1988

Wood Anatomy of Acanthaceae: A Survey

Sherwin Carlquist
Rancho Santa Ana Botanic Garden; Pomona College

Scott Zona
Rancho Santa Ana Botanic Garden

WOOD ANATOMY OF ACANTHACEAE: A SURVEY

SHERWIN CARLQUIST

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

AND

SCOTT ZONA

*Rancho Santa Ana Botanic Garden
Claremont, California 91711*

ABSTRACT

Qualitative and quantitative wood features are reported for 38 species representing 22 genera, including the scandent genera *Mendoncia* and *Thunbergia*. Woods of Acanthaceae are characterized by relatively narrow vessels with simple perforation plates and alternate lateral wall pitting, septate libriform fibers, scanty vasicentric axial parenchyma, rays both multiseriate and uniseriate, erect ray cells abundant in rays (some species rayless or near-rayless), numerous small crystals or cystoliths in ray cells in a few genera (first documented reports of both characters in woods of Acanthaceae), and nonstoried structure. This constellation of features is very closely matched by woods of Gesneriaceae, Scrophulariaceae, Pedaliaceae, Martyniaceae, Bignoniaceae, and Myoporaceae (families listed in order of decreasing resemblance). Narrowness of vessels in tropical Acanthaceae appears related to understory ecology. A few species in warm and seasonally dry areas have narrow, short vessel elements numerous per unit transection. Vasicentric tracheids occur in two nonscandent genera in dry areas. Vessel grouping is roughly proportional to dryness of habitat. *Thunbergia alata, T. laurifolia,* and all collections of *Mendoncia* have interxylary phloem (first report for *Mendoncia*). That feature, plus presence of occasional acicular crystals in rays and axial parenchyma and presence of large gelatinous fibers in phloem ally *Mendoncia* closely with *Thunbergia,* and Mendonciaceae is not justified for this and other reasons. Species of *Thunbergia* differ among themselves, and *T. erecta* and *T. holstii* resemble shrubby Acanthaceae more than they do *Mendoncia* in wood features. *Thunbergia* thus should not be segregated from Acanthaceae.

Key words: Acanthaceae, ecological wood anatomy, interxylary phloem, *Mendoncia*, raylessness, Scrophulariales, *Thunbergia*, wood anatomy.

INTRODUCTION

The present study represents a portion of a survey of wood anatomy in tubiflorous families of dicotyledons. This survey will examine wood features with reference to the ordinal classification system in an effort to achieve more natural groupings. The 43 species of 26 genera included here represent a small portion of the approximately 2500 species in 250 genera conservatively estimated for the family (Cronquist 1981). One should remember that a large portion of the family is herbaceous or minimally woody. Two of the large woody genera, *Graptophyllum* and *Sanchezia,* have been sparsely sampled here because the relative uniformity of habit and habitat type within these genera is likely to be associated with

relatively uniform wood anatomy. A further problem that prevents a more extensive sampling of the family is the lack of determinations on many samples in xylaria; this in turn relates to the lack of monographs of genera in the family or treatments of the family in floras where Acanthaceae are well represented (e.g., Peru). The present study must be considered an exploration of diversity in wood anatomy within the family, and any comparison between wood anatomy and taxonomic categories within the family must await a larger assemblage of woods.

Phylogenetic systems are in agreement that Acanthaceae belong to Scrophulariales (Thorne 1976; Dahlgren 1980; Cronquist 1981; Takhtajan 1987). However, the systems differ with respect to the families between which Acanthaceae are placed. Gesneriaceae, Pedaliaceae, Martyniaceae, and Myoporaceae, respectively, are cited as the closest ally of Acanthaceae about an equal number of times in these systems. One goal of the present paper is to determine which families of Scrophulariales bear the closest relationship to Acanthaceae in terms of wood anatomy.

The predominantly herbaceous or moderately woody nature of such a high proportion of Acanthaceae makes the family potentially interesting with respect to wood anatomy, because patterns in such a group are different from those in predominantly woody families. The families Gesneriaceae (Carlquist and Hoekman 1986a), Myoporaceae (Carlquist and Hoekman 1986b) and Plantaginaceae (Carlquist 1970) are instructive in this regard. At another extreme with respect to habit is *Mendoncia,* a genus of tropical lianas, and *Thunbergia,* which consists of variously woody vines or (*T. erecta*) shrubs. These scandent genera present anatomical patterns that involve abnormal cambial configuration; the histology of these patterns has been in need of study. The xylary peculiarities of *Mendoncia* and *Thunbergia* are also pertinent in connection with systematics, because some accounts have recognized Mendonciaceae as a separate family (Bremekamp 1953; Dahlgren 1980; Cronquist 1981; Takhtajan 1987), and some have considered Thunbergiaceae a worthy segregate family (e.g., Bremekamp 1953; Dalhgren 1980; Takhtajan 1987).

Although the majority of Acanthaceae are characteristic of the humid tropics, some of the Acanthaceae studied here are characteristic of drier or cooler regimes. *Anisacanthus thurberi* occurs along gravelly washes in northwestern Mexico and adjacent Arizona and New Mexico (Johnston 1924; Kearney and Peebles 1960). *Ruellia peninsularis* grows on sea bluffs near La Paz, Baja California (Johnston 1924). *Justicia californica* (formerly considered a species of *Beloperone*) may be found in washes at the northern and western edges of the Colorado Desert (Munz 1974). *Diapedium assurgens* (sometimes included in *Dicliptera*) occurs in disturbed places in shallow coral soils of exposed sites of the Florida Keys and adjacent peninsular Florida (Long and Lakela 1971). *Jacobinia* is an understory plant that ranges from Mexico to Bolivia; it does not occur in moist understory sites, but in shrubby or dry forests, as beneath *Cercidium* (Gentry 1942). Detailed ecological data on Tanzanian Acanthaceae are not at hand, although the data in Dale and Greenway (1961) suggest that genera such as *Himantochilus* and *Pseudoblepharis* characterize relatively dry sites in eastern Africa.

The remaining Acanthaceae studied here are from areas of relatively heavy rainfall. These species are of interest with respect to ecological wood anatomy because dicotyledons with mesomorphic woods have been assumed to be the

norm instead of diverse adaptations to various kinds of humid and moist conditions.

Metcalfe and Chalk (1950) report on the wood features of 15 genera (species not given) of Acanthaceae and the information they give appears accurate. The present study amplifies that account both in qualitative and quantitative aspects. No survey of wood anatomy in Acanthaceae other than their account has appeared elsewhere.

MATERIALS AND METHODS

The majority of specimens studied were available in dried form. Most of these were derived from the SJRw and MADw collection of the Forest Products Laboratory, Madison, Wisconsin (see Table 1). Dried samples were boiled in water and stored in aqueous 50% ethyl alcohol. Other samples from plants in cultivation (Table 1) were preserved in aqueous 50% ethyl alcohol. Sections of woods of most collections were prepared by means of the sliding microtome. However, vining and lianoid species (*Mendoncia, Thunbergia*) cannot be sectioned readily in this way because of the sectioning problems presented by large-diameter vessels and by pockets of thin-walled parenchyma (some of which proved to contain phloem) intercalated among the fibers. For these species, an alternative method involving softening in ethylene diamine, infiltration, embedding in paraffin, and sectioning on a rotary microtome (Carlquist 1982) was used. Sections were stained with a safranin-fast green combination. Macerations were prepared by means of Jeffrey's Fluid and stained with safranin.

Means for wood features were obtained by averaging 25 measurements except for vessel wall thickness, libriform fiber diameter at widest point, and libriform fiber wall thickness. For these latter features, a few typical conditions were measured and averaged. Vessel diameter is taken at the widest point and excludes wall thickness; although this is a less common way of measuring vessel diameter, this method has the merit of representing lumen diameter, which is a dimension more pertinent where physiological and ecological features are being discussed than inclusion of wall thickness (although inclusion of vessel wall thickness does not alter data significantly except in species with very narrow vessels). Vessels per group is based on averaging counts where a solitary vessel = 1, a pair of vessels in contact = 2, etc. Vessels per mm^2 represents a count of all vessels (pores, not vessel groups) within a field. Terminology in wood features follows that of the IAWA Committee on Nomenclature (1964). Growth-ring types are according to Carlquist (1988), which represents essentially the same system presented earlier (Carlquist 1980). Preparation of quantitative data, some of the wood sections and macerations, and some observations on qualitative features are the work of the second author. Preparation of the text, photomicrography, and some observations of qualitative features represent the work of the first author. David A. Hoekman prepared some wood sections and some quantitative data.

Provenance of the specimens is as follows (except for specimens taken from cultivation by the first author): *Acanthus ebracteatus* (New Britain); *Anisacanthus thurberi* (5 miles southwest of Tucson, Arizona); *Aphelandra pulcherrima* (Guyana); *A. scabra* (Guamitas, Venezuela); *A. tetragona* (Colombia); *Asystasia zambiana* (Shaba, West Africa); *Barleria cristata* (cult. Kamehameha School, Hono-

Table 1. Wood characteristics of Acanthaceae.

Taxon	Collection	1 v/g	2 vmm	3 vd	4 vl	5 vwt	6 fd	7 fl	8 fwt	9 mrh	10 mrw	11 urh	12 f/v	13 meso
Acanthus ebracteatus Vahl	SJRw-28606	1.5	83	38	420	3.2	19	665	3.3	359	2.1	172	1.58	192
Anisacanthus thurberi (Torr.) Gray	SJRw-26701	1.6	253	38	201	3.3	13	433	2.5	600	3.7	103	2.15	30
A. pulcherrima (Jacq.) HBK.	SJRw-35876	2.5	113	38	468	3.9	20	822	4.8	432	2.0	202	1.76	157
Aphelandra scabra (Vahl) Sm.	MADw-26634	1.6	169	30	486	3.3	19	779	5.5	489	2.8	187	1.60	86
A. tetragona (Vahl) Nees	SJRw-16435	2.1	129	39	510	3.3	20	886	6.3	560	2.3	314	1.74	154
Asystasia zambiana Brummet & Chisuapa	Tw-39931	2.8	168	53	298	5.4	13	510	2.9	≫	4.5	—	1.71	94
Barleria cristata L.	SJRw-37261	1.5	116	43	566	3.9	22	802	4.3	666	2.0	304	1.42	210
Bravaisia floribunda DC.	MADw-26650	1.0	9	137	774	4.2	29	1460	1.8	753	3.0	340	1.89	11,782
B. integerrima (Spreng.) Standl.	MADw-7158	1.3	14	119	542	4.9	25	1272	2.7	749	2.9	387	2.35	4607
Calycacanthus sp.	SJRw-32146	1.5	122	35	449	2.5	18	748	2.8	556	2.0	277	1.67	129
Diapedium assurgens (L.) Kuntze	SJRw-51436	2.1	282	20	273	2.9	13	540	2.2	—	—	—	1.98	19
Graptophyllum insularum (Gray) A. C. Smith	SJRw-24541	4.1	206	42	379	3.9	15	661	3.1	639	2.4	305	1.74	77
Himantochilus marginatus Linden	SJRw-27563	1.9	102	40	277	4.0	18	676	2.3	343	2.4	144	2.44	109
Jacobinia carnea Nichols.	cult. Claremont	2.6	287	27	320	2.1	18	387	1.1	—	—	—	1.21	30
J. ghiesbrechtiana Benth. & Hook. f.	cult. Orpet Park	2.0	171	36	215	2.6	17	438	2.2	—	—	340	2.04	45
Justicia californica (Benth.) D. Gibson	cult. RSABG	2.1	190	45	225	3.1	20	420	3.1	—	—	—	1.87	53
J. magnifica (Blake) D. Gibson	SJRw-14493	1.5	99	35	547	2.5	18	735	2.2	—	—	—	1.34	193
Megaskepasma erythrochlamys Lindau	cult. PTBG	1.6	66	44	289	2.3	22	494	1.8	430	2.2	227	1.71	193
Mendoncia gigas Lindau	SJRw-44438	1.5	33	181	445	5.8	40	740	4.9	494	2.0	356	1.66	2441
M. microchlamys Leonard	SJRw-44483	2.3	43	158	382	5.2	38	758	3.7	499	2.0	290	1.98	1404
M. retusa Turrill	SJRw-54858	1.3	22	200	338	3.2	30	608	2.4	497	2.1	418	1.80	3072
M. sp.	SJRw-52920	2.6	22	186	414	6.3	40	733	3.5	574	2.0	292	1.77	3500
Pachystachys lutea Nees	MADw-38349	1.4	89	27	507	3.1	19	701	2.4	762	2.3	292	1.38	154
P. spicata (R. & P.) Wassh.	MADw-26785	3.6	116	40	508	3.0	21	848	2.5	830	2.4	361	1.67	175
Pseuderanthemum laxiflorum (A. Gray) Hubbard	SJRw-25683	2.6	139	29	460	2.3	20	787	3.3	550	2.5	233	1.71	96
Pseudoblepharis glischrocalyx Mildbr.	SJRw-27559	1.6	108	48	306	2.9	22	714	2.6	276	2.1	91	2.33	136
Psilanthele jamaicensis Lindau	USw-5946	2.2	87	51	568	3.5	13	969	3.6	695	3.0	228	1.23	333
Razisea spicata Oerst.	SJRw-54840	5.9	132	29	432	2.4	23	626	1.7	530	2.7	42	1.45	95
Ruellia peninsularis (Rose) Johnston	Hunt.-35657	1.7	264	21	162	3.5	18	397	3.6	380	2.5	107	2.45	13
Ruspolia hypocrateriformis (Vahl) Milne-Redhead	Tw-46550	3.2	188	45	301	5.0	11	743	3.2	≫	3.0	—	2.47	72
Salpinxantha coccinea Hook.	USw-5937	1.7	146	34	217	2.2	13	419	2.3	—	—	114	1.93	51

Table 1. Continued.

Taxon	Collection	1 v/g	2 vmm	3 vd	4 vl	5 vwt	6 fd	7 fl	8 fwt	9 mrh	10 mrw	11 urh	12 f/v	13 meso
Sanchezia decora Leonard & Smith	*MADw-38350*	1.3	25	69	989	4.7	28	1417	3.9	2915	3.0	830	1.43	2730
S. nobilis Hook. f.	*cult. Hawaii*	1.8	53	47	538	2.3	30	987	3.2	3700	4.2	493	1.83	477
S. rubriflora Leonard	*MADw-31383*	2.5	26	69	602	3.8	38	1204	4.3	≫	4.1	—	2.00	1598
S. stenomacia Leonard & Smith	*MADw-38352*	2.4	32	57	863	4.1	26	1512	4.4	≫	2.1	1287	1.75	1537
S. williamsii Leonard	*MADw-26799*	1.6	24	86	901	4.7	37	1652	4.6	≫	3.0	277	1.83	3229
Thunbergia alata Bojer	*cult. LASCA*	3.4	53	50	186	3.8	36	263	2.6	—	—	—	1.41	175
T. crispa Brukill	*Tw-45573*	1.0	68	370	213	4.5	12	516	3.2	—	—	—	2.42	1159
T. erecta T. Anders.	*SJRw-37260*	1.0	48	32	295	5.3	25	585	3.7	474	2.2	276	1.98	197
T. holstii Lindau	*cult. UCLA*	1.0	80	47	131	6.1	20	442	2.6	—	—	125	3.37	77
T. laurifolia Lindl.	*cult. LASCA*	2.6	23	81	224	2.2	27	480	2.8	—	—	—	2.14	789
Trichanthera gigantea HBK.	*MADw-1117*	1.2	12	169	822	5.4	54	1592	3.8	1084	3.4	459	1.94	11,576
Whitfieldia colorata C. B. Clarke	*SJRw-15093*	2.6	112	26	846	2.8	25	1152	4.5	1992	3.6	34	1.36	196
Means		2.1	105	70	439	3.7	23	781	3.2	815	2.6	300	1.85	1243

Key to columns: 1 (v/g), mean number of vessels per group as seen in transection; 2 (vmm), mean number of vessels per mm^2 of transection; 3 (vd), mean diameter of vessels at widest point (excluding wall thickness), μm; 4 (vl), mean vessel element length, μm; 5 (vwt), mean wall thickness of vessels, μm; 6 (fd), mean diameter of libriform fibers at widest point, μm; 7 (fl), mean libriform fiber length, μm; 8 (fwt), mean wall thickness of libriform fibers, μm; 9 (mrh), mean multiseriate ray height, μm; 10 (mrw), mean width of multiseriate rays at widest point, cells; 11 (urh), mean height of uniseriate rays, μm; 12 (f/v), ratio, libriform fiber length divided by vessel element length; 13 (meso), Mesomorphy ratio (vessel diameter times vessel element length divided by vessels per mm^2. For further explanations, see Materials and Methods.

lulu, Hawaii); *Bravaisia floribunda* (Colombia); *B. integerrima* (Estrella, Cano Papayal, Bolivar, Colombia); *Calycacanthus* sp. (Urakukur I., Duke of York Group); *Diapedium assurgens* (Florida Keys); *Graptophyllum insularum* (Matuku, Fiji); *Himantochilus marginatus* (Tanzania); *Justicia magnifica* (Belize); *Mendoncia gigas* (Esperanza, Amazonas, Brazil); *M. microchlamys* (Colombia); *M. retusa* (Darien, Panama); *M.* sp. (Aguaytia, Loreto, Peru); *Pachystachys lutea* (Tocache Nuevo, San Martin, Peru); *P. spicata* (Caballo-cocha, Loreto, Peru); *Pseuderanthemum laxiflorum* (Maztasiri, Viti Levu, Fiji); *Pseudoblepharis glischrocalyx* (Tanzania); *Psilanthele jamaicensis* (Jamaica); *Ruspolia hypocrateriformis* (Shaba, West Africa); *Razisea spicata* (Darien, Panama); *Sanchezia decora* (Iparia, Loreto, Peru); *S. rubriflora* (Rio Nanay, Iquitos, Peru); *S. stenomacia* (Tocache Nuevo, San Martin, Peru); *Thunbergia crispa* (Shaba, West Africa); *T. erecta* (cult. Kamehameha School, Honolulu, Hawaii); *Trichanthera gigantea* (Rio Huallaga, Loreto, Peru); *Whitfieldia colorata* (Liberia). The sites of cultivation cited in Table 1 are: Hunt. (Huntington Botanical Gardens, San Marino, California); LASCA (Los Angeles State and County Arboretum, Arcadia, California); Orpet Park (located in Santa Barbara, California); PTBG (Pacific Tropical Botanical Garden, Lawai, Kauai, Hawaii); RSABG (Rancho Santa Ana Botanic Garden); UCLA (Mathias Botanical Garden, University of California at Los Angeles).

ANATOMICAL FEATURES

Growth Rings

Only a minority of Acanthaceae possesses growth rings, and even these would probably not be designated as ring-porous in the ordinary sense of that term. In *Anisacanthus thurberi* (Fig. 1), vessels are wider in earlywood or somewhat after the initiation of earlywood (the rather unusual Type 10 of Carlquist 1988). In this growth-ring type, onset of temperature suitable for growth and beginning of the rainy season are not synchronous. This is observable in the habitat for this species, southern Arizona, in which temperatures suitable for growth occur in early spring months, but the majority of rain does not come until summertime.

Another distinctive type of growth ring is demonstrated by *Whitfieldia colorata* (Fig. 3), in which little change in vessel diameter occurs in growth rings, but in which latewood has libriform fibers thicker walled than in the earlywood (Type 1E of Carlquist 1988). Type 1E is also present in *Bravaisia integerrima* and *Graptophyllum insularum* (Fig. 9).

Thunbergia holstii (Fig. 21) has the unusual Type 12 (Carlquist 1988), in which the wood is diffuse porous and only presence of a parenchyma band defines the beginning of a growth ring. A terminal parenchyma band is present in some growth rings of *Justicia californica,* in which moderate fluctuation of vessel diameter occurs and thus Type 1C (Carlquist 1988) is present.

Diffuse-porous wood with no appreciable evidence of growth-ring activity characterizes the remainder of Acanthaceae studied here, as illustrated for *Beloperone crenata* (Fig. 5), *Sanchezia williamsii* (Fig. 13), *Trichanthera gigantea* (Fig. 24), *Thunbergia laurifolia* (Fig. 25), *T. alata* (Fig. 26), and *Mendoncia gigas* (Fig. 29).

Vessel Elements

Vessel grouping (Table 1, column 1) is moderate in Acanthaceae compared to that in certain other families (e.g., Asteraceae): it is reported here to exceed 2.5
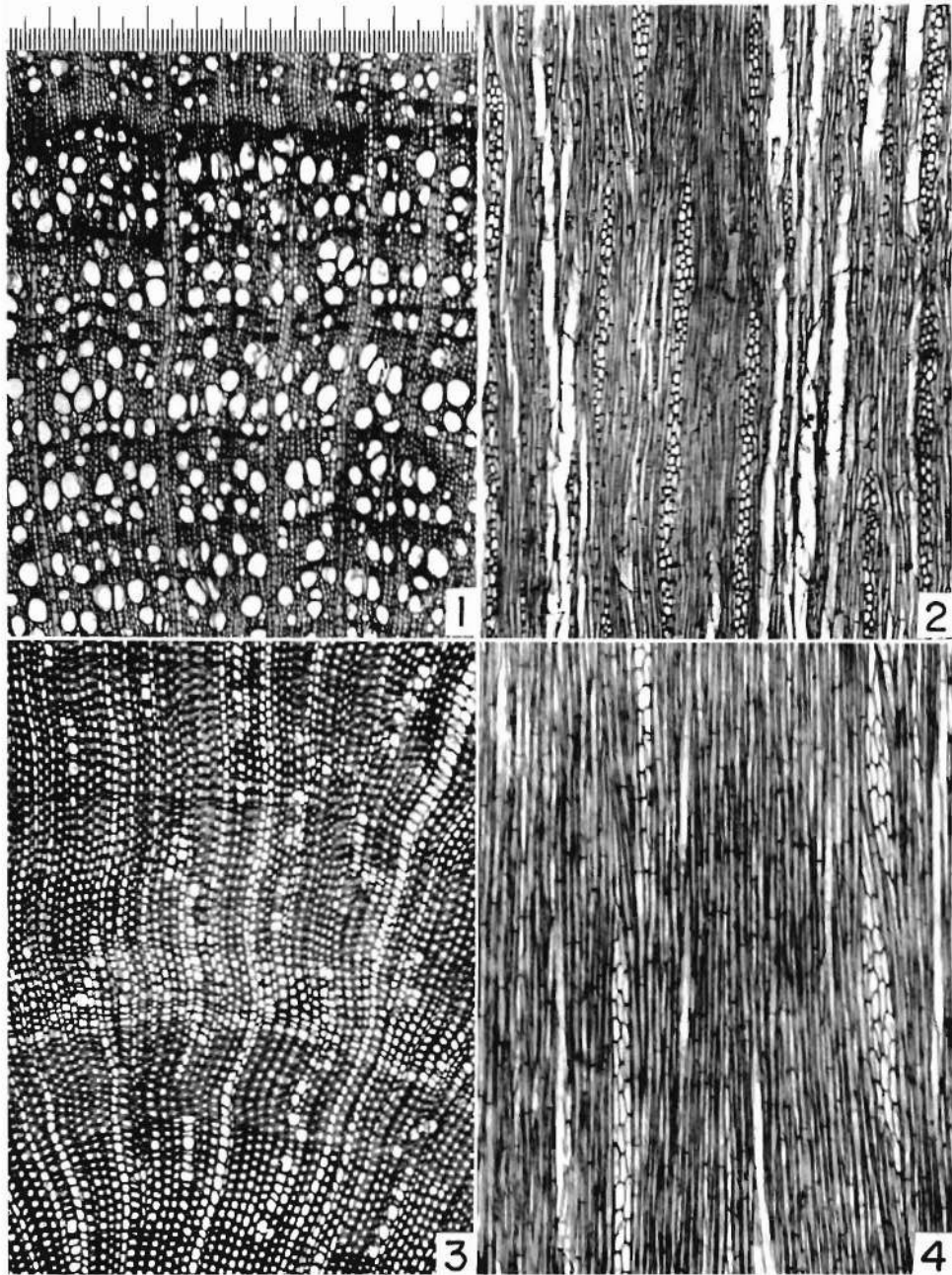
Fig. 1–4. Wood sections of Acanthaceae.—1–2. *Anisacanthus thurberi, SJRw-26701.*—1. Transection, showing growth rings.—2. Tangential section; over half of cells shown are vasicentric tracheids.—3–4. *Whitfieldia colorata, SJRw-15093.*—3. Transection; note narrowness of vessels.—4. Tangential section; multiseriate rays have predominantly erect ray cells. (Fig. 1–4, magnification scale above Fig. 1 [finest divisions = 10 μm].)
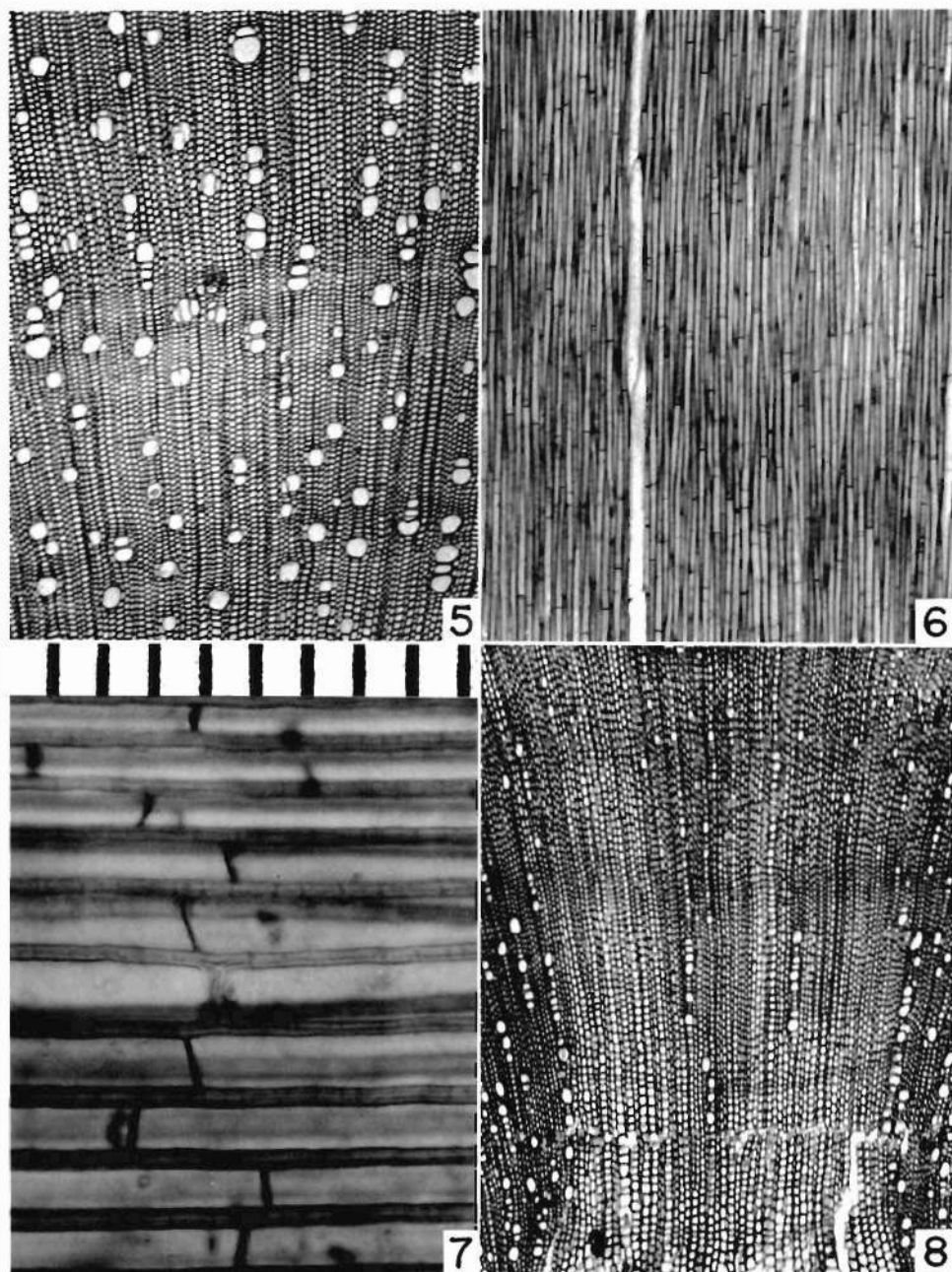
Fig. 5–8.   Wood sections of rayless Acanthaceae. — 5–7. *Justicia magnifica, SJRw-14493.* — 5. Transection; wood is diffuse porous or nearly so. — 6. Tangential section; rays are absent. — 7. Portion of radial section, showing septa and pits in libriform fibers. — 8. *Diapedium assurgens, SJRw-51436.* Transection, showing a broad ray area near pith (below) that has been converted to vessels and libriform fibers (above). (Fig. 5, 6, 8, magnification scale above Fig. 1; Fig. 7, scale above Fig. 7 [divisions = 10 μm].)

vessels per group in *Graptophyllum insularum* (Fig. 9), *Jacobinia ghiesbrechtiana*, *Mendoncia* sp., *Razisea spicata*, *Thunbergia alata* (Fig. 26), *T. laurifolia* (Fig. 25), and *Whitfieldia colorata* (Fig. 3). However, the resemblance in transectional view of very narrow vessels and vasicentric tracheids to libriform fibers results in undermeasurement of vessels per group in *Anisacanthus thurberi* (Fig. 1) and *Justicia californica*, which, therefore, should be added to this listing. Vessel grouping occurs as short radial multiples or as pore clusters. Species with vessels predominantly solitary (1.5 vessels per group or fewer) include *Bravaisia floribunda*, *B. integerrima*, *Sanchezia decora*, *Thunbergia erecta*, *T. holstii* (Fig. 21), and *Trichanthera gigantea* (Fig. 24). More than half of the family averages between 1.5 and 2.5 vessels per group, a moderate figure for a family in which the libriform fiber is the type of tracheary element present (Carlquist 1984).

Vessel density and vessel diameter—figures that tend within limits to be reciprocals of each other in a given group with notable exceptions (e.g., vines and lianas)—are given for Acanthaceae in Table 1 (columns 2 and 3). Metcalfe and Chalk (1950) have commented on the narrowness of vessels in most Acanthaceae. The data of Table 1 in general show that vessels are narrower in the mesic species than one might expect on the basis of other dicotyledonous families (e.g., *Whitfieldia colorata*, Fig. 3). Vessel diameter is probably less in *Anisacanthus thurberi* · and *Justicia californica* than the figures in Table 1 indicate, because narrow vessels grade into vasicentric tracheids in these species, and these cell types are so difficult to distinguish from libriform fibers in transections that overestimating vessel diamter and underestimating vessel density is almost inevitable. Vessel diameter increases with age in stems of *Asystasia zambiana*, *Thunbergia crispa*, and *T. holstii*. The low figures for vessel density in Acanthaceae can be appreciated by comparison with xylem in species of the woody flora of southern California, where relatively high vessel density is to be expected on account of the predominant dryness of this area. In the southern California flora, the mean number of vessels per mm^2 is 257 (Carlquist and Hoekman 1985). Only three of the Acanthaceae studied here have vessel density higher than that figure.

Vessel element length is relatively great in Acanthaceae. The mean vessel element length for the world woody flora is reported by Metcalfe and Chalk (1950) to be 649 μm. To be sure, their sample is probably somewhat biased in favor of trees of relatively moist habitats. The Acanthaceae studied here fall below that figure except for a few species: *Bravaisia floribunda*, *Sanchezia decora*, *S. stenomacia*, *S. williamisii*, *Trichanthera gigantea*, and *Whitfieldia colorata* (Table 1, column 4).

Figures for vessel wall thickness are given in Table 1 (column 5). Relatively thick vessel walls characterize the genera *Bravaisia*, *Mendoncia* (Fig. 29) and *Ruspolia*, as well as some species of *Thunbergia* (Fig. 22) and *Sanchezia*.

Simple perforation plates characterize all Acanthaceae, although in a few end walls there are two perforations, a distinctly larger perforation accompanied by a smaller one (Fig. 15). However, an interesting feature is characteristic of many of the acanthaceous woods studied: perforation plates appreciably narrower than the vessel elements in which they are located. This is shown for *Sanchezia williamsii* (Fig. 15) and, less markedly, *Graptophyllum insularum* (Fig. 11). This tendency was observed characteristically in the genera *Bravaisia*, *Pseuderanthemum*, and *Sanchezia*.
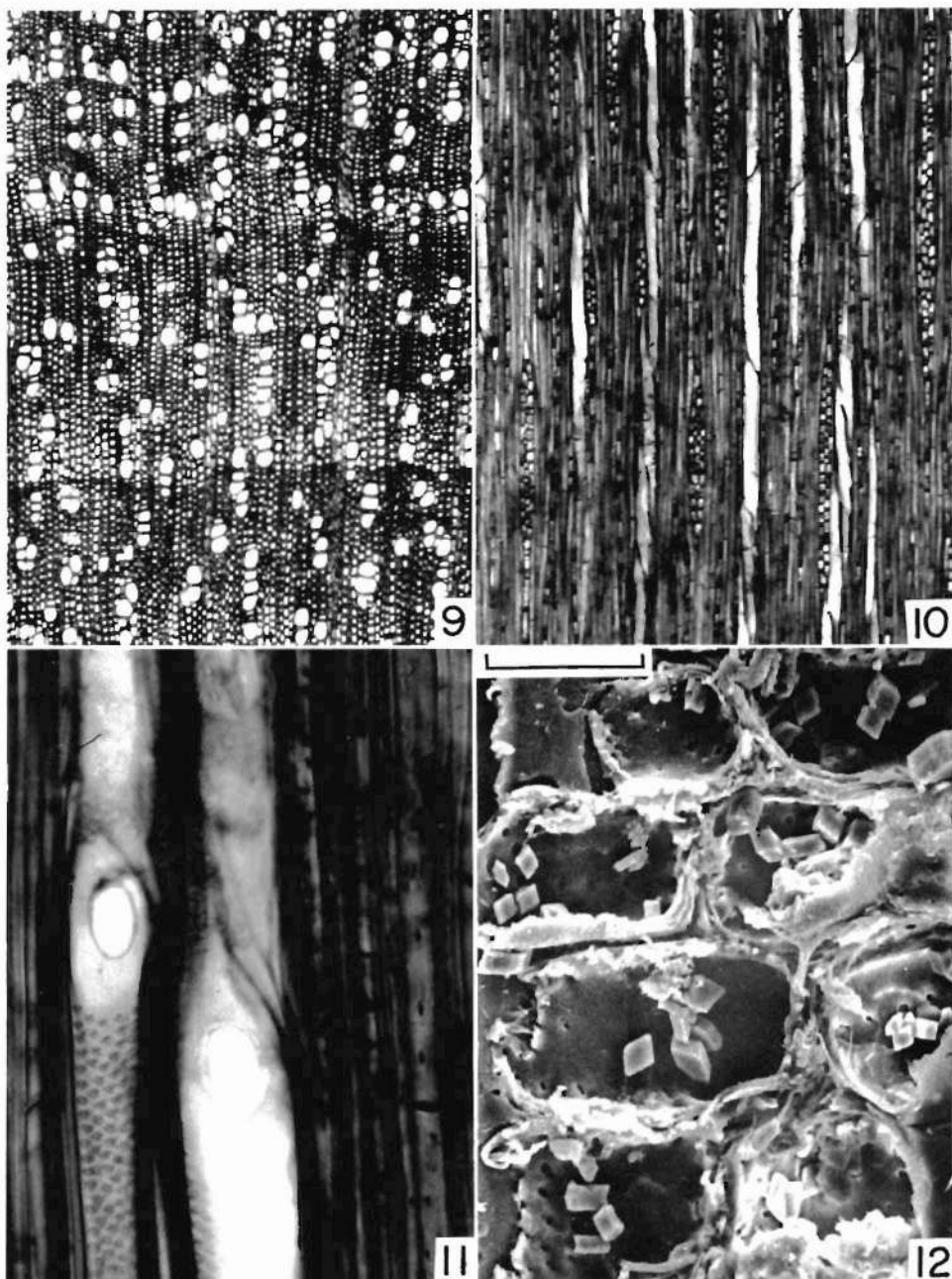
Fig. 9–12. Wood sections of *Graptophyllum insularum, SJRw-24541.* —9. Transection; growth rings demarcated by thick-walled libriform fibers. — 10. Tangential section; multiseriate and uniseriate rays are about equally abundant. — 11. Portion of radial section; perforation plates are appreciably narrower than vessel elements. — 12. SEM photograph of radial section, showing small rhomboidal crystals in ray cells. (Fig. 9, 10, magnification scale above Fig. 1; Fig. 11, scale above Fig. 7; Fig. 12, scale on photograph = 10 μm.)
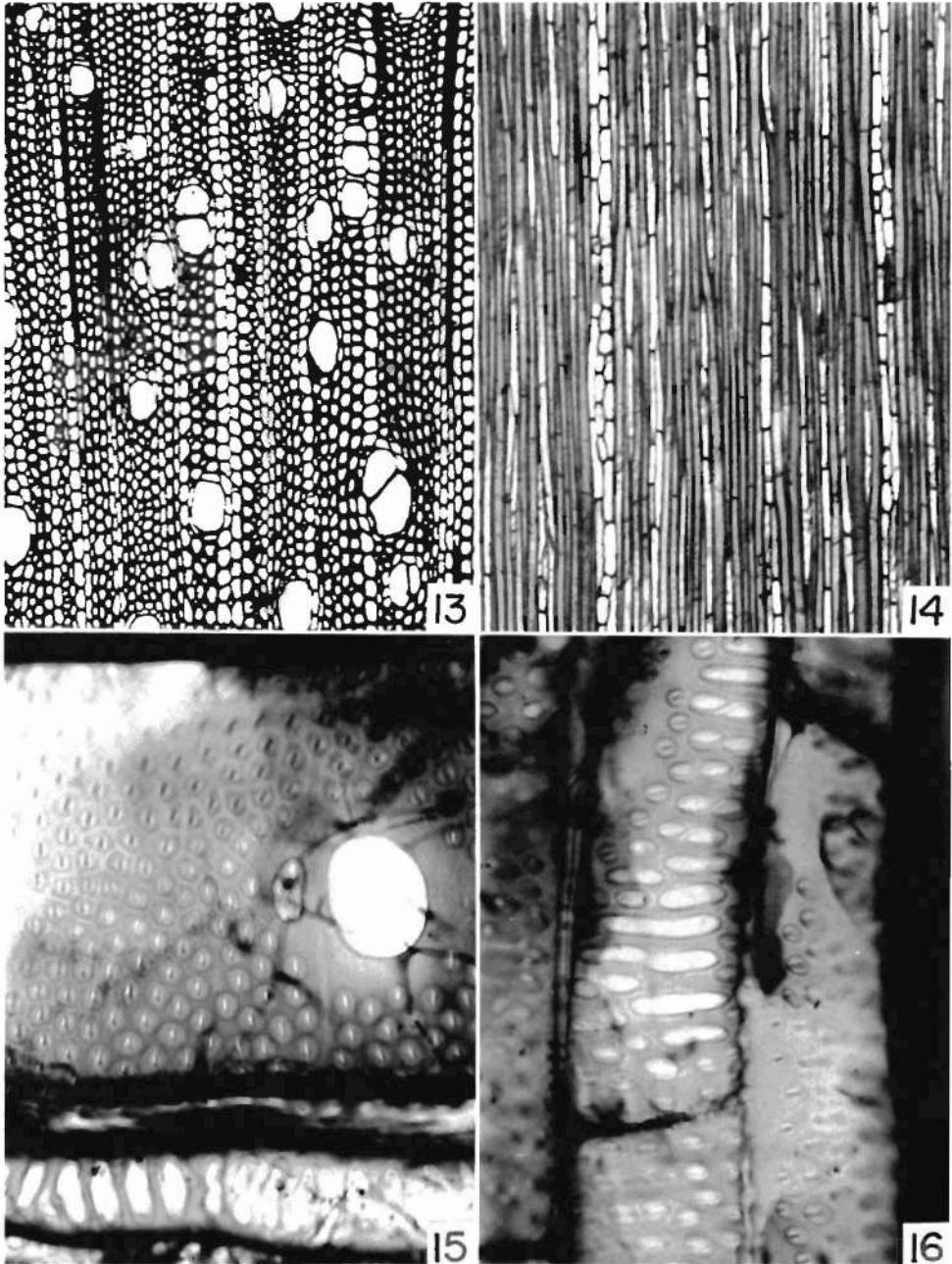
Fig. 13–16.   Wood sections of *Sanchezia.*—13, 15, 16. *S. williamsii, MADw-2677.*—13. Transection; wood is diffuse porous.—14. *S. decora, MADw-38350.* Tangential section; rays are tall, erect cells are predominant.—15. Radial section (vertical axis oriented left to right), showing narrow perforation plate; axial parenchyma cell below.—16. Radial section, showing pitting in axial parenchyma cells. (Fig. 13, 14, scale above Fig. 1; Fig. 15, 16, scale above Fig. 7.)
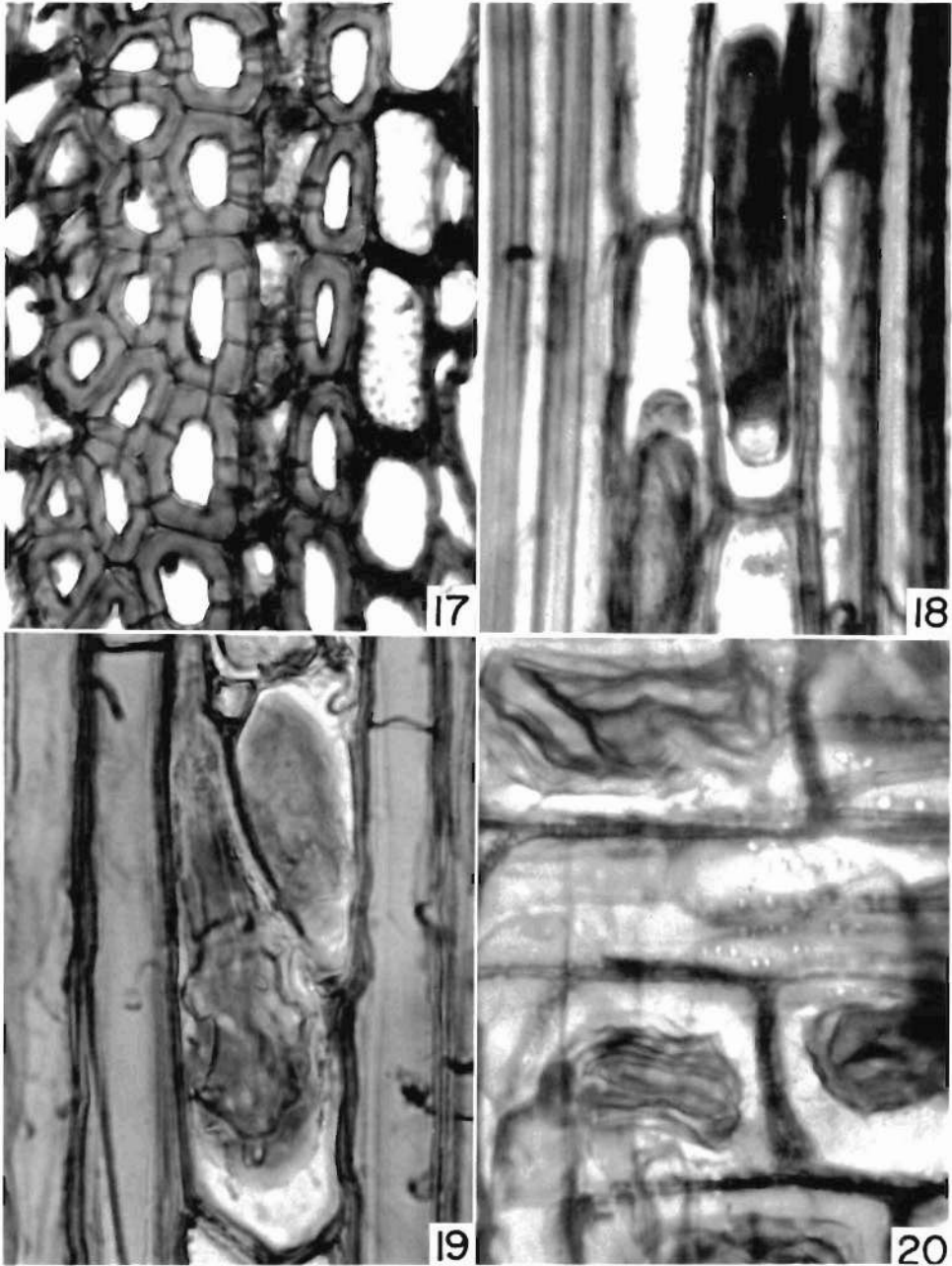
Fig. 17–20.   Wood sections of Acanthaceae.—17. *Sanchezia williamsii, MADw-2677*. Transection, showing simple pits in ray cells.—18. *Sanchezia decora, MADw-38350*. Tangential section; cystoliths in ray cells.—19. *Bravaisia integerrima, MADw-7158*. Tangential section; cystoliths in ray cells.—20. *Bravaisia floribunda, MADw-7154*. Radial section; cystoliths in ray cells. (Fig. 17–20, magnification scale above Fig. 7.)
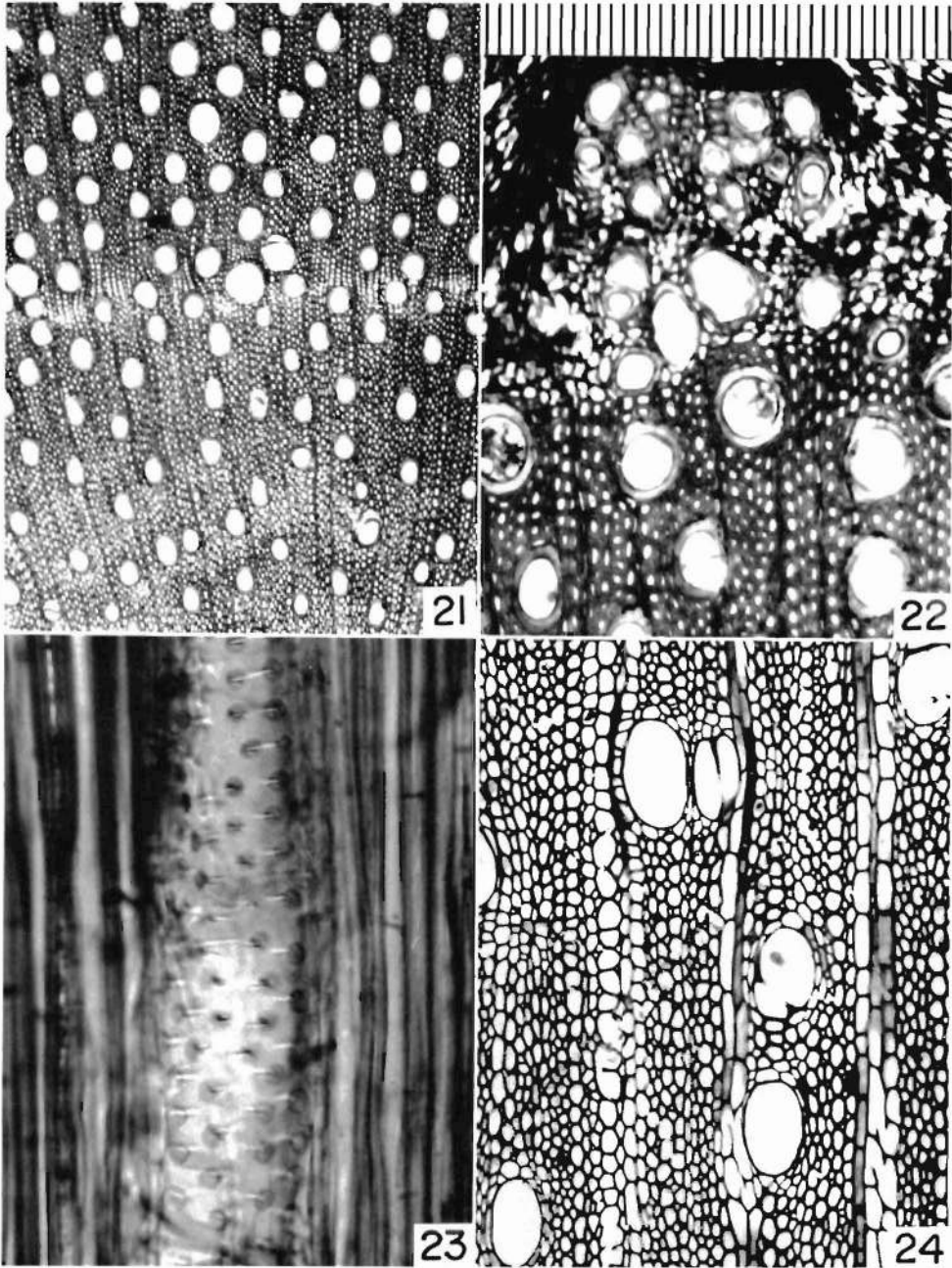
Fig. 21–24. Wood sections of Acanthaceae.—21–23. *Thunbergia holstii, cult. UCLA.*—21. Transection; parenchyma band in center.—22. Transection portion near cambium, showing patch of small vessels extending into phloem, above.—23. Tangential section; vessel has grooves interconnecting pit apertures; septate fibers present.—24. *Trichanthera gigantea, MADw-1117.* Transection; note wide vessel diameter. (Fig. 21, 24, magnification scale above Fig. 1; Fig. 22, scale above Fig. 22 [divisions = 10 μm]; Fig. 23, scale above Fig. 7.)

Lateral wall pitting of vessel-vessel or vessel-libriform fiber pits in the family consists of alternate pits, oval to circular in shape. Size of intervascular pits within the family is as follows (approximate mean given, from which deviation by 1 μm is common): 3 μm: *Aphelandra tetragona, Calycacanthus* sp., *Graptophyllum insularum* (Fig. 11), *Justicia magnifica, Megaskepasma erythrochlamys, Pachystachys lutea, Pseuderanthemum laxiflorum, Psilanthele jamaicensis, Ruspolia hypocrateriformis*; 4 μm: *Aphelandra pulcherrima, A. scabra, Barleria cristata, Diapedium assurgens, Jacobinia carnea, J. ghiesbrechtiana, Justicia californica, Ruellia peninsularis, Salpinxantha coccinea, Thunbergia holstii* (Fig. 23), *Whitfieldia colorata*; 5 μm: *Bravaisia floribunda, B. integerrima, Himantochilus marginatus, Razisea spicata, Sanchezia nobilis, Thunbergia alata* (Fig. 28) *T. crispa, T. erecta*; 6 μm: *Acanthus ebracteatus, Sanchezia stenomacia, Mendoncia gigas, M. microchlamys, M. retusa* (Fig. 31), *M.* sp.; 7 μm: *Sanchezia decora, S. rubriflora, Thunbergia laurifolia, Trichanthera gigantea*.

Pits that are notably elongate radially characterize at least some intervascular pitting of *Bravaisia floribunda, Sanchezia rubriflora, S. stenomacia, S. williamsii* (Fig. 15–16), *Thunbergia alata* (Fig. 28) and *Trichanthera gigantea*. Intervascular pits in Acanthaceae are only infrequently circular in outline, and mostly vary between oval and elliptical in shape. Pit apertures are elliptical to slitlike, more often the latter (Fig. 15, 28), in the majority of the family.

Vessel-axial parenchyma and vessel-ray pitting is like intervascular pitting, but variously more radially elongate. This tendency is shown in a pronounced form in *Mendoncia retusa* (Fig. 31), *Sanchezia williamsii* (Fig. 15, 16), and characterizes the genera *Bravaisia, Mendoncia, Sanchezia*, and *Trichanthera*.

Helical sculpture has not hitherto been reported in vessels of woods of Acanthaceae. Grooves interconnecting pit apertures were observed in *Aphelandra scabra, Asystasia zambiana, Barleria cristata, Bravaisia integerrima, Graptophyllum insularum* (Fig. 11), *Jacobinia ghiesbrechtiana, Justicia californica, Pachystachys spicata, Razisea spicata, Ruellia peninsularis, Thunbergia alata, T. holstii* (Fig. 23), and *Trichanthera gigantea*. Inconspicuous helical thickenings (a band on either side of a groove) were found in *Bravaisia integerrima, Razisea spicata*, and *Trichanthera gigantea*.

Small and numerous thin-walled tyloses were observed in vessels in *Asystasia zambiana, Pachystachys lutea, P. spicata*, and *Ruellia peninsularis*.

Imperforate Tracheary Elements

The imperforate tracheary elements of Acanthaceae (with the exception of the vasicentric tracheids noted below) must all be termed libriform fibers in accordance with the IAWA Committee on Nomenclature (1964), because no borders were observed on pits. This observation is in accord with the findings of Solereder (1908) and Metcalfe and Chalk (1950). Pits in libriform fibers are shown here in a transection of wood of *Sanchezia williamsii* (Fig. 17), in which pits are relatively abundant. Pits are more abundant on radial walls than on tangential walls of libriform fibers in Acanthaceae. Libriform fibers are characteristically septate in the family (e.g., *Justicia magnifica*, Fig. 7), and septate fibers were observed in all collections studied except for *Diapedium assurgens, Ruellia peninsularis, Thunbergia alata, T. crispa, T. erecta*, and *T. holstii*. Metcalfe and Chalk (1950) reported
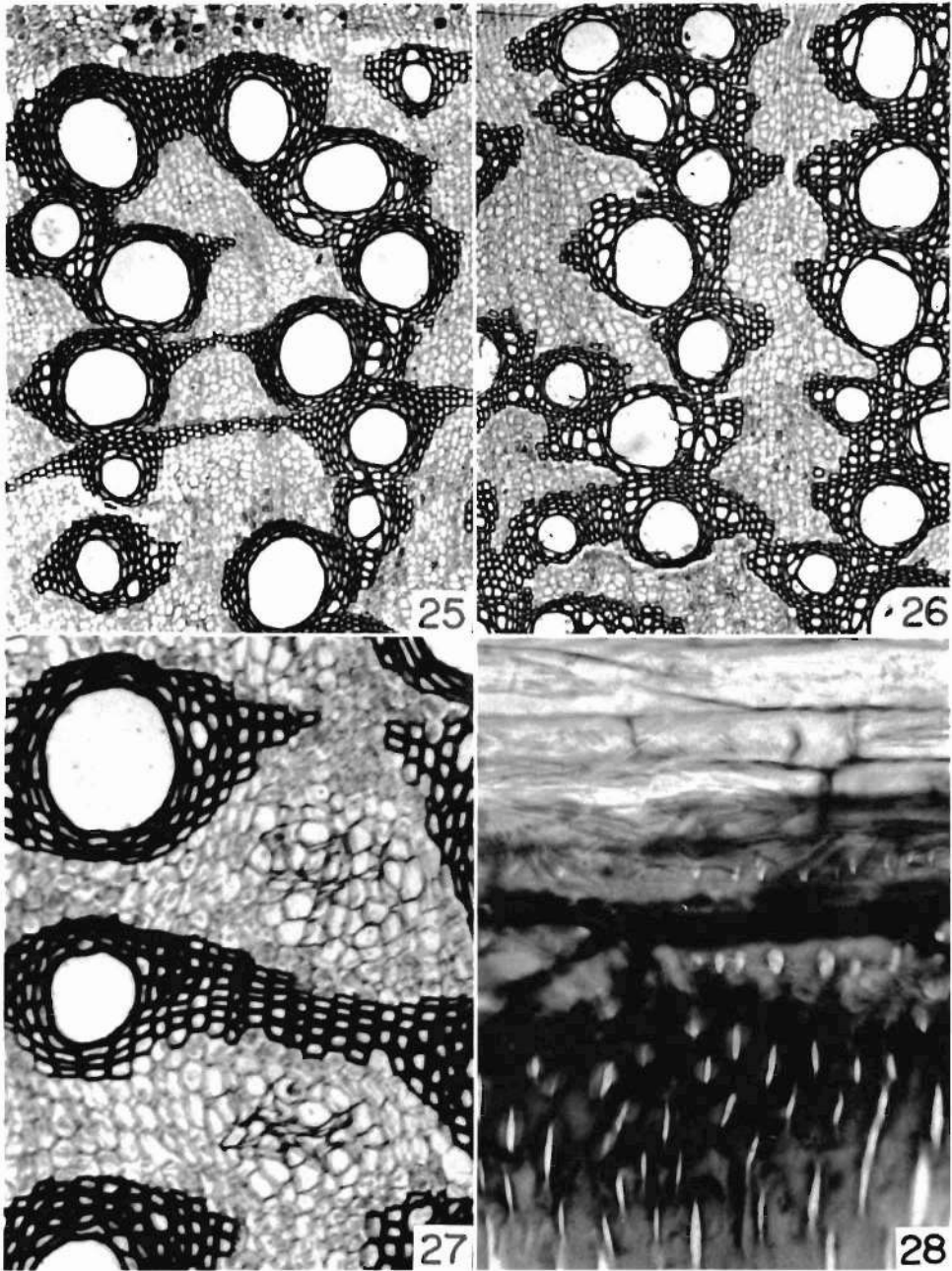
Fig. 25–28. Wood sections of *Thunbergia.*—25. *T. laurifolia, cult. LASCA.* Transection; note gelatinous fibers in phloem, above.—26–28. *T. alata, cult. LASCA.*—26. Transection; as in section of *T. laurifolia,* gray areas = interxylary phloem.—27. Transection portion showing large diameter of sieve tubes, slightly darker, surrounded by parenchyma (gray).—28. Tangential section portion to show vessel (above), with narrow pit apertures. (Fig. 25, 26, magnification scale above Fig. 1; Fig. 27, scale above Fig. 22; Fig. 28, scale above Fig. 7.)
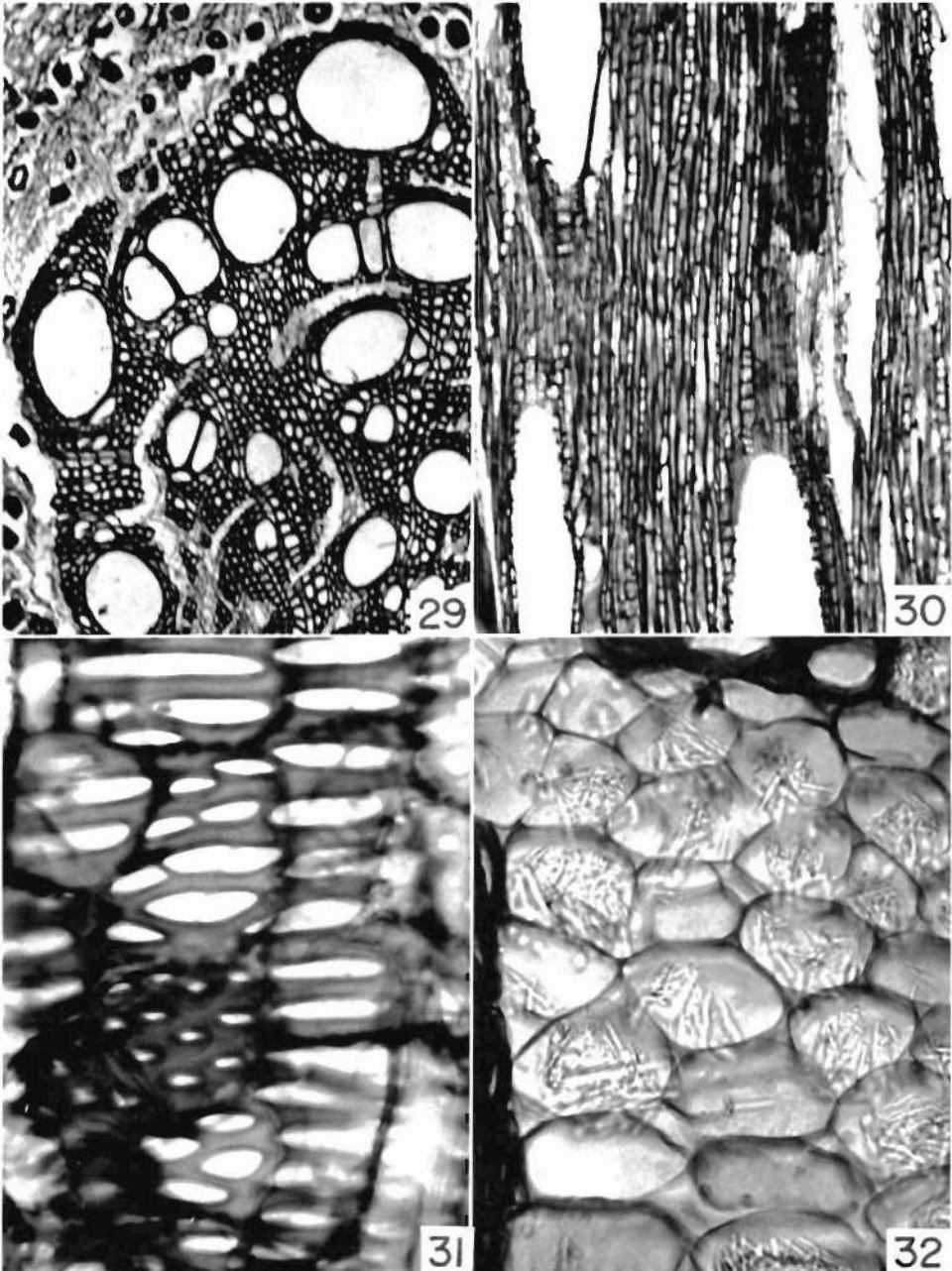
Fig. 29–32.   Wood sections of scandent Acanthaceae.—29–30. *Mendoncia gigas, SJRw-44438.*—
29. Transection of secondary xylem, extraxylary phloem with gelatinous fibers above; interxylary
phloem strands are present within xylem.—30. Tangential section; rays are predominantly uniseriate.—
31. *Mendoncia retusa, SJRw-54858.* Vessel wall from tangential section; vessel-axial parenchyma
pitting shown except for small patch of intervascular pitting below center.—32. *Thunbergia alata, cult.
LASCA.* Transection of secondary xylem showing acicular crystals in parenchyma of interxylary
phloem strand. (Fig. 29, 30, magnification scale above Fig. 1; Fig. 31, 32, scale above Fig. 7.)

nonseptate fibers in *Aphelandra, Pachystachys,* and *Pseudoblepharis.* In those species with septate fibers, the proportion of libriform fibers in which septa may be seen ranges from a small proportion to virtually all. Several septa per fiber (often three) are characteristic of septate fibers.

Libriform fiber length (Table 1, column 6) does not parallel vessel diameter. Exceptionally narrow fibers (less than 15 μm at widest point) were recorded for *Anisacanthus thurberi* (Fig. 1) and *Diapedium assurgens* (Fig. 8). The libriform fibers of the four collections of *Mendoncia* are notably wide, as in *M. gigas* (Fig. 29). Fibers nearly as wide characterize *Sanchezia rubriflora, Thunbergia alata* (Fig. 26, 27), and *Trichanthera gigantea* (Fig. 24).

Libriform fiber length (Table 1, column 7) parallels length of vessel elements, as in other groups of dicotyledons. The ratio between length of libriform fibers and vessel elements (Table 1, column 12) gives a characteristic figure for particular families. The figure for Acanthaceae, 1.85, lies midway between the figure for Gesneriaceae, 1.33 (Carlquist and Hoekman 1986*a*) and that for Myoporaceae, 2.49 (Carlquist and Hoekman 1986*b*).

Libriform fiber wall thickness (Table 1, column 8) is moderate in the family. Relatively thick-walled fibers were observed only in *Aphelandra, Bravaisia, Megaskepasma, Sanchezia* (Fig. 17), and *Whitfieldia.*

Vasicentric tracheids are abundant in *Anisacanthus thurberi,* and represent the majority of the cells shown in Figures 1 and 2, although the magnifications shown in those photographs do not provide details that document this. A few vasicentric tracheids mixed with narrow vessels were observed in all four collections of *Mendoncia* and in *Ruspolia hypocrateriformis* and *Thunbergia alata.* Vasicentric tracheids were previously reported for the family in *Justicia californica* (Carlquist 1985*a*). The "tracheids" reported by Solereder (1908) for *Thunbergia* are doubtless what would now be termed vasicentric tracheids.

Axial Parenchyma

Metcalfe and Chalk (1950) have characterized the axial parenchyma of Acanthaceae as vasicentric scanty, and the present study confirms this. Axial parenchyma forms a complete or partial sheath one cell thick around vessels or vessel groups in all collections studied; such parenchyma is illustrated for *Sanchezia williamsii* (Fig. 13). Vasicentric parenchyma was observed to be very scarce in *Barleria cristata, Diapedium assurgens,* and *Pseudoblepharis glischrocalyx.*

Record and Hess (1943) report terminal and diffuse parenchyma in *Anisacanthus.* Our material of *A. thurberi* reveals that in the growth rings, parenchyma is probably initial rather than terminal. In this species, the vessels are narrow at first in growth rings, with wider vessels appearing somewhat later in the earlywood; latewood may be defined by the libriform fibers of narrowest radial diameter. Similar short bands of thin-walled parenchyma were observed in *Justicia californica.* The report by Record and Hess of diffuse parenchyma in *Anisacanthus* is very likely a result of the fact that so many narrow vessels and vasicentric tracheids, cell types that resemble libriform fibers in transection, occur in *Anisacanthus.* Parenchyma scattered among narrow vessels and vasicentric tracheids should be called vasicentric parenchyma in accord with current usage.

The wood of *Thunbergia holstii* (Fig. 21, center) possesses parenchyma in a

band that may be at the end of a growth ring, but no fluctuation in vessel diameter can be used to define such a ring. This parenchyma is thin walled and nonseptate, and may represent a kind of fiber dimorphism (Carlquist 1958, 1980, 1988). In other species of Acanthaceae, axial parenchyma is generally in strands of two to five (often three) cells.

Mendoncia and two species of *Thunbergia, T. alata* and *T. laurifolia,* have large pockets of thin-walled apotracheal axial parenchyma (Fig. 25–27, 29), but these contain interxylary phloem and are considered below under that heading. In *T. crispa,* the earlier-formed secondary xylem begins without apotracheal parenchyma, but later-formed wood contains strands of apotracheal parenchyma like those of *T. alata* and *T. laurifolia* but somewhat smaller and with no phloem.

Vascular Rays

Acanthaceae show a wide range of expressions in presence of uniseriate or multiseriate rays. Multiseriate rays much more common than uniseriate rays were observed in *Anisacanthus thurberi* (Fig. 2), *Razisea spicata, Sanchezia nobilis, S. rubriflora,* and *S. williamsii.* Multiseriate rays somewhat more common than uniseriate rays were seen in *Acanthus ebracteatus, Aphelandra tetragona, Bravaisia floribunda, B. integerrima, Justicia californica, Sanchezia decora, Trichanthera gigantea,* and *Whitfieldia colorata* (Fig. 4).

Multiseriate rays about as numerous as uniseriate rays occur in *Aphelandra pulcherrima, A. scabra, Calycacanthus* sp., *Graptophyllum insularum* (Fig. 10), *Himantochilus marginatus, Megaskepasma erythrochlamys, Mendoncia retusa, Pachystachys lutea, P. spicata, Pseuderanthemum laxiflorum, Pseudoblepharis glischrocalyx, Ruellia peninsularis, Sanchezia stenomacia,* and *Thunbergia erecta.* Multiseriate rays fewer than uniseriate rays characterize *Barleria cristata, Mendoncia gigas* (Fig. 30), *M. erythrochlamys,* and *M.* sp.

Various degrees of raylessness characterize some Acanthaceae. Species with few rays (and those all uniseriate) include *Jacobinia ghiesbrechtiana, Salpinxantha coccinea,* and *Thunbergia holstii.* The ontogenetic development of a rayless condition can be seen in *Diapedium assurgens* (Fig. 8). Woods observed to be entirely rayless include *Jacobinia carnea, Justicia magnifica* (Fig. 5, 6), and *Thunbergia laurifolia* (Fig. 25).

In species of Acanthaceae in which rays are present, a large proportion have abundant erect cells in the multiseriate portions of multiseriate rays. Erect cells only were observed in *Thunbergia erecta* and *T. holstii.* Erect cells almost exclusively, with a few square cells, characterize multiseriate portions of multiseriate rays in *Acanthus ebracteatus, Anisacanthus thurberi* (Fig. 2), *Asystasia zambiana, Barleria cristata, Calycacanthus* sp., *Graptophyllum insularum* (Fig. 10), *Justicia californica, Megaskepasma erythrochlamys, Pachystachys lutea, P. spicata, Razisea spicata, Ruellia peninsularis, Sanchezia nobilis, S. rubriflora, S. stenomacia, S. williamsii,* and *Whitfieldia colorata* (Fig. 4). A few procumbent cells and square cells, but otherwise erect cells, occur in multiseriate portions of multiseriate rays in *Aphelandra pulcherrima, A. tetragona,* and *Sanchezia decora* (Fig. 14). Predominance of square or nearly square cells in multiseriate portions of multiseriate rays, was observed in *Aphelandra scabra, Mendoncia gigas* (Fig. 30), *M. microchlamys, M. retusa, M.* sp., *Pseuderanthemum laxiflorum, Pseudoblepharis glischrocalyx,* and *Ruspolia hypocrateriformis.* In only a few species of Acanthaceae

are procumbent cells abundant (along with some erect cells) in multiseriate portions of multiseriate rays: *Bravaisia floribunda, B. integerrima, Himantochilus marginatus, Psilanthele jamaicensis,* and *Trichanthera gigantea.* Erect cells characterize uniseriate rays and uniseriate portions of multiseriate rays except in the species listed above in which procumbent cells are common in multiseriate portions of multiseriate rays; in these latter species, square or procumbent cells are occasional but the majority of cells are erect in uniseriate rays and uniseriate portions of multiseriate rays. Thus, upright cells bulk very large in rays of all but a few Acanthaceae. The species with wider rays (Table 1, column 10) tend to have a higher proportion of procumbent cells in multiseriate portions of multiseriate rays: *Anisacanthus thurberi, Aphelandra deppeana, Bravaisia floribunda, B. integerrima,* and *Trichanthera gigantea* could be cited in support of this trend. Rays are characteristically narrow in Acanthaceae: the mean width of multiseriate rays at their widest point is only 2.6 cells for the family at large (Table 1, column 12), and in only seven species does the figure exceed 3.0 cells.

Ray cell walls are only moderately thick in the family (Fig. 2, 4, 10, 14, 19, 20, 24, 30), but all ray cells were lignified except in *Thunbergia alata,* in which rays are very few. Pits interconnecting ray cells were simple in all species studied with the exception of a few pits of ray cells in *Aphelandra pulcherrima.*

Ray heights are shown in Table 1, columns 10 and 11. In general, ray heights parallel length of vessel elements or libriform fibers. The genera *Sanchezia* and *Trichanthera* have long vessel elements and also exceptionally tall multiseriate rays.

Cystoliths

Cystoliths have been reported for various Acanthaceae by Solereder (1908), who has even provided (p. 616–617) a key to the various types of cystoliths in the family. However, the organographic distribution of cystoliths in the family is not given by Solereder (1908) nor by Metcalfe and Chalk (1950), and no account to date has indicated in which genera in the family cystoliths occur in wood.

In the present study, cystoliths were observed in some ray cells of *Bravaisia floribunda* (Fig. 20), *B. integerrima* (Fig. 19), *Sanchezia decora* (Fig. 18), *S. nobilis, S. rubriflora, S. williamsii,* and *Trichanthera gigantea.* All of these cystoliths could be referred to the same basic type: they are oval to elongate structures that tend to conform in their shape to the shape of the cells in which they are contained. Hyaline outer layers or tips (Fig. 18) can be seen on some, while others exhibit a knobby appearance (Fig. 19, center). Cystolith lamellae that stain brightly with fast green, and which therefore probably represents nonlignified cellulosic layers, can be seen in all cystoliths observed in Acanthaceae. These layers are illustrated in Fig. 20.

Crystals

Calcium oxalate crystals have not hitherto been reported in Acanthaceae. In the present study such crystals were uncovered only in three species. In *Graptophyllum insularum* (Fig. 12), crystals are small, rhomboidal, and numerous per ray or axial parenchyma cell. Although crystals are rather uniformly small in *G. insularum,* there are a few larger rhomboidal crystals in ray or axial parenchyma

cells of this species. Small and relatively short acicular crystals were numerous in ray cells of *Aphelandra tetragona*. Acicular crystals of this nature were observed in ray cells and apotracheal parenchyma of *Thunbergia crispa*, and in axial parenchyma associated with interxylary phloem in *T. alata* (Fig. 28, bottom; Fig. 32) and *T. laurifolia* as well as all four collections of *Mendoncia*.

Amorphous Deposits

Irregularly shaped accumulations of tanninlike materials were observed in ray cells of *Aphelandra pulcherrima*, *A. tetragona*, *Pseudoblepharis glischrocalyx*, *Ruellia peninsularis*, and *Salpinxantha coccinea*. Such deposits are to be expected in other species of the family, because in various dicotyledonous woods, amorphous deposits seem to occur without reference to taxonomic groupings.

Interxylary Phloem and Other Cambial Variants

Although "fissured xylem" has been reported for *Mendoncia* and *Thunbergia* (Metcalfe and Chalk 1950), interxylary phloem has been reported in Acanthaceae only for *Thunbergia* (Mullenders 1947). Interxylary phloem is present in *Thunbergia alata* (Fig. 26, 27), *T. laurifolia* (Fig. 25), *Mendoncia gigas* (Fig. 29), *M. microchlamys*, *M. retusa*, and *M.* sp. In *Thunbergia alata* and *T. laurifolia*, the phloem strands are sheathed in parenchyma cells that have a smaller diameter than the sieve tube elements and thus are easily distinguished from them. The remaining xylem areas consist of vessels, libriform fibers, and vasicentric tracheids, cell types that have thick, lignified walls, and thus are quite distinct from the parenchyma-sheathed interxylary phloem zones (Fig. 25–27).

The interxylary phloem of *Thunbergia alata* and *T. laurifolia* lacks fibers, although large scattered gelatinous fibers do characterize the extraxylary phloem of these species (Fig. 25, top). In *Mendoncia gigas* and other species of *Mendoncia*, gelatinous fibers identical to those of *Thunbergia* occur not only in extraxylary phloem (Fig. 29, top and left) but also in some of the interxylary phloem strands.

In *Thunbergia holstii*, a small cambial anomaly was noted; although the xylem cylinder was otherwise normal, a patch of vessels embedded in parenchyma (Fig. 22, top) outside of the xylem cylinder was observed. The cambium presumably is external to the patch of vessels at this point. The apotracheal parenchyma strands in later-formed wood of *Thunbergia crispa* represent a conditional transition between the absence of such parenchyma bands (*T. erecta*) and the strands of parenchyma that contain interxylary phloem in *T. alata* and *T. laurifolia*.

SYSTEMATIC CONCLUSIONS

The features that characterize Acanthaceae include: vessels with simple perforation plates and lateral-wall pitting of medium-sized alternate bordered pits; imperforate tracheary elements with simple pits and therefore libriform fibers (vasicentric tracheids also present in a few genera); libriform fibers septate in most genera; axial parenchyma vasicentric scanty (also initial or terminal in a few genera); rays both multiseriate and uniseriate, the former mostly biseriate (some species rayless or nearly rayless); multiseriate portions of multiseriate rays with procumbent cells in a few genera, rays otherwise paedomorphic (see Carlquist

1962, 1980, 1988) by virtue of predominance of erect cells; cystoliths present in ray cells in a few genera; small rhomboidal or acicular crystals present in axial and ray parenchyma of a few genera; wood nonstoried.

All of the features listed in the above paragraph are matched by those in wood of Gesneriaceae, except for cystolith presence (Carlquist and Hoekman 1986a). The presence of septate libriform fibers in both Gesneriaceae and Acanthaceae provides a striking similarity, and the two families are also alike in presence of paedomorphosis and raylessness in a number of genera. Raylessness could be claimed to form an instance of parallel evolution in the two families, indicative of a similar range of herbaceousness in both families. The entire family Planta-ginaceae is rayless or nearly so (Carlquist 1970), but is probably not as close to either Gesneriaceae or Acanthaceae as it is to Scrophulariaceae, a family which also has some rayless species in genera such as *Hebe*. One genus of Gesneriaceae, *Coronanthera*, has fiber-tracheids (Carlquist and Hoekman 1986a), but the re-maining genera have libriform fibers. Fiber-tracheids characterize some Scroph-ulariaceae, although many have septate libriform fibers and a few (e.g., *Hebe*) have tracheids (Metcalfe and Chalk 1950). In Pedaliaceae and Martyniaceae, libriform fibers are present; they are septate in *Sesamothamnus* of the Pedaliaceae (Carlquist 1987).

Bignoniaceae have aliform-confluent axial parenchyma, and thus represent a slightly greater departure from Acanthaceae than the above families; imperforate tracheary elements in Bignoniaceae are fiber-tracheids or libriform fibers, the latter septate in vining genera (Metcalfe and Chalk 1950). Myoporaceae share vasicentric scanty parenchyma with Acanthaceae, but Myoporaceae differ in having fiber-tracheids rather than libriform fibers and a predominance of procumbent rather than erect cells in rays (Carlquist and Hoekman 1986b). Occasional bands of parenchyma, probably the result of fiber dimorphism, such as those observed in *Thunbergia holstii,* may be found in some Myoporaceae (Carlquist and Hoekman 1986b), Scrophulariaceae (Michener 1986) and Pedaliaceae (Carlquist 1987), but these may not be indicative of relationship because they appear to have originated independently in a number of dicotyledon families. Storying is present in some Scrophulariaceae (Michener 1983, 1986), *Drymonia* of the Gesneriaceae (Carl-quist and Hoekman 1986a), some Myoporaceae (Carlquist and Hoekman 1986b), and many Bignoniaceae (Metcalfe and Chalk 1950). The lack of storying in Acan-thaceae may be significant because the number of collections of Acanthaceae surveyed was large in comparison to collections studied in the other families. Presence of inconspicuous forms of helical sculpture in a scattering of Acanthaceae should probably be interpreted more as an ecological adaptation to dry conditions (Carlquist 1966) than as an indicator of systematic relationship.

Although the families of Scrophulariales (Bignoniales of some authors) do de-viate from one another with respect to wood anatomy, the order is remarkably uniform with respect to wood features compared with other dicotyledonous orders in which wood heterogeneity is much greater. This may aid in defining Scrophu-lariales and in determining the degree of relationship among the component families.

The present study offers significant evidence about the status of families some-times segregated from Acanthaceae. Bremekamp (1953) and Cronquist (1981), who recognize Mendonciaceae as a monogeneric family, cite absence of cystoliths

and a specialized seed dispersal mechanism as reasons for segregating *Mendoncia*. However, cystoliths are not present in all Acanthaceae (Metcalfe and Chalk 1950). In addition, three highly distinctive wood features link *Mendoncia* with the scandent *Thunbergia* species (*T. alata*, *T. laurifolia*): presence of large, scattered gelatinous fibers in extraxylary phloem; presence of interxylary phloem; and presence of acicular crystals in the parenchyma associated with interxylary phloem. With such a constellation of unusual features linking the two genera, segregation of *Mendoncia* from Acanthaceae seems inadvisable unless *Thunbergia* is also excluded from Acanthaceae. *Thunbergia* has been segregated from Acanthaceae by some workers (e.g., Dahlgren 1980). However, wood of two species of *Thunbergia*, *T. erecta* and *T. holstii*, does not share the features cited for *Mendoncia* but is, instead, compatible with the wood of remaining Acanthaceae. Thus, segregation of *Thunbergia* from Acanthaceae is not supported here.

Specific and generic characters probably exist in Acanthaceae (e.g., cystolith presence or absence), but the sampling of the family in the present study is insufficient to establish such features with any degree of validity. Study of wood anatomy in genera with diversity among species (e.g., *Justicia*) in habit and ecology is likely to reveal some wood features that correspond with species limits.

ECOLOGICAL CONCLUSIONS

Although the majority of Acanthaceae occur in moist tropical habitats, some range into dry tropical and even desert (*Anisacanthus, Justicia*) localities, although the two genera named occur in desert washes, where moisture availability is very likely greater than on desert flats. In viewing woods of Acanthaceae, therefore, one is likely to find mesomorphic adaptations.

The vessels of Acanthaceae from the wet tropics are much narrower than one would expect on the basis of observations on wood of tropical trees. Mean vessel diameter for the world flora (admittedly a sample that favors tree species) is 94 μm (Metcalfe and Chalk 1950, p. 1360), whereas the mean vessel diameter for Acanthaceae is 70 μm (Table 1, column 3). Moreover, the presence in several genera (e.g., *Bravaisia, Sanchezia*) of perforation plates appreciably narrower than the vessels in which they occur, suggests a suboptimal conformation of vessels where flow of volume per unit time is concerned. If one views the characteristic habitats of genera such as *Sanchezia*, the nature of quantitative vessel features in the family becomes evident. Tropical Acanthaceae are typically understory plants. Plants in this habitat would transpire lower volumes per unit time than plants with canopy status, so a conductive system adapted to moderate transpiration is not surprising.

The genus *Jacobinia* occupies understory habitats where seasonal drought occurs (see Introduction), and thus the canelike shoots of limited duration in that genus are understandable when one compares *Jacobinia* to genera with single trunks, such as *Sanchezia*. We may take the Mesomorphy ratio value of about 50, well below the family mean of 1361 (Table 1, column 13), as the threshhold below which woody dicotyledons are xeromorphic (Carlquist and Hoekman 1985). *Jacobinia* falls close to that threshhold, as does *Justicia*. Notably low Mesomorphy values are represented by *Anisacanthus thurberi* (30), *Diapedium assurgens* (19), and *Ruellia peninsularis* (13). Desert shrubs of southern California have a Mesomorphy value (20.9) in about the same range (Carlquist and Hoekman 1985),

and correlated with the habitats of these three species (see Introduction). The specimen of *Ruellia peninsularis* was obtained from a cultivated plant receiving regular watering, demonstrating that xeromorphic wood features may be heritable with less phenotypic modification than a scattering of comments in the literature on wood anatomy might lead one to expect.

The range of Mesomorphy-ratio values in Acanthaceae is relatively great, and the figures obtained do appear to be reliable indicators of ecology. However, a species with a value of 10,000 probably should not be considered ten times as mesomorphic as one with a value of 1000: values in this range may indicate differences in ability to conduct volumes per unit time, but values at the low end of the Mesomorphy scale are probably more significant with respect to order of magnitude of numerical values, because they indicate conductive safety (ability to maintain water columns intact through a dry season).

Vessel element length, one of the dimensions on which the Mesomorphy ratio is based, very clearly correlates with ecology in Acanthaceae. If one notes which species in Table 1 have a vessel element length greater than the world flora mean, 649 μm (Metcalfe and Chalk 1950), one finds that they are all broadleaved shrubs of moist tropical forest understory habitats. Degree of vessel grouping is held to be proportional to xeromorphy in woody dicotyledons that have libriform fibers or fiber-tracheids (Carlquist 1984). With respect to this criterion, species of Acanthaceae appear mostly mesomorphic (Table 1, column 1). In this connection, one should note that the vessel per group figures for *Anisacanthus thurberi* and *Justicia californica* are not accurate because narrow vessels and vasicentric tracheids are difficult to distinguish from libriform fibers, and if the former cell types could have been counted accurately, a much higher vessel per group figure would have been obtained for those species.

In addition to features involving vessel dimensions, one should note that presence of vasicentric tracheids in *Anisacanthus thurberi* and *Justicia californica* is of great importance as a probable mechanism for survival of drought, as noted earlier (Carlquist 1985a). Growth-ring presence and presence of helical sculpture in vessels, although both of these are present in relatively moderate forms in the Acanthaceae that possess them, seem to correlate with relative dryness of habitat.

One must remember that features of the vegetative apparatus other than wood may be of overriding importance to survival. For example, if *Jacobinia* stems are moderately succulent, leaves tend to be drought-deciduous, and shoots are of short duration and can die back to the woody caudex without causing any loss in ability to produce flowers the following year.

CONCLUSIONS RELATIVE TO HABIT

Paedomorphosis in dicotyledon wood (Carlquist 1962, 1980, 1988) is indicated by a series of structural features characteristic of wood of herbs and herblike plants (particularly their metaxylem and early secondary xylem) that are protracted indefinitely into the secondary xylem. One of these tendencies is predominance of erect cells in rays, especially in the multiseriate part of multiseriate rays, in which procumbent cells are normally abundant in wood of typically woody dicotyledons. This tendency is remarkably common in Acanthaceae; erect ray cells predominate in multiseriate rays of all but the woodiest of the Acanthaceae studied here.

Raylessness is a form of paedomorphosis in which ray cells are not only so erect that they resemble imperforate tracheary elements in length, they also are like libriform fibers rather than ray cells in morphology (cells are fusiform rather than blunt). Raylessness has been considered as an indicator of secondary woodiness (Carlquist 1970) or an increase in strength involving relatively slender but tall stems in herbs or herblike plants, as in certain species of *Phacelia* (Carlquist and Eckhart 1984). The slender stems of *Plantago princeps* Cham. (Carlquist 1970) and of *Jacobinia,* both good examples of raylessness, may be representative of both tendencies.

The genera *Mendoncia* and *Thunbergia* show adaptation in wood structure to the vining habit. In the genus *Thunbergia, T. alata, T. crispa,* and *T. laurifolia* show the most pronounced expressions of these modifications; *T. erecta* and *T. holstii* are more nearly shrubs than vines in habit and in wood anatomy. *Thunbergia alata, T. laurifolia,* and the various species of *Mendoncia* have vasicentric tracheids in addition to very narrow vessels. Thus, they illustrate the dimorphism in vessel diameter that is characteristic of scandent woody dicotyledons (Carlquist 1981), and they also exemplify the tendency for vines and lianas with libriform fibers (or fiber-tracheids) to have vasicentric tracheids (Carlquist 1985b). Acanthaceae should be added to the list of families with vasicentric tracheids given in Carlquist (1985b). Vasicentric tracheids are theorized to offer a form of safety in vines and lianas, because they could be more resistant to embolism spread than vessels, and thereby could continue to conduct if the wide vessels were temporarily disabled.

A sheath of starch-rich parenchyma around vessels in vines and lianas is also theorized to be a potential conductive safety mechanism (Carlquist 1985b), because hydrolysis of starch into sugar, followed by transfer of sugar into the vessels, could increase volume of water within the vessels by osmotic pressure. *Thunbergia alata, T. laurifolia,* and the four collections of *Mendoncia* studied here all show vasicentric parenchyma unusually abundant for the family (sheaths around vessels usually two cells thick). Dobbins and Fisher (1986) support the idea that presence of parenchyma may help regeneration of conductive tissue following wounding, as might happen when a liana falls from its host tree. While their studies do show callus formation and cambial renewal after artificial wounding, they do not show that this process helps in survival of damaged lianas in the wild. One might expect that evolutionary mechanisms that prevent damage to the conductive system would have greater selective value than those that repair damage; disruption to conductive tissue of a liana could be fatal.

The role of parenchyma in providing flexibility and thereby potentially reducing damage to liana stems has been stressed by various authors (see Carlquist 1985b). The parenchyma sheaths around phloem in *Thunbergia alata* and *T. laurifolia* are quite prominent and suggest a function in protecting the integrity of the interxylary phloem. This function might be in those species related to the abundant acicular crystals in those cells, potentially an herbivore deterrence mechanism rather than a flexibility mechanism. Another possible function of parenchyma abundance in stems of lianas and vines is providing sites for fissuring of the xylem into separate units. Fissuring of the xylem in *Mendoncia* has been mentioned by Metcalfe and Chalk (1950) and by Obaton (1960). When fissuring is active, interxylary phloem provides a mechanism for close phloem association with the fragmented xylem strands.

Wide vessel diameter has long been noted as a characteristic of scandent di-cotyledons (for a review, see Carlquist 1985*b*). Vessels in *Thunbergia alata, T. laurifolia,* and the four collections of *Mendoncia* do not appear exceptionally wide according to the data of Table 1, column 3. However, the presence of numerous narrow vessels in those species undoubtedly masks, in averaging vessel diameters, the existence of exceptionally wide vessels revealed in preparations such as those illustrated in Figure 25, 26, and 29. The presence of numerous narrow vessels in a lianoid species, as in *Asystasia zambiana,* may have a function in improving conductive safety much like the safety conferred by vasicentric tracheids, for very narrow vessels may resist embolisms nearly to the degree that vasicentric tracheids do so (see Carlquist 1988).

The exceptionally thick walls of vessels in *Thunbergia crispa* and *T. holstii* are unusual in Acanthaceae. Walls of this nature might represent a mechanism for maintaining the integrity of water columns in vessels. This possibility should be investigated, and additional instances of notably thick walls in lianas should be reported. As a generalization one may say that wider vessels in dicotyledons have thicker walls. The degree to which this is true deserves study; if wider vessels do tend to be notably thick walled, the function of this thickness may be in main-taining integrity of the water column, because mechanical strength of the stem itself could be achieved much more readily by a moderate increase in thickness of libriform fibers. Thicker vessel walls might also characterize species in which imperforate tracheary elements also tend to be thicker walled, so that an increase in wall thickness of one type of cell tends to be applied, for genetic reasons, to other cell types as well.

The rayless or nearly rayless wood of *Thunbergia alata* and *T. laurifolia* and the relatively ray-poor wood of *T. crispa* may seem curious in view of the prom-inence of wide rays in scandent families such as Aristolochiaceae and Vitaceae. However, raylessness has been reported in another woody vine, *Cobaea* (Carlquist, Eckhart and Michener 1984). The abundant parenchyma of *Cobaea* and the two *Thunbergia* species may serve not only the functions of axial parenchyma in scandent woody plants cited above, it may also substitute very effectively for rays in these species, in which stem diameter may not exceed about 1 cm. *Asystasia zambiana* is a lianoid species that does correspond to the *Aristolochia* pattern, for it has notably wide primary rays altered little during secondary growth.

The possible function of raylessness as a way of conferring mechanical strength to stems of short duration has been mentioned above. Thick-walled libriform fibers appear related to habit in Acanthaceae, because they are most prominent in genera that are large shrubs or even small trees (*Sanchezia, Trichanthera*). The ratio between imperforate tracheary element length and vessel element length is of potential interest with relation to habit. The ratio has a comparatively low value in Gesneriaceae, an intermediate value in Acanthaceae, and a high value in Myoporaceae. This may accord with the fact that woody Gesneriaceae are relatively small shrubs, woody Acanthaceae are medium-sized to large shrubs, and Myoporaceae are medium-sized shrubs to trees.

LITERATURE CITED

Bremekamp, C. E. B. 1953. The delimitation of Acanthaceae. Prog. Kong. Ned. Akad. Wetensk. 56: 533–541.

Carlquist, S. 1958. Wood anatomy of Heliantheae (Compositae). Trop. Woods 108:1030.

———. 1962. A theory of paedomorphosis in dicotyledonous woods. Phytomorphology 12:30–45.

———. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. Aliso 6(2):25–44.

———. 1970. Wood anatomy of insular species of *Plantago* and the problem of raylessness. Bull. Torrey Bot. Club 97:353–361.

———. 1980. Further concepts in ecological wood anatomy, with comments on recent work in wood anatomy and evolution. Aliso 9:499–553.

———. 1981. Wood anatomy of Nepenthaceae. Bull. Torrey Bot. Club 108:321–330.

———. 1982. The use of ethylenediamine in softening hard plant structures for paraffin sectioning. Stain Techn. 57:311–317.

———. 1984. Vessel grouping in dicotyledon wood: significance and relationship to imperforate tracheary elements. Aliso 10:505–525.

———. 1985a. Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions; review of vasicentric tracheids. Aliso 11:37–68.

———. 1985b. Observations on functional wood histology of vines and lianas: vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels, and parenchyma. Aliso 11:139–157.

———. 1987. Wood anatomy of Martyniaceae and Pedaliaceae. Aliso 11:473–483.

———. 1988. Comparative wood anatomy. Springer Verlag, Heidelberg, Berlin, and New York (in press).

———, and V. M. Eckhart. 1984. Wood anatomy of Hydrophyllaceae. II. Genera other than *Eriodictyon*, with comments on parenchyma bands containing vessels with large pits. Aliso 10: 527–546.

———, ———, and D. C. Michener. 1984. Wood anatomy of Polemoniaceae. Aliso 10:547–572.

———, and D. A. Hoekman. 1985. Ecological wood anatomy of the woody southern California flora. IAWA Bull., n.s., 6:319–347.

———, and ———. 1986a. Wood anatomy of Gesneriaceae. Aliso 11:279–316.

———, and ———. 1986b. Wood anatomy of Myoporaceae: ecological and systematic considerations. Aliso 11:317–335.

Cronquist, A. 1981. An integrated system of classification of flowering plants. Columbia Univ. Press, New York. 1262 p.

Dahlgren, R. M. T. 1980. A revised system of classification of flowering plants. Bot. Not. 124:451–472.

Dale, I. R., and P. J. Greenway. 1961. Kenya trees and shrubs. Buchanan's Kenyan Estates, Ltd., in association with Hatchard's, London. 654 p.

Dobbins, D. R., and J. B. Fisher. 1986. Wound responses in girdled stems of lianas. Bot. Gaz. (Crawfordsville) 147:278–289.

Gentry, H. S. 1942. Rio Mayo plants. Carnegie Inst. Washington Pub. 527. Carnegie Inst. Washington, Washington, D.C. 328 p.

IAWA Committee on Nomenclature. 1964. Multilingual glossary of terms used in wood anatomy. Verlagsanstalt Buchdruckerei Konkordia, Winterthur, Switzerland. 186 p.

Johnston, I. M. 1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. The botany (the vascular plants). Proc. Calif. Acad. Sci. Ser. 4, 12:951–1218.

Kearney, T. H., and R. H. Peebles. 1960. Arizona flora. ed. 2. University of California Press, Berkeley and Los Angeles. 1085 p.

Long, R. W., and O. Lakela. 1971. A flora of tropical Florida. Univ. Miami Press, Coral Gables, Florida. 962 p.

Metcalfe, C. R., and L. Chalk. 1950. Anatomy of the dicotyledons. Clarendon Press, Oxford. 1500 p.

Michener, D. C. 1983. Systematic wood anatomy of Californian Scrophulariaceae. I. *Antirrhinum, Castilleja, Galvezia,* and *Mimulus* sect. *Diplacus.* Aliso 10:471–487.

———. 1986. Systematic and ecological wood anatomy of Californian Scrophulariaceae. II. *Penstemon* subgenus *Saccanthera.* Aliso 11:365–375.

Mullenders, W. 1947. L'origine du phloème interxylérien chez *Stylidium* et *Thunbergia.* Étude anatomique. La Cellule (Louvain) 51:7–48.

Munz, P. A. 1974. A flora of southern California. Univ. California Press, Berkeley and Los Angeles. 1086 p.

Obaton, M. 1960. Les lianes ligneuses à stucture anormale des forêts dense d'Afrique occidentale. Ann. Sci. Nat. Bot., Sér. 12, 1:111–220.

Record, S. J., and R. W. Hess. 1943. Timbers of the New World. Yale Univ. Press, New Haven. 660 p.

Solereder, H. 1908. Systematic anatomy of the dicotyledons (trans. by L. A. Boodle and F. E. Fritsch). Clarendon Press, Oxford. 1182 p.

Takhtajan, A. L. 1987. Systema magnoliophytorum. Officina Editoria "NAUKA," Leningrad. 439 p.

Thorne, R. F. 1976. A phylogenetic classification of the angiosperms. Evol. Biol. 9:35–106.