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WOOD ANATOMY OF SENECEONEAE (COMPOSITAE)

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INTRODUCTION

The tribe Senecioneae contains the largest genus of flowering plants, *Senecio* (between 1,000 and 2,000 species). Senecioneae also encompasses a number of other genera. Many species of *Senecio*, as well as species of certain other senecionean genera, are woody, despite the abundance of herbaceous Senecioneae in the North Temperate Zone. Among woody species of Senecioneae, a wide variety of growth forms is represented. Most notable are the peculiar rosette trees of alpine Africa, the subgenus *Dendrosenecio* of *Senecio*. These are represented in the present study of *S. aberdaricus* (dubiously separable from *S. batescombei* according to Hedberg, 1957), *S. adnivalis*, *S. cottonii*, and *S. johnstonii*. The *Dendrosenecios* have been discussed with respect to taxonomy and distribution by Hauman (1935) and Hedberg (1957). Cotton (1944) has considered the relationship between ecology and growth form of the *Dendrosenecios*, and anatomical data have been furnished by Hare (1940) and Hauman (1935), but these authors furnish little information on wood anatomy. Interestingly, the same rosette-tree habit of growth occurs in the Mexican species *Senecio praecox*, which belongs in another section of the genus. This species has been studied morphologically and anatomically by Reiche (1921).

Many of the woody Senecioneae fall in the category of small trees or various-sized shrubs. These include *Senecio mannii* of West Africa and *S. multicorymbosus* of Angola. *Senecio ecuadoriensis* (northwestern South America), *S. petasioides* (South America), *S. picridis* (Mexico), *S. rivalis* (Cuba) and *S. salignus* (Mexico) are also shrubby to arborescent. Among the other genera, bushy or tree-like plants represented in this study include species of *Gynoxys* (Ecuador, Colombia), *Liabum* (Mexico, Central America, northern South America), and *Neurolaena* (Mexico, Central America).

The genus *Mikania* is composed of twining or vine-like plants. The species included in the present study, *M. cordifolia*, like other South American species, has considerable accumulation of secondary xylem and may be considered a small liana.

The tendency of Compositae to be represented on oceanic islands by woody species is well demonstrated by Senecioneae. *Senecio leucadendron* (which has also been regarded under the segregate genera *Pladaroxylon* and *Lachanodes*) is an arborescent endemic of St. Helena Island. *Faujasia* is a shrubby genus characteristic of the Mascarene islands Mauritius and Reunion. On the Juan Fernandez Islands, the endemic genera *Robinsonia*, *Rhetinodendron* and *Symphyochaeta* occur as curious rosette shrubs. The taxonomy of these genera follows that given by Skottsberg (1922, 1951); additional data and illustrations are given by Skottsberg (1922, 1953) and Kunkel (1957). *Brachyglottis* is a small tree from New Zealand (Hooker, 1867). Various species of *Senecio* in New Zealand are shrubby (Hooker, 1867). Those included in the present study are *S. eleagnifolius*, *S. huntii* (a Chatham Island endemic), and *S. kirkii*. *Senecio palmeri* is a prostrate shrub restricted to Guadalupe I., Mexico.

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The shrubby habit characteristic of desert and chaparral plants of the southwestern United States is also found in Senecioneae. *Peucephyllum* is a fountain-shaped shrub of the California deserts. The genus *Tetradymia* forms wiry, thorn-bearing shrubs, branched from the base, in deserts of the southwestern United States. *Senecio douglasii* is a common weedy shrub of dry chaparral areas in the Coast Ranges of southern and central California.

Many herbaceous Senecioneae are capable, under suitable conditions, of accumulating considerable secondary xylem. The specimen of *Erechtites hieracifolia* was collected in the Hawaiian Islands, where it is an introduced weed. The particular plant collected was about six feet tall during flowering (which terminated the life of the plant). This plant suggests that a more woody habit can be achieved by herbs when uniform conditions typical of some oceanic islands (and other localities) release them from seasonal cycles of growth. *Erechtites hieracifolia* is normally a small, short-lived annual in temperate climates.

The above example suggests that a large number of species, both in *Senecio* and in the other genera, could have provided sufficient secondary xylem for study. The number of species studied could have been expanded almost indefinitely, if intensive representation of members of the tribe had been desired, and if facilities and time for collecting had been available. The purpose of this series of papers on wood anatomy of Compositae, however, is a survey of woods of the family, and a construction of modes of evolution of wood in this highly-evolved family. The species actually studied here represent a wide variety in wood structure, perhaps as great a gamut as could have been secured by study of a larger number of Senecioneae. The variety of wood structure demonstrated here, however, suggests that intensive study of wood anatomy of particular groups of Senecioneae would be important.

MATERIALS, METHODS AND ACKNOWLEDGMENTS

Woods were sectioned according to techniques described earlier (Carlquist, 1958). Wood samples were from larger trunks or branches except for *Rhetinodendron berterii* and *Robinsonia gayana*. The specimen of *Senecio aberdaricus* had less than a centimeter of secondary xylem accumulation. Wood samples were obtained from various sources. Most important were the samples sent to me by Dr. William L. Stern from the Samuel J. Record Collection of Yale University during Dr. Stern's association with that institution. Dr. Carl Skottsberg provided wood samples of Juan Fernandez Senecioneae. Dr. Olov Hedberg furnished wood samples of several of the African Dendrosenecios. Some samples were obtained from the wood collections of the Arnold Arboretum of Harvard University through the good offices of Dr. I. W. Bailey. The kindness of these individuals in contributing materials for this study is gratefully acknowledged. Additional wood samples were collected by the writer from localities in southern California. In table 1, institutional accession numbers of wood samples are given, with abbreviations according to Stern and Chambers (1960). Voucher specimens, if known, are also listed in table 1, together with herbarium abbreviations according to Lanjouw and Stafleu (1959).

Many of the sections were prepared by Mr. Charles F. Quibell, Mr. Alfred G. Diboll, and Mr. Loran C. Anderson. In the photographs illustrating this paper, transections are shown with the most recently-formed elements above, except for fig. 9 and fig. 36, where more recent elements are at right. Collection numbers of samples are not indicated in legends because they are given in the table; where more than one wood sample of a species was studied, collection number of the illustrated specimen is given in the legend.

ANATOMICAL DESCRIPTIONS

Table 1 contains a summary of qualitative and quantitative features, much the same as those given in earlier papers on wood anatomy of Compositae by the writer. These features appear best to express differences as well as similarities among the taxa of Senecioneae studied. Those characters which cannot be expressed conveniently in chart form are discussed below under the appropriate headings. Absence of a figure (uniseriate rays) indi-

cates that few or no such structures are present. The column labelled "Elements distinguishing rings" indicates the elements in early wood which differ from those in late wood. These features are discussed further below under "Growth Rings."

Explanation of symbols in table 1:

- bp = banded parenchyma
- cb = coarse bands on vessel walls (helical thickenings)
- cg = continuous grooves (grooves interconnecting many pits in a helix on a vessel wall)
- f = libriform fibers
- fb = fine bands on vessel walls (helical thickenings)
- ff = a few, or some, libriform fibers
- g = grooves interconnecting two or several pits in a helix on a vessel wall
- mv = more numerous vessels
- p = axial parenchyma
- r = some rays
- tf = thin-walled libriform fibers
- v = vessel elements
- vt = vascular tracheids
- wv = wider vessels
- + = presence of characteristic
- = presence of characteristic to a limited extent
- 0 = absence of characteristic
- ? = impossible to measure

VESSELS

Dimensions, shapes, types.—As table 1 indicates, the range in size of vessel elements in Senecioneae is wide. Exceptionally small vessel elements, both with respect to diameter and length, occur in *Peucephyllum schottii* (fig. 1, 2), *Tetradymia argyraea* (fig. 3, 4) and other species of *Tetradymia*. The small average dimensions of vessel elements in these two genera is probably related to the xeric habitats in which these two genera have evolved. Reduction in vessel diameter at the end of growth rings in *Tetradymia* is extreme (fig. 3), and some of the late-wood vessels are imperforate (vascular tracheids). Confirmation of relation between small vessel elements and dry environments may be suggested by vessel dimensions in the chaparral shrub *Senecio douglasii*. Other Senecioneae which have an average vessel diameter of less than 30 microns include species from drier areas of Mexico and South America, such as *Senecio palmeri* (fig. 26, 27), *S. picridis* (fig. 28, 29), *S. salignus*, and *S. ecuadoriensis* (fig. 30, 31). These species of *Senecio* could also be said to have relatively short vessel elements.

The relatively small dimensions of vessels of *Robinsonia gayana*, as compared with other species of *Robinsonia*, is probably related to the fact that only a twig was available for study. The narrow diameter and short length of vessel elements in the Juan Fernandez genera *Rhetinodendron*, *Robinsonia*, and *Symphyochaeta* is readily apparent, however. Because the habitat of these species could not be considered a xeric one, the small vessel-element size of this group of genera is a characteristic which must be explained in some other way.

At the opposite extreme of vessel-element size, the very long vessel elements of "*Faujasia blixana*" deserve mention. Relatively long vessel elements also characterize *Gynoxys verrucosa* var. *grandifolia* (fig. 11) and other species of *Gynoxys* except *G. florulenta*. Long vessel elements are characteristic of all the species of *Liabum*, such as *L. bonplandii* (fig. 6) and *L. pichinchense* (fig. 8) and all the species of *Neurolaena* studied, such as *N. lobata* (fig. 23). The length of vessel elements in the *Dendrosenecios* is above average for the

TABLE 1. *Wood Characteristics of Senecioneae*

SPECIES	COLLECTION	DIAMETER WIDEST VESSEL, μ	DIAMETER VESSELS, AVERAGE, μ
<i>Brachyglottis repanda</i> Forst.	Aw-2614	65	45.0
<i>Erechtites hieracifolia</i> Raf.	Carlquist 511 (RSA)	119	63.7
" <i>Faujasia blixand</i> "	Imper. For. Inst. 1174, Yw-32090	76	58.2
<i>Gynoxys florulenta</i> Cuatr.	Cuatrecasas 20148 (Y), Yw-44417	108	82.6
<i>Gynoxys ballii</i> Hieron.	Rimbach 788 (Y), Yw-32978	140	69.7
<i>Gynoxys indurata</i> Cuatr.	Cuatrecasas 20546 (Y), Yw-44429	151	110.1
<i>Gynoxys verrucosa</i> var. <i>grandifolia</i> Cuatr.	Cuatrecasas 20615 (Y), Yw-44445	162	108.1
<i>Liabum bonplandii</i> Cass.	Rimbach 797 (Y), Yw-32977	110	62.0
<i>Liabum klattii</i> Rob. & Greenm.	R. King 2499 (TEX)	140	105.8
<i>Liabum pichinchense</i> Hieron.	Rimbach 783 (Y), Yw-32975	302	154.8
<i>Mikania cordifolia</i> (L.E.) Willd.	Rimbach 854 (Y), Yw-34199	270	65.5
<i>Neurolaena lobata</i> (Sw.) R. Br.	Cuatrecasas 14975 (Y), Yw-42819	86	60.5
<i>Neurolaena macrophylla</i> Greenm.	Skutch 2055 (A)	130	70.6
<i>Peucephyllum schottii</i> A. Gray	C. B. Wolf 2890 (RSA)	86	36.9
<i>Rhetinodendron berterii</i> Hemsl.	Bertero V-1830 (GH)	63	34.8
<i>Robinsonia evenia</i> Phil.	Yw-27425	108	56.3
<i>Robinsonia gayana</i> Dcne.	Skottsberg III-9-1955 (SBT)	65	22.9
<i>Robinsonia thurifera</i> Dcne.	Skottsberg III-9-1955 (SBT)	75	46.1
<i>Senecio aberdareicus</i> R. E. Bro. & Th. Fr. jr.	O. Hedberg 1593 (UPS et al.)	119	55.6
<i>Senecio adnivalis</i> Stapf	Aw-1939	108	68.0
<i>Senecio adnivalis</i> Stapf	O. Hedberg 708 (UPS et al.)	86	62.6
<i>Senecio cottonii</i> Hutchins. & G. Taylor	Goodwin 70 (A), Aw-23715	119	91.3
<i>Senecio douglasii</i> DC.	Carlquist 490 (RSA)	108	37.5
<i>Senecio douglasii</i> DC.	Carlquist 620 (RSA)	65	36.4
<i>Senecio ecuadoriensis</i> Hieron.	Rimbach 155 (Y), Yw-24094	54	22.8
<i>Senecio elegnifolius</i> Hook.	Sinnott & Eames s.n. (A), Aw-20678	49	16.2
<i>Senecio huntii</i> F. Muell.	Aw-1873	70	43.1
<i>Senecio johnstonii</i> Oliv.	Schlieben s.n., Yw-29404	130	84.0
<i>Senecio kirkii</i> Hook. f. ex T. Kirk	Hambling 29, RSAw	76	43.8
<i>Senecio leucadendron</i> Benth. & Hook.	Aw-1868	108	61.9
<i>Senecio mannii</i> Hook. f.	Metcalfe s.n., Yw-34537	162	110.6
<i>Senecio multicorymbosus</i> Klatt	Schlieben 4308, Yw-29384	173	108.0
<i>Senecio multicorymbosus</i> Klatt	Goodwin 80, Aw-20691	130	87.5
<i>Senecio palmeri</i> A. Gray	Carlquist 260 (RSA)	65	27.8
<i>Senecio petasioideus</i> Greenm.	Edwards 179, Aw-20691	108	55.7
<i>Senecio petasitis</i> DC.	Carlquist 499 (RSA)	75	46.8
<i>Senecio pircridis</i> Schauer	D. Wiens 2577 (RSA)	54	23.2
<i>Senecio praecox</i> DC.	R. King 2530 (TEX)	119	85.5
<i>Senecio rivalis</i> Greenm.	Yw-40048	76	50.2
<i>Senecio salignus</i> DC.	R. King 2636 (TEX)	56	27.5
<i>Symphphyochaeta macrocephala</i> (Dcne.) Skottsbg.	Skottsberg XII-13-1916 (GB)	59	33.5
<i>Tetradymia argyraea</i> Munz & Roos	Everett & Balls 23895 (RSA)	56	18.8
<i>Tetradymia axillaris</i> Nels.	Balls & Everett 23197 (RSA)	65	18.9
<i>Tetradymia glabrata</i> A. Gray	Carlquist 434 (RSA)	59	17.2
<i>Tetradymia stenolepis</i> Greene	Carlquist 432 (RSA)	84	19.5

TABLE 1. *Wood Characteristics of Senecioneae*

VESSELS PER GROUP, AVERAGE	LENGTH VESSEL ELEMENTS, AVERAGE, μ	LENGTH LIBRIFORM FIBERS, AVERAGE, μ	MAXIMUM WIDTH LIBRIFORM FIBERS, AVERAGE, μ	WALL THICKNESS FIBERS, μ	PIT DIAMETER, μ	HELICAL SCULPTURE ON VESSELS	ELEMENTS DISTINGUISHING RINGS	STORIED ELEMENTS	HEIGHT MULTISERiate RAYS, AVERAGE, MM.	HEIGHT UNISERiate RAYS, AVERAGE, μ	MAXIMUM WIDTH MULTISERiate RAYS, AVERAGE, CELLS	RAY CELLS ISODIAMETRIC TO PROCUMBENT	RAY CELLS ISODIAMETRIC TO ERECT
1.57	280	432	16.7	2-3	4			f, p, v	1.17		4.8	0	+
2.64	243	464	15.6	1-3	4				2.19		11.9	0	+
1.40	713	906	21.9	5	3				.49		4.3	+	0
2.10	326	426	32.8	4	3	g, cg		ff	1.11		4.2	+	+
2.00	445	713	27.2	2-4	4	g	wv, tf	ff	> 10		4.7	0	+
1.27	404	583	32.8	3	5			f, p, v	.65	100.4	3.2	+	+
2.60	420	615	38.0	4-5	6			ff	.53	152.7	3.8	+	+
2.22	322	442	23.0	2-3	3	g	wv	f	> 10		5.3	-	+
1.41	463	617	39.2	2-4	6		wv, tf	f, p, v	> 10		6.5	0	+
3.30	540	716	27.8	2-4	6				> 10		10.4	+	+
6.17	230	296	29.3	3	6			f, p, v	> 10		.4	+	0
1.68	412	707	36.3	2	4	g			> 5		6.2	0	+
1.32	456	640	34.7	2-3	5	g		ff	> 10		7.8	0	+
2.83	141	255	22.1	5	4	g	wv		.66		8.6	+	+
3.29	208	299	28.7	3-4	4		wv, f	ff, bp, v	> 5		4.3	-	+
1.78	245	356	32.5	3	3		wv, f	f, bp, v	.41	105.6	3.1	-	+
2.55	176	248	16.1	3	3		wv, f	ff	.64		4.8	-	+
2.05	292	428	26.8	3	4		bp	ff, bp, v	1.09		4.1	-	+
3.38	317	464	35.4	5	6				> 5		3.8	+	+
1.88	330	563	55.2	4-5	5				.91	140.7	5.3	+	+
2.25	247	495	53.6	4-5	5				1.13	108.5	6.1	+	+
1.58	270	458	44.0	4-5	5			ff	1.33		6.2	+	+
1- ∞	154	259	31.2	4-5	4		wv		2.32	69.6	5.3	+	+
1.96	190	297	25.3	4	3				2.59	54.2	5.8	-	+
∞	260	330	25.0	3-5	5	cb	wv	f, p, v, r	1.22		9.3	+	+
1- ∞	258	339	28.4	5	4	g, fb	wv	f, p, v, r	.25	157	2.1	+	+
5.33	205	283	27.5	4	5	cb	wv	f, p, v	.35	71.8	5.3	+	+
1.77	353	495	32.7	3-4	6				.88		6.3	+	+
3.92	281	326	41.3	4-5	4	g, fb	bp, wv	f, p, v	.80		4.3	-	+
2.20	356	457	28.2	4	4	g			1.50		7.7	+	+
1.16	427	678	33.0	3	8				2.80		4.6	0	+
1.40	397	606	31.9	2-4	7		wv, tf	ff	2.61		6.2	+	+
1.62	408	529	25.0	2-3	7		wv, tf		4.34		5.3	-	+
1- ∞	209	335	32.8	4-6	3		wv		2.27	77.5	4.5	0	+
2.08	495	712	26.7	2-3	4			ff	> 10		3.9	0	+
2.93	340	567	27.5	2-3	4		mv, f	bp, ff	> 10		7.3	0	+
1- ∞	266	457	27.2	3	5		wv		2.37		4.7	+	+
1.70	224	338	45.2	1-3	5		bp	bp, f, v	.82		5.8	+	+
5.15	405	734	36.0	7	2		bp		1.06	118.8	2.6	+	+
3.51	211	367	21.0	2-3	5			f, p, v	.97		4.0	-	+
1.79	292	306	22.6	3-4	3	g	bp	ff, bp, v	4.80		3.5	+	+
1- ∞	114	198	16.0	3-5	6	cb	wv	v, vt	1.24		4.6	+	-
1- ∞	152	248	15.6	3-5	5	fb, cg	wv	v, vt	1.42		2.8	0	+
1- ∞	199	292	19.0	3-5	5	cb	wv	v, vt	1.36		4.2	+	+
1- ∞	162	302	15.0	3-5	6	fb, cg	wv	v, vt	1.51		3.8	+	+

tribe, as shown here by *S. adnivalis* (fig. 13) and *S. johnstonii* (fig. 15). Other *Senecios* with relatively long vessel elements include *S. mannii* (fig. 19), *S. multicorymbosus* (fig. 17), *S. petasioides* and *S. rivalis*. The fact that relatively long vessel elements occur in such specialized woods as these is interesting, and is not easily explained.

If an average vessel diameter of more than 60 microns is taken to indicate relatively wide (for *Compositae*, at least) vessels, one may say that wide vessels characterize *Gynoxys verrucosa* var. *grandifolia* and other species of *Gynoxys*, *Liabum bonplandii* (fig. 5) *L. klattii*, *L. pichinchense* (fig. 7) and the species of *Neurolaena* (viz, fig. 22). All of the *Dendrosenecios*, such as *S. adnivalis* (fig. 12) and *S. johnstonii* (fig. 14) have wide vessels, as do *S. mannii* (fig. 18), *S. multicorymbosus* (fig. 16), *S. praecox* (fig. 20), and *S. leucadendron*. Interestingly, the species mentioned in this paragraph are nearly the same as those mentioned as having rather long (for *Compositae*) vessel elements.

Other species with notably wide vessels include *Mikania cordifolia* (fig. 9). In this species, some of the larger vessel elements are, in fact, wider than they are long. This is not surprising, considering the twining habit of the plant. In *Mikania cordifolia*, many of the exceptionally wide vessels are surrounded by narrower vessels, a fact reported for *Mikania* by Metcalfe and Chalk (1950). The two species of *Liabum* illustrated differ markedly in vessel diameter, seemingly a taxonomic characteristic here: *L. bonplandii* (fig. 5) has vessels much narrower than those in *L. pichinchense* (fig. 7).

With respect to shape, the tendency of some vessels to be somewhat caudate was apparent in *Rhettinodendron berterii*, *Robinsonia gayana*, and *Senecio picridis*. Vessel elements in "*Faujasia blixana*" were observed to be frequently and markedly caudate. Vessel elements in *Symphyochaeta macrocephala* (fig. 39) have rather oblique end walls. Various oblique end walls are not uncommon in *Senecioneae*. *Mikania cordifolia*, however, has markedly transverse end walls.

Perforation Plates.—*Compositae* are characterized by simple perforation plates. However, a number of *compositae* have been reported to possess multiperforate perforation plates. These may be highly distorted structures, as in some *Cichorieae* (Carlquist, 1960), or nearly scalariform. The *Senecioneae* which have multiperforate plates conform to the latter type. They may have few bars, as in "*Faujasia blixana*" (fig. 48), or many, where vessels are wider, as in *Liabum klattii*. One or more multiperforate plates were observed in *Brachyglottis repanda*, "*Faujasia blixana*", *Liabum klattii*, *Senecio eleagnifolius*, *S. huntii*, *S. mannii*, *S. multicorymbosus*, *S. petasioides*, *S. praecox*, and *S. rivalis*. Exhaustive observations could probably add other species of *Senecioneae* to this list. No explanation can at present be offered for the relatively frequent occurrence of multiperforate plates in a family which characteristically has simple plates, and no evidence of stages in phylogenetic reduction to this type (e.g., bars with one or two plates occurring occasionally).

Lateral-Wall Pitting.—The occurrence of circular bordered pits, alternate in arrangement, with near-transverse apertures, and with an average pit cavity diameter of three to five microns is typical in *Compositae* and in most *Senecioneae*. Deviations from this type are discussed here, therefore. Unless otherwise noted, figures and data refer to intervascular pitting. Relatively large pits (5 microns or larger) characterize the *Dendrosenecios* and *Tetradymia*. Pits of this size are also found in *Gynoxys verrucosa* var. *grandifolia*, *Liabum klattii*, *L. pichinchense*, *Senecio multicorymbosus*, and *S. rivalis*. The largest pits observed were those of *S. mannii* (fig. 45).

In some of the *Senecioneae* studied here, pits are crowded, so that the outline of the pit cavities is angular, and forms a honeycomb-like appearance. This was illustrated for *Hymenoclea salsola* (Carlquist, 1958, fig. 31), and is shown here for *Senecio praecox* (fig. 44) and *S. mannii* (fig. 45). Other species in which this condition was observed include *S. multicorymbosus* and *S. aberdaricus*.

Horizontal elongation of pits is not at all unusual in *Senecioneae*. Species in which pits

oval in outline in this manner were observed are *Liabum pichinchense*, *Senecio kirkii*, *S. leucadendron*, *S. multicorymbosus* and *S. petasitis*. A more pronounced condition, in which

Fig. 1-4. Fig. 1-2. *Peucephyllum schottii*.—Fig. 1. Transection; note grouping of vessels.—Fig. 2. Tangential section. Note wide rays, tortuous course of vessels and fibers.—Fig. 3-4. *Tetradymia argyraea*.—Fig. 3. Transection. About six growth rings are shown; large vessels in early wood, narrow vessels and vascular tracheids in late wood.—Fig. 4. Tangential section. Ray cells are relatively thick-walled, vessel elements and vascular tracheids stored. All, $\times 65$.

pits are markedly elongate horizontally, and thus form a nearly scalariform condition on vessel walls, is present in a few Senecioneae. *Senecio praecox* (fig. 43, 44) shows this condition clearly, and ordinary circular pitting is less common than a scalariform-like condition in this species. Some pitting of this nature is also present in *Senecio leucadendron*, *S. mannii* (fig. 45), *S. multicorymbosus*, all of the Dendrosenecios studied, and *Symphyochoaeta macrocephala*. Scalariform-like intervacular pitting has been reported earlier in a number of Compositae (Carlquist 1957, 1958, 1960a). The explanation previously offered for this phenomenon (Carlquist, 1958), namely, that it represents primary xylem pitting carried over into secondary xylem, still seems valid.

A peculiarity shown by a number of Senecioneae is the occurrence of pits in which the aperture is widened, forming a broad ellipse instead of a narrow slit. This may be regarded as a reduction of the pit border. Such pits were observed in all of the species of *Gynoxys* and *Liabum*, as well as in the Dendrosenecios studied (*S. aberdaricus*, *S. adnivalis*, *S. cottonii*, and *S. johnstonii*) as well as *Senecio mannii*. The phylogenetic or ecological interpretation of this phenomenon is not clear at present.

Another type of pit, that in which the pit aperture is nearly circular in outline, and thus like a pit of a gymnosperm tracheid, was observed in *Senecio picridis*.

Helical Sculpture.—As the column headed "Helical sculpture on vessels" in table 1 illustrates, Senecioneae possess two main types, grooves which connect only two or several pits ("g"), or form a continuous groove around the vessel wall ("cg"), and bands which are fine ("fb") and usually occur as a pair of thickenings accompanying a continuous groove, or coarse bands ("cb"), which are probably derived from the finer bands phylogenetically (Carlquist, 1958). Bands are probably characteristic of plants of drier habitats, and their occurrence in *Senecio ecuadoriensis*, *S. eleagnifolius*, *S. huntii*, *S. kirkii* and all of the species of *Tetradymia* (viz, fig. 46) seems to confirm this. Abundance of bands in Astereae (Carlquist, 1960b) is probably related to the frequency of this tribe in drier regions. Because many of the Senecioneae studied here do not grow in xeric habitats, a lower frequency of helical thickenings in vessels in this tribe would be expected.

The occurrence of grooves has previously been recorded for *Senecio* (no species given) by Metcalfe and Chalk (1950). As table 1 shows, they are characteristic of a scattering of the Senecioneae studied here.

Vessel Grouping.—Most Senecioneae are characterized by fairly frequent, or large groupings of vessels, although at least a few solitary vessels may be found in all species. Grouping of vessels is most pronounced in dry-country species, such as *Senecio ecuadoriensis* (fig. 30), *S. eleagnifolius*, *S. palmeri* (fig. 26), *S. picridis* (fig. 28) and the various species of *Tetradymia* (viz, fig. 3). Minimal vessel grouping occurs in species from relatively moist habitats, such as *Gynoxys verrucosa* var. *grandifolia* (fig. 10), the Dendrosenecios (fig. 12, 14), *Senecio mannii* (fig. 18), and *S. petasitis* (fig. 24). Short radial chains of vessels characterize some Senecioneae, such as *S. aberdaricus*, *S. adnivalis* (fig. 12) and *S. petasitis* (fig. 24). Longer radial chains may be seen in "*Faujasia blixana*" (fig. 35), *Liabum bonplandii* (fig. 5), *Peucephyllum schottii* (fig. 1), *Rhetinodendron berterii* (fig. 26), *Senecio ecuadoriensis* (fig. 30), *S. palmeri* (fig. 26), *S. petasoides*, *S. picridis* (fig. 28) and *S. salignus*. Bands which vary from radial to diagonal in orientation occur in *Senecio eleagnifolius* and *S. huntii* (fig. 32). These bands may occasionally be tangential in *S. huntii*.

Groupings of vessels which relate to growth-ring phenomena are discussed below under "Growth Rings."

Fig. 5–9. Fig. 5–6. *Liabum bonplandii*.—Fig. 5. Transection. Note size, grouping of vessels.—Fig. 6. Tangential section. Rays are high, abundant.—Fig. 7–8. *Liabum pichinchense*.—Fig. 7. Transection. Note large size of vessels.—Fig. 8. Tangential section. Tyloses are visible in vessels at right.—Fig. 9. *Mikania cordifolia*.—Transection. Large vessels in this liana are associated with smaller vessels; rays are thin-walled, non-lignified. Fig. 5–8, $\times 65$. Fig. 9, $\times 93$.

FIGURES 5-9

TRACHEIDS

Hauman (1935) has reported observation of tracheids in a tangential section of wood of the *Dendrosenecio* *S. friesiorum*, and figures what he claims to be these. He reports vessels in a transverse section (also figured). I believe that Hauman failed to note perforations plates on vessel elements in the tangential section. A tangential section of a wood may show a vessel wall in which perforation plates are not clear, but walls of parenchyma cells which underlie or overlie the vessel may appear to be septa of the vessel. In all likelihood, tracheids are absent from *S. friesiorum*, as they are from the other *Dendrosenecios* and in fact, all other *Compositae* (except for vascular tracheids, which seem very unlikely to occur in the *Dendrosenecios*).

LIBRIFORM FIBERS

Dimensions; Wall-Thickness.—Dimensions of libriform fibers are related to dimensions of vessel elements, in that shorter fibers occur in species with shorter vessel elements, and this paralleling of dimensions is clearly shown by table. For example, the longest fibers were observed in species with the longest vessel elements, such as "*Faujasia blixana*". Differences of taxonomic interest do occur with respect to diameter of fibers and wall thickness. Notably wide fibers occur in the rosette-tree *Senecios*, namely the *Dendrosenecios* such as *S. adnivalis* (fig. 12) and *S. johnstonii* (fig. 14), as well as in the Mexican rosette-tree *S. praecox* (fig. 20). Woods with narrow fibers in the present study include *Brachyglottis repanda*, *Erechtites hieracifolia*, *Robinsonia gayana*, and all the species of *Tetradymia* (viz, fig. 3). Among the *Senecioneae* with unusually thick-walled fibers are "*Faujasia blixana*" (fig. 35), *Peucephyllum schottii* (fig. 1), *Senecio ecuadoriensis* (fig. 30), *S. eleagnifolius*, *S. rivalis*, and the *Dendrosenecios*, illustrated here by *S. adnivalis* (fig. 12) and *S. johnstonii* (fig. 14). Thus, the *Dendrosenecios* combine prominent fiber width with relatively great fiber-wall thickness, a fact shown for *S. (Dendrosenecio) friesiorum* by Hauman (1935). Notably thin-walled fibers occur in *Brachyglottis repanda*, *Erechtites hieracifolia*, the various species of *Liabum* (fig. 5, 7), *Neurolaena* (viz, fig. 22), *Senecio multicorymbosus* (fig. 16), *S. petasitoides*, *S. petasitis* (fig. 24), *S. praecox* (fig. 20) and *S. salignus*.

Septate Fibers.—Septate fibers were observed to be abundant in "*Faujasia blixana*", *Liabum klattii*, and *Liabum pichinchense*. In the last-named species, two or more septa per fiber are characteristic.

Fiber Dimorphism.—Data relating to this topic are discussed under the following heading.

AXIAL PARENCHYMA

A type of paratracheal parenchyma, scanty, is present almost uniformly throughout *Compositae*, and this also proves to be true of *Senecioneae*. Paratracheal parenchyma cells are usually subdivided into strands of two cells, a condition which may be observed clearly in the *Dendrosenecios* (fig. 13, 15), where parenchyma cells are especially large. Strands of two cells may also be seen here in the illustration of *Senecio praecox* (fig. 21). Strands of three cells are common in *S. mannii*, and vary between two and four cells in *S. petasitis*. Strands of paratracheal parenchyma cells vary between four and six in *Liabum klattii*.

Apotracheal parenchyma is present as bands of relatively short, thin-walled cells, often subdivided (not merely septate), which can be shown, in plants for which living material is available, to have living contents. These cells represent a phenomenon I have termed fiber dimorphism (Carlquist, 1958, 1961), because various *Compositae* possess all degrees of differentiation of fibers from none at all to the presence of unmistakable bands of short parenchyma cells alternating with long libriform fibers. Parenchyma cells in *Senecioneae*, and all *Compositae* I have studied, may be shorter than, the same length, or longer than vessel elements, as illustrated here in one section for *Robinsonia evenia* (fig. 42). Therefore, various degrees of elongation from fusiform cambial initials are involved in the formation of these parenchyma bands. The term "nucleated fiber" does not seem acceptable

in Compositae, because this would signify that appreciable elongation of parenchyma cells as compared to the cambial initials from which they are derived occurred. While the term "nucleated fiber" would cover long parenchyma-like cells, it would not cover ones inter-

Fig. 10-13. Fig. 10-11. *Gynoxys verrucosa* var. *grandifolia*.—Fig. 10. Transection.—Fig. 11. Tangential section. Some fibers are stored.—Fig. 12-13. *Senecio adnivalis*, Aw-1939.—Fig. 12. Transection; Vessels in radial chains; fiber diameter relatively wide.—Fig. 13. Tangential section. Note large size of ray cells. All, $\times 65$.

mediate in length or shorter than vessel elements. There is no reason to believe that parenchyma-like cells of all lengths are not products of the same general phenomenon, so the term "apotracheal parenchyma" is applied uniformly here to indicate parenchyma cells

Fig. 14-17. Fig. 14-15. *Senecio johnstonii*.—Fig. 14. Transection. Note similarity to fig. 12.—Fig. 15. Tangential section. Some fibers are storied; note similarity to fig. 13.—Fig. 16-17. *Senecio multicorymbosus*, Yw-29384.—Fig. 16. Transection. Fiber diameter is relatively small; growth ring ends just above center.—Fig. 17. Tangential section. All, $\times 65$.

which occur in bands. The most distinctive instance of apotracheal parenchyma bands illustrated here is that shown for *Robinsonia evenia* (fig. 40–42). Parenchyma bands also occur in other species of *Robinsonia*, as well as *Rhetinodendron berterii* (fig. 36, 37) and *Sym-*

Fig. 18–21. Fig. 18–19. *Senecio mannii*.—Fig. 18. Transection. Fibers are thin-walled.—Fig. 19. Tangential section. Uniseriate rays are absent.—Fig. 20–21. *Senecio praecox*.—Fig. 20. Transection. Fibers are thin-walled; a band of parenchyma above center may be seen.—Fig. 21. Tangential section. Ray cells are relatively small; fibers are short, wide, and storied. All, $\times 65$.

phyochaeta (fig. 38, 29). Highly distinctive parenchyma bands were also seen in *Senecio rivalis*, in which the difference in length of elements and wall thickness was extreme. In *S. rivalis*, the apotracheal parenchyma cells are almost invariably subdivided into strands of two cells.

Other Senecioneae in which fiber dimorphism leading to the production of apotracheal parenchyma bands was observed include *Senecio kirkii* (most fibers rather parenchyma-like), *Senecio praecox* (fig. 20, 21), and *S. petasitis* (fig. 24, 25). The sample of *S. aberdaricus* studied was small, but the secondary xylem present appeared to have a band of parenchyma at its conclusion.

VASCULAR RAYS

Types.—Elimination or loss of uniseriate rays is common in Compositae. Senecioneae illustrate this clearly, and in only one species, *Senecio eleagnifolius* (fig. 34), were uniseriate rays found to be abundant. In this species, they were approximately as frequent as multiseriate rays, which rarely exceed two cells in width. In the remaining Senecioneae, uniseriate rays are very limited in height, and may be only one cell in height, as they typically are in *Senecio adnivalis*.

Very wide rays were observed in *Erechtites hieracifolia*, which can only be called an herb. Obviously relatively little breakup of primary rays had taken place in the specimen studied, although the process was occurring. Extremely wide rays are characteristic of *Peucephyllum schottii* (fig. 2). In this wood, the course of vessels and fibers around rays is often quite tortuous. Wide rays are also characteristic of *Neurolaena* (viz, fig. 23), *Senecio ecuadoriensis* (fig. 31), *S. leucadendron*, and *S. petasitis* (fig. 25).

Relatively short rays (limited in vertical extent) are possessed by *Gynoxys indurata*, *G. verrucosa* var. *grandifolia* (fig. 11), *Peucephyllum schottii* (fig. 2), *Robinsonia evenia* (fig. 41, 42), the New Zealand Senecios (*S. eleagnifolius*, fig. 34; *S. huntii*, fig. 33; *S. kirkii*), and *Senecio praecox* (fig. 21). The Dendrosenecios (fig. 13, 15) also have relatively low rays.

Many Senecioneae have rays so high that the vertical extent of few was complete within a tangential section (usually more than 2 cm. in length in my preparations). The symbol for "greater than 10 mm" is entered in table 1 because no precise idea of their height could be obtained. Such species include *Gynoxys hallii*, the species of *Liabum* (fig. 6, 8), *Mikania cordifolia*, the species of *Neurolaena* (viz, fig. 23), *Senecio petasioides* and *S. petasitis* (fig. 25). The high rays indicated for *Rhetinodendron berterii* and *Senecio aberdaricus* are probably related to the relative youth of the samples from which these figures were obtained. Ray abundance was not measured, but the large area occupied by rays in *Liabum bonplandii* (fig. 6) is notable.

Histology.—Heterocellular rays, that is, rays in which both erect and procumbent cells occur, are the most common type in Senecioneae. There is a tendency in a few Senecioneae toward the elimination of erect cells. No erect cells were observed in "*Faujasia blixana*." Even square cells were wholly lacking in rays of *Mikania cordifolia*. Erect cells are infrequent in rays of *Gynoxys verrucosa* var. *grandifolia* and *Tetradymia argyrea*.

The absence, or near absence, of procumbent cells (although square cells may be present) characterize many Senecioneae. These rays must be termed homocellular according to accepted terminology, because square cells are considered morphologically equivalent to erect cells. Species in this category include *Brachyglottis repanda*, *Erechtites hieracifolia*, *Gynoxys hallii*, *Liabum klattii*, *Neurolaena lobata* (fig. 23), *Rhetinodendron berterii*, *Robinsonia* spp. (viz, fig. 41, 42), *Senecio kirkii*, *S. mannii* (fig. 19), *S. petasioides*, *S. petasitis* (fig. 25), *S. salignus*, *Symphyocheata macrocephala* (fig. 39), and *Tetradymia axillaris*. The abundance of erect cells in rays of these species makes the limits of rays obscure, because erect ray cells stimulate adjacent libriform fibers in length and wall characteristics.

In *Neurolaena macrophylla*, erect cells in rays are present to the exclusion of procumbent

Fig. 22-25. Fig. 22-23, *Neurolaena lobata*.—Fig. 22. Transection. Fibers are thin-walled.—Fig. 23. Tangential section. Rays are high, abundant.—Fig. 24-25. *Senecio petasitis*.—Fig. 24. Transection. Fibers are thin-walled, vessels narrow in diameter.—Fig. 25. Tangential section. Fibers are stored; rays are high, with cells square to erect exclusively. All, $\times 65$.

Fig. 26-29. Fig. 26-27. *Senecio palmeri*.—Fig. 26. Transection. End of growth ring near bottom.—Fig. 27. Tangential section. Ray cells are square to erect exclusively.—Fig. 28-29. *Senecio picridis*.—Fig. 28. Transection. Vessels are very narrow, in large groupings.—Fig. 29. Tangential section. Rays are multiseriate exclusively, very high and wide. All, $\times 65$.

Fig. 30-33. Fig. 30-31. *Senecio ecuadoriensis*.—Fig. 30. Transection. End of growth ring above center; note small diameter of vessels, large groupings.—Fig. 31. Tangential section. Rays are often wide, high; fibers are short, storied.—Fig. 32-33. *Senecio buntii*.—Fig. 32. Transection. Vessels are in large groups and tend to form tangential bands or diagonal patterns.—Fig. 33. Tangential section. Rays are low; tracheary elements are short and storied. All, $\times 65$.

or even square cells. Even when transversely subdivided, the ray cells are still erect.

Wall thickness of ray cells varies within Senecioneae. In most species, ray-cell walls are thin, but with lignified secondary walls. *Mikania cordifolia* (fig. 9) has ray cells which are thin-walled and non-lignified. Ray cells of *Tetradymia* are relatively thick-walled, as shown in fig. 3 and fig. 4, but occasionally they may be quite thin-walled in some late-wood zones. This was observed in *Tetradymia argyraea*, and has been reported earlier for *T. glabrata* (Carlquist, 1961).

Prominent pitting of ray cells (abundant, conspicuous on account of the thick walls of ray cells) was observed in "*Faujasia blixana*".

Perforated Ray Cells.—Perforated ray cells are difficult to regard either as vessel elements or ray cells, because they are vessel elements derived from ray initials. They are related to breakup of rays, ontogenetically (Chalk and Chattaway, 1933). Perforated ray cells were reported in Astereae (Carlquist, 1960b). Because ray breakup is active in Senecioneae, they probably occur in a number of species of the tribe. In the present study, perforate ray cells were observed in *Brachyglottis repanda*, *Erechtites hieracifolia*, and *Senecio rivalis* (fig. 47).

TYLOSES

Tyloses were observed in *Liabum pichinchense* and in the late wood of *L. klattii*. In *L. pichinchense* they are thin-walled and numerous (fig. 8).

GROWTH RINGS

Growth rings are of several types in Senecioneae. In *Erechtites hieracifolia*, termination of the growth of this herb (as indicated by flowering) is accompanied by diminution in the diameter of vessels.

A simple type of growth ring is represented by species in which wider fewer vessels are present in early wood, usually accompanied by narrower, more numerous vessels in late wood. Species with this condition include *Liabum bonplandii* (fig. 5), *Peucephyllum schottii* (fig. 1), *Senecio douglasii*, *S. ecuadoriensis* (fig. 30), *S. buntii*, *S. picridis* (fig. 28), and the various species of *Tetradymia* (viz. fig. 3). All of these species may be said to have some tendency toward a ring-porous condition, but this is most pronounced in *Tetradymia*, the species of which are clearly ring-porous.

Where fiber dimorphism is present, thin-walled fibers may be present in early wood, with thicker-walled fibers in the late wood. This condition was seen in *Gynoxys ballii* and *Liabum klattii*. If actual parenchyma bands are present, these are related to growth-ring phenomena. Marginal parenchyma bands were observed in *Rhetinodendron berterii*, *Senecio kirkii*, *S. multicorymbosus*, *S. petasitis*, *S. praecox*, *S. rivalis*, and *Symphyochaeta macrocephala*. As the data in table 1 show, species with these parenchyma bands may or may not be characterized by wider or more numerous vessels in the early wood of rings.

STORIED WOOD STRUCTURE

Storying of wood is very common in Senecioneae, more common than casual observation might suggest. For instance, the wood of *Senecio douglasii* did not exhibit any appreciable storying, but sections which showed the vascular cambium revealed that fusiform cambial initials were, in fact, storied. Thus, elongation of fibers destroys the storied pattern. The varied expression of storying, that is, whether it is evident in fibers alone, or whether all axial elements conform to the storied pattern, or whether only a few fibers appear storied, indicate relatively minor differences in storying. Species in which a few fibers, most fibers, or fibers plus cells of the parenchyma bands appear storied include the following: *Gynoxys florulenta*, *G. ballii*, *G. verrucosa* var. *grandifolia* (fig. 11), *Liabum bonplandii* (fig. 6), *Rhetinodendron berterii* (fig. 37), *Robinsonia* spp. (viz. fig. 41, 42), *Senecio ecuadoriensis* (fig. 31), *S. praecox* (fig. 21), and *Symphyochaeta macrocephala* (fig. 39). In addition to storying of axial elements, some rays are storied in *Senecio eleagnifolius* (fig. 34) and *S.*

buntii (fig. 33). Because of elongation of fibers, only vessels and vascular tracheids appear storied in species of the genus *Tetradymia* (fig. 4).

RESIN-LIKE DEPOSITS

Deposits of resin-like materials occur in Senecioneae either as massive deposits or as droplets, or both. The following species were observed to have massive deposits in vessels:

Fig. 34-37. Fig. 34. *Senecio eleagnifolius*.—Tangential section. Uniseriate rays are common, multi-seriate rays low and narrow; tracheary elements are short and storied.—Fig. 35. "*Faujasia blixana*."—Transverse section. Fibers are wide, vessels tend to occur in radial chains.—Fig. 36-37. *Rhetinodendron berterii*.—Fig. 36. Transverse section. A parenchyma band occurs at left.—Fig. 37. Tangential section. Fiber dimorphism is evident: long, thick-walled fibers at left; short, wide, thinner-walled and clearly storied elements (parenchyma) at extreme right. Fig. 34-35, $\times 65$. Fig. 36-37, $\times 307$.

Rhetinodendron berterii, *Robinsonia* (all spp., viz *R. evenia*, fig. 40), *Senecio palmeri*, and *S. salignus*. Droplets in parenchyma cells (ray and axial) were seen in *Liabum pichinchense* and *Senecio multicorymbosus*. Droplets both in parenchyma and in other cells were noted in *Liabum klatti* (with massive deposits in late-wood vessels, in addition), *Peucephyllum schottii* (note dark appearance of ray cells, fig. 2), *Mikania cordifolia*, *Senecio kirkii*, and *S. rivalis* (massive deposits in vessels, also).

Secretory canals may be present in the rays of *Mikania cordifolia*. Because the thin-walled ray cells in this species are altered by drying, this could not be clearly determined in the specimen studied. The abundance of secretory canals in the genus *Senecio* suggest that this is to be expected.

CRYSTALS

All species of the genus *Tetradymia* were observed to have prismatic crystals in ray cells. These crystals are much like those figured for *Gutierrezia microcephala* by Carlquist (1960b) or for *Proustia pungens* by Metcalfe and Chalk (1950). Crystals were relatively fine in *T. agyraea*, coarse in *T. stenolepis*.

CONCLUSIONS

SPECIES DIFFERENCES

The varying sources of material make precise descriptions of anatomical differences among species in a genus impossible. However, there are some clear distinctions worthy of mention. In all the species cited, relatively old wood samples were used, so that a fairly secure basis is provided for these comparisons.

In the genus *Gynoxys*, two of the species studied possessed rays with both procumbent and erect cells, but in *G. hallii*, procumbent cells were not observed, whereas in *G. verrucosa* var. *grandifolia*, erect cells were found to be lacking. Also, *G. hallii* has very high rays, whereas they are limited in vertical extent in the other species. Grooves were observed in vessels in two of the species, but not in the other two.

In the genus *Liabum*, *L. pichinchense* is distinctive because of its large vessels, and the presence of procumbent cells in rays. Pits in vessels of *L. bonplandii* are notably smaller than those in the other two species studied.

There is little true difference among the species of *Robinsonia* with respect to wood anatomy. Likewise, the *Dendrosenecios* studied showed little difference from each other, and the drawings given for one of this group not studied here, *S. friesiorum*, by Hauman (1935) suggest this it conforms to the patterns established here.

Within the genus *Senecio*, however, some apparently natural species groups are evident. The *Dendrosenecios* form a tightly-knit group, united by the following characteristics: relatively long vessel elements; relatively small degree of vessel grouping; fibers quite wide, but relatively thick-walled; a tendency toward reduced apertures on pits in vessels; a tendency toward horizontally-widened (scalariform-like) pitting on vessels; relatively few vessels per unit area of transection; large size of both axial and ray parenchyma cells; low wide rays, composed of both erect and procumbent cells; absence of uniseriate rays. Interestingly, the Mexican species *Senecio praecox*, which also has a rosette-tree habit, shows many similarities, although fibers are thin-walled, ray cells are smaller, and both vessel elements and fibers are shorter than in the *Dendrosenecios*. Also, parenchyma bands are characteristic of this species, whereas fiber dimorphism is apparently not characteristic of the *Dendrosenecios*.

The New Zealand *Senecios* studied (*S. eleagnifolius*, *S. buntii*, *S. kirkii*) also show many points of resemblance among themselves: narrow, relatively short vessel elements; large groups of vessels; presence of helical sculpture in vessels; presence of growth rings; relatively low rays, composed of both procumbent and erect cells; all elements storied, including (in some places) rays.

Fig. 38–42. Fig. 38–39. *Symphyochaeta macrocephala*.—Fig. 38. Transection. A parenchyma band is present across center.—Fig. 39. Tangential section. Parenchyma most clearly visible at left, fibers at upper right.—Fig. 40–42. *Robinsonia evenia*.—Fig. 40. Transection. Three parenchyma bands can be seen; note resin-like deposits in vessels.—Fig. 41–42. Tangential sections, representing photographs of two portions of the same section. Fig. 41 shows fibers, fig. 42 parenchyma cells. All, $\times 65$.

Fig. 43-48. Fig. 43-44. *Senecio praecox*.—Portions of vessels from tangential sections, showing intervascular pitting. Note elongate, scalariform-like pitting. Fig. 43 shows pit apertures clearly; in fig. 44, the outlines of the pit cavities, which are wide and angular in outline, may be seen.—Fig. 45. *Senecio mannii*.—Portion of a vessel wall from a tangential section, showing intervascular pitting. Note irregular nature of pit shapes, and crowded, angular shape of pits.—Fig. 46. *Tetradymia argyreaea*.—Vessel

Other species of *Senecio* have distinctive characteristics. *Senecio rivalis* is notable for its wide, thick-walled fibers, and its distinctive parenchyma bands, composed of cells in strands of two. *Senecio palmeri* and *S. picridis* both have very narrow vessels in large aggregations. Other species could also be cited, but comparison of a much larger group of *Senecios* would be desirable for more useful conclusions as to characteristics of sections of the genus, or distinctions within them.

GENUS CHARACTERISTICS AND RELATIONSHIPS

Without study of more numerous species, little can be said about characteristics of most of the genera studied here. However, representation of some genera is relatively good. For example, *Tetradymia* seems characterized by a ring-porous condition, presence of narrow vessels and vascular tracheids, large groupings of vessels, short vessel elements, prominent helical thickenings on vessel walls, and low, narrow rays composed of thick-walled cells. Of especial interest is the presence of crystals in ray cells of all four species of this genus.

The genus *Robinsonia* possesses relatively narrow, short vessel elements, parenchyma bands, and growth rings. The fiber dimorphism and storied wood structure characteristic of *Robinsonia* is also present in *Rhetinodendron* and *Symphyochaeta*. Although Skottsberg has segregated *Symphyochaeta* from *Robinsonia* and contends (personal communication) that *Rhetinodendron* is not closely allied to *Robinsonia*, the three genera from the Juan Fernandez Islands do seem to form a natural group.

The specimen identified as "*Faujasia blixana*" possesses some exceptional features: the type of rays and the great length of vessel elements. Hand-sections of wood of twigs of specimens of *F. flexuosa* and *F. pinifolia* from the British Museum revealed much shorter (ca. 300 microns) vessel elements, and narrow rays consisting of square to erect cells. The identification of the specimen "*Faujasia blixana*" (an unpublished name, apparently) can therefore be questioned, a conclusion which has also been reached by Lawrence Chalk (personal communication).

RELATIONSHIPS TO GROWTH FORM AND ECOLOGY

Wood anatomy of many of the species studied here suggests close adaptation to growth form and ecology. Evolutionary changes related to these factors may be evident in the features listed above as distinctive in the *Dendrosenecios*. Are these features indicative of an herb-ancestry for the *Dendrosenecios*? The growth form and anatomy of the *Dendrosenecios* and of *Senecio praecox* very much suggests that they are herb derivatives, despite the likelihood that primitive *Compositae* were woody. There is no reason to suppose that *Compositae* cannot have proceeded from woody to herbaceous, and then have become woodier again in a few cases. This, in fact, seems to be the simplest explanation for the *Dendrosenecios*. If so, the characteristics of the *Dendrosenecios* and *S. praecox* would become important in suggesting characteristics one might expect to find in the relatively small number of herbaceous dicots which have increased production of secondary xylem phylogenetically. Anyone who wishes to interpret characteristics of these species as indicators of such an ancestry, however, will find that interpretations cannot be simply or easily made.

Certain features of wood anatomy of *Liabum*, *Gynoxys*, and *Neurolaena* invite interpretation. These features include the relatively long, wide vessel elements, the wide fibers, and the predominance of erect cells in rays. The explanation of these features is not readily apparent. The wood anatomy of *Gynoxys*, however, suggests a relatively unspecialized condition for *Senecioneae*. The majority of *Senecioneae* appear specialized in one way or another, even for *Compositae*.

from tangential section. Helical bands on vessel wall are evident.—Fig. 47. *Senecio rivalis*.—Portion of a radial section, showing a perforated ray cell.—Fig. 48. "*Faujasia blixana*."—Portion of a radial section, showing a multiperforate perforation plate. Bars are relatively few and irregular in course. Fig. 43–44, $\times 500$. Fig. 45, $\times 1500$. Fig. 46, $\times 833$. Fig. 47, $\times 520$. Fig. 48, $\times 695$.

The dry-country or desert-inhabiting Senecioneae show the highest degrees of specialization. These specializations are much the same as those in xerophytic Astereae (Carlquist, 1960b), Heliantheae (Carlquist, 1958), and Helenieae (Carlquist, 1959). Narrow vessels, including presence of vascular tracheids, large groupings of vessels, presence of helical sculpture in vessels, and storied wood structure are all found in such species as the New Zealand Senecios, as well as in *S. douglasii*, *S. palmeri*, *S. picridis*, *Peucephyllum schottii*, and the four species of *Tetradymia*. Because of parallelism among tribes of Compositae with respect to xerophytic characteristics, one cannot be sure from wood anatomy that a genus such as *Lepidospartum* belongs to Astereae or Senecioneae. *Lepidospartum* was included in the writer's (1960b) studies on woods of Astereae for purposes of comparison to woods of that tribe.

Because of the sensitivity of evolutionary adjustment by species and genera of Senecioneae to particular ecological conditions, one would not expect subtribal or tribal characteristics to be illustrated by wood anatomy. Understanding of generic and subtribal groupings within Senecioneae is apparently not far advanced at present. Hoffmann (1889-1894) recognizes two subtribes, Liabinae and Senecioninae. Of the genera studied here, only *Liabum* belongs to the former subtribe, and the anatomy of this genus offers nothing which is not characteristic of some of the remaining genera studied here.

Senecioneae do offer excellent material for study of adaptations in wood anatomy to particular ecological conditions or growth forms, or both. The genus *Senecio* is of especial potential value on account of the fact that this genus has radiated into a large number of habitats and has assumed such diverse growth forms, and intensive study of wood anatomy in *Senecio* would undoubtedly offer much basic information of an evolutionary nature.

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