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WOOD ANATOMY OF LAMIACEAE. A SURVEY, WITH COMMENTS ON VASCULAR AND VASICENTRIC TRACHEIDS

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ABSTRACT

Quantitative and qualitative data are presented for 44 collections representing 42 species in 27 genera. Lamiaceae basically have: vessels with simple perforation plates; vessel-to-vessel pitting alternate; imperforate tracheary elements all libriform fibers, fibers commonly septate; axial parenchyma scanty vasicentric; rays Heterogeneous Type IIB. These features ally Lamiaceae closely with Verbenaceae. In addition to the Mesomorphy ratio (based on vessel element dimensions), features that indicate wood xeromorphy in Lamiaceae, in probable increasing order of importance are: presence of indistinct to marked growth rings; presence of helical thickenings in vessels; presence of vasicentric or vascular tracheids; presence of vessel groups averaging three or more vessels per group. More mesomorphic woods in Lamiaceae occur in species that are arborescent to shrubby, and that occur in areas that have no prolonged drought. Helical sculpture in vessels is expressed not only as thickenings, but also as grooves interconnecting pit apertures (coalesced pit apertures), and inconspicuous thickenings in pairs along the grooves. Vascular tracheids (at ends of growth rings) occur in several genera. Where growth rings are very narrow (*Salvia*, *Trichostema*), vessels and tracheids are intermixed, thereby justifying description as vasicentric tracheids of what may have originated phylogenetically as vascular tracheids. This may represent one pathway for origin of vasicentric tracheids. Wide bands of axial parenchyma in *Cuminia* and *Leptosceptrum* have originated as a result of fiber dimorphism. Abundance of upright cells in numerous Lamiaceae is indicative of paedomorphosis, and may point to secondary woodiness in some instances; the family as a whole appears ancestrally moderately woody. The ratio between libriform fiber length and vessel element length marks Lamiaceae as specialized. Crystal presence and cambial variants are newly reported for the family.

Key words: helical sculpture in vessels, helical thickenings, Labiatae, Lamiaceae, vascular tracheids, vasicentric tracheids, wood anatomy.

INTRODUCTION

Although Lamiaceae are a large family (180 genera and 3500 species according to Willis 1985), their wood anatomy has been little studied to date. The main sources of information are the summary for the family by Metcalfe and Chalk (1950) and the more recent study of woods of the subtribe Hyptidinae by Rudall (1981). A few data on wood anatomy of Lamiaceae were offered by Greguss (1959) and by Hatzoupoulou-Belba and Psaras (1985). The lack of studies on wood of Lamiaceae is related to the stature of plants in the family: only a few are large shrubs or small trees (e.g., some species of *Hyptis*, *Leucosceptrum*, *Prostanthera*, and *Westringia*). The purpose of the present study is to survey woods in the family for characters of ecological, evolutionary, and systematic significance. The present study is a contribution to a survey of woods of tubiflorous families of dicotyledons, a summary of which is in progress.

Lamiaceae proved to have diverse expressions in wood anatomy, including some features that have not been reported for the family: banded axial parenchyma; axial parenchyma forming the background tissue for the wood; grooved

vessel walls (coalesced pit apertures); various types of helical thickenings in vessels; occurrence of crystals in ray cells; and occurrence of variant cambial activity.

The number of species surveyed (42 species in 27 genera) is not exceptionally great considering the size of the family. An attempt has been made to study samples of optimal size, so that a mature pattern of wood anatomy is available. Twig material has not been used. Exclusion of smaller wood samples has lowered the number of species that could be included. Only a small proportion of Lamiaceae typically develop stems in excess of one cm in diameter at the base. The selection of species here nevertheless represents a broad systematic coverage. The species studied would be distributed in the following infrafamilial categories in the system offered by Briquet (1895):

Ajugoideae:

Ajugeae: *Leucosceptrum*, *Teucrium*, *Tinnea*, *Trichostema*

Rosmarineae: *Rosmarinus*

Prostantheroideae: *Hemiandra*, *Prostanthera*, *Westringia*.

Prasioideae: *Phyllostegia*

Scutellarioideae: *Salazaria*

Stachyoideae:

Lamiinae: *Leonotis*

Salviae: *Salvia*

Meriandreae: *Dorystoechas*

Lepechiniae: *Lepechinia*

Mellisinae: *Poliomintha*

Hyssopinae: *Hyssopus*

Thyminae: *Bystropogon*, *Monardella*, *Origanum*

Menthinae: *Cuminia*

Ocimoideae:

Hyptidinae: *Hyptis*

Petranthinae: *Hoslundia*, *Plectranthus*

Moschosminae: *Hemizygia*, *Ocimum*, *Orthosiphon*

The significance of this listing is more in showing coverage of the family than in demonstrating any correlations between wood anatomy and the systematics within the family. The sampling is too small to permit any such correlations. Those interested in comparing subfamilial systems will want to consult the work of Wunderlich (1967) and Cantino and Sanders (1986). Cantino (personal communication) is developing new information that may lead to a more definitive system for the family.

The relationships between Lamiaceae and other families are not controversial. The family is placed in an order usually called Lamiales, along with Boraginaceae, Verbenaceae, Lennoaceae, and sometimes Hydrophyllaceae (e.g., Thorne 1976; Cronquist 1988). However, there are additional families recognized in this order if they are segregated from Verbenaceae: Avicenniaceae, Chloanthaceae (Dicrastylidaceae), Hoplostigmataceae, and Wellstedtiaceae. The occurrence of several classes of iridoids in Lamiales (Jensen, Nielsen, and Dahlgren 1975) influenced acceptance not only of the concept of Lamiales as an order, but also the idea that Lamiales are close to Scrophulariales and Gentianales (Thorne 1976; Cronquist 1988). An attempt is made here to delineate features by which Lamiaceae may be related to other families.

The ecological interest of wood anatomy of Lamiaceae is considerable. Lamiaceae as a whole occupy moderately dry, or seasonally dry, sites. The majority of the taxa studied here are characteristic of Mediterranean-type climates. The prominence of specimens from California, the Canary Islands, South Africa, and Australia demonstrates this. Mechanisms for survival of the dry season in Mediterranean-type climates are the chief point of interest. In this connection, the question of vasicentric tracheids is pertinent. Vasicentric tracheids are considered a potential mechanism for drought survival in woody dicotyledons (Carlquist 1985a, b). Several Lamiaceae were noted earlier as having vasicentric tracheids (Carlquist 1985a:49). However, in that reference and in a later book (Carlquist 1988a:135), Lamiaceae were mentioned as exemplifying both vascular and vasicentric tracheids. In some species of the family, vascular tracheids (tracheids formed only in the last several layers of a growth ring) are formed in such abundance that vessels of the latewood are intermixed with them, and therefore those tracheids surrounding the vessels could justifiably be termed vasicentric. The nature of the transition between vascular and vasicentric tracheids in Lamiaceae will be examined and documented here. Features such as vessel diameter, vessel density, vessel element length, and helical thickenings (and other forms of helical sculpture) in vessels have been shown to be indicative of wood xeromorphy (Carlquist 1966). These features prove of great interest in analysis of woods of Lamiaceae.

The samples of Lamiaceae studied here come from both cultivated specimens and plants growing in the wild. Cultivated specimens are often thought to have greater water availability than wild-occurring specimens. By comparing wood samples of Lamiaceae from cultivation to those collected in the wild, one can infer to what degree such features as vessel diameter and vessel density are altered by the conditions of cultivation. Bissing (1982) has shown differences between specimens collected in the wild and cultivated specimens with respect to wood features for a series of Californian native plants. However, his results indicated that degree of environmental modification differed among the species he studied.

Certain features of wood of Lamiaceae are of interest with respect to wood evolution. The ratio between libriform fiber length and vessel element length may be indicative of specialization (Carlquist 1975). The origin of axial parenchyma bands, present in two genera of Lamiaceae (whereas vasicentric parenchyma characterizes the entire family) provides another question of phylogenetic interest. Many Lamiaceae are herbs, but a larger number are at least moderately woody at the base. The nature of the habit ancestral within the family is unclear, and wood anatomy may offer a few features useful in this regard. Predominantly upright ray cells, for example, have been cited as an indicator of juvenility in wood (Carlquist 1962), and may point to secondary woodiness.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Woods were available in dried condition. Samples were boiled in water and stored in aqueous 50% ethyl alcohol. Sections were prepared on a sliding microtome; softening techniques were not required. Some sections of selected species were dried between clean glass slides and examined with scanning electron microscopy. Sections of all species were stained with safranin and, in most species, counterstained with fast green to highlight pit details.

Table 1. Wood Characteristics of Lamiaceae.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Collection	VG	VD	VM	VL	VW	PD	FD	FW	FL	RH	MH	MW	UH	RT	ME
<i>Bystropogon canariensis</i> L'Her.	1.40	36	108	260	1.3	3	25	2.2	604	U	680	2.0	300	1.1	87
<i>B. plumosus</i> L'Her.	1.54	45	41	312	2.5	3	34	2.5	569	usP	464	5.7	270	1.2	342
<i>Cuminia eriantha</i> Benth.	1.96	54	48	277	4.0	6	23	2.0	436	USP	453	3.5	139	0.7	312
<i>C. fernandeziana</i> Colla	1.67	40	48	303	2.3	6	25	2.4	434	USP	560	4.9	142	1.2	211
<i>Dorystoechas hastata</i> Boiss. & Heldr.	2.37	26	219	191	1.2	5	16	2.6	400	USP	770	2.9	140	1.8	23
<i>Hemiandra pungens</i> R. Br.	2.36	39	327	224	1.8	4	25	2.2	328	USP	634	4.5	136	1.5	224
<i>Hemizygia obermayerae</i> Ashby	2.24	39	46	303	2.5	5	23	2.3	616	USP	2143	4.5	215	1.1	257
<i>Hoslundia opposita</i> Vahl	1.07	86	31	354	2.0	7	28	2.2	728	usP	772	3.3	153	2.0	982
<i>Hyptis arborea</i> Benth.	1.71	72	34	378	2.0	5	25	3.2	717	usP	954	3.6	—	1.5	80
<i>H. emoryi</i> Torr.	1.60	64	49	248	2.0	4	34	2.6	542	usP	2030	2.9	243	1.2	332
<i>H. mutabilis</i> Briq.	1.30	64	62	267	1.7	5	25	5.1	521	usP	862	3.2	132	1.3	276
<i>Hyssopus officinalis</i> L.	1.83	26	228	130	2.4	5	21	0.4	270	USP	305	2.0	127	0.9	15
<i>Lavandula dentata</i> L.	1.48	28	170	199	2.3	3	23	2.5	360	USP	813	4.7	62	2.2	33
<i>Leonotis leonurus</i> R. Br.	1.77	52	65	260	2.2	6	32	2.3	513	USP	1098	3.5	87	1.0	208
<i>Lepechinia calycina</i> (Benth.) Epling	3.76	52	65	223	2.0	5	28	4.8	461	usP	776	3.7	177	3.0	64
<i>L. cardiophylla</i> Epling	7.52	25	316	181	2.0	6	23	3.5	408	USP	1034	5.0	110	2.4	14
<i>L. fragrans</i> (Greene) Epling	6.40	21	200	227	2.0	6	21	2.6	490	USP	803	3.7	244	2.7	24
<i>L. ganderi</i> Epling	9.52	22	280	171	2.5	6	34	4.5	363	USP	764	4.0	134	2.7	13
<i>L. hastata</i> (A. Gray) Epling	2.08	32	147	284	2.3	6	28	2.7	645	US	1407	4.2	231	2.2	54
<i>Leucosceptrum canum</i> Sm.	1.70	60	31	267	3.0	5	23	3.5	728	usP	492	6.1	128	2.0	517
<i>Monardella linoidea</i> A. Gray	1.88	29	342	190	2.0	4	23	2.2	365	Us	404	2.1	124	0.3	16
<i>Ocimum basilicum</i> L.	1.79	26	257	257	2.2	5	18	0.6	460	US	596	2.2	214	2.0	26
<i>Origanum majorana</i> L.	1.93	22	323	303	1.4	4	21	2.2	573	Us	302	2.0	181	1.5	21
<i>Orthosiphon labiatus</i> N. E. Brown	1.60	29	131	244	2.5	4	18	4.0	443	USP	1385	3.4	314	2.5	54
<i>Phyllostegia lantanoides</i> Sherff	1.48	69	59	294	3.2	5	27	2.6	647	USP	2307	5.0	—	0.5	343
<i>Plectranthus barbatus</i> Andr.	1.17	55	17	308	2.0	8	27	2.1	593	USP	2069	4.4	—	1.2	996
<i>Polionanthus longiflora</i> A. Gray	1.41	28	366	189	1.6	4	21	2.6	339	US	530	2.0	297	1.2	14
<i>Prostanthera aspalanthoides</i> A. Cunn.	>5	13	330	231	2.7	4	16	4.0	338	USP	313	3.5	168	2.0	9
<i>P. rotundifolia</i> R. Br.	>10	20	603	322	2.0	5	18	4.0	488	SP	408	3.3	162	2.6	11

Table 1. Continued.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Rosmarinus officinalis</i> L.	Carlquist 8150	>10	17	427	167	4.0	5	16	5.2	530	USP	305	3.0	96	2.0	7
<i>Salazaria mexicana</i> Torr.	RSABG 10848	8.00	12	386	159	2.4	5	16	2.6	406	US	—	—	114	2.0	5
<i>Salvia apiana</i> Jepson	Carlquist 8152	2.35	25	234	174	1.8	5	21	2.2	310	USP	306	4.8	97	2.2	19
<i>S. canariensis</i> L.	Carlquist 2592	2.03	31	105	190	2.5	6	23	4.1	403	USP	1321	5.3	156	2.6	56
<i>S. canariensis</i> STEM	Carlquist 15952	2.96	28	68	251	2.2	6	23	3.0	401	USP	4539	5.1	—	2.4	103
<i>S. canariensis</i> ROOT	Carlquist 15952	2.73	85	32	203	2.2	6	27	2.5	510	USP	1510	8.1	—	1.5	539
<i>S. dorrii</i> (Kellogg) Abrams	Carlquist 15860	5.30	19	762	150	1.1	5	16	3.0	349	US	495	2.0	191	2.1	4
<i>S. funerea</i> M. E. Jones	DeBuhr 861	7.52	20	489	231	2.0	5	23	2.6	435	USP	532	3.0	110	2.3	9
<i>S. lanceolata</i> Brouss.	Carlquist 8060	2.36	33	113	191	2.5	5	21	2.7	423	USP	1336	4.0	148	2.0	56
<i>S. mellifera</i> Greene	Carlquist 8153	5.36	20	240	143	2.2	5	18	1.2	333	USP	662	3.3	151	1.8	12
<i>Teucrium flavum</i> L.	Carlquist 8046	3.76	28	158	201	2.0	4	27	4.7	366	US	535	2.5	251	2.5	36
<i>T. heterophyllum</i> L'Her.	Carlquist s. n.	2.96	18	231	110	2.0	2	16	2.8	302	usP	308	3.6	113	2.5	9
<i>Tinnea rhodesiana</i> S. Moore	LASCA 80-5-674	4.10	27	328	243	2.3	2	23	5.0	509	USP	476	2.5	186	2.0	20
<i>Trichostema lanatum</i> Benth.	Carlquist 8149	4.25	15	410	173	2.0	5	16	2.2	413	USP	295	2.4	97	1.2	6
<i>Westringia rosmariniformis</i> S. Moore	Carlquist 15915	2.30	26	235	296	2.6	5	27	4.2	475	USP	571	3.6	137	2.2	33
FAMILY MEANS		3.47	36	211	234	2.2	5	23	2.9	488		899	3.8	166	2.2	163

Legends for columns: 1 (VG), mean number of vessels per group; 2 (VD), mean lumen diameter of vessels at widest point, μm ; 3 (VM), mean number of vessels per mm^2 ; 4 (VL), mean vessel element length, μm ; 5 (VW), mean vessel wall thickness, μm ; 6 (PD), mean diameter of lateral wall pits of vessels, μm ; 7 (FD), mean diameter of libriform fibers widest point, μm ; 8 (FW), mean wall thickness of libriform fibers, μm ; 9 (FL), mean libriform fiber length, μm ; 10 (RH), ray histology (u = upright, square = square, p = procumbent, the commonest cell types designated by upper case); 11 (MH), mean height of multiseriate ray, μm ; 12 (MW), mean width of multiseriate rays at widest point, μm ; 13 (UH), mean height of uniseriate rays, μm ; 14 (RT), mean thickness of ray cell walls, μm ; 15 (ME), Mesomorphy Index (mean vessel lumen diameter times mean vessel element length divided by mean number of vessels per mm^2).

Quantitative data in Table 1 are means based on 25 measurements, except for vessel wall thickness, libriform fiber diameter, libriform fiber wall thickness, and ray cell wall thickness. For these latter features, a few typical conditions were measured for each sample. Wood terminology follows that of the IAWA Committee on Nomenclature (1964). The growth-ring classification used is that of Carlquist (1988a).

Provenance of specimens collected in their native habitats is as follows: *Bystropogon canariensis*, Carlquist 2578, laurel forest, Barranca de la Virgen via Valleseco Road, Tenerife, Canary Islands; *B. plumosus*, Carlquist 2717, Volcan San Antonio, La Palma, Canary Islands; *Cuminia eriantha*, Solbrig 3848, Masatierra, Juan Fernandez Islands; *C. fernandeziana*, Solbrig 3909, Masatierra, Juan Fernandez Islands; *Hyptis arborea*, Carlquist 7099, between Tarma and San Ramon, Peru; *H. mutabilis*, Carlquist 8008, between Moctezuma and Hermosillo, along the Rio Sonora, Sonora, Mexico; *Lepechinia calycina*, Michener 4112, Bolinas Ridge, Marin Co., California; *L. cardiophylla*, Michener 4167, Corona, Orange Co., California; *L. fragrans*, Carlquist 1826, Santa Catalina Island, California; *L. ganderi*, Michener 4170, San Miguel Mt., San Diego Co., California; *Phyllostegia lantanoides*, Carlquist 2366, Konahuanui Summit, Koolau Mts., Oahu, Hawaii; *Plectranthus barbatus*, Carlquist 8070, weedy margins of gully, Newlands, Cape Province, South Africa; *Salvia apiana*, Carlquist 8152, lower San Antonio Canyon, Los Angeles Co., California; *S. canariensis*, Carlquist 2592, between Santa Lucia and Aguimes, Tenerife, Canary Islands; *S. dorrii*, Carlquist 15860, between Kelso and Baker, Mohave Desert, San Bernardino Co., California; *S. funerea*, DeBuhr 861, Titus Canyon, Death Valley, Inyo Co., California; *S. melifera*, Carlquist 8153, lower San Antonio Canyon, Los Angeles Co., California.

The following specimens were obtained from plants cultivated in the Royal Botanic Gardens, Kew, England: *Dorystoechas hastata*, Carlquist 8047; *Teucrium flavum*, Carlquist 8046. Cultivated in the Rancho Santa Ana Botanic Garden, Claremont, California, were: *Hyptis emoryi*, Carlquist 8154; *Leonotis leonurus*, Carlquist 8147; *Lepechinia hastata*, Carlquist 8148; *Monardella linoides*, RSABG prop. no. 6483; *Prostanthera aspalanthoides*, Carlquist 15912; *Salazaria mexicana*, RSABG prop. no. 10848; *Trichostema lanatum*, Carlquist 15912. Cultivated in the Huntington Gardens, San Marino, California, were: *Hemiandra pungens*, Carlquist 15955; *Hyssopus officinalis*, Carlquist 15956; *Lavandula dentata*, Carlquist 15959; *Origanum majorana*, Carlquist 15957; *Poliomintha longiflora*, Carlquist 15958; and *Teucrium heterophyllum*, Carlquist s.n. Specimens taken from plants cultivated in the Los Angeles State and County Arboretum, Arcadia, California, are: *Salvia canariensis*, Carlquist 15952; *Tinnea rhodesiana*, LASCA 80-5-574. Samples taken from plants cultivated in Kirstenbosch Botanic Gardens, Claremont, Cape Province, South Africa, are: *Hemizygia obermayerae*, Carlquist 8066; *Orthosiphon labiatus*, Carlquist 8068; *Salvia lancolata*, Carlquist 8060. Cultivated in Dunedin, New Zealand was: *Prostanthera rotundifolia*, Carlquist 15912. The following were cultivated at my residence in Claremont, California: *Ocimum basilicum*, Carlquist 8155; *Rosmarinus officinalis*, Carlquist 8150. Most voucher specimens are at the Rancho Santa Ana Botanic Garden (*Cuminia* specimens at the Gray Herbarium).

Gratitude is expressed to the Botanic Gardens listed in the above paragraphs for the use of their materials. Dr. David C. Michener kindly placed his collections

of *Lepechinia* at my disposal. The Building Research Establishment at Princes Risborough, England (PRFw), provided the samples of *Hoslundia* and *Leucosceptrum*. I would also like to acknowledge Dr. Otto Solbrig, who donated the samples of *Cuminia*.

ANATOMICAL DESCRIPTIONS

Growth Rings

In some lamiaceous woods, there is only minimal differentiation of earlywood from latewood (Type 1B of Carlquist 1988a). This type is represented here by *Leucosceptrum canum* (Fig. 1). It is also represented among the collections studied by *Bystropogon plumosus*, *Cuminia eriantha*, *C. fernandeziana* (Fig. 30), *Hemizygia obermayerae*, *Hoslundia opposita*, *Leonotis leonurus*, *Lepechinia hastata* (Fig. 3), *Origanum majorana*, *Orthosiphon labiatus*, *Phyllostegia lantanoides* (Fig. 7), *Plectranthus barbatus*, *rostanthera rotundifolia*, *Rosmarinus officinalis* (Fig. 25), *Teucrium heterophyllum*, *Tinnea rhodesiana*, and *Westringia rosmariniformis*. Variants of this type can be found in some collections of *Lepechinia calycina*, *Prostanthera aspalanthoides* (Fig. 6), and *Salazaria mexicana* (Type 1C: earlywood vessels both wider and more numerous than latewood vessels). Type 1D (wider vessels and wider libriform fibers in earlywood) was found in *Bystropogon canariensis* and *Hyptis mutabilis*. The majority of Lamiaceae corresponds to Type 3 (vessels at least twice as wide in earlywood, on the average, as latewood vessels). Type 3 growth rings are well illustrated here by *Monardella linoides* (Fig. 2). Other collections that have this type include *Hemiandra pungens* (Fig. 5), *Hyptis arborea*, *H. emoryi*, *Hyssopus officinalis*, *Lepechinia calycina* (Fig. 26), *L. fragrans* (Fig. 22), *Poliomintha longiflora*, *Salvia canariensis* (Carlquist 2592), *S. canariensis* (Carlquist 15952 root), *S. dorrii* (Fig. 24), *S. funerea*, *S. lanceolata*, *Teucrium flavum*, and *Trichostema lanatum*.

The growth ring termed Type 10 was recognized only recently (Carlquist 1980), based upon an evergreen chaparral shrub, *Eriodictyon* of the Hydrophyllaceae. In this type, the growth ring begins with vessels of moderate diameter, then continues with wider vessels and concludes with narrow latewood vessels. This has been interpreted as a response to commencement of woody cylinder growth during a cool wet season when peak conduction has not yet been achieved, followed by production of wider vessels suited to peak conduction at the onset of warm weather (Carlquist 1980). Type 10 growth rings are clearly illustrated here by *Lepechinia fragrans* (Fig. 4). I can report Type 10 also for *Dorystoechas hastata*, *Lavandula crenata*, *Salvia apiana*, *S. canariensis* (Carlquist 15952 stem), and *S. mellifera* (Fig. 32). These are all shrubs of Mediterranean-type climates where the climatic regime mentioned above does occur.

Cambial Variants

In several of the species studied, secondary xylem is laid down in increments varying in thickness around the stem. One such example is illustrated for *Monardella linoides* (Fig. 2), in which several growth rings are markedly wider at the left side of the photograph than at the right.

A much more extreme condition is represented here for *Hemiandra pungens* (Fig. 5). In the portion illustrated, the most recent additions to the wood (left two

Fig. 1-4. Transections of Lamiaceae to show growth rings.—1. *Leucosceptrum canum*, PRFw-22600, nearly diffuse porous.—2. *Monardella linoides*, RSABG 6483, thickness of growth rings differs at various points around stem.—3. *Lepechinia hastata*, Carlquist 8148, weakly demarcated growth rings.—4. *Lepechinia fragrans*, Michener 4267, Type 10 growth rings (vessels narrower at beginning of ring, then larger, followed by narrow latewood vessels). (Fig. 1-4, magnification scale above Fig. 1 [divisions = 10 μ m].)

Fig. 5–8. Wood sections of Lamiaceae.—5. *Hemiandra pungens*, Carlquist 15955, transection to show cambial variant: wood in left two thirds of photograph perpendicular to wood at right because it has originated from a cambium formed in the ray.—6. *Prostanthera aspalanthoides*, Carlquist 15912, transection to show narrow vessels.—7. *Phyllostegia lantanoides*, Carlquist 2366, transection with relatively wide vessels (some contain tyloses) in background composed of axial parenchyma.—8. *Plectranthus barbatus*, Carlquist 8070, vessel-to-vessel pitting on lateral vessel wall from radial section. (Fig. 5–7, scale above Fig. 1; Fig. 8, scale above Fig. 8 [divisions = 10 μ m].)

thirds of the photograph) have been deposited in an orientation perpendicular to that of the earlier-formed wood (right third of photograph). Stems tend to split along rays in this species. Accordingly, cambia originate in these rays, and the wood produced from these ray cambia is perpendicular to that of the original woody cylinder. Although Lamiaceae have not hitherto been reported to have variant cambial structure ("anomalous secondary thickening"), the condition illustrated by *Hemiandra pungens* qualifies as an exemplar of this category.

Quantitative Vessel Element Features

The mean number of vessels per group for the species studied is shown in Table 1, column 1. However, one must note that for some samples, no accurate figure for the number of vessels per group can be obtained. For example, in *Rosmarinus officinalis* (Fig. 25), cells easily identified in transection as vessels are intermixed with narrower cells that could be either narrow vessels or vasicentric tracheids (macerations reveal both of these cell types). Vessels per group can be calculated only on the basis of transections, yet macerations are required to distinguish between narrow vessels and vasicentric tracheids definitively. Similarly, the late-wood of the temperate species of *Lepechinia* (Fig. 26, 27) contains narrow vessels that grade into vascular tracheids. In transection there is no way that one can establish what proportion of these are narrow vessels and what proportion are vascular tracheids. In *Salvia apiana*, *S. dorrii*, *S. funerea*, *S. mellifera*, and *Trichostema lanatum*, similar considerations apply. The figures given in Table 1, column 1, for the species discussed in this paragraph are doubtless minimal.

For species other than the above, the number of vessels per group is relatively low and ranges from 1.07 (*Hoslundia opposita*) to 4.10 (*Tinnea rhodesiana*). Relatively low degrees of vessel grouping are seen in Figures 1 and 7; somewhat greater degrees of vessel grouping are represented in Figures 2, 3, 4, 5, and 6.

Mean vessel diameter cannot be accurately determined from transections for species with vasicentric or vascular tracheids for reasons given above. Conceding that figures for those species may be slightly inaccurate, there is still a very wide range in mean vessel diameter in Lamiaceae (Table 1, column 2). Narrow vessels characterize the species with relatively large numbers of vasicentric or vascular tracheids, as well as *Origanum majorana*, *Prostanthera aspalanthoides*, *Salazaria mexicana*, and *Teucrium heterophyllum*. Metcalfe and Chalk (1950) cite two genera with vessels less than 25 μm in mean diameter, *Phlomis* and *Rosmarinus*. Relatively wide vessels (more than 60 μm in diameter) were observed in the present study in *Hoslundia opposita*, the species of *Hyptis*, *Leucosceptrum canum*, *Phyllostegia lantanoides* (Fig. 7), and *Salvia canariensis* (Carlquist 15952, root only).

Vessel density (Table 1, column 3) cannot be accurately determined for species with vascular or vasicentric tracheids, for reasons cited earlier. Aside from those species, moderately high vessel density (>200 vessels per mm^2) is reported here for *Dorystoechas hastata*, *Hemiandra pungens* (Fig. 5), *Hyssopus officinalis*, *Monardella linoides*, *Ocimum basilicum*, *Origanum majorana*, *Poliomintha longiflora*, *Prostanthera aspalanthoides* (Fig. 6), *P. rotundifolia*, *Salazaria mexicana*, *Teucrium heterophyllum*, *Tinnea rhodesiana*, and *Westringia rosmariniformis*. Interestingly, material of all of these is from cultivated specimens. One might have expected specimens in cultivation to have wider vessel diameter and lowered

vessel density compared to specimens collected in the wild (Bissing 1982), but evidently this effect, if present, is not strongly expressed within Lamiaceae. Low vessel density ($<50/\text{mm}^2$) was recorded in *Bystropogon plumosus*, *Cuminia eriantha*, *C. fernandeziana* (Fig. 30), *Hemizygia obermayerae*, *Hyptis arborea*, *Leucosceptrum canum* (Fig. 1), and *Plectranthus barbatus*.

Mean vessel element length (Table 1, column 4) ranges from 130 μm (*Hyssopus officinalis*) to 378 μm (*Hyptis arborea*). The mean for the family, 234 μm , is relatively low: one notes family mean of 379 μm for Gesneriaceae (Carlquist and Hoekman 1986) and 439 μm for Acanthaceae. In Lamiaceae, the species with greater vessel element length ($>300 \mu\text{m}$) include *Bystropogon plumosus*, *Cuminia fernandeziana*, *Hemizygia obermayerae*, *Hoslundia opposita*, *Hyptis arborea*, *Origanum majorana*, *Plectranthus barbatus*, and *Prostanthera rotundifolia*. These are mostly from relatively moist localities and also are relatively large in plant size (and thus in wood sample diameter). The shortest vessel elements ($>200 \mu\text{m}$) are reported for *Dorystoehas hastata*, *Hyssopus officinalis*, *Lavandula dentata*, *Lepechinia cardiophylla*, *L. ganderi*, *Monardella linoides*, *Poliomintha longiflora*, *Rosmarinus officinalis*, *Salazaria mexicana*, all of the species of *Salvia* except *S. funerea*, *Teucrium heterophyllum*, and *Trichostema lanatum*.

Vessel wall thickness (Table 1, column 5) shows an appreciable range in Lamiaceae, although the photomicrographs in the present study do not demonstrate this clearly. The species in the present study with the greatest mean vessel diameter, *Phyllostegia lantanoides*, also has relatively thick (3.2 μm) vessel walls and illustrates a correlation often seen in dicotyledons. *Leucosceptrum canum* similarly has wide vessels with thick walls. However, the thickest vessel walls in woods of the present study (4.0 μm) were observed in *Rosmarinus officinalis*, which has relatively narrow vessels. Thus, more than one factor may be related to thickness of vessel walls.

Lateral walls of vessels in Lamiaceae bear alternate pits on vessel-to-vessel contacts. In size, these pits range from 2 μm in diameter in *Teucrium heterophyllum* and *Tinnea rhodesiana* to 8 μm in *Plectranthus barbatus* (Table 1, column 6). The mean for the family (approximately 5 μm) is close to the figure reported for pit diameter in most species.

Morphological Features of Vessel Elements

Vessel-to-vessel pits in Lamiaceae are alternate and circular in outline. Where crowded, pits may be somewhat angular in outline (Fig. 8). Apertures of pits are narrowly elliptical, as illustrated in Figure 8.

Two types of helical sculpture are present on vessel walls. One of these takes the form of grooves interconnecting two or more pit apertures (these have also been termed coalesced pit apertures), as illustrated in Figure 9. Short grooves interconnecting a few pit apertures, and without other forms of helical sculpture, were observed in vessels in *Bystropogon canariensis*, *Hemizygia obermayerae*, *Hyptis arborea*, *H. mutabilis*, *Lavandula dentata*, *Leucosceptrum canum*, *Ocimum basilicum*, *Orthosiphon labiatus*, *Phyllostegia lantanoides*, *Salvia canariensis* (Carlquist 2592), *S. lanceolata*, *Teucrium flavum*, and *T. heterophyllum*. Longer grooves were observed in vessels of *Salvia apiana*.

Grooves that are often flanked by pairs of wall thickenings occur in vessels of a few Lamiaceae. Most notable in this regard are *Hemiandra pungens* (Fig. 14),

Fig. 9–12. SEM photographs of vessel walls from tangential sections.—9–10. *Salvia funerea*, DeBuhr 861.—9. Grooves on vessel wall; several of the grooves interconnect two pit apertures.—10. Paired thickening bands beside grooves (left) and more prominent thickenings (vessel at right).—11–12. *Poliomintha longiflora*, Carlquist 15958.—11. Junction between two vessel elements; pairs of thickenings flank pit apertures.—12. Another vessel, showing long grooves interconnecting pit apertures. (Fig. 9, 10, 12, magnification scale at top of Fig. 9 [bar = 1 μ m]; Fig. 11, scale at top of Fig. 12 [bar = 1 μ m].)

Poliomintha longiflora (Fig. 11, 12), and *Salvia funerea* (Fig. 10). Less conspicuous paired thickening bands were seen in *Trichostema lanatum* (Fig. 18) and *Westringia rosmariniformis*.

Helical striations were observed on vessel walls of *Hemizygia obermayerae* (Fig. 13). These striations are very likely produced by slight irregularities in cellulosic wall deposition, and are not to be confused with helical thickenings. These striations are not visible with light microscopy, but may occasionally be seen in a scattering of dicotyledon vessels when studied with SEM.

Helical thickenings in vessels of Lamiaceae are illustrated in Figures 10 (especially at right), 11, and 12. Fainter thickenings are shown in Figures 14 and 18, coarser thickenings in Figures 15 and 16. Helical thickenings without grooves interconnecting pit apertures are illustrated clearly by *Dorystoechas hastata* (Fig. 15), *Prostanthera rotundifolia* (Fig. 16), and *Trichostema lanatum* (Fig. 18). Such thickenings were also seen in *Prostanthera aspalanthoides* and *Rosmarinus officinalis*. Helical thickenings combined with grooves interconnecting pit apertures are illustrated most clearly by *Salvia funerea* (Fig. 10) and *Poliomintha longiflora* (Fig. 11, 12). This condition was also observed in *Bystropogon plumosus*, *Lepechinia calycina* (narrow vessels), *L. ganderi* (narrow vessels), *Salazaria mexicana*, *Salvia apiana* (fine thickenings), *S. dorrii* (fine thickenings), *S. funerea*, *S. mellifera*, and *Westringia rosmariniformis*.

Vessel-to-ray pitting is either like vessel-to-vessel pitting or is composed of more elongate pits (Fig. 19). Categorizing these pits as scalariform, pseudoscalariform, or transitional is difficult and perhaps unnecessary. Pits of this nature were observed in vessels of *Hemizygia obermayerae*, *Hyptis arborea*, *H. emoryi* (Fig. 19), *H. mutabilis*, *Leonotis leonurus*, *Salvia canariensis* (Carlquist 2592), and *S. canariensis* (Carlquist 15952 root). Pit apertures larger than those of vessel-to-vessel pitting were observed on vessel-to-ray pits of *Plectranthus barbatus*.

Only simple perforation plates were observed in the woods of Lamiaceae studied, except for a few bars on one plate of *Salvia lanceolata*. Solereder (1908) observed bars on a perforation plate of *Cymaria elongata* Benth. These bars, however, were at right angles to the usual (radial) orientation of bars in scalariform perforation plates.

Libriform Fibers

Libriform fiber diameter at widest point is shown in Table 1, column 7. These mean diameters range from 16 to 34 μm . The wide diameters occur in *Bystropogon plumosus*, *Hyptis emoryi*, and *Lepechinia ganderi*.

Libriform fiber wall thickness (Table 1, column 8) averages almost 3 μm for the family as a whole. Species in which wall thickness is 4.0 μm or more include *Hyptis mutabilis*, *Lepechinia calycina*, *L. ganderi*, *Prostanthera aspalanthoides*, *P. rotundifolia*, *Rosmarinus officinalis*, *Salvia canariensis* (Carlquist 2592), *Teucrium flavum*, *Tinnea rhodesiana*, and *Westringia rosmariniformis*. All three species have smooth, hard woods in which the hardness may be attributed to the wall thickness of the libriform fibers. Notably thin walls characterize *Hyssopus officinalis* (0.4 μm) and *Ocimum basilicum* (0.6 μm). In *Ocimum basilicum* the wall thickness ranges from 0.3 to 2.0 μm . The thinner walls characterize the first-formed libriform fibers in this species; libriform fibers become thicker walled as growth proceeds in this annual.

Fig. 13–16. SEM photographs of vessel walls from tangential sections.—13. *Hemizygia obermayrae*, Carlquist 8066, striations probably caused by uneven wall deposition.—14. *Hemiandra pungens*, Carlquist 15955, vessel juncture showing faint thickenings bands on wall.—15. *Dorystoechas hastata*, Carlquist 8047, prominent helical thickenings.—16. *Prostanthera rotundifolia*, Carlquist 8106, thickenings run close to pit apertures. (Fig. 12, 15, scale at top of Fig. 11; Fig. 14, 16, scale at top of Fig. 9.)

Fig. 17-21. Wood sections of Lamiaceae.—17-18. *Trichostema lanatum*, Carlquist 8149. 17. Transverse section; between upper and lower pair of arrows are two growth rings that consist of vasicentric tracheids and vessels; libriform fibers in top and bottom third of photograph.—18. Tangential section of latewood, showing vessel near left (lighter) and tracheids; thickening bands may be seen on both cell types.—19. *Hyptis emoryi*, Carlquist 7099, vessel to ray pitting from radial section.—20. *Cuminia eriantha*, Solbrig 3848, radial section, septate fibers with minute pits.—21. *Plectranthus barbatus*, Carlquist 8070, radial section, portion of two septate fibers containing starch grains. (Fig. 17, scale above Fig. 17; Fig. 18-21, scale above Fig. 8.)

Libriform fiber length in Lamiaceae (Table 1, column 9) ranges from a low of 302 μm (*Teucrium heterophyllum*) to a high of 717 μm in *Hoslundia opposita* and 728 μm in *Leucosceptrum canum*. These latter two species are small trees.

The length of libriform fibers does seem to vary with plant size. However, a figure worth consideration is the ratio between libriform fiber length and vessel element length (sometimes termed "F/V ratio"). For Lamiaceae as a whole, the figure for this ratio is 2.09. A low (1.29) is reached in *Lepechinia cardiophylla*. High ratios are represented by *Leucosceptrum canum* (2.73) and *Rosmarinus officinalis* (3.17). Vessel elements in *Rosmarinus officinalis* are relatively short. Within certain limits, the ratio of libriform fiber length to vessel element length is an indication of phyletic advancement. Differences within genera or among genera within a family in this ratio probably cannot be interpreted in this way for the most part, but differences among dicotyledon families in this ratio can be significant.

Libriform fibers are often septate in Lamiaceae, as in *Cuminia eriantha* (Fig. 20) and *Plectranthus barbatus* (Fig. 21). Septate fibers were observed in *Bystrypogon canariensis*, *B. plumosus*, *Cuminia eriantha* (Fig. 20), *C. fernandeziana*, *Hoslundia opposita*, *Hyptis arborea*, *H. emoryi*, *H. mutabilis*, *Lepechinia fragrans*, *L. hastata*, *Leucosceptrum canum*, *Orthosiphon labiatus*, *Plectranthus barbatus* (Fig. 21), *Prostanthera rotundifolia*, *Salvia canariensis* (all samples), *S. lanceolata*, and *Teucrium heterophyllum*. More than one septum per fiber is characteristic of *Plectranthus barbatus*, and may be seen occasionally in species of the above list. Starch may be seen in septate fibers, most notably those of *Plectranthus barbatus* (Fig. 21), which are quite parenchymalike.

Walls of libriform fibers in Lamiaceae bear minute slitlike pits, rarely much more than 1 μm long (Fig. 20). Pits are simple, although in *Dorystocheas hastata*, a very vestigial border was observed on some pits, although not on others, in libriform fibers. Libriform fibers are not lignified in *Hemizygia obermayerae* and *Ocimum basilicum* (earlier formed fibers). In *Hyssopus officinalis* and *Phyllostegia lantanoides*, the imperforate tracheary elements are supplanted by what I am terming a background of axial parenchyma.

Vascular and Vasicentric Tracheids

In earlier work (Carlquist 1985a, b, 1988a), the terms vascular tracheid and vasicentric tracheid were defined in a way that I believe corresponds closely to the usage of other authors (e.g., Metcalfe and Chalk 1950) and the intent of the IAWA Committee on Nomenclature (1964). In my usage, vascular tracheids are formed at the end of a growth ring where vessels become progressively narrower, so that some of the last-formed vessels are very narrow, lack perforation plates, and therefore must be termed vascular tracheids. Vasicentric tracheids, on the other hand, characteristically occur around and adjacent to vessels, and they occur earlier than the last few layers of a growth ring (they may occur in diffuse porous woods). Although vasicentric tracheids are best known to wood anatomists in *Quercus*, where they form wide sheaths around vessels, they occur in many other families (Metcalfe and Chalk 1950; Carlquist 1985a, b, 1988b) and woods in these families satisfy all of the criteria that have been applied to *Quercus*. In the instances cited for both vascular and vasicentric tracheids, the woods also contain either

Fig. 22-25. Wood sections of Lamiaceae.—22-23. *Lepechinia fragrans*, Michener 4166.—22. Transection; earlywood vessels are embedded in initial parenchyma.—23. Tangential section; narrow vessels and a few vascular tracheids from latewood.—24. *Salvia dorrii*, Carlquist 15860, transection; below pairs of arrows are a series of narrow growth rings in which vessels and tracheids but no libriform fibers are present.—25. *Rosmarinus officinalis*, Carlquist 8150, transection, showing vessels in diagonal aggregations (Fig. 22-24, scale above Fig. 17; Fig. 25, scale above Fig. 1.)

fiber-tracheids (with vestigially bordered pits) or libriform fibers (with simple pits). The IAWA Committee on Nomenclature (1964) defines these terms in this fashion. In woods in which tracheids are the only kind of imperforate tracheary element present, true tracheids are said to be present (Carlquist 1985a, 1988a).

Vascular tracheids, according to the above definitions, are represented by *Lepechinia fragrans* (Fig. 22, 23, 27) and *L. calycina* (Fig. 26). Only in the last two or three layers of a growth ring do the vessels lack perforation plates and therefore qualify as vascular tracheids. Perforation plates in some latewood vessels, but not all, can be seen in Figure 23.

On the other hand, *Rosmarinus officinalis* (Fig. 25) has vasicentric tracheids intermixed with groups of vessels throughout each year's accumulation of wood. This corresponds to the classic definition of vasicentric tracheids and shows the tendency toward diagonal vessel aggregations that characterize certain species with vasicentric tracheids, usually those in drier habitats (Carlquist 1987). By any definition, *Rosmarinus* has vasicentric tracheids but not vascular tracheids.

In other woods of Lamiaceae, however, there are transitional situations. For example, in *Trichostema lanatum* (Fig. 17), narrow growth rings in dry years form only tracheids and narrow vessels, and no libriform fibers. The narrow growth ring between the pairs of arrows in Figure 17 may be likened to latewood without any earlywood. The top and bottom third of Figure 17 shows wood that contains vessels plus libriform fibers. The difference between libriform fibers and tracheids cannot be readily seen in halftones, but there is a color difference in the preparations, and differences of pitting confirm the significance of the color differences. Thus, in the narrow growth rings of *Trichostema*, vessels are present and are embedded in tracheids. This can be demonstrated in a longisection (Fig. 18), in which one vessel (left, lighter in tone) is accompanied by tracheids. The term tracheid here can be used more specifically as "vasicentric tracheid" because the vessels are intermixed with the tracheids.

A situation similar to that of *Trichostema lanatum* is illustrated for *Salvia dorrii* (Fig. 24). Above the pair of arrows at the top of the photograph is a growth ring that begins with large vessels and that contains libriform fibers. Below the pair of arrows are several short growth rings that consist wholly of vessels plus tracheids that should be termed, because of their cooccurrence with vessels, vasicentric tracheids. *Salvia dorrii* is a shrub of the Mohave Desert, where there may be a succession of dry years that result in narrow growth rings such as the ones depicted.

All species of *Lepechinia* have vascular tracheids (Fig. 22, 23, 26, 27) except for *L. hastata*, in which latewood is not strongly different from earlywood. Lamiaceae other than those noted in the above paragraphs that are like *Trichostema lanatum* or *Salvia dorrii* include *Dorystoechas hastata*, *Prostanthera aspalanthoides* (Fig. 6), *P. rotundifolia*, *Salvia funerea*, and *S. mellifera*. A few tracheids, which are probably best termed vascular tracheids because they were observed only in latter portions of growth rings, were observed in *Hemiandra pungens*, *Lavandula dentata*, *Monardella linoides*, *Ocimum basilicum*, *Salazaria mexicana*, *Salvia apiana*, and *Teucrium flavum*. Should one or more narrow growth rings with few libriform fibers succeed each other in these woods, one could say that vascular tracheids transitional to vasicentric tracheids occur, as in *Trichostema lanatum* and *Salvia dorrii*.

Fig. 26-29. Wood sections of Lamiaceae.—26. *Lepechinia calycina*, Michener 4108, transection; last two or three layers of latewood are vascular tracheids.—27. *Lepechinia fragrans*, Michener 4166, radial section; juncture between latewood vascular tracheids and earlywood, containing initial parenchyma, to left of center.—28-29. *Phyllostegia lantanoides*, Carlquist 2366.—28. Transection; vessels contain tyloses, darkly staining compounds.—29. Radial section; background of wood is all axial parenchyma. (Fig. 26-29, scale above Fig. 17.)

Axial Parenchyma

Scanty vasicentric parenchyma is present in most Lamiaceae as a complete or incomplete sheath, usually one cell thick, around vessels or vessel groups. The number of cells per strand in vasicentric axial parenchyma is typically two in *Bystropogon plumosus*, *Dorystoechas hastata*, *Hemiandra pungens*, *Lepechinia cardiophylla*, *Monardella linoides*, *Ocimum basilicum*, *Origanum majorana*, *Poliomintha longiflora*, *Rosmarinus officinalis*, *Salazaria mexicana*, *Salvia canariensis*, *S. funerea*, *S. lanceolata*, *Teucrium flavum*, *Trichostema lanatum*, and *Westringia rosmariniformis*. Strands mostly of three cells were recorded for *Bystropogon canariensis*, *Cuminia eriantha*, *C. fernandeziana*, *Hemizygia obermayerae*, *Hoslundia opposita*, *Hyptis emoryi*, *H. mutabilis*, *Lavandula dentata*, *Lepechinia fragrans*, *L. ganderi*, *L. hastata*, *Leptosceptrum canum*, *Orthosiphon labiatus*, *Phyllostegia lantanoides*, *Plectranthus barbatus*, *Salvia apiana*, *S. mellifera*, and *Tinnea rhodesiana*. Strands consisting of four cells occur commonly in *Hyptis arborea*, *Leonotis leonurus*, and *Lepechinia calycina*. The number of cells per strand is roughly correlated with vessel element length, which in turn is based upon length of fusiform cambial initials.

Axial parenchyma consisting of nonsubdivided cells was recorded for *Salvia dorrii*. No axial parenchyma cells were observed in *Prostanthera aspalanthoides*, *P. rotundifolia*, and *Teucrium heterophyllum*.

Wide bands of axial parenchyma occur in a few Lamiaceae. These bands are figured here for *Cuminia fernandeziana* (Fig. 30, 31). Banded parenchyma of this kind also occurs in *C. eriantha* and *Leucosceptrum canum*. These bands are composed of cells that are subdivided into strands of two or three cells or, less commonly, not subdivided.

Initial parenchyma was recorded in wood of a few Lamiaceae. The earlywood vessels figured for *Lepechinia fragrans* (Fig. 22) are surrounded by initial parenchyma; libriform fibers are laid down only after the first vessels and their adjacent parenchyma are formed (top of photograph). Initial parenchyma is present, but in smaller quantities, in wood of *Lepechinia calycina* (Fig. 26). Subdivision of axial parenchyma into strands is illustrated for *L. fragrans* in Figure 27. Initial parenchyma of this sort also occurs in *Lepechinia ganderi* and *Monardella linoides*. A more limited quantity of initial parenchyma—often only a single cell layer—is illustrated for *Salvia dorrii* (Fig. 24).

The entire background of the wood is parenchyma in a few species of Lamiaceae. If one views a transection of *Phyllostegia lantanoides* wood (Fig. 28), one sees what might be interpreted as thin-walled libriform fibers. In longisection, however, most such cells proved to be strands of thin-walled axial parenchyma (Fig. 29). This is also true of the wood of *Hyssopus officinalis*.

Rays

In a few Lamiaceae, one may see large rays that are continuations of large primary rays, as in *Salvia mellifera* (Fig. 32, center). Such rays are eventually broken into smaller rays, if the stem has a long enough duration. Otherwise, rays in Lamiaceae are, at most, multiseriate rays a few cells wide. Multiseriate rays are more abundant than uniseriate rays in *Bystropogon plumosus*, *Cuminia eriantha*, *C. fernandeziana* (Fig. 31), *Dorystoechas hastata*, *Hyptis arborea*, *H. mu-*

Fig. 30-33. Wood section of Lamiaceae.—30-31. *Cuminia fernandeziana*, Solbrig 3909.—30. Transection; bands of axial parenchyma may be seen as horizontal paler gray areas.—31. Tangential section; lower and right, cells from axial parenchyma band.—32. *Salvia mellifera*, Carlquist 8153, transection, showing a large primary ray, center.—33. *Leucosceptrum canum*, PRFw-22600, radial section; ray cells (center) are all procumbent. (Fig. 30-32, scale above Fig. 1; Fig. 33, scale above Fig. 17.)

tabilis, *Lavandula dentata*, *Leonotis leonurus*, *Lepechinia hastata*, *Orthosiphon labiatus*, *Phyllostegia lantanoides*, *Plectranthus barbatus*, *Salvia apiana*, *S. canariensis* (Carlquist 1952, stems and roots), and *Teucrium flavum*. Uniseriate rays are more common than uniseriate rays in *Bystropogon canariensis*, *Hemiandra pungens*, *Hyssopus officinalis* (Fig. 37), *Lepechinia cardiophylla*, *L. fragrans* (Fig. 34), *L. ganderi*, *Monardella linoides*, *Poliomintha longiflora*, *Prostanthera rotundifolia*, *Salazaria mexicana*, and *Salvia dorrii*. Species not listed in either of the above categories have multiseriate and uniseriate rays about equally abundant, as in *Lepechinia fragrans* (Fig. 34), *Leucosceptrum canum* (Fig. 35), and *Trichostema lanatum* (Fig. 36). Uniseriate wings occur on a few multiseriate rays (Fig. 34, 36), particularly if uniseriate rays are common. The tendency for uniseriate rays to occur on multiseriate rays in this case is a result of the fact that when uniseriate rays are abundant, a few will be formed in contact with the tip of a multiseriate ray.

In Table 1, column 10, a formula for ray histology is given. The species of Lamiaceae differ markedly from each other in ray histology. Lamiaceae can be said basically to have Heterogeneous Type IIB rays, using the terminology of Kribs (1935). In this ray type the center of the multiseriate ray is composed of procumbent cells, as shown for *Leucosceptrum canum* in Figure 33. The margins of the rays contain upright cells, as shown for *L. canum* in Figure 35. The formula usP corresponds to this type, and is also reported here for *Hoslundia opposita*, *Hyptis arborea*, *Lepechinia calycina*, and *Teucrium heterophyllum*. One notes that this list includes the woodiest of the Lamiaceae studied. A moderate departure from this type, represented by the formula USP in Table 1, column 10, was recorded in *Cuminia eriantha*, *Dorystoechas hastata*, *Hemizygia obermayerae*, *Hyptis mutabilis*, *Lepechinia cardiophylla*, *Prostanthera rotundifolia*, *Rosmarinus officinalis*, *Salvia apiana*, *Tinnea rhodesiana*, and *Trichostema lanatum*. A further departure from the typical Heterogeneous Type IIB pattern, in which multiseriate rays have relatively few procumbent cells (USp), was observed in *Cuminia fernandeziana*, *Hyssopus officinalis*, *Lavandula dentata*, *Leonotis leonurus*, *Lepechinia fragrans*, *L. ganderi*, *Orthosiphon labiatus*, *Phyllostegia lantanoides*, *Plectranthus barbatus*, *Prostanthera aspalanthoides*, *Salvia canariensis*, *S. funerea*, *S. lanceolata*, *S. mellifera*, and *Westringia rosmariniformis*. These are all clearly shrubby species.

Lack of procumbent cells in multiseriate rays (U, US, Us) has been cited as strongly indicative of paedomorphosis (Carlquist 1962), and has been utilized in a modification of Kribs's ray classification (Carlquist 1988a). Such paedomorphic ray conditions are reported for *Bystropogon canariensis*, *Monardella linoides*, *Ocimum basilicum*, *Origanum majorana*, *Poliomintha longiflora*, *Salazaria mexicana*, *Salvia dorrii*, and *Teucrium flavum*. These could be called shrubs or subshrubs. *Ocimum* is an annual, or at least a facultative annual.

Height of multiseriate rays is given in Table 1, column 11. *Salazaria mexicana* lacks multiseriate rays altogether; in *Hyssopus officinalis*, rays are mostly uniseriate with a few biseriate rays (Fig. 37); the latter were measured as multiseriate rays. Tall rays are characteristic of some species, such as *Hemizygia obermayerae* (2143 μm), *Hyptis emoryi* (2030 μm), *Phyllostegia lantanoides* (2307 μm), and *Plectranthus barbatus* (2069 μm). Interesting with regard to these species is that there is no correlation between multiseriate ray height and vessel element length, although one frequently finds such a correlation in dicotyledons at large.

Fig. 34-37. Tangential sections to show rays.—34. *Lepechinia fragrans*, Michener 4269, uniseriate rays and tall multiserial rays are present.—35. *Leucosceptrum canum*, PRFw-22600, rays are typical of Heterogeneous Type IIB.—36. *Trichostema lanatum*, Carlquist 8149; rays are all biseriate or uniseriate.—37. *Hyssopus officinalis*, Carlquist 15956, most rays are uniseriate, composed of upright cells. (Fig. 34-37, scale above Fig. 1.)

Multiseriate ray height also does not correlate with multiseriate ray width. The multiseriate rays of *Lepechinia fragrans* (Fig. 34) are narrower but taller than those of *Leucosceptrum canum* (Fig. 35). Multiseriate rays of Lamiaceae as a whole (Table 1, column 12) average 3.8 cells at the widest point. Notably wide rays were recorded for *Bystropogon plumosus*, *Cuminia fernandeziana*, *Lavandula dentata*, *Leucosceptrum canum* (Fig. 35), *Plectranthus barbatus*, *Salvia apiana*, *S. canariensis* (Carlquist 1952, notably roots), and *S. lanceolata*.

Uniseriate ray height (Table 1, column 13) is rather great ($>250\ \mu\text{m}$) in *Bystropogon canariensis*, *B. plumosus*, *Orthosiphon labiatus*, *Poliomintha longiflora*, and *Teucrium flavum*. Most of these species have narrow multiseriate rays, and two of them have no rays wider than two cells.

Ray-cell wall thickness (Table 1, column 14) is perhaps most notable in Lamiaceae by virtue of the thinness of walls throughout the family, as shown in tangential sections, Figures 31, 34–37. The thinnest ray cell walls, those of *Monardella linoides* and *Phyllostegia lantanoides*, are nonlignified. Borders are common on pits of rays cells in the species with lignified ray cell walls, especially on tangentially oriented ray cell walls. Bordered pits clearly outnumbered simple pits in ray cells of *Dorystoechas hastata*, *Hoslundia opposita*, *Gyptis mutabilis*, *Lavandula dentata*, *Lepechinia calycina*, *L. cardiophylla*, *L. fragrans*, *L. ganderi*, *Ocimum basilicum*, *Origanum majorana*, *Poliomintha longiflora*, *Prostanthera aspalanthoides*, *P. rotundifolia*, *Rosmarinus officinalis*, *Salvia apiana*, *S. dorrii*, *S. funerea*, *S. lanceolata*, *S. mellifera*, *Teucrium heterophyllum*, *Trichostema lanatum*, and *Westringia rosmariniformis*.

Perforated ray cells were recorded in *Phyllostegia lantanoides* and *Tinnea rhodesiana*. Very likely perforated ray cells could be located in other Lamiaceae. Although perforated ray cells are a notable morphological phenomenon, their occurrence has not demonstrated phyletic or systematic significance. They may be more common in species with wide and tall rays than in species with short, narrow ones.

Tyloses

Thin-walled tyloses are illustrated for *Phyllostegia lantanoides* (Fig. 28). Thin-walled tyloses with nonlignified walls were also recorded for *Lepechinia ganderi*, *Orthosiphon labiatus*, *Poliomintha longiflora*, *Rosmarinus officinalis*, *Salazaria mexicana*, *Salvia mellifera*, and *Trichostema lanatum*. Tyloses with moderately thick but definitely lignified walls were observed in *Hyptis arborea*, *H. mutabilis*, and *Salvia canariensis* (Carlquist 1952, stem).

Storying

In several species, a few libriform fibers appeared storied. However, this condition was so vague and inconsistent that no storying can be claimed for the family.

Crystals and Other Cellular Contents

Metcalf and Chalk (1950) do not report crystals in secondary xylem of Lamiaceae. Prismatic crystals about three times as long as wide were observed most abundantly in *Salazaria mexicana* (Fig. 38). The only other species observed to

Fig. 38–39. Radial sections to show crystals.—38. *Salazaria mexicana*, RSABG 10848, elongate prismatic crystals.—39. *Westringia rosmariniformis*, Carlquist 15915, mixture of small and large rhomboidal crystals. (Fig. 38, 39, scale above Fig. 8).

have prismatic crystals of this description in ray cells was *Plectranthus barbatus*, in which crystals are sparser than they are in *Salazaria mexicana*.

Rhomboidal crystals are somewhat more common in woods of Lamiaceae. They are figured here for *Westringia rosmariniformis* (Fig. 39), in which they occur commonly in ray cells. Large and small crystals occur intermixed in ray cells of this species. Rhomboidal crystal occurrence of this nature was recorded for ray cells of *Leonotis leonurus* and *Salvia canariensis* (all collections).

Starch was observed abundantly in ray cells and septate fibers of *Plectranthus barbatus* (Fig. 21). Had wood samples for this study been preserved in liquid rather than dried, more instances of starch occurrence in ray cells and septate fibers would likely have been recorded.

Darkly staining deposits of resinlike compounds are not common in Lamiaceae. They were most conspicuous in *Rosmarinus officinalis* (Fig. 25), in which they fill some vessels as well as other cells.

ECOLOGICAL CONCLUSIONS

Three quantitative features are combined in the ratio termed Mesomorphy (Carlquist 1977): vessel diameter times vessel element length divided by number of vessels per mm². This ratio has been computed for Lamiaceae (Table 1, column 15). Notably low ratios (<15) occur in *Lepechinia cardiophylla*, *L. ganderi*, *Mon-*

ardella linoides, *Poliomintha longiflora*, *Prostanthera aspalanthoides*, *P. rotundifolia*, *Rosmarinus officinalis*, *Salazaria mexicana*, *Salvia dorrii*, *S. funerea*, *S. mellifera*, *Teucrium heterophyllum*, and *Trichostema lanatum*. Certainly all of these are species from regions with a prolonged dry season. The six species with the greatest Mesomorphy ratio figures (in descending numerical order) are *Hoslundia opposita*, *Hyptis arborea*, *Leucosceptrum canum*, *Phyllostegia lantanoides*, *Bystropogon plumosus*, and *Cuminia eriantha*. All of these six species are from relatively wet areas, in which either the dry season is not prolonged or is modified by high humidity or occasional condensation from clouds.

Helical thickenings in vessels have been correlated with climates that are cool or dry or both (Carlquist 1975, 1983). The Mesomorphy ratios for the species with helical thickenings in vessels are given in parentheses: *Bystropogon plumosus* (342), *Dorystoechas hastata* (23), *Hemiandra pungens* (224), *Lepechinia calycina* (64), *L. ganderi* (13), *Monardella linoides* (16), *Ocimum basilicum* (26), *Poliomintha longiflora* (14), *Prostanthera aspalanthoides* (9), *P. rotundifolia* (11), *Rosmarinus officinalis* (7), *Salazaria mexicana* (5), *Salvia apiana* (19), *S. canariensis* (56), *S. dorrii* (4), *S. funerea* (9), *S. mellifera* (12), *Trichostema lanatum* (6), *Westringia rosmariniformis* (33). The Mesomorphy ratio for these species averages 47, well below the average for the family as a whole (163). The list of species with the lowest Mesomorphy ratio is very similar to the list of species with helical thickenings. This seems to validate the idea that helical thickenings function in wood xeromorphy. Although in some groups of dicotyledons, helical thickenings may be related to cold, in others they are clearly related to drought instead: the Lamiaceae listed do not occur in localities with extreme cold. The citation of helical thickenings in desert and chaparral shrubs by Webber (1936) underlines the relationship between helical thickenings and drought, because the species studied by Webber are not from areas cold in winter.

The other form of helical sculpture in vessels of Lamiaceae is represented by grooves interconnecting pit apertures ("coalesced pit apertures"). These structures occur in Lamiaceae with woods less xeromorphic than those with helical thickenings.

The number of vessels per group has been claimed to be associated with wood xeromorphy (Carlquist 1966). The Lamiaceae with more than three vessels per group, together with their Mesomorphy figures given in parentheses, are: *Lepechinia calycina* (64), *L. cardiophylla* (14), *L. fragrans* (24), *L. ganderi* (13), *Prostanthera aspalanthoides* (9), *P. rotundifolia* (11), *Rosmarinus officinalis* (7), *Salazaria mexicana* (5), *Salvia dorrii* (4), *S. funerea* (9), *S. mellifera* (12), *Teucrium flavum* (36), *Tinnea rhodesiana* (20), and *Trichostema lanatum* (6). Mesomorphy ratio figures for these species average 17, well below the average Mesomorphy figure for the family as a whole (163).

Although one is accustomed to thinking of growth rings as an accommodation to peak flow by virtue of wider earlywood vessels, the adaptation to dry conditions by means of latewood conductive safety (narrow vessels, more numerous per mm²) needs to be stressed, especially in such a family as Lamiaceae, in which many species occur in relatively dry localities. The majority of Lamiaceae have growth rings. Therefore, it is easier to cite the species that lack growth rings. These diffuse porous species are, together with their respective Mesomorphy figures in parentheses: *Cuminia fernandeziana* (211), *Hemiandra pungens* (224), *Hemizygia*

obermayerae (257), *Hoslundia opposita* (982), *Hyptis arborea* (800), *Leonotis leonurus* (208), *Lepechinia hastata* (53), *Leucosceptrum canum* (517), *Origanum majorana* (21), *Orthosiphon labiatus* (54), *Phyllostegia lantanoides* (343), and *Plectranthus barbatus* (996). Some of these might have growth rings had they not been in cultivation. However, for these species, the mean Mesomorphy ratio figure is 389, well above the family mean (163). The mean Mesomorphy figure for the remaining Lamiaceae (with growth rings indistinct to prominent) is 78.

The occurrence of vascular or vasicentric tracheids has been cited as an indicator of wood xeromorphy (Carlquist 1985a, b). The method used above for citing Mesomorphy figures for species can be used for the species of Lamiaceae with vascular or vasicentric tracheids: *Dorystoechas hastata* (23), *Hemianandra pungens* (224), *Lavandula dentata* (33), *Lepechinia calycina* (64), *L. cardiophylla* (14), *L. fragrans* (24), *L. ganderi* (13), *Monardella linoides* (16), *Ocimum basilicum* (26), *Poliomintha longiflora* (14), *Prostanthera aspalanthoides* (9), *P. rotundifolia* (11), *Rosmarinus officinalis* (7), *Salazaria mexicana* (5), *Salvia dorrii* (4), *S. funerea* (9), *S. mellifera* (12), *Teucrium flavum* (36), and *Trichostema lanatum* (6). The average Mesomorphy figure for these species is 29, well below the figure for the family as a whole (163).

One can use the Mesomorphy ratio as a key to features other than the quantitative vessel element features directly involved in the ratio, as the paragraphs above indicate. By way of summarizing the findings of the above paragraphs, one can rank the average Mesomorphy figures for the species with those features: growth rings (78), helical thickenings in vessels (47), presence of vascular or vasicentric tracheids (47), presence of more than three vessels per group, average (17). One should note that any degree of growth-ring demarcation from indistinct to marked is recognized in the computation; had only strongly ring-porous conditions been recognized, a lower Mesomorphy figure for species with growth rings would have been obtained.

The above calculations are valid if wood from cultivated specimens is not much more mesomorphic than wood of specimens collected in the wild. To be sure, the cultivated *Salvia canariensis* stem had a higher Mesomorphy figure (103) than the stem from the natural habitat (56). However, most of the collections with very low Mesomorphy figures are cultivated specimens: *Hyssopus officinalis* (15), *Monardella linoides* (16), *Ocimum basilicum* (26), *Origanum majorana* (21), *Poliomintha longiflora* (14), *Prostanthera aspalanthoides* (9), *P. rotundifolia* (11), *Rosmarinus officinalis* (7), *Salazaria mexicana* (5), *Teucrium heterophyllum* (9), and *Trichostema lanatum* (6). Gardens may not be as mesic compared to the wild as one might think, but a more likely explanation is that cultivation for these species does not alter quantitative wood features to a major extent.

In an earlier study (Carlquist 1985a), a correlation was noted between vascular tracheids and drought-deciduous foliage on the one hand, and vasicentric tracheids and evergreen foliage on the other. The hypothesis was offered that if conductive cells other than vascular tracheids cavitated, the cambium would be protected but pathways to leaves would not be protected. In species with vasicentric tracheids, the pathways of vessels to leaves are accompanied by vasicentric tracheids, so that a subsidiary conductive system (vasicentric tracheids) could supply leaves even if the vessels were embolized. In Lamiaceae, this correlation is evident. *Rosmarinus*, with clear vasicentric tracheids, has evergreen leaves. *Lepechinia*,

with vascular tracheids, tends to have drought-deciduous leaves. *Salvia* and *Trichostema*, in which a condition transitional between vascular and vasicentric tracheids occurs, have leaves that crisp somewhat during the hot months, but tend to persist.

MORPHOLOGICAL CONCLUSIONS

Vessel elements of Lamiaceae show both grooves interconnecting pit apertures (coalesced pit apertures) and helical thickenings. A condition perhaps intermediate, represented in several Lamiaceae, is the formation of thickenings on either side of a groove (Fig. 11). This was termed "paired bands" in my earlier papers on wood of Asteraceae. Neither of these phenomena is as well recognized as helical thickenings in vessel elements. Attention is called to the three phenomena, each of which is in itself diverse.

Both the diameter and density of vessels of *Hemiandra pungens* are above the means for Lamiaceae as a whole, despite the fact that wider vessel diameter tends to be associated with lowered vessel density. The nature of these features in *Hemiandra pungens* suggests the wood of a vine (Carlquist 1975), and indeed, the stems of *Hemiandra pungens* could be likened to those of a prostrate vine. In this connection, one should note that *Hemiandra pungens* has unusual cambial activity: cambia formed from rays. Cambial variants of this sort are more common in vines and lianas (Carlquist 1985b). The relatively long stems of *Phyllostegia lantanoides* also remind one of vine wood structure in terms of their wide vessels (Fig. 7), although the mean vessel diameter in this species is not as great as one finds in most vines. *Phyllostegia* can be called a sprawling shrub, the stems of which extend through shrubbery and extend outward from the plants on which they climb. The relatively wide vessels of *Hoslundia opposita*, *Hyptis arborea*, and *Leucosceptrum canum* are related to the arborescent habit and relatively moist habitats of these species.

Septate fibers occur in the majority of Lamiaceae. These may be a site for storage of starch, as is observable in *Plectranthus barbatus*. Septate fibers can form a parenchymalike tissue. Axial parenchyma is not abundant in most dicotyledon woods with septate fibers, and Lamiaceae are no exception. Axial parenchyma was not observed in *Prostanthera aspalanthoides*, *P. rotundifolia*, and *Teucrium heterophyllum*. Because of the paucity of axial parenchyma in dicotyledons with septate or living fibers, the development of imperforate tracheary elements into a parenchymalike tissue may phylogenetically be accompanied by lessening or even disappearance of axial parenchyma.

The axial parenchyma of *Cuminia* and *Leucosceptrum canum* is a good example of fiber dimorphism, a phenomenon discovered in Asteraceae (Carlquist 1958), but now reported in other families (Carlquist 1988a). The parenchyma that results from fiber dimorphism does not represent a modification of preexisting parenchyma, but an innovation of parenchyma from a new source. A phenomenon allied to evolution of parenchyma bands in woods of *Cuminia* and *Leucosceptrum* is the conversion of the ground tissue of wood of *Hyssopus officinalis* and *Phyllostegia lantanoides* into parenchyma. The earlier-formed imperforate tracheary elements of *Ocimum basilicum* are nonlignified and like parenchyma, although the later-formed imperforate tracheary elements are typical libriform fibers. I am unaware of another example like this, where formation of cells producing mechanical strength is deferred. Initial parenchyma occurs in a few Lamiaceae, most

notably *Lepechinia*; this parenchyma may originate as an expansion of vasicentric parenchyma around the earlywood vessels.

Vascular and vasicentric tracheids are of ecological significance, as discussed under Ecological Conclusions above. A further point of interest is the mode of origin of these cells. In Lamiaceae such as *Salvia dorrii* and *Trichostema lanatum*, narrow growth rings are like latewood without any accompanying earlywood, and consist of vessels plus tracheids intermixed with vessels (the tracheids therefore are termed vasicentric tracheids here). Vascular tracheids (tracheids only at the end of latewood) occur in various genera of Lamiaceae, such as *Lavandula*, *Lepechinia*, *Prostanthera*, *Salazaria*, and *Salvia*, where vasicentric tracheids clearly occur in *Rosmarinus*. The distribution of tracheids in woods of Lamiaceae leads me to hypothesize that origin of vasicentric tracheids in Lamiaceae begins with production of vascular tracheids, followed by expansion of these latewood tracheids into earlier portions of a growth ring. *Lepechinia* would represent an early stage, *Salvia dorrii* and *Trichostema lanatum* an intermediate stage, and *Rosmarinus* the end product in such a hypothetical phyletic. This pathway is different from the tracheid dimorphism mode of origin of vasicentric tracheids hypothesized for Rosaceae and Ericaceae subfamily Arbutioideae (Carlquist 1988b).

Hatzoupoulou-Belba and Psaras (1985) designate tracheary elements of *Phlomis* and *Thymus* as vessel elements and tracheids and do not mention libriform fibers. They evidently have not paid attention to details of pitting, and the cells they cite as tracheids are very likely libriform fibers, at least in part. Greguss (1959) correctly figures the imperforate tracheary elements of *Lavandula* and *Rosmarinus* as both libriform fibers and tracheids.

Upright ray cells are more common in Lamiaceae than they typically are in a woody family characterized by Heterogeneous Type IIB rays, as Lamiaceae are. The exceptional prominence of upright ray cells in such cases, as in Asteraceae or Campanulaceae subfamily Lobelioideae, is indicative of paedomorphosis (Carlquist 1962). Rays composed predominantly or exclusively of upright cells are one possible indication of secondary woodiness in a family. On this basis, secondary woodiness might be considered possible in a few genera of Lamiaceae, such as *Monardella*, *Ocimum*, *Origanum*, and *Plectranthus*. Within the family as a whole, however, some degree of woodiness (e.g., subshrub) may be primitive. Rudall (1981) in her study of wood anatomy of Hyptidinae subscribed to a woody ancestry for Lamiaceae, although the evidence she cites is, quite plausibly, from inflorescence structure compared to habits in the family rather than from wood evolution.

SYSTEMATIC CONCLUSIONS

The following features are basic in wood of Lamiaceae: vessels with simple perforation plates; lateral wall pitting alternate on vessel-vessel interfaces (alternate, transitional or pseudoscalariform on vessel-ray interfaces); imperforate tracheary elements with simple pits (therefore libriform fibers), often septate; axial parenchyma scanty vasicentric; rays Heterogeneous Type IIB; wood nonstoried. All of these basic features characterize Verbenaceae, according to the data offered by Metcalfe and Chalk (1950). One could add features found in individual genera in both Lamiaceae and Verbenaceae that differ from these basic patterns, but various apomorphies are to be expected. The essential closeness of Lamiaceae to Verbenaceae in wood anatomy is evident. One can ask if families other than

Verbenaceae (or families segregated from Verbenaceae, such as Avicenniaceae, Chloanthaceae, or Stilbaceae) show resemblances to Lamiaceae with respect to wood anatomy. To answer that question, one must invoke comparisons of wood features for numerous families of tubiflorous dicotyledon families. Accomplishment of that goal is planned for the forthcoming final paper in this series.

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