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WOOD ANATOMY OF BRUNIACEAE: CORRELATIONS WITH
ECOLOGY, PHYLOGENY, AND ORGANOGRAPHY

Sherwin Carlquist

Abstract.—Wood of Bruniaceae is very primitive according to widely-accepted criteria. Vessels are relatively long, with scalariform perforation plates having numerous bars, fully or vestigially bordered. Many aberrations in disposition of bars and perforations in perforation plates are present, and no species has exclusively normal perforation plates. Lateral wall pitting of vessels, both intervascular and between vessels and rays, is scalariform to opposite. Vessels are solitary or nearly so, angular to round in transection. Helical thickenings are present in vessels of only a single species. All imperforate elements are thick-walled tracheids, some with gelatinous walls. Tracheids are only slightly longer (in two instances shorter) than the vessel elements they accompany in any given species. Axial parenchyma is diffuse, with very slight tendencies toward aggregates or vasicentric scanty. Rays are heterocellular, with a predominance of upright cells, or upright cells exclusively in species with very narrow multiseriate rays. Multiseriate rays vary from biseriate to an average of more than five cells in width, according to species. Uniseriate wings are present on at least some multiseriate rays in all species. Borders are frequently present on the tangential walls of ray cells, which tend to be thick. Uniseriate and multiseriate rays are present in all species. Growth rings vary from absent to conspicuous, the latter mostly in montane species. Inconspicuous growth rings feature narrow vessels or narrow tracheids in latewood. More pronounced growth rings have more numerous as well as wider vessels in earlywood; vessels may be absent or nearly so in latewood, which would thus constitute an all-tracheid band produced annually. Crystals are present in rays of most species, sometimes chambered in subdivided ray cells. A few species have crystals in chambered axial parenchyma cells. Droplets or massive deposits of amorphous dark-staining compounds are present in all species. Woods of Bruniaceae are exemplary, considering their primitiveness, for adaptation to xeromorphy, based on current concepts of wood xeromorphy. Vessels are notably narrow or numerous per mm² of transection, or both. The nature of growth rings and of perforation plate modifications are suggestive of xeromorphy. Although species of moister habitats do have quantitatively more mesomorphic wood features, the span within Bruniaceae is not great, suggesting that wood of the family as a whole is adapted to extremes of water stress in accordance with the dry, hot summers, high incidence of wind, and porous sandstone soils of Cape Province, South Africa. Lignotubers have woods more parenchymatous and mesomorphic than wood of stems in the lignotuber-bearing species. Wood of stems does not differ appreciably from that

of roots. Bruniaceous woods are most closely comparable to those of Geis-solomataceae and Grubbiaceae, although other "rosoid" families have similar woods. This agrees with the "rosoid" placement accorded Bruniaceae by most phylogenists.

Introduction

Wood anatomy of the South African family Bruniaceae is of special interest for several reasons. Remarkably little is known on this topic, and the brief account in Metcalfe and Chalk (1950) is very largely derived from the scanty data of Solereder (1908) and of Nieden-zu and Harms (1930). All of these accounts are based upon twig material of a few species. One can say fairly that Bruniaceae, although a clearly woody family, have been neglected by wood anatomists because of their nonarboreal status. Only two species, *Berzelia commutata* Sond. and *B. lanuginosa* Brongn., become small trees. Most species are shrubs of various sizes, ranging downward to rock-crevice species such as *Linconia cuspidata* Swartz and *Staavia pinifolia* Willd., which do not exceed 3 dm in height. Thus, wood samples of Bruniaceae are extremely rare in wood collections. During my 1973 field work in Cape Province, South Africa, I attempted to collect as many species as possible.

Bruniaceae contain 12 genera in which approximately 75 species have been recognized (Pillans, 1947). Of these, about 15 species are known only from one or several collections. Of the remainder, only two, *Berzelia lanuginosa* and *Staavia radiata* Dahl, could be said to be at all common. Only one species, *Raspalia trigyna* Dümmer, occurs outside Cape Province; it is endemic to Natal. The remainder are all endemic to Cape Province, and occur either on Table Mountain sandstone or soils derived from that formation. A large proportion of the species are montane, some limited to just a few summits or a small portion of a short mountain range. Thus, collecting woods of a majority of the species provided unusual problems. During my field work in South Africa in 1973 I focused on Bruniaceae and obtained wood samples of 47 species belonging to all 12 genera (Table 1).

Woods of Bruniaceae prove to be exceptionally interesting with regard to their high degree of primitiveness as judged on widely-accepted criteria. Why do such primitive woods exist in Cape Province, in which the vast majority of dicotyledons have highly specialized woods (Carlquist 1975a)? Bruniaceae prove not to be exceptions to the rule that groups with primitive xylem tend to exist in mesic situations, as discussed later with regard to ecological preferences of the family.

The relationships of Bruniaceae are thought to be rosalean (e.g., Wettstein, 1935; Cronquist, 1968) or hamamelidalean (Hutchinson, 1959). Thorne's Pittosporales (1968, 1976), in which he places Bruniaceae, is a

rosoid group, ranked under his superorder Rosiflorae. Thus, there is not much disagreement over the general position of the family. If one is to select one or several families close to Bruniaceae, however, lists vary rather considerably from one author to another. Wood anatomy proves at least initially helpful in confirming a generalized "rosoid" placement as well as in suggesting what families might be most closely compared to Bruniaceae.

The diversity of wood anatomy within Bruniaceae is quite noteworthy, which is why a more than token number of illustrations are presented here. Obviously the various expressions are variations on a basic plan. However, these variations are more diverse than one would expect for the size of the family. These expressions tend to reinforce generic lines and groupings of genera. The diversity in wood anatomy within the family appears to be the product of evolution into a wide variety of woody growth forms as well as into a number of distinctive habitats.

Materials and Methods

Wood samples were collected in the field and preserved by means of drying. Herbarium vouchers were prepared. Wood samples of roots and lignotubers were taken in addition to stem samples (Table 1). Wood samples of stems were selected so as to obtain portions of maximal diameter for any given species. Obviously species in which numerous stems sprout from a lignotuber, such as *Audouinia capitata* or *Staavia radiata*, tend to be much smaller than those of single-stemmed species. For *Berzelia commutata*, a log 16 cm in diameter was obtained; for *B. lanuginosa*, a log 9 cm in diameter was selected. Most stems range between 0.5 and 4.0 cm in diameter, and were collected so as to obtain the largest stems within a population of a given species. *Linconia cuspidata* and *Staavia pinifolia* are rock-crevice species exclusively. Some other Bruniaceae occur sometimes as rock-crevice plants: the collections *Raspalia globosa*, *Carlquist 4811a*, and *R. microphylla*, *Carlquist 5012*, represent rock-crevice shrublets. The region of the *Linconia cuspidata* lignotuber studied represents a transitional region between the stem and lignotuber proper, and is therefore not fully representative of lignotuber anatomy. The photomicrographs illustrate stems almost exclusively, because the twisted grain of lignotubers results in oblique sections of most cells in any given section. Of the species studied here, the following characteristically have lignotubers: *Audouinia capitata*, *Berzelia abrotanoides*, *B. burchellii*, *B. cordifolia*, *Brunia laevis*, *Linconia alopecuroides*, *L. cuspidata*, *Lonchostoma myrtoides*, *L. pentandrum*, *Nebelia paleacea*, *Staavia capitella*, *S. pinifolia*, *S. radiata*, *Thamnea diosmoides*, and *Tittmannia esterhuyseniae*. The remaining species in the present study lack lignotubers. This matter is of interest, for the difference between lignotuber-bearing and nonlignotuberous species within genera is sharply defined, but

Table 1. Wood characteristics of Bruniaceae.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Audouinia capitata</i> Brongn.	4610	S	137	23	594	690	1.16	14.3	b, v	50	1.16	O	O	5.8	507	352	2.47	0.17	101
		L	92	28	513	599	1.17	16.0	v	90	1.24	O	O	5.8	442	240	—	0.30	154
		R	263	21	373	574	1.54	16.0	b, v	30	1.48	S-O	S	5.3	268	144	3.47	0.08	29
<i>Berzelia abrotanoides</i> Brongn.	4478	S	263	30	889	1010	1.14	28.8	v, a	80	1.36	S-O	S-O	2.9	1213	524	2.80	0.11	98
	5015	S	427	26	570	643	1.13	19.0	a	75	1.48	O	O	3.4	609	240	3.33	0.06	34
		R	299	29	662	751	1.15	16.9	v, a	90	1.36	O	S-O	2.8	526	262	3.40	0.10	66
<i>Berzelia bruchelli</i> Dümmer	4542	S	350	24	1071	1146	1.07	33.0	v, a	75	1.24	S-O	S-O	4.6	990	617	2.73	0.07	75
		L	137	30	791	964	1.22	28.9	v	85	1.24	S-O	S	4.8	475	313	3.67	0.22	174
<i>Berzelia commutata</i> Sond.	4736	S	179	46	706	966	1.37	20.4	v, a	80	1.20	S-O	S	4.0	533	253	3.33	0.26	184
<i>Berzelia cordifolia</i> Schlecht.	4690	S	337	28	693	700	1.01	27.7	b, v	80	1.20	O	S-O	4.8	608	381	2.45	0.08	55
<i>Berzelia ecklonii</i> Pillans	4965	S	120	33	900	989	1.10	33.0	v	80	1.36	S-O	S-O	5.0	1230	766	3.33	0.27	43
<i>Berzelia galpinii</i> Pillans	4541	S	265	31	863	880	1.02	26.4	v, a	80	1.36	S-O	S-O	3.6	565	366	2.40	0.12	104
<i>Berzelia intermedia</i> Schlecht.	4729	S	276	29	821	964	1.17	29.3	v, a	95	1.12	O	S-O	4.4	865	673	2.47	0.11	90
		L	163	29	522	583	1.12	27.2	v, a	70	1.04	S-O	S	4.3	965	490	3.00	0.18	94
<i>Berzelia lanuginosa</i> Brongn.	4835	S	119	43	866	1055	1.22	22.2	v, a	50	1.12	O	S-T	4.4	491	226	4.13	0.36	311
<i>Berzelia rubra</i> Schlecht.	4961	S	158	26	843	772	0.92	29.9	v	85	1.50	O	S-O	4.0	791	457	2.60	0.16	135
<i>Berzelia squarrosa</i> Sond.	4646	S	338	27	737	884	1.20	23.6	a	80	1.16	O	S	3.5	971	122	3.47	0.08	58
	4845	S	218	28	1196	1234	1.03	30.2	b	80	1.12	T-O	S-O	4.0	616	421	2.80	0.13	155
<i>Brunia albiflora</i> Phillips	4576	S	155	32	852	900	1.06	29.7	v	80	1.12	T-O	S-O	4.6	488	329	2.60	0.21	179
<i>Brunia alopecuroides</i> Thunb.	4944	S	488	23	971	1090	1.12	18.9	v	98	1.28	O	S-O	3.6	907	385	2.13	0.05	49
<i>Brunia laevis</i> Thunb.	4695	S	218	29	477	627	1.31	22.0	a	80	1.16	S-O	S	4.4	749	252	4.00	0.13	62
		L	162	21	688	775	1.13	25.1	b, v	70	1.16	S-O	S-O	4.4	485	342	?	0.13	89
<i>Brunia nodiflora</i> Linn.	4608	S	240	28	768	849	1.10	19.4	b	95	1.16	O	S-O	4.3	1290	491	4.33	0.12	92
<i>Brunia stokoei</i> Phillips	4679	S	106	32	739	849	1.15	44.3	b	95	1.08	O	S-O	5.9	542	227	3.27	0.30	221
<i>Linconia alopecuroides</i> Linn.	2510a	S	218	24	826	950	1.15	33.6	v	20	1.12	S	S	4.0	855	636	2.00	0.08	66
<i>Linconia cuspidata</i> Swartz	4943	S	182	20	546	706	1.29	30.8	b	20	1.16	S	S	5.3	967	512	3.40	0.11	60
		L	251	21	451	728	1.61	22.0	b	20	1.44	S	S	4.8	1197	373	5.60	0.08	36
<i>Lonchostoma esterhuyseniae</i> Strid	4982	S	218	29	734	779	1.06	41.8	v	98	1.16	O	O	4.6	1007	514	2.20	0.13	95
<i>Lonchostoma monogyna</i> (Vahl) Pillans	4682	S	283	25	851	938	1.10	38.8	b	80	1.32	O	S-O	4.9	—	430	2.00	0.09	77
<i>Lonchostoma myrtilloides</i> (Vahl) Pillans	5020	LS	79	33	532	634	1.16	30.8	b	95	1.28	S	S-O	5.3	1086	545	4.67	0.42	223
		US	146	27	764	883	1.16	26.1	b	95	1.20	S-T	S-O	3.4	1143	617	5.67	0.18	138

Table 1. Continued.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Lonchostoma pentandrum</i> (Thunb.) Pillans	4645	S	227	24	732	738	1.01	32.6	a	80	1.20	O	O	2.9	706	559	2.00	0.11	81
		L	173	23	595	647	1.09	29.0	b, v	70	1.44	S-O	S-O	4.4	887	370	3.40	0.13	77
<i>Lonchostoma purpureum</i> Pillans	4930	S	287	31	659	755	1.15	30.8	b, v	80	1.28	O	O	3.6	502	537	2.00	0.11	72
<i>Mniothamnea bullata</i> Schlecht.	4715	S	159	28	778	998	1.28	40.4	v	80	1.12	O	S	4.8	—	822	2.00	0.18	140
	5100	S	275	27	665	757	1.39	34.0	b	70	1.08	T	T	4.0	—	443	2.00	0.10	66
<i>Mniothamnea callunoides</i> Niedenzu	4720	S	382	22	799	876	1.10	40.3	v	85	1.12	O	T-O	4.3	544	413	2.00	0.06	48
		R			800	839	1.05			90									
<i>Nebelia fragarioides</i> O. Kuntze	4670	S	527	25	674	796	1.18	33.6	b	90	1.40	O	O	3.8	871	287	3.93	0.05	34
<i>Nebelia paleaceae</i> Sweet	4522	S	180	27	613	669	1.09	27.9	b, v	98	1.20	O	S	4.0	891	553	3.27	0.15	92
<i>Nebelia sphaerocephala</i> O. Kuntze	4614	S	432	23	760	899	1.18	27.1	v	80	1.20	O	S	3.3	696	512	3.73	0.05	38
<i>Nebelia stokoei</i> Pillans	5022	S	308	26	594	768	1.29	23.1	v	80	1.16	T-O	S-O	3.0	917	371	4.20	0.08	48
<i>Pseudobaeckea africana</i> (Burm. f.) Pillans	4588	S	193	33	1011	1237	1.22	41.4	b	100	1.20	T-O	O	4.1	1308	559	3.93	0.17	172
<i>Pseudobaeckea cordata</i> Niedenzu	4615	S	177	39	895	1019	1.14	35.2	b	80	1.16	T	T	3.1	815	308	4.40	0.22	197
<i>Raspalia globosa</i> (Lam.) Pillans	4811	S	307	26	914	903	0.99	36.1	v	40	1.20	T-O	T	5.0	488	392	4.47	0.08	73
	4811a	S	175	25	574	798	1.39	36.2	b, v	75	1.12	T-O	T-O	4.1	1332	373	5.43	0.14	80
	4811a	R	292	29	716	904	1.26	37.8	b, v	50	1.24	O	T-O	3.8	1018	647	3.40	0.10	72
<i>Raspalia microphylla</i> Brongn.	4673	S	189	26	982	1001	1.02	25.8	b, v	80	1.12	T-O	T	4.8	711	420	4.45	0.14	137
	5012	S	304	24	946	1041	1.10	34.8	b	40	1.12	T	T	5.3	1241	466	4.13	0.08	76
<i>Raspalia stokoei</i> Pillans	5053	S	245	23	608	725	1.19	30.3	b, v	80	1.12	O	O	4.5	636	341	3.50	0.09	55
<i>Raspalia variabilis</i> Pillans	4680	S	287	27	643	828	1.29	36.4	v	70	1.12	S-O	S-O	4.5	1186	539	3.20	0.09	58
<i>Raspalia virgata</i> (Brongn.) Pillans	4936	S	327	28	838	963	1.15	47.7	b, v	60	1.20	T	T	4.0	908	842	2.00	0.09	75
		R	205	35	987	1102	1.12	30.8	b, v	80	1.20	O	T-O	3.4	1380	463	4.13	0.17	168
<i>Staavia capitella</i> Sond.	4819	S	361	22	830	957	1.15	28.1	b, v	35	1.16	S-T	T	4.4	1083	565	2.00	0.06	50
		L	158	25	431	526	1.22	29.6	b	60	1.24	O	T-O	5.3	789	290	3.75	0.16	69
<i>Staavia dodii</i> Bolus	4620	US	130	26	871	1004	1.15	28.4	b, v	60	1.04	O	O	5.5	597	405	2.40	0.20	174
		LS	126	26	817	956	1.17	20.9	b	75	1.08	O	O	6.0	797	463	3.07	0.21	172
		R	134	26	680	818	1.20	20.2	b	80	1.08	O	S-O	5.0	872	399	2.80	0.19	129
<i>Staavia glutinosa</i> Dahl	4768	S	358	30	986	1132	1.15	25.0	v, a	50	1.32	S-T	S-T	6.3	777	562	2.10	0.08	79
		R			898	1018	1.32												
<i>Staavia pinifolia</i> Willd.	4754	S	450	29	548	655	1.20	24.6	b, v	20	1.32	S-O	S-O	3.8	1012	537	2.20	0.06	33

Table 1. Continued.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
<i>Staavia radiata</i> Dahl	4601	S	356	20	773	1015	1.31	25.8	v	35	1.40	T-O	S-T	3.9	1065	492	2.33	0.06	46
		L	260	25	582	671	1.15	26.4	b, v	60	1.20	T-O	S-O	3.8	1415	574	4.60	0.10	58
	4483	L	239	27	803	937	1.17	30.0	b	25	1.28	T-O	S-T	4.1	1723	651	3.53	0.11	88
<i>Thamnea diosmoides</i> Oliver in Hook.	4665	S	315	22	597	696	1.17	15.0	b	55	1.24	O	T-O	4.4	—	255	2.00	0.07	42
		L	165	23	441	493	1.12	14.2	b	30	1.04	O	O	3.6	340	218	3.47	0.14	62
		R	176	30	470	621	1.32	13.6	b	25	1.16	O	T	5.0	460	321	3.47	0.17	80
<i>Thamnea massoniana</i> Dümmer	4852	S	150	27	380	428	1.13	15.4	b, v	65	1.08	T-O	T	4.5	452	180	2.47	0.18	68
<i>Tittmannia esterhuyseniae</i> Powrie	5040	S	200	26	452	564	1.25	14.6	b	60	1.12	O	O	5.1	483	282	2.40	0.13	59
		L	118	25	400	491	1.23	13.1	b	40	1.12	O	O	5.1	655	308	6.20	0.21	84
<i>Tittmannia laevis</i> Pillans	4850	S	127	26	475	621	1.31	17.6	b	60	1.04	O	O-T	4.8	458	246	3.07	0.20	95
<i>Tittmannia laxa</i> Presl	5051	S	194	25	570	650	1.14	12.6	b	50	1.04	O	O	5.9	708	224	3.60	0.13	74

Key to Table. 1. Carlquist collection number, full set of specimens in RSA and duplicates distributed to other herbaria. 2. Portion of plant: S = stem; L = lignotuber; R = root; LS = lower (basal) stem; US = upper stem (branch). 3. Mean number of vessels per mm² of transection. 4. Mean vessel diameter, μm . 5. Mean vessel-element length, μm . 6. Mean tracheid length, μm . 7. Ratio of tracheid length to vessel-element length. 8. Mean number of bars per perforation plate. 9. Nature of bars on perforation plate: b = fully bordered; v = vestigial borders present; a = borders absent or nearly so. 10. Approximate percentage of perforation plates in which deviations from a perfectly scalariform condition (forked bars, semimultiperforate, etc.) occur. 11. Mean number of vessels per group as seen in transection. 12. Nature of intervacular lateral-wall pitting of vessels: O = opposite; S = scalariform; T = transitional between scalariform and opposite. 13. Nature of vessel-ray pitting on lateral walls of vessels: symbols as in 12. 14. Mean tracheid wall thickness, μm . 15. Mean height of multiseriate rays, μm . 16. Mean height of uniseriate rays, μm . 17. Mean width of multiseriate rays, number of cells at widest point in ray. 18. Vulnerability (vessel diameter divided by number of vessels per mm² of transection). 19. Mesomorphy (vulnerability figure multiplied by vessel-element length). Quantitative data for items 3, 4, 5, 6, 7, 8, 10, 11 based on average of 50 measurements. Quantitative data for other items based on average of 10 measurements.

has not been cited by Pillans (1947) or other authors. Species without lignotubers tend to grow in very wet places or have fruits or seeds resistant to fire. The significance of lignotuber evolution is primarily a mechanism for fire resistance, and possibly secondarily a means for photosynthate and water storage.

Woods were sectioned and macerated according to the usual techniques. Accumulation of the data in Table 1 is the work of Dr. Donald R. Bissing and Dr. Larry DeBuhr. Descriptions of localities and some ecological data can be found in the monograph by Pillans (1947).

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Anatomical Descriptions

Vessel Elements

Dimensions.—As shown in Table 1, vessel elements in Bruniaceae as a whole are relatively long for dicotyledons at large. They are probably primitively long, in accordance with the concepts of Frost (1930a, b) and Carlquist (1975a). One might expect even longer vessel elements if Bruniaceae were arboreal, for fusiform cambial initials in typically woody plants (which Bruniaceae clearly are) tend to increase with age (Bailey and Tupper, 1918; Carlquist, 1962). That average vessel-element length exceeds 1,000 μm in some Bruniaceae (e.g., *Pseudobaeckea africana*) therefore, is all the more remarkable for a family of shrubs. Further reinforcing the interpretation of length of vessel elements as primitive in Bruniaceae is the fact that the ratios for tracheid length to vessel-element length are remarkably low (Table 1, column 7). Markedly low tracheid length to vessel-element length ratios were hypothesized to be primitive (Carlquist, 1975a), and subsequent studies (e.g., Carlquist 1975b, c, 1976a, b) seem to confirm this. Of special interest is the fact that ratios lower than 1.00 occur in two Bruniaceae, *Berzelia rubra* Schlecht. and *Raspalia globosa* (Table 1). The only other instances in which ratios lower than 1.00 have been reported include *Myro-*

Fig. 1-4. *Audouinia capitata*, Carlquist 4610, wood sections of stem.—1. Transection, showing narrow, sparse, vessels.—2. Tangential section; rays are few, predominantly biseriate.—3. Perforation plate from radial section. Resinlike compounds outline the perforations, which are arranged in a semimultiperforate fashion.—4. Radial section showing rhomboidal crystals in ray cells, upper left and lower right. To the left of the crystal (lower right) is a pair of crystals in a horizontally subdivided ray cell.

thamnus Welw. (Carlquist, 1976a) and *Grubbia* Bergins (Carlquist, 1977a). All of these are shrubs of relatively finite size, which may be correlated with lowered intrusiveness of tracheids, as hypothesized in the two papers cited.

Quantitative features of vessel elements (vessel diameter, vessel-element length, and number of vessels per mm²) show a rather broad range within Bruniaceae. These variations have ecological explanations and are therefore discussed below in a section devoted to ecological interpretations.

Perforation plates.—Perforation plates of Bruniaceae can all be described as basically scalariform. As can be seen from Table 1, the range in means for number of bars per plate is considerable, however. Fewer than 20 bars per plate characterize *Audouinia capitata* (Fig. 3), *Berzelia abrotanoides*, *Brunia alopecuroides*, *B. nodiflora* (Fig. 16, 17), *Thamnea diosmoides* (Fig. 74), *T. massoniana* (Fig. 73), *Tittmannia esterhuyseniae* (Fig. 77, 78), *T. laevis*, and *T. laxa*. An average of more than 40 bars per plate was observed in *Brunia stokoei*, *Mniothamnea bullata*, *M. callunoides*, *Pseudobaeckea africana* (Fig. 47, 48), and *Raspalia virgata*. Species in which the mean falls between 20 and 30 (Table 1) are illustrated here: *Berzelia cordifolia* (Fig. 44), *Lonchostoma esterhuyseniae* (Fig. 33), *L. purpureum* (Fig. 24, 25), *Nebelia stokoei* (Fig. 43), *Staavia pinifolia* (Fig. 68), and *S. dodii* (Fig. 79). Number of bars per perforation plate is correlated roughly with mesomorphy, and is discussed in the section on ecological interpretations below.

Bruniaceae are notable for their numerous modifications of the scalariform perforation plate. One can say that no species of Bruniaceae has "perfectly" scalariform plates uniformly (Table 1, column 10). The variations observed include literally all the anomalies known for dicotyledons. The most common of these is presence of forked bars. This condition is shown here for *Brunia nodiflora* (Fig. 16, 17) and *Staavia pinifolia* (Fig. 68). The proportion of perforation plates with this anomaly is high in all species of Bruniaceae. The second most common anomaly can be loosely described as "multiperforate." By this, I mean that where one would expect an unbroken elliptical perforation, two or more perforations occur across the width of the perforation plate, like opposite pitting on the lateral walls of a vessel. These perforation plates are not so extreme in Bruniaceae as those described for other families of dicotyledons by MacDuffie (1921) or Parameswaran and Liese (1973), in which circular perforations distributed randomly on the perforation plate are figured. Multiperforate perforation plates with more than a single series of perforations across the width of a plate are shown here for *Audouinia capitata* (Fig. 3), *Berzelia cordifolia* (Fig. 44), *Lonchostoma*

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(Magnifications shown by photograph of stage micrometer enlarged at same scale as applicable photomicrograph. Fig. 1–2, magnification scale above Fig. 1 (finest division = 10 μ m); Fig. 3–4, magnification scale above Fig. 3 (divisions = 10 μ m).)

Fig. 5-8. *Berzelia ecklonii*, Carlquist 4965, wood sections of stem.—5. Transection, showing prominent growth ring.—6. Tangential section. Gummy deposits prominent in the ray cells.—7. Radial section. At left, a strand of axial parenchyma which has been subdivided into crystalliferous sclereids. At right, predominantly scalariform vessel-ray pitting visible.—8. Enlarged view of crystalliferous sclereids shown in Fig. 7; smaller crystals can be seen in the lower cell. (Fig. 5-6, scale above Fig. 1; Fig. 7, magnification scale above Fig. 7 (divisions = 10 μ m); Fig. 8, scale above Fig. 3.)

purpureum (Fig. 24, 25), *Staavia dodii* (Fig. 69), and *Tittmannia esterhuyseniae* (Fig. 78). Perforation plates of this type have been figured for *Myrothamnus flabellifolia* Welw. (Carlquist, 1976a), *Vaccinium leschenaultii* Wight. (Jane, 1956), and for *Warburgia ugandensis* Sprague, *Cinnamosma madagascariensis* Danguy, and *Canella alba* Murr. by Wilson (1960).

A third anomaly of a striking nature is the subdivision of the perforation plate into several portions by bands of nonperforated wall material. These "multiple" perforation plates were observed most frequently in *Nebelia stokoei* (Fig. 43), *Staavia dodii*, and *Tittmannia laevis*.

A fourth anomaly is represented by a basically scalariform plate in which thin strands of wall material interconnect bars. This is illustrated here for *Pseudobaeckea africana* (Fig. 48) and was also observed in *P. cordata*. Bars of this sort occur in *Epacris heteronema* Labill. (Solleder, 1908), *Warburgia stuhlmannii* Engl. (Wilson, 1960), *Carpenteria californica* Torr. (Carlquist, 1961), and *Myrothamnus flabellifolia* (Carlquist, 1976a).

A fifth type of anomaly is represented by the disposition of bars in a mesh-worklike pattern. This condition is illustrated here for *Lonchostoma esterhuyseniae* (Fig. 33) and was also observed in *Mniothamnea bullata*. Mesh-like perforation plates have also been described and illustrated for another South African plant, *Roridula dentata* Linn. (Carlquist, 1976b).

Borders on bars of perforation plates are very common in Bruniaceae. As Table 1 shows, only a few species were not observed to have borders, although I suspect intensive examination of these would reveal at least some vestigial borders. A rather large number of Bruniaceae were found to have fully bordered bars. Prominently bordered bars are illustrated here for *Audouinia capitata* (Fig. 3), *Berzelia cordifolia* (Fig. 44), *Brunia nodiflora* (Fig. 16), *Lonchostoma purpureum* (Fig. 24, 25), *Pseudobaeckea africana* (Fig. 47), *Staavia dodii* (Fig. 69), *Thamnea diosmoides* (Fig. 74), *T. masoniana* (Fig. 73), and *Tittmannia esterhuyseniae* (Fig. 77, 78). Frost (1930a, b) considers presence of borders on bars of perforation plates to be a primitive feature. One is not inclined to demur, in view of the probable origin of perforations from bordered pits on end walls of tracheids. However, if this is a primitive feature, it has been retained in some dicotyledons with relatively specialized scalariform perforation plates. For example, the few, thick bars on perforation plates of Rhizophoraceae are fully bordered, whereas borders are absent or vestigial in such primitive woods as *Cercidiphyllum* Sieb. & Zucc. or *Illicium* Linn. I have interpreted retention of borders on bars of perforation plates as a possible strengthening mechanism (Carlquist, 1975a). Borders could hypothetically counter xylem tension that might deform or break very thin borderless bars. This may explain the presence of borders on bars of other primitive South African woods, such as *Geissoloma marginatum* Kunth (Carlquist, 1975c), *Roridula dentata* (Carlquist, 1976b), and the three species of *Grubbia* (Carlquist, 1977a).

Fig. 9-13. Wood sections of *Brunia*.—9-11. *Brunia laevis*, Carlquist 4965.—9. Tangential section of aboveground stem. Rays shown are all multiseriate.—10. Radial section of lignotuber, photographed with partially polarized light. Several strands of crystalliferous axial parenchyma cells may be seen, as well as dark-staining compounds in ray cells.—11. Tangential section, showing ray cells, from stem. More than half of the ray cells are sclereids.—12-13. *Brunia stokoei*, Carlquist 4679, stem sections.—12.

Lateral-wall pitting.—As shown in Table 1, all Bruniaceae have scalariform to opposite intervascular and vessel-ray pitting on lateral walls of vessels. By "transitional" pitting is connoted the tendency for a scalariform pattern to be partly subdivided into series of opposite circular pits (Fig. 7, 49). Quite notably, no alternate lateral-wall pitting occurs in Bruniaceae. If we accept Frost's (1931) hypothesis that scalariform, followed by opposite, pitting are primitive expressions, and that alternate pitting (which occurs in by far the majority of dicotyledonous vessels) is specialized, Bruniaceae are quite primitive. I believe presently available data show that Frost's hypothesis is in general justified, one may wonder why such families as Tremandraceae (Carlquist, 1977b) have scalariform vessel-ray pitting. In Tremandraceae, almost all wood features other than vessel-ray pitting qualify as highly specialized. Alternative explanations for presence of scalariform lateral-wall pitting of vessels doubtless obtain in some instances. A series of these fall under the hypothesis of paedomorphosis (Carlquist, 1962). However, woods of Bruniaceae show none of the criteria of paedomorphosis. I believe the scalariform to opposite lateral-wall pitting of vessels of Bruniaceae to be a genuine expression of a primitive feature. This would be reinforced by the wood of the possibly related family Geissolomataceae (Carlquist, 1975c), which is similarly primitive. Possibly related families from South Africa according to Thorne's (1968, 1976) scheme, Myrothamnaceae (Carlquist, 1976a), Roridulaceae (Carlquist, 1976b), and Grubbiaceae (Carlquist, 1977a) have scalariform vessel-ray pitting, but mostly alternate intervascular pitting. Thus Bruniaceae has lateral-wall pitting somewhat more primitive than that of those putatively allied families.

In only two species of Bruniaceae, *Lonchostoma esterhuyseniae* (Fig. 32) and *L. purpureum*, were helical grooves observed in vessel walls. This feature, although not to be interpreted unequivocally (Baas, 1973; Carlquist, 1975a), seems generally an indication of xeromorphy, as in Asteraceae (Carlquist, 1966).

Vessel grouping.—The number of vessels per group in Bruniaceae ranges from 1.04 to 1.48 (Table 1, column 11). This range is a remarkably narrow one, compared with other groups of dicotyledons: Onagraceae would be more typical in their broader range (Carlquist, 1975b). A summary description of woods of Bruniaceae would read "vessels mostly solitary." The transections shown here (Fig. 1, 6, 14, 18, 20, 22, 26, 35, 37, 41, 45, 50, 52, 58, 60, 62, 66, 70, 72, 75) show this clearly. Some vessels as seen in transection

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Radial section, showing crystalliferous axial parenchyma strand among tracheids.—13. Portion of radial section. Two erect ray cells subdivided into tetrads of crystalliferous cells may be seen. (Fig. 9, scale above Fig. 1; Fig. 10–12, scale above Fig. 7; Fig. 13, scale above Fig. 3.)

Fig. 14–17. *Brunia nodiflora*, Carlquist 4508, wood sections of stem.—14. Transection. No growth rings present.—15. Tangential section. Prominent multiseriate and uniseriate rays visible.—Fig. 16–17. Scalariform perforation plates from radial section, shown in their entirety.—16. Plate showing prominent borders on bars (staining aided by presence of gummy compounds). Borders on pits of tracheids evident at right.—17. Longer perforation plate with narrow borders present on perforations. (Fig. 14–15, scale above Fig. 1; Fig. 16–17, scale above Fig. 3.)

Fig. 18-21. Sections of *Linconia*.—18-19. *Linconia alopecuroidea*, Carlquist 2510a, wood sections of twig.—18. Transection. Growth ring evident at top of photograph.—19. Tangential section. All rays shown are uniseriate.—20-21. *Linconia cuspidata*, Carlquist 4943.—20. Transection wood of stem, showing dark-staining compounds in some ray cells.—21. Radial section, secondary phloem, photographed with partially polarized light. Strands of crystalliferous phloem parenchyma which include large and smaller crystals are visible. (Fig. 18-21, scale above Fig. 7.)

appear paired (e.g., Fig. 18), but are actually single vessels subdivided by a vertically oriented perforation plate. The low degree of vessel grouping may be interpreted as a primitive feature, but note must be taken that vessel grouping is also characteristically low in some families with highly specialized wood, such as Goodeniaceae (Carlquist, 1969).

Vessel shape in transection.—Vessels in Bruniaceae can be said to be generally angular in transection, but more nearly rounded in earlywood of some markedly ring porous species (Fig. 22, 50). Vessel walls in Bruniaceae are relatively thick, although somewhat thinner than those of tracheids (e.g., Fig. 64). The fact that vessels are moderately thick walled undoubtedly contributes to the fact that vessels in Bruniaceae are less angular, in general, than in some other families. Where vessels are thin walled in dicotyledons, wall material does not fill in the angles, which thus makes the vessels more angular in appearance. The relatively thick walls of vessels in Bruniaceae may correlate with mechanical strength of these woods or with resistance to tensions in water columns of the xylem.

Tracheids

As can be seen in the transections just cited—but more particularly in Fig. 18, 20, 29, and 64—tracheids in Bruniaceae are all relatively thick walled. The figures in Table 1 (column 14) show tracheids to be generally thicker walled than imperforate elements in other families, for which figures are available, such as Onagraceae (Carlquist, 1975b). The thick tracheid walls in Bruniaceae can often be described as gelatinous because of staining reactions (Fig. 29) or shrinkage patterns. One can see in longitudinal sections of wood on prepared (and therefore dehydrated) slides that shrinkages take the form of splits in tracheid walls. These splits are extensions quite often of the elliptical apertures of tracheid pits (Fig. 30), which is to be expected because these apertures run parallel to microfibrils, between which splits would naturally occur in the case of gelatinous wall structure. These splits, if interpreted as naturally long apertures rather than artifacts, would force one to designate imperforate elements in Bruniaceae as fiber-tracheids. However, careful examination confirms that these splits are artifacts. Diameter of the pit cavity (and therefore border width) is roughly the same throughout all Bruniaceae; if fiber-tracheids were present, one would expect reduction in border width with increasing length of pit aperture. Therefore, tracheids are the only type of imperforate element present in Bruniaceae (Fig. 16). Species in which elongate pit apertures were observed include *Audouinia capitata*, *Berzelia abrotanoides*, *B. lanuginosa*, *B. rubra*, *Lonchostoma* Wikstr. (all species), *Mniothamnea bullata*, *Nebelia paleacea*, *Pseudobaeckea cordata*, *Raspalia* Brongn. (all species), *Staavia* Dahl (all species), *Thamnea* Soland. ex Brongn. (all species), *Tittmannia*

Fig. 22-25. *Lonchostoma purpureum*, Carlquist 4930, wood sections of stem.—22. Transection, showing sharply defined growth rings.—23. Tangential section. All rays shown are uniseriate.—24-25. Perforation plates from radial sections.—24. Perforation plate scalariform above, somewhat multiperforate below.—25. Entire perforation plate with bordered bars; some anomalies are evident. (Fig. 22-23, scale above Fig. 1; Fig. 24-25, scale above Fig. 3.)

Fig. 26-31. *Lonchostoma esterhuyseniae*, Carlquist 4982, wood sections of stem.—26. Transection, showing numerous growth rings.—27. Tangential section. Most rays are uniseriate.—28. Transection, enlarged; latewood consists of tracheids, lacks vessels.—29. Portion of transection. Gradations in coloration of staining in tracheid walls indicates gelatinous nature. Dark material in spaces among tracheids, above left, is primary wall.—30. Radial section, showing apertures of tracheids elongate owing to shrinkage

esterhuyseniae, and *T. laevis*. Thus, over half of the species of Bruniaceae have tracheids with gelatinous walls.

Crassulae.—Thickenings of primary walls between tracheids and vessels or among tracheids were observed in *Berzelia abrotanoides* and *Staavia dodii* (Fig. 29, 31). These could be termed crassulae ("bars of Sanio").

Storied structure.—Neither tracheids nor any other axial elements of the woods of bruniaceae show any storied pattern.

Axial Parenchyma

Axial parenchyma is basically diffuse in distribution in Bruniaceae, as the transections illustrated here show. One would expect diffuse axial parenchyma distribution within a family with such a large number of primitive features. Deviations from a purely diffuse pattern are very few, and the condition in all species could be characterized as "diffuse." Occasional parenchyma cells in contact with vessels in a slightly more than random fashion (vasicentric scanty) were observed in *Berzelia burchellii*, *B. galpinii*, *B. intermedia*, *B. rubra*, *B. squarrosa*, *Lonchostoma pentandrum*, *Mniothamnea bullata*, *M. callunoides*, and *Nebelia fragarioides*. Occasional pairs of parenchyma cells, which could be called a rudimentary form of diffuse-in-aggregates, were observed in *Brunia alopecuroides*, *B. laevis*, *B. stokoei*, *Lonchostoma esterhuyseniae*, *L. monogyna*, *L. myrtoides*, *Nebelia paleacea*, *N. stokoei*, and *Raspalia variabilis*.

Axial parenchyma cells are subdivided into strands ranging from two to seven cells. By far the most common condition is three to four cells, and that range can be said to characterize three-quarters of Bruniaceae. Notable exceptions occur where axial parenchyma strands are subdivided into crystalliferous square cells (Fig. 7, 8, 12, 21), which will be discussed below in connection with crystal occurrence. In no species of Bruniaceae is axial parenchyma either abundant or absent.

Ray Parenchyma

Ray dimensions.—Figures for mean heights of rays are given in Table 1 (columns 15, 16). As can be seen, there is a rough correlation between ray height and vessel-element length. Taller rays tend to occur in the species with longer vessel elements, such as *Berzelia ecklonii* (Fig. 6), *Pseudobaeckea africana* (Fig. 46), *P. cordata* (Fig. 51), and *Raspalia globosa* (Fig. 52). Obviously, this correlation is a loose one, in part because species and

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of gelatinous wall.—30. Portion of radial section showing crassulae (primary wall thickenings) on tracheids. (Fig. 26–27, scale above Fig. 1; Fig. 28, scale above Fig. 7; Fig. 29–31, scale above Fig. 3.)

Fig. 32-36. Wood sections of *Lonchostoma* and *Mniothamnea* stems.—32-33. Radial sections of *L. esterhuyseniae*, Carlquist 4982.—32. Vessel wall showing helical grooves in wall.—33. Perforation plate with meshlike arrangement of bars.—34. *Lonchostoma myrtoides*, Carlquist 5020. Ray cell from tangential section, photographed in partially polarized light to show small rhomboidal crystal.—35-36. *Mniothamnea bullata*, Carlquist 4715.—35. Transection, showing numerous growth rings.—36. Tangential section. Erect ray cells predominate. (Fig. 32-34, scale above Fig. 3; Fig. 35-36, scale above Fig. 1.)

genera which have wide multiseriate rays also tend, in many cases, to have taller rays. Species in which multiseriate rays are at most biseriate or triseriate tend to have somewhat shorter rays.

Ray width also bears a relationship to relative abundance of multiseriate rays. Those genera and species in which multiseriate rays are biseriate or at the most triseriate tend to have a higher proportion of uniseriate rays. This is especially true in the genera *Linconia* Linn. (Fig. 19), *Lonchostoma* (Fig. 23, 27) and *Mniothamnea* (Oliv.) Niedenzu. In these genera, a rough estimate reveals that between 70 and 95 percent of rays are uniseriate. In the remaining genera, uniseriate rays are approximately as abundant as multiseriate rays, as shown in Fig. 2, 6, 9, 15, 38, 42, 46, 51, 53, 59, 61, 63, 67, 71, and 76. Individual species—and plant portions—differ with respect to rays. In the slender, wiry upright stems of *Thamnea diosmoides*, uniseriate rays were found exclusively, although in the lignotuber of that species, multiseriate rays are approximately equal in number to uniseriate rays. Multiseriate rays are so frequent as to be virtually absent in *Lonchostoma monogyna*, *Mniothamnea bullata* (Fig. 36), and *M. callunoides*.

Differences in multiseriate ray width characterize particular genera and species (Table 1, column 17). *Linconia* and *Lonchostoma* have exceptionally narrow rays; multiseriate rays in *Mniothamnea*, if present at all, are biseriate. The three species of *Raspalia* illustrated (Fig. 53, 59, 61) show clear differences in ray width.

Histology.—The wider the multiseriate rays in any particular species, the greater is the likelihood that procumbent cells will be present. This generalization could be made for many families of dicotyledons as a whole as well as for Bruniaceae. Uniseriate rays in Bruniaceae consist mostly of upright cells with a few square cells, as suggested by the tangential sections of Fig. 19, 23, and 27. This tends to be true in narrow multiseriate rays, and thus procumbent cells are absent or very scarce in rays of the genera *Linconia*, *Lonchostoma*, and *Mniothamnea*, as well as in *Staavia glutinosa*. Upright cells tend to predominate (square and procumbent cells are also present) in multiseriate rays of *Audouinia capitata* (Fig. 2), *Berzelia* Brongn. (all species except *B. commutata* and *B. lanuginosa*), *Brunia* Linn. (all species), and *Raspalia virgata*. Predominance of both upright and square cells (procumbent cells are also present) characterize multiseriate rays of *Nebelia* Neck. ex Sweet. (all species), *Pseudobaeckea* Niedenzu (both species), *Raspalia* (all species except *R. virgata*), *Staavia* (all species) and *Tittmannia* Brongn. (all species). Predominance of procumbent cells characterize multiseriate rays of the material studied of *Berzelia commutata* and *B. lanuginosa*. The samples of this pair of species consisted of relatively large logs. Increase in proportion of procumbent cells with age in a woody dicotyledon is often to be expected (e.g., Carlquist, 1975b), so this is not surprising. Horizontal subdivision of ray initials probably occurs gradually with age.

Fig. 37-40. *Nebelia paleacea*, Carlquist 4522, wood sections of stem.—37. Transverse section. No growth rings occur.—38. Tangential section. Relatively wide multiseriate rays can be seen.—39. Radial section oriented with ray running vertically to show procumbent ray cell subdivided into quartet of crystalliferous cells.—40. Radial section with ray oriented horizontally to show erect ray cell subdivided into a pair of crystalliferous cells. (Fig. 37-38, scale above Fig. 1; Fig. 39-40, scale above Fig. 3.)

Pillans (1947) seems to have recognized the closeness of *Linconia* and *Lonchostoma* on the basis of gross morphology. Ray histology does seem to ally *Linconia*, *Lonchostoma*, and *Mniothamnea*. Limited stem diameter in *Mniothamnea* may account for absence of procumbent cells, but this is obviously not a factor in the equally narrow stems available in the case of *Audouinia* Brongn., which had procumbent cells. The similarity of *Brunia* and *Berzelia* claimed by Pillans (1947) is evident on grounds of ray histology. Uniseriate wings are present on multiseriate rays of Bruniaceae in at least half the rays in any tangential section. Naturally, wings are more abundant in rays that are biseriate than in wider multiseriate rays.

In Bruniaceae, then, both multiseriate and uniseriate rays are present (except in some stems of *Mniothamnea* and *Thamnea*). In multiseriate rays, upright, square and procumbent cells are present (with exceptions as noted above). Procumbent cells would probably be present in all rays if large stems were formed by all species. With this understandable partial exception, rays are heterocellular. Uniseriate wings are generally present on multiseriate rays. Thus, basically rays of Bruniaceae correspond, with some exceptions, to the most primitive type of ray ("Heterogeneous Type I") hypothesized for dicotyledons by Kribs (1935).

Cell size.—Examination of the tangential sections of woods of Bruniaceae herewith reveals considerable differences from species to species in size of ray cells. For example, ray cells are relatively small in *Audouinia* (Fig. 2), but relatively large in *Berzelia* (Fig. 6), *Brunia* (Fig. 15), *Pseudobaeckea* (Fig. 45, 51), and *Nebelia paleacea* (Fig. 38).

Cell walls.—Ray cell walls are lignified in all Bruniaceae, but not excessively thick walled. The only exception to this was observed in *Brunia laevis* (Fig. 11), where numerous ray cells become sclereids. However, radial sections reveal that tangential walls of rays of many Bruniaceae are notably thicker. These tangential walls contain prominent pits, and radial sections show that with increased wall thickness, there is a tendency for pits in ray cells to develop borders. Such bordered ray cell pits were observed (along with simple pits) in *Audouinia capitata*, *Berzelia* (all species), *Brunia* (all species), *Lonchostoma myrtoideus* (lignotubers), *L. pentandrum*, *L. purpureum*, *Nebelia* (all species), *Pseudobaeckea* (both species), *Raspalia* (all species), *Thamnea* (all species), and *Tittmannia* (common in all species). Tendency to lack bordered pits on ray cells tends to underline the similarity among *Linconia*, *Lonchostoma*, and *Mniothamnea*. The prominence of bordered pits on ray cells distinguishes *Tittmannia*.

Bordered pits on ray cells are not as scarce in dicotyledons as one might imagine. They evidently have escaped notice, but are easily visible in radial sections. They have been reported in a number of families probably allied to Bruniaceae, such as Geissolomataceae (Carlquist, 1957c), Roridulaceae (Carlquist, 1976b), Grubbiaceae (Carlquist, 1977a) and Tremandraceae

Fig. 41–44. Wood sections of *Nebelia* and *Berzelia* stems.—41–43. *Nebelia stokoei*, Carlquist, 5022.—41. Transection. Two well-marked growth rings are evident.—42. Tangential section. Multiseriate rays are relatively narrow, tall.—43. Portion of radial section to show perforation plate subdivided into three portions.—44. *Berzelia cordifolia*, Carlquist 4690. Portion of radial section to show portions of perforation plates. Plate at left shows vestigial borders. Plate at right shows intergradation between perforations and lateral wall pitting (bottom). (Fig. 41–42, scale above Fig. 1; Fig. 43–44, scale above Fig. 3.)

(Carlquist, 1977b). They are not limited to families with a predominance of primitive features, as the data of Kribs (1935) might imply. They can be found in myrtalean families, such as Myrtaceae (Sastropadja and Lamoureux, 1969), Penaeaceae (Carlquist and DeBuhr, 1977), and Onagraceae (Carlquist, 1977c). Careful examination will doubtless reveal bordered pits in ray cells of a wide range of families. Although their significance is unclear, bordered pits may be indicative of mechanical strength of ray cells (Carlquist, 1975a).

Crystals

Bruniaceae are unusually rich in occurrence of crystals in parenchyma. Rhomboidal crystals in ordinary ray cells were observed in *Berzelia abrotanoides*, *B. lanuginosa*, *B. squarrosa*, *Brunia* (all species), *Linconia* (both species), *Lonchostoma myrtoides* (Fig. 34), *L. purpureum*, *Mniothamnea* (sparse in both species), *Nebelia fragarioides*, *N. paleacea*, *Pseudobaeckea africana*, *Raspalia stokoei*, *R. virgata*, *Thamnea diosmoides*, and *Tittmannia esterhuyseniae*. Large rhomboidal crystals plus smaller crystals aggregated in various degrees as druses were observed in ray cells of *Audouinia capitata*, *Berzelia commutata*, *Raspalia globosa* (Fig. 55, 57), *R. microphylla*, *R. variabilis*, and *Thamnea massoniana*.

In a number of species in which crystals were observed in ray cells, single rhomboidal crystals occur within two to four cells subdivided from an erect ray cell (Fig. 13, 40, 56, 60, 65) or occasionally within cells subdivided from a procumbent ray cell (Fig. 39). Species which contained crystals both in subdivided and nonsubdivided ray cells include *Audouinia capitata* (Fig. 4), *Berzelia* (all species except *B. rubra*), *Brunia stokoei* (Fig. 13), *Nebelia paleacea* (Fig. 39, 40), *Raspalia globosa* (Fig. 56), *Staavia capitella*, *S. dodii* (Fig. 65), and *S. radiata*. Occurrence of subdivided crystal-bearing ray cells may be expected in species in addition to those listed.

Crystals in subdivided axial parenchyma cells were observed in a number of Bruniaceae. These strands, rather than three or four cells in length, are at least 10 cells long, as shown for *Brunia stokoei* in Fig. 12. Subdivided crystalliferous axial parenchyma strands were most conspicuous in *Berzelia ecklonii* (Fig. 7, 8), in which cells of the strand become rounded and form sclereidlike thick lignified walls around the crystals. Chambered rhomboidal crystals in axial parenchyma cells were observed in *Berzelia burchellii*, *B. commutata*, *B. cordifolia*, *B. galpinii*, *B. intermedia*, *B. lanuginosa*, *Brunia albiflora*, *B. alopecuroides*, *B. laevis*, *B. stokoei*, *Lonchostoma myrtoides* (stems), *Raspalia globosa*, *R. stokoei*, and *Staavia radiata*.

The occurrence of crystals in subdivided axial parenchyma in wood of Bruniaceae is probably less frequent and conspicuous than occurrence of similar chambered crystals in secondary phloem of Bruniaceae. For example, such crystals in strands were seen prominently in secondary phloem

Fig. 45-49. *Pseudobaeckea africana*, Carlquist 4558, wood sections of stem.—45. Transection, showing abundance of vessel elements.—46. Tangential section. Dark-staining compounds evident in parenchyma cells.—47. Portion of "normal" perforation plate from radial section. Bars are bordered.—48. Portion of perforation plate from radial section, showing interconnections between bars.—49. Intervascular pitting from radial section, showing opposite and scalariform configurations. (Fig. 45-46, scale above Fig. 1; Fig. 47-49, scale above Fig. 3.)

of *Linconia cuspidata* (Fig. 21), *Staavia capitella*, and *Thamnea diosmoides*, but not in wood of these species. Crystals were observed in traumatic wood parenchyma and in pith parenchyma of *Tittmannia esterhuyseniae* (Fig. 79). These records are random, for no systematic effort was made to survey bark or pith in Bruniaceae. One has the impression that crystals occur more abundantly in axial parenchyma of secondary phloem than of secondary xylem, and that degree of crystal occurrence in wood is a relative matter. Perhaps more instances of crystal occurrence in wood could have been added to the above listings if more numerous wood samples had been examined. Occurrence of crystals more abundantly in phloem than in wood is probably to be expected in many families of dicotyledons. This was observed in Tremandraceae (Carlquist, 1977b). Unfortunately, wood anatomists rarely study bark of the species on which they are making observations on wood anatomy.

Amorphous Deposits

Woods of all Bruniaceae contain deposits of dark-staining amorphous compounds. The nature of these compounds is not known, but may contribute to the faint but distinctive scent characteristic of herbage of Bruniaceae, especially when it is being dried. Sometimes these deposits occur as minute droplets and are not conspicuous, as in *Audouinia capitata* (Fig. 4). Droplets plus large amorphous masses can be seen in Fig. 6, 7, 10, 20, 21, 38, 63, and 65. The genera in which these deposits are least conspicuous include *Audouinia*, *Lonchostoma*, *Mniothamnea*, and *Thamnea*.

Ecological Interpretations

Growth Rings

Growth rings are considered here rather than under the above descriptive text because they bear such a direct relation to ecology and to probable water-conductive characteristics of particular woods. Growth rings in Bruniaceae seem mostly to be indicators of fluctuation in water availability. Water availability may be lowered by either drought or freezing. Absence of growth rings certainly does not necessarily indicate absence of drought conditions in habitats of Bruniaceae. For example, *Audouinia capitata* lacks growth rings (Fig. 1) but grows in a very exposed site: the summit of a sandstone hill, Karbonkelberg, which is subjected to summer heat and drought and is much too low in elevation to experience condensation of moisture from summer winds, which do moisten high montane slopes. One can hypothesize that *Audouinia* has a foliar apparatus which anatomically or physiologically, or both, restricts transpiration to a very low and probably constant rate. However, high-montane Bruniaceae tend to have pronounced growth rings. In montane situations, summer winds bring some moisture,

Fig. 50-53. Wood sections of *Pseudobaeckea* and *Raspalia* stems.—50-51. *Pseudobaeckea cordata*, Carlquist 4615.—50. Transection, showing a prominent growth ring.—51. Tangential section. Rays abundant, heterocellular.—52-53. *Raspalia globosa*, Carlquist 5811.—52. Transection. Only faint growth ring activity is present.—53. Tangential section. Multiseriate rays are notably large. (Fig. 50-53, scale above Fig. 1.)

but probably result in greater evaporation than condensation. Montane situations experience summer heat and drought terminated by winter freezing. However, spring provides more abundant moisture than is true of lowland localities. Montane Bruniaceae favor seeps, streams, or south-facing localities where soil moisture is probably retained until summer heat becomes intense. Therefore, Bruniaceae with suitable growth ring phenomena probably take advantage of these sites by means of wood anatomy.

Absence of growth rings characterizes *Audouinia capitata* (Fig. 1), *Berzelia lanuginosa*, *B. rubra*, *Brunia laevis*, *B. nodiflora* (Fig. 14), *Linconia cuspidata* (Fig. 20), *Nebelia paleacea* (Fig. 37), *Pseudobaeckea africana* (Fig. 45), *Raspalia globosa* (Fig. 52), *R. virgata*, all species of *Staavia*, *Tittmannia laevis*, and *T. laxa*. All of these are shrubs of lowland localities, low to middle montane elevations, or else are rock-crevice shrublets (*Linconia cuspidata*, *Staavia pinifolia*). One can hypothesize that water availability for these species is either uniformly low, as in the case of the rock-crevice shrublets, or uniformly high, as in the case of the riparian species *Berzelia lanuginosa* and *Pseudobaeckea africana*.

Very mild growth-ring activity, evidenced only by occurrence of narrower tracheids in latewood (but no perceptible changes in vessel diameter or frequency) characterize some Bruniaceae. Species in this category include (stems unless otherwise indicated) *Berzelia burchellii*, *B. galpinii*, *B. intermedia* (lignotubers), *Linconia alopecuroidea* (Fig. 18), *Mniothamnea bullata*, *Nebelia fragarioides*, *Thamnea massoniana* (Fig. 71), and *Tittmannia esterhuyseniae* (Fig. 75).

Another form of mild growth ring activity, closely allied to the above, is constituted by presence of vessels slightly wider in earlywood than in latewood, but with little or no change in abundance of vessels during the year. Species which fall in this category include *Berzelia squarrosa*, *Raspalia microphylla* (Fig. 58), and *Thamnea diosmoides*.

Marked growth ring activity characterizes only those Bruniaceae which have wider vessels, wider tracheids, and more numerous vessels in earlywood than in latewood. Species characterized by this habit are *Berzelia abrotanoides*, *B. cordifolia*, *B. ecklonii* (Fig. 5), *B. intermedia*, *Brunia alopecuroides*, *B. stokoei*, *Lonchostoma esterhuyseniae* (Fig. 26), *L. monogyna*, *L. purpureum* (Fig. 22), *Nebelia sphaerocephala*, *N. stokoei* (Fig. 41), *Pseudobaeckea cordata* (Fig. 50), *Raspalia variabilis* (Fig. 60), and *R. virgata* (stems; growth rings absent in roots). Over half of these species are high-montane. Notable in this type of growth-ring activity, as dramatized by the enlarged transection of Fig. 28, is the absence of vessels in latewood. Thus, in latewood, the conducting system is an all-tracheid system, essentially that of a gymnosperm. The physiological significance of this is interesting, in that an all-tracheid system is more resistant to spread of air embolisms under conditions of high water stress (Carlquist, 1975a), and is thus very

Fig. 54-57. *Raspalia globosa*, Carlquist 5811, wood sections of stem to show crystal occurrence.—54. Tangential section. Crystals are visible in ray (right) and strand of axial parenchyma (upper left).—55. Crystals, photographed with polarized light, in ray cells of radial section. Both large rhomboidal and smaller crystals in various degrees of aggregation are present.—56-57. Radial sections photographed in partially polarized light.—56. Erect ray cells subdivided in pairs, containing rhomboidal crystals, in sheathing cells of a multiseriate ray.—57. Large and small rhomboidal crystals in ray cells of multiseriate rays. (Fig. 54, 56-57, scale above Fig. 7; Fig. 55, scale above Fig. 3.)

Fig. 58-61. Wood sections of *Raspalia* stems.—58-59. *Raspalia microphylla*, Carlquist 4673.—58. Transection. One faint growth ring present.—59. Tangential section. Multiseriate rays are wide, filled with dark-staining compounds.—60-61. *Raspalia variabilis*, Carlquist 4680.—60. Transection. Numerous growth rings present.—61. Tangential section. Uniseriate rays with erect ray cells predominate. (Fig. 58-61, scale above Fig. 1.)

Fig. 62-65. *Staavia dodii*, Carlquist 4620, wood sections of stem.—62. Transection. Tracheids are notably thick walled.—63. Tangential section. Many ray cells are occluded with dark-staining compounds.—64. Portion of transection to show thick inner gelatinous portion of tracheid secondary walls.—65. Portion of radial section to illustrate dark-staining deposits and a quartet of crystal-bearing cells formed by subdivision of an erect ray cell. (Fig. 62-63, scale above Fig. 1; Fig. 64-65, scale above Fig. 3.)

high in "safety" (or low in "vulnerability"). In addition, more numerous vessels in latewood provide more "redundancy" in the vessel system, a situation discussed below under the concept of vulnerability.

Vulnerability

Production of narrow tracheary elements (both tracheids and vessel elements) seems to connote greater resistance to tensions in water columns of secondary xylem (Carlquist, 1975a; Rundell and Stecker, 1977). More numerous vessels per mm² connote greater resistance to water stress, in that disabling of some vessels by air embolisms is less serious if a large number of vessels provide "safety in numbers" (Carlquist, 1977b, 1977c, 1977d; Carlquist and DeBuhr, 1977). One might expect that number of vessels per mm² of transection is nearly a perfect inverse of vessel diameter. However, the proportion varies a great deal, within extreme limits (Carlquist and DeBuhr, 1977). Thus, these two measures are independent expressions of wood xeromorphy, and have been calculated as independent variables in the papers cited above. "Vulnerability," the vessel diameter divided by the number of vessels per mm² of transection, is an index which, at low values indicates xeromorphy quite reliably based on the species in various families to which I have thus far applied it. This figure is presented for Bruniaceae in Table 1, column 18. As can be seen, the range in figures is from 0.05 to 0.42. If all the figures for "vulnerability" in Table 1 are averaged, one obtains a mean of 0.14. This mean is remarkably low for dicotyledons at large. The vulnerability figure, when calculated for various groups of dicotyledons, ranges as high as 2.29 for an assemblage of primitive mesic woods and as low as 0.08 for an assemblage of North American desert shrubs (Carlquist, 1977d). The figure 0.14 matches exactly the mean obtained for shrubs from sand heath areas of Western Australia (Carlquist, 1977d). This coincidence is an interesting one, because habitats for Bruniaceae are much like those of the sand heath shrubs: acid, porous sands, or crevices in sandstone rocks. These sands can dry markedly in the hottest portions of the summer, approximating deserts. Not surprisingly, shrubs of deserts, either from North America or from Australia, have figures for vulnerability in the same range as do Bruniaceae. The microphyllly of Bruniaceae is an external indicator which might lead one to expect this. Bruniaceae appear to have woods which have retained many primitive features but which are adapted to extremes of summer drought.

Species with notably low vulnerability figures (below 0.14) illustrated here include *Brunia nodiflora* (Fig. 14), *Linconia alopecuroidea* (Fig. 18), *L. cupsidata* (Fig. 20), *Lonchostoma esterhuyseniae* (Fig. 26), *L. purpureum* (Fig. 22), *Nebelia stokoei* (Fig. 41), *Raspalia globosa* (Fig. 54), *R. microphylla* (Fig. 58), *R. variabilis* (Fig. 60), *Staavia pinifolia* (Fig. 66)

Fig. 66-69. Wood sections of *Staavia* stems.—66-68. *Staavia pinifolia*, Carlquist 4754.—66. Transection. Note great density of narrow vessels.—67. Tangential section. Dark-staining deposits abundant in parenchyma cells.—68. Portions of two perforation plates from radial section. Borders are nearly absent.—69. *Staavia dodii*, Carlquist 4620. Perforation plate from radial section. Perforation plate is semimultiperforate, perforations are bordered. (Fig. 66-67, scale above Fig. 1; Fig. 68-69, scale above Fig. 3.)

and *S. radiata* (Fig. 70). Some species, such as *Audouinia capitata* (Fig. 1) have narrow but sparse vessels. Others, such as *Pseudobaeckea africana* (Fig. 45), have relatively large but numerous vessels. This shows the independence of vessel diameter and vessel density, either of which may be indicators of xeromorphy. As in Penaeaceae (Carlquist and DeBuhr, 1977), rock crevice species (*Linconia cupsidata* and *Staavia pinifolia*) have notably low vulnerability figures. Relatively high vulnerability figures are shown by characteristically riparian species such as *Berzelia commutata*, *B. lanuginosa*, and *Pseudobaeckea africana*. The range in vulnerability figures for the entire family is not very great, however, suggesting that Bruniaceae are adapted to drought extremes in their wood formulation.

Mesomorphy

Greater length of vessel elements, as well as wider ones, can be said to be indicative of mesomorphy (Carlquist, 1975a). If the figure for vulnerability is multiplied by vessel element length, a figure that can be termed "mesomorphy" (Carlquist, 1977d) is obtained. As can be seen from Table 1 (column 19), the values in Bruniaceae range from 29 to 311. The mean for all mesomorphy figures in Table 1 is 95. This figure would place Bruniaceae between the sand heath shrubs of Western Australia ($M = 43$) and shrubs from granitic coastal bluffs of Western Australia ($M = 119$) according to figures developed earlier (Carlquist, 1977d). These Western Australian habitats approximate the temperature, rainfall and soil porosity ranges of the Table Mountain Sandstone areas where Bruniaceae grow. To be sure, relatively high M values occur in the wet forest or riparian tree *Berzelia commutata* and the riparian shrubs *B. lanuginosa* and *Pseudobaeckea africana*. The range of M values within Bruniaceae is not great, however, when one considers that an assemblage of primitive mesic woods I studied earlier have an M value of 3172 (Carlquist, 1977d). Bruniaceae can be said to be "buffered" in wood anatomy: capable of resisting strong extremes in drought, but able to take advantage of moisture availability.

In this connection, one must remember that the apparent mesic nature of habitats of Bruniaceae may feature water availability higher than that of most niches in the Table Mountain Sandstone, but the habitats are still subject to extremes. The sandstone soils have extremely poor water-holding capacity, notably when dry in summer. Moreover, the incidence of windy conditions in Cape Province, a factor difficult to measure quantitatively but apparent to the field botanist, promotes greater water evaporation and tightens the water economy of plants of the region considerably. Primitive woods such as those of Bruniaceae, even when modified by narrowing of vessels and more numerous vessels per unit area, seem adaptive, judging from field observations, only to the most mesic microclimates. These include

Fig. 70-74. Wood sections of *Staavia* and *Thamnea* stems.—70-71. *Staavia radiata*, Carlquist 4601.—70. Transection. No growth rings are evident.—71. Tangential section. Rays are biseriate and uniseriate.—72-73. *Thamnea masoniana*, Carlquist 4852.—72. Transection. Faint growth rings are present.—73. Perforation plate from a radial section. Bars are vestigially bordered.—74. *Thamnea diosmoides*, Carlquist 4665. Perforation plate from radial section. Bars are few bordered. (Fig. 70-72, scale above Fig. 1; Fig. 73-74, scale above Fig. 3.)

flats with underlying hardpan where water collects (*Berzelia ecklonii*, *B. lanuginosa*); streamsides (*Berzelia lanuginosa*, *Pseudobaeckea africana*); montane seeps (*Berzelia galpinii*, *Lonchostoma monogyna*, *L. myrtoides*, *L. pentandrum*, *Mniothamnea callunoides*, *Raspalia stokoei*, and *R. virgata*); south-facing slopes, especially where boulders or bluffs provide shade and channeling of rainwater (*Berzelia burchellii*, *B. intermedia*, *B. squarrosa*, *Brunia albiflora*, *B. stokoei*, *Linconia alopecuroidea*, *Lonchostoma esterhuyseniae*, *L. purpureum*, *Mniothamnea bullata*, *Nebelia fragarioides*, *N. sphaerocephala*, *N. stokoei*, *Pseudobaeckea cordata*, *Raspalia globosa*, *Staavia glutinosa*, *Thamnea diosmoides*, *T. massoniana*, *Tittmannia laevis*, and *T. laxa*); among boulders underneath which water may be retained (*Audouinia capitata*, *Berzelia cordifolia*, *B. rubra*, *Brunia alopecuroides*, *B. laevis*, *B. nodiflora*, *Nebelia paleacea*, *Raspalia microphylla*, *R. variabilis*, *Staavia capitella*, and *S. dodii*). Some species occur on open sandy flats (*Berzelia abrotanoides*, *Staavia radiata*) where water availability would appear to be low, but large taproot systems coupled with underlying geological formations may compensate for a sandy soil surface prone to drying.

Borders on bars, semimultiperforate perforation plates, and relatively wide bars on perforation plates are suggestive of possibly greater resistance to water tensions in xylem, if my (1975a) hypotheses are valid. These features are extraordinarily common in Bruniaceae, as mentioned in the section on vessel elements. The perforation plate characteristics, as well as the growth ring phenomena, must, then, be considered as supplementary to the features used in calculation of vulnerability and mesomorphy.

Organographic Analysis of Wood

Differences between stem and lignotuber wood have been described for other South African families, such as Geissolomataceae (Carlquist, 1975c), Grubbiaceae (Carlquist, 1977a) and Penaeaceae (Carlquist and DeBuhr, 1977). Findings in these families parallel what was observed in those Bruniaceae (Table 1, column 2) in which both stem and lignotuber woods were studied. Vessels are fewer per unit transection in lignotubers (except in the sample of *Linconia cuspidata*, which was probably not truly representative of lignotuber structure). Vessel diameter is the same or wider in lignotubers than in stems (except in *Brunia laevis*). Vessel element length is shorter in lignotubers than in stems (except in *B. laevis*). The wood of lignotubers is contorted, and in contorted woods, shorter tracheary elements are to be expected (Bailey and Tupper, 1918; Carlquist, 1975a). Rays are wider in lignotubers of all Bruniaceae than they are in stems. Thus, lignotubers can be said to be sites of photosynthate storage and perhaps a modest degree of water storage, in accordance with greater parenchymatization. These structural modes are demonstrable quantitatively, and thus lignotubers of Bruniaceae have higher values for vulnerability than do stems. Lignotubers

Fig. 75-79. *Tittmannia esterhuyseniae*, Carlquist 5040, wood sections of stem.—75. Transection. Marked growth rings are present.—76. Tangential section. Rays are numerous, short.—77-78. Perforation plates from radial sections.—77. A normal scalariform perforation plate.—78. Perforation plate with two rows of perforations.—79. Quartet of crystalliferous cells derived from transverse subdivision of pith cell from radial section of woody stem. (Fig. 75-76, scale above Fig. 1; Fig. 77-79, scale above Fig. 3.)

also have higher values for mesomorphy, despite the tendency toward shorter vessel elements (except in *Linconia cuspidata*).

Differences between wood of stems and roots in particular species have been found in some groups of woody plants, although differences are not always consistent with a given pattern (Carlquist, 1975a). However, as the data in Table 1 show, few consistent differences between wood of stems and that of roots can be demonstrated for Bruniaceae. There are more vessels per mm² in roots except for *Thamnea diosmoides*. However, this difference is sufficiently minor so that vulnerability values and mesomorphy values compared for roots and stems show no trends in Bruniaceae. In attempting to explain this, one might note the extremely porous nature of soils derived from the Table Mountain Sandstone, which would subject roots to considerable water stress during drought. In most groups of dicotyledons for which comparative data are available, wood features of roots appear more mesomorphic than those of stems (Carlquist, 1975a).

Phylogenetic Relationships

Bruniaceae obviously have very primitive woods according to the criteria of Frost (1930a, b, 1931) and Kribs (1935, 1937). Bruniaceae are specialized, according to the considerations of these authors, only in lack of uniseriate wings on some multiseriate rays, and in a *slight* degree of grouping of axial parenchyma cells in *some* species. Thus, in whatever phylogenetic line one places Bruniaceae, one must consider it the most primitive with respect to woods. If one compares Bruniaceae with families grouped with it by Thorne (1968, 1976) in Pittosporales, one finds that Geissolomataceae (Carlquist, 1975c), Myrothamnaceae (Carlquist, 1976a), Roridulaceae (Carlquist, 1976b) and Grubbiaceae (Carlquist, 1977a) are only slightly more specialized with respect to wood anatomy. When one looks at floral morphology of certain Bruniaceae such as *Linconia* or *Lonchostoma*, with ovaries superior or nearly so, carpels follicular in fruit, corollas choripetalous, and calyx lobes united slightly, one sees a floral plan more primitive than those of the other families just cited.

One has difficulty in separating wood features indicating level of specialization from those indicating phylogenetic relationship. As I have stated earlier (1975c), one probably should not consider level of specialization similarities entirely irrelevant in assessing relationships if there are other features that suggest relationships between families.

Wood features of Bruniaceae unrelated to level of specialization include a predominance of upright ray cells, presence of borders on pits of ray cells, occurrence of droplets or massive deposits of amorphous dark-staining compounds, and occurrence in ray cells of large rhomboidal crystals together with smaller ones. These features would tend to ally Bruniaceae with Geissolomataceae and Grubbiaceae, as I (1975c) have noted. Van Tieghem

(1897) claimed a relationship between Bruniaceae and Grubbiaceae, and cited other authors with a similar viewpoint. Subdivided ray cells containing crystals, characteristic of many Bruniaceae, can be found in Tremandraceae (Carlquist, 1977b) and Pittosporaceae (unpublished data), a pair of families which also are included by Thorne (1968, 1976) in Pittosporales. Axial parenchyma subdivided into crystalliferous strands, a feature of numerous Bruniaceae, is a characteristic that occurs in a number of dicotyledonous families (e.g., Santalaceae, Sapindaceae, Sapotaceae, and most of the myrtalean families) but does not occur, as far as known at present, in other families of Pittosporales. Excessive stress should not be placed on crystal occurrence, however. The reader will have noted that crystals were not observed at all in woods of some species of Bruniaceae.

One can conclude that Bruniaceae are, on the basis of wood anatomy alone, allied to Grubbiaceae and Geissolomataceae, but that similarities to other "rosoid" and hamamelidoid families exist as well. Placement of Bruniaceae in Rosales has been advocated by such phylogenists as Cronquist (1968) and Wettstein (1935). Thorne's (1968, 1976) concept of Pittosporales is essentially rosoid, since he includes it within his superorder Rosiflora. Jay (1968) finds Bruniaceae to be rosalean on the basis of flavonoids. Even conceding a generalized "rosoid" placement for Bruniaceae, however, any attempt to make precise groupings and sequences on the basis of limited information would be premature.

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