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SYSTEMATIC AND ECOLOGICAL WOOD ANATOMY OF
CALIFORNIAN SCROPHULARIACEAE. I. *ANTIRRHINUM*,
CASTILLEJA, *GALVEZIA*, AND *MIMULUS*
SECT. *DIPLACUS*

David C. Michener

INTRODUCTION

The woody Scrophulariaceae of the California Floristic Province (Raven and Axelrod 1978) constitute a distinctive, although minor, element of the flora. The presence of suffrutescent to truly shrubby species among seven genera (Table 1) representing four of the five or six tribes (Wettstein 1897, Pennell 1935; respectively) native in the floristic province indicates that the development of woody habits has been selectively advantageous in this province in this essentially herbaceous family. How are these woods constructed? Are they secondarily woody? What systematic and ecological patterns do the woods present; has there been structural convergence among the drought-deciduous taxa due to the mediterranean-type climate regardless of tribal ancestry? Are any of the woods (as of the evergreen *Galvezia*) modally distinct? These questions, and the dearth of information on woods of Scrophulariaceae, prompted this series. This paper presents the descriptive wood anatomy of *Antirrhinum*, *Castilleja*, *Galvezia*, and *Mimulus* sect. *Diplacus* as well as a discussion of the ecological patterns within *Mimulus* sect. *Diplacus*. The subsequent paper will present the descriptive wood anatomy of *Penstemon* and *Scrophularia* species as well as a discussion of the ecological patterns within *Penstemon*. The wood anatomy of *Keckiella* is presented in Michener (1981). Since these genera enter an overlapping array of habitat sites, and as several taxa were collected from the same site or similar habitats, an inclusive presentation of intergeneric convergences (and exceptions) will conclude the work.

Castilleja, *Mimulus*, and *Galvezia*—*Antirrhinum* represent three distinct phylogenetic lineages of the Scrophulariaceae, yet all include woody taxa of various habits in the floristic province. Few species of *Castilleja* are shrubby (although woody root crowns are present in some perennial species). The two *Castilleja* species studied here are distinctly shrubby (to ca. 1 m tall), drought-deciduous, insular endemics. *Mimulus* sect. *Diplacus* comprises six extant species of shrubs (to ca. 1.5 m tall) and one suffrutescent perennial, *M. clevelandii*. All are drought-deciduous. The species of this section are native to rocky or disturbed sites in a wide range of low to mid elevation plant communities throughout the montane parts of the floristic province. Both of the *Galvezia* species native to the province are shrubs attaining a

Table 1. Native woody Scrophulariaceae in the California Floristic Province.

Genus	Tribe	Woody species in C.F.P.	Total species in C.F.P.
<i>Antirrhinum</i> L.	Antirrhineae	3	12
<i>Castilleja</i> Mutis.	Rhinantheae	4	34
<i>Galvezia</i> Domb. ex Juss.	Antirrhineae	2	2
<i>Keckiella</i> Straw	Cheloneae	7	7
<i>Mimulus</i> L. sect. <i>Diplacus</i> (Nutt.) Gray	Gratiolaeae	7	7
<i>Penstemon</i> Mitch.	Cheloneae	ca. 30	54
<i>Scrophularia</i> L.	Cheloneae	1	4

Woodiness includes suffrutescence in this count. Data from Munz and Keck (1959) and Wiggins (1980). Tribal arrangement follows Wettstein (1897); tribal placement for these genera is congruent between Wettstein (1897) and Pennell (1935). *Scrophularia* may be misplaced in the Cheloneae (Thieret 1967).

span of up to 2 m. The green-stemmed *G. juncea* of Baja California is drought-deciduous (Shreve and Wiggins 1964, Mooney 1977) whereas *G. speciosa*, an insular endemic, is evergreen. None of the Californian species of *Antirrhinum* are consistently suffrutescent; most are annuals. The specimen of *A. nuttallianum* is included for systematic completion and for comparison with the closely related genus, *Galvezia*.

Only limited references to the wood anatomy of these genera are present in the literature. Born (1886) included observations on *Antirrhinum orontium* L. [= *Misopates orontium* (L.) Raf. (Rothmaler 1956)], *A. majus* L., *Castilleja arvensis* Schlecht. et Cham., *C. canescens* Benth. [= *C. tenuiflora* Benth. (Holmgren 1976)], and *Mimulus luteus* L. Of these, *Antirrhinum majus* may become suffrutescent and *Castilleja tenuiflora* is shrubby (Grant 1924, Holmgren 1976, 1978, Rothmaler 1956). Herbst (1894) described the primary and secondary ray structure of *Antirrhinum orontium*. Solereder (1908) repeated some of the observations of Born and presented original observations on *Castilleja*. Metcalfe and Chalk (1950) included species of *Antirrhinum*, *Galvezia* (as *Antirrhinum junceum* A. Gray), *Castilleja*, and *Mimulus* sect. *Diplacus* in their survey. This work extends, quantifies, and emends these reports.

All of these genera are taxonomically complicated at the specific level, and even the generic limits are not always clear. *Antirrhinum* has been variously circumscribed. One concept includes the Californian species of *Galvezia* as *A.* sect. *Gambelia* (Nutt.) Gray (see Wettstein 1897), leaving to *Galvezia* only the two South American species. Wettstein (1897) also retained *Antirrhinum orontium* within the genus under *A.* sect. *Orontium*. Many authors treat sect. *Diplacus* of *Mimulus* as a distinct genus; in this paper I follow the generic concepts of *Mimulus* presented by Grant (1924) and Vickery (1978). The nomenclature used in this paper is presented in Table

2 and follows Munz (1974) if the taxon is present in that flora. The exceptions are some taxa in *Mimulus* (nomenclature follows Munz and Keck 1959) and *Galvezia juncea* (nomenclature follows Wiggins 1980).

The ecological (vegetational) literature on these taxa is limited. This is due in large part to the low cover the taxa possess in most communities. For example, *Mimulus aurantiacus* is a typical member of coastal sage scrub (Munz and Keck 1959, Thorne 1976). Westman's (1983) survey of 99 sites in coastal sage scrub lists *M. aurantiacus*; its cover (when present) peaks in the 5–9% class. Recent vegetational works which refer to species of *Mimulus* sect. *Diplacus* include Barbour and Major (1977), Brown (1982), and Rzedowski (1978).

MATERIALS AND METHODS

All specimens with my collection numbers were collected from natural habitats except for *Mimulus fleminigii*. This sample was collected from the botanic garden on San Clemente Island (the island to which the species is endemic) where it was grown without supplemental water. In all cases I collected the lower segment of the largest stem(s). All samples were pickled in FAA. The remaining collections are from the xylarium or herbarium of RSA. A complete set of voucher specimens and permanent slides of wood sections and macerations is deposited at RSA. A list of collection localities can be obtained from the author. Wood samples large enough to be clamped in a sliding microtome were prepared, sectioned, stained, and mounted according to the methods in Michener (1981). The smaller wood samples, and samples which tore excessively on the sliding microtome, were over-softened in ethylemediamine, embedded in paraffin, and sectioned on a rotary microtome following the method of Carlquist (1982). These sections were handled according to standard paraffin techniques and then stained and mounted in the same manner as the woods above. Jeffry's solution (Johansen 1940) was used in making all of the macerations. Only wood from the outermost growth rings was used for macerations; in *A. nuttallianum* and *M. clevelandii* only xylem attributable to the second year was macerated. Dilute IKI (Johansen 1940) was used for identifying starch grains.

All anatomical measurements were made with a light microscope. Sample size for vessel-element length, vessel-element width (from macerations and transections, respectively), and fiber length and width is 30; for vessels per mm² it is 15 (fields). Sample size for vessels per group varied from 54 to 118 vessels. In Table 3, sample sizes for vessel-element length are given parenthetically. The sample sizes in Table 2 vary as I measured all the given cells in a complete radial strip for the given growth ring(s) to avoid introducing a seasonal bias (from measuring only part of a year's growth). Sample sizes in Table 3 vary as complete metaxylary elements are infrequent in the

Table 2. Wood features of *Antirrhinum*, *Castilleja*, *Galvezia*, and *Mimulus* sect. *Diplacus*.

Species	Collection	1	2	3	4	5	6	7	8	9
<i>Antirrhinum nuttalianum</i> Benth.	<i>Michener 4225</i>	a	152 ± 39	34 ± 12	259 ± 30	30 ± 7	4.8 ± 5.0	6.1	106 ± 19	49.0
<i>Castilleja grisea</i> Dunkle	<i>Michener 4196</i>	4	131 ± 32	23 ± 11	265 ± 34	19 ± 4	2.0 ± 1.5	27.4	456 ± 198	6.8
<i>C. hololeuca</i> Greene	<i>Balls 23666</i>	2	167 ± 33	25 ± 9	297 ± 44	17 ± 2	3.2 ± 2.6	11.0	565 ± 162	7.4
<i>Galvezia juncea</i> (Benth.) Ball.	<i>Michener 4216</i>	a	139 ± 21	46 ± 12	271 ± 42	30 ± 4	2.4 ± 1.7	15.7	49 ± 31	131.0
	<i>Michener 4227</i>	a	169 ± 43	37 ± 11	355 ± 42	27 ± 5	2.2 ± 1.7	24.0	85 ± 46	74.1
	<i>Michener 4271</i>	a	171 ± 34	30 ± 13	350 ± 62	23 ± 5	2.4 ± 1.6	16.0	106 ± 38	48.7
<i>G. speciosa</i> (Nutt.) Gray	<i>Michener 4192</i>	a	125 ± 21	36 ± 9	297 ± 45	25 ± 4	2.7 ± 2.8	19.5	89 ± 47	51.4
	<i>Michener 4195</i>	a	166 ± 28	26 ± 13	310 ± 52	22 ± 3	2.2 ± 2.1	20.8	136 ± 56	32.7
<i>Mimulus aridus</i> (Abrams) Grant	<i>Michener 3987</i>	4	187 ± 52	14 ± 6	297 ± 53	14 ± 1	3.1 ± 2.6	12.7	1300 ± 270	2.0
<i>M. aurantiacus</i> Curt.	<i>Michener 4032</i>	4	206 ± 53	31 ± 8	367 ± 69	21 ± 3	1.4 ± 0.8	50.0	268 ± 97	24.2
ssp. <i>aurantiacus</i>	<i>Michener 4041</i>	4	192 ± 46	41 ± 9	337 ± 66	25 ± 5	1.7 ± 0.9	29.2	208 ± 66	38.1
	<i>Michener 4066</i>	6	229 ± 41	22 ± 14	364 ± 56	20 ± 3	2.4 ± 2.1	19.2	446 ± 86	11.7
	<i>Michener 4096</i>	5	184 ± 50	25 ± 13	372 ± 61	21 ± 3	2.0 ± 1.8	26.4	238 ± 80	19.7
	<i>Michener 4111</i>	3	222 ± 56	28 ± 8	362 ± 64	18 ± 3	1.6 ± 1.0	32.1	294 ± 83	21.6
	<i>Michener 4117</i>	6	177 ± 54	20 ± 9	299 ± 82	19 ± 4	4.2 ± 6.2	6.3	472 ± 151	7.6
	<i>Michener 4150</i>	7	199 ± 56	20 ± 13	317 ± 65	18 ± 2	3.0 ± 2.4	10.3	767 ± 358	8.6
ssp. <i>australis</i> (McMinn) Munz	<i>Michener 3975</i>	8	174 ± 55	22 ± 10	322 ± 47	18 ± 3	3.0 ± 2.0	8.9	568 ± 177	6.8

Table 2. Continued.

Species	Collection	1	2	3	4	5	6	7	8	9
<i>ssp. lompocensis</i> (McMinn) Munz	Michener 4067	5	223 ± 45	14 ± 7	311 ± 48	17 ± 3	4.2 ± 3.1	6.6	887 ± 159	3.7
<i>M. bifidus</i> Penn. <i>ssp. bifidus</i>	Michener 4019	10	150 ± 35	16 ± 13	250 ± 38	16 ± 4	5.0 ± 4.6	6.6	1147 ± 192	2.2
<i>ssp. fasciculatus</i> Penn.	Michener 4033	4	164 ± 39	19 ± 9	262 ± 58	18 ± 3	1.9 ± 1.5	6.6	720 ± 86	4.4
× <i>M. aurantiacus</i>	Michener 4082	6	143 ± 37	15 ± 9	261 ± 36	16 ± 2	4.6 ± 4.9	10.1	1068 ± 167	2.0
<i>M. clevelandii</i> Bdg.	Michener 4042	2	111 ± 29	15 ± 3	b	b	3.8 ± 3.9	7.3	584 ± 148	2.9
<i>M. flemingii</i> Munz	Michener 4200	7	202 ± 65	22 ± 8	337 ± 68	18 ± 3	1.8 ± 1.9	35.3	315 ± 84	14.4
<i>M. longiflorus</i> (Nutt.) Grant	Michener 3969	5	212 ± 36	25 ± 14	311 ± 63	19 ± 4	2.0 ± 1.2	23.0	561 ± 77	5.6
<i>ssp. calycinus</i> (Eastw.) Munz	Michener 4061a	5	143 ± 38	21 ± 11	295 ± 59	20 ± 4	3.2 ± 2.8	12.6	480 ± 104	6.4
	Michener 4063a	6	266 ± 57	27 ± 13	414 ± 77	19 ± 3	2.5 ± 2.1	15.9	383 ± 131	18.8
<i>ssp. longiflorus</i>	Michener 3981	3	197 ± 58	23 ± 16	402 ± 72	24 ± 3	3.5 ± 7.3	15.5	558 ± 614	8.2
	Michener 4162	3	192 ± 49	21 ± 10	369 ± 63	23 ± 4	1.8 ± 1.7	36.5	366 ± 149	11.3
	Michener 4165	3	214 ± 45	25 ± 17	377 ± 71	22 ± 4	2.0 ± 2.2	29.6	244 ± 69	22.3
<i>M. puniceus</i> (Nutt.) Steud.	Carlquist 1829	5	183 ± 55	19 ± 11	386 ± 83	22 ± 3	2.6 ± 2.4	16.8	260 ± 104	14.0
	Michener 3661	6	242 ± 64	32 ± 15	350 ± 21	21 ± 4	2.6 ± 4.2	21.5	267 ± 57	29.6
	Michener 4048	4	200 ± 43	29 ± 16	366 ± 39	21 ± 4	1.6 ± 2.2	40.3	332 ± 167	17.7
	Michener 4215	3	267 ± 45	36 ± 13	529 ± 75	23 ± 4	1.5 ± 1.0	41.8	302 ± 126	32.2

Key to columns: 1, Number of growth rings (a = growth flushes obscure or replace distinct growth rings).—2, Vessel-element length, μm .—3, Vessel-element diameter (internal), μm .—4, Libriform-fiber length, μm (b = lignified fibers lacking).—5, Libriform-fiber diameter, μm (b = lignified fibers lacking).—6, Vessels per group.—7, Vessels, percent solitary.—8, Vessels per mm^2 .—9, Mesomorphy ratio (vessel-element diameter divided by vessels per mm^2 multiplied by vessel-element length). All entries (except columns 7 and 9) are the mean and standard deviation; for sample sizes, see methods. Ray tissue is described in the text.

sections, and vessel-element members in the secondary xylem were counted from entire vertical series of cells rather than counting only to a given sample size.

ANATOMICAL DESCRIPTIONS

Table 2 summarizes over 6000 wood cell measurements and provides the quantitative basis for the descriptions. Ray characteristics, presented below, were only qualitatively assessed. The wood of these genera is highly specialized: 1) the mechanical tissue is composed of libriform fibers, and both the libriform fibers and the vessel-element members are very short (the libriform fibers average less than twice the length of the vessel-element members); 2) fiber dimorphism is conspicuous; and 3) the woods are paeodomorphic. Furthermore, in *Mimulus*, the elimination of rays has advanced to the point that one species is nearly rayless. Since the woods are so specialized and fundamentally similar, the anatomical descriptions are by cell and tissue type rather than by taxon. The parenthetical values are averages from Table 2.

Vessel-element members are short (111–267 μm), and narrow (14–46 μm). Perforation plates are primarily simple, but scalariform perforation plates are found in *Antirrhinum nuttallianum*, *Galvezia juncea*, *Mimulus aurantiacus*, *M. flemingii*, *M. longiflorus*, and *M. puniceus*. In *M. aurantiacus* ssp. *aurantiacus* (Michener 4096), 35.2% ($n = 159$) of the vessel elements scored in maceration counts had scalariform perforation plates (see Fig. 17). Sclariform perforation plates were also noted in the metaxylem of *M. puniceus* (Fig. 16). Intervascular pitting is of alternate circular bordered pits. Vessels are typically grouped (6–50% solitary), often into radial rows (Fig. 1, 5, 7, 9, 11, 13, 15). Grouping into radial rows is prominent in latewood. The number of vessels per group is quite variable (Table 2, column 6); the standard deviations are high due to the grouping of vessels in latewood (see Fig. 6). Prominent tertiary helical thickenings are found in the latewood vessels of *Castilleja* and *Mimulus*. Vascular tracheids were occasionally noted in *Castilleja*, *Galvezia*, and *Mimulus*.

Libriform fibers are short (250–520 μm) and narrow (14–30 μm); their length ranges from 1.3 to 2.3 times that of the vessel-element members. Although libriform fibers do intergrade with the truncate fibers (considered below), the two classes are modally distinct; the libriform fibers are longer, lack truncate ends, and have narrower, simple pits.

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Fig. 1–4. Wood sections of *Antirrhinum* and *Galvezia*. — 1. *A. nuttallianum* (Michener 4225). Transection: distinct growth flush; vessels in radial rows; mesomorphy ratio is 49. — 2. *G. juncea* (Michener 4271). Transection: growth rings marked by wide earlywood vessels; vessels tend to radial rows; mesomorphy ratio is 48. — 3. 4. *G. speciosa* (Michener 4192). Mesomorphy ratio

is 51.—3. Transection: growth flushes indistinct.—4. Tangential section: rays tall, wide; erect cells common. (Fig. 1, magnification scale above Fig. 15; Fig. 2–4, magnification scale above Fig. 6. Divisions = 10 μ m.)

Axial parenchyma, rather than consisting of septate strands, consists of the truncate fibers. These fibers are easily mistaken for erect ray cells (Fig. 8, 10, 12, 14). The truncate fibers can be distinguished from the erect ray cells on the basis of pitting with the vessels; the truncate fiber:vessel pitting is of broad, narrowly bordered to simple pits whereas the ray:vessel pitting is of alternate circular bordered pits. (Pitting between the truncate fibers and between the ray cells is of slightly bordered pits and is thus not useful in resolving the cell type.) The truncate fibers are produced in distinct seasonal bands: this band varies from one cell in width in one sample of *Galvezia juncea* (Fig. 2) to a continuous zone several cells wide from the last-formed latewood to the earlywood in *Mimulus bifidus* (Fig. 6, 7). Figure eight, a tangential section through part of the latewood, shows the abundance of truncate fiber cells.

Ray characteristics vary between the genera and within *Mimulus*. Uniseriate rays are infrequent in all four genera. The multiseriate rays are composed of erect, square, and procumbent cells; procumbent cells are absent in *Mimulus bifidus* (both subspecies) and one sample of *M. puniceus* (Michener 3661). Procumbent ray cells are uncommon in *Mimulus aridus*, *M. aurantiacus* spp. *lompocensis* (Fig. 10), *M. longiflorus* ssp. *calycinus* (Michener 4061a, 4063a), and *M. longiflorus* ssp. *longiflorus* (Michener 4165). The multiseriate rays range from 115 cells tall and 12 cells wide in *Galvezia speciosa* (Fig. 4) to 19 cells tall and 9 cells wide in *G. juncea*. The rays in *Antirrhinum* and *Castilleja* are smaller: from 33 to 19 cells tall and from 8 to 5 cells wide. Rays of *Mimulus* are strikingly different: figures 12, 14, and 10 show the range from well-defined multiseriate rays, to poorly defined multiseriate rays, to multiseriate rays locally absent. This example of elimination of rays can not be ascribed to stem age as the three samples are all five to six years old. Furthermore, the oldest stem illustrated (Fig. 8; *M. bifidus*) is 10 years old and shows no sign of multiseriate rays.

Two pedomorphic features are present in the woods. First, the change in vessel-element length with age (from the metaxylem through the outer years of the secondary xylem) shows no division and subsequent elongation of the cambial initials at the beginning of secondary growth (Table 3). All four genera show a continuous decline in vessel-element length, with a leveling of the rate of decrease in the later years. This is the prima facie evidence

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Fig. 5-8. Wood sections of *Castilleja* and *Mimulus*.—5. *C. grisea* (Michener 4196). Transection: growth ring terminates with a zone of very narrow vessels; wide vessels not in the first-formed earlywood. Mesomorphy ratio is 6.—6, 7, 8. *M. bifidus* ssp. *bifidus* (Michener 4019). Mesomorphy ratio is 2.—6. Transection: detail of growth ring from Fig. 7 showing very narrow latewood vessels that are narrower than the fibers.—7. Transection: growth rings distinct, terminated by a band of narrow, thick-walled vessels and thin-walled (dimorphic) fibers.—8.

Tangential section: multiseriate rays lacking; apparent uniseriate rays are series of fibers (see text). (Fig. 5, 7, magnification scale above Fig. 6; Fig. 6, 8, magnification scale above Fig. 15. Divisions = 10 μ m.)

of paedomorphosis as established by Carlquist (1962). Second, the presence of scalariform perforation plates in the secondary xylem of all of the genera except *Castilleja* is indicative of paedomorphosis; the existence of meta-xylem vessel members with scalariform plates buttresses this interpretation. The absence of scalariform perforation plates in the secondary xylem of *Castilleja* may reflect the semiparasitic nutritional mode of the genus: wood of parasites is expected to be more xeromorphic than their host's (Carlquist 1975). The inverse correlation of scalariform perforation plates to wood xeromorphy in *Mimulus* is presented below.

Crystalline deposits of starch were noted in *Castilleja* and *Galvezia*. These starch granules were present both in ray cells and fiber cells.

DISCUSSION

The data presented above describe how the woods of *Antirrhinum*, *Castilleja*, *Galvezia*, and *Mimulus* sect. *Diplacus* are constructed: the woods are highly specialized and somewhat stereotyped. The independent, paedomorphic origin of woody taxa in these lineages is not necessarily an insular phenomena in the California floristic province even though woody insular endemics are present in *Castilleja*, *Galvezia*, and *Mimulus* sect. *Diplacus*. Woodiness is certainly polyphyletic in *Castilleja*: *C. tenuiflora* of the pine belt of mainland Mexico is distinctly shrubby (Holmgren 1976). In *Mimulus* sect. *Diplacus* the insular species, *M. flemingii*, is not considered particularly unspecialized; *M. clevelandii* of interior southern California is considered the least specialized taxon. Instead of considering the origin of woody taxa in these genera in relation to insular habitats, it is preferable to consider the role of an equitable (essentially frost-free) climate. This has been suggested by Carlquist (1970) and will be developed in the subsequent paper once *Penstemon* and *Scrophularia* can be considered as well.

Mimulus woods.—The 25 *Mimulus* samples represent a broad survey of the geographic, elevational, and habitat diversity within the sect. *Diplacus*. All taxa native to the province are represented other than a color variant of *M. longiflorus*. However, the geographically restricted *M. aridus*, *M. clevelandii*, and *M. flemingii* are represented only by single samples.

The wood mesomorphy ratios of Table 2 are taken as the single measure

←
Fig. 9–12. Wood sections of *Mimulus*.—9, 10. *M. aurantiacus* ssp. *lompopensis* (Michener 4067). Mesomorphy ratio is 3.—9. Transection: growth rings distinct, vessels in latewood band thick walled.—10. Tangential section: apparent uniseriate rays are primarily series of fibers (see text).—11, 12. *M. aurantiacus* ssp. *aurantiacus* (Michener 4096). Mesomorphy ratio is 19.—11. Transection: growth rings as in Fig. 9.—12. Tangential section: multiseriate rays of erect, square, and procumbent cells. (Fig. 9–12, magnification scale above Fig. 6. Divisions = 10 μ m.)

Table 3. Vessel-element length by age class.

Species and collection	1	2	3	4	5
<i>Antirrhinum nuttallianum</i> 4225	185 ± 35 (5)	196 ± 32 (6)	175 ± 24 (7)	127 ± 22 (4)	
<i>Castilleja grisea</i> 4196	358 ± 78 (7)	197 ± 15 (10)	184 ± 18 (6)	125 ± 21 (6)	110 ± 12 (7)
<i>C. hololeuca</i> 32666	355 ± 65 (6)	193 ± 20 (5)	184 ± 18 (6)	176 ± 32 (7)	
<i>Galvezia juncea</i> 4216	298 ± 74 (6)	200 ± 71 (9)	163 ± 25 (7)	155 ± 32 (9)	166 ± 37 (9)
<i>G. speciosa</i> 4195	265 ± 46 (4)	240 ± 33 (6)	160 ± 7 (8)	149 ± 27 (11)	
<i>Mimulus aridus</i> 3987	407 ± 35 (4)	202 ± 39 (8)	180 ± 54 (8)	58 ± 16 (11)	
<i>M. aurantiacus</i> 4111	369 ± 96 (7)	239 ± 43 (7)	240 ± 25 (10)	218 ± 39 (12)	196 ± 35 (15)
<i>M. clevelandii</i> 4042	280 ± 68 (5)	226 ± 44 (6)	97 ± 33 (10)		
<i>M. flemingii</i> 4200	427 ± 115 (4)	258 ± 74 (9)	190 ± 49 (9)	175 ± 72 (9)	153 ± 42 (8)
<i>M. longiflorus</i> 4162	501 ± 31 (4)	424 ± 69 (5)	222 ± 56 (8)	193 ± 29 (9)	187 ± 44 (8)
<i>M. puniceus</i> 3661	330 ± 74 (5)	292 ± 65 (6)	249 ± 47 (7)	219 ± 69 (9)	212 ± 38 (8)

Key to columns: 1, Metaxylem.—2, Early secondary xylem of the first year.—3, Earlywood of the second year.—4, 5, Earlywood of successive year(s) to the end of the section; the interval between columns 4 and 5 may represent several years. Stem age (growth rings) is given in Table 2. The values for *A. nuttallianum* 4225 span only two years. All lengths in microns. Sample sizes for the averages given in parentheses.

best reflecting the drought severity of the microhabitat. When the 25 samples are ranked by mesomorphy value, the species sequence (and average mesomorphy value) is: *M. puniceus* (23.3), *M. aurantiacus* (15.7), *M. flemingii* (14.4), *M. longiflorus* (12.1), *M. bifidus* (3.3), *M. clevelandii* (2.9), and *M. aridus* (2.0). The mesomorphy values divide the species into two groups: species found in areas of maritime influence (*M. puniceus*, *M. aurantiacus*, *M. flemingii*, *M. longiflorus*) and species restricted to interior ranges (*M. aridus*, *M. bifidus*, *M. clevelandii*). Ranking the samples within species is even more revealing. The most widespread species is *M. aurantiacus*. Here the four highest mesomorphy values (38.1 to 19.7) represent plants from the immediate coast and coastal-facing ridges in the central Coast Ranges. The intermediate values (11.7 to 7.6) represent plants from the interior Transverse Ranges, the interior North Coast Ranges, and the foothills of the Sierra Nevada. The two values of lowest rank represent *M. aurantiacus* ssp. *australis* (6.8) of the Santa Ana Mountains of southern California, and *M. aurantiacus* ssp. *lompopensis* (3.7) of the extreme western Transverse Ranges. This last sample, although growing less than 10 km from the coast, had the most xeromorphic wood in the species—evidently the water relations of the sandy soils overcomes any mitigating maritime influence as temperature or cloud-cover. In *M. longiflorus*, the two subspecies present a similar pattern where the highest values (22 to 18) are from chaparral sites in the San Gabriel or San Jacinto mountains, with lower values (8.2 to 6.4) from coastal sage scrub sites. The lowest value in *M. longiflorus* ssp. *calycinus* (5.6), however, is from a rock crevice plant from the Tehachapi Mountains (an interior range). *Mimulus bifidus* and *M. puniceus* are not considered further due to the small sample size.

The presence of scalariform perforation plates corresponds well with mesomorphy values in *Mimulus*. In *M. aurantiacus*, scalariform perforation plates were found in samples 4041, 4096, and 4111; these represent three of the four highest mesomorphy values in the species. In *M. longiflorus*, scalariform plates were noted only in sample 4165, which has the highest mesomorphy value in the species; in *M. puniceus* the scalariform-perforate sample 3661 had the second highest mesomorphy value in the species. The scalariform-perforate wood sample with the lowest mesomorphy value is that of the insular endemic, *M. flemingii*. This is a clear pattern: scalariform perforation plates, ancestrally (although not necessarily predominately) present in these paedomorphic woods, have not been selectively advantageous in the habitats where the most xeromorphic woods are produced. This indicates that survival to reproductive age of these shrubs has been adversely affected by the scalariform perforation plates, or the vessel-element members that bear them.

The elimination of rays that is demonstrated by the *Mimulus* samples does not present any simple pattern. Barghoorn (1941) noted that the re-

duction of ray tissue was associated with a tendency to a herbaceous habit and considered it a highly specialized condition. The woods of *Mimulus* fit his scheme for the elimination of rays by the enlargement of ray initials.

Finally, the literature is incorrect on one substantial point: the condition of the perforation plate. Solereder (1908) and Metcalfe and Chalk (1950) both list the perforation plate as always simple. The presence of scalariform perforation plates in *Antirrhinum*, *Galvezia*, and *Mimulus* and the paedomorphic origin of these woods suggests that other paedomorphic, scrophulariaceous genera may be similar. In this light, the report of Bierhorst and Zamora (1965) of at least occasional scalariform to transitional perforation plates in the protoxylem to metaxylem of *Scrophularia*, *Verbascum*, and *Veronica* is intriguing, as woody taxa are present in these, or related, genera.

SUMMARY

The secondary xylem of *Antirrhinum*, *Castilleja*, *Galvezia* and *Mimulus* sect. *Diplacus* is highly specialized. Specialized features include the very short and narrow proportions of the vessel-element members, the short stature of the libriform fibers, the presence of dimorphic fibers, and the paedomorphic nature of the woods. In *Mimulus*, elimination of ray tissue by the enlargement of ray initials is well developed. Within *Mimulus*, wood mesomorphy values are indicative of apparent habitat drought severity, and correlate inversely with the presence of scalariform perforation plates. I interpret this to indicate that vessel elements bearing scalariform perforation plates have been strongly selected against in the most xeric habitats entered by species of *Mimulus*.

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Fig. 13–17. Wood sections of *Mimulus*.—13, 14. *M. puniceus* (Michener 3661). Mesomorphy ratio is 14.—13. Transection: growth rings distinct, narrow, thick-walled latewood vessels few.—14. Tangential section: multiseriate rays lack procumbent cells; rays poorly defined.—15. *M. clevelandii* (Michener 4042). Transection: vessels above the growth ring are of the second year; fiber walls not lignified in the second year.—16. *M. puniceus* (Michener 3661). Radial section of vessel in metaxylem; perforation plate scalariform.—17. *M. aurantiacus* ssp. *aurantiacus* (Michener 4096). Radial section of vessels in wood several years old; perforation plates scalariform. (Fig. 13, 14, magnification scale above Fig. 6; Fig. 15, magnification scale at top; Figs. 16–17, magnification scale above Fig. 17. Divisions = 10 μ m.)

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