1984

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Carlquist, Sherwin (1984) "Wood Anatomy of Loasaceae with Relation to Systematics, Habit, and Ecology," *Aliso: A Journal of Systematic and Floristic Botany*. Vol. 10: Iss. 4, Article 7.
Available at: <https://scholarship.claremont.edu/aliso/vol10/iss4/7>

WOOD ANATOMY OF LOASACEAE WITH RELATION TO SYSTEMATICS, HABIT, AND ECOLOGY

Sherwin Carlquist

INTRODUCTION

Loasaceae is one of a number of predominantly herbaceous families of dicotyledons which have received little study with respect to wood anatomy. No data on wood features of Loasaceae, for example, are offered by Metcalfe and Chalk (1950). As in other families of this nature, some species of Loasaceae in warmer areas are shrubby; one (*Mentzelia arborescens* Urban & Gilg) is even a tree, and *Fuertesia domingensis* Urban is a vine with moderate wood accumulation. Through the efforts of Dr. David C. Michener and Dr. Henry J. Thompson, wood samples of several Loasaceae which otherwise could not have been studied were made available to me. Because so many of the Loasaceae with appreciable secondary xylem accumulation are present in the materials used for this study, a paper on this topic is offered at this time.

Wood anatomy may be able to offer some information with respect to the systematic position of Loasaceae. Although Loasaceae traditionally has been placed in Violales or a similar grouping based on possession of parietal placentation, recent systems diverge from that view. Cronquist (1981) has retained this placement, although he notes that the placement of the Loasaceae is uncertain: "the unitegmatic ovules with chalazal and micropylar haustoria are aberrant in the Dillenidae and suggest the Asteridae, as does the frequent presence of iridoid compounds." Emphasis on presence of iridoid compounds in Loasaceae (Kooiman 1974) has led authors to compare Loasaceae to "Corniflorae-Lamiiflorae-Gentianiflorae" (Jensen et al. 1975; Dahlgren 1980). Presence of secoiridoids, according to Dahlgren, indicates a "Cornalean-Dipsacalean or Gentianifloreal affinity." The families in these groups are sympetalous, so that inclusion of Loasaceae among the families I have recently been surveying from the tubiflorous (in the broad sense) dicotyledons is entirely logical. In fact, the idea that Loasaceae are chori-petalous, although cited by some authors (Dahlgren 1980) is erroneous, since sympetaly may be found in the genera *Eucnide*, *Mentzelia*, *Petalonyx* and, as the generic name suggests, *Sympetaleia* (Gilg 1925). Even before the discovery of iridoids in Loasaceae, Wunderlich (1959) claimed that the family might have a place in one of the sympetalous orders on the basis of embryological features. She named Gentianales, Campanulales, and Tubiflorae as possibilities.

Wagenitz (1977) accepts Loasaceae within Asteridae, and Takhtajan (1980) agrees with this while saying that the family should be put "in a separate order placed after Dipsacales and before Polemoniales." Thorne (1983) considers Loasaceae to be the sole family of a superorder, Loasiflorae (a category Dahlgren also accepts), and places Loasiflorae between Rosiflorae and Myrtiflorae.

The genera of Loasaceae are grouped as follows in the system of Gilg (1925):

Gronovioideae

Gronovieae: *Gronovia*, *Fuertesia*, *Cevallia*, *Petalonyx*

Mentzelioideae

Mentzelieae: *Mentzelia*, *Schismocarpus*

Eucnideae: *Eucnide*, *Sympetaleia*

Loasoideae

Loaseae: *Loasa*, *Scyphanthus*, *Cajophora*, *Blumenbachia*

Kissenieae: *Kissenia*

Klaprothieae: *Klaprothia*, *Sclerothrix*

However, Davis and Thompson (1967) in their revision of *Petalonyx* stress the need for revision of the systematics of the family. They regard "*Petalonyx*, *Cevallia*, and the *Gronovia-Fuertesia* alliance to be three divergent groups whose affinities lie with other genera in the family and not with each other." Similarly, Leins and Winhard (1973) propose exclusion of *Mentzelia* from the family as a monogeneric family. The need for revision of the family makes anatomical data valuable, although wood anatomy may offer less than, for example, trichome morphology, where intergeneric problems are concerned.

Does wood anatomy of Loasaceae bear a close relationship to ecology, or does the apparent succulence of stems and roots in this family alter the adaptation of wood anatomy to the dry habitats typically occupied by members of Loasaceae? For convenience of comparison, habitats of the species utilized in the present study are given here (data based on Darlington 1934; Davis and Thompson 1967; Gilg 1925; Munz 1974; and Weberbauer 1945).

Eucnide urens Parry occupies rocky slopes in desert areas of southern California, portions of Baja California, Arizona, Sonora, and southwestern Utah. *Eucnide cordata* Kell. occupies similar sites in portions of Baja California. *Fuertesia domingensis* is a vine from dry slopes in southern Haiti and the Dominican Republic. *Kissenia capensis* R. Br. is a shrub of the Namaqualand deserts of southern Africa and is possibly conspecific with plants known as *K. spathulata* R. Br. from southern Arabia; other than these two species, the family is reported only from the New World. *Loasa picta* Hook. is an annual, somewhat woody at the base, in dry rocky grasslands between 1200 and 2000 m on the Pacific slope of the Andes of Peru. *Loasa*

incana R. & P. is a small shrub from elevations around 1000 m on the Pacific slope of the Andes of Peru. The specimen in the present study was collected on a talus slope dominated by *Cereus macrostibas* (K. Schum.) Berg. *Mentzelia arborescens* is a tree (albeit a rather small and succulent one) native to Oaxaca, Mexico. The specimen used in the present study is from a plant cultivated in the Mildred E. Mathias Botanic Garden of the University of California at Los Angeles. *Mentzelia humilis* (Gray) Darlington occurs on clay cliffs in Colorado and Utah and extends southward to Texas and adjacent northern Mexico. The specimen of *Mentzelia laevicaulis* (Dougl.) T. & G. was on a granitic talus slope at about 1800 m on Mt. San Antonio, near Claremont, California; it is perhaps best described as a biennial or triennial rosette plant in which the succulent root becomes woody. When the plant flowers, a moderate amount of secondary xylem may be found in the stem, all of which above the leaf rosette may be considered as an inflorescence axis. The four species of *Petalonyx* studied here are all shrubs, but are well differentiated from each other with respect to habitat. *Petalonyx crenatus* Gray occurs on sandy plains, gypsum mesas, and dry troughlike valleys in Coahuila, Mexico. *Petalonyx linearis* Greene may be found in sandy soil below 1000 m in Creosote Bush Scrub of southwestern Arizona, Baja California, Sonora, and the islands of the Gulf of California. *Petalonyx nitidus* S. Wats. is known from rocky canyons, washes, open desert, and roadbanks above 1150 m in Creosote Bush Scrub, Joshua Tree Woodland, and Pinyon-Juniper Woodland of southern California, southern Nevada, southwestern Utah, and southwestern Arizona. *Petalonyx thurberi* Gray occupies the *Covillea* and *Artemisia* belts of the Mojave and Colorado deserts of California, Nevada, Arizona, Baja California, and Sonora.

The monotypic genus *Schismocarpus* may not belong to Loasaceae (Dr. Henry J. Thompson, personal communication). Its affinities will be examined in a subsequent study.

MATERIALS AND METHODS

Woods of Loasaceae were available as liquid-preserved samples for the species *Cevallia sinuata* Lag., *Eucnide cordata*, *E. urens* (Michener 4203), *Mentzelia arborescens*, *M. humilis*, *M. laevicaulis*, *Petalonyx crenatus*, *P. nitidus*, and *P. thurberi*. Material of the remaining taxa studied was available as dried portions. Dried material was boiled in water and then stored in 50% ethyl alcohol.

The woods of Loasaceae range from relatively soft to quite succulent. *Mentzelia arborescens* and *M. humilis* exemplify the latter condition. The harder loasaceous woods could be cut on a sliding microtome with moderate success; the softer woods were not suitable for this procedure. The large vessels of *Fuertesia* and the very thin walls of parenchyma in *Mentzelia*

Table 1. Wood characteristics of Loasaceae.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Cevallia sinuata</i>	Michener 4304 (RSA)	84	46	394	1.14	2.7	30	696	3.5	Db	70	3.3	>3000	—	U	1.83	719
<i>Eucnide cordata</i>	Michener 4247 (RSA)	72	22	296	1.15	2.4	25	423	3.0	Db	114	5.8	1452	276	Usp	3.32	982
<i>E. urens</i>	Michener 4203 (RSA)	86	29	269	1.60	2.5	35	640	2.0	DA	269	10.0	2594	—	USp	2.93	788
	Wolf 3186 (RSA)	61	34	192	1.20	2.0	28	463	3.7	DA	151	8.5	1876	—	USp	1.78	342
<i>Fuertesia domingensis</i>	Zanoni et al. 24495 (MO)	326	11	477	1.00	4.6	41	1165	4.6	D	149	7.8	>5000	272	U	30.2	14,398
<i>Kissenia capensis</i>	Barker 2068 (RSA)	71	31	257	1.20	2.4	32	721	3.3	D	151	6.3	2113	187	USp	2.33	594
<i>Loasa incana</i>	Carlquist 7001 (RSA)	60	32	324	1.33	1.8	25	494	2.2	0	51	6.3	634	269	Us	1.89	611
<i>L. picta</i>	Stork 10950 (UC)	44	21	378	1.37	2.2	30	600	3.1	d	139	6.0	1622	240	USp	2.06	777
<i>Mentzelia arborescens</i>	Prigge 5507 (LA)	139	8	291	1.37	2.4	27	815	2.4	DB	587	14.0	>5000	—	Usp	18.1	5253
<i>M. humilis</i>	Michener 4397 (RSA)	47	121	160	1.32	4.1	23	323	3.9	DA	255	12.3	1020	—	USP	0.39	62
<i>M. laevicaulis</i>	Carlquist 4354 (RSA) stem	61	46	490	1.90	2.1	23	826	2.2	0	51	3.1	1628	299	Us	1.33	653
	Carlquist 4354 (RSA) root	79	29	415	2.16	2.5	28	646	1.8	0	55	3.3	662	120	USP	2.69	1115
<i>Petalonyx crenatus</i>	Michener 4381 (RSA)	46	166	161	1.11	2.4	23	265	3.0	D	—	—	—	—	U	0.28	45
<i>P. linearis</i>	Wolf 3173 (RSA) root	63	36	258	1.17	3.4	32	483	3.4	Db	198	9.8	>3000	—	USp	1.76	455
<i>P. nitidus</i>	Michener 4060 (RSA)	59	65	220	1.23	2.3	25	522	2.2	D	139	9.7	>3000	—	USp	0.96	199
<i>P. thurberi</i>	Michener 4953 (RSA)	81	57	247	1.08	2.5	23	536	3.2	Db	74	5.8	>3000	—	USp	1.43	353

Legend for columns: 1 = mean vessel diameter, μm ; 2 = mean number of vessels per mm^2 of transection; 3 = mean vessel-element length, μm ; 4 = mean number of vessels per group; 5 = mean vessel wall thickness, μm ; 6 = mean fiber-tracheid diameter at widest point, μm ; 7 = mean length of fiber-tracheids, μm ; 8 = mean fiber-tracheid wall thickness, μm ; 9 = axial parenchyma (A = abundant, pervasive; B = wide bands; b = few or narrow bands; D = diffuse, abundant; d = diffuse, scarcer; 0 = absent); 10 = mean width of multiseriate rays at widest point, μm ; 11 = mean width of multiseriate rays at widest point, cells; 12 = mean height of multiseriate rays, μm ; 13 = mean height of uniseriate rays, μm ; 14 = ray histology (u = upright, s = square, p = procumbent; upper case indicates predominant types); 15 = Vulnerability ratio (vessel diameter divided by vessel number per mm^2); 16 = Mesomorphy ratio (vulnerability multiplied by vessel element length). Data for *Fuertesia domingensis* include wide vessels but not fibriform vessels.

humilis would be virtually impossible to section well on a sliding microtome. Consequently an alternative procedure involving softening of woods with ethylene diamine followed by sectioning of paraffin-embedded portions on a rotary microtome (Carlquist 1982a) was invoked. This method proved uniformly successful not merely for the softest woods but for the others as well. Sections were stained in a safranin-fast green combination. This proved especially advantageous in species in which some cells lack lignified walls (which would therefore stain less well with safranin alone). Membranes of bordered pits were made more easily visible by the counterstaining, and thus the extent of border presence could be detected more readily. Ethylene diamine tends to hydrolyze starch somewhat, but otherwise alters histological details little.

Macerations were prepared by means of Jeffrey's Fluid and stained with safranin.

The quantitative data of Table 1 represent means obtained from 25 measurements, although fewer measurements were made where a particular feature was uncommon (e.g., uniseriate rays). Where rays were mostly so long that both ends were not confined within a single section, a minimal ray length was estimated (e.g., $>3000\ \mu\text{m}$). The samples listed in Table 1 are all from stems unless otherwise shown.

ANATOMICAL DESCRIPTIONS

Growth rings.—Some of the Loasaceae studied have inconspicuous growth rings characterized by wider vessels in earlywood, narrower vessels in latewood. In their least pronounced form, such growth rings may be seen in *Eucnide cordata* (Fig. 1) and *Mentzelia arborescens* (Fig. 25). More pronounced growth rings of this type may be seen in *Mentzelia humilis* (Fig. 20), *Petalonyx crenatus*, *P. linearis* (Fig. 14), *P. nitidus* (Fig. 16), and *P. thurberi*. Parenchyma bands mostly do not seem related to growth-ring activity, but a parenchyma band coinciding with narrow latewood vessels was observed in *P. thurberi*. Of the Loasaceae studied, those not mentioned in this paragraph lack growth rings.

Vessel elements.—With respect to diameter, the vessels of Loasaceae (Table 1, column 1) range from means of $44\ \mu\text{m}$ in the annual *Loasa picta* to $139\ \mu\text{m}$ in the tree *Mentzelia arborescens* (Fig. 25). *Fuertesia domingensis* ($326\ \mu\text{m}$) exceeds this range considerably. However, one should note that this figure is biased because *Fuertesia* (Fig. 27) demonstrates vessel dimorphism, a phenomenon often seen in vines (Carlquist 1981). The narrower vessel elements may be termed fibriform vessel elements and are difficult to distinguish from imperforate tracheary elements in transection; hence, they were not taken into account in measuring vessel diameter. Thus the actual

Fig. 1-4. Wood sections of *Eucnide cordata* (Michener 4247).—1. Transection. A very small degree of vessel grouping is present.—2. Tangential section; ray cells are mostly upright.—3. Vessels from a radial section showing scalariformlike pits.—4. Fiber-tracheids from a tangential section; pits are fully bordered. (Fig. 1-2, magnification scale above Fig. 1 [finest divisions = 10 μ m]. Fig. 3-4, magnification scale above Fig. 3 [divisions = 10 μ m].)

vessel diameter of *Fuertesia* is much less than indicated. Fibriform vessel elements were observed to be present sparingly in *Mentzelia laevicaulis*.

The number of vessels per mm² in the species studied (Table 1, column 2) ranges from a low of eight in *Mentzelia arborescens* (Fig. 25) to a high of 166 in *Petalonyx crenatus*. The figure 11 has been reported for *Fuertesia domingensis* (Fig. 27), but that refers only to wide vessels and does not include the fibriform vessels.

The shortest vessel elements (mean = 160 μ m) were observed in *Mentzelia humilis* (Fig. 21), the longest (mean = 490 μ m) in *M. laevicaulis*. If one scans the lengths of vessel elements in the family (Table 1, column 3), one finds that vessel elements are not long for dicotyledons as a whole, but they fall between 250 μ m and 400 μ m mostly.

The number of vessels per group is uniformly relatively low in the family (Table 1, column 4), ranging from 1.08 in *Petalonyx thurberi* to 2.16 in roots of *Mentzelia laevicaulis*. The value of 1.00 in *Fuertesia domingensis* is artificially low because narrow vessels were not included in the calculations. The fact that none of the larger vessels are in contact with each other in this species (Fig. 27) is interesting, however.

Loasaceae fall within a narrow range with respect to vessel wall thickness (Table 1, column 5). Notably thick-walled vessels occur in *Fuertesia domingensis* (Fig. 27) and in *Mentzelia humilis* (Fig. 20, 22).

Perforation plates are basically simple throughout the family. However, altered versions of scalariform plates or plates with other aberrant configurations were observed in *Loasa picta* (Fig. 7–11) and *Mentzelia humilis* (Fig. 24). These do not seem to represent minor deviations from scalariform plates and they are not common in any case. Those most similar to scalariform conditions show interconnections between bars (Fig. 7, 24). Others represent meshworklike configurations (Fig. 8) or pitlike appearances (Fig. 9–11). In *Mentzelia humilis*, slender vessel elements with helixlike or networklike thickening bands and without perforation plates may be found adjacent to larger vessel elements. These narrow cells might technically be called vasicentric tracheids, but they do not represent that concept adequately, since vasicentric tracheids are, in other families, different in morphology and fully functional cells rather than vestigial in appearance. These tracheary elements in *Mentzelia humilis* may represent vessel elements the enlargement of which was preempted by the growth of neighboring vessel elements.

Lateral wall pitting of vessels in Loasaceae consists in most species of pits ranging from circular (6 μ m $\times$ 6 μ m) to oval (6 μ m $\times$ 8 μ m). Slightly larger pits (about 7 μ m in diameter when circular) occur in *Mentzelia arborescens*. Pits more elongate laterally than oval pits are common in most species of Loasaceae. Pits laterally widened so as to extend the width of a vessel face occur in some species, such as *Eucnide cordata* (Fig. 3). These pits may be

Fig. 5-11. Wood sections of *Loasa*.—5,6. *Loasa incana* (Carlquist 7001).—5. Transection; no growth rings are present.—6. Tangential section; multiseriate rays are narrow.—7-11. *Loasa picta* (Stork 10950), aberrant perforation plates from radial sections.—7. Plate with forked bars.—8. Plate with meshworklike pattern.—9-11. Plates with variously distorted circular pits. (Fig. 5-6, magnification scale above Fig. 1. Fig. 7-11, scale above Fig. 3.)

termed scalariform. In *Mentzelia arborescens*, *M. humilis* (Fig. 23) and *M. laevicaulis* these laterally elongate pits may be subdivided by narrow vertical strands of lignified wall material. Pits in vessel elements of all the Loasaceae studied could be said to have "gaping" pits, that is, pits with wide, mouthlike pit apertures (Fig. 23, 24).

All vessels in Loasaceae are circular in outline as seen in transection (Fig. 1, 5, 12, 14, 16, 18, 20, 25, 27).

Fiber-tracheids.—The Loasaceae studied may be said to have various fiber-tracheids. These imperforate tracheary elements mostly have fully bordered pits with slitlike apertures. These pits are about 6 μm in diameter in fiber-tracheids of *Eucnide cordata* (Fig. 4), *E. urens*, *Fuertesia domingensis*, and *Mentzelia humilis*. Fully bordered pits 5 μm in diameter characterize fiber-tracheids in *Cevallia sinuata*, *Mentzelia arborescens*, *Petalonyx crenatus*, *P. linearis* (Fig. 19), *P. nitidus*, and *P. thurberi*. Fully bordered pits 4 μm in diameter but with pit apertures gaping rather than slitlike were observed in *Mentzelia laevicaulis* stems and roots.

Fiber-tracheids of the above taxa sometimes approach tracheids in morphology and size of pits; only in density of pits do they fall short, and for this reason are termed fiber-tracheids.

Pits with slitlike apertures and with vestigial borders (circular pit apertures 2–3 μm in diameter) were observed on fiber-tracheids of the Southern Hemisphere Loasaceae studied: *Kissenia capensis*, *Loasa incana*, and *L. picta*. Fiber-tracheids of these species approach libriform fibers rather closely.

Diameter of fiber-tracheids (Table 1, column 6) is somewhat greater in Loasaceae than in most other families of dicotyledons. Fiber-tracheid wall thickness (Table 1, column 8) is not unusual for dicotyledons at large, however.

With respect to length (Table 1, column 7), fiber-tracheids of Loasaceae come very close to approximating twice the length of vessel elements for any given species.

Axial parenchyma.—A variety of expressions of axial parenchyma occurs in Loasaceae, as shown in Table 1, column 9. The basic condition may be described as diffuse. No axial parenchyma was observed in *Loasa incana* stems, or in the roots of *Mentzelia laevicaulis*. A few diffuse parenchyma cells were observed in the earliest secondary xylem of stems of *M. laevicaulis*, but otherwise axial parenchyma was absent in that species. Axial parenchyma is scarce in *Loasa picta*.

Axial parenchyma is abundant in some Loasaceae, however. If so, it may be present in moderately conspicuous bands, as in *Cevallia sinuata*, *Eucnide cordata*, *Petalonyx linearis* (Fig. 14), and *P. thurberi*. Conspicuous bands may be seen in *Mentzelia arborescens* (Fig. 25). Axial parenchyma when most abundant replaces fiber-tracheids so pervasively that parenchyma dis-

Fig. 12-15. Wood sections of *Kissenia* and *Petalonyx*.—12, 13. *Kissenia capensis* (Barker 2068).—12. Transection; latewood above center of photograph.—13. Tangential section. Multiseriate rays are much more abundant than uniseriate rays.—14, 15. *Petalonyx linearis* (Wolf 3173).—14. Transection; parenchyma band above center of photograph.—15. Tangential section. Ray cells are upright (procumbent cells mostly the result of subdivision of upright cells). (Fig. 12-15, magnification scale above Fig. 1.)

tribution cannot be described in terms of bands. Such pervasive parenchyma is exhibited by *Mentzelia humilis* (Fig. 20, 21).

Axial parenchyma was observed typically in strands of two cells in all of the Loasaceae studied.

Vascular rays.—Presence of both multiseriate and uniseriate rays characterizes many Loasaceae, such as *Eucnide cordata* (Fig. 2), *Fuertesia domingensis* (Fig. 28), *Kissenia capensis* (Fig. 13), *Loasa incana*, *L. picta* (Fig. 6), and *Mentzelia laevicaulis*. Uniseriate rays are few or none in *Eucnide urens*, *Mentzelia arborescens* (Fig. 26), *M. humilis* (Fig. 21), and the four species of *Petalonyx* (Fig. 15, 17). In only *Fuertesia domingensis*, where multiseriate rays are tall and wide, can uniseriate rays outnumber multiseriate rays (Fig. 28).

Dimensions of multiseriate rays are shown in Table 1, columns 10 through 13. Relatively narrow rays characterize *Mentzelia laevicaulis*; the widest rays in this study occur in *Mentzelia arborescens* (Fig. 26). However, note should be taken of the fact that Loasaceae as a whole have notably tall, wide rays compared to those of most families of dicotyledons.

As may be seen in Table 1, column 14, the rays of Loasaceae consist predominantly of upright (erect) cells; square cells are present or not, and procumbent cells are scarce or absent, depending on the species; only in *Mentzelia humilis* stems (Fig. 21) and in roots of *Mentzelia laevicaulis* were procumbent cells judged to be at all abundant. Erect ray cells in *M. humilis* are horizontally subdivided where they contain crystals. Procumbent cells in the rays of *Loasa incana* are present only by subdivision of erect cells. Throughout Loasaceae, procumbent cells, where present, occur only in the central portions of multiseriate rays. In stems of *M. laevicaulis*, uniseriate wings composed of erect cells often occur on multiseriate rays. Uniseriate wings are ordinarily not common on multiseriate rays of Loasaceae.

Rayless conditions were observed in two species of Loasaceae. Wood of *Petalonyx crenatus* was observed to be wholly rayless except for scattered upright cells. In *P. nitidus*, wood begins rayless, although rays develop during the second year (Fig. 16–18). In *P. linearis*, rays are infrequent at first, but become more common as growth continues (Fig. 14, 15).

Ray cell walls of Loasaceae are generally relatively thin walled but lignified. Exceptions may be observed in *Petalonyx nitidus* (Fig. 18), in which later-formed portions of secondary xylem had thin-walled ray cells (evident by virtue of absence of ray cells, because of collapse, Fig. 18 upper left). In *Fuertesia domingensis*, ray cells fluctuate between lignified and nonlignified (Fig. 27, 28). In *Mentzelia humilis* (Fig. 20, 21), all ray cells are nonlignified.

Crystals.—Druses may be seen in the rays of *Mentzelia humilis* (Fig. 20, 21); some druses may be observed in the rather extensive axial parenchyma in this species.

Fig. 16-19. Wood sections of *Petalonyx nitidus* (Michener 4060).—16. Transection near center of stem, showing growth ring.—17. Tangential section; multiseriate rays are composed of upright cells.—18. Transection from periphery of stem (thin-walled cells collapsed in ray area, upper left).—19. Fiber-tracheids from radial section; bordered pits are evident. (Fig. 17-18, magnification scale above Fig. 1. Fig. 19, scale above Fig. 3.)

Fig. 20-24. Wood sections of *Mentzelia humilis* (Michener 4397).—20. Transection; axial parenchyma cells more abundant than fiber-tracheids.—21. Tangential section. Numerous druses are visible in rays.—22. Transection, showing druses, above; fiber-tracheids and vessel portions are below.—23. Portion of vessel wall from radial section; laterally elongate pits with wide apertures evident.—24. Perforation plate which is like a small aggregation of pits, from radial section. (Fig. 20-21, magnification scale above Fig. 1. Fig. 22-24, scale above Fig. 3.)

Fig. 24–28. Wood sections of *Mentzelia* and *Fuertesia*.—25, 26. *Mentzelia arborescens* (Prigge 5507).—25. Transection; parenchyma band above center.—26. Tangential section. Note the large size of ray cells.—27, 28. *Fuertesia domingensis* (Zanoni et al. 24495).—27. Transection, showing large diameter of vessels.—28. Tangential section; vessel at extreme right; rays contain both thick-walled and thin-walled cells. (Fig. 25–28, magnification scale above Fig. 1.)

Starch.—Starch was observed in abundance in rays and axial parenchyma of *Mentzelia arborescens*, and rather more sparsely in septate fiber-tracheids in that species.

SYSTEMATIC CONCLUSIONS

The range of wood structure within Loasaceae is greater than is typical for a small family. Most of this diversity seems related to ecological adaptations, mostly at the species level. Only a few characters seem to interconnect genera in systematic patterns. To be sure, the Davis and Thompson (1967) commentary casts doubt on systems which have hitherto been offered (e.g., Gilg 1925). Thereby one cannot securely compare data to a system for the family at present.

The imperforate tracheary elements of Loasaceae may all be called fiber-tracheids, but they may be divided into those which are tracheidlike by virtue of presence of wide borders on pits and those which are like libriform fibers by virtue of presence of vestigial borders on pits. The latter may be seen in *Kissenia* and *Loasa*. This would seem to support both the inclusion of *Kissenia* and *Loasa* within the subfamily Loasoideae and the placement of Loasoideae as the last subfamily in Gilg's (1925) system, thereby implying that subfamily should be richer in specialized features.

To what families and orders is Loasaceae related? Phylogenists are not united on this question, although some recent opinions seem to favor Gentianales and Dipsacales. For purposes of comparison, one may look for distribution of wood features of Loasaceae such as vessels with simple perforate plates, vessels solitary, imperforate tracheary elements which are fiber-tracheids (some like tracheids, some like libriform fibers), rays predominantly multiseriate, with erect cells more common than procumbent cells, and axial parenchyma present and diffuse in distribution. These features are all commonly present in Goodeniaceae (Carlquist 1969) and Dipsacaceae (Carlquist 1982b). In Loganiaceae (*sensu lato*) all of these features may be found, although not in a majority of species, judging from the data of Menega (1980). Most Loganiaceae have vasicentric parenchyma, libriform fibers, and relatively narrow (compared to those of Loasaceae) multiseriate rays. One must remember that Loganiaceae in the broad sense is such a diverse group that match of individual features in particular genera is not a very convincing indication of affinity.

The families included by Cronquist in Violales include, in addition to Loasaceae, 23 families notable for parietal placentation (or alliance to such families). Of these families, all lack two key features of loasaceous woods: diffuse axial parenchyma and bordered pits on imperforate tracheary elements (judging from the data for these families in Metcalfe and Chalk, 1950). Within these groups, one can only find a few genera in which the loasaceous features are matched (and then not closely), such as *Cistus*.

Although conclusions based upon wood alone must be very tentative, the closest similarity to wood of Loasaceae may be found in Dipsacaceae, Gooeniaceae, and, to a lesser extent, Loganiaceae. Other comparisons seem more remote, so that citation of additional families at this point is not justified.

WOOD ANATOMY AND HABIT

Perhaps the most striking alterations in wood anatomy with respect to habit are seen in *Fuertesia domingensis*. The wide, thick-walled vessels in that species correlate with the vining habit. The presence of fibriform vessel elements in *Fuertesia* is a good example of the vessel dimorphism (smaller vessels preempted from widening by the wider vessels) as outlined earlier (Carlquist 1981).

Some of the features of wood in Loasaceae seem clearly related to the herblike nature of the plants. The relatively long vessel elements of *Cevallia sinuata*, *Loasa incana*, *L. picta*, and *Mentzelia laevicaulis* may reflect the limited accumulation of secondary xylem in these species. This would accord with the theory of paedomorphosis and the descending curve cited for *Talinum guadalupense* Dudley by Carlquist (1962). Species which show paedomorphosis do not show the sharp decrease in length of fusiform cambial initials which typically occurs in woody plants with the onset of secondary growth. Therefore vessel elements and imperforate tracheary elements in plants which often show paedomorphosis (stem succulents, rosette trees, herbs and herblike shrubs) tend to be longer than one would expect on the basis of studies of characteristically woody species. The presence of oddly-perforated perforation plates in vessels of *Loasa picta* may represent a feature from primary xylem carried into secondary xylem, and thus would be an indication of paedomorphosis. In the 1962 survey of paedomorphosis, I cited laterally-widened (often scalariform or scalariformlike) pits (frequently with wide "gaping" pit apertures) on lateral walls of vessels of such species as *Begonia coccinea* Hook., *Brighamia insignis* A. Gray, *Carica candamarcensis* Hook., *Cereus giganteus* Engelm., *Macropiper excelsum* Miq., *Sedum praealtum* A. DC., and *Talinum guadalupense*. All of these are succulents. The succulent nature of stems of Loasaceae may be related to such vessel wall pitting in *Mentzelia arborescens* and *M. humilis*, both of which are certainly succulent on the basis of abundance in the xylem of thin-walled nonlignified parenchyma cells. To a lesser extent, all Loasaceae have laterally elongate pits on vessel walls, and Loasaceae as a whole may be regarded as succulent on the basis of having thick cortex composed of large parenchyma cells with thin nonlignified walls.

Abundance of erect cells in rays may also be an indicator of paedomorphosis in "woody herbs" (Carlquist 1962). Certainly Loasaceae fall into this

habit class. Although erect cells can certainly be found in the rays of most woody plants, their presence is by no means as pervasive as it is in Loasaceae: upright cells are usually restricted to a sheathing layer on multiseriate rays or to wings on multiseriate rays (Kribs 1935). In fact, Kribs (who worked with "woody" species exclusively) did not report rays composed wholly of upright cells; such rays were not reported until later (Carlquist 1961) when they had been discovered in "woody herbs." The predominance of erect ray cells in Loasaceae is doubtless related to the herbaceous nature of the group.

Although tall, wide rays are sometimes viewed as a characteristic more of herbs than of woody plants, such a stereotype is quite unjustified. Even within Loasaceae, that does not hold: the widest, tallest rays occur in the tree *Mentzelia* and in the species of *Petalonyx*, all of which may be regarded as shrubs. The width (and to a lesser extent, height) of rays in Loasaceae seems more clearly related to succulence in Loasaceae as a whole. However, width of rays in *Petalonyx* and in *Mentzelia arborescens* may be related to the relative longevity of stems in these species; width of rays and abundance of procumbent cells within rays increase over time, as the studies of Barghoorn (1941a) show.

Absence or rarity of parenchyma in *Loasa incana*, *L. picta*, and *Mentzelia laevicaulis* may be related to habit. Selective value of axial parenchyma in shortlived stems may be minimal. Similar considerations probably also apply to presence of rays, which perhaps explains why at least some woods which are rayless eventually acquire rays (Barghoorn 1941b; Carlquist 1970). The function of both ray and axial parenchyma—storage of photosynthates—presumably is important if a stem continues growth, but may be of minimal significance in stems with finite lifespan. If the starch of parenchyma functions in renewing (or continuing) conduction by virtue of upped osmotic concentration when starch is hydrolyzed to sugar, one can understand this parenchyma distribution. Braun (1983) hypothesized this function for paratracheal parenchyma of trees, but it may apply to other parenchyma distributions and to nonwoody plants in some hitherto unappreciated ways. The narrow rays of *Mentzelia laevicaulis* may be correlated with lack of succulence or lack of storage in that either characteristic would be of minimal selective value in a plant with a short and finite lifespan.

ECOLOGICAL CONCLUSIONS

The ecological preferences of Loasaceae as a whole can be described as xeric, ranging from only moderately dry conditions in which a vine can flourish (*Fuertesia domingensis*) to true desert areas in which shrubs (*Eucnide*, *Petalonyx*) are adaptive. Are the woods of Loasaceae xeromorphic? The features which are generally accepted as indicative of xeromorphy are not expressed in a xeromorphic way in Loasaceae, with some exceptions. If

vessel diameter, number of vessels per mm², and vessel-element length are combined into ratios termed Vulnerability and Mesomorphy (Table 1, columns 15 and 16), the values for these ratios in Loasaceae are high, which would indicate mesomorphy. Mesomorphy values below 50 can generally be expected for woody desert plants or even shrubs of Mediterranean-type climates. In the Loasaceae studied, only *Petalonyx crenatus* falls below that value.

The explanation for this paradox lies in the markedly succulent stems and roots of Loasaceae. When stems and roots are succulent, wood structure is no longer a prime tool for dealing with extremes of water availability, since water storage within parenchyma removes that role. This can be seen from the quantitative values for plants of various habits and habitats given earlier (Carlquist 1975, p. 206). In those samples, the desert shrubs have a Mesomorphy value of 18, whereas stem succulents have a value of 290. Each group of succulents will have its own characteristic values, and those of Loasaceae are within the ranges of mesomorphy values which can be calculated for other groups of stem and root succulents.

The tendencies toward succulence are shown in Loasaceae not merely by wide and tall rays, but by parenchymatization of axial xylem as well. Some Loasaceae have merely diffuse axial parenchyma, slightly more abundant than is typical for dicotyledons with diffuse parenchyma. *Kissenia capensis* has such "abundant" diffuse parenchyma. However, in some other Loasaceae, replacement of fiber-tracheids by parenchyma may be seen. This parenchyma may take the form of bands, as in *Cevallia sinuata*, *Eucnide cordata*, and *Mentzelia arborescens*. However, in *Eucnide urens* and in *Mentzelia humilis*, portions of axial xylem more extensive than what could be termed bands are converted to axial parenchyma. In these, axial xylem may be more abundant than fiber-tracheids with respect to volume occupied, in fact. If banded parenchyma in Loasaceae showed transitions between diffuse and banded types of occurrence (e.g., diffuse-in-aggregates), or if extensive parenchymatization were absent, one could conclude that banded parenchyma was an evolutionary modification of diffuse parenchyma. Because those conditions are not met, one must instead hypothesize that axial parenchyma cells have been introduced into woods which ancestrally contained more fiber-tracheids. This process may be somewhat like that described earlier as fiber dimorphism (Carlquist 1958). However, parenchyma cells in Loasaceae cannot be regarded as products of a divergence in which some libriform fibers become more fiberlike, others more parenchymalike. The presence of bordered pits on fiber-tracheids of Loasaceae would introduce a problem, because borders would have to be lost on fiber-tracheids (ordinarily probably a slow process phyletically) before they could be converted into parenchyma-like cells. Instead, the parenchymatization of succulents is probably different

from fiber dimorphism in that the cambium produces more numerous parenchyma cells, fewer imperforate tracheary elements, during secondary growth.

Vessel grouping is uniformly low in Loasaceae except for *Mentzelia laevicaulis*, in which number of vessels per group exceeds 2.0. According to a hypothesis in an accompanying paper (Carlquist 1984), vessel grouping occurs in woods of (1) species in which the imperforate tracheary elements are not tracheids; and (2) species which occur in physiologically dry conditions, at least seasonally. On these grounds, one would expect more numerous Loasaceae to show a higher degree of vessel grouping than they do. To be sure, some Loasaceae have fiber-tracheids which approach tracheids very closely, and if those cells do serve as a subsidiary conducting system then they would forestall evolution of vessel grouping. However, succulence in woods of Loasaceae may also play a part, since existence of water-storing parenchyma as a means of countering water shortage would tend to deter evolution of wood features (e.g., narrow vessels, as mentioned above) which typically preserve the integrity of water columns during dry periods. *Mentzelia laevicaulis* is less succulent than other Loasaceae, occurs in a highly seasonal environment (in which freezing as well as drought occurs) and also has imperforate tracheary elements which are like libriform fibers rather than like tracheids. Therefore *Mentzelia laevicaulis* satisfies the conditions requisite for evolution of vessel grouping whereas other Loasaceae do not satisfy all of these conditions.

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

Footnote

The writer is grateful to the National Science Foundation for a grant, DEB 81-09910, which has assisted this study.