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WOOD ANATOMY OF BUDDLEJACEAE

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ABSTRACT

Quantitative and qualitative data are presented for 23 species of *Buddleja* and one species each of *Emorya*, *Nuxia*, and *Peltanthera*. Although crystal distribution is likely a systematic feature of some species of *Buddleja*, other wood features relate closely to ecology. Features correlated with xeromorphy in *Buddleja* include strongly marked growth rings (terminating with vascular tracheids), narrower mean vessel diameter, shorter vessel elements, greater vessel density, and helical thickenings in vessels. Old World species of *Buddleja* cannot be differentiated from New World species on the basis of wood features. *Emorya* wood is like that of xeromorphic species of *Buddleja*. Lateral wall vessel pits of *Nuxia* are small (2.5 μm) compared to those of *Buddleja* (mostly 5–7 μm). *Peltanthera* wood features can also be found in *Buddleja* or *Nuxia*; Dickison's transfer of *Sanango* from Buddlejaceae to Gesneriaceae is justified. All wood features of Buddlejaceae can be found in families of subclass Asteridae such as Acanthaceae, Asteraceae, Lamiaceae, Myoporaceae, Scrophulariaceae, and Verbenaceae. Wood anatomy of Buddlejaceae relates to species ecology and size of wood sample, and is not useful in demonstrating that Buddlejaceae are closer to any particular one of these families; such evidence must be sought in molecular data and elsewhere.

Key words: Asteraceae, Asteridae, ecological wood anatomy, Lamiales, Scrophulariaceae, Verbenaceae, xeromorphy.

INTRODUCTION

A survey of wood anatomy of Buddlejaceae (as tribe Buddlejeae of Loganiaceae) was provided by Mennega (1980) as part of the Pflanzenfamilien monograph of Loganiaceae. Her survey had the merit of providing descriptions of wood of the component genera, together with illustrations of wood sections by means of light microscopy. In these respects, Mennega's account represents an advance on the coverage of this group offered by Metcalfe and Chalk (1950). The present study expands coverage of wood anatomy of *Buddleja* and especially relates to a monograph of New World species of *Buddleja*, currently in preparation for *Flora Neotropica* by Dr. Eliane Norman. In addition, quantitative data accumulated in the present study permit analysis of *Buddleja* woods and those of other genera of Buddlejaceae with respect to ecology. *Buddleja* woods reflect sensitive adaptation to a diverse range of ecological sites, and the genus is therefore an exemplary one in which to demonstrate the relationship between wood anatomy and ecology. Ecology accounts for most of the variation patterns of the woods and few features can be said to correlate with infrageneric systematics. A scattering of Old World species of *Buddleja* has been included in order

to determine if there are any features of Old World species not also found in the New World species.

By way of examining the question of the generic composition of Buddlejaceae, studies of two other genera, *Nuxia* and *Peltanthera*, have been included here, and Mennega's (1980) data on *Androya* and *Gomphostigma* are considered. *Peltanthera*, a monotypic genus, has been claimed not to be close to *Buddleja*. Hunziker and Di Fulvio (1958) favor the retention of *Peltanthera* in Loganiaceae, although they claim "strong affinities with some genera of Scrophulariaceae." Punt's (1980) phylogenetic scheme for Loganiaceae s. l. based on pollen data shows *Androya*, *Emorya*, *Nuxia*, and *Peltanthera* as derivatives of *Buddleja*, which becomes the basal genus of the group recognized here as Buddlejaceae. The genus *Sanango* has now been removed from Buddlejaceae, and its position in Gesneriaceae appears likely (Dickison 1994).

A question of broader phylogenetic significance to which wood data can be applied is whether Buddlejaceae should be included in Asteridae, and, if so, in the order Lamiales (Scrophulariales of some authors). A database on woods of Asteridae (Carlquist 1992a) provides data for comparisons. The cladograms of Olmstead et al. (1993) and Olmstead and Reeves (1995), based on *rbcL* analysis and other molecular data from the families of Asteridae, offer a convenient framework to which patterns from various kinds of data sets may be compared. However, one must keep

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in mind that wood anatomy of a group such as Buddlejaceae should not be considered primarily interpretable in phylogenetic terms. In the Asteridae especially, woods often reflect rapid change with respect to ecology of species rather than other phyletic factors. This is particularly notable, for example, in the huge family Asteraceae, where most of the diversity is interpretable in terms of ecology and habit, and relatively few patterns are attributable to systematic relationships (Carlquist 1966).

MATERIALS AND METHODS

Woods were mostly available in dried form; a few were pickled in 50% ethanol. The distinction in results based on the two methods of preservation is minimal, because one can find cytoplasmic remnants and starch in sections derived from dried specimens. Portions of dried specimens were boiled in water and stored in 50% ethanol preparatory to sectioning on a sliding microtome. Wood of *Nuxia verticillata* proved excessively hard, and the method of Kukachka (1977) was applied in order to obtain good sections. Wood sections were stained with a safranin-fast green combination. A few wood sections were left unstained, dried between clean glass slides, mounted on aluminum stubs, sputter coated, and examined with a Bausch and Lomb Nanolab scanning electron microscope (SEM) to reveal details of sculpturing on vessel walls or crystal content of cells. Macerations were prepared from woods by means of Jeffrey's fluid and stained with safranin.

Terms are according to the IAWA Committee on Nomenclature (1964), except for ray type terms and the term "vascular tracheid," which is defined according to Carlquist (1988). Vessel diameter is measured as lumen diameter rather than outside diameter as commonly done, and the lumen diameter recorded is an average of the widest and the narrowest diameter. This method should be a more accurate reflection of the hydraulic capabilities of a vessel than taking the widest lumen diameter or the tangential diameter. In Buddlejaceae, vessel elements are often at least a little wider radially than tangentially. Those who wish to compare my vessel data to data in other studies in which vessel diameter is based on outside diameter can easily do so by adding twice the mean wall thickness of vessels to the diameter (vessel wall thickness is given in Table 1, column 5).

The sources of the materials are as follows: *Buddleja alternifolia* Maxim., cult. Connecticut (native to China), SJRW-45028; *B. americana*, SJRW-16684; *B. anchoensis* Kuntze, Bolivia, SJRW-46201; *B. araucana* Philippi, cult. Kew (native to Argentina); *B. asiatica* Lour., Crater Rim Road near Waldron Lodge, Kilauea, Hawaii National Park (*Linda Pratt s. n.*); *B. bullata*

Benth., Ecuador (*coll. A. Rimbach*), SJRW-23118; *B. colvilei* Hook. f. et Thoms., cult. Kew (native to Nepal, s. n.); *B. cordobensis* Griseb., Lago San Roque, Argentina, Norman A2; *B. davidii* Franch., cult. Maryland, RSAw (from USw); *B. domingensis* Urban, with tree ferns, *Brunellia*, *Tabebuia*, etc., between La Nuez and Tetero de Media, Prov. Peravia, Cordillera Central, Dominican Republic, Zanon 40654 (NY); *B. globosa* Hope, Chile, Carlquist 7278 (RSA); *B. indica* Lam., cultivated at the Marie Selby Botanical Gardens, Sarasota, Florida (collected by E. Norman); *B. mendozensis* Gillies, Lago San Roque, Argentina, Norman A1; *B. parviflora* HBK., Dist. Fed., Mexico, Iltis 106 (WIS); *B. parviflora*, Dist. Fed., Mexico, Iltis 167 (WIS); *B. racemosa* Torr., bluffs on the south side of the Colorado River, Austin, Davis Co., Texas, Mayfield 2118 (TEX); *B. rufescens* Willd. ex Schultes et Schultes, cult. UCB Bot. Gard. (*Hutchison 3406*); *B. salviifolia* (L.) Lam., SJRW-37626; *B. scordioides* Kunth in Humb., Zech & Manning 60; *B. skutchii* Morton, cult. UCBBG (source: *Pinus-Quercus* forest, slope E of San Cristobal de las Casas, 2300 m, Chiapas, Mexico, Bartholomew 986, UC); *B. stachyoides* Cham. & Schlecht., 22 km W from Alpichili, Prov. Park Cochuna, Tucuman, Argentina, Norman A7; *B. tubiflora* Benth., near El Tio, Cordoba, Argentina, Norman A15; *B. tucumanensis* Griseb., 5 km W of Andalgalá, Catamarca, Argentina, Norman A12; *B. utahensis* Cov., E Mojave Desert, California, Thorne 44537 (RSA); *B. utahensis*, E Mojave Desert, California, Wolf 9833 (RSA); *Emorya suaveolens* Torr., limestone canyon 54 km S of Castaños, Puerto de San Lazaro, Sierra de San Lazaro, Coahuila, Mexico, Johnston 4331 (LL); *Nuxia verticillata* Lam., Mauritius, SJRW-33200; *Peltanthera floribunda* Benth., San Jose, Puesto Carara, 200 m., Costa Rica, Hammel 19855 (MO).

ANATOMICAL DESCRIPTIONS

Growth Rings

Most species of *Buddleja* show at least a little differentiation in diameter between latewood and earlywood vessels; in many species, narrower vessels occur only in the last-formed latewood, and narrowing is not gradual over much of a growth ring. Likewise, relatively wide vessels tend to occur only in a limited portion of the earlywood. Virtually no difference between latewood and earlywood (diffuse porous) was observed in *B. globosa* (Fig. 1) and *B. rufescens* (Fig. 3). Moderate degrees of differentiation in vessel diameter are shown for *B. alternifolia* (Fig. 10). A strong differentiation in diameter between earlywood and latewood vessels is illustrated by *B. parviflora* (Fig. 14), a species in which latewood as defined by notably narrow vessels is extensive. In this species, latewood vessels are not only narrower but also more numerous.

Table 1. Wood characteristics of Buddlejaceae.

Species	Collection	1 VG	2 VD	3 VM	4 VL	5 VW	6 PD	7 LL	8 LW	9 MR	10 MW	11 UR	12 FV	13 ME
<i>Buddleja alternifolia</i>	SJRw-45028	3.2	32	263	234	4.0	7	550	4.5	235	3.5	106	2.35	28
<i>B. americana</i>	SJRw-16684	1.6	26	99	355	1.4	6	794	4.0	433	2.7	181	2.24	93
<i>B. anchoensis</i>	SJRw-46021	1.4	41	104	331	2.0	5	780	3.2	361	2.9	136	2.36	130
<i>B. araucana</i>	cult. Kew	2.3	22	357	245	1.5	6	375	2.2	352	2.2	125	1.53	15
<i>B. asiatica</i>	Pratt s. n.	1.2	66	71	346	3.0	6	834	2.8	371	2.5	193	2.41	322
<i>B. bullata</i>	SJRw-23118	2.2	56	19	336	3.1	7	751	4.8	376	2.8	103	2.24	990
<i>B. colvilei</i>	cult. Kew	2.7	26	177	528	1.4	5	749	2.5	828	2.5	291	1.41	78
<i>B. cordobensis</i>	Norman A2	3.5	31	190	346	2.3	5	635	3.0	678	2.1	237	1.84	56
<i>B. davidii</i>	USw-2156 (RSAw)	3.4	37	188	267	1.4	7	589	2.0	377	3.6	108	2.21	38
<i>B. domingensis</i>	Zanoni 40654	1.5	55	49	356	1.8	6	831	3.0	433	2.8	219	2.33	400
<i>B. globosa</i>	Carlquist 7278	2.1	29	149	364	2.0	7	662	3.2	377	2.6	171	1.81	71
<i>B. indica</i>	cult. Selby B. G.	1.2	29	82	398	2.0	3	952	2.0	326	2.9	113	2.39	140
<i>B. mendozensis</i>	Norman A1	2.2	20	289	209	1.8	4	346	2.4	296	3.0	296	1.66	14
<i>B. parviflora</i>	Ilitis 106	3.9	39	124	239	1.2	5	718	2.3	299	2.5	121	3.00	75
<i>B. parviflora</i>	Ilitis 167	5.2	27	239	313	2.2	8	673	3.5	367	2.4	162	2.15	35
<i>B. racemosa</i>	Mayfield 2118	2.5	32	282	186	1.4	3	384	2.4	409	2.9	135	2.06	21
<i>B. rufescens</i>	Hutchison 3406	2.0	45	50	368	2.5	7	745	2.5	636	2.9	222	2.02	331
<i>B. salviifolia</i>	SJRw-37626	2.7	52	119	304	2.4	5	622	4.5	499	2.5	95	2.04	133
<i>B. scordioides</i>	Zech 60	1.6	15	381	166	2.2	5	375	3.1	364	2.3	90	2.26	6
<i>B. skutchii</i>	Bartholomew 926	1.7	30	136	308	2.4	7	628	2.8	349	2.3	111	2.04	68
<i>B. stachyoides</i> STEM	Norman A7	2.1	26	271	300	2.3	6	552	2.6	308	2.3	183	2.03	29
<i>B. stachyoides</i> ROOT	Norman A7	1.9	26	144	236	0.8	5	551	2.0	288	2.5	92	2.33	43
<i>B. tubiflora</i>	Norman A15	2.1	23	268	254	2.2	4	504	3.2	456	2.5	145	1.98	22
<i>B. tucumanensis</i>	Norman A12	2.4	25	245	317	2.5	4	595	3.0	406	2.2	152	1.88	32
<i>B. utahensis</i>	Thorne 44537	2.5	18	663	152	1.7	4	340	2.5	292	4.1	100	2.24	5
<i>B. utahensis</i>	Wolf 9833	1.9	25	340	184	2.3	5	371	2.5	455	2.2	156	2.02	14
<i>Buddleja</i> species, averaged		2.3	32	205	294	2.0	5.4	460	3.0	406	2.8	156	2.10	134
<i>Emorya suaveolens</i>	Johnston 4331	2.5	15	325	162	4.6	4.8	443	4.8	608	2.3	141	2.73	7
<i>Nuxia verticillata</i>	SJRw-33200	1.1	45	19	445	0.9	2.5	918	4.6	410	4.9	281	2.06	1054
<i>Peltanthera floribunda</i>	Hammel 19855	1.4	101	9	772	2.5	2.5	1509	4.6	926	5.7	442	2.09	8102

Key to columns: 1 (VG), mean number of vessels per group; 2 (VD) mean diameter of vessel lumen μm ; 3 (VM), mean number of vessels per mm^2 of transection; 4 (VL) mean vessel element length, μm ; 5 (VW), mean vessel wall thickness, μm ; 6 (PD) mean vertical diameter of pit cavity, lateral vessel wall, μm ; 7 (LL), mean length of libriform fibers, μm ; 8 (LW), mean libriform fiber wall thickness, μm ; 9 (MR), mean height of multiseriate rays, μm ; 10 (MW), mean width of multiseriate rays at widest point, cells; 11 (UR), mean height of uniseriate rays, μm ; 12 (FV), "F/V ratio" (libriform fiber length divided by vessel element length; 13 (ME), Mesomorphy Ratio Value (vessel diameter times vessel element length divided by vessel number per mm^2 transection). For further collection information and information concerning data, see Materials and Methods.

Latewood with vessels both narrower and more numerous than those of earlywood was also observed in *B. alternifolia*, *B. araucana*, *B. mendozensis*, *B. racemosa*, *B. scordioides*, *B. utahensis* (Fig. 18), and *Emorya suaveolens*. The latewood vessels of *B. parviflora* (Fig. 14) are distinctive in being in tangential bands; the narrowest vessels are similar in diameter to the surrounding libriform fibers. About six layers of initial parenchyma were observed in earlywood of *B. salviifolia* and *Peltanthera floribunda* (Fig. 26).

The continuum in the genus *Buddleja* between well-marked growth rings and wood in which minimal differentiation between earlywood and latewood occurs illustrates the difficulty of applying the terms "ring porous" and "diffuse porous." The term ring porous was invented primarily in terms of north temperate woods in which strong seasonal change in temperature coincidental with change in water availability is related to much greater size of earlywood vessels. In many

woods in which growth rings relate to seasonal decrease in water availability rather than winter freezing, growth rings that do not fit definitions of "ring porous" or "diffuse porous" well are characteristic, and this intermediacy is certainly exemplified by *Buddleja*.

Quantitative Vessel Features

Mean numbers of vessels per group for the species studied are given in Table 1, column 1. The range is considerable, from 1.4 (*B. anchoensis*, *P. floribunda*) to 5.2 (*B. parviflora*). The true figures for the latter species and for *Emorya suaveolens* may actually be higher than calculated, because identification of very narrow latewood vessels (similar in diameter to libriform fibers) is so difficult in transections. The fact that the average number of vessels per group in *Buddleja* is 2.4 indicates that solitary vessels do not predominate, a statement supported by transections such as

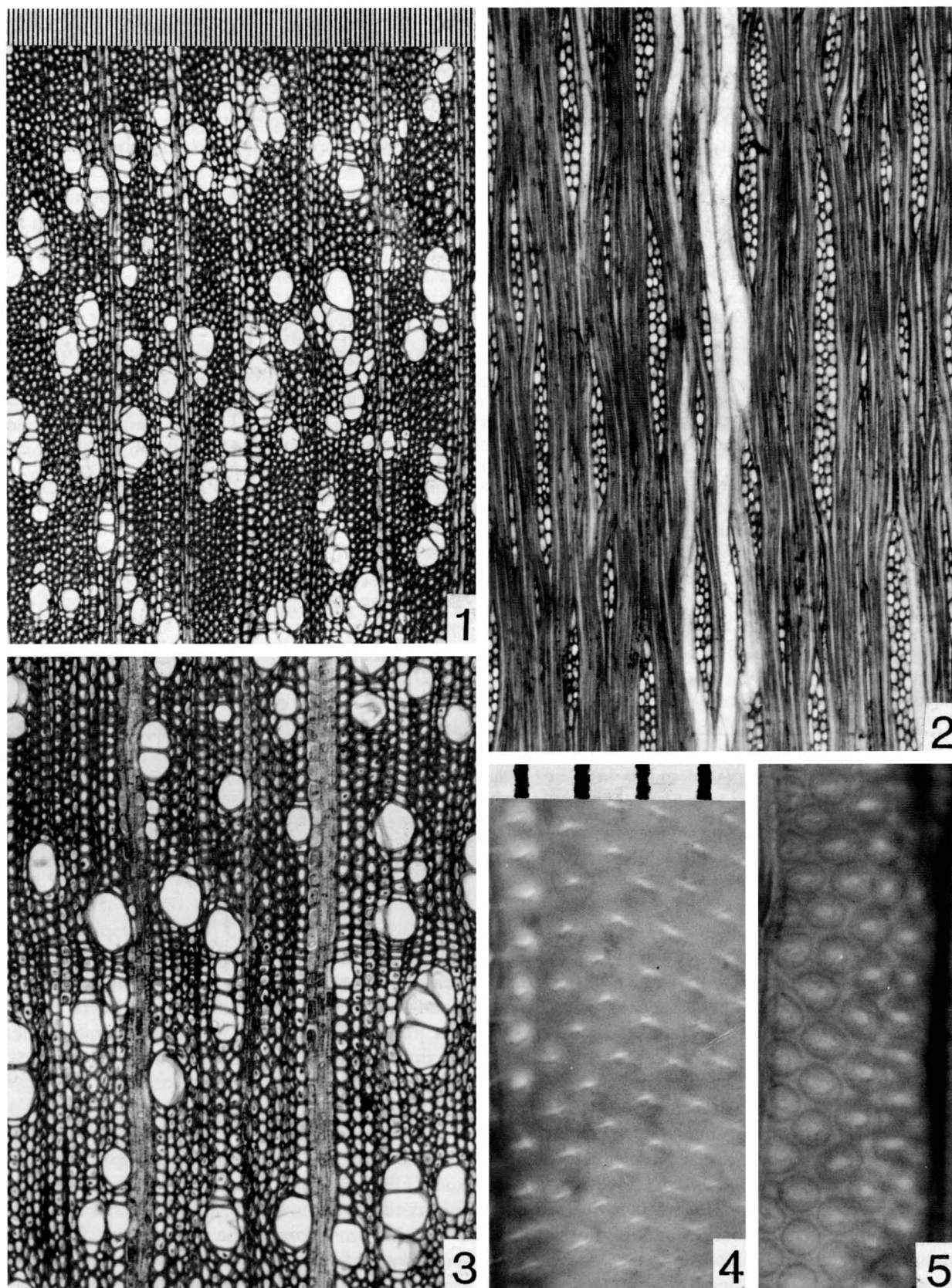


Fig. 1-5. Wood sections of *Buddleja*.—1-2. *B. globosa*—1. Transection, to show vessel typical sizes and arrangements.—2. Tangential section; multiseriate rays outnumber uniseriate rays.—3. *B. rufescens*, transection; larger vessels typical of the more mesomorphic species of *Buddleja*.—4-5. Vessel walls from tangential sections to show typical pitting, lack of helical thickenings.—4. *B. domingensis*; pit apertures are narrowly elliptical.—5. *B. araucana*; pits are nearly circular, apertures widely elliptical. (Fig. 1-3, magnification scale above Fig. 1 [divisions = 10 μm]; Fig. 4-5, scale above Fig. 4 [divisions = 10 μm].)

those shown in Fig. 1, 3, 10, and 14. Solitary vessels predominate in *Nuxia verticillata* (Fig. 22) and *Peltanthera floribunda* (Fig. 26), but also in some *Buddleja* species, such as *B. anchoensis*, *B. asiatica*, and *B. indica*.

Mean vessel diameter (Table 1, column 2) within *Buddleja* ranges from 14 to 56 μm . A condition close to average for the genus is shown by *B. globosa* in Fig. 1. Wider vessels are exemplified by *B. rufescens* (Fig. 3). *Buddleja parviflora* (Fig. 14) tends to have two vessel diameter classes, but the mean vessel diameter in this species is closer to the mean for the genus nonetheless. Similarly, in *B. alternifolia* (Fig. 10) smaller vessels are often grouped near larger vessels; vessels near the median for that species are not common.

Vessel density (Table 1, column 3) relates inversely to vessel diameter with minor deviations. The species with the greatest mean vessel diameter, *B. bullata*, has the lowest number of vessels per mm^2 . Likewise, notably narrow vessels occur in species with relatively high density (>300 vessels per mm^2), as in *B. araucana*, *B. scordioides*, and *B. utahensis* (Fig. 18). The range of vessel density in *Buddleja* is very considerable, as can be seen by comparison of the transections (Fig. 1, 2, 10, 14, 18). Vessel densities are relatively low in *Nuxia verticillata* (Fig. 22) and *Peltanthera floribunda* (Fig. 26). Ecological interpretation of vessel density is offered later section.

Mean vessel element length (Table 1, column 4) for the family as a whole (294 μm) is close to that for families claimed to be phylogenetically close to Buddlejaceae. Mean vessel element length is a little shorter in Convolvulaceae (Carlquist and Hanson 1991), Lamiaceae (Carlquist 1992b), and Myoporaceae (Carlquist and Hoekman 1986a), but familial means somewhat greater than in Buddlejaceae occur in Acanthaceae (Carlquist and Zona 1988), Gesneriaceae (Carlquist and Hoekman 1986b), and Solanaceae (Carlquist 1992c). Vessel element length is significant with relation to ecology and habit (see discussions below).

Mean diameter of lateral wall pits of vessels (Table 1, column 6) varies widely within *Buddleja*. The most common pit size (mean for *Buddleja* = 5.4 μm) is represented in the photographs of vessels of *B. domingensis* (Fig. 4) and *B. araucana* (Fig. 5). However, notably small pits can also be found in the genus: *B. racemosa* has a mean pit diameter of 3 μm . This figure is noteworthy because pits of approximately this size occur in *Nuxia* (Fig. 24) and *Peltanthera* (Fig. 28).

Vessel wall thickness (Table 1, column 5) is included in this study because of the great range in figures for this feature: from 0.8 μm (*B. stachyoides*) to 4.0 μm (*B. bullata*). The mean vessel wall thickness in *Buddleja* (2.0 μm) is relatively small. Much thicker vessel walls characterize woods in other dicotyledon-

ous families, and are especially common in lianas (Carlquist and Hanson 1991).

Qualitative Vessel Features

Perforation plates are simple throughout Buddlejaceae. Lateral wall pitting consists of alternate pits with pit cavity circular to oval in outline; pit apertures are elliptical (Fig. 4, 5).

Grooves interconnecting pit apertures ("coalescent pit apertures" of some authors) were observed in *B. americana*, *B. indica*, *Nuxia verticillata* (Fig. 25), and *Peltanthera floribunda* (Fig. 28). There are paired thickenings that accompany the grooves in *Buddleja indica* and *Nuxia verticillata* (Fig. 25, light bands adjacent to grooves).

Helical thickenings occur on vessel walls of most species of *Buddleja*. Helical thickenings on the walls of all vessels were observed in *B. alternifolia*, *B. araucana* (Fig. 7), *B. cordobensis*, *B. globosa*, *B. mendozensis* (Fig. 8), *B. racemosa*, *B. tubiflora*, and *Emorya suaveolens*. Very similar to this condition are woods in which helical thickenings are present in most vessels, but are lacking only in a few earlywood vessels: *B. colvillei*, *B. davidii*, *B. scordioides*, *B. stachyoides*, *B. tucumanensis* (Fig. 9), and *B. utahensis*. Helical thickenings are notably fine in *B. colvillei* (Fig. 8) and *B. stachyoides*. Thickenings are much coarser in the remaining species (e.g., Fig. 7, 9). Helical thickenings were not recorded at all in vessels of *B. anchoensis*, *B. asiatica*, *B. domingensis*, *B. rufescens*, *B. salviifolia*, *B. skutchii*, and *Peltanthera floribunda*.

Imperforate Tracheary Elements

In species with more xeromorphic wood, vessels become progressively narrower in latewood, and those formed at the terminus of a growth ring may be extremely narrow radially and lack perforation plates; these latewood cells are termed vascular tracheids (Carlquist 1985, 1988). Presence of vascular tracheids must be determined with the use of macerations, because a portion of a cell bearing a small perforation plate may be cut away in a longisection. Vascular tracheids were observed in small numbers in *B. araucana*, *B. colvillei*, *B. davidii*, *B. mendozensis*, *B. parviflora* (both collections), *B. racemosa*, *B. tubiflora*, and *B. utahensis*. Many vascular tracheids were observed in *B. scordioides* and *Emorya suaveolens*.

Aside from vascular tracheids, all imperforate tracheary elements in Buddlejaceae are libriform fibers. In no specimen could vestigial borders be observed on pits of the libriform fibers, either in transections or longisections of pits or in face view of pits. Although the length of libriform fibers (Table 1, column 7) shows a considerable range (from 375 μm in *B. scordioides* to 1509 μm in *Peltanthera floribunda*), much

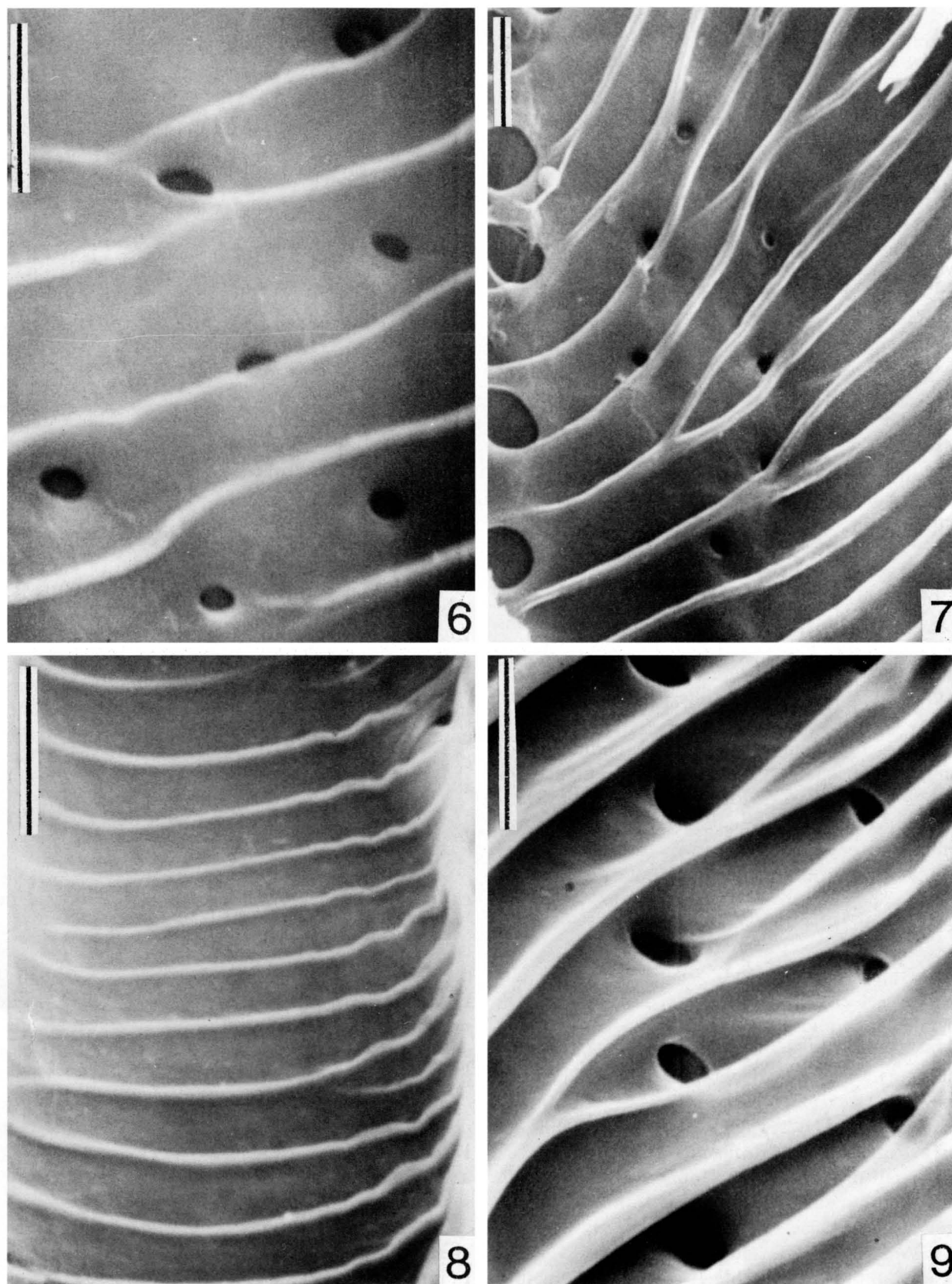


Fig. 6-9. SEM photographs of vessel walls from tangential sections of *Buddleja* wood to show helical thickenings.—6. *B. colvilei*, widely spaced thickenings.—7. *B. araucana*, forked and anastomosing thickenings.—8. *B. mendozensis*, fine thickenings on a wall devoid of pits.—9. *B. tucumanensis*, very pronounced thickenings. (Magnification shown by bars at upper left in each photograph [scale bar = 10 μm].)

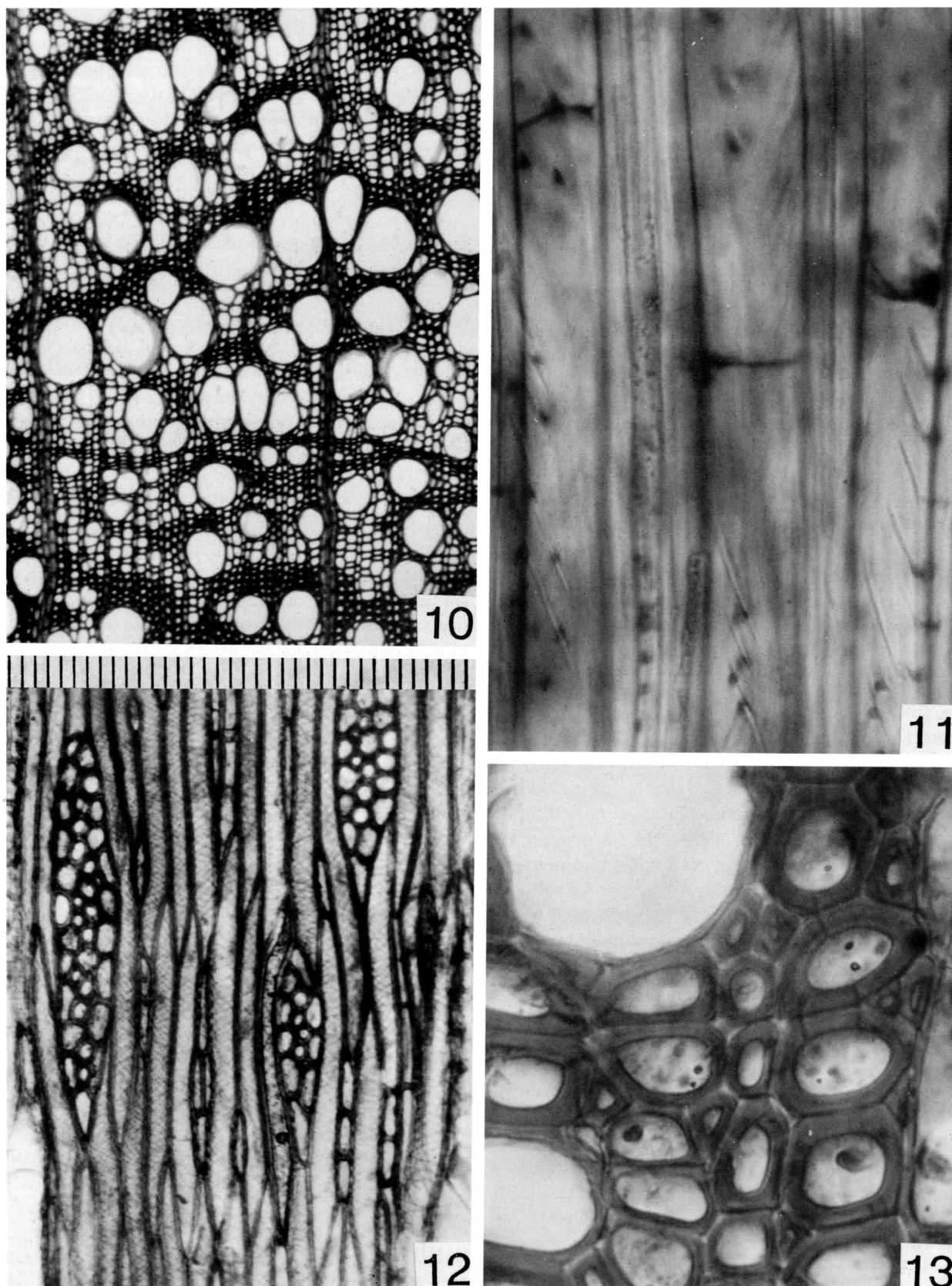


Fig. 10–13. Wood sections of *Buddleja* to show details of vessels and imperforate tracheary elements.—10. *B. alternifolia*, narrow vessels accompany many of the wider vessels.—11. *B. bullata*, libriform fibers from radial section to show septa and splits in wall, extending from pit apertures.—12. *B. alternifolia*, tangential section through a zone of narrow vessels; vague storying is suggested in the vessel elements.—13. *B. colvillei*, transection to show vessel (upper left) and libriform fibers which contain starch grains (hila of starch grains appear as black dots). (Fig. 10, scale above Fig. 1; Fig. 11, 13, scale above Fig. 4; Fig. 12, scale above Fig. 12 [divisions = 10 μ m].)

of the range can be explained in terms of stem diameter (see discussion on habit and ecology below).

Libriform fibers of *Nuxia verticillata* (Fig. 22) and *Peltanthera floribunda* (Fig. 26) are thicker walled (4.6 μm) than any but three collections of *Buddleja* (*B. alternifolia*, *B. bullata*, and *B. salviifolia*). Notably thick- or thin-walled fibers might possibly be species characteristics in *Buddleja*, but the majority of the species have fibers that are typical for the genus in wall thickness (3.0 μm).

Wolkinger (1970) cited two species of *Buddleja*, *B. alternifolia* and *B. davidii*, as having living fibers. The present study confirms that libriform fibers likely have prolonged longevity, and could therefore be called living fibers, in all species of *Buddleja*. Septa in libriform fibers are an indication of prolonged longevity, and were observed in *B. araucana*, *B. bullata* (Fig. 11), *B. indica*, *B. parviflora* (Iltis 167), *B. stachyoides* (stem and root), *B. tubiflora*, *B. tucumanensis*, *Nuxia verticillata*, and *Peltanthera floribunda*. Nonseptate fibers that contained cytoplasm remnants were observed in *B. americana* and *B. skutchii*. Both cytoplasm and starch were observed in libriform fibers of *B. colvillei* (Fig. 13). If liquid-preserved material had been available for all taxa, more indicators that the libriform fibers are long lived doubtless would have been seen.

Axial Parenchyma

Degree of axial parenchyma presence is often closely correlated with presence of living fibers. Living fibers can be regarded as a kind of pervasive parenchymalike tissue that renders axial parenchyma superfluous or nearly so (Carlquist 1988). In no species of Buddlejaceae examined here is axial parenchyma abundant except for the bands of initial parenchyma observed in *B. salviifolia* and *Peltanthera floribunda*. Very scanty vasicentric (paratracheal) parenchyma was observed in *B. davidii*, *B. globosa*, *B. rufescens*, *B. scordioides*, *B. skutchii*, *B. stachyoides*, *B. utahensis*, and *Peltanthera floribunda*. No axial parenchyma was observed in *B. indica*, *B. mendozensis*, and *Nuxia verticillata*. In *B. bullata* and *B. parviflora* (Iltis 167), axial parenchyma was not abundant, but it did form a nearly complete sheath one cell in thickness around vessels or vessel groups.

As seen in longisection, axial parenchyma consists of strands of two to five cells. The cells of the strand are surrounded by relatively thin (ca. 1.0–1.4 μm) lignified walls.

Rays

Both multiseriate and uniseriate rays occur in all Buddlejaceae. Uniseriate rays are less common than multiseriate rays in all species except *B. alternifolia*, *B. globosa*, *B. rufescens*, and *B. utahensis* (Wolf 9833).

In these four, uniseriate rays are about as common as multiseriate rays.

The ray type of Buddlejaceae can be assigned to Heterogeneous Type IIB of Kribs (1935), although several-celled uniseriate tips on multiseriate rays, a characteristic of Heterogeneous Type IIA, can be seen occasionally in most species of *Buddleja* as well as in *Peltanthera*.

The wood samples of *Buddleja*, *Nuxia*, and *Peltanthera* used in this study can be divided into those that are less than 1 cm in diameter and those that are wider than 1 cm. Samples less than 1 cm in diameter include *B. americana*, *B. araucana*, *B. colvillei*, *B. indica*, *B. mendozensis*, *B. racemosa*, *B. scordioides*, *B. skutchii*, *B. stachyoides* (stems and roots), *B. tubiflora*, *B. tucumanensis*, *B. utahensis* (Wolf 9833), and *Emorya suaveolens*. In all of the samples less than 1 cm in diameter, upright cells comprised at least half of the tissue of multiseriate rays, and therefore the rays in these samples conform to Paedomorphic Type I (Carlquist 1988). In the remaining wood samples, which were more than 1 cm in diameter, upright cells were confined to the tips of multiseriate rays (with occasional upright sheath cells on the sides of multiseriate rays). Uniseriate rays are composed of upright cells only, a characteristic of either Heterogeneous Type IIA or Type IIB of Kribs (1935).

Mean height of multiseriate rays (Table 1, column 9) ranges between one and two times the mean length of vessel elements. The photographs of tangential sections (Fig. 2, 12, 15, 19, 23, and 27) show relatively little disparity among the species, although the rays of *Peltanthera floribunda* (Fig. 27) are taller than those of *Buddleja*. If most multiseriate rays are, indirectly, derived from fusiform cambial initials, a height for multiseriate rays somewhat in excess of that of vessel elements (which are roughly the same length as fusiform cambial initials) is to be expected.

Mean width of multiseriate rays (in terms of cell number) is shown in Table 1, column 10. In most species of *Buddleja*, rays are 2–4 cells wide at their widest point (Fig. 2, 12, 15). In *B. utahensis* (Thorne 44537: Fig. 19), *Nuxia verticillata* (Fig. 19), and *Peltanthera floribunda* (Fig. 27), rays average more than four cells wide.

Uniseriate rays (Table 1, column 11) are typically more than one cell in height. The mean uniseriate ray height for *Buddleja* (156 μm) corresponds to rays two or three cells in height. Although not conspicuous, uniseriate rays can be found in the tangential sections shown in Fig. 2, 12, 15, and 23.

Perforated ray cells were observed in *Buddleja globosa*, *B. utahensis* (Thorne 44537), and *Peltanthera floribunda*. Ray cell wall thickness mostly ranges between 1.0 and 1.8 μm , and only lignified walls were observed. In the Buddlejaceae studied, bordered pits

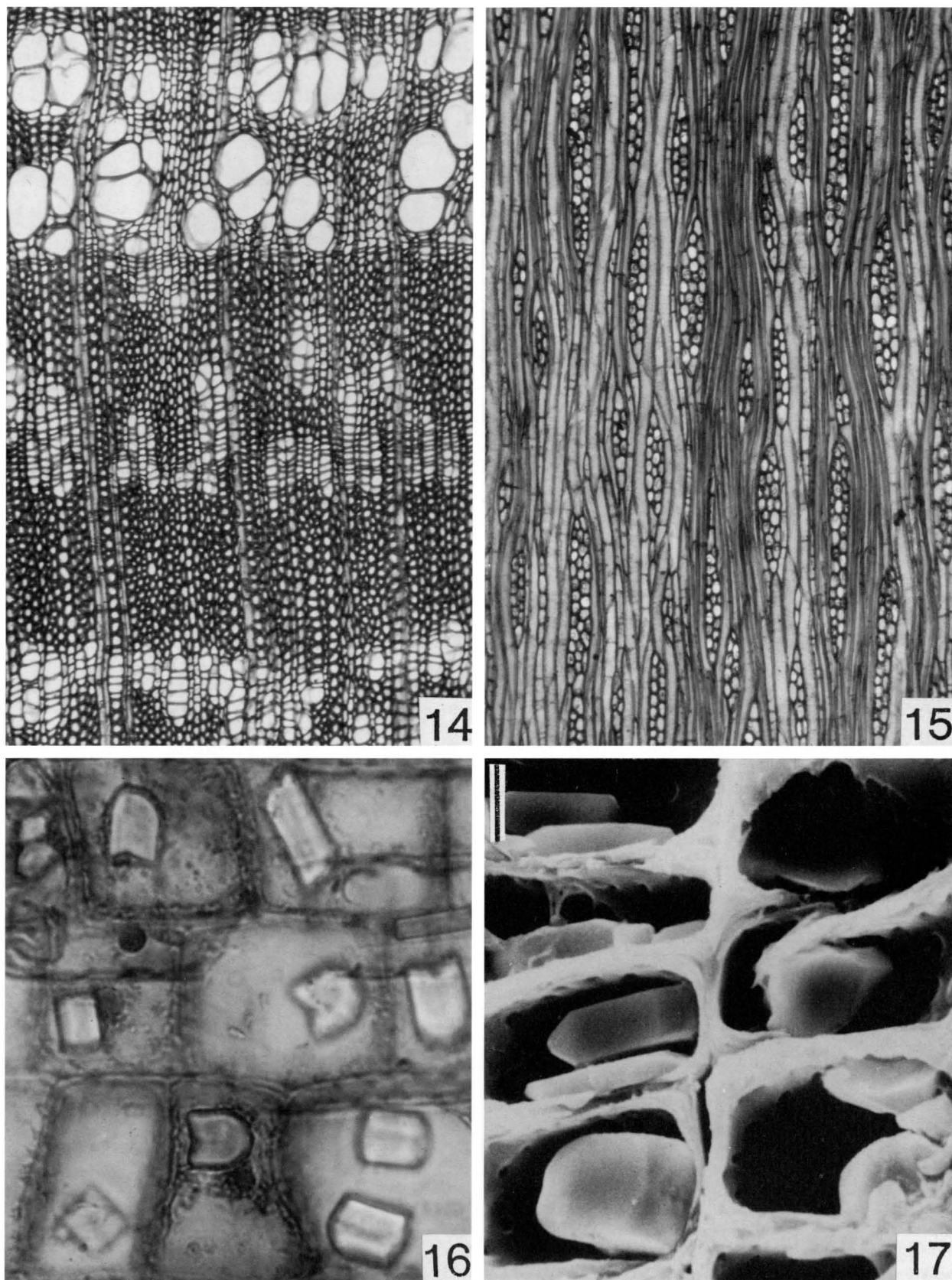
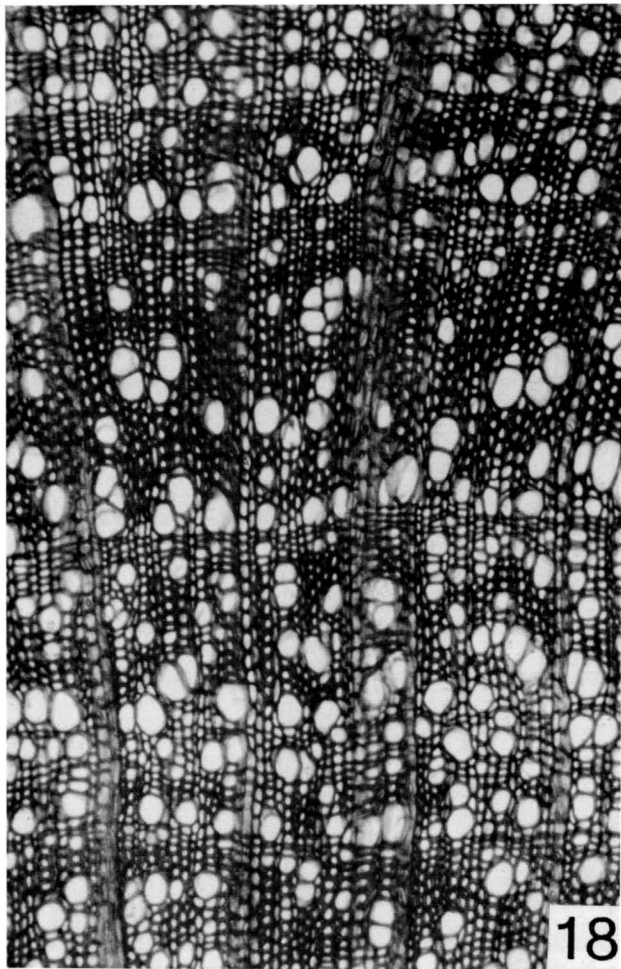
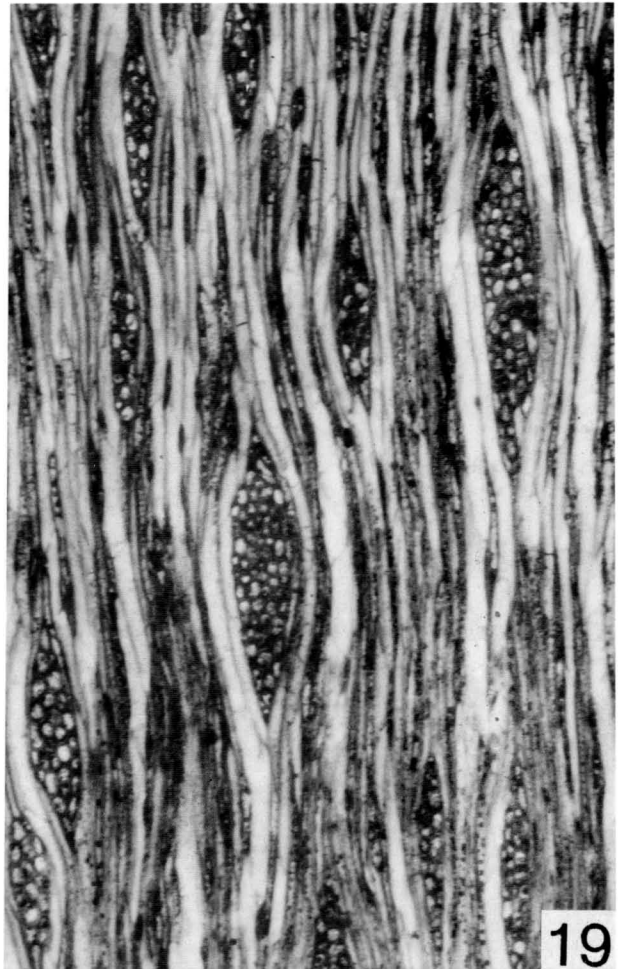


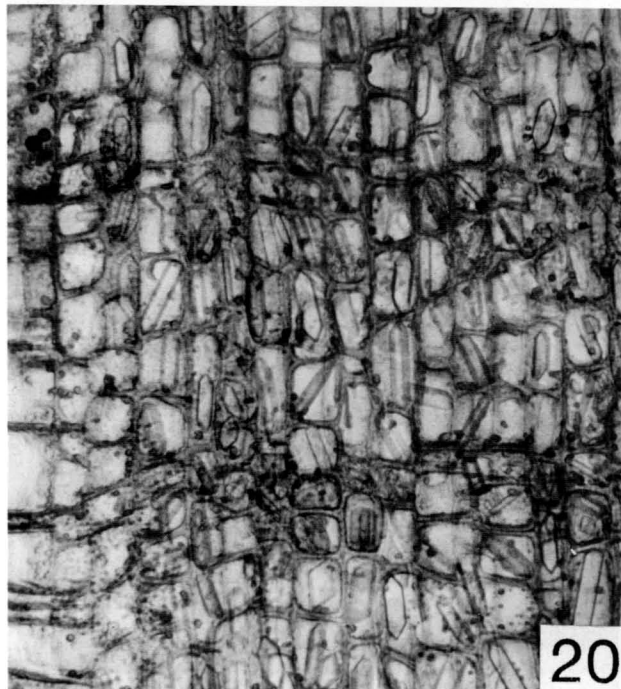
Fig. 14–17. Wood sections of *Buddleja*.—14–15. *B. parviflora*.—14. Transection, showing pronounced difference in diameter and abundance between earlywood vessels (top quarter of photograph) and latewood vessels (bottom three-quarters of photograph).—15. Tangential section; the darker patches are libriform fibers, the lighter areas are narrow vessel elements.—16. *B. parviflora*, ray cells from radial section, showing crystals of medium size for the genus; several form mirror-image pairs.—17. *B. mendozensis*, SEM photograph of ray cells from radial section; crystals are relatively large (portions sectioned from several crystals). (Fig. 14, 15, scale above Fig. 1; Fig. 15, scale above Fig. 4; Fig. 17, scale at upper left = 10 μm .)



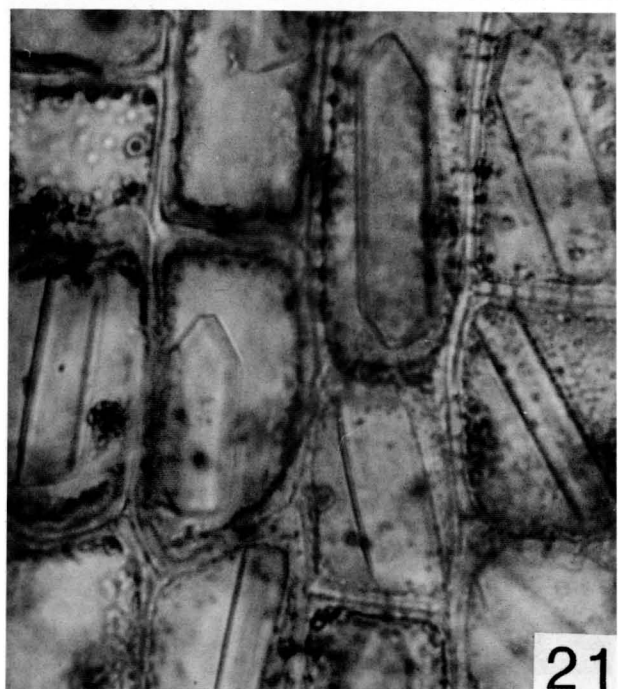
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Fig. 18–21. Wood sections of *Buddleja utahensis*, Thorne 44537.—18. Transection, illustrating narrowness of vessels; approximately five growth rings are present.—19. Tangential section; rays are mostly four or more cells wide.—20–21. Radial sections, horizontal axis of ray oriented vertically in photographs.—20. Portion of multiseriate ray to show that almost every cell contains one large crystal.—21. Several ray cells to show that crystals are chiefly oriented parallel to the long axis of the cell. (Fig. 18, 19, scale above Fig. 1; Fig. 20, scale above Fig. 12; Fig. 21, scale above Fig. 4.)

are quite frequent on tangential walls of ray cells, somewhat less common on transverse and radial walls. One must observe borders as seen in radial sections; most workers have looked for borders in face view, and borders on ray cells are not readily detected in this fashion. A few thin-walled tyloses were observed in *B. alternifolia*, *B. asiatica*, and *Peltanthera floribunda*.

Storying

No easily recognized storying was observed in any Buddlejaceae. In Fig. 12, a series of narrow vessel elements show a tendency toward storying. Study of stems of large diameter would be more likely to reveal storying than study of stems less than 1 cm in diameter.

Crystals and Deposits

Crystals, often hexagonal in shape (Fig. 17), are elongated and in some species (Fig. 21, 29, 30). In a few instances, paired mirror-image crystals are common, as in *B. parviflora* (Fig. 16, center right). Large crystals were observed in *B. cordobensis*, *B. mendozensis* (Fig. 17), and *B. utahensis* (Fig. 21). Medium-sized crystals occur in *B. parviflora* (Fig. 16). Small crystals were observed in *B. tubiflora* as well as in *Peltanthera floribunda* (Fig. 29, 30). Mennega (1980) says, concerning crystals of *Peltanthera*, "In nearly all cells very fine needle crystals present," but the crystals are not truly needlelike, and were observed in the present study only in ray cells. In dicotyledons at large, crystals are not reported from vessels (except in tyloses), are very rarely present in imperforate tracheary elements, and essentially occur only in parenchyma. Crystals like those illustrated for *Peltanthera* (Fig. 29, 30) were also observed in pith cells of *Buddleja skutchii*. One to several crystals occur in *Buddleja* ray cells, but if more than one crystal is present, one is larger than the others. No crystals were observed in *B. alternifolia*, *B. americana*, *B. asiatica*, *B. dominicensis*, *B. indica*, *B. salviifolia*, *B. skutchii*, *Emorya suaveolens*, and *Nuxia verticillata*.

Sphaeroidal droplets of resinlike appearance were observed in wood cells of *B. asiatica* and *B. utahensis*.

PHYLOGENETIC AND TAXONOMIC CONCLUSIONS

Crystal presence or absence and a few other wood features have been used as species criteria in dicotyledons. The number of features in wood of *Buddleja* is too small and the coverage of the genus too sparse to permit citation of any wood features as species or infrageneric criteria within the genus. Characters other than those in secondary xylem must be relied upon for classification within *Buddleja*.

Generically, *Buddleja*, *Nuxia*, and *Peltanthera* are

distinguishable in terms of wood features. *Emorya suaveolens* has wood like that of a xeromorphic *Buddleja*, and has no features not seen in *Buddleja*. No feature is truly diagnostic for any one or two of the genera. The lateral wall pits of *Nuxia* and *Peltanthera* vessels are slightly smaller than the smallest in *Buddleja*, but not much smaller than those of *B. racemosa*. Multiseriate rays are wider in *Nuxia* and *Peltanthera* than those reported in *Buddleja*. However, the difference is not great, and might derive from the fact that wood samples of these two genera were likely larger in diameter than those available for *Buddleja*, although diameter of stems from which samples were taken cannot always be estimated readily from xylarium samples. Rays tend to grow wider with increase in diameter of stems (see Carlquist 1988). The sample of *Peltanthera floribunda* was about 8 cm in diameter. The sample of *Peltanthera floribunda* studied by Mennega (1980) was relatively small in diameter (a twig), and not surprisingly, she reports relatively narrow rays compared with the rays figured here (Fig. 27). The rays described by Mennega (1980) for this species also contain a higher proportion of upright cells, a fact that tends to indicate a relatively juvenile condition. The old stem (as indicated by their numerous growth rings) of *B. utahensis* (Thorne 44537) had relatively wide rays (Fig. 19); this stem was 1.8 cm in diameter. The grooves interconnecting pit apertures on lateral vessel walls of *Peltanthera floribunda* were observed in *B. indica* and *B. salviifolia*. Thus, no feature of *Peltanthera* wood can be used to segregate it from that of *Buddleja*. The wood of *Peltanthera* is somewhat more similar to wood of *Buddleja* than is the wood of *Nuxia verticillata*. *Nuxia* wood features do not exclude that genus from Buddlejaceae, based on the present data and that offered by Mennega (1980). The information given by Mennega (1980) about wood of *Androya* and *Gomphostigma* does not exclude these two genera from Buddlejaceae. Mennega (1980) cites radial files of vessels, presence of procumbent cells exclusively, and presence of marginal parenchyma bands in these two genera as indications for their distinctness. All of these features are present in *Buddleja* (initial parenchyma is a form of marginal parenchyma). The idea, mentioned by Mennega (1980), that *Gomphostigma* might belong to Oleaceae, is not warranted in terms of information from wood anatomy. In fact, the phylogenetic tree presented by Mennega (1980, p. 157), shows *Buddleja* as a basal group from which *Androya*, *Gomphostigma*, *Nuxia*, and *Peltanthera* have been derived. A similar concept is offered by the phylogenetic tree given by Punt (1980) on the basis of pollen structure; Punt also gives *Buddleja* as the basal genus. Hunziker and Di Fulvio (1958) in their study of *Peltanthera* say on the basis of data from macromorphology that *Peltanthera* should be included in Loganiaceae

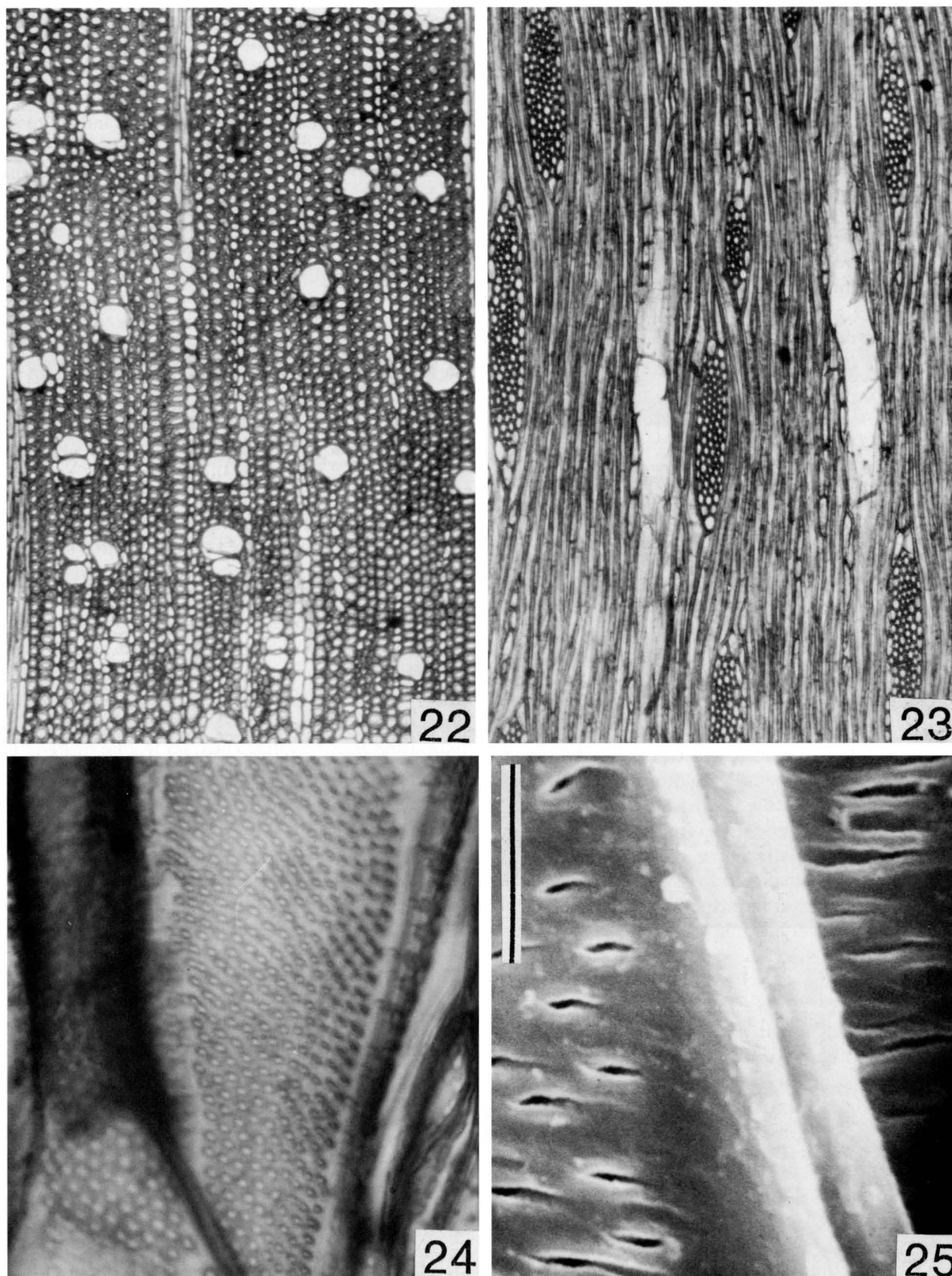


Fig. 22–25. Wood sections of *Nuxia verticillata*.—22. Transection; vessels are relatively sparse and mostly solitary.—23. Tangential section; multiseriate rays are at least four cells wide and lack long uniseriate wings.—24. Portions of vessel wall from tangential section, to show minute size of pits.—25. SEM photograph of juncture between two vessel elements, from tangential section, to show that pairs of thickenings accompany the pit apertures. (Fig. 22, 23, scale above Fig. 1; Fig. 24, scale above Fig. 4; Fig. 25, scale bar at upper left = 10 μm .)

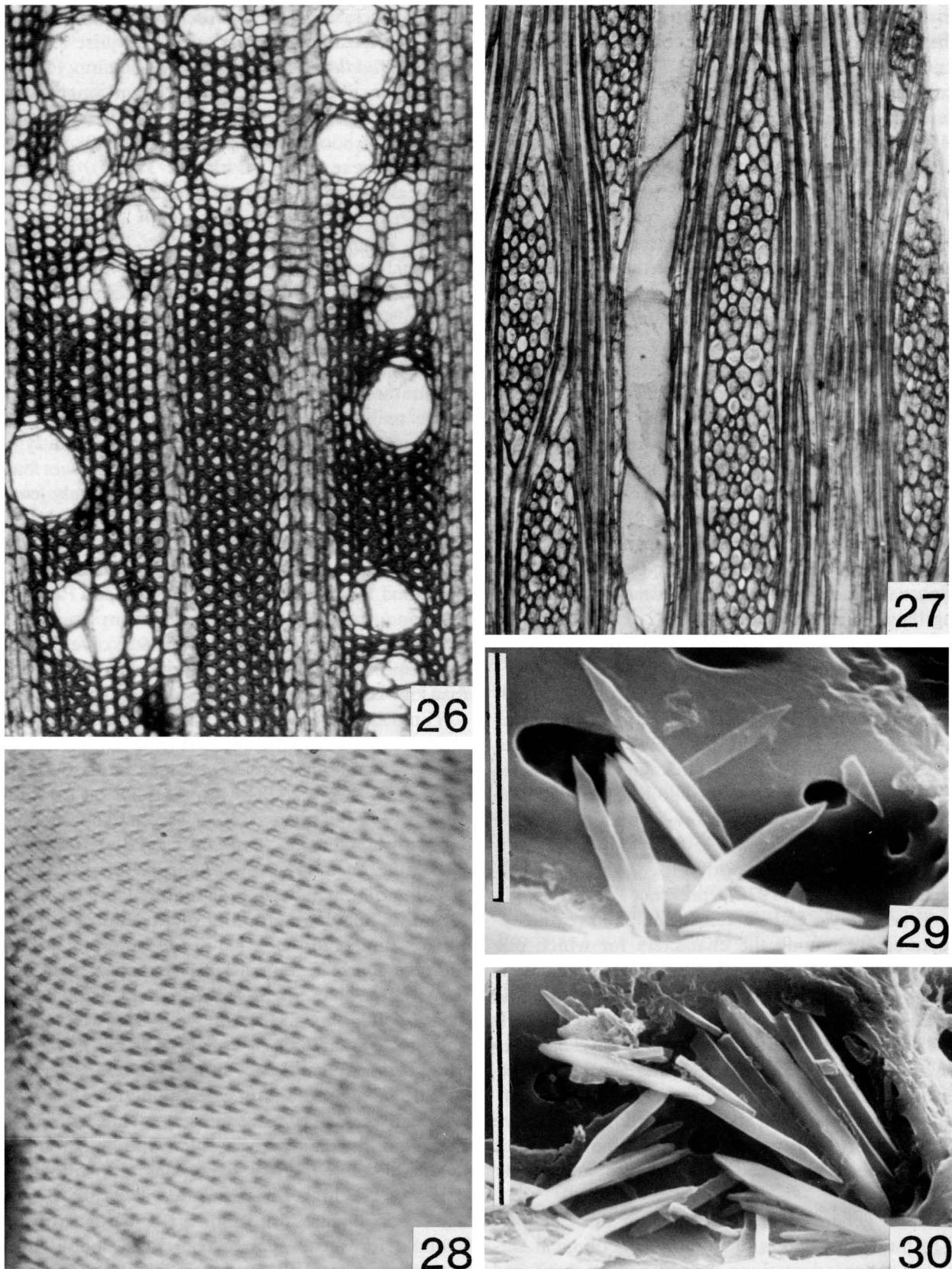


Fig. 26–30. Wood sections of *Peltanthera floribunda*.—26. Transection, showing large diameter of most vessels.—27. Tangential section; most rays are more than 5 cells wide.—28. Portion of vessel wall from tangential section to show small size of pits and a few inconspicuous grooves interconnecting pit apertures.—29–30. SEM photographs of ray cells from transection to show styloid-like crystals.—29. Crystals with tapered ends.—30. Large number of crystals typical of many ray cells. (Fig. 26, 27, scale above Fig. 1; Fig. 28, scale above Fig. 4; Fig. 29, 30, scale bars at left = 10 μm .)

(which at that time included the buddlejoid genera), but that *Peltanthera* has "strong affinities with some genera of the Scrophulariaceae." This conclusion is difficult to interpret.

The exclusion of *Sanango* from Buddlejaceae (Dickson 1994) is justified because it has some features not found in Buddlejaceae. The transfer to Gesneriaceae, tentatively advocated by Dickson (as well as by authors of papers that accompany his paper) seems advisable. In fact, one important feature quite infrequent in Lamiales (Scrophulariales) reported for *Sanango* is presence of scalariform perforation plates in vessels (Dickson 1994). Although not cited by Dickson, scalariform perforation plates have been reported in a genus of Gesneriaceae, *Kohleria* (Carlquist and Hoekman 1986b).

If one looks at the families of Asteridae s. l. as defined by Olmstead et al. (1993), one finds great diversity in woods because of the numerous families in that subclass. However, if one looks at a single order of Asteridae, Lamiales, as defined by Olmstead et al. (1993) (Acanthaceae, Bignoniaceae, Buddlejaceae, Lamiaceae, Martyniaceae, Oleaceae, Pedaliaceae, and Verbenaceae), one finds a great deal of similarity among these families (Carlquist 1992a). For example, I cannot with certainty separate wood of Asteraceae from wood of these families.

In the cladogram of Olmstead et al. (1993), Buddlejaceae are shown as a sister group of Verbenaceae. Does wood anatomy support this view? Some features common in *Buddleja* (helical thickenings in vessels, crystals in ray cells) are not common in Verbenaceae, but they do occur in at least a few genera of Verbenaceae (Metcalf and Chalk 1950). Presence of libriform fibers (living fibers reported for *Vitex* of the Verbenaceae: Wolkinger 1970), presence of Heterogeneous Type II rays, and all vessel and axial parenchyma features are among the characters for which one can cite resemblance between Buddlejaceae and Verbenaceae. Olmstead and Reeves (1995) place *Buddleja* in a clade they call "Scrophulariaceae I." Septate fibers (a concept similar to living fibers) have been reported for some genera of Scrophulariaceae by Metcalfe and Chalk (1950), and all vessel, axial parenchyma, and ray features cited above for Buddlejaceae have also been reported in at least some of the genera of Scrophulariaceae examined by Metcalfe and Chalk (1950).

Particular genera or groups of genera show adaptations to particular habits or particular ecological settings, but these adaptations should not be confused with synapomorphies indicative of phyletic relationship. However, the "F/V ratio" (length of imperforate tracheary elements divided by length of vessel elements) is indicative of degree of phyletic advancement, within limits, in a phylad. An F/V ratio of 4.0

or more is rare; F/V ratios below 1.20 are indicative of primitive dicotyledon woods (Carlquist 1975). The ratio in *Buddleja* is 2.10 (Table 1, column 12), indicative of a degree of phyletic advancement slightly above average for dicotyledons; the figure for Acanthaceae is 1.85 (Carlquist and Zona 1988). The figure for Lamiaceae, 2.09 (Carlquist 1992b), is virtually identical with that for Buddlejaceae.

CONCLUSIONS ON ECOLOGY AND HABIT

In woods that do not have tracheids as imperforate tracheary elements, but rather have fiber-tracheids or libriform fibers, degree of vessel grouping is proportional to xeromorphy (Carlquist 1984). The mean figure for vessels per group in *Buddleja*, 2.3, is not far above or below the figure for the individual species, and could show that *Buddleja* most frequently characterizes habitats that are not perpetually wet but experience some seasonal drying. The relatively low vessel per group figures for *Nuxia verticillata* (1.1) and *Peltanthera floribunda* show that these species grow in areas where soil dries very little: *Nuxia verticillata* is a cloud forest element of Mauritius, and *Peltanthera floribunda* occurs in moist forests from Costa Rica to Bolivia (Hunziker and Di Fulvio 1958). Vessel grouping is probably a less sensitive indicator of ecology than the vessel features discussed below.

Three quantitative features of vessel elements are physiologically significant and indicate relative xeromorphy or mesomorphy. These can be combined into a ratio I have termed the Mesomorphy Ratio (Carlquist 1988): vessel diameter times vessel element length divided by number of vessels per mm². The figures for this Ratio obtained for Buddlejaceae are given in Table 1, column 13. The range of figures is unusually great for a monophyletic group of dicotyledons: 5 to 8,102. This is similar to the range in Mesomorphy values for Pittosporaceae (Carlquist 1981), except that Mesomorphy Ratio values in *Buddleja* extend much lower, as in *B. mendozensis* (14), *B. scordioides* (6), *B. utahensis* (5, 14), and *Emorya suaveolens* (7). Values this low occur only in desert shrubs (Carlquist and Hoekman 1985), and the four species cited occupy habitats about as xeric as those of deserts. Thus, the diversity in quantitative data on vessels in Buddlejaceae reflects to a remarkable degree adaptations to a wide range of habitats. The high Mesomorphy values for *B. bullata* and *B. domingensis* are indicative of relatively moist habitats for those species, but note should also be taken that these samples are relatively large in diameter, and larger diameter samples tend to have wider vessels at their peripheries because as a tree or large shrub increases in size, its roots tend to go deeper and tap more soil levels in which moisture fluctuates less and is more abundant. The habitats of the species for

which wood has been studied here are not discussed in detail because I do not have direct knowledge of the ecology of these habitats, but the data that will be included in a forthcoming monograph of neotropical Buddlejaceae by Dr. Eliane Norman can be examined to show that close correlations between ecology and Mesomorphy Ratio values exist.

In addition to quantitative vessel data, the occurrence of growth rings (in which narrow vessels are predominant and wide vessels are relatively narrow compared with those of dicotyledons at large) as shown for *B. parviflora* (Fig. 14) is indicative of adaptation to dry habitats. The growth rings of *Buddleja* species with lower Mesomorphy Ratio values feature latewood in which appreciably narrower vessels are formed. Narrow vessels are indicative of xeromorphy because they embolize less readily than wider vessels (Hargrave et al. 1994). In several species of *Buddleja*, the last one or two layers of latewood vessels are so narrow that perforation plates are lacking, and thus vascular tracheids are present (e.g., *B. parviflora*, *B. mendozensis*, *B. scordioides*, *B. tubiflora*, and *B. utahensis*). Vascular tracheids are strongly indicative of xeromorphy, and probably resist embolism formation better than vessels. Vascular tracheids tend to occur in plants with drought-deciduous leaves, as opposed to plants that are evergreen throughout the dry season, as in chaparral or macchi (Carlquist 1985), and in which virtually no leaves are lost during the dry season. Vascular tracheids likely permit survival of cambium in stems that cannot support leaves in periods of extreme drought. Vascular tracheids are seen in species that lose some of their leaves during the dry season, as happens in *Buddleja*. Woods of *Buddleja* with more xeromorphic woods also have, as one might expect, smaller leaf sizes as compared to the leaf sizes of species in wetter habitats.

Within a phylad of woody dicotyledons, helical thickenings are more common in species occupying drier or colder areas (Carlquist 1988). Because most species of *Buddleja* grow in areas that are at least moderately dry, presence of helical thickenings in most species of the genus is understandable. Interestingly, all of the species of *Buddleja* that have helical thickenings in vessels have Mesomorphy Ratio values below 100; this is also true in *Emorya suaveolens*. On the other hand, species that lack helical thickenings (together with their Mesomorphy Ratio values) are: *B. asiatica* (322); *B. bullata* (990); *B. domingensis* (400); *B. rufescens* (331) and *B. salviifolia* (133). Not surprisingly, *Nuxia verticillata* (1054) has only the most vestigial helical thickenings, and *Peltanthera floribunda* (8102) lacks thickenings.

Thus, most features of wood of Buddlejaceae relate to ecological adaptation of particular species, and the inherent interest of the family in this respect is very

great. Two features have no obvious relation to xeromorphy, but character expressions in these (degree of crystal presence; diameter of pit cavities of lateral wall pits of vessels) form continua within *Buddleja*, and cannot be readily used for systematic distinctions.

The wood anatomy of Buddlejaceae suggests a phylad that had woody origins, although perhaps shrubby rather than arboreal. One reason for this conclusion is that length of vessel elements does not decrease with increase in stem diameter, as it does in phylads where secondary woodiness has occurred (Carlquist 1962). For example, larger wood samples were available for *B. asiatica*, *B. domingensis* and *B. globosa*, but these three species have relatively long vessel elements. A second reason is that ray structure is not juvenilistic for prolonged periods. In all of the species for which stems with diameters of more than 1 cm were available for study, the multiseriate rays consisted almost exclusively of procumbent cells except in *B. asiatica*, in which procumbent cells comprised about a third of the cells in multiseriate rays at the periphery of the stem. Predominance of upright cells in multiseriate rays, a condition often protracted for the entire life of the plant, characterizes phylads with secondary woodiness (Carlquist 1962, 1988).

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