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Wood Anatomy of Hydrophyllaceae. II. Genera Other Than Eriodictyon, with Comments on Parenchyma Bands Containing Vessels with Large Pits

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WOOD ANATOMY OF HYDROPHYLLACEAE. II. GENERA OTHER THAN *ERIODICTYON,* WITH COMMENTS ON PARENCHYMA BANDS CONTAINING VESSELS WITH LARGE PITS

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INTRODUCTION

Although the family Hydrophyllaceae is largely herbaceous, woody species and genera present a series of interesting problems which invite study by means of wood anatomy. One concern of this paper and its antecedent (Carlquist, Eckhart and Michener 1983) is whether Hydrophyllaceae is basically an herbaceous or woody family. The potential parallel between the distinctive habits of particular genera and species and their wood anatomy provides other questions. For example, is raylessness in some Hydrophyllaceae the result of secondary woodiness, as appears to be the case in other families? Does the wood of *Wigandia,* the most arborescent genus in the family, approach an herbaceous or a woody mode of wood structure more closely?

Eriodictyon is clearly woody, although its roots, from which aerial stems arise, may be larger, older, and more nearly permanent parts of the plant than the stems. *Wigandia,* a genus of two to six species (Constance 1982), is often designated as a kind of herb (Brand 1913; Constance 1982), perhaps because of its sparse branching, tendency to branch from near the base, large leaves, and presence of a relatively large pith in its thickish stems. However, a large cylinder of secondary xylem, sometimes as much as a half meter in diameter, can develop at the base of a *Wigandia* plant. *Wigandia* can innovate aerial shoots from roots (observation based on material of *W. caracasana* H.B.K. in cultivation at Santa Barbara, California), but this form of reproduction probably does not account for the majority of shoots seen, because colonial distribution in *Wigandia* is not as conspicuous as it is in *Eriodictyon. Wigandia* often occurs in exposed sites, but in basically moist climatic zones of the tropics from Peru [*W. crispa* (R. & P.) H.B.K. and *W. urens* (R. & P.) Choisy] to Venezuela (*W. caracasana*), Mexico (*W. kunthii* Choisy) to Cuba and Haiti (*W. reflexa* Brand).

Nama lobbii A. Gray, like *Eriodictyon,* has a horizontal root system from which the stems arise; often, roots contain more wood than the stems. This habit may be related to habitat: *N. lobbii* occurs in cinders, sand, or scree. *Nama johnstonii* C. L. Hitchcock and allied species (*N. constancei* J. D. Bacon and *N. hitchcockii* J. D. Bacon) are suffrutescent short-lived perennials

(Bacon 1981). Most other species of *Nama* can be regarded as herbaceous with little wood accumulation.

Likewise, *Phacelia* consists mostly of annuals. The perennial species of what may be termed the "*Phacelia magellanica* (Lam.) Cov. complex" (Heckard 1960) have woody taproots, but the stems which branch from the taproot do not contain much wood and are mostly annual. *Phacelia pedicellata* A. Gray is an annual, although one of relatively large stature, growing in desert regions but only during the period of a wet year when the soil is moist enough to permit lush growth.

Four species of *Phacelia* may be regarded as insular (or nearly so) in distribution: *P. floribunda* Greene (San Clemente, Santa Barbara, and Guadalupe Is.), *P. ixodes* Kell. (Cedros, Natividad, San Martin, and Todos Santos Is.; adjacent coast of Baja California near Ensenada), *P. lyonii* A. Gray (San Clemente and Santa Catalina Is.), and *P. phyllomanica* A. Gray (Guadalupe I.). Munz (1974) regards *P. floribunda* and *P. lyonii* as annuals; of *P. ixodes,* Howell (1942) says, "on examination the plant seems definitely an annual, but its bush habit gives it the appearance of a perennial." However, plants in these species may survive into a second year, as new growth on old stems indicates. Stems two years old were studied here in the case of *P. ixodes* and *P. phyllomanica.* The insular species of *Phacelia* can be described as annuals which may persist into a second year by virtue of the moderate insular climates which may, at least in some years, feature summers with temperatures cool enough and with sufficient fog and humidity so that plants do not die during the summers. *Phacelia ramosissima* Dougl. ex. Benth. may be related to the insular species; it may be described as a perennial, as Munz (1974) does, but it should be considered a short-lived perennial in which shoots may be innovated from near the base, so that the stem below the innovations may contain wood from more than one year.

Codon royenii L. is a short-lived perennial from dry regions (e.g., the Karoo Desert) of South Africa; it does not appear to reproduce by forming shoots from roots. *Hydrolea* is a genus of annuals or short-lived perennials from wet or marshy areas of Africa, South America, the West Indies, and the southeastern United States (Brand 1913). *Hydrolea paraguayensis* Chodat was selected for study here because its wood accumulation, although not very great, was optimal for the genus. *Turricula parryi* (Gray) Macbr. occurs in montane California and adjacent Baja California. The single species of its genus, *T. parryi* is a large perennial, branched from near the base, with prominent leaf rosettes and succulent cortex on stems and roots. It grows on slides and similarly disturbed exposed habitats.

The range of habitats occupied by Hydrophyllaceae is sufficiently wide in terms of water availability so that one can reasonably search for correlations between that factor and wood anatomy. However, in doing so one must be cautioned that annuals which grow only during the wet part of the year

should not be expected to show xeromorphy even if their locality has low annual rainfall (e.g., *Phacelia pedicellata*). Also, genera in which shoots are innovated from long-lived and somewhat succulent roots (*Eriodictyon*) cannot be expected to show as great xeromorphy in wood as those which lack such roots.

Constance (1963) and Constance and Chuang (1982) have outlined subdivisions and groupings of genera. The latter study was inspired by examination of pollen morphology as well as other features; the former shows the influence of studies on chromosome number. Wood is not as sensitive an indicator of systematic affinity as pollen, largely because variations in wood anatomy within the family are related primarily to ecological adaptations. The number of genera and species in the present study represents a selection more nearly than a comprehensive survey, and the data herewith would be inadequate for systematic purposes in any case. However, data from other areas of anatomy (trichomes, leaf anatomy, seed coat anatomy) would be promising where systematics is concerned, and hopefully studies on these aspects will be undertaken by those interested in this family. Although the species selected represent many of the woodier Hydrophyllaceae, they do not represent all systematic parts of the family equally well. However, the assemblage of species studied probably can reveal whether all have a basic plan on which variations have occurred, or whether more than one basic plan might be present and therefore there might be several distinct portions of the family.

MATERIALS AND METHODS

Wood samples were available chiefly in dried form; wood of *Turricula parryi* was pickled in 50% ethyl alcohol. Other woods were boiled to remove air and stored in 50% ethyl alcohol. Wood of *Wigandia, Turricula,* and a few other species (e.g., *Nama johnstonii*) were then sectioned on a sliding microtome. However, most wood samples were either too small in size or too soft in texture to be sectioned successfully on a sliding microtome. Additionally, imperforate tracheary elements and vessel elements in Hydrophyllaceae have various degrees of what may be termed gelatinous wall structure, providing difficulty in sectioning on a sliding microtome. Consequently, the vast majority of species in the present study with the exception of species of *Wigandia* were sectioned by means of an alternative procedure involving softening, embedding in paraffin, and sectioning on a rotary microtome (Carlquist 1982a). Some sections were stained with safranin only, others with safranin followed by fast green. The latter procedure was advisable for staining of unlignified cell walls.

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

Table 1. Wood characteristics of Hydrophyllaceae.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Codon royenii	*cult. Berkeley, s.n.* (UC)	SS	53	92	260	1.64	1.5	520	20	2.0	312	187	2.2	37	0.58	150
Draperia systyla	*Bolt 166* (UC)	R	48	180	187	1.80	3.0	322	20	2.5	853	125	4.4	92	0.27	50
Hydrolea paraguayensis	*Pedersen 10060* (UC)	SS	44	125	458	1.20	2.8	905	23	4.5	1690	113	2.4	39	0.35	161
Nama johnstonii	*Michener 4386* (RSA)	SS	49	149	225	1.87	2.3	318	28	2.8	619	101	3.0	45	0.33	74
N. lobbii	*Wolf 6017* (RSA)	SS	57	155	250	1.96	2.0	572	20	2.5	593	133	2.5	78	0.37	92
Phacelia floribunda	*Raven 17243* (RSA)	SS	50	56	240	3.28	2.5	341	20	2.0	1146	131	3.8	54	0.89	215
P. heterophylla subsp. *virgata*	*Follet 92* (RSA)	R	44	241	169	4.40	2.0	229	30	1.1	—	—	—	—	0.18	31
P. ixodes	*Moran 15139* (RSA)	SS	38	121	245	2.72	2.7	379	21	2.4	—	—	—	—	0.31	77
P. lyonii	*Thorne 34886* (RSA)	R	43	96	203	2.12	2.5	264	28	2.0	314	290	2.9	39	0.45	91
P. oreopola subsp. *simulans*	*Carlquist 7393* (RSA)	R	48	100	135	1.33	2.3	182	23	1.5	—	—	—	—	0.48	65
P. pedicellata	*Castagnoli 169* (RSA)	SS	51	86	221	1.64	1.3	340	33	1.1	—	—	—	—	0.60	131
P. phyllomanica	*Franceschi 43* (POM)	SS	40	190	244	1.44	2.5	609	15	2.5	—	—	—	—	0.21	51
P. ramosissima	*Munz 11404* (RSA)	SS	53	205	101	1.55	2.5	154	23	2.0	—	—	—	—	0.26	26
Turricula parryi	*Carlquist 15637* (RSA)	R	99	35	354	1.47	1.5	690	18	2.0	291	94	3.4	37	2.83	1001
		S	53	127	343	1.43	2.0	572	15	2.0	260	62	4.2	47	0.42	143
Wigandia caracasana	*MADw-9914*	S	92	34	343	1.20	2.0	1030	32	4.0	281	84	4.6	50	2.71	928
	MADw-22081	S	85	24	510	1.08	1.5	963	23	2.0	297	99	2.4	28	2.54	1806
W. crispa	*Carlquist 7048* (RSA)	S	87	34	447	1.28	2.0	832	28	3.5	297	143	3.1	43	2.56	1143
	Carlquist 7097 (RSA)	S	78	31	354	1.28	2.0	874	33	2.5	291	99	4.0	48	2.52	891
W. kunthii	*Henrickson 2061A* (RSA)	S	99	34	420	1.30	3.0	894	25	3.0	260	73	2.9	33	2.91	1223
	MADw-23974	S	131	24	364	1.24	3.0	957	20	3.0	322	73	3.2	33	5.46	1987
W. reflexa	*SJRw-3822*	S	97	16	385	1.27	3.0	978	21	4.0	374	94	4.2	58	6.06	2334

Legend for numbered columns: 1, plant portion (R = root, S = stem of maximal diameter near base of plant, SS = a small stem, but of maximal diameter for the species concerned). 2, mean vessel diameter, μm. 3, mean number of vessels per mm^2. 4, mean vessel-element length, μm. 5, mean number of vessels per group. 6, mean vessel wall thickness, μm. 7, mean length of imperforate tracheary elements, μm. 8, mean diameter of imperforate tracheary elements at widest point, μm. 9, mean wall thickness of imperforate tracheary elements. 10, mean height of multiseriate rays, μm. 11, mean height of uniseriate rays, μm. 12, mean width of multiseriate rays at widest point in number of cells. 13, mean width of multiseriate rays at widest point in μm. 14, vulnerability ratio (mean vessel diameter divided by mean number of vessels per mm^2). 15, mesomorphy ratio (vulnerability ratio multiplied by mean vessel element length).

Dimensions of various wood features given in Table 1 were based on 25 measurements per feature. Vincent M. Eckhart made the majority of slides and measurements; the balance of the paper is the work of the senior author.

Appreciation is expressed to the Herbarium of the University of California, Berkeley, for the first three wood samples listed in Table 1. Several wood samples were made available through the kindness of the U.S. Forest Products Laboratory collection (MADw, incorporating SJRw). Dr. David C. Michener thoughtfully collected the sample of *Nama johnstonii* for use in the present study.

<div align="center">ANATOMICAL FEATURES</div>

Growth rings.—Little variation in vessel diameter is seen in certain species with one or a few years of xylem accumulation, such as *Codon royenii* (Fig. 1), *Hydrolea paraguayensis* (Fig. 3), *Nama johnstonii,* and *Phacelia pedicellata.* Very moderate changes in vessel diameter or little at all may be found in the stems of *Wigandia* (Fig. 5, 8) in which an indefinite number of years of xylem accumulation can be studied. Moderate growth-ring activity of this type has been termed Type IB in a scheme proposed elsewhere (Carlquist 1980). In *Phacelia floribunda* and *P. lyonii,* imperforate tracheary elements are narrower and thicker-walled in latewood, and are thus referable to Type ID. Also referable to that growth-ring type are the woods studied of *P. ixodes* and *P. phyllomanica,* in which two years of accumulation were visible; fluctuation of vessel diameter was accompanied by narrowing of latewood fibers, which are also thicker-walled. *Nama lobbii* (Fig. 10) and *Turricula parryi* (Fig. 12) tend to have vessels markedly wider in earlywood but also more numerous at the beginning of a growth ring as compared to latewood. These are referable to Type VI in the scheme just mentioned, provided that the definition is modified so as to include fiber-tracheids as well as libriform fibers as the imperforate tracheary element type present accompanying vessels in the wood. The remaining taxa of the present study differ from Type VI only in that parenchyma bands are present at some point and to various degrees in relation to seasons. Parenchyma is visible in latewood in *Phacelia heterophylla* Pursh subsp. *virgata* (Greene) Heckard (Fig. 21) and *P. ramosissima* (Fig. 14); those species should be included in Type XIC. In *P. oreopola* Heckard subsp. *simulans* Heckard, the specimen studied showed a rayless first year followed by a second year in which vessel-bearing areas, markedly widening outward, and parenchymatous areas were present in earlywood although the second year's xylem accumulation ended with what could be called very short libriform fibers in areas outward from the zones of parenchyma. Much variation is to be expected in expression of banded parenchyma in herbaceous or "woody-herbaceous" species of dicotyledons, such as is discussed in a terminal section of this paper, and the
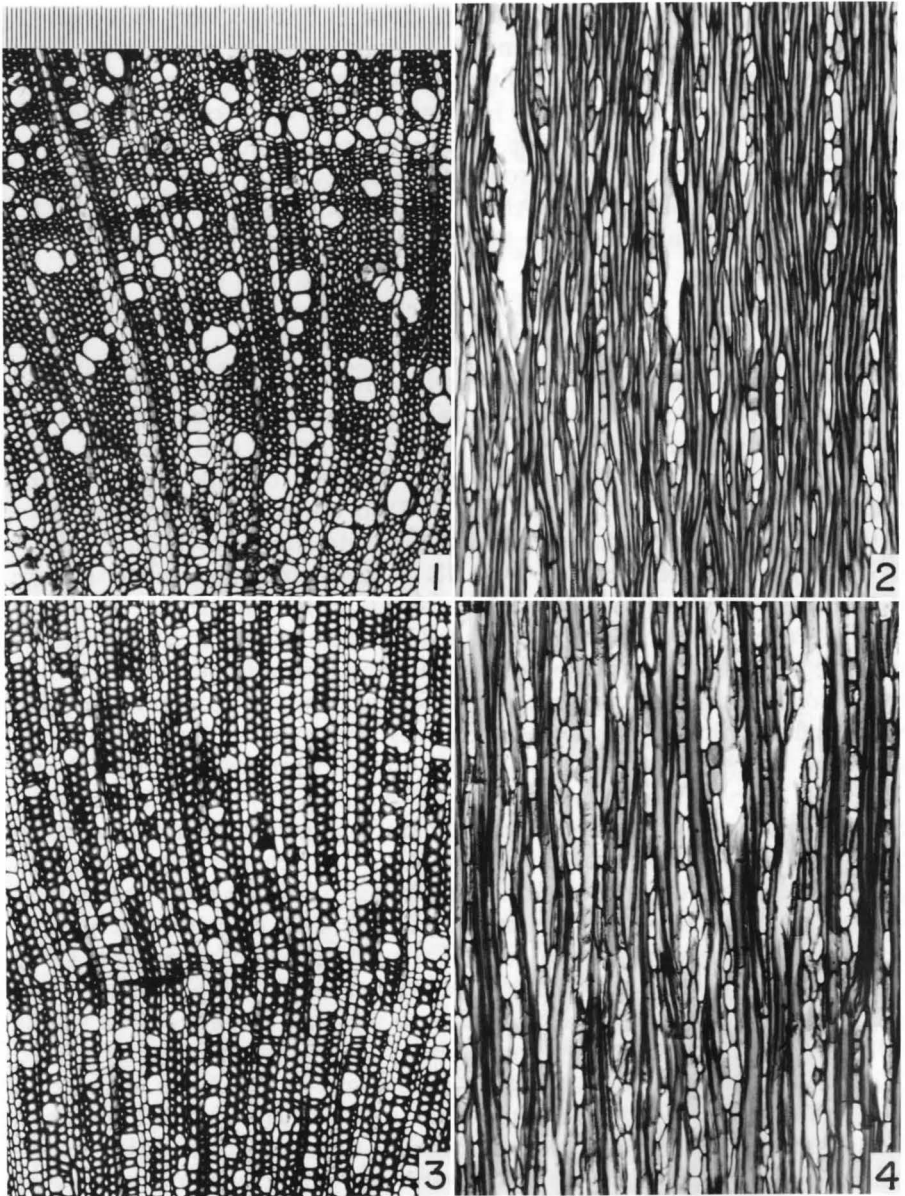
Fig. 1–4.   Wood sections of stems of *Codon* and *Hydrolea.*— 1–2. *Codon royenii* (*cult. Berkeley,* UC).— 1. Transection; very little growth-ring activity evident.— 2. Tangential section; multiseriate and uniseriate rays are both frequent.— 3–4. *Hydrolea paraguayensis* (*Pedersen 10060,* UC).— 3. Transection; vessels are narrow, not grouped.— 4. Tangential section; most ray cells are upright. (Fig. 1–4, magnification scale above Fig. 1 [finest divisions = 10 μm].)

species selected may not represent the full range of growth-ring activity for the family. Indeed, different growth-ring phenomena might occur in successive years with different climatic events for a single species.

Vessel elements. — Perforation plates in the vessels elements of the Hydrophyllaceae studied are characteristically simple. Occasional scalariform perforation plates (or an aberrant form based on a scalariform pattern) were seen in *Hydrolea paraguayensis* (Fig. 17). Double perforation plates (Fig. 18) could occasionally be observed; these were more frequent in the genera with more abundant fibriform vessel elements: *Eriodictyon* (Carlquist et al. 1983), *Turricula,* and *Wigandia*; they were somewhat less common in the other genera and species (e.g., *Phacelia ixodes*). Fibriform vessel elements, so characteristic of *Eriodictyon,* can also be reported for all of the species studied here, although *Turricula* and *Wigandia* have more than twice the frequency of these cells than do the other genera reported here.

Lateral walls of vessels bear alternate circular bordered pits. However, somewhat widened pits with tapered ends characterize vessels of *Phacelia ramosissima* (Fig. 16). Vessel elements surrounded by parenchyma in the latewood bands of *P. heterophylla* subsp. *virgata* (Fig. 21, 22) have lateral-wall pits which are even more markedly widened laterally; pit apertures are also very large. Such vessel walls given an appearance superficially like that of helically (spirally) banded primary xylem tracheary elements. That appearance is misleading, however, for vertical strands of wall material demonstrate that uninterrupted gyres are not present; the bands are not truly spiral even if one neglected these interconnecting strands. The pattern is merely one in which alternate bordered pits have become very much enlarged.

Mean vessel diameter is shown in Table 1, column 2. One can see that vessel diameter is close to 50 μm in most species, but vessel diameter is notably greater in *Wigandia* (Fig. 5, 8) and in the roots of *Turricula parryi.* Notably large numbers of vessels per mm^2 (Table 1, column 3) occur in *Phacelia heterophylla* subsp. *virgata* (Fig. 19), especially in a latewood band (Fig. 20), as well as in *P. ramosissima* (Fig. 14). Notably low numbers of vessels per mm^2 occur in *Wigandia* stems (Fig. 5, 8) and in the roots of *Turricula.* Vessel-element lengths (Table 1, column 4) are notably long in *Wigandia* and *Turricula,* but also in *Hydrolea.* The mean number of vessels per group is not uniform in the family. Although this figure is near 1.5 in *Phacelia oreopola* subsp. *simulans* and in *Turricula* (Fig. 12), a notably lower figure is registered by *Hydrolea paraguayensis* (Fig. 3) and by the various species of *Wigandia* (Fig. 5, 8). High numbers of vessels per group may be found in *Codon royenii* (Fig. 1), *Draperia systyla* Torrey, *Nama johnstonii, N. lobbii* (Fig. 10), *Phacelia floribunda, P. ixodes, P. lyonii, P. pedicellata,* and, most notably, *P. heterophylla* subsp. *virgata* (Fig. 19, 21).
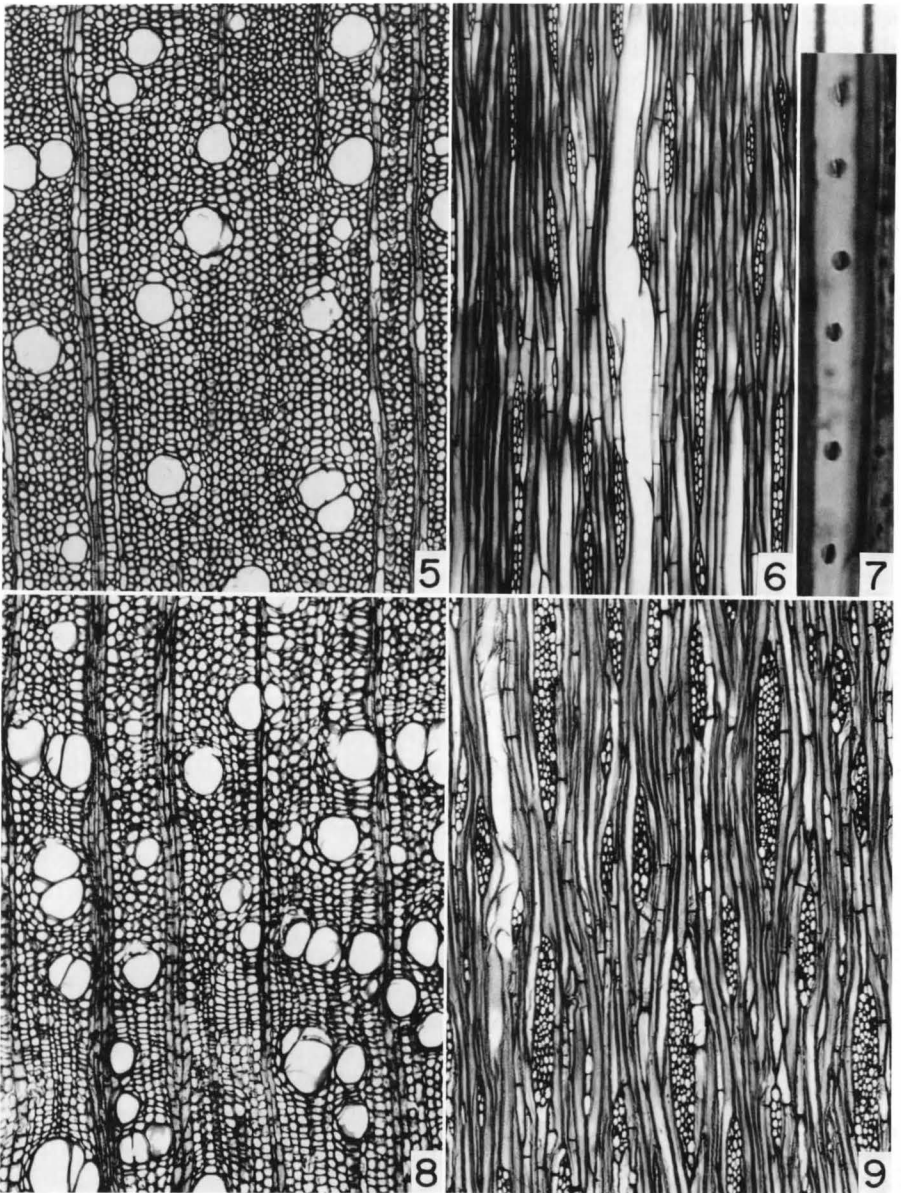
Fig. 5–9. Wood sections of stems of *Wigandia.*—5–7. *Wigandia caracasana* (*MADw-22081*).—5. Transection; vessels are sparse, not grouped.—6. Tangential section; rays short, narrow, but composed mostly of procumbent cells.—7. Fiber-tracheid from radial section, showing bordered pits.—8–9. *Wigandia crispa* (*Carlquist 7097*, RSA).—8. Transection; no growth-ring activity evident.—9. Tangential section. Rays are wide, high, composed mostly of procumbent cells. (Fig. 5–6, 8–9, magnification scale above Fig. 1. Fig. 7, magnification scale above Fig. 7 [division = 10 μm].)

Imperforate tracheary elements. — Nature of pits defines types of tracheary elements in dicotyledons. Tracheids can be defined as imperforate cells in which bordered pits are similar to those on the lateral walls of a vessel of any given species. Bordered pits which are sparser or have borders reduced as compared to those of lateral wall pitting of vessels characterize fiber-tracheids. Libriform fibers can be said to occur if borders are absent on pits of imperforate tracheary elements. Most Hydrophyllaceae can be said to have fiber-tracheids because pit borders are vestigial on imperforate tracheary elements. However, all of the taxa of *Phacelia* studied here must be characterized as having libriform fibers according to the above definitions. Of the Hydrophyllaceae in the present paper, *Wigandia* has fiber-tracheids which are transitional to tracheids in presence of pit borders, although the density of pits is less than is typical for tracheids (Fig. 7).

Walls of imperforate tracheary elements in all genera of Hydrophyllaceae studied here could be said to be gelatinous. Although shrinkage patterns are not marked, they can occasionally be seen, and use of counterstains replaces safranin more conspicuously than is the case with fully lignified imperforate tracheary elements. Some of the fiber-tracheids in *Draperia systyla* and *Hydrolea paraguayensis* were observed to be septate.

As shown in Table 1, column 7, mean length of imperforate tracheary elements in most Hydrophyllaceae is approximately twice the mean length of vessel elements. The ratio falls lower in the stems of *Phacelia ramosissima* (Fig. 14) and the roots of *P. heterophylla* subsp. *virgata* (Fig. 20) and *P. oreopola* subsp. *simulans.*

Axial parenchyma. — In *Eriodictyon,* axial parenchyma was observed to be uniformly diffuse in distribution (Carlquist et al. 1983). This is also clearly true in *Nama lobbii, Turricula parryi,* and all of the species *Wigandia* studied. However, diffuse axial parenchyma is very scarce in *Codon royenii, Nama johnstonii,* and *Phacelia ramosissima.* No diffuse axial parenchyma was observed in *Draperia systyla, Hydrolea paraguayensis, Phacelia floribunda, P. heterophylla* subsp. *virgata, P. ixodes, P. lyonii, P. oreopola* subsp. *simulans, P. pedicellata,* and *P. phyllomanica.* In the genera where axial parenchyma is present, strands of 2–4 cells (often 3) are characteristic. Occurrence of banded parenchyma is discussed above in connection with growth rings.

Vascular rays. — All of the species of *Phacelia* can be described as rayless at first; some acquire rays during the process of secondary growth, whereas others, such as *P. heterophylla* subsp. *virgata* (Fig. 20), *P. oreopola* subsp. *simulans, P. pedicellata, P. phyllomanica,* and *P. ramosissima* (Fig. 20) do not. Rays of the stem of *P. ixodes* studied were composed wholly of erect cells; these rays were few and no attempt to obtain ray dimensions was therefore made. The stems of *P. floribunda* and *P. lyonii* studied were only one year old, but xylem accumulation for that year was appreciable, and
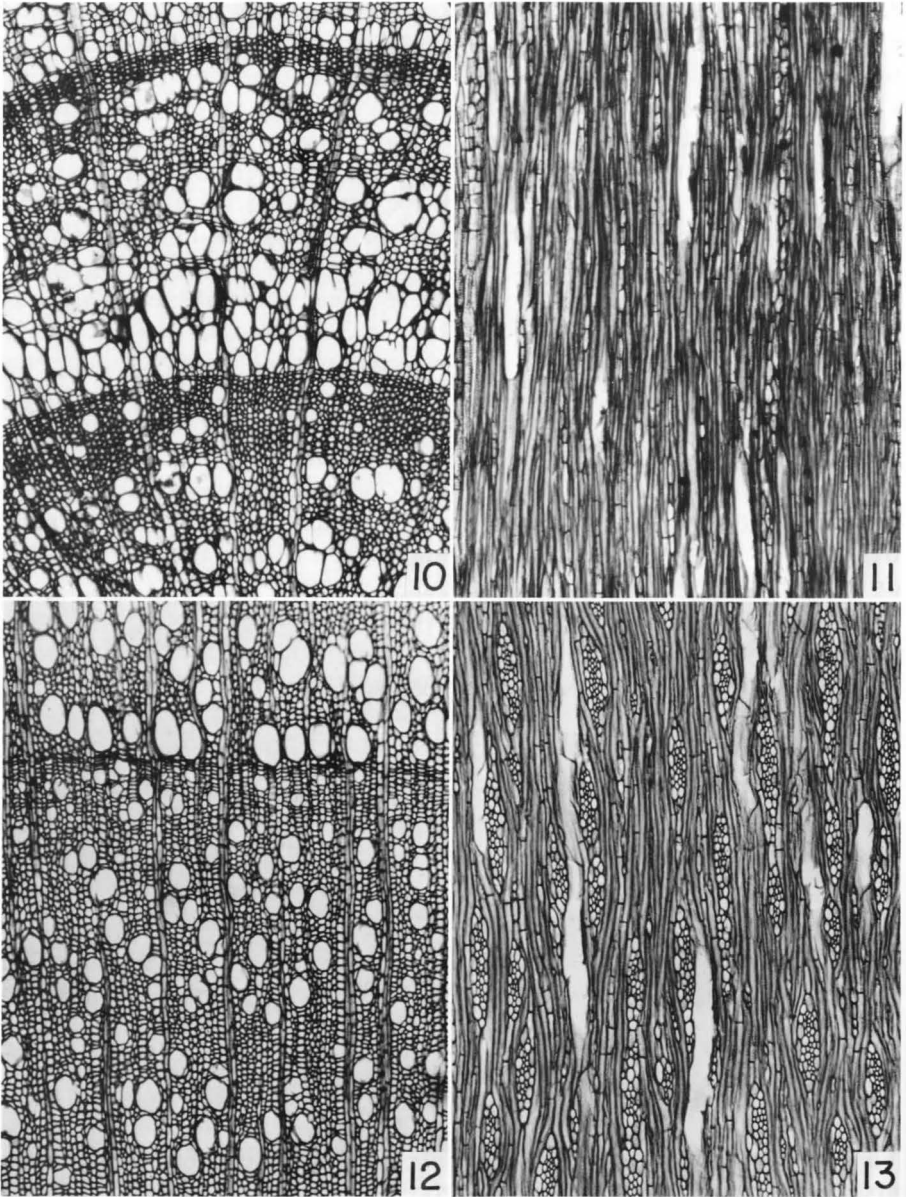
Fig. 10–13. Wood sections of stems of *Nama* and *Turricula.*—10–11. *Nama lobbii* (*Wolf 6017*, RSA).—10. Transection; two growth rings clearly evident.—11. Tangential section; erect cells abundant in rays, but procumbent cells present in central portions of larger rays.—12–13. *Turricula parryi* (*Carlquist 15637*, RSA).—12. Transection; earlywood of growth ring near top of photograph.—13. Tangential section; rays short, wide. (Fig. 10–13, magnification scale above Fig. 1.)

thereby rays apparently had a greater opportunity to develop. Rays in these two species consisted of erect, square, and procumbent cells, but only erect cells were common.

The remainder of the species studied here divide into those in which procumbent ray cells predominate (*Turricula, Wigandia*) and those in which erect ray cells predominate (*Codon, Draperia, Hydrolea, Nama johnstonii*). Procumbent and erect cells are about equally frequent in rays of *Nama lobbii*. The difference between the extreme types can be demonstrated by comparing rays of *Codon royenii* (Fig. 2) or *Hydrolea paraguayensis* (Fig. 4) with those of *Turricula parryi* or those of any of the species of *Wigandia* (Fig. 6, 9). As shown by *Turricula* (Fig. 13), procumbent cells where present occur in the central portions of rays chiefly; where procumbent cells are very abundant in rays, as in *Wigandia crispa* (Fig. 9), even some marginal cells of rays are procumbent. Increase in proportion of procumbent ray cells with age is evident in *Wigandia* (the smallest sample studied was that of *W. kunthii* [*Henrickson 2061A*] in which erect cells are more frequent than in the other samples of *Wigandia*). The width of rays also apparently increases with age in Hydrophyllaceae. These ontogenetic trends are familiar because Barghoorn (1941) found that they characterize dicotyledons at large.

Perforated ray cells, reported common in many collections of *Eriodictyon* (Carlquist et al. 1983), may be seen frequently in the stems of *Nama lobbii*.

Other features.—Storied structure is not present in woods of any of the Hydrophyllaceae studied. Druses occur in vegetative portions of Hydrophyllaceae (a few species), as noted by Metcalfe and Chalk (1950). However, druses have not hitherto been recorded in the wood itself of the family. Druses were observed in the earlywood parenchyma portions of the second year's growth in roots of *Phacelia oreopola* subsp. *simulans.*

SYSTEMATIC CONCLUSIONS

While one would be mistaken in underestimating possible systematic significance of data from wood anatomy in dicotyledons at large, Hydrophyllaceae in common with many other families show that distinctions in wood anatomy do not relate primarily to generic and specific divisions. Rather, features of wood anatomy tend to reflect habit, ecology, and age of specimen. If one seeks anatomical features which reflect systematic divisions, one must look for a structure in which various configurations can equally well accomplish a particular function. For example, in pollen grains numerous colpar configurations can insure proper germination and change in volume of the grain; numerous surface ornamentation patterns are equally successful in attaching a grain to an insect vector or performing functions related to that. In embryology, a number of different sequences of nuclear divisions or configurations are apparently equally successful in the reproductive cycle.
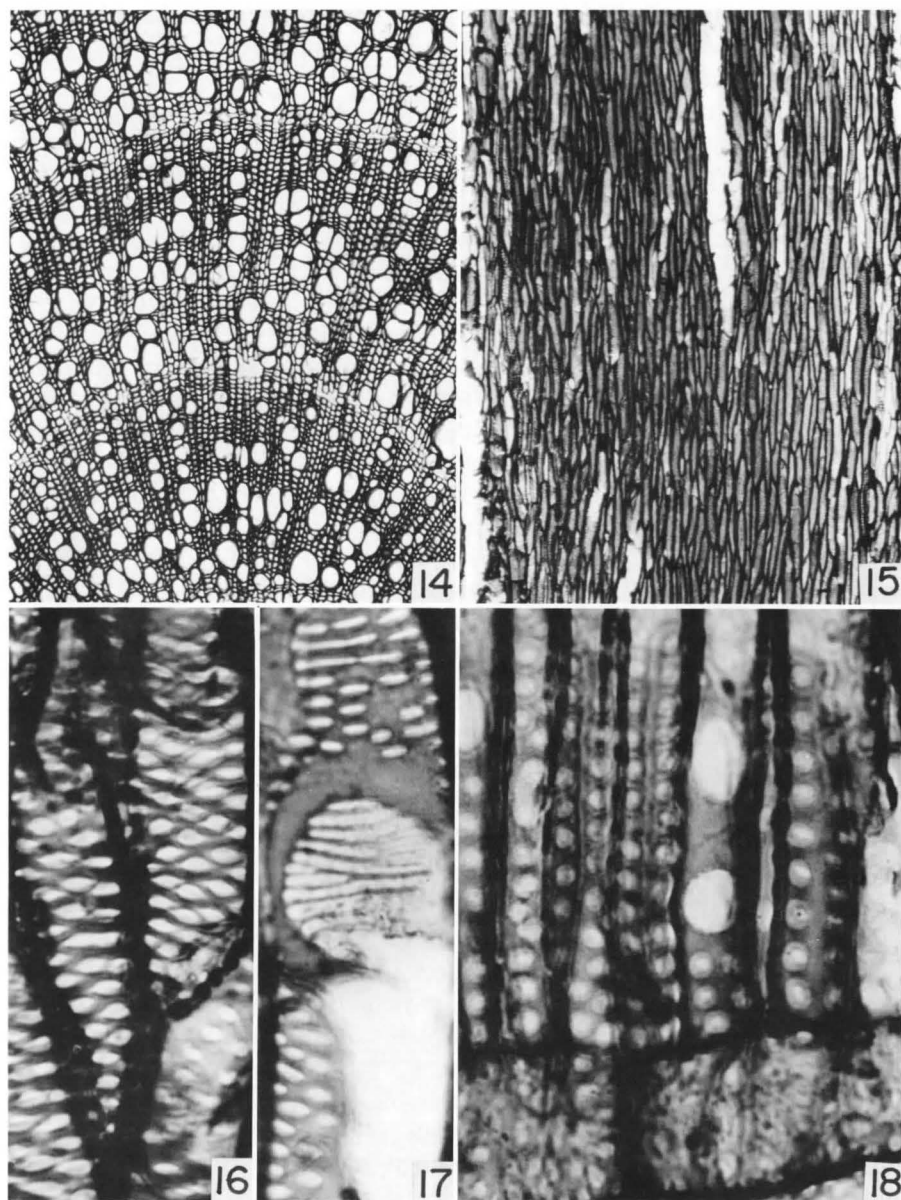
Fig. 14–18. Wood sections of stems of *Phacelia, Hydrolea,* and *Turricula.*— 14–16. *Phacelia ramosissima (Munz 11404,* RSA).— 14. Transection; margins of two growth rings shown.— 15. Tangential section; rayless nature of wood evident.— 16. Vessel from tangential section, showing laterally widened pits with tapered ends.— 17. *Hydrolea paraguayensis (Pedersen 10060,* UC), scalariform perforation plate of vessel from radial section.— 18. *Turricula parryi (Carlquist*

Thus the present study does not particularly reinforce, nor does it in any way negate, systems for Hydrophyllaceae such as those offered by Brand (1913), Constance (1963), or Constance and Chuang (1982). Information from wood anatomy does tend to confirm that Hydrophyllaceae is a natural family. The presence of fibriform vessel elements, tracheids (with various degrees in reduction of pit size and density, culminating in complete loss of borders with production thereby of libriform fibers), and diffuse axial parenchyma is an unusual combination of features in tubiflorous dicotyledon families. These features all occur in *Eriodictyon, Nama, Turricula,* and *Wigandia,* which would represent one of Brand's three tribes (Phacelieae) and two of the four generic groups of Constance and Chuang. *Phacelia,* which differs from the remainder of the family in being rayless at first and in having libriform fibers rather than tracheids or fiber-tracheids, is put in a subfamilial group by itself by Constance and Chuang, although Brand includes genera other than *Phacelia* in his Phacelieae. Moderately gelatinous imperforate tracheary elements characterize all of the species in the present study, as well as *Eriodictyon;* however, one is not likely to choose this as a feature certifying monophylesis of Hydrophyllaceae, for it occurs in various families.

Gelatinous imperforate tracheary elements, presence of tracheids or fiber-tracheids, and presence of diffuse axial parenchyma characterizes three other tubiflorous dicotyledon families: Convolvulaceae (Metcalfe and Chalk 1950), Dipsacaceae (Carlquist 1982b), and Goodeniaceae (Carlquist 1969) share these features. Convolvulaceae, like Hydrophyllaceae, have fibriform vessel elements (Mennega 1969). Fibriform vessel elements may be found in groups not closely related to these tubiflorous families, however: the term was devised by Woodworth (1935), who found these cells in Passifloraceae.

Anatomical features of primary stems are basic to Brand's main subdivisions for the family. More study of primary stems would be advisable, and with such studies could be combined studies of trichomes and of leaf anatomy. Because trichomes often are relatively conservative with respect to systematic divisions of families, examination of these features of vegetative anatomy is likely to yield interesting systematic dividends.

ECOLOGICAL CONCLUSIONS

Vessel diameter, vessel-element length, and number of vessels per mm^2 of transection have been combined into ratios termed Vulnerability (Table 1, column 14) and Mesomorphy (column 15). First used in an earlier paper

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15637, RSA), portion of radial section, showing a double perforation plate in a vessel element which is probably a fibriform vessel element. (Fig. 14–15, magnification scale above Fig. 1. Fig. 16–18, magnification scale above Fig. 7.)
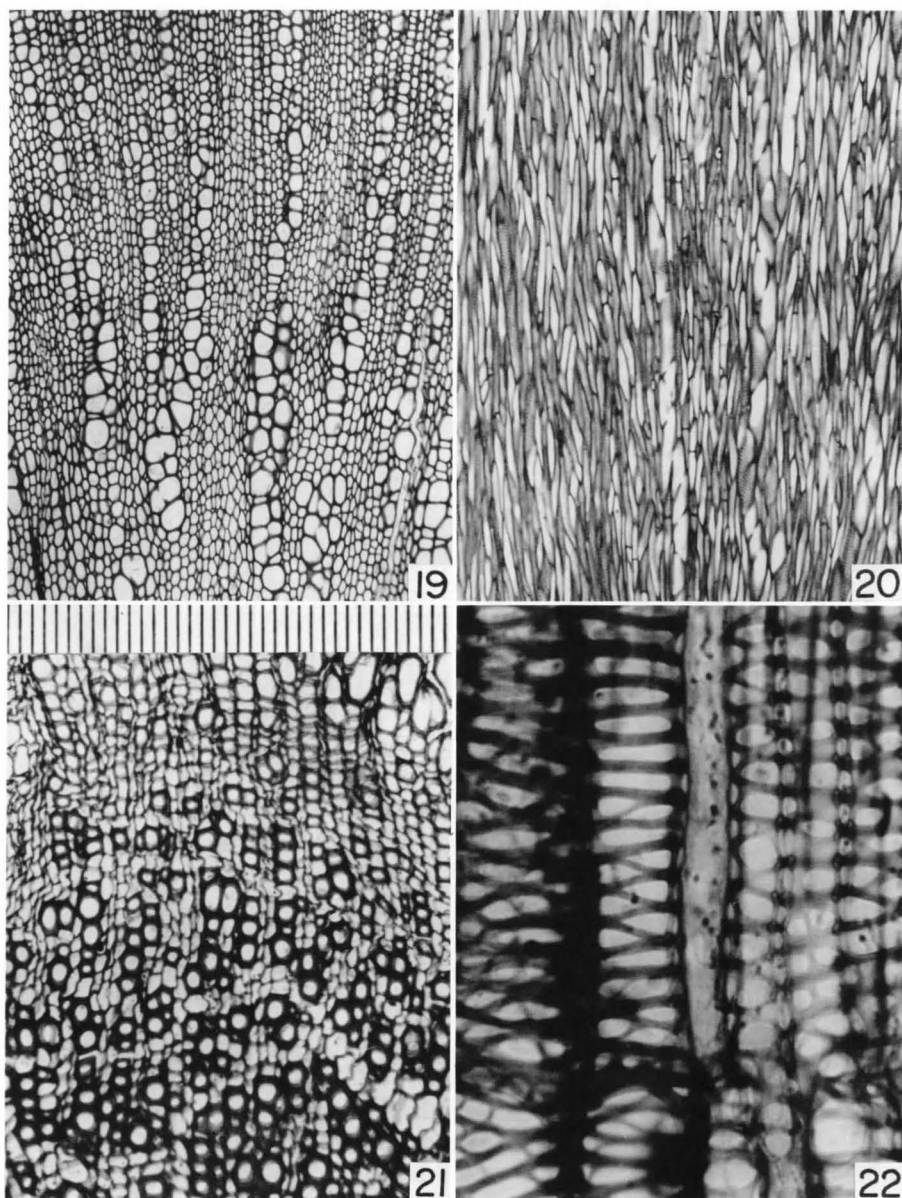
Fig. 19–22. Wood sections of root of *Phacelia heterophylla* subsp. *virgata* (*Follet 92*, RSA).—
19. Transection, showing vessels in large groupings; vessel diameter decreases upward into
latewood.—20. Tangential section; wood is essentially rayless, although an occasional ray cell
may be seen.—21. Portion of latewood of growth ring from transection (a few earlywood vessels
at extreme upper right corner); vessels mixed with parenchyma.—22. Radial section, showing

(Carlquist 1977), these ratios have proved sensitive indicators of adaptation to variously dry or wet habitats. The stems of Hydrophyllaceae other than *Wigandia* in the present study have vulnerability figures below 0.60; the same was true for *Eriodictyon* (Carlquist et al. 1983). Values for roots are much higher; *Eriodictyon* is much like *Turricula* in this respect. *Wigandia* has vulnerability and mesomorphy values typical of a mesic tropical tree, an entirely appropriate ranking for this genus, which grows in openings in tropical areas which are basically moist, probably exceeding 150 cm of rainfall per year. The broad leaves of *Wigandia* do not resist low humidity well; in California, *W. caracasana* can only be cultivated successfully near the coast. *Eriodictyon* and *Turricula* have fairly high vulnerability and mesomorphy values, as noted in the earlier paper on *Eriodictyon,* considering that they occupy some rather dry habitats. These elevated values are undoubtedly related to the succulent roots with long duration in these genera; perhaps the foliage in both genera has an intermediary role in water economy of the plants as well, a role lacking in genera with drought-deciduous leaves. The relatively low vulnerability and mesomorphy values in the genera other than *Eriodictyon, Turricula,* and *Wigandia* are understandable; those genera grow in relatively dry places except for *Hydrolea. Hydrolea paraguayensis* has the highest values for the genera other than *Eriodictyon, Turricula,* and *Wigandia.* The specimen of *Codon royenii* studied here was from cultivation, so its values may be higher than would be found in a specimen from the wild. *Phacelia pedicellata* has values higher than might be expected in a plant of its range (Mojave Desert), but it grows only during a moist part of a moist year and thus lives very little under drought conditions. This is perhaps also true of *Nama johnstonii. Draperia systyla, Nama lobbii,* and the species of the *Phacelia magellanica* complex have the advantage of dying back to perennial roots; these taxa, however, have fairly shallow roots compared with those of *Eriodictyon,* so relatively low mesomorphy values are not unexpected. *Phacelia ramosissima* does not have a succulent root, yet is a perennial living a few seasons; its highly xeromorphic wood reflects this difficult combination of habit and habitat. In this species, the upper stem does die back at the end of the growing season. The four insular species of *Phacelia* (*P. floribunda, P. ixodes, P. lyonii,* and *P. phyllomanica*) have vulnerability and mesomorphy values higher than that of *P. ramosissima.* These values may reflect not a wetter habitat than that of *P. ramosissima,* but their facultative annual nature. If the season is excessively dry, they can

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vessels from parenchymatous latewood; laterally widened pits evident. (Fig. 19–20, magnification scale above Fig. 1. Fig. 21, magnification scale above Fig. 21 [divisions = 10 μm]. Fig. 22, magnification scale above Fig. 22.)

persist as seeds rather than as vegetative structures in which xeromorphic wood must play a role in survival. However, *Phacelia pedicellata* has wood more mesomorphic than that of the insular species despite its desert habitat, but it is an obligate annual and grows only in wet years; no growth occurs nor does any xylem function when soil is dry.

The occasional scalariform perforation plates observed in *Hydrolea paraguayensis* probably represent manifestations of paedomorphosis: persistence of metaxylem features into the secondary xylem. However, persistence of this feature into the secondary xylem appears to characterize only mesomorphic species, as noted earlier (Carlquist 1983).

Vessel grouping seems to occur in species with libriform fibers or fiber-tracheids, and represents an adaptation to xeromorphy (Carlquist 1984). The small mean figure of vessels per group in *Wigandia* and in *Eriodictyon* is notable. Does this represent wetter habitats for these genera, or does it represent compensation for a rather dry habitat by means of succulent cortex, long-lived roots from which stem innovations can originate, or are other factors involved? The numbers for vessels per group in these genera are only slightly above chance contact of vessels (ca. 1.2 or less). Perhaps more importantly, *Wigandia* and *Eriodictyon* have imperforate tracheary elements which are close to true tracheids; according to the theory cited (Carlquist 1984), tracheids serve as a subsidiary conductive system so that vessel grouping is not of selective value in a tracheid-bearing wood. Few genera of dicotyledons are in transition between tracheids and fiber-tracheids in secondary xylem. In Hydrophyllaceae, the genera other than *Eriodictyon* and *Wigandia* have fiber-tracheids with reduced borders on pits or else libriform fibers, and they also have higher numbers of vessels per group (Table 1, column 5). Only *Hydrolea paraguayensis* and some *Phacelia* species among these genera escape from a greater degree of vessel grouping, and they probably do so by virtue of growth under moist conditions; the plant body in these species probably ceases to function after drought occurs. These facts are in accord with the hypothesis on vessel grouping.

If one calculates a ratio between length of imperforate tracheary elements and length of vessel elements, the value for most Hydrophyllaceae is about 2.0, but it falls well below that in the roots of *Phacelia heterophylla* subsp. *virgata, P. lyonii,* and *P. oreopola* subsp. *simulans,* as well as in the stems of *P. ramosissima.* The relatively short length of imperforate tracheary elements in these species might indicate diminished mechanical strength, but the difference among species of Hydrophyllaceae for this ratio is not significant.

RAYLESSNESS AND EVOLUTION OF HABIT

Hydrophyllaceae have both multiseriate and uniseriate rays; the multiseriate rays have procumbent cells in the central portions, and uniseriate rays

may contain both procumbent and erect cells. Thus the Heterogeneous Type IIB of Kribs (1935) may be said to be present. Older stems have wide multiseriate rays, and a higher proportion of procumbent cells may be found at the periphery of older stems as compared to portions nearer the pith. Both of these are common trends in dicotyledons (Barghoorn 1941). The scarcity of procumbent cells in rays of *Codon, Draperia, Hydrolea,* and *Nama* is in accordance with the theory of paedomorphosis in dicotyledon woods.

Phacelia is distinctive in being rayless, at least at the beginning of secondary growth, in all seven species studied. The development of rays ultimately in some of these species as secondary growth proceeds (rapidly in the case of *P. floribunda* and *P. lyonii*) is not an exception to raylessness; many rayless species ultimately develop rays if stems become large enough. Phacelia can be said to be more specialized than the remainder of Hydrophyllaceae in having no perceptible borders on pits of imperforate tracheary elements. *Phacelia* is a large genus in which many species are annuals; conceivably, annuals are basic to *Phacelia* species as a whole. If, as has been claimed earlier (Carlquist 1970), raylessness characterizes herbaceous taxa in phylesis toward a woodier stature, one would have to hypothesize the annual habit as ancestral to the *Phacelia* species studied. However, Hydrophyllaceae as a whole appear to have been a woody group ancestrally. There is nothing to contradict the idea that Hydrophyllaceae were woody in their inception in the data of the present paper or the earlier study of *Eriodictyon.* Wood like that of *Eriodictyon* or *Wigandia* does not look like wood of an herb; most notably, the rays show no evidence of herbaceous modes of structure. *Eriodictyon, Turricula,* and *Wigandia* have more primitive tracheary elements than do the other genera. *Eriodictyon, Nama, Turricula,* and *Wigandia* have diffuse parenchyma, which has evidently been lost in the remaining genera. Loss of diffuse parenchyma would be expected in species with short-lived stems, where selective value for parenchyma, with its photosynthate storage function, is minimal because pith and cortical parenchyma as well as phloem parenchyma are not separated by wide zones of xylem and erect ray cells may substitute well for axial parenchyma cells in what little xylem is present.

Raylessness may represent a substitution of libriform fibers for ray cells as a way of securing increased mechanical strength in a small stem or root. If so, that could explain why an annual species of *Phacelia* might have rayless secondary xylem.

SIGNIFICANCE OF PARENCHYMA BANDS CONTAINING VESSELS WITH LARGE PITS

Parenchyma bands in growth rings are a noteworthy phenomenon because Hydrophyllaceae as a family basically have diffuse parenchyma. The absence of diffuse parenchyma (with minor exceptions) in *Codon, Draperia, Hydro-*

lea, Nama, and *Phacelia* may be related to the relatively small size and short duration of woody cylinders in these genera. The function of axial parenchyma is not entirely clear, although Braun (1983) has advanced our understanding considerably. Braun claims that wood parenchyma acts as a water reservoir and also can, by releasing osmotically active substances (sugars), induce uptake in a plant—for example, when trees begin function in early spring before leafing out. These functions would be of little importance in stems of short duration, such as those of annuals or short-lived perennials. However, perennials which go through a dry season, at the end of which conduction must be renewed (and through which a few intact water columns must be preserved) could benefit from the two functions mentioned above. The parenchyma bands in *Phacelia heterophylla* subsp. *virgata* (Fig. 21), *P. oreopola* subsp. *simulans,* and *P. ramosissima* are relevant to the ideas expressed above for perennials. The parenchyma bands in these species are probably the result of fiber dimorphism, a phenomenon discovered in Asteraceae (Carlquist 1958) but applicable to other families as well.

Other examples similar to the three species of *Phacelia* mentioned in having parenchyma bands containing vessels with large pits include *Hemizonia minthornii* Jepson (Carlquist 1958); *Stephanomeria blairii* Munz & Johnston and *S. guadalupensis* Brandegee (Carlquist 1960) and *Mimulus bifidus* Pennell and *M. clevelandii* Brandegee (Michener 1983). Slides of *Penstemon bridgesii* A. Gray prepared by Donald R. Bissing also show such bands. Noteworthy in regard to all of these species is that they grow in Mediterranean-type climates, in which they must persist through dry seasons, and in which water retention by parenchyma and osmotic activity by parenchyma would therefore be adaptive.

The vessels in parenchyma bands in these species tend to have notably enlarged pits. The pits are most often laterally widened. The vertical bands of thick wall material may be relatively inconspicuous, whereas the horizontal bands of thickened wall material are comparatively more evident. Thus there is a superficial resemblance to the spiral (helical) bands of primary xylem tracheary elements. This phenomenon has evidently been noted by Metcalfe and Chalk (1950) in the case of *Alyssum spinosum* L., which those authors thought did have "spirally thickened" vessels which they therefore thought represented a "juvenile form of xylem." The vessels seen in *Alyssum spinosum* should be regarded as a special phenomenon, not related to primary xylem or to juvenilism (e.g., paedomorphosis). Paedomorphosis is ruled out in the case of *Alyssum spinosum* because an unbroken sequence from metaxylem to the allegedly spiral elements in pitting type does not occur. Paedomorphosis can be cited where vessels and vascular tracheids in secondary xylem with scalariform or spiral-banded wall patterns are connected with similar vessels in metaxylem; the globular cacti mentioned below are an example where paedomorphosis is operative.

In addition to perennials of Mediterranean-type climates, succulents form another group in which there are vessels with wide pits, some simulating vessels with spiral thickenings when the vertical bands of thickened wall material are inconspicuous. *Aeonium* and *Crassula* are good examples of this tendency. In some globular cacti, vessels and vascular tracheids with true spiral thickenings can be found; Gibson (1973) figures these for *Echinopsis calochlora* K. Schum. and *Ferocactus townsendianus* Britton & Rose. This true spiral thickening seems related to ability of globular cacti to shrink during dry periods. Are vessels with wide pits simulating to some degree spirally-thickened vessels, such as those of *Aeonium* and *Crassula,* also devices to accommodate shrinkage and expansion? Braun (1970, 1983) mentions enlarged pits as characteristics of "Kontaktparenchyma," but the pits of vessels figured for *Phacelia heterophylla* subsp. *virgata* exceed in size considerably those included by Braun in that terminology. If parenchyma serves as a water reservoir in the stems of Mediterranean-climate perennials and succulents, shrinkage might be expected to occur, although this possibility was not mentioned in the examples cited by Braun, who has discussed trees or large shrubs and not other growth forms.

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