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WOOD AND STEM ANATOMY OF CONVULVULACEAE: A SURVEY

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ABSTRACT

Quantitative and qualitative features of wood and stem anatomy are presented for 44 collections of 16 genera and 35 species of Convolvulaceae. Markedly furrowed xylem characterizes the genera of tribe Cresseae. Successive cambia occur in 11 of the genera studied. Large patches of axial parenchyma occur in many of these; only in one species was interxylary phloem (formed internally by the cambium) observed in the parenchyma patches. Intraxylary phloem at the periphery of the pith is universal in Convolvulaceae, but newly reported is the fact that in many species, cambial activity adds secondary phloem to the intraxylary phloem strands. These cambia were also observed to add limited amounts of secondary xylem externally in *Ericybe* and *Operculina*. Fragmentation of the vascular cylinder by growth from the inner cambia leads to initiation of radially oriented cambia (ray cambia) along the ray zone where fracture occurs. Three new types of vessel restriction patterns (nonrandom distribution of vessels in wood or absence of vessels within some parts of the secondary xylem) are reported for the family (and dicotyledons). Rays are predominantly uniseriate; ray histology and quantitative vessel features show little change ontogenetically in species with successive cambia, suggesting that this cambial mode deters the kinds of progressive changes that occur in dicotyledons with a single cambium. Vessels are much wider in lianoid Convolvulaceae than in shrubby species; the lianoid species of *Ipomoea* have vessels twice the diameter of those in arborescent species of *Ipomoea*. Conjunctive parenchyma may serve for water storage in *I. arborescens* and other species, but this tissue and abundance of axial parenchyma in lianas might also aid flexibility and damage resistance. Septate fiber-tracheids and septate libriform fibers occur in a few species and represent tracheid dimorphism. Occurrence of tracheids together with fibriform vessel elements in woods of many Convolvulaceae suggests relationship of Convolvulaceae to Polemoniaceae and Hydrophyllaceae; intraxylary phloem and other wood features suggest relationship between Convolvulaceae and Solanaceae.

Key words: Cambial variants, Convolvulaceae, fibriform vessel elements, furrowed xylem, intraxylary phloem, lianas, ray cambia, vessel restriction patterns, wood anatomy.

INTRODUCTION

Convolvulaceae are currently regarded as containing 58 genera with 1550 species (Mabberley 1987). The 16 genera and 35 species represented in the present study may seem a remarkably small fraction of the family for the purpose of a survey. Despite the smallness of this sample, wood anatomy is reported for several genera not hitherto studied. More significantly, modes of anatomical structure newly described for dicotyledons are presented here: presence of secondary growth associated with intraxylary phloem; presence of three distinctive types of vessel

restriction patterns; and presence of a continuum between tracheids and fibriform vessel elements.

The predominantly herbaceous nature of the family—as represented particularly in the larger genera such as *Convolvulus* and *Ipomoea*—accounts in part for the scanty representation of the family in studies of wood anatomy. Most of the species that are woody are lianas, and wood samples of lianas tend not to be collected as often as those of trees or even shrubs. Many of these species have successive cambia, so that large amounts of soft tissue (phloem, conjunctive tissue) in addition to hard tissue (wood, sclereid nests) are present in stems. The soft tissues are not preserved well by drying, although a number of preparations made for this study from dried specimens show soft tissue details to a surprising extent. Lack of liquid-preserved samples may have deterred investigations of wood anatomy of Convolvulaceae. In the present study, liquid-preserved specimens provided a baseline for the understanding of the nature of nonlignified tissues in the genera and species they represent. New information about cambial activity was developed for this reason.

Metcalf and Chalk (1950) attribute most of our knowledge of stem and wood anatomy to Solereder (1908), and add little data of their own. Among the most important subsequent contributions are those of Metcalf (1935) on *Convolvulus*; Obaton (1960) on *Bonamia*, *Neuropeltis*, and *Prevostea*; Mennega (1969) on *Dicranostyles*; Pant and Bhatnagar (1975) on *Argyreia*; and Lowell and Lucansky (1986) on *Ipomoea hederifolia*. These contributions complement the present study because the species studied here are mostly not those viewed by the above authors.

This paper is one of a series of studies of wood anatomy of families of tubiflorous dicotyledons. The relationships of these families may be clarified by knowledge of wood anatomy. Data on wood anatomy of Convolvulaceae prove to be important in showing a relationship to Solanaceae. The wider relationships of Convolvulaceae and Solanaceae will be discussed in a final paper in this series.

The diversity of wood structure in Convolvulaceae is great and invites comparison to the system of subfamilies and tribes. The system of Peter (1896), which is based upon fruit type, has been influential; a modification based on information from pollen was appended to the volume in which Peter's monograph appeared (authorship not indicated). These and other schemes are reviewed by Austin (1973), who has proposed his own scheme. Austin's system is influenced by information on chromosome number. One of the distinctive groupings offered by Austin is one he calls "merremioids" (*Aniseia*, *Hewittia*, *Merremia*, *Operculina*, and *Tetralocularia*). Although Austin suggested that these genera, included in tribe Ipomoeae in earlier systems, might be an independent tribe, he did not offer a tribal name for them. Austin (1973) also combined Dichondreae and Wilsonieae; on account of the distinctive habit and wood of *Wilsonia*, I prefer to retain Wilsonieae. With that exception, the genera studied or mentioned here are listed according to Austin's scheme as a framework for discussing similarities and differences; all of the tribes are represented in the present paper except for Poraneae and Dichondreae. The purpose of giving the system below is in part to give a basis for comparison to data from wood anatomy, but, more importantly, to show that the family has been broadly sampled. By sampling all of the tribes with woody species, more diversity in wood anatomy is likely to be uncovered.

Ericybeae: *Dicranostyles*, *Ericybe*, *Lysiostyles*, *Maripa*

Cresseae: *Bonamia*, *Breweria*, *Neuropeltis*, *Prevostea*

Poraneae: *Porana*

Convolvuleae: *Convolvulus*

"merremioids": *Merremia*, *Operculina*

Ipomoeae: *Exogonium*, *Ipomoea*, *Stictocardia*, *Turbina*

Argyreieae: *Argyria*

Dichondreae: *Dichondra*

Wilsonieae: *Wilsonia*

Because of its lack of secondary growth, *Cuscuta*, sometimes recognized under Cuscutaceae, is not considered in the present account.

With respect to habit, not all of the species studied here are lianas, but the majority are. "Liana" is held to apply to woody climbers; "vine," therefore, connotes a scandent herb. *Mina lobata* can be considered a vine rather than a liana, because it is an annual. In *Ipomoea*, *I. adenoides*, *I. arborescens*, *I. fistulosa*, *I. intrapilosa*, *I. murucoides*, and *I. pauciflora* are small to medium-sized trees. *Convolvulus cneorum* is a small shrub; *C. floridus* and *C. scoparius* are large shrubs. *Wilsonia humilis* is a prostrate microphyllous subshrub. The specimen of *Turbina stenosisiphon* studied was from a small shrub, although ultimately plants of this species become climbers. Wood anatomy is related to the range of growth forms in the family. Lianas have a number of distinctive characters in wood anatomy (Schenck 1893; Carlquist 1975a, 1985, 1991). The lianoid Convolvulaceae studied here will be compared to features reported as typical for lianas. Among the shrubs, *Wilsonia* is from dry areas of southwestern Australia; *Convolvulus floridus* and *C. scoparius* are from dry scrub of the Canary Islands; *C. cneorum* occurs in *macchi* of southern Europe. The wood anatomy of these four shrubby species can be compared to these ecological regimes. The arborescent species of *Ipomoea* have successive cambia; the vascular bands are interspersed with succulent conjunctive tissue. The nature and function of this tissue is examined here.

MATERIALS, METHODS, AND ACKNOWLEDGMENTS

Wood samples were available in dried or liquid-preserved form. Dried wood samples were mostly those supplied from the SJRw and MADw collections of the Forest Products Laboratory, Madison, Wisconsin, through the courtesy of Donna J. Christensen and Regis B. Miller. The samples from the Musée Royal de l'Afrique Centrale (Tw) were contributed through the kindness of Roger Dechamps. The sample of *Ericybe coccinea* was provided by the Forestry Commission of New South Wales. Also in dried form were the collections of *Convolvulus floridus* and *C. scoparius*. Other Carlquist specimens were preserved in formalin-acetic-alcohol, as were those of Oscar Dorado. Appreciation is expressed to Oscar Dorado for his collections of *Ipomoea* in Mexico, as well as for his help during a collecting trip to Sonora in March, 1988. Liquid-preserved material of *Turbina stenosisiphon* was available through the courtesy of the Los Angeles State and County Arboretum. This study was aided by a grant from the National Science Foundation, BSR-84119469.

Dried wood samples were boiled in water and stored in aqueous 50% ethyl alcohol. The species of *Argyria*, *Convolvulus*, and *Wilsonia* have relatively hard wood and were sectioned on a sliding microtome without pretreatment. The

remaining species presented problems because soft and hard tissues are intermixed in stems. Therefore, most collections were softened in ethylene diamine, embedded in paraffin, and sectioned on a rotary microtome according to the schedule of Carlquist (1982). This method provided remarkably good sections of convolvulaceous woods, particularly those with exceptionally wide vessels. Sections were stained with safranin and counterstained with fast green. Some paraffin sections were attached to aluminum SEM mounts in much the same way that paraffin sections are mounted on glass slides. After removal of paraffin, these sections were coated with gold and examined with an ISI WB-6 scanning electron microscope.

Locality data for the specimens collected are as follows: *Argyrea obtusifolia* (Liang 63095 RSA), Yaichow, Hainan I., China; *Bonamia maripoides* (SJRw-555483), border between Est. Bolivar and Terr. Delta Amacuro, Venezuela; *Breweria menziesii* (SJRw-26329), W. Maui, Hawaii; *Convolvulus cneorum* (Carlquist 15941 RSA), cult. in Claremont, California (native to Mediterranean coasts of southern Europe); *C. floridus* (Carlquist 2486 RSA), Barranco del Infierno, Tenerife, Canary Islands, Spain; *C. scoparius* (Carlquist 2501 RSA), Barranca de San Andres, Tenerife, Canary Islands, Spain; *Dicranostyles densa* (SJRw-40316), Manaos, Brazil; *D. holostyla* (MADw-14066), São Paulo de Olivença, Amazonas, Brazil; *Erycibe coccinea* (SFCw-R1229-2), New Guinea; *Exogonium bracteatum* (Carlquist 8005 RSA), between Moctezuma and Hermosillo, 23 km from Ures, Sonora, Mexico; *E. bracteatum* (Carlquist 8024 RSA), 30 km S of Quiriga, Sonora, Mexico; *E. bracteatum* (Henrickson 2093 RSA), 24 km S of Izucar de Matamoros, Puebla, Mexico; *Ipomoea adenoides* (MADw-37405), 5 km from Pereira de Eca on road to Arthur de Paiva, Angola; *I. arborescens* var. *arborescens* (Dorado 624-7 RSA), 60 km S of Morelia, near Iranche, Michoacán, Mexico; *I. arborescens* var. *arborescens* (Henrickson 2087 RSA), 5 km S of Izucar de Matamoros, Puebla, Mexico; *I. arborescens* var. *glabrata* (Carlquist 8027), summit of road between Rosario and Nuri, Sonora, Mexico; *I. arborescens* var. *glabrata* (Dorado 1584 RSA), 20 km N of Los Mochis, Sinaloa, Mexico; *I. bona-nox* (SJRw-25081), W side of Mt. Tantalus, Oahu, Hawaii; *I. cardiosepala* (SJRw-35995), Guayana; *I. fistulosa* (Carlquist 15939 RSA), cultivated in Claremont from seed collected near San Ramon, Peru; *I. intrapilosa* (Dorado 633-1 RSA), Volcan Tequila, Jalisco, Mexico; *I. mauritiana* (Tw-41314), Shaba, W. Africa; *I. murucoides* (Dorado 1646 RSA), 5 km N of Tamazulapan, on road to Tepelmeme de Morelos, Oaxaca, Mexico; *I. murucoides* (Iltis 816 MAD), Mexico; *I. murucoides* (SJRw-53328), Mexico; *I. pauciflora* (Dorado 620-1 RSA), 3 km from Valle de Vasquez on road to Quilamula, Morelos, Mexico; *I. pauciflora* (Dorado 638-1 RSA), 6 km N of Campo Acorta, Jalisco, Mexico; *I. prismatosiphon* (MADw-37551), 5 km from Mussolo on road to Cuque, Angola; *I. tiliaceae* (SJRw-54734), Prov. Darien, Panama; *I. tuba* (SJRw-51483), Florida Keys, Florida; *I. verbascoidea* (Tw-35138), Shaba, W. Africa; *Lysistyles scandens* (SJRw-41774), Venezuela; *Maripa janusiana* (MADw-38476), Alto Nanay, Maynas, Loreto, Peru; *M. panamensis* (SJRw-54969), Prov. Darien, Panama; *Merremia cissoides* (Carlquist 8016 RSA), Bahia San Carlos, NW of Guaymas, Sonora, Mexico; *M. nymphaeifolia* (SJRw-37593), Tuevessi, Rotuma, Fiji Is.; *M. peltata* (MADw-41005), near Lasanga, SE of Lae, New Guinea; *Mina lobata*, cultivated at Pomona College, Claremont, California; *Operculina palmeri* (Carlquist 8021 RSA), 24 km from Navojoa on road to Al-

amos, Sonora, Mexico; *O. palmeri* (Carlquist 8022 RSA), between Alamos and Navojoa, Sonora, Mexico; *O. passifloroides* (SJRw-32648), Brazil; *Stictocardia benaviensis* (Tw-21212), Shaba, W. Africa; *Turbina stenosphon*, cult. at Los Angeles State and County Arboretum, Arcadia, California (prop. no. 80-5-56); *Wilsonia humilis* (Gibbons 359 RSA), 1 km SE of Kingston, S.A., Australia.

Terms used are according to the IAWA Committee on Nomenclature (1964) except for terms relating to cambial variants; those follow Carlquist (1988a). Vessel diameter is measured as the widest dimension of the lumen (regardless of orientation). A continuum between tracheids and fibriform vessel elements occurs in many Convolvulaceae; citing features of this cell type continuum provides problems that cannot be resolved by use of a single term. The number of vessels per mm² is based on the "obvious" vessels and omits fibriform vessel elements (which are identical to tracheids as seen in transection). This figure cannot have the same significance as in a species without fibriform vessel elements.

Means in Table 1 are based on 25 measurements per feature except for diameter and wall thickness of fibriform vessel elements/tracheids; figures for these are based on conditions judged to be typical. Means were based on fewer than 25 measurements per feature if the anatomical structure was scarce (e.g., multiseriate rays, scarce in some species and absent in others) or not well preserved (unlignified rays in dried specimens).

ANATOMICAL RESULTS

Cambial Variants

Of primary importance in discussing woods of Convolvulaceae is detailing the nature of cambial activity. Without such a discussion, correlations with other anatomical data cannot be understood. For example, occurrence of conjunctive tissue in stems with successive cambia provides a source of water-storage tissue. Species of Convolvulaceae with successive cambia do not show the rise in tracheary element length that characterizes stems with single cambia. In Table 1, column 1, types of cambial variants are cited. These types are also illustrated photographically.

Furrowed xylem is demonstrated well by *Bonamia maripoides* (Fig. 1-3). In Figure 1, a lobe of secondary xylem is surrounded on three sides by secondary phloem. In Figure 2, a secondary xylem portion beginning with the pith and primary xylem (lower left) and continuing into lobe formation is illustrated. In Figure 3, center left, a semicircular strand of secondary xylem has been added to the wood at one point. The formation of such markedly furrowed secondary xylem is achieved by production of less secondary xylem in the grooves than in the lobes of the wood. *Breweria menziesii* also has furrowed xylem, but to a less marked degree (Fig. 5). Obaton (1960) figures markedly furrowed xylem for *Neuropeltis acuminata* Benth. & Hook. and *N. prevostioides* G. Mangenot and less strongly furrowed xylem for *Bonamia cymosa* H. Hallier. All of these species lack successive cambia. Furrowed xylem in *Prevostea* appears to be similar to that of *Bonamia* and *Neuropeltis*, but in addition, parenchymatous zones within the secondary xylem undergo cell proliferation, expand, and split the secondary xylem into numerous segments (Obaton 1960).

Furrowed xylem occurs, to a very moderate degree, in the species of the present

Table 1. Continued.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>I. cardiosepala</i> Meissn.	SJRw-35995	SC	23	1.36	235	5.8	10	8	124	667	30	4.0	P, W, VS	—	—	—	Usp
<i>I. fistulosa</i> Martius	Carlquist 15939	IP, SC	16	1.20	88	3.0	11	5	139	496	34	1.7	N, W, VS	1.2	541	220	USP
<i>I. intrapilosa</i> Rose	Dorado 633-1	IP, SC	14	1.44	140	4.4	11	9	159	777	23	3.5	VS	2.9	2196	916	US
<i>I. mauritiana</i> Jacq.	Tw-41314	SC	15	1.04	216	8.0	10	7	188	633	30	4.3	P, W, VS	—	—	—	USP
<i>I. murucoides</i> Roem. & Schult.	Dorado 1646	SC	17	1.29	123	4.9	10	7	150	846	27	2.3	D, VS	6.8	1278	846	Usp
	Iltis 816	SC	3	1.20	147	5.8	12	6	150	889	27	2.5	N, VS	—	—	—	Usp
	SJRw-53328	SC	14	1.30	153	5.8	12	6	172	967	27	2.5	T, VS	7.4	931	254	Usp
<i>I. pauciflora</i> Mart. & Gal.	Dorado 620-1	IP, SC	8	1.14	130	4.0	10	7	158	705	25	2.4	VS	6.0	705	301	Usp
<i>I. prismatosiphon</i> Welw.	Dorado 683-1	IP, SC	14	1.22	115	4.3	11	7	173	862	30	4.5	N, VS	3.0	—	—	1010 USP
<i>I. tiliaceae</i> (Willd.) Choisy	MADw-37551	SC	18	1.19	156	4.5	10	8	532	901	34	4.8	V	—	—	—	Usp
	MADw-54734	IP	20	1.08	443	8.0	15	12	490	789	34	5.0	P, VS	—	—	—	Usp
<i>I. tuba</i> (Schlecht.) G. Don	SJRw-51483	SC	16	1.17	218	6.2	10	7	163	717	28	6.2	D, P, VS	—	—	—	USP
<i>I. verbascoidea</i> Choisy	Tw-35138	SC	16	1.28	147	5.0	10	10	238	575	32	6.0	D, P, VS	—	—	—	Us
<i>Lysostyles scandens</i> Benth.	SJRw-41774	IP, SC	15	1.20	148	4.5	15	8	411	659	18	5.0	A, VS	2.8	837	340	USP
<i>Maripa janusiana</i> D. Austin	MADw-38476	SC	14	1.12	226	6.5	12	10	332	824	25	4.4	AC, VS	—	711	280	USP
<i>M. panamensis</i> Hemsl.	SJRw-54959	SC	12	1.12	283	6.2	14	12	395	843	25	2.3	SC, VS	3.3	701	280	USP
<i>Merremia cissoides</i> (Lam.) H. Hallier	Carlquist 8016	IP, SC	28	1.08	141	4.8	10	8	253	696	23	2.0	W, P, VS	—	—	—	Us
<i>M. nymphaeifolia</i> H. Hallier	SJRw-37593	SC	15	1.04	396	7.2	12	7	136	1340	28	2.5	D, P, VS	—	—	—	USP

Table 1. Continued.

Species	Collection	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>M. peltata</i> (L.) Merrill	MADw-41005	IP, SC	10	1.08	461	7.3	14	14	150	716	46	5.0	AC, P, VS	3.9	949	264	USP
<i>Mina lobata</i> Liave & Lex.	cult. Claremont	—	46	1.38	156	2.6	7	5	147	478	25	1.8	P, VS	—	402	210	Usp
<i>Operculina palmeri</i> (Wats.) Howe	Carlquist 8021	F, IPX	31	1.04	242	5.2	10	9	181	651	23	2.6	P, VS	2.2	846	372	USP
	Carlquist 8022S	F, IPX	29	1.04	223	7.0	14	10	219	717	32	4.8	P, VS	2.0	577	478	Usp
	Carlquist 8022L	F, IPX, R	26	1.16	294	7.0	14	7	219	717	30	5.0	P, VS	2.0	356	273	USP
<i>O. passifloroides</i> (Benth.) Ducke	SJRw-32646	SC	10	1.04	334	7.3	12	9	462	980	32	5.0	AC, P, VS	2.6	667	241	USP
<i>Stictocardia benawiensis</i> (Vatke) H. Hall.	Tw-212121	IP, SC	25	1.16	278	9.6	15	12	218	816	38	5.0	P, VS	2.0	378	305	USP
	Tw-212120	IPX, SC	21	1.04	353	9.0	15	12	218	816	38	5.0	P, VS	2.0	458	267	USP
<i>Turbina stenosphon</i> (H. Hall) A. Meeuse	LASCA-80-5-56	IP, SC, X	12	1.12	164	4.8	12	7	222	676	32	2.6	P, VS	3.2	1571	457	USp
<i>Wilsonia humilis</i> R. Br.	Gibbons 359	—	307	1.20	20	4.4	5	4	165	249	16	5.1	VS	—	—	169	U
Lianas, Means ($n = 28$)			20	1.13	256	8.4	12	9	282	792	30	4.5	—	2.6	696	311	—
Shrubs, Means ($n = 4$)			121	1.21	50	4.3	8	6	257	589	14	4.9	—	3.6	775	146	—

Legends for columns: Collections column: letters following collection numbers (I = inner, L = large, O = outer, S = small); 1, cambial variants (F = furrowed xylem, IP = secondary phloem produced by intraxylary phloem cambium, IPX = xylem and phloem produced by intraxylary phloem cambium, R = ray cambia, X = interxylary phloem in thin walled axial parenchyma); 3, mean number of vessels per group; 4, mean vessel diameter, μm ; 5, mean vessel wall thickness μm ; 6, vertical diameter of vessel to vessel pits, μm ; 7, diameter of pits of tracheids or fibriform vessel elements, μm ; 8, mean length of vessel elements, μm ; 9, mean length of tracheids and/or fibriform vessel elements, μm ; 10, mean diameter at widest points of tracheids and/or fibriform vessel elements, μm ; 11, Mean wall thickness of tracheids and/or fibriform vessel elements, μm ; 12, apotracheal parenchyma distribution (A = aliform, AC = aliform-confluent, D = diffuse, N = narrow bands, P = patches of thin-walled parenchyma; V = vasicentric, VS = vasicentric scanty, W = wide bands); 13, mean width of multiseriate rays, no. of cells; 14, mean height of multiseriate rays, μm ; 15, mean height of uniseriate rays, μm ; 16, ray histology (p = procumbent cells, s = square cells, u = upright cells, upper case letters indicate predominant type or types).

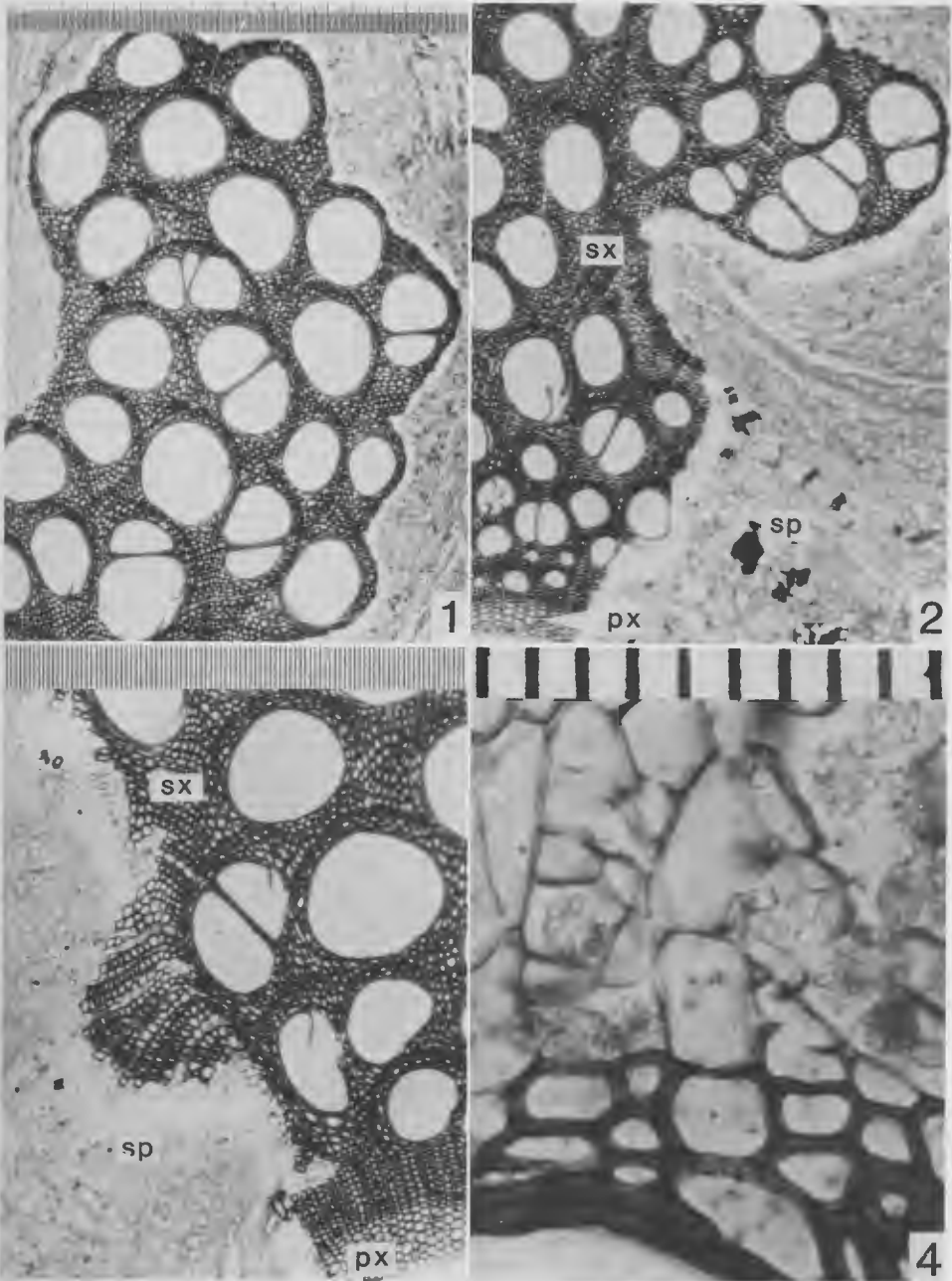


Fig. 1-4. Wood transections of *Bonamia* and *Breweria*.—1-3. *Bonamia maripoides* (SJRw-55483).—1. Lobe of secondary xylem surrounded by secondary phloem except at bottom, which connects to the vascular cylinder.—2. Portion of the furrowed xylem, primary xylem at extreme lower left, break in vascular cylinder bottom, center.—3. Portion of furrowed xylem showing addition of a bulge of secondary xylem (center); primary xylem at lower right.—4. *Breweria menziesii* (SJRw-26329), portion of vessel (lower left), thick-walled vasicentric parenchyma adjacent to the vessel (near bottom), and thin-walled parenchyma containing druses. Labels: px = protoxylem, sp = secondary phloem, sx = secondary xylem. (Fig. 1, 2, scale for magnification above Fig. 1 [finest divisions = 10 μ m]; Fig. 3, scale above Fig. 3 [divisions = 10 μ m]; Fig. 4, scale above Fig. 4 [divisions = 10 μ m].)

study in which successive cambia occur. An undulate outline of the secondary xylem, as seen in transection, is evidence of this and can be seen in *Dicranostyles densa* (Fig. 21, top), *Ipomoea adenoides*, *I. pauciflora* (Fig. 33, bottom), *Maripa janusiana* (Fig. 37, right), *Operculina palmeri* (Fig. 42, top), and *O. passifloroides* (Fig. 50, top).

Successive cambia characterize all of the genera studied here except for *Bonania*, *Breweria*, *Convolvulus*, *Mina*, and *Wilsonia*. Obaton's (1960) figures indicate successive cambia are lacking in *Neuropeltis* and *Prevostea*. Successive cambia are designated by means of the term "concentric interxylary phloem" in earlier literature. This is a misnomer, because the phloem formed by successive cambia is formed externally to each of the cambia (just as in dicotyledons with a single "normal" cambium), and therefore is not within the xylem at all. The term "interxylary phloem" is now reserved for instances in which phloem strands, embedded within secondary xylem, are produced internally by a cambium. Most instances of true interxylary phloem occur in species with only a single cambium, and thus for clarity that variant can be termed "interxylary phloem produced by a single cambium."

Successive cambia can be indefinite in number, as in *Ipomoea arborescens*, where larger stems have numerous concentric rings of vascular tissue (Fig. 27: This specimen is 6 cm in diameter, and stems in this species can exceed 30 cm in diameter.). Paucity of successive cambia was observed in *Ipomoea fistulosa*, in which the cultivated specimen had only a single cambium in the stem at the time it was harvested (when the "tree" was 2.5 m tall), but in the main root, a second cambium had formed. Only a single cambium was observed in the material available of *I. tiliaceae*, but a larger stem of this species (or the root) might well prove to have more than one cambium, because all of the remaining species of *Ipomoea* studied had two or more cambia. Vascular products—xylem, phloem, and conjunctive tissue—of more than one cambia are shown here for *Dicranostyles densa* (Fig. 21), *Ipomoea pauciflora* (Fig. 33, 34), and *Maripa janusiana* (Fig. 37). For other species with successive cambia, only portions of secondary xylem produced by one of the cambia are illustrated here (Fig. 22, 23, 25, 28, 29, 31, 36, 39, 41, 42, 43, 45, 49, 50, 53).

Convolvulaceae are well known for possessing intraxylary phloem: strands of phloem at the periphery of the pith, internal to the primary xylem (Fig. 31). An unexpected finding of the present study is that in lianoid Convolvulaceae, cambial action occurs at the inner face of the intraxylary phloem (Table 1, column 1, "IP" and "IPX"). This cambial activity is evident not just in the crushing of earlier-formed phloem (which one could attribute merely to crushing of protophloem by metaphloem as the latter matures without evidence of this cambial activity) but by formation of tangential divisions in the cambium associated with intraxylary phloem. The amount of phloem produced by the cambium is quite extensive in some species, in which it obliterates the pith. These cambial divisions were seen on the outer face of intraxylary phloem in all of the lianoid species studied here in which pith portions were present.

In several species, prolonged action by the intraxylary phloem cambium produces a limited amount of secondary xylem as well. This is shown for *Operculina palmeri* (Fig. 45—three vessels internal to primary xylem; Fig. 47—one vessel; Fig. 48—four vessels and associated lignified fibriform cells). The intraxylary

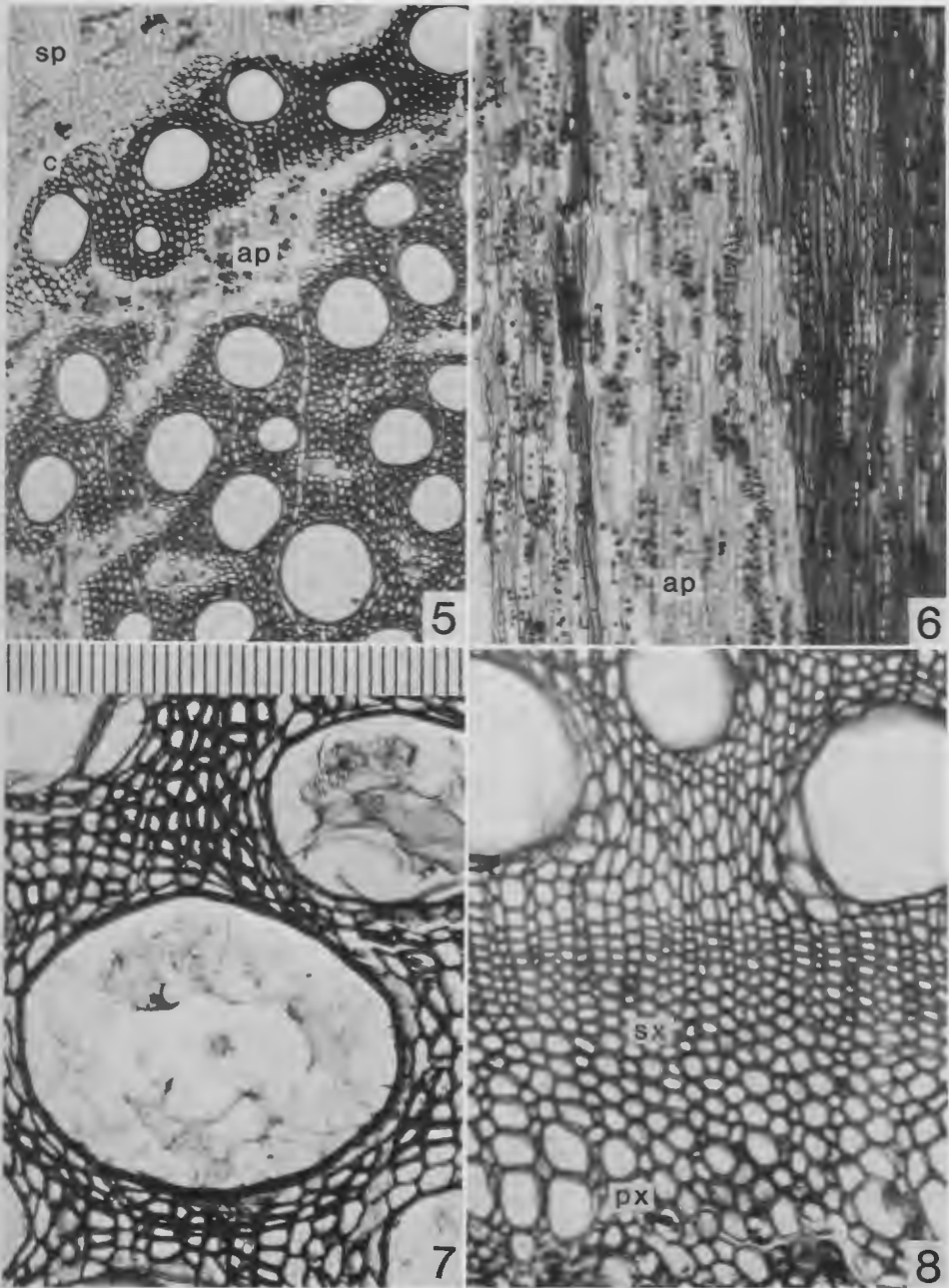


Fig. 5-8. Wood sections of *Breweria* and *Exogonium*.—5-6. *Breweria menziesii* (SJRw-26329).—5. Transection; numerous patches of thin-walled druse-containing parenchyma within the wood; periphery of the wood near top.—6. Tangential section; thin-walled parenchyma in left two thirds of photograph.—7-8. *Exogonium bracteatum* (Carlquist 8024), transections of wood portions.—7. Vessels containing thin-walled tyloses that contain druses.—8. Section near inside of vascular cylinder, pith at bottom; metaxylem vessels are succeeded by wood containing only tracheids (and fibriform vessel elements), then (top) wood containing wide vessels. Labels: ap = axial parenchyma; c = cambium; px = primary xylem; sp = secondary phloem; sx = secondary xylem. (Fig. 5, 6, scale above Fig. 3; Fig. 7, 8, scale above Fig. 7 [divisions = 10 μ m].)

phloem cambium is well illustrated in Figure 47. The dark grey crescent at the bottom of Figure 45 is an extensive mass of crushed secondary phloem. Note should be taken of the inverted nature of the xylem (produced externally by the intraxylary phloem cambium). Inverted vascular strands in the pith of three species of *Prevostea* figured by Obaton (1960) probably represent the cambial action described above.

The occurrence of cambial activity in the pith, with consequent increase in the tissue volume of the pith region there, may be the cause for splitting of the vascular cylinder. Where this occurs, new tissues are formed in the fracture, which is radial in orientation. This activity, termed ray cambium here (Table 1, column 1), produces xylem and phloem. This activity is shown for *Bonamia maripoides* (Fig. 2, lower right), but more conspicuously in *Operculina palmeri*, in which the edges of the vascular cylinder fractured apart are shown (Fig. 46, top and bottom). The ray cambium produces phloem adjacent to the fractured xylem face, and xylem distal to the fractured xylem face. In the section shown, there are two cambia in the fractured area, so that the products from top to bottom are secondary phloem of upper cambium, secondary xylem of upper cambium (thicker-walled cells), secondary xylem from lower cambium, secondary phloem from lower cambium ("upper" and "lower" used here merely with reference to position in photograph, Fig. 46). Photographic evidence that cambial activity in the pith region leads to fracture of the vascular cylinder is not presented here because scanning of portions at low power is required to see the nature of this activity. We will be happy to share slides with investigators interested in seeing this process.

Axial parenchyma patches within the secondary xylem (conjunctive tissue is excluded from this by definition) is common in lianoid Convolvulaceae. These patches are denoted by "P" in Table 1, column 12. These patches have thin nonlignified walls, in contrast to the vasicentric parenchyma that characterizes all Convolvulaceae (Table 1, column 12) and that has thicker, lignified walls. This contrast can be seen in Figure 4, in which the thin-walled parenchyma occupies the top two thirds of the photograph; the thick-walled vasicentric parenchyma is above the crescentlike portion of the vessel wall. Druses are common in the patches of thin-walled parenchyma (Fig. 4, 5, 6), just as they are in phloem parenchyma of most Convolvulaceae. The similarity of the thin-walled axial parenchyma patches to phloem parenchyma in such respects as druses and wall thickness leads one to ask whether this axial parenchyma contains sieve-tube elements. Careful examination revealed sieve-tube elements only in the axial parenchyma patches of *Turbina stenosiphon*. In this species, occasional sieve-tube elements, usually with two sieve areas per sieve plate (rather than the more numerous sieve areas per sieve plate in the secondary phloem) and inconspicuous sieve areas on lateral walls of sieve-tube elements, were clearly observable. The liquid preservation of stems of this species doubtless aided detection of these sieve-tube elements. Thus, *Turbina stenosiphon* has true interxylary phloem (phloem produced externally by the successive cambia is excluded, as noted earlier). Interxylary phloem like that of *Turbina stenosiphon* has been reported and clearly shown by Lowell and Lucansky (1986). Although sieve-tube elements were not observed in other species that have the druse-containing patches of thin-walled parenchyma, one cannot categorically state that sieve-tube elements are always absent in these patches: study of liquid preserved material is recommended. Cells in these areas in dried

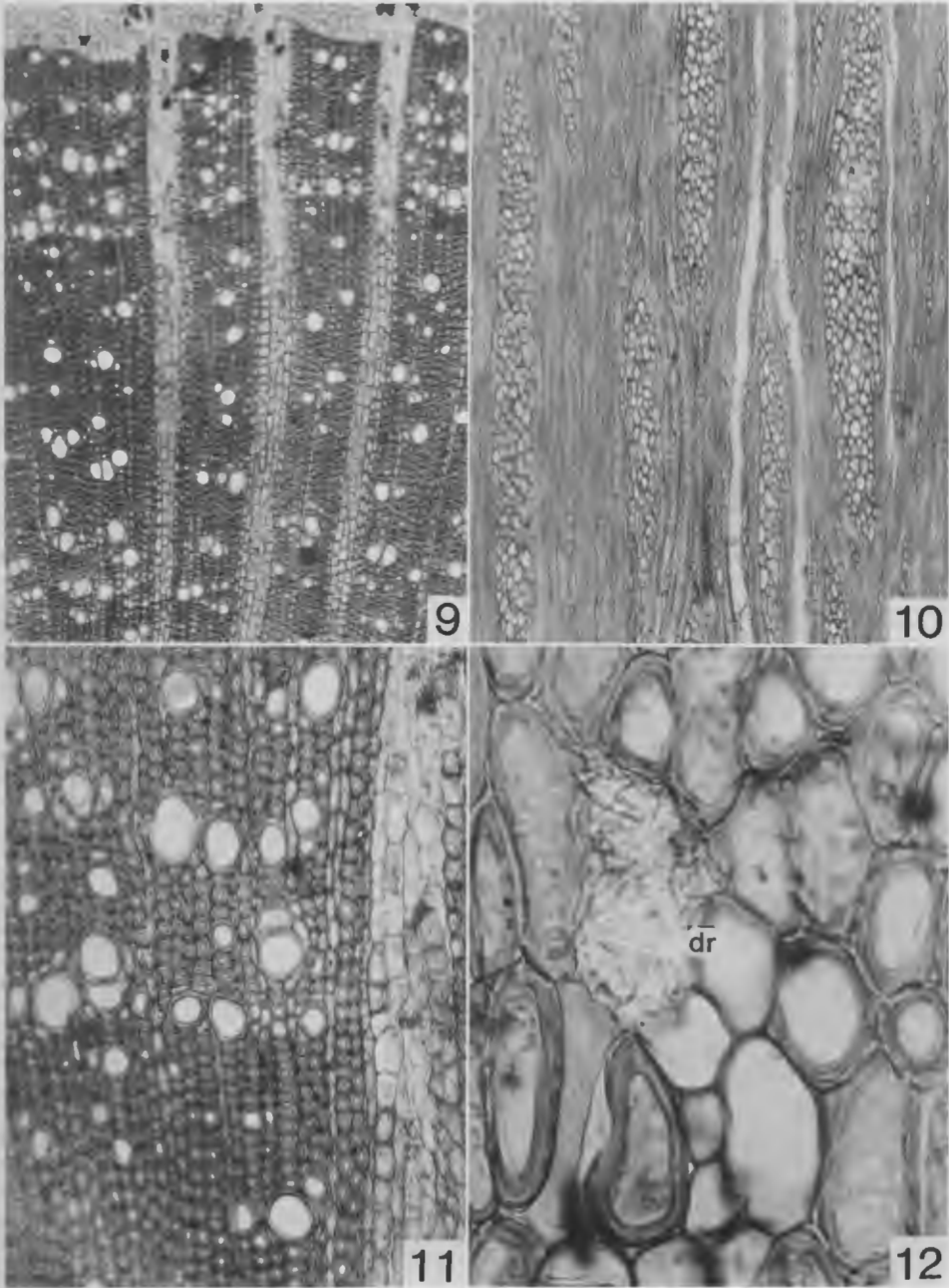


Fig. 9-12. Wood sections of *Convolvulus cneorum* (Carlquist 15941).—9. Transection; vessels notably small in diameter.—10. Tangential section; multiseriate rays are conspicuous.—11. Transection; tracheids are notably thick walled.—12. Portion of ray from tangential section; druse in thin-walled cell, above. Label: dr = druse (Fig. 9, 10, scale above Fig. 3; Fig. 11, scale above Fig. 7; Fig. 12, scale above Fig. 4.)

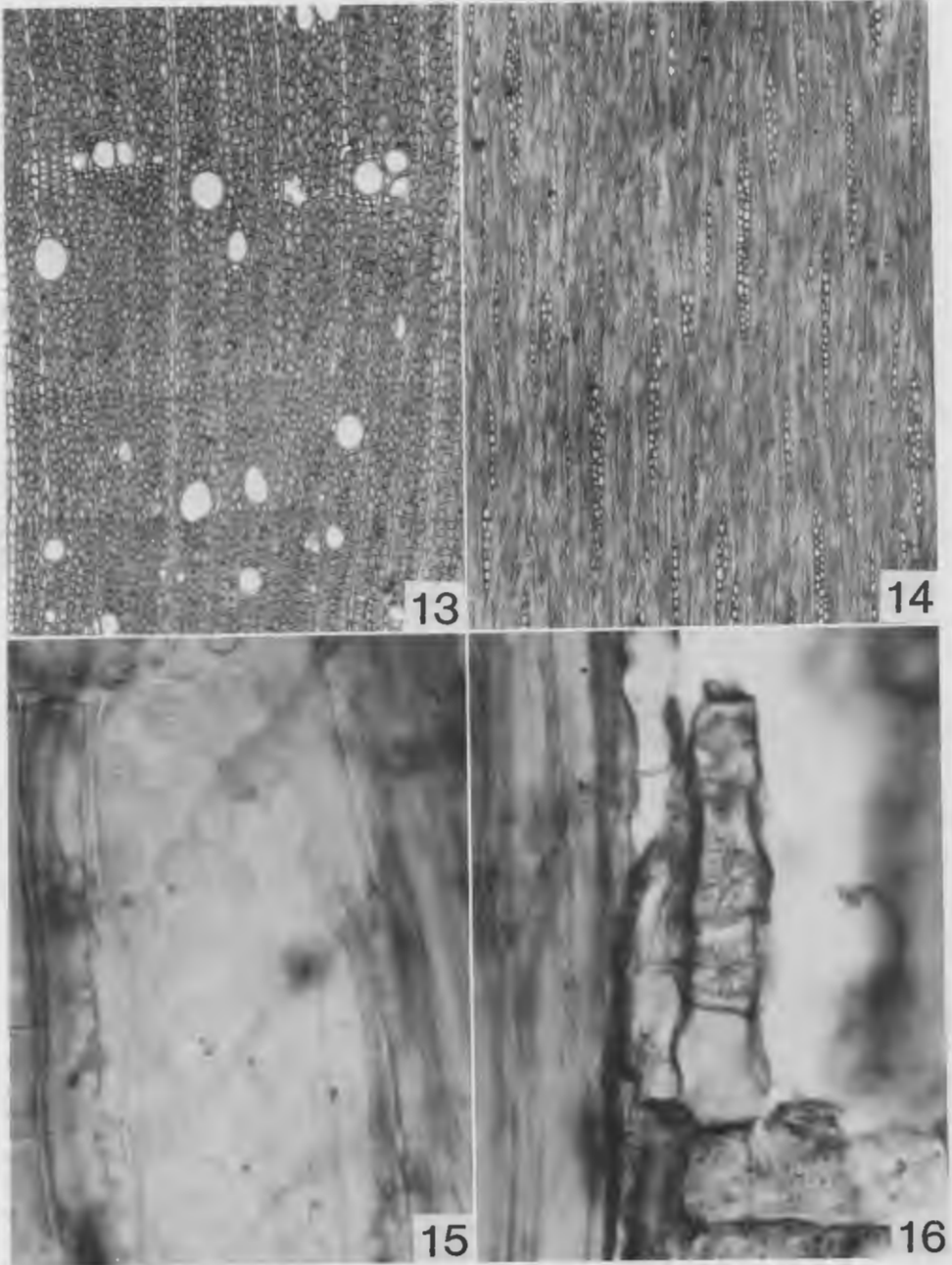


Fig. 13–16. Wood sections of *Convolvulus floridus* (Carlquist 2501).—13. Transection; vessels are sparse.—14. Tangential section; rays are biseriate or uniseriate.—15. Vessel from radial section; pits and pit apertures are circular in outline.—16. Thin-walled parenchyma from radial section; druses are present in the cells. (Fig. 13, 14, scale above Fig. 3; Fig. 15, 16, scale above Fig. 4.)

specimens (Fig. 36, 41, 42) show various degrees of preservation, and do not yield reliable conclusions—particularly if sieve-tube elements are sparse, as they are in the interxylary phloem of *Turbina stenosphon*. Axial parenchyma, no matter how abundant, in the stems of Convolvulaceae (and other families) is not considered an “anomaly” or cambial variant (Carlquist 1988a), unless it contains interxylary phloem.

Growth Rings

Although some of the Convolvulaceae studied occur in climates with marked seasonality (especially with respect to rainfall), there is little evidence of growth-ring activity in any of the collections. Vessels are, however, slightly larger at the beginning of seasonal increments in woods in *Convolvulus floridus* and *C. scoparius*. Metcalfe (1935) cites “thin-walled fibers” as indicating growth rings in *C. scoparius*, but these “fibers” may, in fact, be what we have identified as axial parenchyma (Fig. 17). In Convolvulaceae with successive cambia, the cambia are not initiated annually. One can occasionally see cell layers within the secondary xylem produced by successive cambia that suggest brief cessation of growth (Fig. 25). These layers are not annual in occurrence, however. Terminal parenchyma, a phenomenon related to growth-ring activity, was identified in *Ipomoea murucoides* (SJRw-53328).

Vessel Density

Vessel density bears a direct relationship to presence of successive cambia. Because the stems of species with successive cambia contain conjunctive tissue (tissue between successive vascular rings) as well as secondary phloem, the number of vessels per mm² is less if stems are randomly scanned than if the number of vessels per mm² is based on scanning secondary xylem only. We have chosen to base the figure on random scanning of an entire stem. The rationale for this procedure is that the degree of parenchymatization within a stem should be reflected in this figure rather than excluded from it. If, however, one does wish to compare how much greater the number of vessels per mm² would be if one scanned only secondary xylem, we can furnish comparative figures. In the following species, the first figure in parentheses is based on secondary xylem only, the second on scanning the entire stem (inside the cortex): *Ipomoea mauritiana* (38, 15), *I. murucoides* (10, 3), *Maripa janusiana* (27, 14), *M. panamensis* (25, 12), *Merremia peltata* (16, 10), *Operculina passifloroides* (16, 10). The figures for these species when averaged can be expressed: (22, 11). Thus, with appreciable deviations, the density of vessels if based only on secondary xylem is about twice what one calculates on the basis of the stem inside the cortex. The four species with “normal” cambia (*Convolvulus*, *Wilsonia*) have a much higher average number of vessels per mm² (121).

The figure for number of vessels per mm² in the lianoid Convolvulaceae is, in fact, moot because in all of these species there are fibriform vessel elements as well as tracheids. These cell types appear identical to each other in transection, and one cannot obtain a figure for the proportion of each in a given wood for reasons given in connection with fibriform vessel elements. Therefore, fibriform vessel elements were excluded from vessel density calculations, and only “obvi-

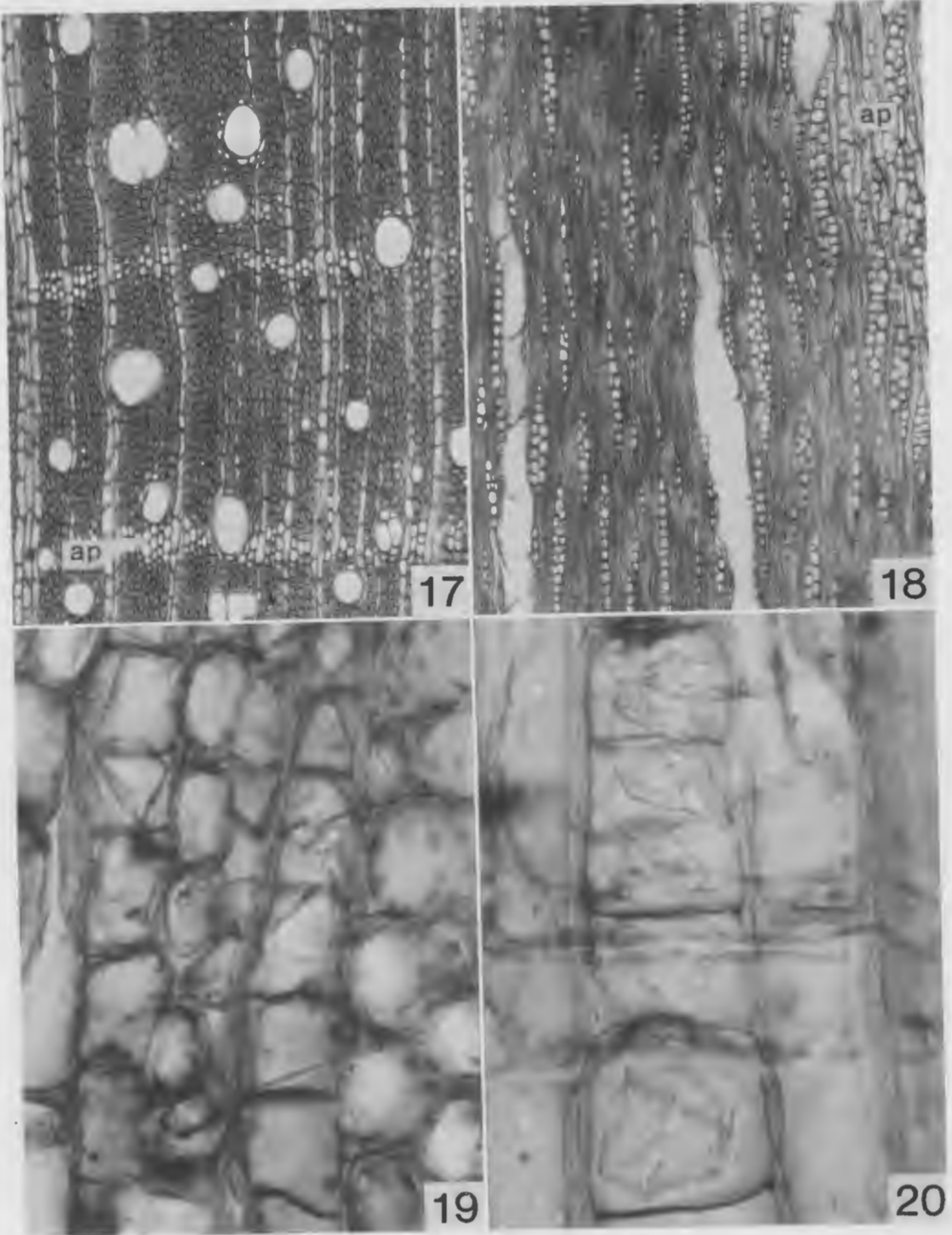


Fig. 17-20. Wood sections of *Convolvulus scoparius* (Carlquist 2486).—17. Transection; two narrow bands of parenchyma shown.—18. Tangential section; portion of parenchyma band, upper right.—19. Axial parenchyma containing chambered rhomboidal crystals from radial section.—20. Procumbent ray cells (running vertically in photograph) containing chambered rhomboidal crystals. Label: ap = axial parenchyma. (Fig. 17, 18, scale above Fig. 3; Fig. 19, 20, scale above Fig. 3.)

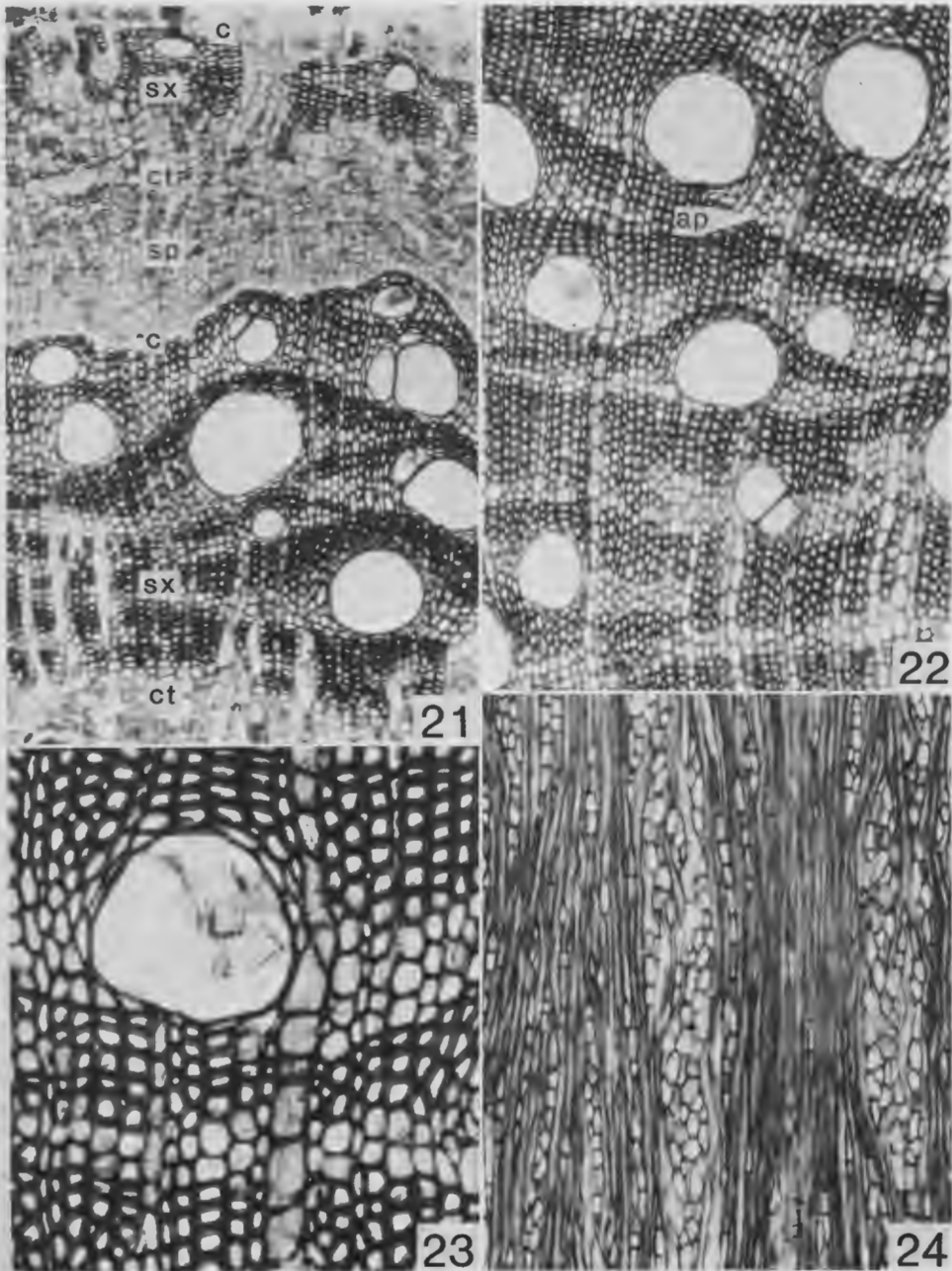


Fig. 21-24. Wood sections of *Dicranostyles densa* (SJRw-40316).—21. Transection, showing vascular tissue produced by two successive cambia (smaller xylary band above).—22. Transection; axial parenchyma is aliform-confluent.—23. Transection; vasicentric scanty parenchyma around vessel in which there are tyloses containing rhomboidal crystals.—24. Tangential section; multiseriate and uniseriate rays are about equally frequent. Labels: ap = axial parenchyma; c = cambium; ct = conjunctive tissue; sp = secondary phloem; sx = secondary xylem. (Fig. 21, 22, 24, scale above Fig. 3; Fig. 23, scale above Fig. 7.)

ous" vessels as seen in transection were counted. Thus the actual number of vessels per mm² in the lianoid species is considerably greater than the figures given, no matter which of the two bases for calculation is used.

Vessel Grouping

If one disregards fibriform vessel elements and bases observations only on vessels obvious as seen in transection, one can say that vessels are mostly solitary in Convolvulaceae (Table 1, column 3). Although the figures show a range for the family, they are sufficiently low so that one can say that in most species contact between vessels is essentially random. Because vessels in Convolvulaceae are relatively large, random contact between vessels is inevitable. The mean number of vessels per group for lianoid Convolvulaceae (1.13) is essentially the same as for the four shrubs (1.21). Species with characteristically nearly solitary vessels are illustrated in Figures 1, 2, 5, 9, 13, 17, 22, 25, 28, 29, 33, 34, 41, 42, and 45. *Argyreia obtusifolia* has a notably high number of vessels per group (1.82), a circumstance that will be discussed in a later section.

Vessel Restriction Patterns

The term "vessel restriction patterns" (Carlquist 1988a, Carlquist and Zona 1988a) has been applied to instances in which vessels are rarely in contact with rays, and thus show a nonrandom distribution in woods such as *Valeriana glauca* Poepp. (Carlquist 1983), *Hunnemannia fumariaefolia* Sweet (Carlquist and Zona 1988a), and *Isomeris arborea* Nutt. (new record). The tendency of vessels to be absent from the latewood—half or more of each growth ring—in growth-ring types 5A and 5C (Carlquist 1988a) might also be regarded as a type of vessel restriction.

In contrast to the above types of vessel restriction patterns, we are recognizing several new types of vessel restriction that occur in Convolvulaceae (fibriform vessel elements are disregarded in these examples, and only vessels with terminal perforation plates are considered). One type of vessel restriction is the tendency for vessels to be absent or rare early in the secondary xylem of each vascular band yet abundant in the later-formed secondary xylem of each band (Fig. 28). This tendency is clearly represented in *Ipomoea pauciflora* (Fig. 33, 34), in which each cambium tends to produce strands of wood in which vessels are abundant, strands which extend outward from the vascular band. The tendency for vessels to be restricted to the latter part of wood in each vascular band was observed in all collections of *I. arborescens* and *I. pauciflora*, so this type of vessel restriction is probably characteristic of particular species.

A second type of vessel restriction pattern in Convolvulaceae is represented by *Ipomoea fistulosa* (Fig. 29). In this species, vessels tend to occur in radial strips separated from each other by vessel-free secondary xylem.

A third anatomical condition possibly referable to the concept of vessel restriction patterns is formed in Convolvulaceae by the rather sudden shift between earlier-formed secondary xylem and the secondary xylem—presumably formed later in the first year—in which large vessels are present. This is illustrated for *Bonamia maripoides* (Fig. 2, lower left corner, Fig. 3, lower right), *Exogonium bracteatum* (Fig. 8—pith at bottom), and *Operculina palmeri* (Fig. 45). This pattern was also observed in *Breweria menziesii*, most species of *Ipomoea* studied (primary

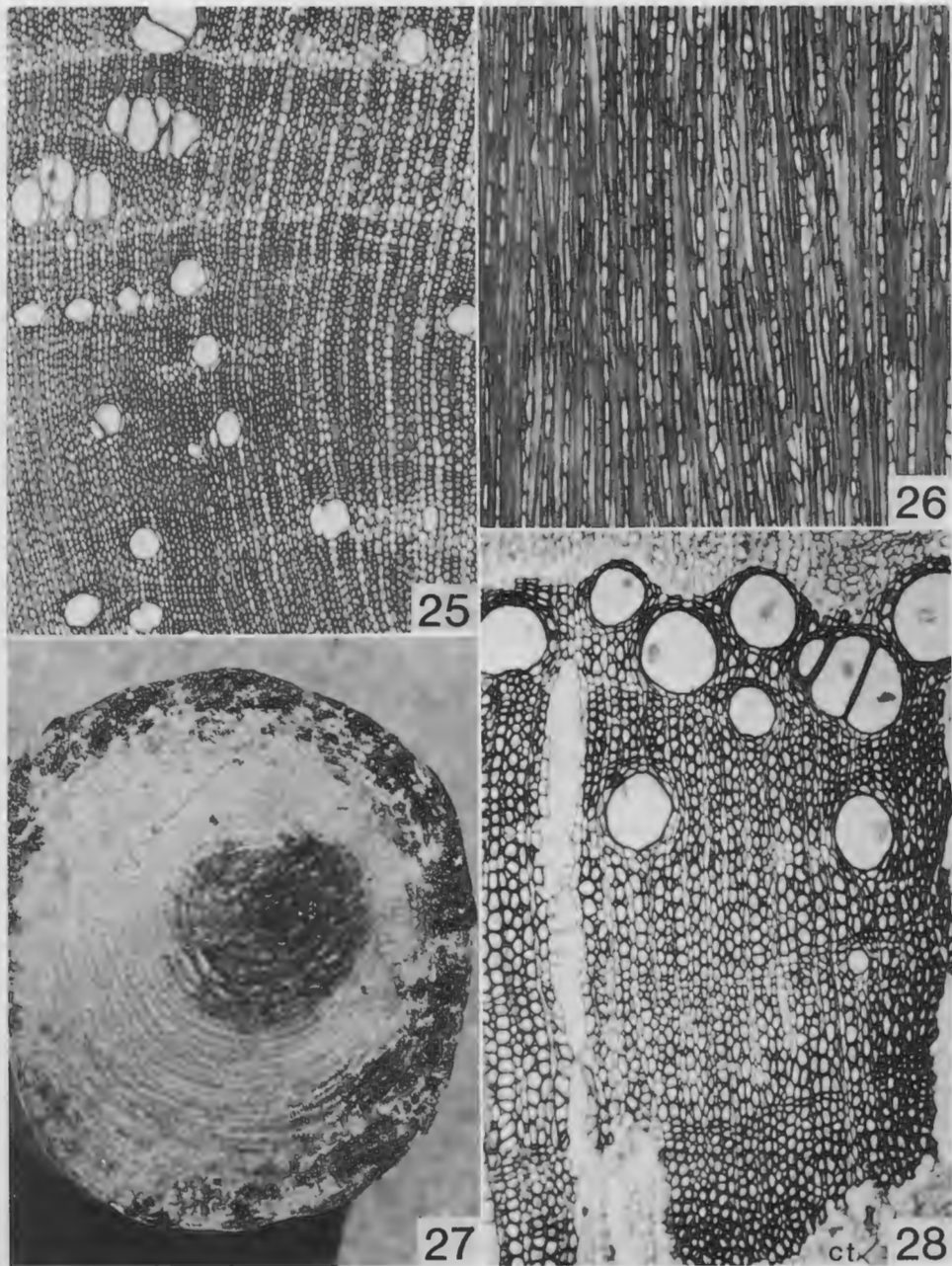


Fig. 25-28. Wood of *Ipomoea*.—25-26. *I. adenoides* (MADw-37405).—25. Transection; axial parenchyma is present as narrow bands.—26. Tangential section; rays are mostly uniseriate with upright cells predominant.—27-28. *I. arborescens* var. *glabrata* (Carlquist 8027).—27. Freshly cut stem transection with about 30 concentric rings of vascular tissue; dark patches are dried latex.—28. Transection of xylem of one vascular band, showing tendency of vessels to be produced late in the band. (Fig. 25, 26, 28, scale above Fig. 3; widest diameter of stem in fig. 27 is 4.2 cm.)

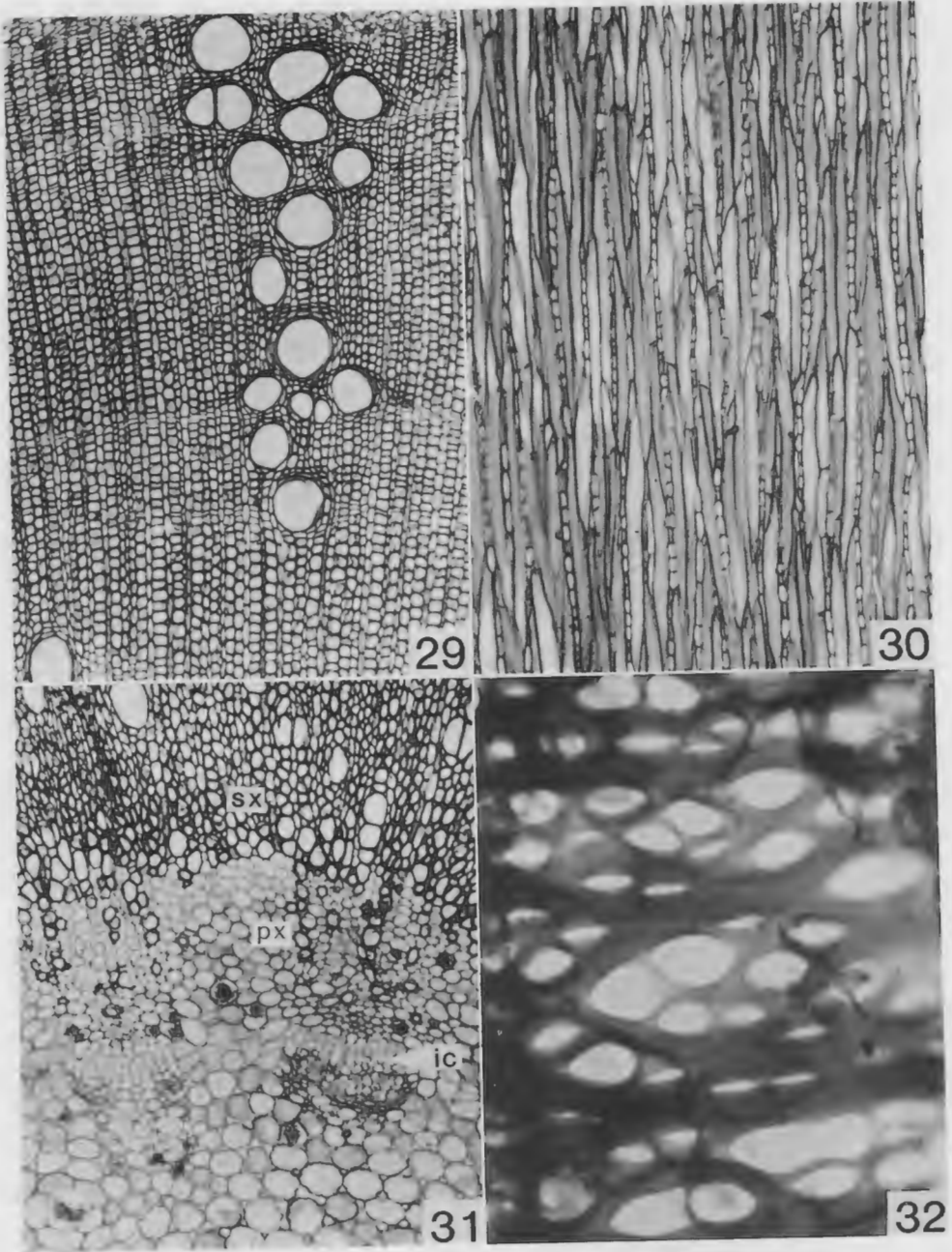


Fig. 29-32. Wood sections of *Ipomoea*.—29-30. *I. fistulosa* (Carlquist 15931).—29. Transection; vessels are restricted to radial groupings.—30. Tangential section; rays are uniseriate with upright cells.—31. *I. intrapilosa* (Dorado 633-1), transection of stem near pith; intraxylary phloem, below; primary xylem in center.—32. *I. verbascoidea* (Tw-35188), portion of vessel wall from radial section, showing vessel to axial parenchyma pitting. Labels: ic = intraxylary phloem cambium; px = primary xylem; sx = secondary xylem. (Fig. 29-31, scale above Fig. 3; Fig. 32, scale above Fig. 4.)

xylem was not present in all of the specimens available for study), *Maripa janusiana*, *Operculina passifloroides*, and *Turbina stenosphon*. One sees radial rows of vessels in metaxylem (possibly transitional to secondary xylem). Subsequent to production of this metaxylem, vessel formation ceases and only tracheids (or fibriform vessel elements) are formed, but after that, wood containing large vessels is produced. The vessel-free zone can be seen in Figure 8, center. This phenomenon is evident in the figures of Lowell and Lucansky (1986) for *Ipomoea hederifolia*.

Vessel Diameter

Wide vessels (Table 1, column 4) have been noted as characteristic of lianas (Schenck 1893; for a review, see Carlquist 1991); therefore, occurrence of wide vessels in lianoid Convolvulaceae is not surprising. Notably wide vessels are illustrated in Figures 3, 5, 21, 25, 28, 29, 34, and 37. All of these are at the same scale of magnification (the scale above Figure 3 applies to all of these). One can compare the vessel diameter of these lianas to that of the three shrubby species of *Convolvulus* (Fig. 9, 13, 17) shown at the same magnification. The narrowest vessels in the family, noted by Solereder (1908), are those of *Wilsonia humilis*. The shrubs have a mean vessel diameter of 50 μm , which is one fifth the mean vessel diameter of the lianoid species (256 μm ; *Argyreia obtusifolia*, for which wood from an herbarium specimen was studied, is omitted from this calculation). Vessel diameter is not greater in all species with successive cambia: the four collections of the tree *Ipomoea arborescens* have a mean vessel diameter of 132 μm —relatively large, but only half the mean diameter of the lianoid species.

Morphology and Wall Features of Vessels (Excluding Fibriform Vessel Elements)

Simple perforation plates were observed without exception in all Convolvulaceae.

Vessel wall thickness (Table 1, column 5) ranges from 3.0 μm in *Ipomoea fistulosa* (Fig. 29) to 11.3 μm in *Bonamia maripoides* (Fig. 1–3). Mean vessel wall thickness in the lianas is 8.4 μm , which is almost twice that of the shrubs (4.3 μm).

Lateral wall pitting of vessels is uniformly alternate in Convolvulaceae. Pits tend to be laterally elongate, and therefore oblong or elliptical in shape, in vessel-to-vessel contacts of *Bonamia maripodes* and *Breweria menziesii* (the vertical dimension only of pits are shown in Table 1, column 5). Vessel-to-vessel pits tend to be isodiametric in shape, whereas vessel-to-axial-parenchyma and vessel-to-ray pits are somewhat more laterally elongate (Fig. 32, 44). Vessel-to-vessel pits have a circular outline most frequently (Fig. 15), but pits polygonal in outline characterize *Argyreia obtusifolia*, *Exogonium bracteatum*, *Ipomoea arborescens*, *I. bona-nox*, *I. cardiosepala*, *I. fistulosa*, *I. intrapilosa*, *I. murucoides*, *I. pauciflora*, *I. tiliaceae*, *Merremia peltata*, and *Mina lobata*. Vessel-to-axial-parenchyma and vessel-to-ray pits have wide, gaping apertures, as shown in Figures 32 and 44. Vessel-to-vessel pits most often have elliptical apertures, but they are circular in some species (Fig. 15). Vessel-to-parenchyma pits tend to be grouped, with slender strips of wall material separating them (Fig. 32), and some of these pits have

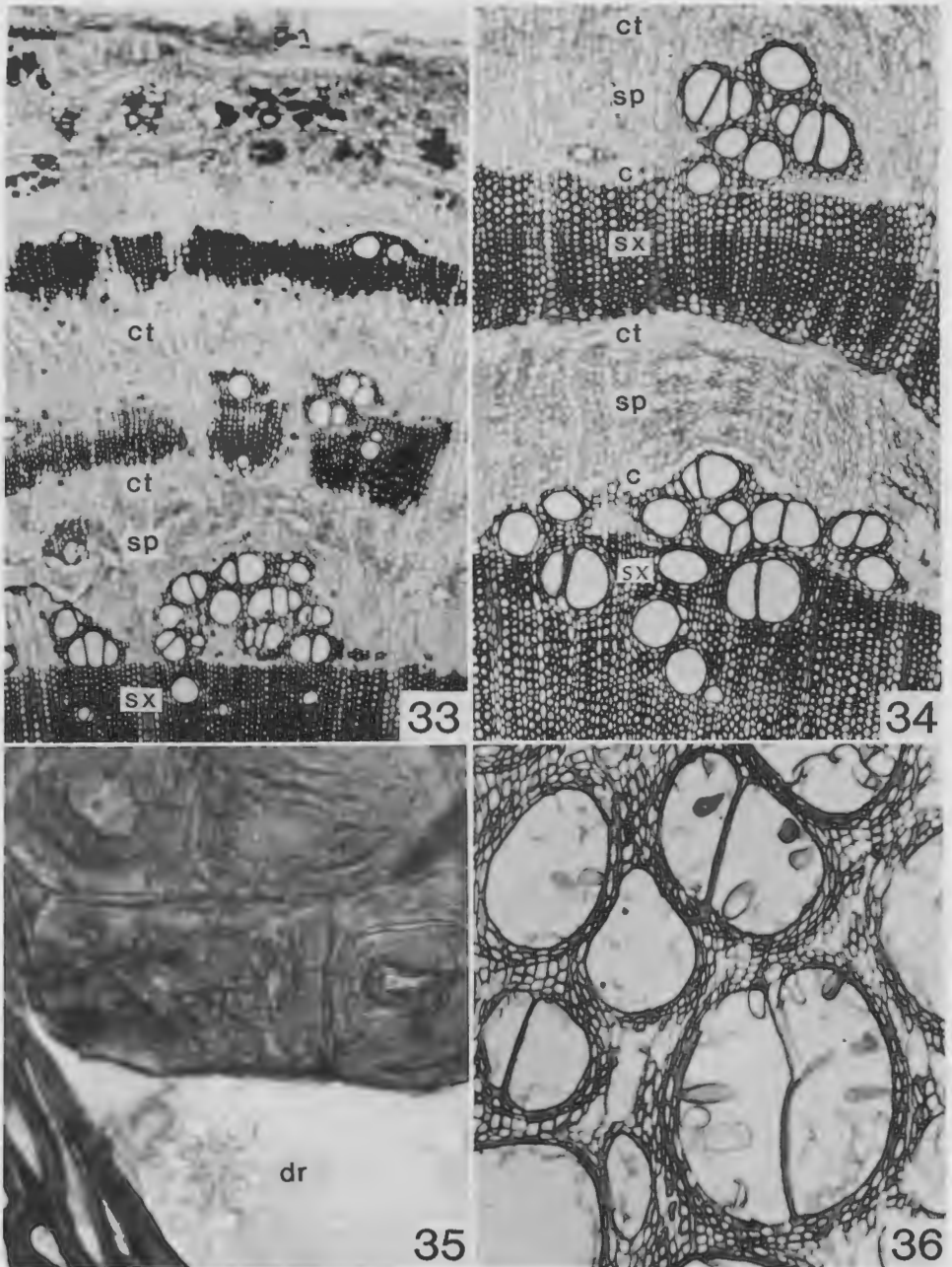


Fig. 33–36. Wood sections of *Ipomoea*.—33–34. *I. pauciflora* (Dorado 638-1).—33. Transection of stem, showing periderm (top), xylem produced by three successive cambia (dark).—34. Transection; vessels occur at outer portion of secondary xylem bands, which have irregular outline at close of cambial activity.—35. *I. cardiosepala* (SJRw-35995), sclerosed tyloses from transection; druse (presumably from thin-walled tylosis) below.—36. *I. tiliaceae* (SJRw-54734), transection; thin-walled sclerosed tyloses in vessels. Labels: c = cambium; ct = conjunctive tissue; dr = druse; sp = secondary phloem; sx = secondary xylem. (Fig. 33, scale above Fig. 1; Fig. 34, 36, scale above Fig. 3; Fig. 35, scale above Fig. 4.)

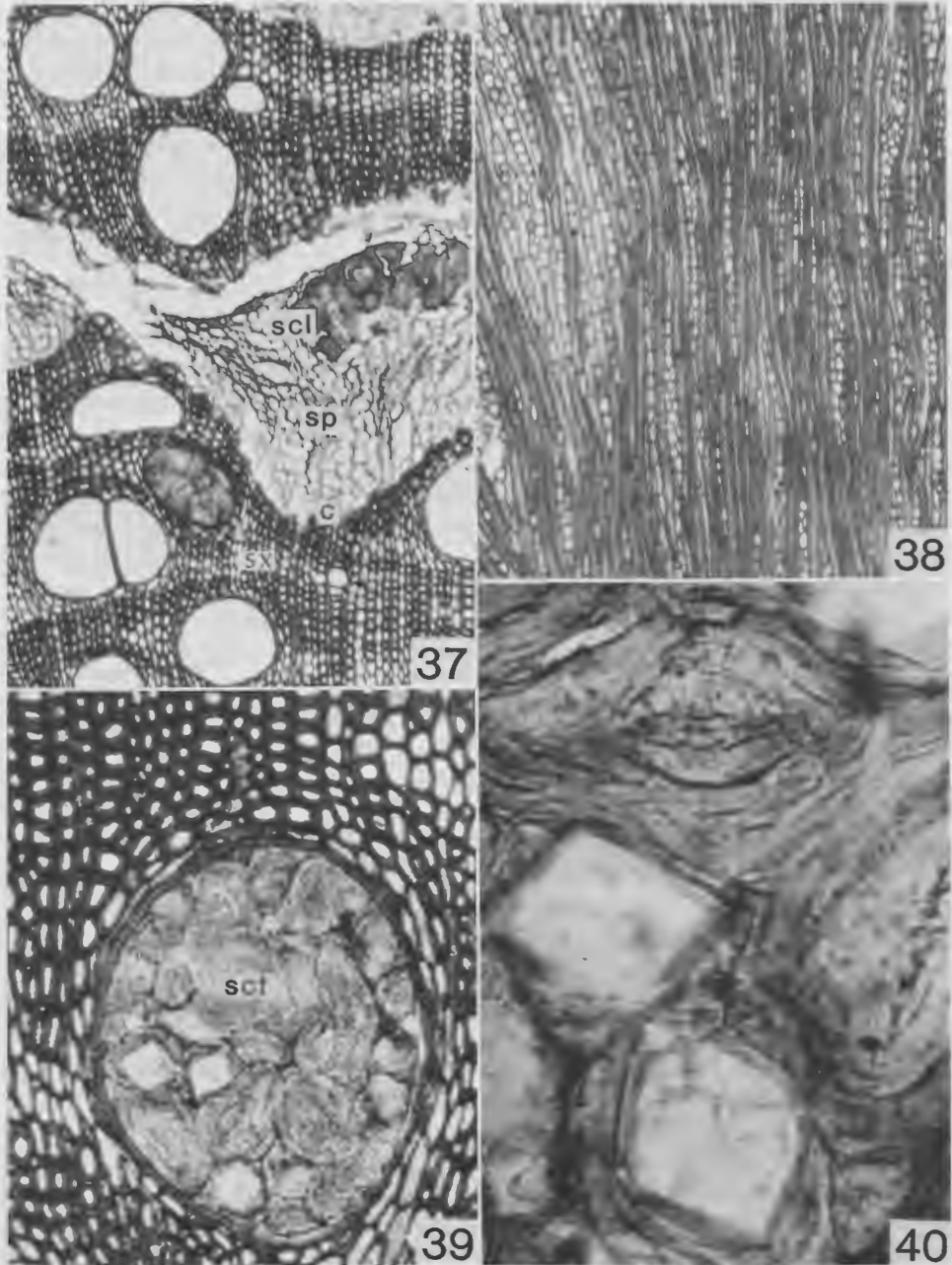


Fig. 37-40. Wood sections of *Maripa janusiana* (MADw-38476).—37. Secondary xylem of two vascular bands; sclereids in conjunctive tissue, center right.—38. Tangential section of secondary xylem; rays are uniseriate and multiseriate.—39. Vessel filled with sclerosed tyloses from transection.—40. Two rhomboidal crystals in sclerosed tyloses, from wood transection. Labels: c = cambium; scl = sclereid group; sct = sclerosed tyloses; sp = secondary phloem; sx = secondary xylem. (Fig. 37, 38, scale above Fig. 3; Fig. 39, scale above Fig. 7; Fig. 40, scale above Fig. 3.)

grooves interconnecting them (Fig. 44). Scanning electron microscope photographs reveal that grooves interconnecting pit apertures characteristically occur on vessel walls of *Operculina palmeri* (Fig. 54, left; 55). In this species, occasional thickenings on the vessel walls were also observed (Fig. 54, right). In no species of Convolvulaceae were true helical thickenings observed.

The range in size in vessel-to-vessel pits is shown in Table 1, column 6. These pit sizes are notably large when compared to those of dicotyledons at large (Metcalfe and Chalk 1950). The mean size for vessel-to-vessel pits in lianas (12.4 μm) is appreciably greater than that of the shrubs (7.5 μm).

Fibriform Vessel Elements

In Convolvulaceae, fibriform vessel elements characterize the majority of species. This term is used in the sense proposed by Woodworth (1935). The terms "perforated fiber-tracheid" (Woodworth 1934) and "perforated fiber" (Lemesle 1946) have been proposed, but should be abandoned because they are merely synonyms for fibriform vessel elements. Fibriform vessel elements are fusiform cells that are like imperforate tracheary elements except for the occurrence of a small subterminal perforation plate near each end of the cell. Fibriform vessel elements were observed in small but appreciable numbers, together with tracheids, in *Bonamia maripoides*, *Breweria menziesii*, *Convolvulus cneorum*, and *Ericybe coccinea*, whereas only tracheids were observed in *Convolvulus floridus*, *C. scoparius*, and *Wilsonia humilis*. In all other species studied here, fibriform vessel elements are abundant with some tracheids also present, but no clear demarcation between these two cell types exists in terms of length in these species. One would like to be able to discriminate between fibriform vessel elements and tracheids on the basis of perforation presence, but perforation presence is not easy to establish. One can see obvious subterminal perforations at the ends of fibriform vessel elements in some species (Fig. 51). However, in other species, one sees wide pits (perforations?) scattered along fusiform cells in addition to narrow pits. These latter pits certainly have pit membranes (Fig. 52, top; 56), which often can be seen by means of careful light microscope examination. The ideal way to distinguish between perforations and wide pits is to examine them by means of a scanning electron microscope. Using this technique, we were able to show that pit membranes can be present in what one would have called small perforations on the basis of light microscopy (Fig. 57). This observation may or may not apply to all such "perforations" in fibriform vessel elements of Convolvulaceae. Absence of pit membranes in some of these "perforations" might be the result of handling and preservation techniques rather than a natural occurrence. Another circumstance that leads one to question whether the wide pits are ever perforations is the fact that one can frequently observe wide pits, equivalent in size to what one might call small perforations on lateral walls of fibriform vessel elements, on interfaces between the fusiform cells and ray cells. Perforations between vessel elements and ray cells are absent except in the special case of perforated ray cells. Therefore, any given cell with large pits (small perforations?) cannot unequivocally be called a fibriform vessel element or a tracheid in this family. Probably fibriform vessel elements can be designated where the perforations are relatively large and tend to occur in radial rows (as seen in radial sections: e.g., Fig. 51). However, cells such as those shown in Figure 52, in which a few slightly wider pits (small

perforations?) are present may be tracheids more often than would be suggested by light microscopy. For these reasons, no positive distinction between fibriform vessel elements and tracheids is made in Table 1, columns 7, 9, and 11.

The pit diameter of lateral walls of fibriform vessel elements or tracheids is less than that of lateral wall pits on vessels (Table 1, column 7), although in most species studied, only 20–40% less.

Vessel Element Length

Vessel element length was measured for the wider vessels readily recognized as vessel elements and not for fibriform vessel elements. There is no difficulty in distinguishing between these two cell types, either in sections or in macerations.

Mean vessel element lengths in the species studied range from 124 μm to 467 μm (Table 1, column 8). In the shrubby species, vessel elements are only slightly shorter (257 μm) than in the lianoid species (279 μm). In some lianoid species, vessel elements are only a little longer than wide. Vessel elements that are a little shorter than they are wide characterize *Ipomoea bona-nox*, *I. cardiosepala*, *I. mauritiana*, *I. tuba*, *Merremia nymphaeifolia*, *M. peltata*, *Mina lobata*, *Operculina palmeri*, and *Stictocardia benaviensis*. Certainly these species have vessel elements shorter than those of arboreal dicotyledons from comparable habitats.

Tracheids and Fibriform Vessel Elements: Quantitative Features

In Table 1, column 9, the length of tracheids and/or fibriform vessel elements is given. If both are present in a species, an equal number of each (judged by apparent presence or absence of the small perforation plates) are included in the computation of the mean; otherwise the cell type that is much more abundant (see under *Fibriform Vessel Elements* above) is the basis of the mean. Separate means were computed in a few cases, and these show relatively small differences within a species between the two cell types. The mean tracheid length (first within parentheses) and fibriform vessel element length (second within parentheses) for several species are: *Exogonium bracteatum*, Carlquist 8005 (800, 787); *E. bracteatum*, Carlquist 8024, small stem (869, 801); *E. bracteatum*, Henrickson 2093 (775, 711); *Ipomoea adenoides*, MADw-37405 (804, 779); *I. arborescens* var. *arborescens*, Dorado 624-7 (858, 800). The small but consistent difference in length between the two cell types shows both that a small degree of differentiation is present, and that a continuum between the two cell types exists. The length of fibriform vessel elements when computed separately from that of tracheids does show that "ordinary" vessel elements and fibriform vessel elements do not form a continuum; the data, when plotted, yield a markedly bimodal curve.

Diameter of fibriform vessel elements and/or tracheids is given in Table 1, column 10. In combination with fibriform vessel element/tracheid wall thickness (Table 1, column 11), quantitative data convey a picture of how thick the walls are relative to cell diameter. For example, in *Convolvulus*, the tracheid wall thickness is approximately one third the diameter (therefore the lumen comprises one third the diameter). The prominently thick walls of tracheids in *Convolvulus* are evident in Figures 9, 11, 13, and 17. The reverse tendency, thin walls combined with relatively wide fibriform vessel elements and/or tracheids, is illustrated by *Exogonium bracteatum* (Fig. 7), *Dicranostyles densa* (Fig. 23), *Ipomoea adenoides*

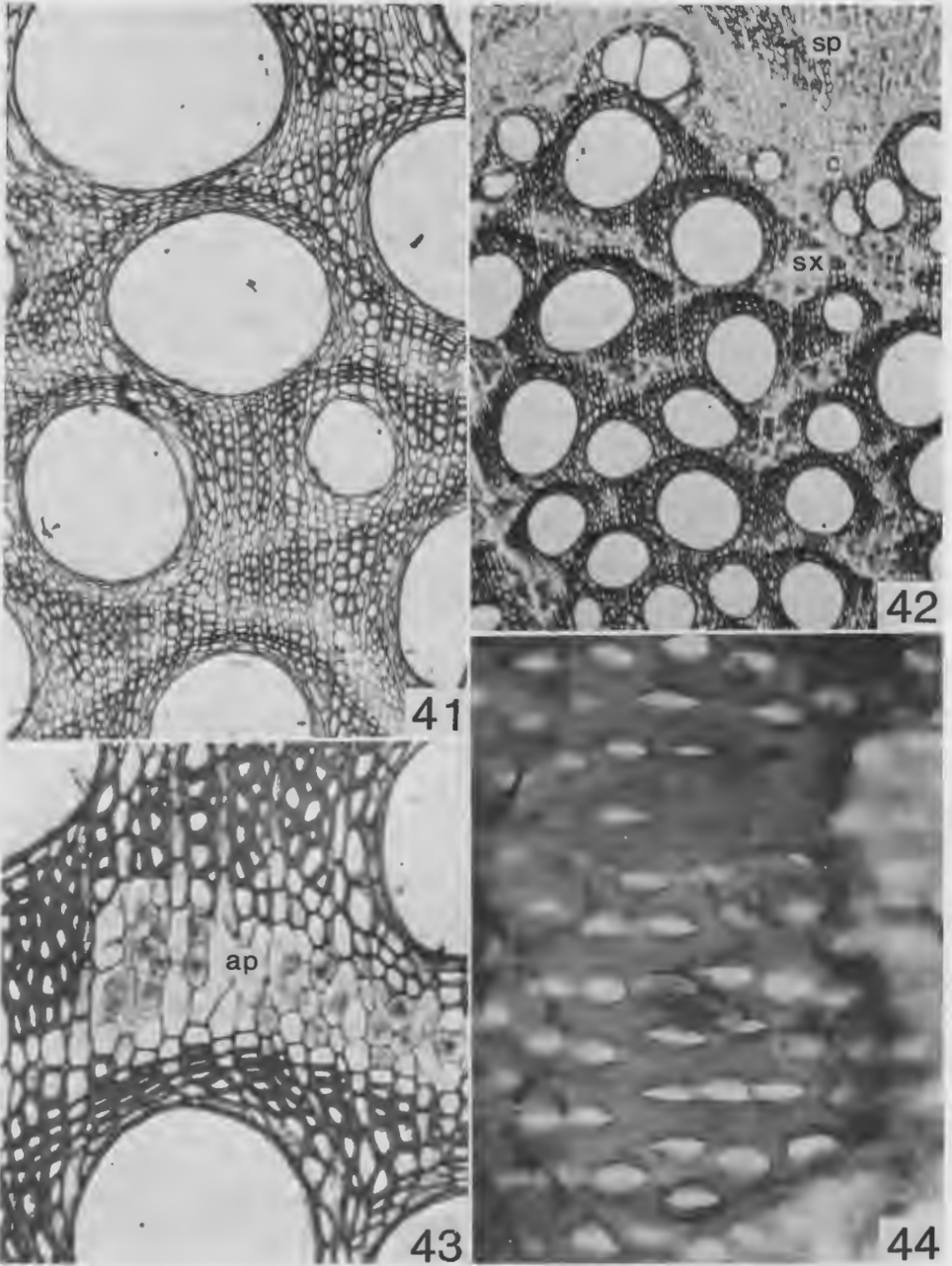


Fig. 41-44. Wood sections of *Merremia* and *Operculina*.—41. *M. peltata* (MADw-41005), transection; vessels are notably large, axial parenchyma in a modified aliform conformation.—42-44. *Operculina palmeri* (Carlquist 8022).—42. Transection, secondary phloem above; patches of axial parenchyma scattered among vessels.—43. Transection portion with a patch of axial parenchyma containing druses but no phloem.—44. Vessel wall from radial section, showing vessel to axial parenchyma pitting. Labels: ap = axial parenchyma; c = cambium; sp = secondary phloem; sx = secondary xylem. (Fig. 41, scale above Fig. 3; Fig. 42, scale above Fig. 1; Fig. 43, scale above Fig. 7; Fig. 44, scale above Fig. 4.)

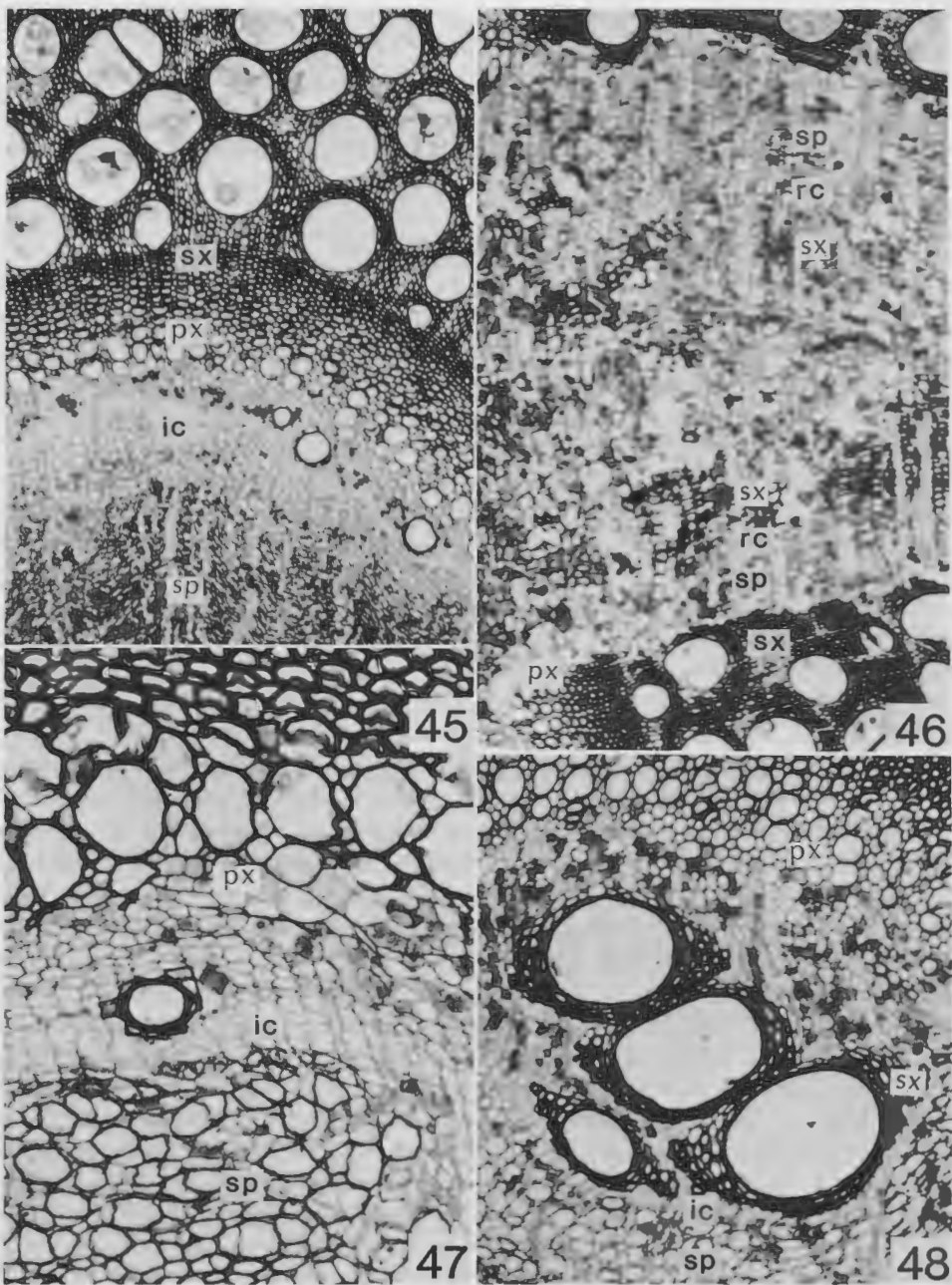


Fig. 45–48. Wood transections of *Operculina palmeri* (Carlquist 8021).—45. Section from near center of stem; dark zone below is secondary phloem produced by intraxylary phloem cambium, which has produced three secondary xylem vessels at periphery of pith zone also.—46. Portion of secondary xylem fractured radially, with xylem and phloem produced by the ray cambium filling the space (phloem is closer to each fractured surface, xylem more distal).—47. Section of pith region; from top to bottom: secondary xylem, primary xylem, vessel (sheathed by dark cells) produced by intraxylary phloem cambium, intraxylary phloem cambium, secondary phloem produced by intraxylary phloem cambium.—48. Four vessels produced by intraxylary phloem cambium in pith region of stem. Labels: ic = intraxylary phloem cambium; px = primary xylem; rc = ray cambium; sp = secondary phloem; sx = secondary xylem. (Fig. 45, 46, scale above Fig. 1; Fig. 47, scale above Fig. 7; Fig. 48, scale above Fig. 3.)

(Fig. 25), *I. arborescens* var. *glabrata* (Fig. 28), and, especially, *I. fistulosa* (Fig. 29). The hardness of woods of *Convolvulus* is in marked contrast with that of other Convolvulaceae, and wall thickness of tracheids and/or fibriform vessel elements explains the textural differences observed.

Imperforate Tracheary Elements: Terminology and Diversity

The most commonly encountered tracheary elements of Convolvulaceae, judged on the basis of macerations to be most likely imperforate, are termed tracheids in accordance with the terminology of Bailey (1936) and the IAWA Committee on Nomenclature (1964). The fully bordered nature of pits in convolvulaceous tracheids, and the relatively great diameter of these pits (Table 1, column 7) are criteria for calling these cells tracheids (density of pits is one criterion for recognition of a cell as a tracheid; see Carlquist 1988a). The density of pits on imperforate tracheary elements is great in *Bonamia*, *Breweria*, and *Wilsonia*, so clearly those genera have tracheids. The pits on the cells of *Ipomoea* that might be either fibriform vessel elements or tracheids (depending on whether small "perforations" do have pit membranes or not) are not so densely placed (Fig. 52, 56). However, supposing that the wide pits do, in fact, have pit membranes (and thus are not perforations), such wide pit membrane area would compensate for pit density, and would confer enhanced conductive capability on these cells—a conductive capability comparable to that of a densely pitted tracheid.

Fibriform vessel elements are mentioned in the studies on convolvulaceous woods by Mennega (1969), Pant and Bhatnagar (1975), and Lowell and Lucansky (1986) as present in the species these authors studied, respectively. Both tracheids as well as fiber-tracheids are reported for *Dicranostyles* by Mennega (1969) and *Ipomoea hederifolia* L. by Lowell and Lucansky (1986). These authors may base their distinction on degrees of pit density; although there is some diversity in degrees of pit density among imperforate tracheary elements in the species of *Dicranostyles* and *Ipomoea* in the present study, the differences are not sufficient to justify designation of the two classes of cells. Presence of septate imperforate tracheary elements, discussed below, constitutes an exception. Convolvulaceae, incidentally, do not appear to have vasicentric tracheids. Except for *Convolvulus* and *Wilsonia*, in which axial parenchyma cells adjacent to tracheids are few (and tracheids are present throughout the woods in these genera anyway), vessels of Convolvulaceae are completely sheathed by axial parenchyma. To be sure, fibriform vessel elements occur in many Convolvulaceae, but these do not have pitting so dense as that characteristic of vessel walls, so that tracheids adjacent to fibriform vessel elements would be likely to have only pitting of equally moderate density and would not be called vasicentric tracheids.

In the present study, septate imperforate tracheary elements with reduced pit border width and pit diameter compared to that of the tracheids they accompany were found in *Dicranostyles holostyla*, *Ipomoea arborescens* var. *arborescens* (Henrickson 2087), *I. prismatosiphon*, and *Turbina stenosisiphon*. These septate fiber-tracheids are less abundant than the tracheids in these species. Pant and Bhatnagar (1975) claimed not only tracheids and fiber-tracheids, but also libriform fibers for the wood of two species of *Argyreia*. Such a wide range of imperforate tracheary elements within a single wood would be unusual, so *A. obtusifolia* was also investigated by us. This *Argyreia* has nonseptate tracheids with large bordered pits,

septate fiber-tracheids with smaller bordered pits, and septate libriform fibers with simple pits as reported for *Argyreia* by Pant and Bhatnagar (1975). The significance of these findings will be explored in a later section of this paper.

Axial Parenchyma

There is a great diversity in distribution of axial parenchyma in Convolvulaceae, (Table 1, column 12). The basic form of axial parenchyma in Convolvulaceae is scanty vasicentric. Very few parenchyma cells surround the vessels in the species of *Convolvulus* (Fig. 9, 13, 17) and *Wilsonia*. In these genera, some vessels may be associated with only one or sometimes no parenchyma cells. This pattern is least well developed in *C. cneorum* (Fig. 9), in which the axial parenchyma is often abaxial or diffuse apotracheal rather than vasicentric. The presence of scanty vasicentric parenchyma is not readily seen in most Convolvulaceae (although it is present) because the parenchyma cells have lignified walls only a little thinner than those of imperforate tracheary elements. Also, the parenchyma cells surrounding the vessels are flattened parallel to the vessel wall and are thus inconspicuous. These conditions may be seen in *Operculina palmeri*, in which the vasicentric parenchyma is relatively abundant rather than scanty. The vessel of *Turbina stenosphon* (Fig. 53, left) shows the presence of vasicentric parenchyma that is typical for the family.

Various types of banded axial parenchyma characterize more than half of the Convolvulaceae studied. Apotracheal bands may be seen in the transection of *Convolvulus scoparius* (Fig. 17), as well as in the tangential section (Fig. 18, upper right). *Ipomoea adenoides* has more numerous apotracheal bands (Fig. 25). However, these bands of parenchyma frequently show a greater degree of association with vessels and must be given a term other than vasicentric. In *Dicranostyles densa*, for example, the parenchyma extends laterally from vessels in aliform extensions or in bands that qualify as confluent, aliform, or aliform-confluent (Fig. 21–23). *Maripa janusiana* (Fig. 37), *Merremia peltata* (Fig. 41), and *Operculina passifloroides* (Fig. 49, 50) show variations of aliform-confluent patterns. In *Argyreia obtusifolia*, axial parenchyma cells are very similar to imperforate tracheary elements (or fibriform vessel elements) in transection, and the distribution in transection, therefore, is difficult to establish. Comparison with longitudinal sections of this species demonstrate that the parenchyma is present in aliform patterns. Pant and Bhatnagar (1975) did not report on axial parenchyma distribution in the woods of *Argyreia* they studied. Examples of aliform-confluent axial parenchyma distribution are cited in Table 1, column 12.

In woods of some Convolvulaceae there are zones of apotracheal parenchyma that do not conform to banded patterns. In these species, parenchyma is abundant and thin walled, in contrast to the vasicentric parenchyma (which is also present in these species). Thin-walled parenchyma zones are designated as "patches" here (Table 1, column 12). Examples of parenchyma patches are shown for *Breweria menziesii* (Fig. 5, transection; Fig. 6, tangential section), and *Operculina palmeri* (Fig. 42, 43), whereas in *Convolvulus floridus* only a few small patches of thin-walled parenchyma occur. One of these patches is located about one fourth of the way from the top, just right of center in Fig. 13. Cells in the thin-walled parenchyma of this species contain druses or sphaerocrystals (Fig. 16). The druses occur in "chambered" cells (horizontally subdivided axial parenchyma, with one druse

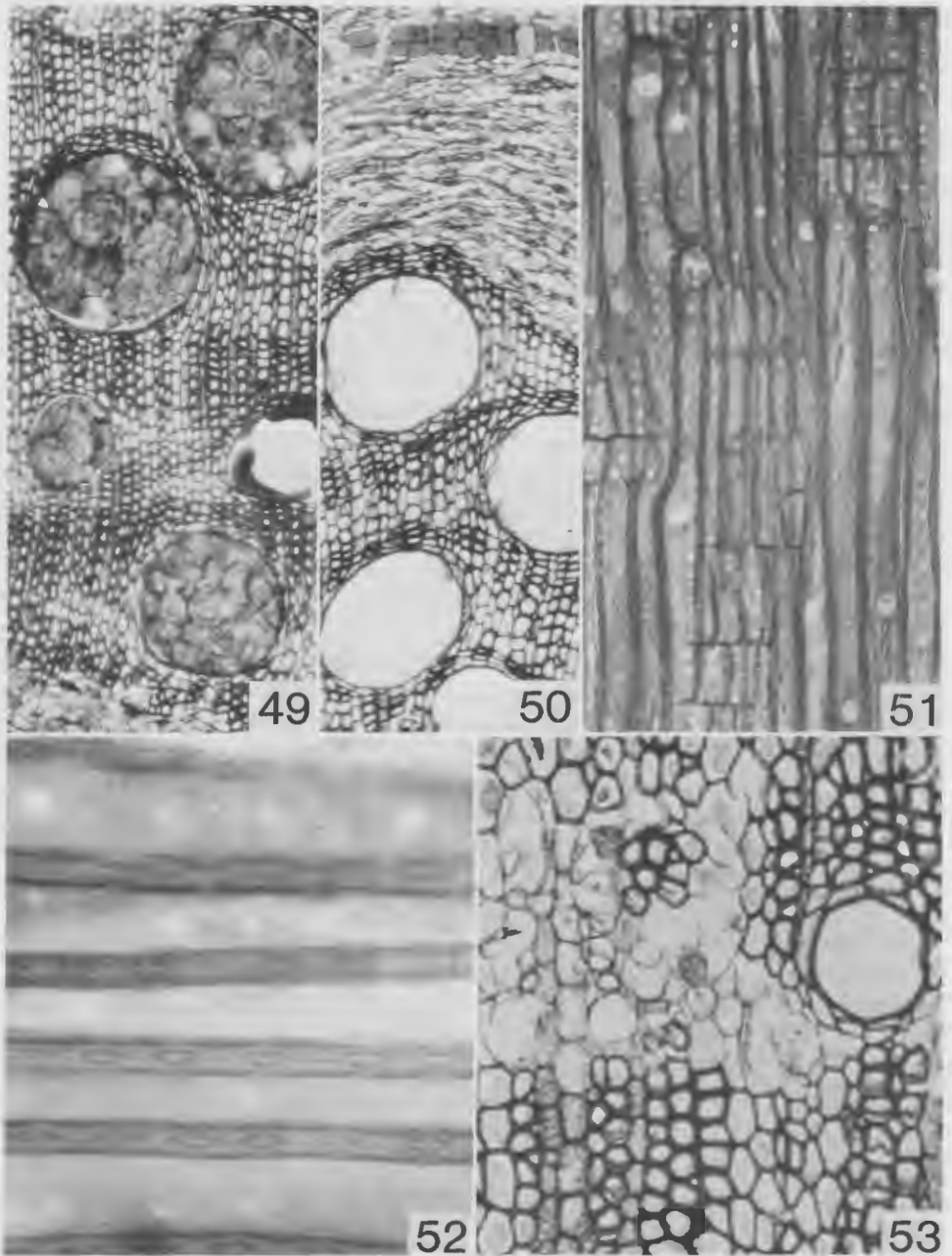


Fig. 49–53. Wood sections of *Operculina* and *Turbina*.—49–50. Transections of *O. passifloroides* (SJRw-32648).—49. Sections of vessels filled with sclerosed tyloses.—50. Outer part of secondary xylem (aliform axial parenchyma adjacent to vessels); phloem with laticifers (gray band near top of photograph) above.—51–53. *T. stenosphon* (LASCA-80-5-56).—51. Radial section; the small perforation plates are in fibriform vessel elements.—52. Pits (or possibly small perforations) seen in face view, also in sectional view in the walls, from radial section.—53. Patch of thin-walled parenchyma from transection; a few thin-walled sclereids have formed in this band. (Fig. 49, 50, scale above Fig. 3; Fig. 51, 53, scale above Fig. 7; Fig. 52, scale above Fig. 4.)

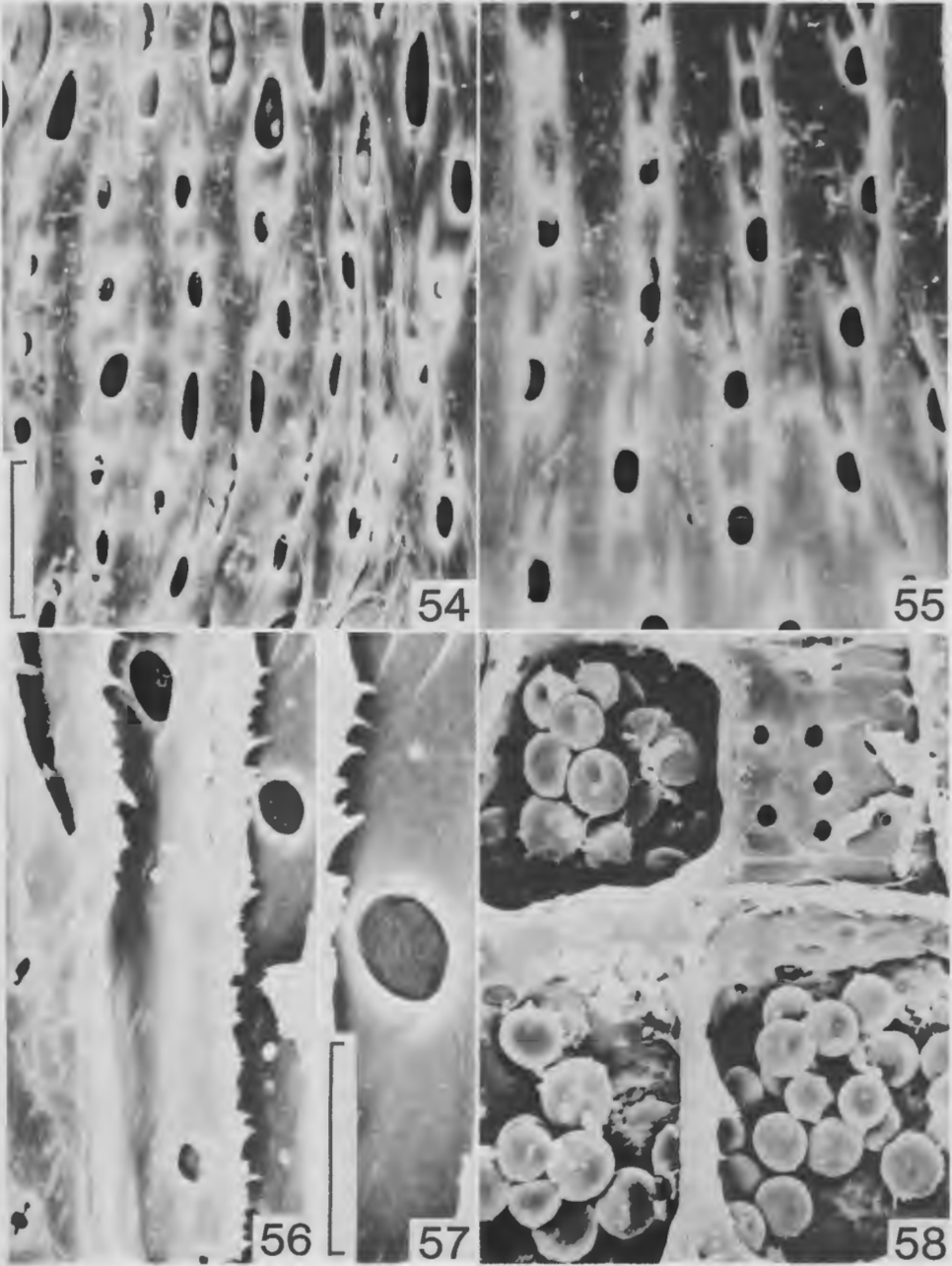


Fig. 54–58. SEM photomicrographs of *Operculina* and *Ipomoea* wood.—54–55. *O. palmeri* (Carlquist 8021), vessel walls from radial section.—54. Wall with variously sized pit apertures; inconspicuous thickenings in right third of photograph.—55. Grooves interconnecting pit apertures (but no helical thickenings).—56–58. *Ipomoea arborescens* var. *glabrata* (Carlquist 8027), radial sections.—56. Variation in pit aperture size, in fibriform vessel elements (or tracheids).—57. Pit aperture intact in pit (which resembles a small perforation) with relatively wide pit aperture.—58. Starch grains in ray cells. (Fig. 54, 55, 56, 58, bracket at left in Fig. 54 applies [bracket = 10 μ m]; Fig. 57, bracket at lower left in Fig. 57 applies [bracket = 10 μ m].)

per cell). Metcalfe (1935) reported similar parenchyma patches in *Convolvulus scoparius* as "traumatic," but parenchyma of this sort is characteristic of woods of the Canarian *Convolvulus* species, and is referable to the concept of parenchyma patches used here.

No interxylary phloem was found in the parenchyma patches of *Convolvulus floridus* by either Metcalfe (1935) or by us. The reason for expecting sieve tubes in this thin-walled parenchyma is that similar thin-walled parenchyma containing chambered druses may be found in secondary phloem. In older secondary phloem, sieve tubes are crushed, so that this tissue is, in effect, only parenchyma. In fact, sieve-tube elements do occur in the parenchyma patches of *Turbina stenosphon* (Fig. 53). Lowell and Lucansky (1986) illustrated sieve tubes (interxylary phloem) in one of the patches (which they term "islands") of axial parenchyma in *Ipomoea hederifolia*, but other patches in their sections apparently lacked phloem. In species of the present study (other than *Turbina stenosphon*), no sieve-tube elements occur in the patches of thin-walled axial parenchyma. Although the use of dried rather than liquid-preserved material would not be expected to favor observation of sieve-tube elements, the condition of thin-walled parenchyma in some species was remarkably good, and sieve tubes probably are infrequent in the patches of thin-walled parenchyma. In *Turbina stenosphon*, the sieve tubes were few in number in the parenchyma patches, and never abundant or in strands. This situation is different from the usual mode of occurrence of interxylary phloem, in which thin-walled axial parenchyma contains sieve tubes regularly and in considerable numbers (e.g., Onagraceae: Carlquist 1975*b*). Even in Onagraceae, however, thin-walled axial parenchyma always does sheathe the phloem.

Rays

Woods of Convolvulaceae have abundant uniseriate rays (Fig. 6, 10, 14, 18, 24, 26, 30, 38). In addition to uniseriate rays, multiseriate rays may be present in some species. Species in which biseriate rays are more common than pluriseriate rays have multiseriate ray width barely or not exceeding 2.0 cells, and these species may be identified by the data in Table 1, column 13. *Convolvulus floridus* (Fig. 14) and *C. scoparius* (Fig. 18) have uniseriate plus biseriate rays and few pluriseriate rays. In other Convolvulaceae, wider multiseriate rays are present, as in *Convolvulus cneorum* (Fig. 10), *Dicranostyles densa* (Fig. 24), *D. holostyla*, *Ipomoea arborescens*, *I. murucoides*, *I. pauciflora*, *Merremia peltata*, and *Turbina stenosphon* (see Table 1, column 13). Some Convolvulaceae have rays that are nearly all uniseriate, as shown for *I. adenoides* (Fig. 26) and *I. fistulosa* (Fig. 30); no data for multiseriate ray width (Table 1, column 13) is given for such species, but presence of a figure for uniseriate ray height (Table 1, column 15): e.g., *Exogonium bracteatum*. If one views the first-formed secondary xylem of Convolvulaceae, one finds uniseriate rays abundantly (e.g., Fig. 8, center), with virtually no multiseriate rays.

Multiseriate ray height is less than 1000 μm in the majority of Convolvulaceae (Table 1, column 14). The mean height for multiseriate rays in all species studied is 904 μm . Multiseriate rays of the lianas average 696 μm , whereas that of the shrubs averages 775 μm . These figures are slightly lower than those of comparable families of dicotyledons; for example, mean multiseriate ray height in Acanthaceae (which has multiseriate rays more frequently) is 815 μm (Carlquist and Zona

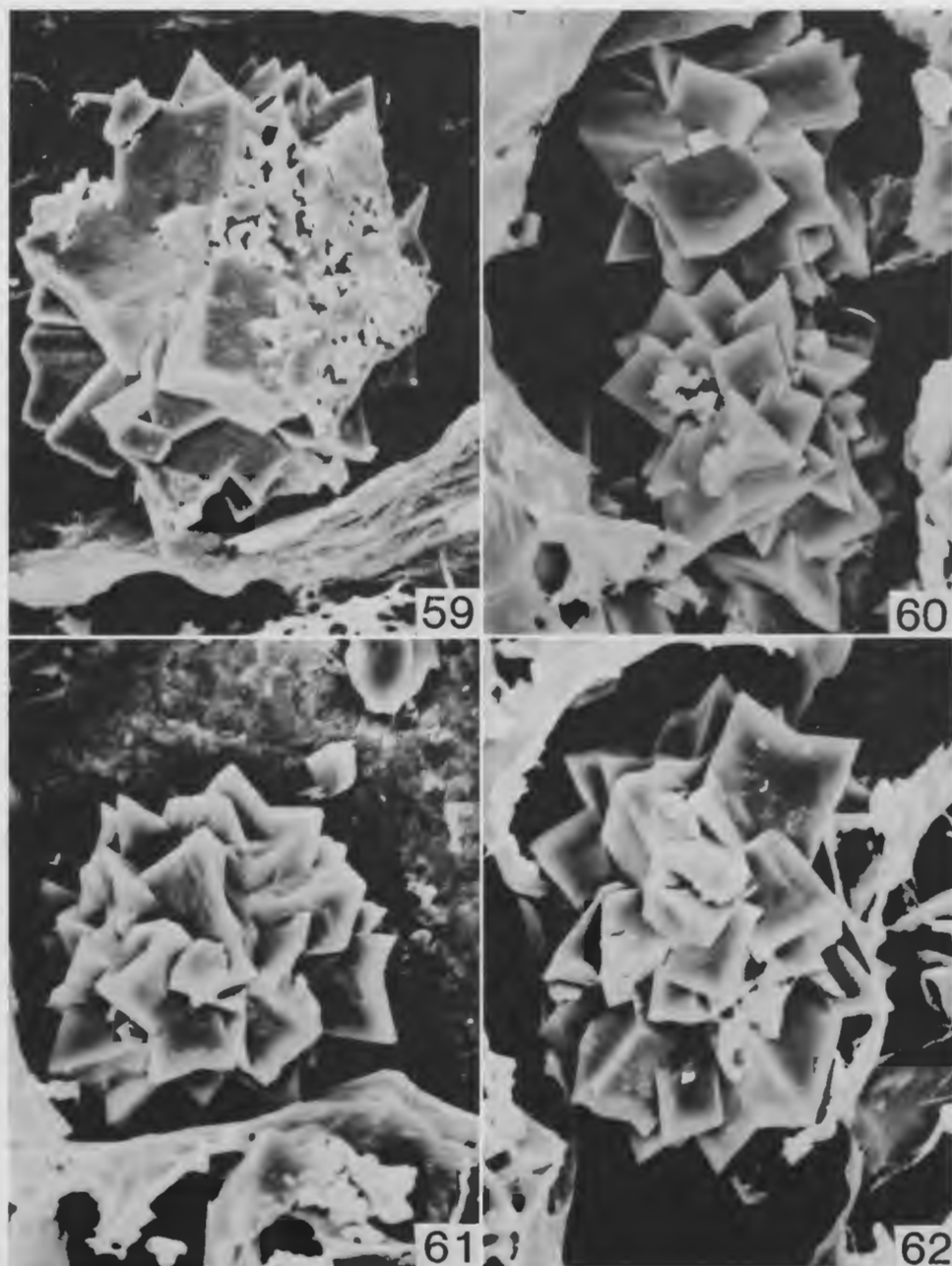


Fig. 59–62. SEM photographs of druses from radial sections of *Ipomoea*.—59. *I. arborescens* var. *glabrata* (Carlquist 8027); druse with small crystals agglutinated to surface, from conjunctive tissue.—60–62. *I. cardiosepala* (SJRW-3599).—60. Pair of small druses from axial parenchyma.—61. Druse hemispherical in outline from conjunctive tissue.—62. Larger druse from conjunctive tissue. (Fig. 59–62, scale at lower left in Fig. 57 applies.)

1988b). The mean uniseriate ray height in Acanthaceae is 300 μm , almost exactly the same as that of the lianoid Convolvulaceae (311 μm). The shrubby Convolvulaceae have a mean uniseriate ray height of 146 μm (Table 1, column 15), which may be related to the rather short vessel element length (257 μm) in these species. Uniseriate ray height is omitted for some species in Table 1; if multiseriate ray height is also omitted for these same species, data were impossible to obtain because ray cells are collapsed on account of their lack of lignified walls.

Abbreviations representing ray histology are given in Table 1, column 16. Convolvulaceae have mostly upright ray cells according to the tabulation. In many species, procumbent cells are scarce or absent. Procumbent ray cells are common only in *Bonamia maripoides*, *Convolvulus floridus*, *C. scoparius*, *Ipomoea bona-nox*, *I. fistuloides*, *I. tuba*, *Lysiostyles scandens*, *Maripa janusiana*, *Merremia cissooides*, *M. nymphaeifolia*, *Operculina palmeri*, *O. passifloroides*, *Stictocardia benaviensis*, and *Turbina stenosisiphon*. The two Canarian species of *Convolvulus* (*C. floridus*, *C. scoparius*) are the only Convolvulaceae in which ray cells are procumbent exclusively (Fig. 14, 18). Note should be taken of the fact that in the species for which procumbent ray cells are abundant, multiseriate rays also are common (as indicated by a multiseriate ray width of more than 2.2 cells).

Ray cell walls in Convolvulaceae are lignified and 2–3 μm thick in most species (Fig. 6, 10, 14, 18, 24, 26, 30, 38). Ray cells are especially thick walled in *Convolvulus cneorum* (Fig. 12). Ray cells less than 1.5 μm thick were recorded in *Breweria menziesii*, *Exogonium bracteatum*, *Ipomoea arborescens*, *I. fistulosa*, *I. mauritiana*, *I. pauciflora*, *I. verbascoidea*, *Merremia cissooides*, *M. nymphaeifolia*, *M. peltata*, *Stictocardia benaviensis*, and *Turbina stenosisiphon*.

Bordered pits can often be seen on walls of ray cells of dicotyledons, but one should look at pits in sectional view in radial sections. Bordered pits on both tangential and horizontal walls were typically observed in *Breweria menziesii*, *Eriybe coccinea*, *Exogonium bracteatum*, *Maripa janusiana*, *M. panamensis*, *Operculina palmeri*, *O. passifloroides*, and *Wilsonia humilis*. Bordered pits only on tangential walls were frequently observed in *Argyreia obtusifolia*, *Bonamia maripoides*, *Convolvulus scoparius*, *Ipomoea adenoides*, *I. murucoides*, *I. pauciflora*, *Lysiostyles scandens*, *Merremia peltata*, and *Turbina stenosisiphon*. In Convolvulaceae not included in the two lists above, bordered pits were less common; bordered pits are absent in species of Convolvulaceae in which ray cells have only primary walls, such as *Ipomoea bona-nox*, *I. cardiosepala*, *I. fistulosa*, *I. mauritiana*, *Merremia cissooides*, *M. nymphaeifolia*, and *Mina lobata*.

Tyloses

Tyloses are common in Convolvulaceae, although not universal. Tyloses are structurally diverse in the family. Every type of variation reported for tyloses in dicotyledons can be found in Convolvulaceae. Most tyloses are thin walled, as shown for *Exogonium bracteatum* (Fig. 7) and *Dicranostyles densa* (Fig. 23); thin-walled tyloses were also observed in *Bonamia maripoides*, *Convolvulus cneorum*, *Dicranostyles holostyla*, *Eriybe coccinea*, *Ipomoea arborescens* var. *arborescens*, *I. bona-nox*, *I. cardiosepala*, *I. mauritiana*, *Maripa panamensis*, *Merremia cissooides*, *Operculina palmeri*, and *Stictocardia benaviensis*. Starch was observed to be abundant in tyloses of *Eriybe coccinea*, *Exogonium bracteatum*, and *Merremia cissooides*. Druses were observed in the tyloses of *Bonamia maripoides*, *Exogonium*

bracteatum (Fig. 7), *Ipomoea cardiosepala* (Fig. 35, bottom), *I. mauritiana*, *Operculina palmeri*, and *Stictocardia benaviensis*. Rhomboidal crystals were observed in thin-walled tyloses of *Dicranostyles densa* (Fig. 23). Markedly sclerosed tyloses containing rhomboidal crystals are illustrated here for *Ipomoea cardiosepala* (Fig. 35) and *Maripa janusiana* (Fig. 39, 40). Similarly sclerosed tyloses were noted in *Maripa panamensis* and *Operculina passifloroides* and they occasionally contained rhomboidal crystals. Sclerosed tyloses with relatively thin walls occurred *Ipomoea tiliaceae* (Fig. 30), *Ipomoea mauritiana* and *I. murucoides* (in which they contain tanninlike deposits).

Conjunctive Tissue

In the Convolvulaceae with successive cambia, conjunctive tissue ordinarily consists of nonlignified parenchyma that forms a band generally thinner than or about as thick as the band of phloem produced by the cambium internal to it (Fig. 33). As a cambium produces secondary phloem, the proportion of secondary phloem to conjunctive tissue increases. Groups of thick-walled sclereids were observed in conjunctive tissue of *Dicranostyles densa*, *D. holostyla*, *Ericybe coccinea*, *Ipomoea cardiosepala*, *I. fistulosa*, *I. verbascoidea*, *Maripa janusiana* (Fig. 37), and *Operculina passifloroides*. Laticifers are not nearly as common in conjunctive tissue as in secondary phloem, but were observed in *Ipomoea arborescens*, *I. murucoides*, *I. pauciflora*, and *I. verbascoidea*. Occurrence of crystals in conjunctive tissue is included in the section below.

Crystals

Druses occur in the parenchyma throughout stems of Convolvulaceae, but they are not present in all parenchyma tissue in all species. Small druses tend to be common in secondary phloem (Fig. 5, top; Fig. 42, top; Fig. 60; dark gray circular objects in these photographs are druses). In wood, druses tend not to be as common as in cortex, phloem, or pith (Fig. 31), but they are present in woods of many Convolvulaceae. Druses may be present in thin-walled axial parenchyma as noted above (Fig. 4, 5, 6, 16, 42, 43). Ray cells may contain druses (Fig. 61, 62). Druses in *Convolvulus cneorum* and *C. scoparius* occur in idioblastic thin-walled ray cells (Fig. 12) that are scattered among cells that have thick lignified walls. *Ipomoea murucoides* and *I. pauciflora* characteristically have ray cells subdivided into chambered druses. Druses even occur in tyloses of *Exogonium bracteatum* (Fig. 7, upper right) and *Ipomoea cardiosepala* (Fig. 35).

Druses in Convolvulaceae, when viewed with scanning electron microscopy, in some instances have agglutinations of small "crystal fragments," evidently added as the druse is completed (Fig. 59, 60), but more commonly, the small crystals are lacking. The number of component crystals in druses of Convolvulaceae is limited (Fig. 59–62), so that the druses have rough surfaces. In contrast, in some dicotyledons, druses are composed of larger numbers of crystals, so that the surface of the druse is smoother (these latter druses may be called sphaerocrystals).

Systematic and organographic distribution of druses in the Convolvulaceae studied is as follows (ap = axial parenchyma; cj = conjunctive tissue; cx = cortex; ph = secondary phloem; pi = pith; ra = rays; ty = tyloses). *Argyrea obtusifolia*

(ph, ra); *Bonamia maripoides* (cj, ph, pi, ty); *Breweria menziesii* (ap, co, ph, pi); *Convolvulus cneorum* (cx, ph, ra); *C. floridus* (ph); *C. scoparius* (ph, ra); *Dicranostyles densa* (ph); *D. holostyla* (cj, ph); *Ericybe coccinea* (cj, cx, ph); *Exogonium bracteatum* (ap, cj, cx, ph, pi, ra, ty); *Ipomoea adenoides* (cx, ph, pi); *I. arborescens* (ap, cj, cx, ph, pi); *I. bona-nox* (cj, ty); *I. cardiosepala* (ap, cj, ty); *I. fistulosa* (cx, ph, pi); *I. intrapilosa* (cx, pi); *I. mauritiana* (ap, cj, cx, ph, pi, ty); *I. murucoides* (ap, cj, cx, pi, ra); *I. pauciflora* (cj, cx, pi); *I. prismatosiphon* (cj); *I. tiliaceae* (ap, ph, pi); *I. tuba* (cx, ph); *I. verbascoidea* (cj, cx); *Lysiostyles scandens* (cj, cx, pi); *Maripa janusiana* (cj, cx); *M. panamensis* (cj, cx); *Merremia cissoides* (cj, cx, pi); *M. nymphaeifolia* (ph); *M. peltata* (cj, cx); *Mina lobata* (cx); *Operculina palmeri* (cx, ph, pi, ra, ty); *Stictocardia benaviensis* (cj, cx, pi); *Turbina stenosphon* (cj, cx, pi).

Rhomboidal crystals are less abundant than druses in Convolvulaceae. The chambered rhomboidal crystals in axial parenchyma (Fig. 19) and in procumbent cells of xylem rays (Fig. 20) of *Convolvulus scoparius* are distinctive and have not been reported in any other Convolvulaceae. Rhomboidal crystals in tyloses are an unusual occurrence in dicotyledons at large, but occur in at least two species of Convolvulaceae (Fig. 23, 39, 40). Distribution of rhomboidal crystals in Convolvulaceae studied is as follows (abbreviations as above): *Breweria menziesii* (cx, ph, pi); *Convolvulus floridus* (ra); *Dicranostyles holostyla* (cj, cx); *Ericybe coccinea* (cj, ph, ty); *Maripa janusiana* (cx, ty); *Maripa panamensis* (cj, cx, ty); *Stictocardia benaviensis* (cj, ph).

Starch

Starch may occur widely in Convolvulaceae, but it is best retained in liquid-preserved material. Because only a minority of the specimens were observed in liquid-preserved form, the list below is quite incomplete and biased in favor of liquid-preserved specimens. Starch grains are spherical or nearly so in shape, as shown with SEM (Fig. 58). The distribution of starch in the collections studied is as follows (abbreviations as above for druses): *Ericybe coccinea* (ap, cj, ra); *Exogonium bracteatum* (cj, ra, ty); *Ipomoea arborescens* (ap, cj, pi, ra); *I. murucoides* (cj, cx, ph, pi); *Merremia cissoides* (cj, cx, ra, ty); *Operculina palmeri* (ap, ph); *Wilsonia humilis* (cx, pi).

Laticifers

Material of all species was not equally suitable for demonstrating presence of laticifers. Dried specimens of some species showed laticifer presence quite well if contents were retained, as in the transection of *Operculina passifloroides* (Fig. 50). In general, however, laticifer presence is revealed best by liquid-preserved material. Therefore, the listing below is incomplete (abbreviations as above for druses); *Convolvulus cneorum* (cx, ph); *Exogonium bracteatum* (cj, cx); *Ipomoea adenoides* (ph); *I. arborescens* (cj, cx, ph, pi); *I. bona-nox* (ph); *I. cardiosepala* (ph); *I. mauritiana* (ph); *I. murucoides* (cj, ph); *I. pauciflora* (cx, ph, pi); *I. tiliaceae* (cx, ph); *I. verbascoidea* (cj, cx, pi); *Maripa panamensis* (cj); *Merremia cissoides* (cx, ph, pi); *M. nymphaeifolia* (cx, ph, pi); *Operculina palmeri* (cx, ph); *O. passifloroides* (cx, ph); *Stictocardia benaviensis* (cj).

Periderm and Cortex

Older stems of Convolvulaceae characteristically bear a periderm or, as seen in *Operculina palmeri*, successive periderms. The phellem often has thickenings on the internal walls, but other walls remain thin (a small periderm portion is shown in Figure 33, upper left).

Thick-walled sclereids, commonly in groups but less commonly scattered in individual fashion, occur in cortex in *Breweria menziesii*, *Dicranostyles densa*, *D. holostyla*, *Ericybe coccinea*, *Exogonium bracteatum*, *Ipomoea adenoides*, *I. arborescens*, *I. cardiosepala*, *I. intrapilosa*, *I. mauritiana*, *I. pauciflora* (Fig. 33), *I. verbascoidea*, *Maripa janusiana*, *Merremia nymphaeifolia*, *M. peltata*, *Operculina palmeri*, *O. passifloroides*, and *Turbina stenosphon*. Thick-walled protophloem fibers were observed in stems of *Ipomoea mauritiana*, *I. pauciflora* (Fig. 33), and *Operculina palmeri* (primary and secondary phloem, including secondary phloem produced by the intraxylary phloem cambium). Laticifers were observed in the cortex of *Convolvulus cneorum*, *Exogonium bracteatum*, *Ipomoea arborescens*, *I. pauciflora*, *I. tiliaceae*, *I. verbascoidea*, *Merremia cissoides*, *M. nymphaeifolia*, *Operculina palmeri*, and *O. passifloroides* (Fig. 50). Druses are quite common in the cortex of Convolvulaceae (see list under *Crystals* above).

Pith

Pith in Convolvulaceae typically consists of thin-walled parenchyma, but sclereids were, in addition, observed in *Ipomoea adenoides*, *I. arborescens*, *Maripa janusiana*, and *Operculina palmeri*. Laticifers were observed in pith of *Ipomoea arborescens*, *I. pauciflora*, *I. verbascoidea*, and *Merremia cissoides*. Druses are common, rhomboidal crystals less common, in the pith of Convolvulaceae (see listing under *Crystals* above).

DISCUSSION AND CONCLUSIONS

Ecological and Functional Wood Anatomy

The occurrence of wide vessels in the stems of lianas is very clearly exemplified by lianoid Convolvulaceae. Vessel dimorphism (Carlquist 1981) is a term that can be applied to presence of wide plus narrow vessel elements. Fibriform vessel elements, so common in *Argyrea*, *Dicranostyles*, *Exogonium*, *Ipomoea*, *Lysiostyles*, *Maripa*, *Merremia*, *Mina*, *Operculina*, *Stictocardia*, and *Turbina* (and present but less common in some other genera), represent this phenomenon very well. Notable in these genera is the transition from fibriform vessel elements to tracheids, and in various proportions, the lianoid genera of Convolvulaceae have both cell types. Vessel dimorphism is very characteristic of wood of lianas, but the term should be applied broadly to any situation that differs from a modal distribution curve. Any departure from a modal curve in the direction of a bimodal curve can exemplify vessel dimorphism. The term should not be restricted to definitive bimodal curves, although some Convolvulaceae do qualify as examples of the latter because fibriform vessel elements are so much narrower than the ordinary vessel elements in these species. Vessel dimorphism of various kinds is characteristic of lianas (Carlquist 1991).

Tracheids also occur, but without fibriform vessel elements, in some *Convolvulus floridus*, *C. scoparius*, and *Wilsonia humilis* (*Convolvulus cneorum* does have fibriform vessel elements). True tracheids (tracheids in woods that do not also have fiber-tracheids or libriform fibers) were cited for 28 families of dicotyledons in which scandent genera occur (Carlquist 1985). An additional 24 families of dicotyledons in which scandent genera occur have vasicentric tracheids, defined so that these tracheids and true tracheids are mutually exclusive (Carlquist 1985; to that list should be added Acanthaceae, Carlquist and Zona 1988b). The 52 families with either true or vasicentric tracheids represent a very large proportion of climbing dicotyledons and this degree of presence indicates the probable functional importance of tracheids in this growth form. A possible explanation for value of tracheids in scandent dicotyledons is maintenance in these cells of water columns at times of stress when water columns break in the vessels (Carlquist 1985). Another possible explanation is that of water storage, but water storage seems better served by parenchyma, which bulks much larger in stems than do tracheids.

Fibriform vessel elements are probably nearly as effective as tracheids in resisting formation of air embolisms in vessels, because air embolisms form far less commonly in narrow vessels than in wide ones (Ellmore and Ewers 1985). Thus, fibriform vessel elements, which are so common in Convolvulaceae, and other lianas (Passifloraceae: Ayensu and Stern 1964), can form a subsidiary conductive system with virtually as high a degree of conductive safety as that provided by tracheids. Because they have perforation plates, fibriform vessel elements have greater potential conductive efficiency than tracheids.

Successive cambia occur in 30 families of dicotyledons (Carlquist 1988a). Fifteen of these families have lianoid representatives (Carlquist 1991). Thus, successive cambia are much better represented in scandent dicotyledons than if they were randomly distributed throughout dicotyledons. Furrowed secondary xylem (characteristic of *Bonamia*, *Breweria*, *Neuropeltis*, *Prevostea*, and to a lesser extent other Convolvulaceae) is even more dramatically related to the lianoid habit. Of the seven families in which furrowed xylem is known to occur (Carlquist 1988a), all seven have lianoid representatives (Carlquist 1991). Interxylary phloem (this term now restricted to production internally of phloem by a cambium) is reported in Convolvulaceae, with certainty, only in *Ipomoea hederifolia* and *Turbina stenosisiphon*, but it very likely occurs in a scattering of other Convolvulaceae. Interxylary phloem is reported in 19 families of dicotyledons (Carlquist 1988a); of these, seven have scandent representatives (Carlquist 1991). Another phenomenon, not considered a cambial variant *per se* because it occurs in dicotyledons with "normal" cambia such as *Erythrina*, is the occurrence of large parenchyma areas within the secondary xylem. This feature, reported in many species of the Convolvulaceae studied (e.g., Fig. 5, 22, 41, 42, 54) is common in many lianoid dicotyledons (Carlquist 1985, 1991).

One of the pervasive themes of some of the above phenomena is the tendency for the vessels (and associated secondary xylem cells) to be formed in strands surrounded by soft tissues (parenchyma, phloem). One potential advantage claimed for such conformations is that of cable construction: protection of the large and vulnerable vessels from damage during torsion in stems of lianas (Schenck 1893; Carlquist 1975a). This explanation still appears valid, because protection from

injury is presumably a better strategy than recovery from injury. The role of parenchyma in recovery from injury is stressed by Fisher and Ewers (1989). This function cannot be claimed for vining monocotyledons, in which parenchyma proliferation leading to formation of new vascular tissue is not possible. Water storage is another potential function of the large parenchyma zones in a liana stem, but this runs counter to the tendency for a liana stem to have a small volume compared to the large leafy crown it supports. Although water storage is a conceivable function of the parenchyma, and this function may be realized, it cannot be as significant as it is in stems of more succulent dicotyledons. Water storage doubtless is realized in the stem of the tree *Ipomoea arborescens*, in which starch as well as water is stored in parenchyma of the conjunctive tissue. I found that the dry weight of a stem segment of *Ipomoea arborescens* was only 46% of the fresh weight. The highly seasonal habitat of *Ipomoea arborescens* is related to a water storage function for this species: the Sonoran thorn forest is leafless during much of the year, including winter months.

The difference between the tree *Ipomoea* species and the lianoid Convolvulaceae with respect to vessel diameter is prominent: the mean diameter for 11 arborescent *Ipomoea* collections is 130 μm , approximately half the vessel diameter of lianoid Convolvulaceae (256 μm).

The shrubby Convolvulaceae studied here are nonsucculent and have much narrower vessels (mean = 50 μm) than the lianoid species. The wood of the shrubby species is notably xeromorphic—especially that of *Wilsonia*. An anatomical condition of especial significance in these shrubby species is the presence of tracheids (with accompanying fibriform vessel elements, in limited numbers, only in *C. cneorum*). Presence of tracheids as the background cell type constitutes a maximally safe subsidiary conducting system that can serve for conduction without breakage in their water columns should air embolisms form in vessels (Carlquist 1988a).

The presence of tracheids as a background tissue in woods has been hypothesized to deter vessel grouping (Carlquist 1984), and certainly Convolvulaceae support this hypothesis, as the low vessels-per-group numbers (Table 1, column 3) within the family indicate. Fibriform vessel elements are part of the background wood tissue, and are often a preponderant part in some convolvulaceous woods. Because fibriform vessel elements are nearly as “safe” against embolism formation as tracheids, theoretically, and much safer than the ordinary vessel elements, they, too, would tend to deter vessel grouping. Interestingly, the only exception to the low vessels-per-group values is in *Argyreia obtusifolia*, in which septate fiber-tracheids and septate libriform fibers are moderately abundant. In the wood of this species, vessel grouping does represent a way of achieving conductive safety.

Anatomical Features Not Directly Related to Ecology

Intraxylary phloem (phloem strands at the periphery of the pith—not to be confused with interxylary phloem) in Convolvulaceae is associated with a type of secondary growth that has not been appreciated previously. In many of the Convolvulaceae studied, a cambium forms between the phloem of the intraxylary phloem strands and the primary xylem of the first vascular cylinder. This intraxylary phloem cambium produces secondary phloem, often in large quantities, on its internal face. In a few (*Ericybe*, *Operculina*, *Stictocardia*) this cambium even

produces a small amount of secondary xylem externally. The phloem produced by the intraxylary phloem cambium crushes any earlier-formed phloem internal to primary xylem, and the volume of the the pith may not increase appreciably. When xylem, which is relatively noncompressible, is added by this cambium the pith volume may increase and the vascular system may be variously fractured as a result. Fractures occur along rays, and ray cambium parallel to this fracture produces new secondary xylem and phloem. This type of cambial action has not been previously reported in the literature.

Various types of vessel restriction patterns (nonrandom distribution of vessels within the secondary xylem) are reported in the Convolvulaceae studied. These types of vessel restriction patterns are newly reported for dicotyledons: (1) in some species with successive cambia, vessels are not produced at first by each cambium, but vessels, once produced, are successively larger in diameter and more frequent as cambial action proceeds; (2) in other species, vessels occur in radial strips that alternate with vessel-free zones (fibriform vessel elements are not considered in this description); (3) in many Convolvulaceae, the metaxylem vessels form in typical radial sequence, but the subsequently formed secondary xylem is free of obvious vessels (fibriform vessel elements may be present) and then, suddenly, secondary xylem containing large vessels is produced. The significance of these three vessel restriction patterns is uncertain. Correlations with ecological or structural factors cannot be obtained at present because these vessel restriction patterns are known only from a limited number of species.

Tracheids are the basic type of imperforate tracheary element in Convolvulaceae. In *Ipomoea arborescens*, *I. prismatosiphon*, and *Turbina stenosiphon*, septate fiber-tracheids were also observed. In *Argyreia obtusifolia*, septate libriform fibers and septate fiber-tracheids, as well as tracheids, are present; this confirms similar reports for the genus by Pant and Bhatnagar (1975). The tracheids in all of these genera are nonseptate. The species cited all exemplify tracheid dimorphism (Carlquist 1988b), a process in which a phylad with only tracheids as the imperforate tracheary element type gives rise to a group in which both tracheids and septate fiber-tracheids (or septate libriform fibers) occur. The conversion of some of the imperforate tracheary elements to septate cells, which have indefinite longevity, means that the septate cells are essentially nonconductive compared to tracheids, and the bordered nature of pits on the septate elements therefore is, in evolutionary terms, rapidly diminished or lost. Convolvulaceae were cited earlier as exemplifying fiber dimorphism (Carlquist 1988b) on the basis of septate fiber-tracheids in *Ipomoea arborescens*. The species mentioned earlier in this paragraph should also be added as examples of fiber dimorphism. However, one collection cited in the earlier account (Carlquist 1988b), "*Ipomoea macrorrhiza*, USw-1843," should be discounted because further study of that specimen proves that it is vitaceous.

The ray cells of Convolvulaceae as tabulated in Table 1, column 16, appear to be predominantly upright, with procumbent cells present in rays in a minority of species. However, the procumbent cells occur in species with multiseriate rays (compare column 13 and column 16, Table 1), whereas the species in which multiseriate rays are absent or nearly so have upright cells predominantly or exclusively). Convolvulaceae basically have the ray type Kribs (1935) designated as Heterogeneous Type IIB. This type has procumbent cells in the multiseriate rays, but uniseriate rays may be composed either of procumbent cells or of upright

cells. In Convolvulaceae, the uniseriate rays correspond to the upright cell mode of composition, and thus absence of procumbent cells in a species is mostly a measure of absence of multiseriate rays. Pertinent in this finding is the fact that secondary growth in Convolvulaceae begins with rays uniseriate exclusively or nearly so. Those species without successive cambia but with the largest amount of secondary xylem, *Convolvulus floridus* and *C. scoparius*, have procumbent cells exclusively in both multiseriate and uniseriate rays, and are unusual within the family in this respect. Possibly the rays in these two species may, at least in part, represent an ontogenetically mature type of ray pattern for the family. In this case, successive cambia may well have the effect of maintaining a more juvenile condition, in which multiseriate rays are less abundant and uniseriate rays are composed solely of upright cells. The role that successive cambia may or may not play in maintaining juvenile wood conditions has not been investigated to any appreciable extent. One circumstance that suggests that more juvenile conditions may be maintained in stems of Convolvulaceae with successive cambia is the tendency for vessel element (and fibriform vessel element) length to remain steady, rather than to increase over time, as in typical woody dicotyledons (Carlquist 1975a). Comparison of inner and outer stem wood of *Turbina stenosphon* and of smaller and larger stems of *Exogonium bracteatum* (see Table 1) reveals no ontogenetic changes in histology of statistical significance.

Phylogenetic and Systematic Conclusions

There is a high degree of consensus on the relationships of Convolvulaceae. Solanaceae, a family that, like Convolvulaceae, possesses intraxylary phloem, are thought to be closely related to Convolvulaceae by most authors (e.g., Thorne 1976; Dahlgren 1980; Takhtajan 1987; Cronquist 1988). Polemoniaceae are also frequently associated with Convolvulaceae (Thorne 1976; Dahlgren 1980; Takhtajan 1987; Cronquist 1988); polyporate pollen grains are shared by these families. Boraginaceae are also claimed to be allied to Convolvulaceae, although Thorne (1976) places them in Lamiales. Hydrophyllaceae are also claimed to be allied to Convolvulaceae by some recent authors (e.g., Dahlgren 1980). Although all of the tubiflorous orders tended to be grouped together in earlier systems, recent authors separate them into at least two orders or superorders and consider these groupings to be polyphyletic. For example, Dahlgren's (1980) system shows the impact of knowledge of iridoid distribution: Solanales lack iridoids, whereas the orders Gentianales, Lamiales, and Scrophulariales have these compounds (Jensen, Nielsen, and Dahlgren 1975). As noted in the Introduction, Convolvulaceae are thought to be related to Solanaceae, Boraginaceae, Polemoniaceae, Hydrophyllaceae; all of these families lack iridoids (Jensen et al. 1975).

Data from wood anatomy are pertinent to proposed interfamilial relationships. The presence of fibriform vessel elements in certain Hydrophyllaceae such as *Eriodictyon*, a nonlianooid genus (Carlquist, Eckhart and Michener 1983), and in woods of many Polemoniaceae (Carlquist, Eckhart and Michener 1984) is suggestive of these relationships. Completion of the survey of wood anatomy of tubiflorous dicotyledons, to which the present paper is a contribution, will permit a better discussion.

Within the family, comparisons of wood anatomy of the tribes as redefined by Austin (1973: see Introduction) proves instructive, and the present study lends

support to Austin's system. The three species studied here of *Convolvulus*, tribe Convolvuleae, all have "normal" cambia; the only other genus with normal cambia studied here, *Wilsonia*, should probably also be in a tribe by itself, Wilsonieae, in agreement with Peter's (1896) treatment. The genera with strongly furrowed xylem—*Bonamia*, *Breweria*, *Neuropeltis*, and *Prevostea*—were all included by Austin (1973) in the tribe Cresseae, although they were scattered among other tribes in earlier systems, such as that of Peter (1896) and Roberty (1952). The work by Mennega (1969) on wood anatomy of *Dicranostyles* supports the relationship of that genus to *Maripa* (both have successive cambia) rather than to *Bonamia* or *Prevostea*. That idea corresponds to the system of Austin (1973), who grouped *Dicranostyles*, *Ericybe*, *Lysiostyles*, and *Maripa*, in the tribe Ericybeae, although he was apparently unaware of Mennega's (1969) work because he cites no work in wood anatomy.

The representation of specimens in this study is too scanty to permit citation of generic or specific criteria with any certainty. The possible generic distinction of *Breweria* is worth consideration; it lacks the sclerosed tyloses found in *Bonamia*, with which *Breweria* is often united. *Exogonium*, sometimes united with *Ipomoea*, is certainly close to *Ipomoea* on the basis of wood anatomy, but is distinctive in having ray cambia and in having a somewhat higher proportion of tracheids than is typical of *Ipomoea* woods.

The great diversity of wood anatomy in Convolvulaceae, when investigated more thoroughly, will offer excellent possibilities for correlation with the taxonomic system. This diversity also invites phylogenetic interpretation. Very likely, absence of successive cambia is more primitive than presence of them, and this is congruent with Austin's precladistic phylogenetic tree of the family. Presence of both multiseriate and uniseriate rays is considered more specialized than presence of uniseriate rays alone (Kribs 1935), and the absence of multiseriate rays in Convolvulaceae should be considered to exemplify a specialized character state. Presence of uniseriate rays exclusively at the outset of secondary growth may or may not be specialized (for a discussion, see Carlquist 1988a, p. 346). The presence of tracheids combined with fibriform vessel elements in convolvulaceous woods is hypothesized here to precede the condition seen in *Ipomoea arborescens* and other species, in which tracheids are apparently virtually absent in favor of fibriform vessel elements. The presence of septate fiber-tracheids and/or septate libriform fibers is considered a specialized character state within the family, as noted above. The presence of vasicentric scanty axial parenchyma is universal in the family, and thus should be considered primitive. Alternative types or variations on vasicentric parenchyma (aliform, aliform-confluent) would be regarded as advanced character states in the family. Analysis of woods of tubiflorous dicotyledons as a whole may aid in identifying further structural trends of specialization within the family.

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