1966

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Recommended Citation

Carlquist, Sherwin (1966) "Wood Anatomy of Compositae: A Summary, With Comments on Factors Controlling Wood Evolution," *Aliso: A Journal of Systematic and Floristic Botany*: Vol. 6: Iss. 2, Article 3. Available at: <https://scholarship.claremont.edu/aliso/vol6/iss2/3>

WOOD ANATOMY OF COMPOSITAE: A SUMMARY, WITH COMMENTS ON FACTORS CONTROLLING WOOD EVOLUTION

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INTRODUCTION

This paper concludes the writer's survey of wood anatomy of Compositae. The contents of the tribal monographs on which this summary is based provide material for an analysis of trends in wood anatomy in the family as a whole. Such analysis is of unusual interest because of several distinctive features possessed by Compositae.

The family is world-wide in distribution. The great plasticity of composites is evident in their occupation of many regions and ecological niches. Often, woody representatives from more than one tribe may be found in a given locality. The sensitiveness with which Compositae adapt to particular conditions is imprinted clearly on their patterns of wood anatomy. Therefore, the family is excellent for demonstrating how various factors influence wood evolution. The fact that 14 tribes are involved, and that each shows an ability to radiate into a variety of environments means that the family is like an experimental material divided into 14 replications, and each potentially can provide a "control" for comparison with the others.

Growth forms attained by Compositae cover a very broad range of conformations. True trees occur, and are rather more numerous and more truly woody than generally appreciated. Rosette trees and rosette shrubs are also abundant within the family. True shrubs, however, provided the majority of wood samples studied here. An appreciable number of perennials with woody caudices were studied, as were woody annuals and biennials with sufficient wood. Only one vine (*Mikania cordifolia*) was available for study.

Compositae are rich in herbaceous species, and thus investigation of wood anatomy differs in kind, as well as degree, from study of a family which is predominantly or exclusively woody. That some Compositae are truly woody cannot be denied. Thus, one can compare modes of wood structure in herbaceous and woody groups, and suggest how the two modes of wood structure are interrelated, a problem which has not yet received sufficient attention.

¹Completion of this series of papers on wood anatomy of Compositae has been made possible by two grants from the National Science Foundation, NSFG-5428 and NSFG-23396. The writer wishes to express appreciation for this assistance.

Investigation of factors controlling modes of wood evolution requires a large sample in order that results can be expressed statistically and yield reliable distinctions. Obviously there are many ways of adjusting to a particular locality, both within Compositae and in dicotyledonous families at large. A large sample, however, can suggest broad trends. This summary is based upon analysis of 353 samples, representing 328 species in 171 genera. This may not seem a large sample of a family which has been estimated (perhaps conservatively) to contain 20,000 species in 1,000 genera. However, a large proportion of the family is composed of annuals with little or no secondary growth, and such forms could not be investigated.

Systematic conclusions can be served by analysis of woods in the family as a whole. The tribes differ to some extent in wood anatomy, and regardless of the reasons for these differences, they can be used systematically and are to some extent susceptible to phylogenetic interpretation. Because Compositae is a family in which the gamut of wood specialization ranges from advanced to highly advanced, one cannot use a wide range of expression in the major trends of xylem evolution for systematic and phylogenetic purposes, as one can, for example, in Violaceae. The most useful features taxonomically are ones which relate to habit, as well as minor characters which can be expected to occur sporadically within a family: septate fibers, thick- or thin-walled fibers, presence of crystals, etc. Such characters have been discussed in the earlier papers of this series, and need not be repeated here.

Systematists seem often to overestimate the taxonomic value of wood anatomy. Where two groups differ markedly in evolutionary level, and thereby in expressions of the features statistically associated with the vessel elements (the "major trends of xylem evolution"), such a difference can be used both taxonomically and phylogenetically. Compositae, as indicated, encompass only a narrow span of specialization. This span has been traversed many times within the family, in all likelihood, and thus parallelisms are very frequent and conservative characters are few. Woods of Compositae are indistinguishable from woods of other specialized families which may not be at all closely related (e.g., Scrophulariaceae).

With a family of the size of Compositae, one wishing to develop characters of wood anatomy for systematic use must study genera synoptically. Although a few genera have been so studied within the survey of tribes, the survey approach is opposed to monographic understanding of woods within a genus. Availability of wood samples dictated the species studied. Had exhaustive wood collections been made, the analysis of Compositae wood would have been so bulky that the present series of papers would have been almost impossible. However, the taxonomic dividends of such exhaustive study would probably have been relatively small. The present data seem adequate for exposing trends in structure; the data are, in fact, best used for this purpose. Had twice the number of samples been studied, the conclusions permitted would probably have been substantially the same.

The major offering of this paper is in establishment of trends of wood evolution within Compositae. Although major trends of wood evolution have been established within dicotyledons at large, as yet we have little information as to which factors of climate and ecology guide these trends. Also, to what extent

can a particular wood pattern be modified by such processes as paedomorphosis? Assuming irreversibility of the major trends of xylem evolution, can a particular group nevertheless possess wide flexibility in expression, and if so, how does this flexibility operate? The answers to these questions are suggested to some degree by the data on woods of Compositae, and by such studies we may hope to widen and re-shape our ideas of wood evolution.

The papers which contribute data summarized here include the following tribal monographs by the writer: Mutisieae (1957); Heliantheae (1958a); Helenieae (1959); Cichorieae (1960a); Astereae (1960b); Inuleae (1961); Senecioneae (1962a); Vernonieae (1964); Cynareae (1965a); Eupatorieae (1965b); Anthemideae, Ambrosieae, Calenduleae, and Arctotideae (1966). A floristic-anatomical study of Compositae of the Florida Keys (Carlquist, 1958b) contributed data to this program. Investigation of phenomena of juvenilism, or paedomorphosis (Carlquist, 1962b) was inspired by study of woods in certain members of Compositae and other families, and the concepts developed there are basic to interpretations in the present summary.

MATERIALS AND METHODS

The summation of data on wood anatomy of Compositae is presented in table 1. The qualitative and quantitative features given there are similar to those presented in the tribal monographs. Data on growth rings, uniseriate ray height, libriform fiber width, and fiber-wall thickness have been omitted here because these seem characteristic of particular species and genera but unrelated to broader phyletic trends with few exceptions. Data presented in table 1 seem high in significance, but not in all cases. Presentation of some cases with neutral correlation seems important if only as a background to those features which do show correlation.

Factors referable to ecological concepts are shown in the upper half of table 1. Following these, data are summarized on each of the tribes. The last line of table 1 is a summary for the family as a whole. The method employed for obtaining the figures is as follows. For quantitative features (e.g., vessel element length), averages for each species were given in the earlier papers of this series. Such averages were collected into appropriate categories (e.g., Vernonieae; shrubs) and averaged. The advisability of taking an average of averages may be questioned, but there seemed no other way of analysis in this particular summary.

For quantitative characters, the total number not of collections but of species was determined for each category (e.g., the number of species of Astereae, or of shrubs, in which storied wood was observed). The degree of presence has also been computed as a percentage (e.g., of shrubby composites, the percent which have storied wood). Computation of these percentages compensates for different numbers of species in the categories (i.e., 59 species of Astereae were studied, but only 16 Cichorieae).

With such statistics as these, how can one determine whether significant correlations exist? Standard error and standard deviations were not computed, nor were mathematical significance tests used because the nature of the sampling and referral of particular species to categories provide sources for error

well beyond the limits of error in measurement, or variability of measurements within a sample. My knowledge of ecology, distribution, and growth forms of the 328 species is imperfect, and is a source of error. The species for which

TABLE 1.
*Wood Characteristics
of Compositae*

ECOLOGICAL OR SYSTEMATIC CATEGORY	NUMBER OF GENERA STUDIED	NUMBER OF SPECIES AND VARIETIES STUDIED	NUMBER OF COLLECTIONS STUDIED	DIAMETER OF WIDEST VESSEL, AVERAGE OF COLLECTIONS, μ	DIAMETER OF VESSELS, AVERAGE OF COLLECTIONS, μ	VESSELS PER GROUP, AVERAGE OF COLLECTIONS	LENGTH OF VESSEL ELEMENTS, AVERAGE OF COLLECTIONS, μ	LENGTH OF LIBRIFORM FIBERS, AVERAGE OF COLLECTIONS, μ	HELICAL SCULPTURE ON VESSELS, NO. OF SPECIES WHICH HAVE	HELICAL SCULPTURE ON VESSELS, PERCENTAGE OF SPECIES IN CATEGORY WHICH HAVE
<i>Rainfall:</i>										
Mesic		161	177	109	66	3.04	282	448	79	49
Dry		129	136	80	39	5.20	198	334	74	57
Desert		38	40	75	34	8.37	155	301	26	68
<i>Latitude:</i>										
Temperate		191	204	87	51	5.68	191	344	116	61
Tropical		137	149	107	65	2.64	300	501	63	46
<i>Habit:</i>										
Annual or Biennial		35	35	87	46	2.74	186	359	12	34
Caudex Perennial		29	29	77	39	4.45	152	303	22	76
Shrub or Subshrub		173	186	67	45	6.26	240	373	109	63
Tree		38	46	119	84	1.94	312	457	26	68
Rosette Tree or Rosette Shrub		52	56	104	68	2.22	292	446	10	19
<i>Habitat:</i>										
Equatorial Alpine		9	11	113	80	1.90	300	516	0	0
Insular		90	98	91	52	3.62	246	358	38	42
Continental		229	244	94	52	4.83	226	395	142	62
<i>Tribes:</i>										
Ambrosieae	6	15	15	99	44	5.11	187	423	10	67
Anthemideae	5	20	21	69	33	6.35	145	338	20	100
Arctotideae	1	2	2	98	56	3.53	129	357	2	100
Astereae	13	58	69	85	38	8.89	189	293	47	81
Calenduleae	3	4	4	76	41	7.54	158	326	2	50
Cichorieae	8	14	16	102	57	2.44	232	360	0	0
Cynareae	7	18	18	93	48	2.49	185	336	10	56
Eupatorieae	4	19	19	109	62	2.21	287	482	18	95
Helenieae	11	15	15	62	35	4.82	167	302	10	67
Heliantheae	33	53	53	88	48	2.16	255	477	7	13
Inuleae	11	17	19	90	52	4.75	218	338	13	76
Mutisieae	22	24	24	65	38	1.91	272	503	8	33
Senecioneae	12	42	45	102	58	4.07	297	448	16	38
Vernonieae	5	27	33	154	96	1.86	321	567	16	59
<i>All Compositae Studied</i>	141	328	353	94	51	3.62	235	407	179	55

samples were available may or may not be a good cross-section of tree-Compositae, or of Cichorieae. Moreover, different samples represent different degrees of maturation, or may be from divergent parts of plants. Despite these sources

STORIED WOOD STRUCTURE, NO. OF SPECIES WHICH HAVE	STORIED WOOD STRUCTURE, PERCENTAGE OF SPECIES IN CATEGORY WHICH HAVE	HEIGHT MULTISERATE RAYS, AVERAGE OF COLLECTIONS, mm.	RAY MULTISERATE EXCLUSIVELY, NO. OF SPECIES WHICH HAVE	RAY MULTISERATE EXCLUSIVELY, PERCENTAGE OF SPECIES IN CATEGORY WHICH HAVE	MAXIMUM WIDTH MULTISERATE RAYS, AVERAGE OF COLLECTIONS, CELLS	RAY CELLS ISODIAMETRIC TO PROCUMBENT, NO. OF SPECIES WHICH HAVE	RAY CELLS ISODIAMETRIC TO PROCUMBENT, PERCENTAGE OF SPECIES IN CATEGORY WHICH HAVE	RAY CELLS ISODIAMETRIC TO PROCUMBENT EXCLUSIVELY, NO. OF SPECIES WHICH HAVE	RAY CELLS ISODIAMETRIC TO PROCUMBENT EXCLUSIVELY, PERCENTAGE OF SPECIES WHICH HAVE	RAY CELLS ISODIAMETRIC TO ERECT, NO. OF SPECIES WHICH HAVE	RAY CELLS ISODIAMETRIC TO ERECT, PERCENTAGE OF SPECIES IN CATEGORY WHICH HAVE	RAY CELLS ISODIAMETRIC TO ERECT EXCLUSIVELY, NO. OF SPECIES WHICH HAVE	RAY CELLS ISODIAMETRIC TO ERECT EXCLUSIVELY, PERCENTAGE OF SPECIES IN CATEGORY WHICH HAVE
77	48	1.93	72	45	4.7	106	66	39	24	126	78	66	41
48	37	.88	48	37	4.2	86	67	27	21	102	79	41	32
26	68	.87	26	68	4.8	28	74	14	37	21	55	10	26
102	53	.93	65	34	4.4	146	76	50	26	138	72	58	30
49	36	2.24	81	59	4.9	78	57	30	22	97	71	59	43
2	6	1.06	12	34	4.5	23	66	1	3	31	89	11	31
14	48	.94	21	72	5.6	17	59	5	17	22	76	11	38
88	50	1.09	74	43	4.2	127	73	57	33	105	61	51	30
20	52	1.17	27	71	4.8	22	58	12	32	27	71	18	47
26	50	3.40	11	21	5.1	30	58	4	8	50	96	25	48
4	23	2.93	6	67	5.6	8	89	0	0	9	100	1	11
57	63	1.19	40	44	4.0	42	47	15	17	59	66	50	56
90	39	1.45	100	43	4.7	160	70	65	28	167	73	66	29
9	60	1.03	11	73	4.3	8	53	1	7	14	93	7	47
14	70	.50	10	50	5.1	15	75	8	40	12	60	6	30
0	0	.75	1	50	4.5	2	100	0	0	2	100	0	0
44	76	.51	21	36	3.7	54	93	32	55	25	43	5	9
0	0	.35	0	0	3.4	3	75	0	0	3	75	0	0
5	36	.70	1	7	4.8	8	57	2	14	12	86	6	43
3	17	1.17	4	22	4.7	15	83	0	0	18	100	3	17
13	68	2.21	16	84	5.0	11	73	1	5	18	95	7	37
1	7	.73	4	27	4.1	6	40	3	20	8	53	3	20
26	49	1.60	28	53	3.8	20	38	5	9	48	90	36	68
5	29	1.31	11	65	4.5	7	41	4	24	10	59	7	41
2	8	.77	2	8	3.1	9	38	5	21	15	63	15	63
26	62	4.41	30	71	5.3	22	52	2	5	39	93	20	48
3	11	.98	7	26	5.0	26	96	17	63	10	37	2	7
151	45	1.44	146	45	4.6	220	67	80	24	235	72	117	35

of error, meaningful correlations seem obtainable. Characters which lack strong correlation can be compared with those which are positively correlated. For example, the difference in vessel-element length between tropical Compositae (300 μ) and temperate ones (191 μ) seems significant, whereas the same comparison for ray width (4.4 cells vs. 4.9 cells) does not.

Several criteria were used in determining whether comparisons were significant. First, is the gap in figures between the categories wide (e.g., more than 20%)? Second, where categories form a continuous series (mesic-dry-desert), do figures increase or decrease correspondingly? Third, although one cannot predict results in advance of computation, the results should be susceptible to rational interpretation. For example, increased xeromorphy is correlated with increasing grouping of vessels concomitantly with narrowing of vessels, and such a trend would correspond to physiological expectations.

Data on certain wood characteristics were not included consistently in all earlier studies (e.g., libriform-fiber length was not given for Mutisieae: Carlquist, 1957). Such data have been obtained now so that complete and comparable figures could be presented in table 1.

For purposes of calculations, some indefinite quantitative figures given in the papers of the series have been assigned arbitrary values and included in the data in table 1. Vessel grouping noted as "1- ∞ " has been given the value of 10.0, and " ∞ " has been given the value 15.0. In ray height, ">3" has been calculated as 5.0, ">5" as 10.0, and ">10" as 15.0. Similar values were required in a few cases in ray width. The designation of these arbitrary values may have had the effect of heightening differences, but to have omitted these extreme expressions would have been unwarranted.

Errata have occurred in earlier papers, and the following corrections are offered. In Heliantheae (1958a), the last two species in the table (*Grindelia stricta* var. *procumbens* and *Eastwoodia elegans*) seem, by indentation, to be referred to Ambrosiinae. The writer intended that these species names be set on the margin, and no relationship to Ambrosiinae was intended. These two taxa, often placed in Astereae, were included in the survey of Heliantheae because several authors suggest they should be referred to, or are transitional to, Heliantheae. In the survey of Astereae (1960b), *Lepidospartum squamatum* was included because the writer was uncertain whether that genus should be placed in Senecioneae or Astereae. Subsequent studies, such as those on chromosomes, confirm Senecioneae as the correct placement. By error, *Mikania cordifolia* was incorrectly included in the survey of Senecioneae (1962a); it has also been included (correctly) in the study of Eupatorieae (1965b). In the table of data for woods of Inuleae (1961), the infinity sign has been set incorrectly as "oo" in the column of vessels per group, and the name *Brachylaena merana* has been incorrectly set. A few other typographical errors of a routine nature occur in papers of the series; these will be easily recognized by the reader.

FACTORS CONTROLLING WOOD EVOLUTION

Thanks to the work of Bailey and his students, we have a comprehensive picture of the major trends of xylem evolution (for a summary, see Carlquist, 1960c). These trends are alleged to be irreversible. At the same time, flexibility

obviously occurs in some groups, as noted by Bailey (1944). A theory of paedomorphosis (Carlquist, 1962b) was devised to account for certain instances of this flexibility. With such a theory, we can account for various expressions within a framework of irreversibility of the statistically-linked characters included in the major trends of xylem evolution. The totality of data on wood anatomy of Compositae can be applied to demonstrating the major trends, but more importantly, to exploring the degree and method of flexibility. This flexibility is a mechanism which permits Compositae to adapt to ecological conditions in a rapid and sensitive manner. Thus, we can explore the ways in which ecological factors influence wood evolution. One contribution which has been made to understanding of this problem was made by Webber (1936), who noted shortening of vessel-element length as an accompaniment of xeromorphy. The method she employed, a floristic one, is a legitimate method. An alternative is offered here: a single large and plastic group, containing many units which have entered particular niches several or many times. Moreover, conditions other than xeric are included here, so that a contrast is afforded. If Compositae basically have a rather uniform pattern of wood anatomy, adaptations when seen against that basic plan will be readily evident.

To the extent that selection and definition of ecological factors are done perceptively, the conclusions will be valuable. In table 1, these factors take the form of mutually-exclusive categories. Of the categories in table 1, the contrast between insular and continental offers no significant differences of a high degree, probably because insular has been defined too broadly (all kinds of islands, including Australia, were included under "insular"). Future studies on insular woodiness can focus more exactly on various modes of wood structure on islands and various types of islands. With greater discrimination, significant correlations can probably be obtained both in Compositae and in other families.

CORRELATIONS WITH RAINFALL

Habitats were divided into mesic, dry, and desert. These habitats were roughly defined as more than 25 inches of rain annually, 10–25 inches, and less than 10 inches, respectively. Assignment of species to these categories is difficult in some cases. Most annuals were termed mesic, even if they grow in regions of low rainfall. The reason for this is that most annuals complete their growth during moist seasons, and thus secondary growth is not adapted to dry conditions as much as it is in perennials or shrubs.

The error most likely in assigning species to the categories mesic, dry, and desert, would seem the inclusion of too many species in "mesic," too few in "dry." Thus, the differences which are presented in table 1 may be considered conservative. Nevertheless, clear correlations are shown in table 1. With increasing dryness, width of vessels decreases markedly. The increase in number of vessels per group with dryness is also very clear. Vessel-element length shows a sharp decrease with increased dryness, as does length of libriform fibers. The decrease of multiseriate ray height increased dryness would be expected because the subdivisions which form short fusiform cambial initials

may be assumed to be accompanied by subdivision in ray initials. Table 1 indicates that this is probably the case, for correlations are good.

Helical sculpturing ("tertiary" helical thickenings) on vessels becomes more abundant with increasing dryness. Storied woods are more abundant among Compositae in desert localities. The number of desert species with rays multiserial exclusively is higher than in the family at large. With regard to ray histology, figures show a greater proportion of procumbent, a lower proportion of erect cells than in the family at large.

Of the anatomical features given in table 1, all appear to be affected by xeromorphy. Increased in storied woods might be more apparent than real, because the storied condition is more readily exhibited when tracheary elements are short, and minimal libriform fiber elongation does not mask the storied condition of fusiform cambial initials. However, the predominance of storied woods in deserts might also connote the tendency of greater wood specialization in desert areas. This latter explanation seems most applicable to the higher proportion of species with rays multiserial exclusively.

Of all factors listed in table 1, rainfall appears to be the most thoroughgoing in its effect on wood anatomy. The physiological advantage of helical sculpture on vessel elements appears to be that of creating greater surface, and therefore more capillarity, in the vessels. Narrower vessels are correlated with more numerous (grouped) vessels in xeromorphic woods. This can be explained similarly. More numerous, narrower vessels offer greater capillarity per unit volume of wood than do few, wide vessels. The presence of vascular tracheids—an extreme form of vessel narrowing—is clearly a feature of xeromorphy. In some annuals, for example, the last elements formed by the cambium as the soil dries are vascular tracheids. These form a terminal band in which narrow vessels and vascular tracheids are often present to the exclusion of libriform fibers. This is also true within growth rings of desert shrubs (e.g., *Artemisia*). The physiological significance of shorter vessel elements might lie in providing more numerous perforation plates, and thus more capillarity, per unit volume. Helical sculpture would seem much more effective in securing greater surface tension, however.

CORRELATIONS WITH LATITUDE

Latitude denotes more than a single factor, such as temperature, uniformity of seasons, or rainfall. Because desert areas are well developed in the temperate zone, and because Compositae in temperate areas often grow in areas with strongly seasonal rainfall patterns, the tropical-temperate contrast may to a large degree be synonymous with differences in rainfall. If correlations with latitude are more striking (e.g., comparative vessel-element length averages) than are rainfall correlations, then latitude must connote more than rainfall, or else the referral of species to rainfall categories was less accurate than referral to latitude classes. The difference between rainfall correlations and latitude correlations is small enough for vessel-element length and other features so that the latter explanation is reasonable. Uniformity of seasons, however, may in some way aid preservation of longer vessel-element length.

Whatever the explanation ultimately might prove to be, temperate Compositae show the following features when compared with tropical ones: nar-

rower, more extensively grouped vessels; shorter vessel elements and libriform fibers; a greater degree of helical sculpturing on vessels and more prominent storying of wood; and multiseriate rays which are less often present to the exclusion of uniseriate rays, are lower, narrower, and show a greater tendency toward procumbency of ray cells. As suggested, none of these expressions run counter to the xeromorphy correlations.

CORRELATIONS WITH HABIT

The categories annual or biennial, caudex perennial, shrub, tree, and rosette tree or rosette shrub were chosen because they represent the most conspicuous life forms within Compositae. "Caudex perennial" is taken to mean a perennial in which a woody base innovates narrow branches each year. The rosette plants denote sparse branching, with large leaves separated by very short internodes and clustered at the tips of branches. Rosette trees have more limited branching and greater height than do rosette shrubs, but these differences appear to be relatively unimportant, so the two are grouped together. Rosette trees in the sense of *Espeletia* and the Afro-alpine species of *Senecio* (section *Dendrosenecio*) have been presented as a quasi-geographical category ("equatorial alpine") which comprehends only the two groups named.

We can logically say that growth forms are not basic selective factors in evolution, they are the products of such forces. Trees, for example, are generally indicators of more mesic conditions in Compositae. Admitting this, there is still utility in computation of data with regard to wood characteristics, for we should know what modal conditions xylem may be expected to exhibit in various growth forms. Several growth forms may be sympatric (e.g., shrub, annual, caudex perennial) in Compositae.

Annuals are generally thought to be the most specialized of growth forms within many families of dicotyledons. There is nothing in the present data to contradict this, because one must remember that the wood of annuals is also the most highly juvenilistic, and thus by means of paedomorphosis (Carlquist, 1962b), characters regarded as somewhat more primitive are expressed. The presence of such features merely reflects that primary xylem is less specialized than secondary xylem in dicotyledons at large, and juvenilism will, of course, favor primary xylem characters. Annuals have the most limited opportunity to achieve adult patterns. For example, vessel-element length and libriform fiber length is greater in annuals than in caudex perennials—but these average lengths are in turn less than those for shrubs, confirming that annuals are more specialized than shrubs.

The low proportion of helical sculpturing on vessels in annuals seems to relate to the fact that most growth of annuals occurs during the wet season. This would also seem to account for the moderate width of vessels (near the average for Compositae as a whole) and the low degree of grouping of vessels in annual Compositae.

Annual Compositae have a very low degree of storying. This is readily understandable because divisions leading to increase in girth of the cambium are a requisite for storying and annuals have only a limited opportunity for such divisions. The same explanation may account for the predominance of erect

cells in multiseriate rays: subdivisions of ray initials leading to formation of procumbent cells requires more time than is available in the life span of many annuals. The low proportion of annuals with multiseriate rays exclusively may relate to juvenilism also.

Caudex perennials seem transitional between annuals and shrubs in some respects: ray histology, grouping of vessels, and storying. In other features, however, xeromorphy not masked by juvenilism seems exhibited: vessel elements are notably short and narrow, and helical sculpture is abundant on vessels. The rays are multiseriate exclusively in a high proportion of species. The fact that juvenilism does not mask such specialized features as these speaks for an advanced position for caudex perennials.

Shrubs have sufficient xylem accumulation so that juvenilism may be considered to have a minimal effect. The fact that vessel elements in shrubs are longer than those of both annuals and perennials would seem interpretable as a relatively unspecialized condition. If longer vessel elements in shrubs as compared to perennials were an indicator of juvenilism, one would expect other indications of juvenilism, such as predominance of erect ray cells. Instead, shrubs have a lower proportion of species with erect ray cells than in other growth forms. Moreover, presence of exclusively multiseriate rays characterizes fewer shrubs than species in other categories. Both features of ray histology suggest that shrubs are less specialized in Compositae than are other growth forms. The proportion of storied wood is fairly high in shrubs, but it is also high in all other growth forms except annuals, which lack storying for reasons indicated above. The fact that shrubs have a rather high degree of vessel aggregation seems understandable in view of the fact that shrubs are adapted to drier situations than trees or rosette trees, and form more secondary xylem during dry seasons than do annuals and perhaps caudex perennials. Vessels are narrower than in trees, but about the same as in annuals and caudex perennials.

Trees show the longest average figure for vessel-element length and libriform-fiber length. They also have the widest vessels, aggregated into the smallest groups. All of these features also characterize mesic and tropical Compositae, and these factors seem in turn related to the tree habit. Helical sculpture, however, is about as abundant on vessels of trees as on vessels of other growth forms.

A high proportion of tree-Compositae have erect ray cells; the proportion of species with procumbent cells is below the average for the family as a whole. Multiseriate rays are tall; this may explain the relatively high proportion of species with rays multiseriate exclusively, for more extensive multiseriate rays are more likely to include uniseriate segments which, if rays were shorter, would be present as independent uniseriate rays. This combination of features suggests paedomorphosis: fewer transverse divisions in the vascular cambium, less break-up of multiseriate rays. This mechanism also seems responsible for longer vessel elements in tree-Compositae. Longer vessel elements are no doubt adaptively linked with mesic conditions, but can be achieved, to a certain extent at least, by protracted juvenilism. Taller rays and tall ray cells seem a side-effect of this juvenilism rather than primary expressions of favorable rainfall conditions.

The anatomical nature of rosette trees and rosette shrubs proves very interesting because they are, as the writer demonstrated earlier (1962b), clear examples of paedomorphosis. Rosette trees and rosette shrubs are indications of lack of strong seasonalism. Notable in these plants are wide vessels, fewer vessels per group, long vessel elements and libriform fibers, and a low degree of helical sculpture on vessels. Multiseriate rays are extremely wide and high. All of these features are expressions of juvenilism, are correlated with mesic climates, and also reflect parenchymatization. Rosette trees and rosette shrubs are not notable for mechanical strength, and can be considered relatively succulent.

CORRELATIONS WITH HABITAT

The contrast between insular and continental Compositae did not prove to be a well-designed one, for reasons stated earlier. The lack of difference between figures for "insular" and "continental" does show that clear statistical differences for other factors (rainfall, latitude, habit) are significant. There are a few differences between the species designated as insular and continental here, however. Insular species have fewer vessels per group (indicative of more moderate insular climates) and more predominantly erect ray cells (corresponding to the rosette-tree habit common on islands).

The equatorial alpine species show the rosette-tree habit most clearly, and suggest how clear correlations could be obtained if "insular" were subdivided into more numerous groupings, defined more restrictively. The equatorial alpine species have exceptionally wide vessels, few per group. Vessel elements and libriform fibers are quite long, and rays are wide and quite high, with a strong tendency toward erect ray cells. These extreme expressions have undoubtedly been achieved by paedomorphosis; the equatorial alpine rosette-trees are generally conceded to have an herbaceous ancestry. That these expressions can be achieved by paedomorphosis is important, since it indicates the capability of paedomorphosis to alter wood anatomy to a considerable extent.

Equatorial alpine species have sufficient xylem accumulation so that storiness should be exhibited, but it is present in a low proportion of the species, suggesting how pervasive juvenilism is in these plants. The low degree of helical sculpture on vessels suggests that the conditions under which equatorial alpine rosette trees grow can be considered uniformly mesic.

SYSTEMATIC CORRELATIONS

Table 1 contains summaries of wood anatomy for the tribes. Numerous differences among tribes are evident. In view of the foregoing considerations, one might suspect that these differences reflect not old, conservative features, but rather the degree to which particular tribes have adapted to certain of the factors listed at the beginning of table 1. This appears to be true. For example, the figures for Cichorieae are remarkably similar to those of rosette trees and rosette shrubs at large; this is the growth form which predominated in the Cichorieae studied. Likewise, most Cynareae studied fall into the category "annual or biennial", and the figures are remarkably similar to those for annual

and biennial Compositae at large. This can be viewed in other ways, in order to confirm the predominant role of the ecological factors in determining the patterns of wood anatomy in Compositae. Noting the decrease in vessel-element length from tropical to temperate, we can arrange several of the tribes in the order of proportion of species which are tropical and compare this arrangement to average vessel-element length within tribes:

TRIBE	PERCENTAGE OF TROPICAL SPECIES IN SAMPLE STUDIED	AVERAGE VESSEL-ELEMENT LENGTH OF TRIBE, μ
Vernonieae	100	321
Mutisieae	73	272
Senecioneae	72	292
Heliantheae	69	255
Eupatorieae	68	287
Cynareae	5	185
Helenieae	0	167

The agreement is not perfect, but very close. Another method would be to compare within one tribe the average vessel-element length of tropical and temperate species. Tropical Senecioneae average 366 μ , whereas temperate ones average 208 μ .

Admitting that characters of tribes are determined, with respect to wood anatomy, by the degree to which each tribe has responded to the ecological factors listed in table 1, these differences may be considered as systematic characters. Other characters, particularly at the generic and species level, are offered by features not listed in table 1: thickness of fiber walls, septate fibers, crystals, etc. The basic plan of wood anatomy appears to be much the same from tribe to tribe. The opportunity for phylogenetic specialization is small because the basic pattern is already so highly specialized. Consequently, conservative characters are few.

Although pedomorphosis occurs in Compositae, it does not mask completely certain of the major trends of xylem evolution. The very short vessel-element length of Helenieae, or of caudex perennials, would seem examples of this. Eupatorieae have a high proportion of species in which uniseriate rays are few or none, and thus may be regarded as more specialized. Senecioneae have a rather high proportion of species with storied wood structure.

The three tribes with relatively unspecialized wood are Vernonieae, Mutisieae, and Heliantheae. The relatively long vessel-element length in these tribes is probably not wholly the result of juvenilism. These three tribes also offer more numerous primitive characteristics with respect to floral morphology and floral anatomy than do the other tribes. The search by various workers for *one* primitive tribe within the family is pointless, for characters, not tribes, are primitive, and among the three tribes mentioned, none has a marked preponderance of primitive characters over the others. Even derived groups can retain some primitive characteristics (e.g., the imbricate involucre in Astereae).

The tendency for elimination of uniseriate rays may, to a certain extent, be linked with juvenilism, because uniseriate rays seem scarcer in woods with very high, wide rays. However, the correlation is not perfect. In any case, two of the

tribes just mentioned, Vernonieae and Mutisieae, have a low proportion of species lacking uniseriate rays.

A SYNOPSIS OF WOOD EVOLUTION IN COMPOSITAE AND ITS BROADER SIGNIFICANCE

BASIC PLAN

Woods of Compositae have vessel elements with simple perforation plates (occasionally multiperforate: see below). Pits on vessels are alternate, often somewhat larger on walls facing parenchyma. Helical sculpture is often present on vessel walls, usually in the form of grooves which interconnect pit apertures adjacent in a helix; and raised bands which usually accompany the grooves. Vessels are solitary or in groups of various extent, including the tendency of vessels to comprise almost the entire axial portion of the xylem (*Loricaria*; *Dimorphotheca*). Radial chains are common, as are tangential bands (especially where growth rings occur). Libriform fibers, but no tracheids or fiber-tracheids are present. Libriform fibers vary from wide to narrow, thin to thick-walled. Fibers are occasionally septate. Vascular tracheids are present in some species, usually intermixed with very narrow vessels in wood of xeromorphic species.

Axial parenchyma is most commonly present in the form of a scanty paratracheal sheath around a vessel or vessel group. This sheath is usually only a single layer thick, and is often incomplete. Occasionally two or three layers of vasicentric parenchyma are present. In no species is paratracheal parenchyma entirely absent. Banded apotracheal parenchyma occurs in some species (chiefly insular ones). This is believed to have been derived from libriform fibers by fiber dimorphism.

Rays are usually both multiseriate and uniseriate, the former almost always more abundant. Species with exclusively multiseriate rays are more common than those with rays uniseriate exclusively (a few Mutisieae). In multiseriate rays, both procumbent and erect ray cells commonly occur. Procumbent cells usually occupy the central portion of a multiseriate ray. Species in which ray cells are erect exclusively are somewhat more common than those in which ray cells are exclusively procumbent. Species in which erect ray cells are nearly as tall as libriform fibers may approximate raylessness (*Artemisia pycnocephala*). Rayless woods occur in the genera *Baeria*, *Chrysactinia*, *Dyssodia*, *Porophyllum*, *Santolina*, and *Stoebe*. In *Santolina*, multiseriate rays are ultimately formed. Ray cells vary from wide to narrow, from thin to thick walled. They may have thin, unligified primary walls, but lignified walls are more common, and walls often bear conspicuous pits.

Storied wood structure is rather common within Compositae. This may take the form of patches of storied fibers, or vessels, or may extend to all elements of the axial xylem. In only a few species (*Brachylaena merana*, *Olearia paniculata*, *Gochnatia* sp.) are rays also storied.

Growth rings are common in the family, but are usually expressed merely as wider vessel elements at the beginning of a growth ring. The composition of axial xylem within a growth ring may shift however. Wider vessels with para-

tracheal parenchyma and libriform fibers in late wood is one such pattern. Interxylary cork rings are an adaptation to extreme dryness in a few species of *Artemisia* and *Tanacetum*; they are storied in all species studied. Growth ring phenomena are more complex in Compositae from xerophytic regions.

Prismatic crystals occur in a few Compositae (*Baccharis*, *Olearia*, *Proustia*, *Eriocephalus*, *Athanasia*). They are usually found in ray parenchyma. Deposits of resin-like materials (presumably less volatile portions of oleoresins) are common in the family. These deposits most frequently take the form of numerous minute droplets in cell lumina of one or more cell types. In some species, deposition is abundant enough to occlude vessels, fibers, or parenchyma cells. In a few species, secretory canals occur in rays (*Ambrosia hispida*, *Artemisia tridentata*, *Hymenoclea salsola*, *Oxytenia acerosa*). Carbonized intercellular resinous deposits characterize some species.

SHIFTS IN WOOD ANATOMY NOT RELATED TO TYPES OF CAMBIAL DIVISIONS

Some of the tendencies toward xeromorphy which emerge from study of Compositae bear no relationship to length of cambial initials. These include width of vessels, the ultimate product of narrowing being imperforate vessels (vascular tracheids). Grouping of vessels increases, as does the number of vessels per unit area of transection. The presence of helical sculpture on vessels seems to bear a close relationship to xeromorphy. These features may be expressed in a constant form within a particular species, but in terms of phylogeny within the family, they are characters which seem eminently reversible. Such reversibility has doubtless given Compositae a plasticity whereby particular ecological conditions can be rapidly and sensitively exploited. The features listed can vary within a growth ring, so that a continual parallel to seasonal events can occur. The ability of helical sculpture to be virtually absent on wide vessels, prominent on narrow vessels within a ring can be demonstrated, for example, in *Artemisia*. Helical sculpture itself exhibits a range within the family: shallow grooves, prominent grooves, grooves accompanied by pairs of fine bands, grooves accompanied by pairs of coarse bands, and very prominent bands between helices of pits (e.g., *Flotovia*) are increasing degrees of expression.

Features in woods of Compositae which seemingly reflect paedomorphosis but which are not related to cambial-initial length include nature of pitting and the presence of multiperforate perforation plates. Scalariform pitting both between adjacent vessels and between vessels and parenchyma cells occurs in a number of Compositae (Carlquist, 1962b). Pits with wide apertures occur in some juvenilistic woods also. Multiperforate perforation plates have been observed in virtually all tribes of Compositae. Although atypical perforation plates may be alterations of normal scalariform plates in some dicotyledons, this does not appear to be the case in Compositae. Perforation plates with network-like bars appear to reflect juvenilism, for such plates seem more common in herbaceous species (e.g., *Cichorieae*), and have been reported in primary xylem of various dicotyledons with frequency (Bierhorst, personal communication). Where near-scalariform plates occur in Compositae, they are often anomalous in position: bars often run tangentially, not radially. If multiperforate plates were vestiges of true scalariform plates in Compositae, one

would expect some vestigial scalariform plates (plates with one or two bars). Such vestigial plates are not present in the family, however. The systematic distribution of multiperforate plates in Compositae is virtually random in nature.

Introduction of apotracheal bands by means of fiber dimorphism (Carlquist, 1958a, 1960c, 1966) may or may not be related to juvenilism. This condition appears closely associated with insular Compositae (*Argyroxiphium*, *Fitchia*, *Hemizonia*, *Psiadia*, *Robinsonia*, *Rhetinodendron*, *Dubautia*, *Hesperomannia*, and insular species of *Artemisia*). Its significance appears related to (1) uniform growing conditions, so that cessation of cambial activity does not occur; (2), lack of strong selection for mechanical elements, e.g., fibers; and (3), parenchymatous tendencies of rosette shrubs and rosette trees. Abundant parenchyma is present in cortex of such trees, so inclusion of abundant interxylary parenchyma bands may be merely an alternative form of parenchymatization.

SHIFTS IN WOOD ANATOMY RELATED TO CHANGE IN LENGTHS OF CAMBIAL INITIALS

Retention of longer cambial initials, little changed from the length of procambial cells giving rise to cambium, is one feature of paedomorphosis (Carlquist, 1962b). Normal woody plants accompany onset of secondary growth by numerous transverse cambial divisions which shorten cambial initials. In herbs, some shrubs, and other types of plants such as stem succulents and rosette trees, only a limited number of such subdivisions occur. A detailed study of how this process occurs has been offered for one species, *Hibiscus lasiocarpus*, by Cumbie (1963).

When the totality of data concerning wood anatomy of Compositae is reviewed, it becomes obvious that a prime source of diversity is created by differences among taxa with respect to frequency and time of initial-shortening divisions in the cambium. In this feature we have a flexible system for influencing length of cambial initials. Xeromorphism can be served by increasing the number of such divisions, and shorter vessel elements and libriform fibers will result. Adjustment to mesic conditions could feature virtual absence of initial-shortening divisions, so that long vessel elements and libriform fibers could be achieved.

Indeed, shifts of this sort would be expected. Viewing the correlations in table 1, we can see shortening of vessel elements from mesic to dry to desert conditions, from tropical to temperate, and from trees to rosette trees to shrubs to annuals to perennials. Does this mean that a strictly unidirectional phylogeny in the sequence indicated has occurred? Not at all. By means of hastened adulthood or prolonged juvenilism, a great variety in potential length of tracheary elements could be achieved by a particular phylad.

By different pace and timing of subdivisions in cambial initials, we can imagine various types of curves (fig. 1) which would achieve various patterns of element length. Some of these curves have been shown to exist by Carlquist (1962b) and Cumbie (1963). The type of curve characteristic of "normal" woody plants was demonstrated earlier by Bailey and Tupper (1918). With additional study, a great variety in curves, such as those indicated as hypothetical in fig. 1, may be discovered in particular species. Another possibility is

speculatively indicated in fig. 1. The starting point for curves is the procambium, and different species, as shown by Bailey and Tupper (1918), may be expected to start from different lengths of procambium cells. While Bailey and his students have shown that in dicotyledons at large, there is a phylogenetic shortening in cambial (and by inference, procambial) cells, is length of procambial cells unexceptionably destined to phylogenetic shortening, or can, in particular species, long procambium cells be achieved? Under some circumstances, a plant may produce exceptionally long procambial cells (sucker shoots, for example). The possibility of change to a "higher starting point" of this sort is indicated in fig. 1. This possibility may be consistent with the theory of irreversibility of vessel-element shortening and features statistically associated with it (the "major trends of xylem evolution"). However, paedomorphosis alone could achieve such a broad range in cambial initial length that it could indeed account for some of the flexibility which Bailey (1944) noted does exist in dicotyledonous woods. The theory of paedomorphosis can be fitted within the concept of irreversibility of the major trends of xylem evolution very easily (Carlquist, 1962b).

If, by paedomorphosis, fusiform cambial initials fail to subdivide, or only a few subdivide, the same tendency would be expected within a given species with respect to ray initials, as well. As seen in table 1, there is good agreement between trends in vessel-element length and, for example, percentage of species with erect ray cells either exclusively or in combination with procumbent cells. This agreement validates the idea that paedomorphosis affects length not only of fusiform initials, but of ray initials at the same time.

As a footnote, the conditions which promote raylessness may be examined. The average vessel-element length for all rayless Compositae is 201 μ , and this figure is relatively short with reference to the family as a whole. If a species had short vessel elements and libriform fibers, but tall ray cells, the tall ray cells would mimic libriform fibers and a rayless condition would result. In what sort of plant would this be most likely to occur? The most likely answer seems to be a plant in which phylogenetic shortening of fusiform cambial initials has proceeded rather far, but which also is so strongly affected by paedomorphosis that very tall ray initials are formed. The types of plants, according to the results of table 1, which would satisfy this description are herbs. For example, *Baeria macrantha*, being an annual, has very specialized xylem which features very short tracheary elements (derived from short fusiform cambial initials). If paedomorphosis occurs, the fusiform initials would not be shortened, but neither would ray initials, permitting the lengths of the two types of cells to be roughly equal for prolonged periods of secondary growth.

The tendency for introduction of more parenchyma tissue into wood of certain groups of Compositae might be considered juvenilistic. If primary rays are wide and tall, paedomorphosis would alter this condition little.

PHYLOGENY OF GROWTH FORMS WITHIN COMPOSITAE

We have seen that wood anatomy is intimately related to growth form, and we can reasonably expect that some inferences regarding phylogeny of growth forms might be obtained.

An ancestral group of Compositae would be expected to have relatively primitive ray conformation, i.e., both multiseriate and uniseriate rays. Minimal paedomorphosis would be expected of ancestral Compositae, for protracted juvenilism seems more likely to occur sporadically in a group than to be basic in the origin of major groups. If this assumption is warranted, minimal paedomorphosis would be expected not only in tracheary elements, but in rays as well. Thus, vessel-element length or libriform-fiber length approximately

Fig. 1. Patterns of change in vessel-element length during growth. Although vessel-element length is indicated, similar curves could be drawn for libriform fibers or other cell types controlled by length of cambial initials. Phylogenetic shortening according to the major trends of xylem evolution will produce the change from curve I to curve II in normal woody plants. If paedomorphosis is superimposed upon a plant with procambium-cell length like that which begins curve I, the types of curves designated A-C might be formed (B and C have been observed). Similar curves showing paedomorphosis could be drawn at lower levels, such as that of curve II, and such curves could be the result of phyletic change from a plant possessing the paedomorphosis curves shown or from a plant having curve II. Curve III would normally be expected in a more primitive species, and ordinarily phyletic change would yield plants with curves I or II. A possibility exists that occasionally increase in length of procambium might occur, so that the change from I to III is a hypothetical possibility.

median for the family would be expected; rays should be relatively short, and should consist of both procumbent and erect cells. Exceptionally short tracheary elements would be expected to result from great phylogenetic specialization, and thus a median length seems more likely.

According to table 1, only one growth form conforms to these criteria: shrubs. Shrubby Compositae have the lowest proportion of species in which rays are multiseriate exclusively, and the lowest proportion of species in which erect cells are present (either exclusively or in combination with procumbent cells). Vessel elements approximate the median figure for Compositae. Narrowness of rays in shrubs suggests lack of paedomorphosis also.

Cronquist (1955) claimed the herbaceous habit to be primitive for Compositae. His reasons for this are not confirmed by my studies. Cronquist's citation of anomalous secondary growth in Inuleae or the rosette-tree habit of Afro-alpine *Senecios* seems inadvisable, because these are exceptional types which shed no light on the basic nature of the family. His statement that "the woody types that have been studied do not resemble each other anatomically" is not supported by my studies, nor would it be supported by Metcalfe and Chalk (1950), although this situation is not explicitly described by Metcalfe and Chalk. Actually, the uniformity in basic plan of wood anatomy of Compositae is revealed abundantly and repeatedly throughout the family. A shrubby ancestry for the family can be defended easily without reference to plant anatomy, but the data of the present study offer an independent line of support.

The fact that annuals and biennials have a vessel-element length longer than that of caudex perennials suggests paedomorphosis, as does the strong tendency toward erectness of ray cells in annuals and biennials. Very short vessel elements in perennials suggests phylogenetic shortening; an element length longer than in annuals would be expected except for the fact that greater xylem accumulation in perennials lessens the juvenilism likely to be shown. Annuals and biennials would appear a poor ancestral form on other grounds. Cynareae and Cichorieae are groups which have been unable to achieve any truly woody forms, probably because they stem from ancestors in which the ability to form unlimited secondary xylem had already been lost. The paucity of growth forms in Cichorieae and Cynareae, therefore, is probably what we would expect in Compositae as a whole had an annual or biennial been basic to the family. The anatomical features of caudex perennials, judging from table 1, mark them as much more likely to have been derived from shrubby species than to have given rise to shrubs. For example, the exceptionally short vessel-element length suggests an end-product of phylogenetic shortening; ray structure of perennials suggests more juvenilism than does that of shrubs.

Trees seem very likely to have been derived from shrubs in Compositae. Longer vessel elements and libriform fibers in trees could suggest greater primitiveness, but such an interpretation is clearly countered by the presence of juvenilistic features: a high proportion of species with erect ray cells, either erect exclusively or in combination with procumbent cells; relatively wide rays. Tree-Compositae have a high proportion of species with a character which may be regarded as phylogenetically highly specialized, or possibly indicative of paedomorphosis: rays multiseriate exclusively. The fact that islands such as

St. Helena have a higher proportion of tree-Compositae than do continental areas suggests that original immigrants to islands were shrubby, and that increase in arborescence is acquired on islands. This trend on islands has been accepted by workers from Charles Darwin to the present, and can be demonstrated in particular genera, such as *Fitchia*, *Dubautia*, and *Scalesia*. Moreover, tree-Compositae do not belong predominantly to primitive tribes. Among the most spectacular instances of arboreal Compositae are *Bedfordia* (Senecioneae), *Brachyglottis* (Senecioneae), *Brachylaena* (Inuleae), *Olearia* (Astereae), *Senecio* (certain species), and *Tessaria* (Inuleae). Although some tree-composites appear to be primitive in many respects (*Stenopadus*, *Fitchia*), others do not. On the basis of all characters, some arboreal species do not appear to be primitive within their respective tribes at all.

Rosette trees and rosette shrubs are excellent examples of paedomorphosis. One can cite in this regard the strong tendency toward erectness of ray cells, a fact demonstrated in heightened form by the equatorial-alpine rosette trees. These rosette trees also have very high, wide rays. The very long vessel elements in equatorial-alpine rosette trees can only be interpreted as a result of paedomorphosis. Statistical survey alone cannot give much information about which of the other growth forms has given rise to rosette shrubs and rosette trees. In fact, the likelihood seems very great that in Compositae, rosette trees or rosette shrubs have originated from more than one type of ancestor. The more succulent rosette trees, capable of only limited secondary growth, probably originated from more nearly herbaceous ancestors. Other quite woody rosette trees and rosette shrubs might have been derived from shrubs.

The above considerations suggest that a flexible system of wood anatomy has accompanied Compositae in their adaptation to a wide diversity of growth forms. Shrubs seem, for various reasons, more likely to be the ancestral form within the family Compositae. We must not be misled by a supposition that because woody species are primitive, the most woody growth form (trees) is ancestral within a group. In many dicotyledonous families, trees do appear to be primitive. There is no reason to believe in an inflexible tree-to-herb phylysis within all families, however. My studies on Compositae have led me to believe that a wide degree of plasticity is retained within many portions of the family. Some groups of herbs may be unable to regain woodiness, but conversion of shrubs into trees, or into herbs, seems highly probable.

Other families of dicotyledons may retain such plasticity also. One suspects that in highly specialized families where a few arboreal species have originated, tree forms may be secondary. The starting-point for arborescence would, however, be expected to be woody. Families which would appear to suit this description include Scrophulariaceae, Labiatae, Solanaceae, Hydrophyllaceae, and perhaps many others. Examination of wood in such families should be undertaken to reveal if patterns similar to those in Compositae occur, and whether paedomorphosis is a mechanism whereby growth forms and wood anatomy can be altered. I would like to stress that growth forms such as *Espeletia*, which are in their external appearance highly suggestive of juvenility, are by no means the only growth forms in which one may expect wood anatomy to reveal evidences of paedomorphosis.

Wood anatomy seems important in analysis of how a group adapts to various

ecological situations, and which factors are most influential in inducing change of wood. Data from Compositae were not originally planned to answer these questions. Although the results obtained here seem acceptable as a beginning, more refined design of investigations would undoubtedly reveal more significant correlations, and permit less equivocal statements. The broad outlines of the major trends of xylem evolution have become well established, thanks to the work of Bailey, Frost, Kribs, Barghoorn, and Cheadle. Studies on which factors in the environment of a plant influence these trends of wood evolution, and how, can now usefully be pursued. Ultimately, our understanding of wood anatomy must incorporate concepts of ecology and physiology. Although such a synthesis may be difficult and time-consuming, it seems a very rewarding enterprise.

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