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WOOD ANATOMY OF THE BRAZILIAN SPECIES OF SWARTZIA AND CONSIDERATIONS WITHIN THE TRIBE SWARTZIEAE

by

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SUMMARY

Fifty-one Brazilian species and varieties of *Swartzia* Schreber and eight other genera from the tribe Swartzieae were examined. Features with the greatest diagnostic value for the tribe are intervascular pit size, ray width and frequency, storied structure, axial parenchyma strand length, parenchyma band width, and vessel diameter. We analyzed the wood anatomical data using average linkage cluster analysis and canonical discriminant analysis. With weighted features, cluster analysis grouped the species and varieties of *Swartzia* into four distinct groups and tribe *Swartzieae* into seven groups. With unweighted features for both *Swartzia* and *Swartzieae*, the canonical discriminant analysis showed that linear combinations of the variables storied structure, number of tiers per millimetre, axial parenchyma strand length, ray height, intervascular pit size, and exclusively uniseriate rays were good discriminators among the groups. We discuss the grouping of the species of *Swartzia* and compare other genera within the tribe Swartzieae to the four groups of *Swartzia.*

Key words: *Swartzia,* Swartzieae, Leguminosae, Fabaceae, wood anatomy, cluster analysis, canonical discriminant analysis.

INTRODUCTION

Most species of *Swartzia* Schreber occur in tropical Central and South America. The greatest number of species grow in the Amazon region, which appears to be the centre of dispersion (Cowan 1967). Some species occur in the Atlantic forest *(S. myrtifolia, S. glazioviana)* and as far south as the state of Rio Grande do Sul *(S. simplex* var. grandiflora). Other species occur in the central region of Brazil, particularly the state of Mato Grosso *(S. arborescens* and *S. lucida).* Cowan (1967) mentioned that two species *(S. fistuloides* and *S. madagascariensis)* are endemic in Africa. These two species have a different number of chromosomes than the other species. Cowan (1981a) suggests that these African species might be transferred to another genus. Ferguson and Skvarla (1991) support this concept and mention that they have a different pollen

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morphology when compared with the Neotropical species. In 1997 Kirkbride and Wiersema transferred *S. fistuloides* and *S. madagascariensis* to *Bobgunnia fistuloides* (Harms) J.H. Kirkbr. & Wiersema and *B. madagascariensis* (Desv.) J.H. Kirkbr. & Wiersema, respectively. In his wood anatomy paper, Gasson (1996) did not find any compelling reasons to suggest transferring these two species to a new genus.

In 1967, Cowan monographed the Neotropical species of *Swartzia.* He recognized 127 species, many of which were subdivided into varieties. Since 1967, Rizzini & Mattos Filho (1968), Simpson (1975), and Barneby (1991) described additional species. In 1991, Ferguson and Skvarla stated that *Swartzia* consists of about 135 or more species. In 2001, the International Legume Database and Information Service (ILDIS) listed 144 accepted species (http://www.ildis.org/).

Normally the species of *Swartzia* are small to large trees, but some are shrubs. The height ranges from 3–30metres. They grow in non-inundated forests, as well as in riverine forests and cerrado (Cowan 1967). The sapwood is light yellowish brown to almost white and sharply demarcated from the decorative heartwood that varies in colour from reddish-brown to dark-brown or black-brown. The heartwood is hard and heavy and is sometimes similar to Brazilian rosewood *(Dalbergia nigra)* or ebony *(Diospyros* spp.). It is used for flooring, decorative items, turnings, furniture, and small carvings.

The wood of several Brazilian species of *Swartzia* has been described and incorporated into dichotomous keys (Record 1943; Loureiro & Rodrigues 1975; Perez Olvera et al. 1979; Mainieri et al. 1983; Détienne & Jacquet 1983). Gasson (1996) and Gregory (1994) reviewed the wood anatomical literature of *Swartzia* noting the species described. In his study of the tribe Swartzieae, Gasson (1996) examined 19 species of *Swartzia* and analyzed the data using cladistic analysis of 12 wood anatomy features.

Swartzia is by far the largest genus in the tribe Swartzieae, which has been viewed as a basal tribe between Caesalpinioideae and Papilionoideae (Cowan 1981a; Polhill 1981) although recent phylogenetic analysis indicate the tribe is polyphyletic (Herendeen 1995; Pennington et al. 2000,2001). The wood, pollen, and morphological characters are nearly as variable within the genus as to accommodate all species of the tribe Swartzieae. Clearly *Swartzia* needs to be revised and Cowan (1967) mentioned the necessity of more information about the wood anatomy and pollen morphology that could amplify and complement the taxonomic and phylogenetic studies.

We examined and analyzed the wood anatomy of the Brazilian species of *Swartzia* and representative species from eight additional genera of the tribe Swartzieae to determine the most important diagnostic wood anatomical features within *Swartzia,* to group similar species/specimens using statistical methods, and to compare species or species groups within *Swartzia* and the other genera in Swartzieae.

MATERIAL AND METHODS

We examined 51 Brazilian species and varieties of *Swartzia,* represented by 97 samples. We also examined representative species from 8 of the 11 genera within the tribe Swartzieae sensu Cowan (1981b) for a total of 115 specimens. In the Appendix, we list all specimens examined together with the collector's name and number, country

of origin, wood collection designation and number, and whether or not it was cited by Cowan (1967).

Many of the wood samples were very hard, heavy, and contained large amounts of extractive materials. Initially, we tried softening the samples by boiling in water and in a 50/50 solution of glycerin and water. When this method failed, we infiltrated the sectioning blocks with a 4% solution of ethylenediamine and then heated them following the recommendations of Kukachka (1977). Sections (12−20µm thick) were cut on a sliding microtome, stained with safranin, and mounted in a synthetic resin. Macerations were prepared using Jeffrey's solution and mounted in a 50/50 solu-tion of glycerin and ethanol for vessel element and fibre length measurements. For the scanning electron microscopy (SEM), the wood samples were split in radial section, bleached following recommendations of Quirk and Miller (1985), dried, and sputter-coated with gold.

For gathering data and writing descriptions, we followed the recommendation outlined in the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989). The quantitative data were based on 30 measurements for vessel diameters, vessel frequency, vessel element length, fibre length, ray height, and ray frequency. The 30 measurements were analyzed according to Eckblad (1991) ($N = t^2 \times S^2/E^2$; where t = student t, S = standard deviation, E = 0.1 × mean, N = number of measurements). For these features, the overall means were calculated from the means of individual samples. The minimum and maximum values are the lowest and highest means for the taxa. For size of intervascular pits, 10 measurements were taken and only the range reported.

For the statistical approach, we used the SAS system. For the weighted and unweighted analysis we used the Average Linkage Cluster Analysis. We assigned descending weight from the most diagnostic features to the least diagnostic features (scale from 6 to 1). In both analyses, we determined the number of groups in the cluster analysis and then used the canonical discriminant analysis to determine which linear combinations of the variables best discriminated among the clusters.

In general, we followed the taxonomic nomenclature of Cowan (1967). For *Swartzia simplex* var. *continentalis*, we used the revision of McVaugh (1987). Draft descriptions were created using DELTA (Dallwitz et al. 1993) and the character list proposed by DePernia and Miller (1991) with some minor modifications.

RESULTS

The most important anatomical features of *Swartzia* and the other genera of Swartzieae are summarized in tabular form and shown in Table 1. A complete wood anatomical description of the Brazilian species of *Swartzia* follows. A summarized description from direct observation and literature, especially Gasson (1996), Gasson & Webley (1999), and Détienne & Ter Welle (1989), of other genera of Swartzieae is reported. We used the IAWA standard list of features (IAWA Committee 1989) as a guideline. Features not specifically listed in the descriptions are negative or do not apply.

(text continued on page 375)

Table 1. Selected qualitative and quantitative wood characters in Swartzieae.

Vessels: Pits: large (8–10 µm), medium (6–8 µm), small (4–6 µm) – Mean tangential diameter (diam. µm) – Vessels per square millimetre (/sq. mm). – **Rays:** Exclusively uniseriate (ex. uni): – (absent), + (present) – Storied (stor) – (not storied), ± (irregularly storied), + (stoned) - Number of ray tiers per millimetre (tiers/mm) – Number of rays per millimetre (#/mm) – Mean ray height (ht. µm). – **Axial Parenchyma:** Aliform (alif) – Confluent (confl) – **Banded:** - (absent), ± (not predominant), + (predominant) - Band width in cells (bd width) – Number of parenchyma cells per strand (#/str.).

	Vessels			Rays					Parenchyma				
Species / Samples	pits	diam. µm	/sq.mm	ex.uni	stor	tiers/mm	#/mm	ht. µm	alif	confl	banded	bd width	#/str.
Swartzia													
S. acutifolia													
var. *parvipetala*													
MADw 18904	large	73	12	–	+	4	12	246	–	+	±	>4	2
S. apetala													
var. *apetala*													
MADw 36597	large	96	27	–	+	4–5	13	194	–	+	±	3-4	2
S. aptera													
MADw 22714	small	87	16	–	+	3-4	12	182	±	–	+	3-4	2
MADw 22709	small	74	12	–	+	3-4	10	214	+	–	+	3-4	2
S. arborescens													
MADw 18975	medium	65	11	–	±	3-4	10	259	–	±	+	1–2	4
MADw 15920	medium	72	13	–	+	3-4	10	218	–	+	±	1–2	4
MADw 31331	medium	83	19	–	–	–	8	274	–	±	+	3-4	4
MADw 22692	medium	65	14	–	–	–	7	263	–	±	+	3-4	4
S. argentea													
var. *flavescens*													
MADw 45236	small	117	6	–	+	3	9	294	+	+	±	3-4	4
S. benthamiana													
var. *benthamiana*													
MADw 12126	large	146	3	+	+	3	14	271	–	–	+	3-4	4
MADw 19875	large	182	3	+	+	3	13	257	–	–	+	3-4	4
MADw 22847	large	144	2	+	+	3	11	266	–	–	+	3-4	4
MADw 46521	large	170	3	+	+	3	15	271	–	–	+	3-4	4
S. brachyrachis													
var. *brachyrachis*													
MADw 22671	medium	81	11	–	+	3–4	11	245	–	±	+	3-4	4
var. *colombiana*													
MADw 17619	medium	99	3	–	±	3	10	250	–	±	+	3–4	4
MADw 31330	medium	113	4	–	±	3-4	10	262	–	±	+	3-4	4

(S. brachyrachis)													
var. *glabrata*													
MADw 11978	medium	108	6	–	–	–	9	380	–	±	+	1–2	4
SJRw 35768	medium	81	6	–	–	–	8	345	–	±	+	1–2	4
var. *peruviana*													
MADw 22282	medium	151	3	–	±	2–3	9	369	–	+	±	3-4	4
S. cardiosperma													
SJRw 37109	small	110	5	–	±	4	13	286	–	±	+	3-4	4
MADw 31329	small	66	12	–	+	4	12	180	–	±	+	3-4	4
S. conferta													
var. *conferta*													
SJRw 54376	medium	73	10	–	–	–	9	284	+	–	+	1–2	4
S. corrugata													
SJRw 21343	medium	163	2		+	2–3	8	294		+	±	>4	4
INPAw 1621	medium	142	5	–	+	3	9	266	–	+	±	3-4	4
S. cuspidata													
MADw 31326	medium	83	11	–	+	3	11	279	+	±	±	1–2	4
MADw 31327	medium	84	15	–	+	3-4	11	230	+	±	±	3-4	4
S. dipetala													
SJRw 35551	large	109	7	+	+	4	16	206		±	+	3-4	2-4
SJRw 35902	large	104	6	+	+	4	15	214	–	+	±	3-4	2-4
S. euxylophora													
BCTw 11544	large	141	7		+	2–3	11	363	–	–	+	1–2	4
BCTw 11543	large	151	4	–	+	2–3	10	298	–	±	+	1–2	4
S. fasciata													
BCTw 5466	large	135	4	–	+	3-4	9	366	–	+	±	1–2	2-4
S. flaemingii													
var. *flaemingii*													
MADw 13358	large	91	12	–	+	4	11	221	–	±	+	3-4	2
var. psilonema													
BCTw 15558	large	100	17	+	+	4–5	13	184	–	±	+	3-4	2
S. grandifolia													
SJRw 43605	large	71	8	+	+	3	12	258	–	±	+	3-4	4
MADw 22807	large	109	6	+	+	3-4	12	223	–	–	+	3-4	4
S. ingaefolia													
SJRw 21353	large	136	3		+	3	10	282	±	±	+	>4	4
CTFw 30309	large	169	3	–	+	3-4	12	206	±	±	+	>4	4
BCTw 17562	large	174	3	–	+	3	11	221	±	±	+	>4	4
S. krukovii													
MADw 31323	small	104	13	–	+	3-4	12	234	–	+	±	3-4	4

(Table 1 continued)

Species/ Samples	Vessels					Rays			Parenchyma				
	pits	diam. µm	/sq.mm	ex.uni	stor	tiers/mm	#/mm	ht.µm	alif	confl	banded	bd width	#/str.
S. laevicarpa													
SJRw 37175	large	83	6	+	–	–	10	184	–	–	+	1–2	4
SJRw40111	large	98	7	+	+	3	12	274	–	±	+	1–2	4
MADw 22891	large	143	3	+	+	3-4	13	252	–	–	+	3-4	4
S. lamellata var. *lamellata*													
INPAw3628	large	159	5	+	+	3-4	14	253	–	–	+	1–2	4
S. langsdorfii													
BCTw4433	large	106	12	–	+	4	14	187	±	+	±	3-4	2
MADw 13189	large	142	7	–	+	4	14	182	±	+	±	3-4	2-4
S. latifolia													
SJRw 35959	medium	112	14	–	+	4	11	183	±	+	±	3-4	4
SJRw 35810	medium	111	7	–	+	3-4	11	219	±	+	±	3-4	4
SJRw 35554	medium	100	13	–	+	4	11	245	±	+	±	3-4	4
S. laurifolia													
MADw 31321	medium	97	5	–	+	3-4	11	209	±	+	±	3-4	4
S. laxiflora													
MADw 30352	large	130	4	–	+	3	11	238	±	–	+	>4	4
MADw 31320	large	179	2	–	+	3-4	9	244	±	–	+	>4	4
SJRw 45552	large	160	3	–	+	3-4	13	251	±	–	+	>4	4
S. leptopetala													
MADw 31317	small	133	4	–	+	3	8	345	±	+	±	>4	4
S. lucida													
MADw 31314	medium	87	5	–	–	–	8	331	–	+	±	3-4	4
S. multijuga													
BCTw 13288	medium	59	9	–	+	4–5	14	181	–	+	±	3-4	2
S. myrtifolia var. *elegans*													
SJRw 53077	medium	71	19	–	+	4–5	11	163	±	+	±	3-4	4
var. *peruviana*													
MADw 1591*8*	medium	73	11	–	–	–	10	204	±	+	±	3-4	4
var. standleyi													
SJRw 21500	medium	81	18	–	–	–	7	277	–	±	+	3-4	4
S. oblunceolata													
MADw 31308	medium	123	4	–	+	3-4	10	280	±	±	+	3-4	4
MADw 31306	medium	82	14	–	+	4	12	161	–	±	+	3-4	4
MADw 5623	medium	118	6	–	+	3	10	300	±	+	±	3-4	4

S. panacoco												
var. *pariacoco*												
SJRw 49792	large	177	2	−	+	3	12	234	±	–	+	3-4	4
SJRw 12749	large	174	3	+	+	3	12	222	±	–	+	3-4	4
BCTw I6572	large	211	2	–	+	3	12	270	±	–	+	3-4	4
var. *polyanthera*												
MADw 19553	large	213	3	+	+	2–3	11	266	±	–	+	34	4
SJRw 2927	large	122	6	–	+	2–3	9	301	±	–	+	1–2	4
var. *sagotii*												
Uw 31658	large	191	2	+	+	2–3	11	288	±	–	+	3-4	4
Uw 31632	large	183	1	−	+	2–3	11	331	±	–	+	>4	4
CTFw 23400	large	165	2	–	+	2–3	11	283	±	–	+	34	4
S. pendula												
MADw 31311	medium	61	9	–	–	–	10	197	–	±	+	34	4
MADw 31312	medium	55	8	–	–	–	12	189	–	±	+	3-4	4
S. polyphylla												
SJRw 54119	large	194	4	–	+	3	14	317	–	+	±	3-4	4
SJRw 52623	large	123	8	+	+	3	12	279	–	+	±	3–4	4
MADw 12588	large	169	5	−	+	3	12	293	–	+	±	>4	4
S. racemosa												
var. *racemosa*												
MADw 21478	small	84	8	–	+	3	12	212	±	+	±	3-4	4
S. recurva												
MADw 31309	small	122	5	–	+	3	10	268	±	+	±	3-4	4
MADw 31310	small	141	5	–	+	3	10	310	±	+	±	3-4	4
MADw 12590	small	108	5	–	+	3	12	284	±	+	±	3–4	4
S. reticulata												
MADw 22904	large	109	3	+	+	3-4	13	235	–	–	+	1–2	2
INPAw2039	large	121	6	+	+	3-4	11	218	–	–	+	1–2	2
S. schomburgkii												
var. *schomburgkii*												
MADw 5624	large	212	4	+	+	2–3	11	301	–	–	+	3-4	4
Uw 11141	large	111	6	+	+	2–3	10	352	–	–	+	3-4	4
Uw 6884	large	151	6	+	+	2–3	11	304	–	–	+	3-4	4
S. sericea												
var. *sericea*												
SJRw 52410	large	110	9	+	+	3	14	293	–	+	±	3-4	4
INPAw4351	large	118	7	+	+	3-4	12	233	–	+	±	3-4	4

(Table1continued)

Species / Samples	Vessels			Rays					Parenchyma				
	pits	diam. µm	/sq.m	ex.uni	stor	tiers/mm	#/mm	ht.µm	alif	confl	banded	bd width	#/str.
S. simplex													
var. *continentalis*													
SJRw 12283	small	73	15	–	±	4–5	10	185	–	±	+	1–2	4
SJRw 54679	small	53	19	–	+	4	13	205	–	+	±	1–2	4
MADw 31307	small	81	20	–	±	4–5	9	192	–	±	+	1–2	4
var. *grandiflora*													
MADw 4830	small	81	13	–	+	4	11	223	–	±	+	3-4	4
BCTw 2527	small	79	13	–	+	4	12	219	–	+	±	1–2	4
BCTw 18236	small	93	19	–	+	4	11	238	–	+	±	1–2	4
var. *simplex*													
MADw 31302	small	53	18	–	–	–	7	218	–	–	+	1–2	4
MADw 31303	small	53	28	–	–	–	7	242	–	–	+	1–2	4
MADw 31304	small	48	24	–	–	–	9	226	–	–	+	1–2	4
S. tessmannii													
MADw 46437	large	137	1	+	+	2–3	11	273	–	–	+	3-4	4
S. tomentifera													
MADw 12711	large	171	3	+	+	2–3	12	287	–	–	+	3-4	4
S. ulei													
BCTw 9198	large	150	2	+	–	–	11	202	–	–	+	3-4	4
Aldina													
A. insignis													
MADw 1012	medium	274	1	–	+	2–3	6	355	+	±	–	–	4
A. petiolulata													
SJRw 52624	medium	189	2	–	+	3-4	8	218	–	±	+	24	4
Bocoa													
B. alterna													
SJRw 35695	medium	65	25	–	–	–	10	504	–	+	±	3-4	2
MADw 31334	medium	64	20	–	–	–	10	537	–	±	+	3-4	2
MADw 46482	medium	60	13	–	–	–	11	617	–	±	+	3-4	2
B. prouocensis													
MADw 19596	medium	153	3	–	+	3-4	10	260	±	–	+	1–2	2
B. viridiflora													
SJRw 23647	medium	132	4	–	+	2–3	12	296	±	+	±	3-4	4

Candolleodendron													
C. brachystachium													
Oldeman 2291	small	56	61	–	±	5-6	14	291	–	±	+	3-4	2
Cordyla													
C. africana													
SJRw 29961	large	175	2	–	+	4–5	8	160	–	±	+	>4	2-4
SJRw 41353	large	189	2	–	+	4–5	1	220	–	±	+	>4	4
SJRw 49830	large	142	3	–	+	4	8	183	–	±	+	>4	4
Exostyles													
E. venusta													
BCTw 13301	small	15	16	–	±	3-4	10	300	–	±	+	3-4	2-4
BCTw 13328	small	68	11	–	+	3-4	7	271	–	±	+	3-4	2-4
Lecointea													
L. amazonica													
SJRw 20711	small	91	14	–	+	4	11	204	–	±	+	3-4	4
SJRw 16174	small	93	18	–	+	4	12	206	–	±	+	3-4	4
Mildbraediodendron													
M. excelsum													
SJRw 32110	large	187	2	–	+	4	9	224	+	±	–	–	4
MADw 17296	large	185	2	–	+	4	1	220	+	±	–	–	4
Zollernia													
Z. paraensis													
SJRw 5952	small	94	17	–	+	4	1	213	–	±	+	3-4	4

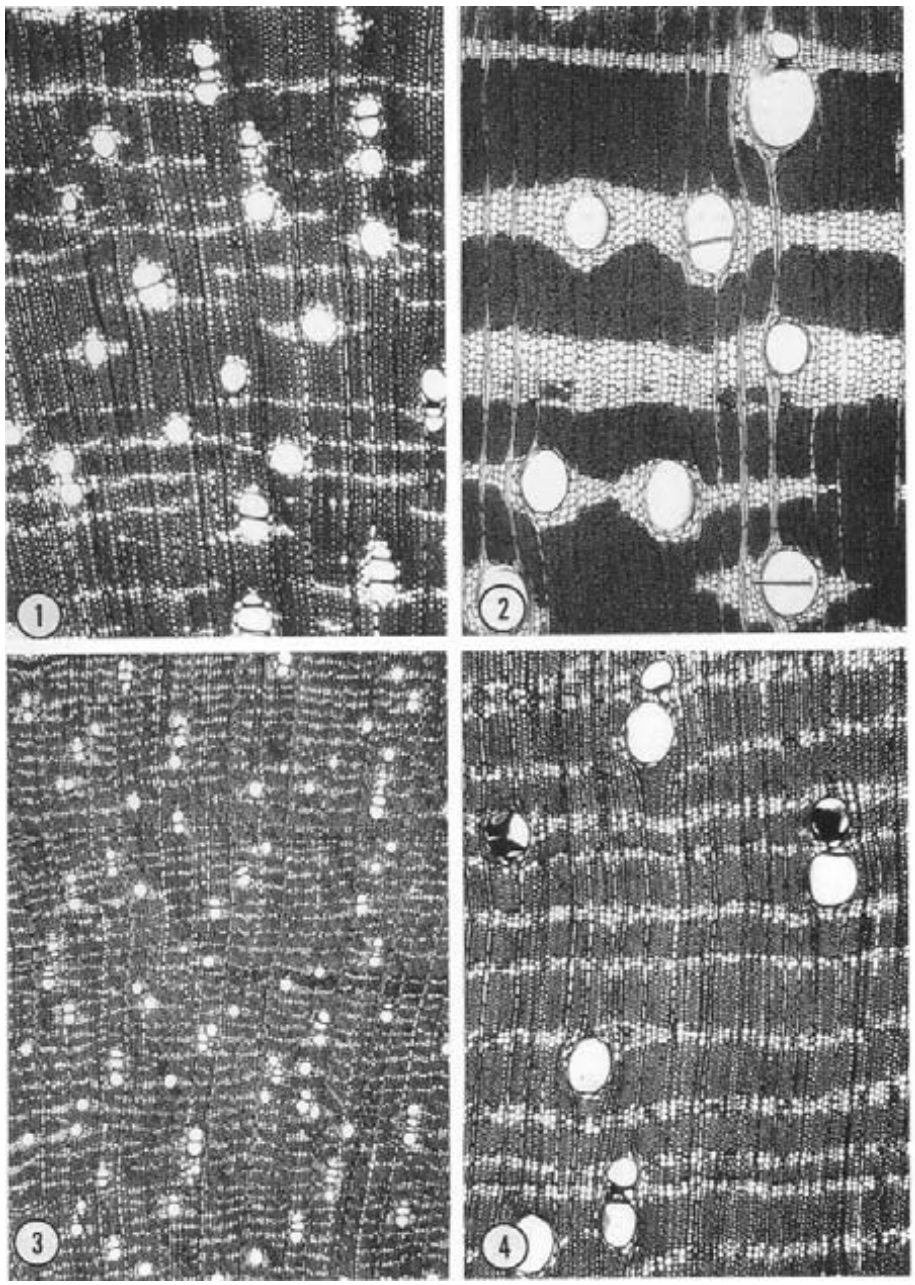

Fig. 1–4.*Swartzia.* Transverse sections. Scale bar 100 µm. - 1: *S. conferta;* aliform and narrow banded parenchyma, vessel diameter < 100 µm. - 2: *S. laxiflora;* aliform and wide banded parenchyma, vessel diameter > 130 µm. - 3: *S. simplex* var. *simplex:* exclusively banded parenchyma, vessel diameter < 55 µm. - 4: *S. benthamiana;* exclusively banded parenchyma, vessel diameter > 130.

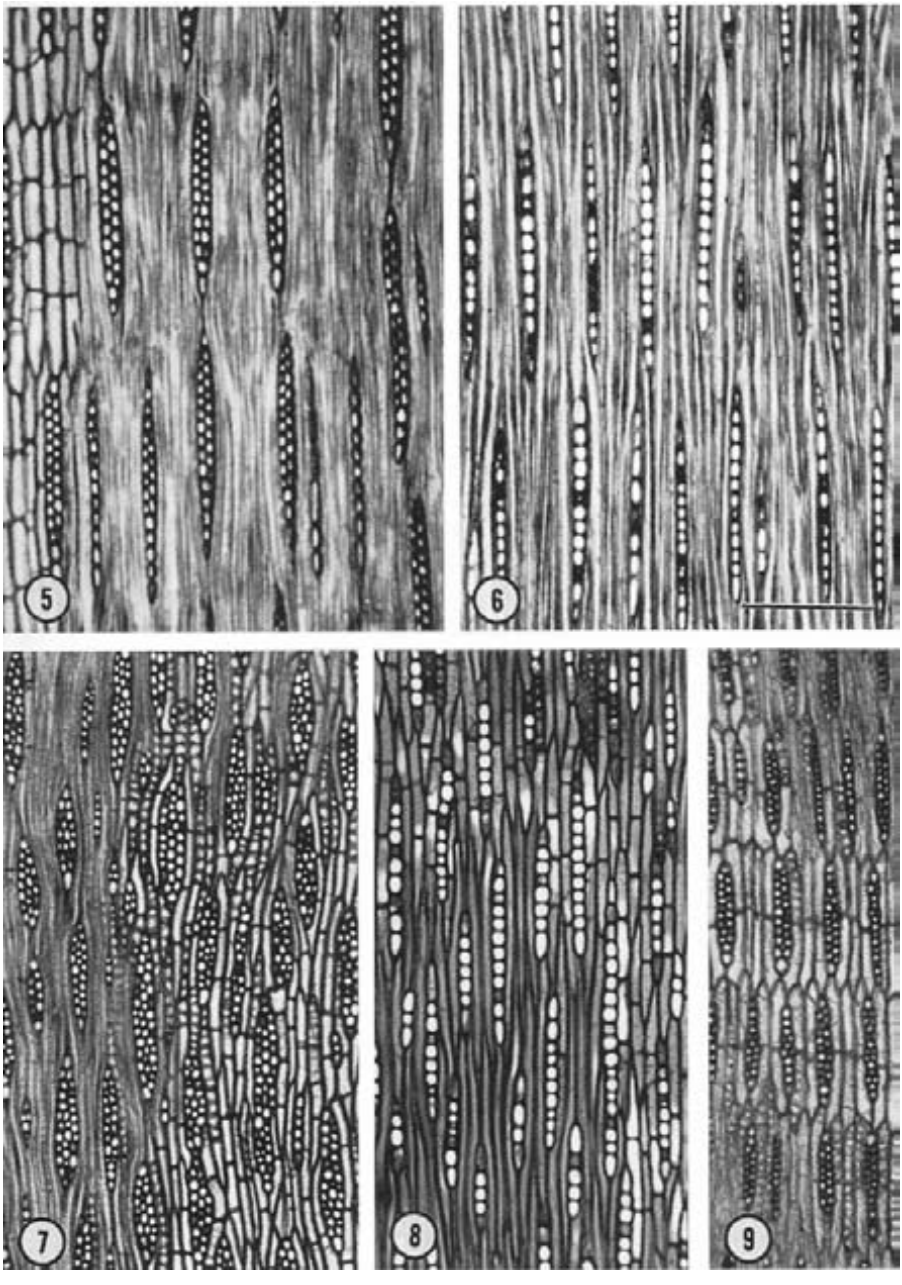

Fig. 5–9.*Swartzia*. Tangential sections. Scale bar 100 µm. - 5: *S. ingaefolia;* storied, biseriate rays, axial parenchyma with 4 cells per strand. - 6: *S. laxiflora:* storied, uniseriate rays. - 7: *S. myrtifolia* var. *peruviana:* non-storied, rays 3 cells wide, axial parenchyma with 4 cells per-strand. - 8: *S. laevicarpa* (SJRw 371 75). non-storied. uniseriate rays, axial parenchyma with 2–4cells per strand. - 9: *S. multijuga;* storied, rays mostly 2 cells wide, axial parenchyma with 2 cells per strand.

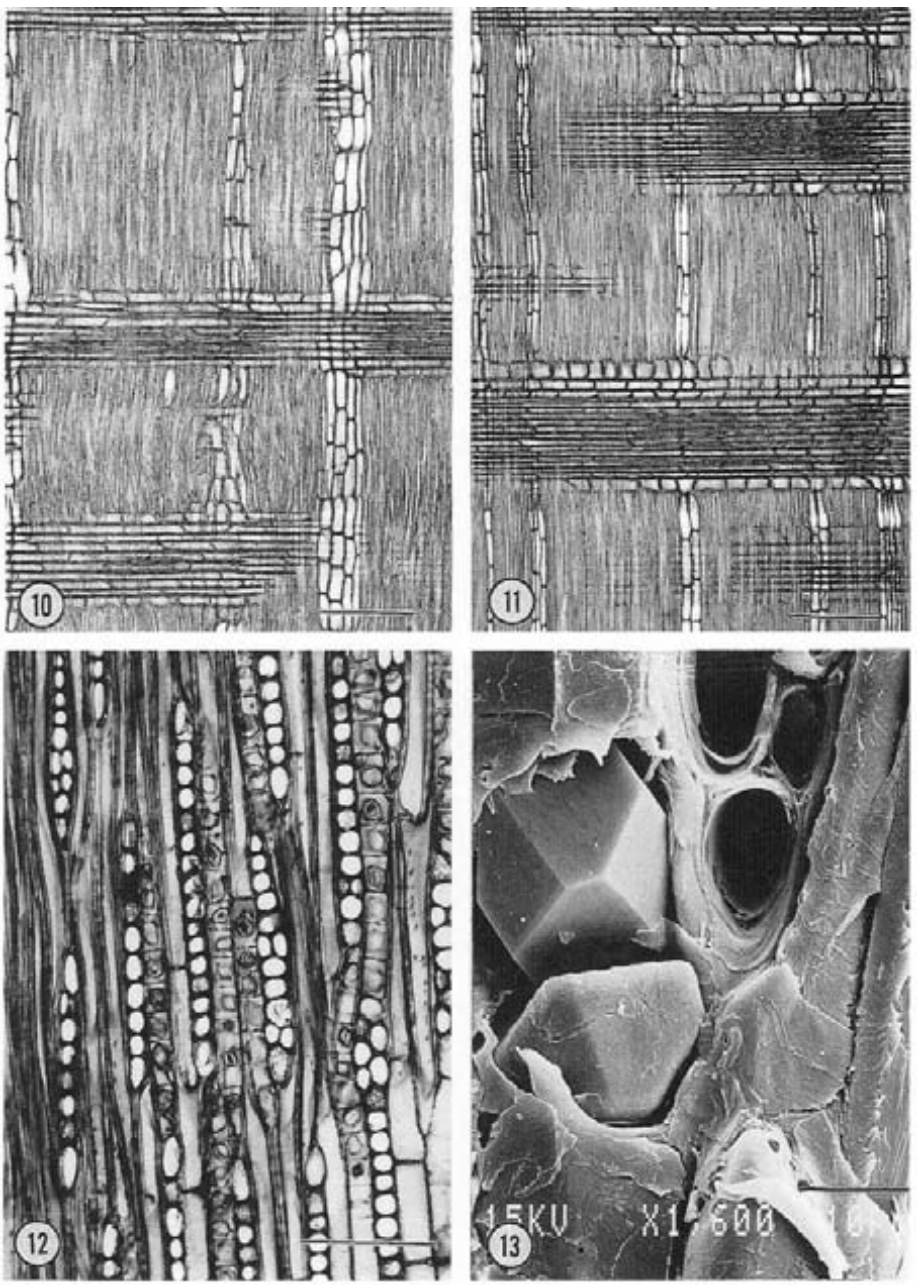

Fig. 10–13.*Swartzia.* - 10 & 11: Radial sections. Scale bar 100 µm. - 10: *S. laurifolia;* homocellular rays. - 11: *S. recurva;* heterocellular rays, with one row of square marginal cells. - 12 & 13: Tangential sections. - 12: *S. laevicarpa;* prismatic crystals in chambered axial parenchyma. Scale bar 100 µm. - 13: *S. simplex* var. *simplex;* prismatic crystals in axial parenchyma (SEM). Scale bar 10 µm.

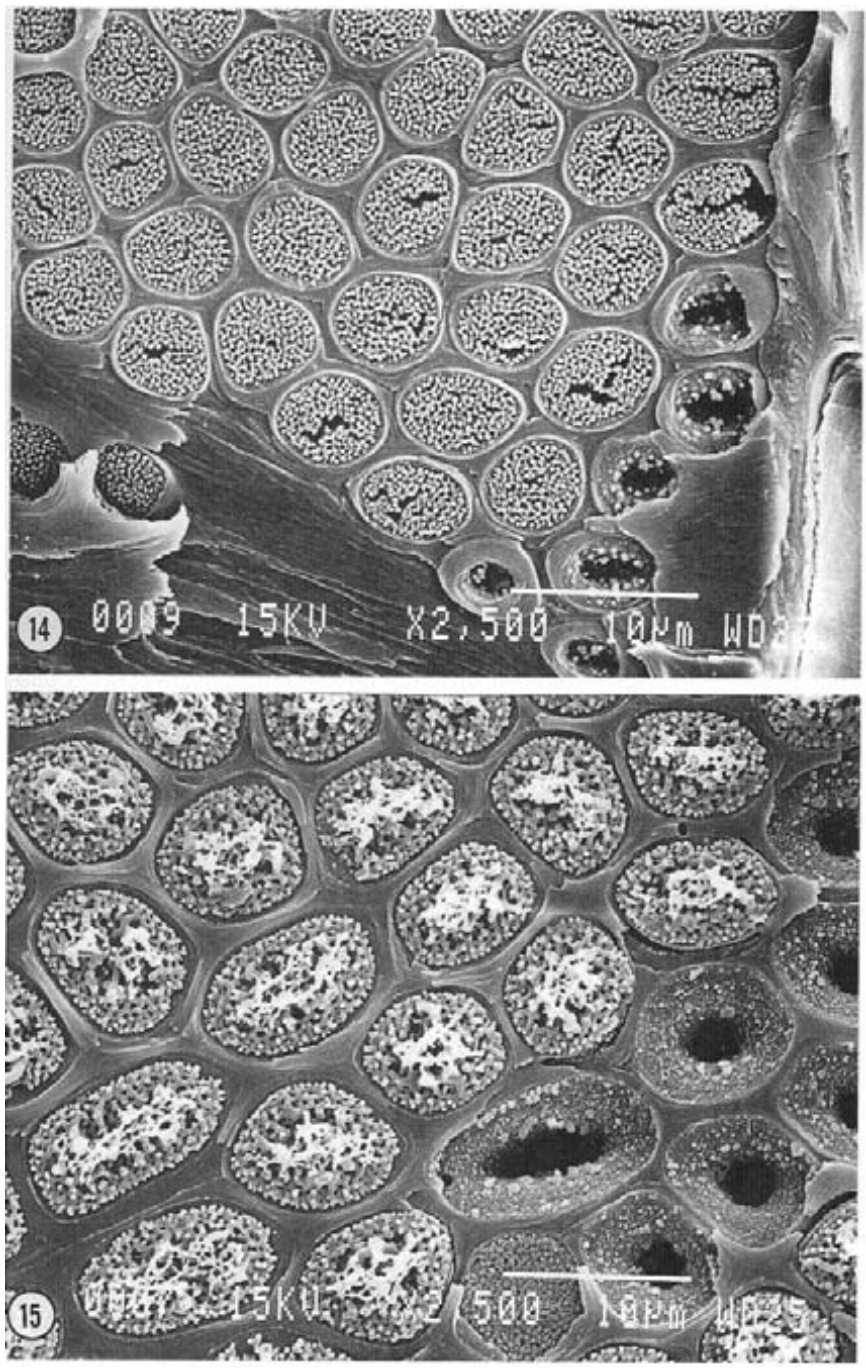

Fig. 14 & 15. *Swartzia.* Tangential sections. Scale bar 10 µm. Intervascular pits vestured (SEM photo taken from the middle lamellae side). - 14: *S. simplex* var. *grandiflora;* small pits (4–6 µm). - 15: *S. benthamiana:* large pits (8–10µm).

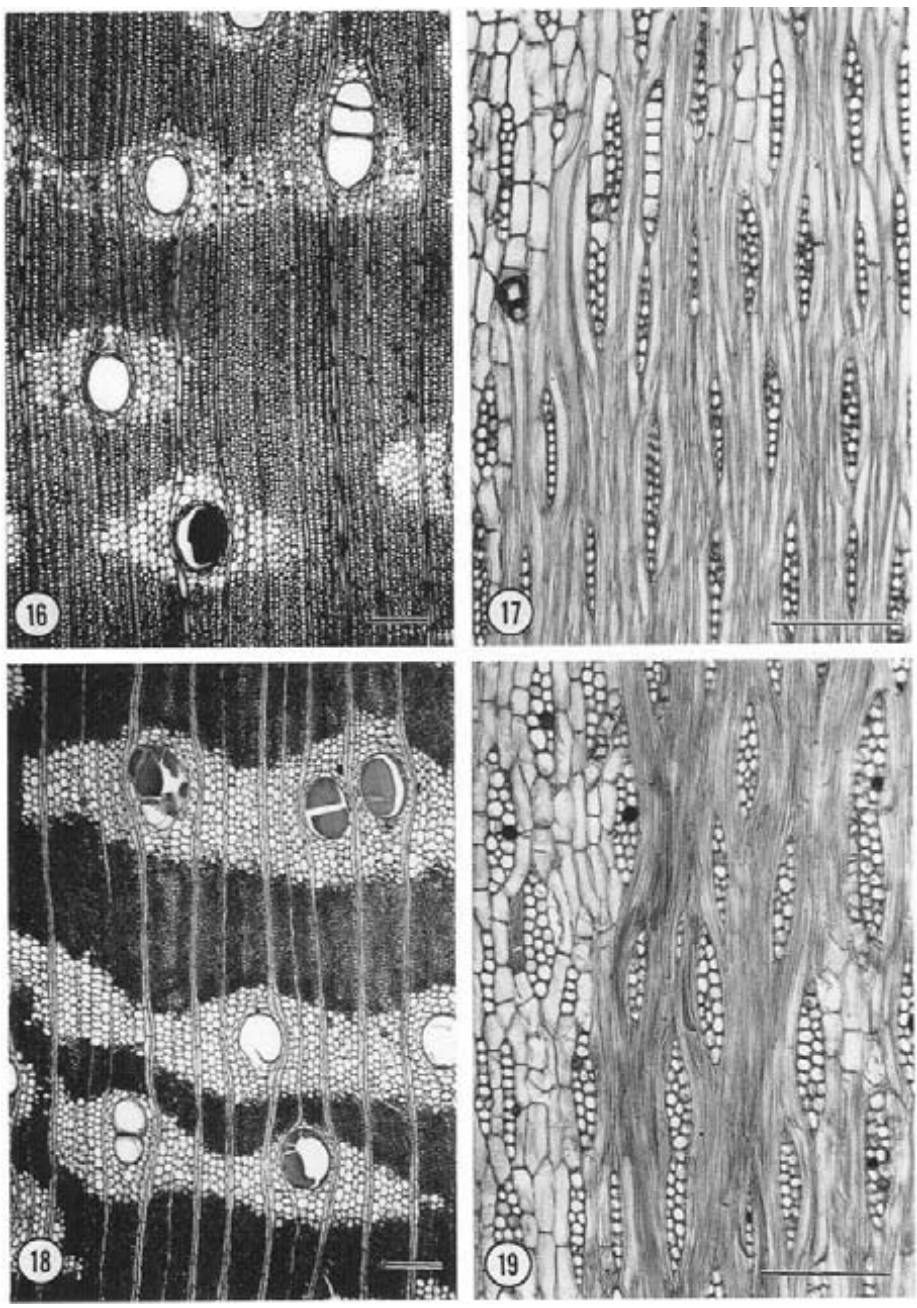

Fig. 16–19.Scale bar 100 µm. - 16 & 17: *Mildbraediodendron excelsum.* - 16: Transverse section; aliform to occasionally confluent parenchyma. - 17: Tangential section; storied, mostly 2–3cells wide. - 18 & 19: *Cordyla africana.* - 18: Transverse section; confluent to banded parenchyma. - 19: Tangential section; storied, mostly 2–3cells wide.

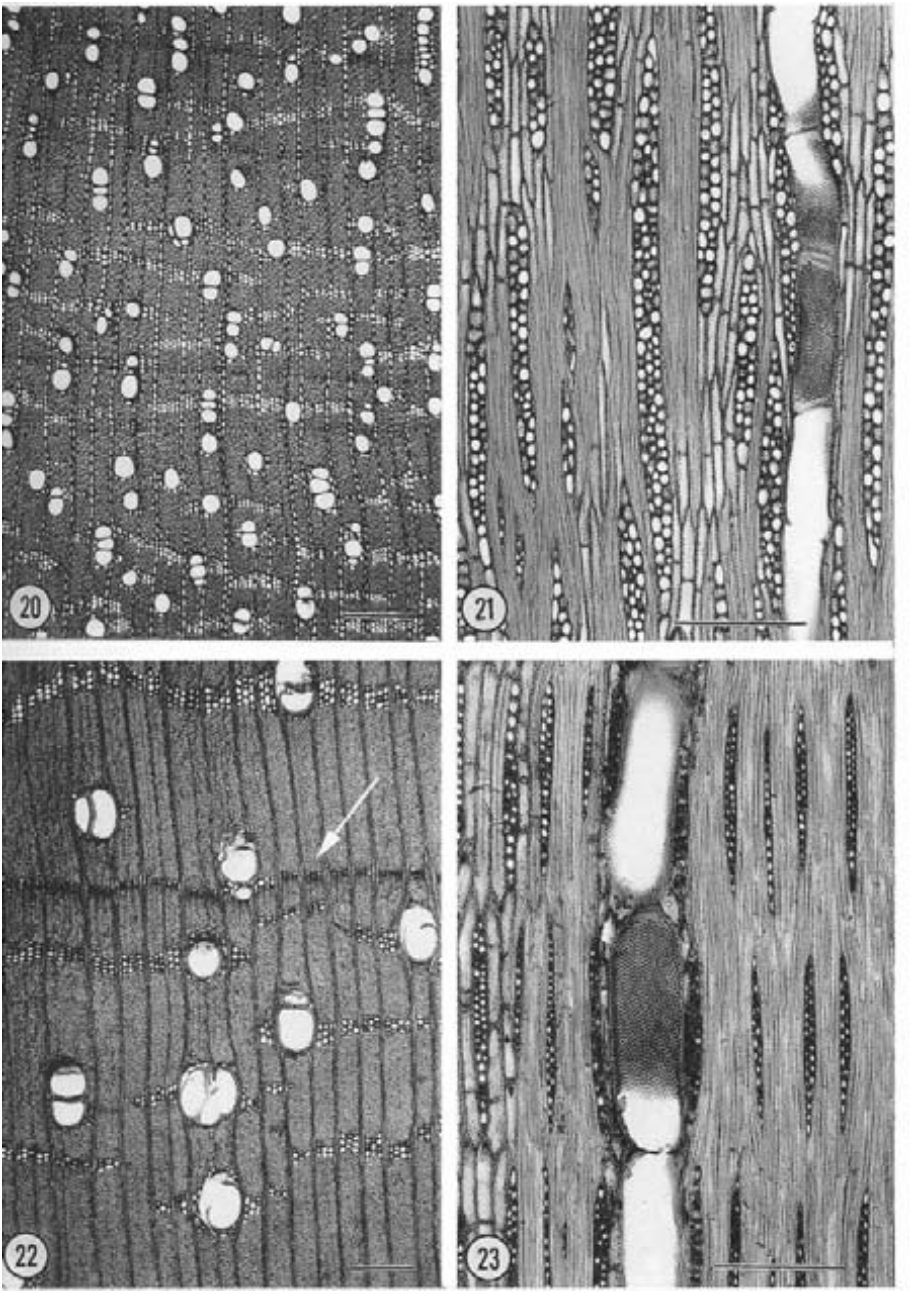

Fig. 20–23.Scale bar 100 µm. - 20 & 21 : *Bocoa alterna.* - 20: Transverse section: confluent to banded parenchyma. - 21 : Tangential section; non-storied, rays tall and heterocellular, axial parenchyma with 2 cells per strand. - 22 & 23: *Bocoa prouacensis.* - 22: Transverse section; aliform to banded parenchyma, also marginal parenchyma (arrow). - 23: Tangential section; storied, rays mostly biseriate. axial parenchyma with 4 cells per strand.

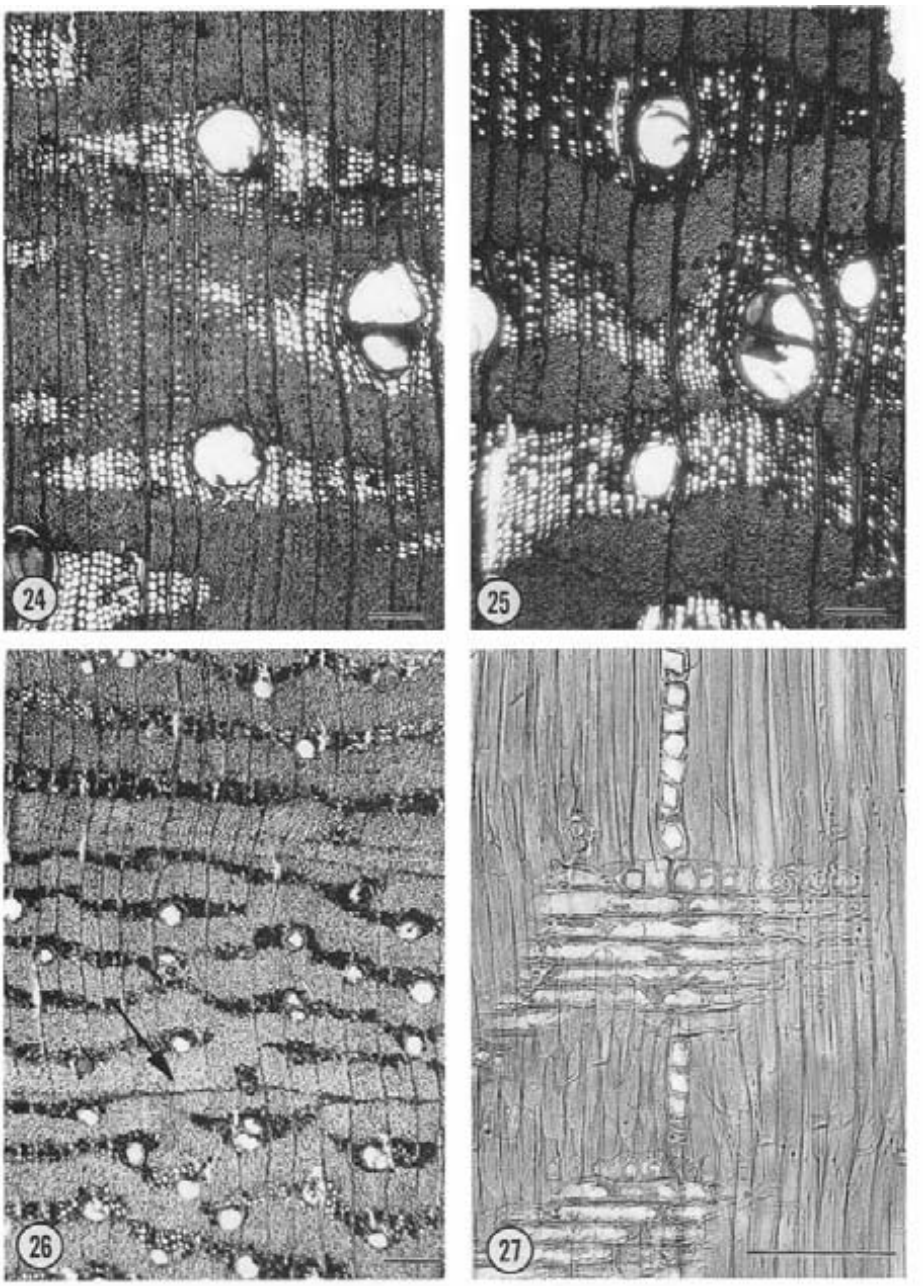

Fig. 24 & 25. *Aldina.* Transverse sections. Scale bar 100 µm. - 24: *A. insignis;* lozenge-type aliform parenchyma. - 25: *A. petiolulata;* confluent to banded parenchyma. - 26 & 27: *Lecointea amazonica.* - 26: Transverse section; confluent to banded parenchyma, also marginal parenchyma (arrow). - 27: Radial section; prismatic crystals in chambered axial parenchyma and in marginal ray cells.

Wood anatomy of *Swartzia*

Heartwood/sapwood: Sapwood light yellowish brown to almost white and sharply demarcated from the dark reddish-brown to dark-brown or black-brown heartwood (present in 30% of the specimens); reddish-brown to dark reddish-brown in *S. benthamiana, S. euxylophora, S. fasciata, S. laevicarpa,* having darker streaks in *S. benthamiana* (Mmw 12126) and *S. laevicarpa;* dark brown to nearly black in *S. corrugata, S. dipetala, S. grandifolia, S. laxiflora, S. leptopetala, S. lucida, S. myrtifolia* var. *peruviana, S. oblanceolata, S. panacoco, S. schomburgkii.* Heartwood surface fluorescence absent; ethanol extract fluoresces blue in *S. benthamiana, S. oblanceolata,* and *S. tessmannii;* water extract fluorescence absent.

Growth rings indistinct to somewhat distinct, if present, demarcated by marginal parenchyma bands 1–2 cells wide and/or a gradual change from aliform-confluent parenchyma to paratracheal banded parenchyma and finally marginal bands.

Vessels diffuse-porous; solitary and in radial multiples of 2 to 4 (Fig. 1–4); (48–)113(–213) µm in diameter; (1–)9(–28) per square millimetre; (243–)335(–508)µm in length. Simple perforation plates. Intervascular pits alternate, circular or oval; small (4–6µm) (Fig. 14), medium (6–8µm) and large (8–10µm) (Fig. 15); vestured (Fig. 14 & 15). Intervascular and vessel-ray pitting of the same size and shape.

Fibres mostly thick to very thick-walled with simple or minutely bordered pits, (886–)1142(–1527)µm long. Not septate.

Parenchyma: Apotracheal parenchyma in marginal bands; mostly 1–2 cells wide. Paratracheal parenchyma variable from aliform to confluent (Fig. 1 & 2) to predominantly banded (Fig. 3 & 4); bands variable in width from narrow (1–2cells) (Fig. 3 & 4), medium (2–4 cells) to wide (> 4 cells) (Fig. 2). Parenchyma strands mostly of 4 cells (Fig. 5,7 and 8), sometimes 2 cells (Fig. 9) in *S. acutifolia, S. apetala* var. *apetala, S. aptera, S. flaemingii* var. *flaemingii, S. flaemingii* var. *psilonema, S. langsdorfii* (BCTw 4433), *S. multijuga,* and *S. reticulata,* or 2–4 cells per strand in *S. dipetala, S. fasciata,* and *S. langsdorfii* (MADw 13 189).

Rays homocellular (Fig. 10), heterocellular with 1 or occasionally 2 rows of square marginal cells (Fig. 11); (7–)11(–16) per millimetre; exclusively uniseriate (Fig. 6 & 8), mostly biseriate (Fig. 5 & 9), or 2–3 cells wide (Fig. 7); (161–)253(–380)µm in height; storied or irregularly storied in most species (Fig. 5,6 & 9), not storied in *S. conferta, S. laevicarpa* (SJRw 37175) (Fig. 8), *S. lucida, S. myrtifolia* var. *peruviana* (Fig. 7), *S. myrtifolia* var. *standleyi, S. pendula, S. simplex* var. *simplex,* and *S. ulei,* mostly 3 or 4 tiers per millimetre, sometimes 2–3 or 4–5 tiers.

Prismatic crystals in chambered axial parenchyma cells, absent in rays (Fig. 12 & 13).

Summarized wood anatomy of *Aldina, Bocoa, Candolleodendron, Cordyla, Exostyles, Lecointea, Mildbraediodendron,* and *Zollernia*

Heartwood/sapwood: Sapwood mostly light brown to almost white; sharply demarcated from heartwood of *Aldina, Bocoa,* and *Zollernia,* but only somewhat demarcated from heartwood in *Cordyla, Lecointea,* and *Mildbraediodendron.* No heartwood

available for *Candolleodendron* and *Exostyles.* Heartwood reddish-brown *(Aldina),* light-brown to medium brown *(Cordyla, Lecointea, Mildbraediodendron),* dark-brown *(Bocoa prouacensis)* to black *(Zollernia paraensis).* Heartwood surface fluorescence absent; ethanol extract fluoresces blue in *Aldina,* weak light blue in *Lecointea* and *Bocoa prouacensis,* and weak light green in *Cordyla;* water extract fluorescence absent.

Growth rings indistinct to slightly distinct, demarcated by marginal parenchyma bands 1–2cells wide in *Bocoa viridiflora, B. prouacensis* (Fig. 22), *Exostyles, Lecointea* (Fig. 26), and *Zollernia.*

Vessels diffuse-porous; mostly solitary and in radial multiples of 2 to 4, some longer radial chains in *Bocoa alterna* (Fig. 20); (56–)76(–94)µm in diameter in *B. alterna, Candolleodendron, Exostyles, Lecointea,* and *Zollernia* and (132–)184(–274)µm in *Aldina, Bocoa prouacensis, B. viridiflora, Cordyla* (Fig. 18), and *Mildbraediodendron* (Fig. 16); (1–)2(–4) per square millimetre in *Aldina, Bocoa prouacensis, B. viridiflora, Cordyla, and Mildbraediodendron,* (11-)17(-25) per square millimetre in *Bocoa alterna, Exostyles, Lecointea,* and *Zollernia,* and 61 per square millimetre in *Candolleodendron;* (203–)303(–532)µm in length. Simple perforation plates. Intervascular pits alternate, circular or oval; small (4–6µm) in *Candolleodendron, Exostyles, Lecointea,* and *Zollernia,* medium (6–8µm) in *Aldina* and *Bocoa,* and large (8–10µm) in *Cordyla* and *Mildbraediodendron;* vestured. Intervascular and vessel-ray pitting of the same size and shape.

Fibres thin to very thick-walled with simple or minutely bordered pits; (888–)1272 (–1905)µm long. Not septate.

Parenchyma: Paratracheal parenchyma mostly aliform to confluent to occasionally wide bands in *Aldina* (Fig. 24 & 25), *Cordyla* (Fig. 18), and *Mildbraediodendron* (Fig. 16); confluent to predominantly banded of variable widths in *Bocoa, Candolleodendron, Exostyles, Lecointea,* and *Zollernia.* Occasional apotracheal irregular or marginal bands, mostly 1–2cells wide. Parenchyma strands mostly of 4 cells, 2-celled in *Bocoa alterna, B. prouacensis,* and *Candolleodendron,* 2–4cells per strand in *Cordyla africana* (SJRw 29961) and *Exostyles.*

Rays homocellular in *Bocoa prouacensis, B. viridiflora, Cordyla, Lecointea, Mildbraediodendron,* and *Zollernia;* homocellular to heterocellular with one row of square marginal cells in *Aldina;* heterocellular with 1–2rows of square to upright cells in *Exostyles;* heterocellular with mixed square and upright cells in *Bocoa alterna;* mostly 2–3cells wide, 1–2cells wide in *Candolleodendron;* (160–)236(–356)µm in height, in *Bocoa alterna* 504–617µm in height (Fig. 21); storied or irregularly storied (Fig. 17, 19 & 23) except in *B. alterna* (Fig. 21); mostly 3–4tiers per millimetre, 5–6in *Candolleodendron.*

Prismatic crystals in chambered axial parenchyma cells in *Aldina, Cordyla, Exostyles, Lecointea, Mildbraediodendron,* and *Zollernia;* in marginal ray cells in *Exostyles, Lecointea* (Fig. 27), and *Zollernia,* rarely in procumbent cells in *Exostyles;* and crystals absent in *Bocoa* and *Candolleodenidron.*

DISCUSSION

The wood anatomy of the 51 Brazilian species of Swartzia shows a wide range of variability for a number of specific characters. If we include *Aldina, Bocoa, Candolleodendron, Cordyla, Exostyles, Lecointea, Mildbraediodendron,* and *Zollernia* from the tribe Swartzieae in our comparison, we find that the total variability does not increase appreciably. In particular, we found that characters for all species of Swartzieae vary as follows: intervascular pits from small to large (4–10 µm); rays homocellular to heterocellular with 1–2rows of upright cells, ray width from exclusively uniseriate to mostly 2–3 cells wide; ray height from a mean of 160 to 617 µm; vessel diameters from a mean of 48 to 274 µm; vessels per square millimetre from a mean of 1 to 61; rays per millimetre mostly 6 to 16; rays from storied to non-storied; number of tiers per millimetre from 2 to 6 (for storied rays); axial parenchyma from aliform with marginal or irregularly banded apotracheal parenchyma to predominantly banded; axial parenchyma band width from 1–2cells to more than 5 cells; and number of cells per parenchyma strand from 2 to 4. To analyze these data for relationships and phylogenetic trends, we initially proposed using a cladistic analysis approach. However, we did not examine all the species of *Swartzia,* and initially we did not include *Ateleia, Cyathostegia* and *Amburana* of Polhill's (1994) Swartzieae. We also did not have sufficient discrete characters to properly analyze the taxa (Herendeen & Miller 2000). As an alternative, we explored various statistical methods to group taxa that might suggest some general relationships. Using the SAS system, we preformed average linkage cluster analyses to identify groups and then performed canonical discriminant analyses to identify linear combinations of the original 13 variables that were effective in discriminating among the groups.

Groups from statistical analysis

The principle of cluster analysis is to group similar entities, in this case, specimens within the tribe Swartzieae. The process is similar to cladistic analysis in that the approach is quantitative and statistical and the data are coded in a similar fashion. However, cladistics is a "method of classification that groups taxa hierarchically into nested sets and conventionally represents these relationships as a cladogram" (Kitching et al. 1998). Cluster analysis is not a substitute for cladistic analysis.

To analyze the anatomical data of the 115 specimens of Swartzieae, we selected 13 variables as follows: vessel diameter, number of vessels per square millimetre, intervascular pit size, storied structure, number of tiers per millimetre, ray height, number of rays per millimetre, rays exclusively uniseriate, axial parenchyma aliform, confluent, or banded, band width in cells, and number of cells per axial parenchyma strand (Table 1). Data based on these variables were analyzed using average linkage cluster analysis. The result produced 10 distinct groups (Table 2). Of the 10 groups, five contained 4 or fewer specimens. Group 10 was *Mildbraediodendron,* group 9 *Aldina insignis,* and group 8 *Bocoa alterna,* suggesting that species in these three groups are not closely related to *Swartzia* or at least to the species of *Swartzia* included in this study.

Table 2. Groups within Swartzieae using unweighted cluster analysis.

Group 1 (7 specimens): *S. acutifolia, S. apetala* var. *apetala, S. flaemingii* var. *flaemingii, S. langsdorfii, S. multijuga, Candolleodendron brachystachium.*

Group 2 (39 specimens): S. arborescens (MADw 18975 & MADw 15920), *S. argentea* var. *flavescens, S. brachyrachis* var. *brachyrachis, S. brachyrachys* var. *colombiana, S. brachyrachis* var. *peruviana, S. cardiosperma, S. corrugata, S. cuspidata, S. krukovii, S. latifolia, S. laurifolia, S. leptopetala, S. myrtifolia* var. *elegans, S. oblanceolata, S. racemosa, S. recurva, s. simplex* var. *continentalis, S. simplex* var. *grandiflora, Bocoa viridiflora, Exostyes venusta, Lecointea amazonica, Zollernia paraensis.*

Group 3 (14 specimens): *S. ingaefolia, S. laxiflora, S. panacoco* var. *panacoco* (SJRw 49792 & BCTw 16572), *S. panacoco* var. *sagotii* (Uw 31632 & CTFw 23400), *Cordyla africana, Aldina petiolulata.*

Group 4 (3 1 specimens): *S. benthamiana, S. dipetala, S. euxylophora, S. fasciata, S. flaemingii* var. *psilonema, S. grandifolia, S. laevicarpa* (SJRw 40111 & MADw 22891), *S. lamellata, S. panacoco* var. *panacoco* (SJRw 12749), *S. panacoco* var. *polyanthera, S. panacoco* var. *sagotii* (Uw 31658), *S. polyphylla, S. reticulata, S. schomburgkii, S. sericea, S. tessmannii, S. tomentifera.*

Group 5 (3 specimens): *S. aptera, Bocoa prouacensis.*

Group 6 (11 specimens): *S. arborescens* (MADw 31331 & MADw 22692), *S. laevicarpa* (SJRw 37175), *S. myrtifolia* var. *peruviana, S. myrtifolia* var. *standleyi, S. pendula, S. simplex* var. *simplex; S. ulei.*

Group 7 (4 specimens): *S. brachyrachis* var. *glabrata, S. conferta, S. lucida.*

Group 8 (3 specimens): *Bocoa alterna.*

Group 9 (1 specimen): *Aldina insignis.*

Group 10 (1 specimen): *Mildbraediodendron excelsum.*

To determine which characters (variables) were the most important in grouping the specimens, we used canonical discriminant analysis. The first canonical discriminator was correlated with storied structure and the number of ray tiers per mm. The second canonical discriminator was correlated with ray height and intervascular pit size. The third discriminator was correlated with exclusively uniseriate rays and the number of cells per axial parenchyma strand. A plot of the first three canonical values (Fig. 28) shows good separation of the non-storied groups 6, 7, and 8 on the left side of the graph. On the right side group 4 (pyramids) shows some separation from the main body of data based mostly on intervascular pit size.

In an effort to eliminate the influence of genera other than *Swartzia,* we analyzed only specimens of *Swartzia* using the same methods as above. In this analysis, we obtained 6 groups (Table 3). Group 2 was *S. aptera,* and group 6 was *S. brachyrachis* var. *glabrata, S. brachyrachis* var. *peruviana, S. conferta,* and *S. lucida.* When we analyzed all Swartzieae (Table 2), *S. aptera* was in group 5 (3 specimens) along with *Bocoa prouacensis. Swartzia brachyrachis* var. *glabrata, S. conferta,* and *S. lucida* of

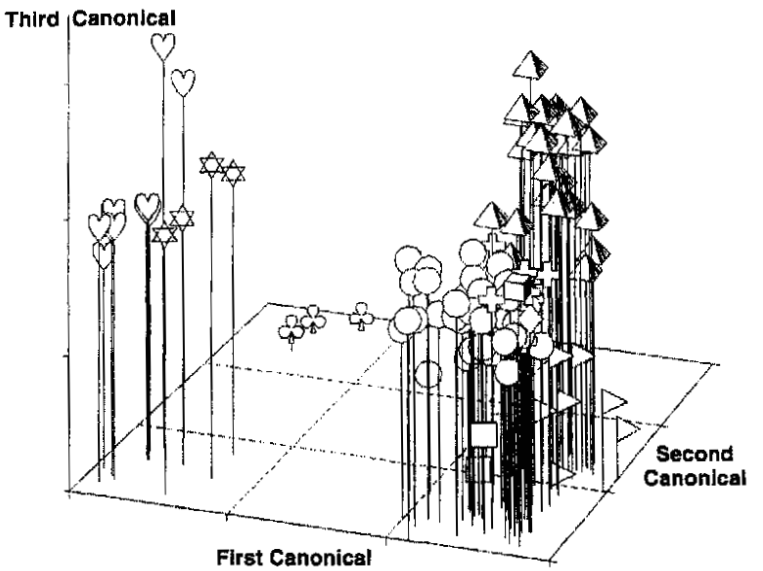

Fig. 28. Plot of first three canonical variables for the unweighted Swartzieae. Legend: Group 1 = flag; Group 2 = circle; Group 3 = cross; Group 4 = pyramid; Group 5 = square; Group 6 = heart; Group 7 = star; Group 8 = club; Group 9 = cube; Group 10 = diamond.

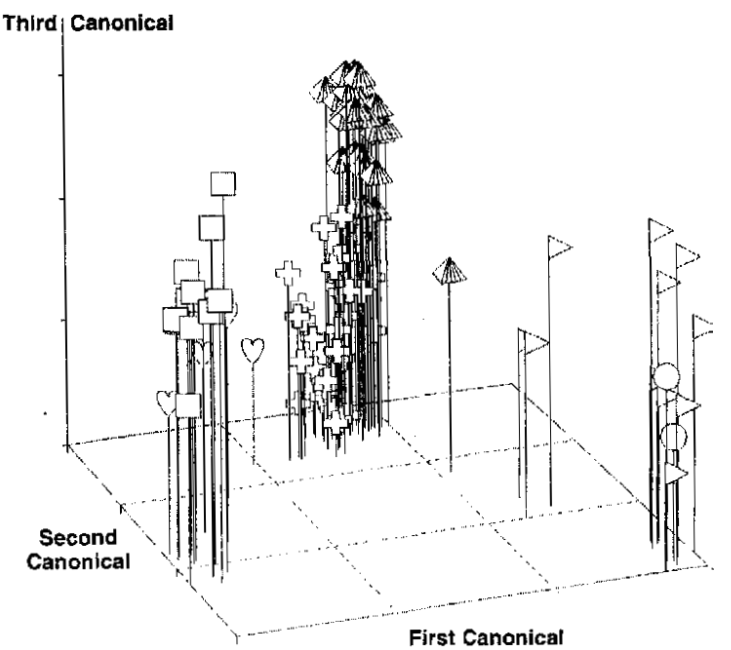

Fig. 29. Plot of first three canonical variables for the unweighted Swartzia. . Legend: Group 1 = flag; Group 2 = circle; Group 3 = cross; Group 4 = pyramid; Group 5 = square; and Group 6 = heart.

Table 3. Groups within *Swartzia* using unweighted cluster analysis.

Group 1 (11 specimens): *S. acutifolia, S. upetala* var. *apetalu, S. dipetala, S. flaemingii* var. *flaemingii, S. flaemingii* var. *psilonema, S. langsdorfii, S. multijuga, S. reticulata.*

Group 2 (2 specimens): *S. aptera.*

Group 3 (37 specimens): *S. arborescens* (MADw 18975 & MADw 15920), *S. argentea* var. *flavescens, S. brachyrachis* var. *brachyrachis, S. brachyrachys* var. *colombiana, S. cardiosperma, S. corrugata, S. cuspidata, S. krukovii, S. latifolia, S. laurifolia, S. leptopetala, S. myrtifolia* var. *elegans, S. oblanceolata, S. polyphylla, S. racemosa, S. recurva, S. sericea, S. simplex* var. *continentalis, S. simplex* var. *grandiflora.*

Group 4 (31 specimens): *S. benthamiana, S. euxylophora, S. fasciata, S. grandifolia, S. ingaefolia, S. laevicarpa* (SJRw 401 11 & MADw 22891), *S. lamellata, S. laxiflora, S. panacoco* var. *panacoco, S. panacoco* var. *polyanthera, S. panacoco* var. *sagotii, S. schomburgkii, S. tessmannii, S. tomentifera.*

Group 5 (11 specimens): *S. arborescens* (MADw 31331 & MADw 22692), *S. laevicarpa* (SJRw 37175), *S. myrtifolia* var. *peruviana, S. myrtifolia* var. *standleyi, S. pendula, S. simplex* var. *simplex; S. ulei.*

Group 6 (5 specimens): *S. brachyrachis* var. *glabrata, S. brachyrachis* var. *peruviana, S. conferta, S. lucida.*

group 6 of *Swartzia* make up the entire group 7 of Swartzieae. *Swartzia brachyrachis* var. *peruviana* of group 6 of *Swartzia* moved to group 2 of Swartzieae, a large group that includes the other varieties of *S. brachyrachis.* Again, the first canonical variable is well correlated with storied structure coupled with number of ray tiers per mm. The second canonical variable, however, is well correlated with the number of cells per axial parenchyma strand, and the third with intervascular pit size. A plot of the first three canonical values (Fig. 29) shows good separation of groups 3 and 4 from groups 1, 2, and 5. Group 6 has one specimen *(S. brachyrachis* var. *peruviana)* within the group 3 specimens (storied); whereas the others are closely associated with specimens of group 5 (not storied). Groups 3 and 4 (both storied) show good separation based mostly on intervascular pit size. Group 5 (not storied) is separate from groups 1 and 2 based mostly on exclusively uniseriate rays.

To explore different possibilities for analyzing our data and to reduce and clarify groupings, we assigned weight to the 13 characters. The values for weight are based on the first three canonical variables for the analysis of *Swartzia* and Swartzieae and the diagnostic value of the characters within Swartzieae, Caesalpinioideae, Papilionoideae, and wood in general. Characters such as intervascular pit size are less affected by environmental conditions, maturity of specimens, or other growth conditions. We also considered subjectivity and interpretation of character states in assigning weights. For example, there is much less subjectivity in determining exclusively uniseriate rays than axial parenchyma patterns. Gasson (2000) also noted that axial parenchyma patterns were difficult to determine and categorize in the papilionoid Leguminosae. The assigned descending weights are as follows: intervascular pit size (6), exclusive-

Table 4. Groups within Swartzieae using weighted cluster analysis.

Group 1 (6 specimens): *S. acutifolia, S. apetala* var. *apetala, S. flaemingii* var. *flaemingii, S. langsdorfii, S. multijuga.*

Group 2 (19 specimens): *S. euxylophora, S. fasciata, S. ingaefolia, S. laxiflora, S. polyphylla* (SJRw 541 19 & MADw 12588), *S. panacoco* var. *panacoco* (SJRw 49792 & BCTw 16572), *S. panacoco* var. *polyanthera* (SJRw 2927), *S. panacoco* var. *sagotii* (Uw 31632 & CTFw 23400), *Cordyla africana.*

Group 3 (2 specimens): *Mildbraediodendron excelsum.*

Group 4 (27 specimens): *S. benthamiana, S. dipetala, S. flaemingii* var. *psilonema, S. grandifolia, S. laevicarpa, S. lamellata, S. panacoco* var. *panacoco* (SJRw 12749), *S. panacoco* var. *polyanthera* (MADw 19553), *S. panacoco* var. *sagotii* (Uw 31685), *S. polyphylla* (SJRw 52623), *S. reticulata, S. schomburgkii, S. sericea, S. tessmannii, S. tomentifera, S. ulei.*

Group 5 (34 specimens): *S. arborescens, S. brachyrachis* var. *brachyrachis, S. brachyrachys* var. *colombiana, S. brachyrachis* var. *glabrata, S. brachyrachis* var. *peruviana, S. conferta, S. corrugata, S. cuspidata, S. latifolia, S. laurifolia, S. lucida, S. myrtifolia* var. *elegans, S. myrtifolia* var. *peruviana, S. myrtifolia* var. *standleyi, S. oblanceolata, S. pendula, Aldina petiolulata, Bocoa alterna, B. prouacensis, B. viridiflora.*

Group 6 (26 specimens): *S. aptera, S. argentea* var. *flavescens, S. cardiosperma, S. krukovii, S. leptopetala, S. racemosa, S. recurva, S. simplex* var. *continentalis, S. simplex* var. *grandiflora, S. simplex* var. *simplex; Candolleodendron brachystachium, Exostyles venusta, Lecointea amazonica, Zollernia paraensis.*

Group 7 (1 specimens): *Aldina insignis.*

ly uniseriate rays (5), vessel diameters (4), rays per millimetre (3), storied rays (2), aliform and banded axial parenchyma (2), number of cells per parenchyma strand (2), and a value of 1 for confluent axial parenchyma, width of axial parenchyma band, number of ray tiers per millimetre (when storied), ray height, and vessels per square millimetre. The resulting dendrogram of the weighted cluster analysis is shown in Figure 30. At first glance, it is obvious that there are at least 3 large groups (groups 1, 2 & 3; group 4; and groups 5 & 6) and the single specimen of *Aldina insignis* if we draw an imaginary horizontal line at 1. However, if we draw a line across the dendrogram slightly lower than the 3 major groups, we show 7 distinct groups. In the unweighted dendrogram 10 groups (Table 2) were shown at approximately the same level and more groups at slightly lower levels. A description of the weighted groups follows, and a list of the species in each group is in Table 4.

Group 1 (6 specimens and 5 species): This group is characterized by large intervascular pits except for medium pits in *S. multijuga*, multiseriate stoned rays that range from 11 to 14 per millimetre, mean vessel diameters 59–142 µm, 7–27 vessels per square millimetre, banded parenchyma 3 to > 4 cells wide, and 2–4 cells per axial parenchyma strand. This group is nearly similar to group 1 in both unweighted analyses (Tables 2 & 3).

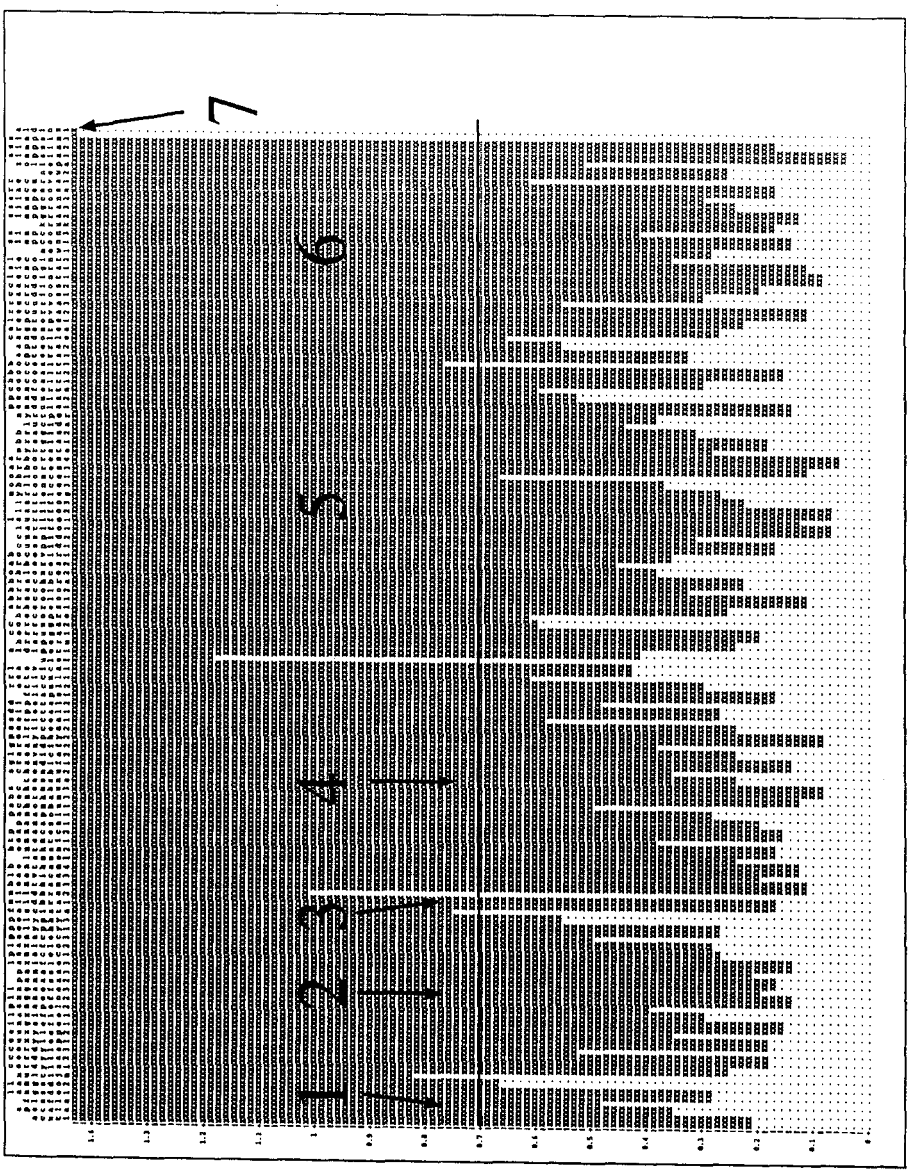

Fig. 30. Dendrogram resulting from the SAS System Average Linkage weighted Cluster Analysis showing the seven groups within Swartzieae. Specimens are listed across the top (see Table 4 for list of species in each group). Scale on left reports average linkage distance between groups and is useful only as a guide. The horizontal black line is arbitrary; if shifted up, there are few groups; if shifted down, more groups.

Group 2 (16 specimens and 8 species/varieties of *Swartzia;* 3 specimens of *Cordyla africana):* This group is characterized by large intervascular pits, multiseriate stoned rays that range from 7 to 13 per millimetre, mean vessel diameters 122–211 µm, 1–7 vessels per square millimetre, banded parenchyma mostly 3 to > 4 cells wide (1–2 cells wide in *S. euxylophora, S. fasciata,* and *S. panacoco* var. *polyanthera* (SJRw 2927)), and mostly 4 cells per axial parenchyma strand. Most of these species and specimens are found in group 4 of unweighted analysis of *Swartzia* and in groups 3 and 4 of Swartzieae. The main difference between the weighted groups 1 and 2 is vessel diameter; group 1 has smaller vessels than group 2.

Group 3 (2 specimens of *Mildbraediodendron excelsum): Mildbraediodendron* is characterized by large intervascular pits, multiseriate storied rays that are 7–9 per millimetre, a mean vessel diameter of 186 µm and 2 vessels per square millimetre, mostly aliform axial parenchyma without bands, and 4 cells per parenchyma strand. This group or genus is similar to species in group 2, but group 2 has mostly a combination of aliform, confluent, and banded parenchyma, whereas *Mildbraediodendron* only has aliform and confluent parenchyma. This grouping suggests that *Mildbraediodendron* is distinct from the main body of *Swartzia.* In addition *Cordyla* (group 2) and *Mildbraediodendron* are similar to each other (Fig. 16–19) but are easily distinguished from *Swartzia* by the shorter and broader axial parenchyma cells (Gasson 1996), heartwood colour, and the abundance of lozenge-type aliform to confluent parenchyma. In morphological (Herendeen 1995), pollen (Ferguson & Schrire 1994), and molecular (Ireland et al. 2000) cladistic studies, *Cordyla* and *Mildbraediodendron* also appear closely related. Groups 1, 2, and 3 form one of the major divisions in the dendrogram (Fig. 30).

Group 4 (27 specimens and 16 species /varieties): This large group forms the second major division in the dendrogram (Fig. 30). It is characterized by large intervascular pits, exclusively uniseriate rays that range from 10 to 16 per millimetre, mostly storied (not storied in *S. ulei* and *S. laevicarpa* (SJRw 37175)), mean vessel diameters 71–213 µm, 1–17 vessels per square millimetre, banded parenchyma mostly 3–4 cells wide (1–2cells wide in *S. laevicarpa* (SJRw 37175 & SJRw 40111l), *S. lamellata,* and *S. reticulata),* mostly 4 cells per axial parenchyma strand (mostly 2 in *S. dipetala, S. flaemingii* var. *psilonema,* and *S. reticulata).* This group is similar to the larger unweighted group 4 of Swartzieae and *Swartzia.* Species missing are mostly in the weighted group 2 and are not exclusively uniseriate. The two specimens that are not storied *(S. ulei* and *S. laevicarpa* (SJRw 37175)) seem out of place in this group. Loureiro and Rodrigues (1 975) also observed these characteristics for these two specimens. Since both specimens are from small diameter stems, it is possible that the lack of regularly storied rays was due to the absence of mature wood. Of course, it is also possible that one or both specimens are misidentified. More mature vouchered wood samples are needed to confirm this variability.

Group 5 (28 specimens and 16 species/varieties of Swartzia; 1 specimen of *Aldina petiolulata;* 5 specimens and 3 species of *Bocoa):* This group is characterized by medium intervascular pits, multiseriate rays that range from 7 to 12 per millimetre, often storied (not storied in *S. arborescens* (MADw 22692 & 31331), *S. brachyrachis* var. *glabrata, S. conferta, S. lucida, S. myrtifolia* var. *peruviana, S. myrtifolia* var. *standleyi, S. pendula, and Bocoa alterna),* mean vessel diameters 55–189 µm, 2–25 vessels per square millimetre, banded parenchyma mostly 3–4 cells wide (1–2 cells wide in *S. arborescens* (MADw 15920 & 18975), *S. brachyrachis* var. *glabrata, S. conferta, S. cuspidata* (MADw 31326), and *Bocoa prouacensis* and > 4 cells wide in *S. corrugata* (SJRw 21343)), mostly 4 cells per axial parenchyma strand. This group is similar to the unweighted group 5 of Swartzieae and group 3 of *Swartzia.* Species in this weighted group that are not in the unweighted groups are mostly those that are not storied.

The species *B. prouacensis* (Fig. 22 & 23) and *B. viridiflora* have a similar anatomy to each other and to *Swartzia,* but *B. alterna* (Fig. 20 & 21) seems out of place in the genus. It has long radial multiples, non-storied rays, exclusively heterocellular rays, and much taller rays than the other species (503–616 µm for *B. alterna* and 160–356 µm for other species). Gasson (1996), Herendeen (1995), Ferguson & Skvarla (1991), and Ireland et al. (2000) also noted differences between *B. alterna* and the other species of *Bocoa* based on wood anatomy, morphology, pollen, and molecular studies. Presently Helen Ireland (pers. comm. 2001) plans to move *B. alterna* to the genus *Trischidium,* a move we fully support.

The presence of *Bocoa prouacensis* and *Aldina petiolulata* in this group agrees with the cladistic studies of pollen (Ferguson & Schrire 1994) and morphology (Herendeen 1995) where *Aldina* and *Bocoa* occur in the same clade. However, recent molecular studies (Ireland et al. 2000) have shown that Aldina is closer to *Cordyla* and *Mildbraediodendron.*

Group 6 (20 specimens and 10 species /varieties of *Swartzia;* 1 specimen of *Candolleodendron brachystachium;* 2 specimens of Exostyles venusta; 2 specimens of *Lecointea amazonica;* 1 specimen of *Zollernia paraensis):* This group is characterized by small intervascular pits, multiseriate rays that range from 7 to 14 per millimetre, mostly storied (not stoned in *S. simplex* var. *simplex),* mean vessel diameters 48–141 µm, 4–28 vessels per square millimetre (61 per square millimetre in *Candolleodendron brachystachium),* banded parenchyma mostly 3–4 cells wide (mostly 1–2 cells wide in *S. simplex* and > 4 cells wide in *S. leptopetala),* mostly 4 cells per axial parenchyma strand (2 cells in *S. aptera* and *Candolleodendron brachystachium).* This group is similar to the unweighted group 2 of Swartzieae and group 3 of *Swartzia.* Species found in other unweighted groups include *S. aptera, S. simplex* var. *simplex,* and *Candolleodendron brachystachium.* Groups 5 and 6 form the third major divisions in the dendrogram (Fig. 30).

Exostyles venusta, Lecointea amazonica, and *Zollernia paraensis* are anatomically similar to *Swartzia.* These three species have crystals in the marginal ray cells, and *Z. paraensis* has rays that are exclusively two cells wide. These two diagnostic characters distinguish these three genera from other species of *Swartzia.* Our results sup-

port the cladistic results of Herendeen (1995) and Ireland et al. (2000), where *Exostyles, Lecointea,* and *Zollernia* appear in the same major clade.

Group 7 (1 specimen of *Aldina insignis): Aldina insignis* is characterized by medium intervascular pits, multiseriate storied rays that are 6 per millimetre, a mean vessel diameter of 274 µm and 1 vessel per square millimetre, mostly aliform axial parenchyma without bands, and 4 cells per parenchyma strand. What makes this group unique is the lack of banded parenchyma and the large vessel diameters. *Mildbraediodendron excelsum* (the only species in group 3) is the only other species in Swartzieae that lacks banded parenchyma. Both groups or species are unique and the grouping suggests that both are distinct from the main body of *Swartzia.*

Comparison to other studies

Comparing our cluster analysis with Gasson's (1996) wood cladistic analysis of the tribe Swartzieae, shows some major differences in character selection. We used intervascular pit size, vessel diameters, number of vessels per square millimetre, ray width and height, rays per millimetre, storied rays, axial parenchyma patterns, number of cells per parenchyma strand, and width of axial parenchyma band. Gasson (1996) used 12 characters and only 2 characters (parenchyma patterns and stoned ray) are the same. In addition, 7 of his 12 characters did not show any variability and thus did not contribute to his analysis. Therefore, his cladistc analysis led to completely unresolved trees.

Ferguson and Schrire (1994) split *Swartzia* into three groups for their cladistic analysis of the pollen morphology of the tribe Swartzieae. *Swartzia* A includes species with Type I pollen of Ferguson and Skvarla (1991); *Swartzia* B includes all species with Types II, III, IV, and V pollen of Ferguson and Skvarla (1991); and Swartzia M includes the two African species of *Swartzia.* Species in Swartzia A that we examined include *S. argentea* var. *flavescens* and *S. racemosa* of group 6 and *S. pendula* of group 5. However, other species in groups 5 and 6 have pollen Types II, III, IV, and V. Group 1 has three species with Type II pollen, and Group 2 has three species with Type III pollen. Ferguson and Skvarla (1991) list no other species in groups 1 and 2. Group 4 has two species with Type III pollen, one with Type II, and one with Type IV. Group 5 has two species with Type III pollen, one with Type I and one with Type V. Group 6 has two species with Type I pollen, two with Type III, one with Type IV, and one with Type V. For the most part, our wood groups are not similar to Ferguson and Schrire's (1994) grouping of Swartzia. Groups 1 and 2 only have one pollen type initially suggesting relationship between pollen and wood, but both pollen types are found in other wood groups. The other wood groups have a variety of pollen types and no trends are evident.

In his cladistic analysis of the tribe Swartzieae, Herendeen (1995) used 29 morphological characters. He split *Swartzia* into two groups based on whether the anthers were dorsifixed (Swartzia-1) or basifixed (Swartzia-2) (Herendeen, pers. comm.). For Swartzia-1 we did not examine any wood from the three species he examined *(S. macrocarpa, S. macrophylla,* and *S. parvifolia).* However, for Swartzia-2 we exam-

ined wood for all three species and all three are in group 5 *(S. elegans* [= *S. myrtifolia* var. *elegans*], *S. myrtifolia,* and *S. oblanceolata).* Herendeen (1995) examined six species and Ferguson and Skvarla (1991) several other species but both only examined *S. macrocarpa.* Without additional species for comparison, we cannot draw any conclusions from Herendeen's analysis.

Cowan's (1967) classification has some similarity to our wood groups. His section *Possira* only contains species that we place in groups 5 and 6. However, several species from groups 5 and 6 are scattered among the subsections and series of section *Swartzia.* Species in group 2 are confined to section *Swartzia* subsection *Terminales* although groups 4,5 and 6 are also represented. Section *Swartzia* subsection *Swartzia* has seven series and has representatives of groups 1, 4, 5 and 6. Series *Benthamianae* and *Orthostylae* only have species of group 4 except for one species of group 6. Series *Acutifoliae* has species of group 1 except for one specimen of *S. flaemingii* var. *psilonema* that we place in group 4. This specimen might possibly be misidentified since it was not cited by Cowan (1967) and often is not in the same group as *S. flaemingii* var. *flaemingii.* The other series contain multiple groups or have only one or two representative species.

Ireland et al. (2000) studied the molecular systematics of Swartzieae sensu Polhill (1994), including representative taxa from the tribes Sophoreae, Dipterygeae, and Dalbergieae. They show four major clades; the vataireoid, lecointeoid, aldinoid, and swartzioid clades. The vataireoid clade contains *Exostyles* and the lecointeoid clade contains *Lecointea* and *Zollernia.* In our study we found that these three genera are quite similar, but differ from the main body of *Swartzia.* The aldinoid clade contains *Aldina, Cordyla, Mildbraediodendron,* and *Amburana.* We concur that *Cordyla* and *Mildbraediodendron* are quite similar to each other and distinct from *Swartzia.* The two species (2 specimens) of *Aldina* that we examined did not fall into the same group as *Cordyla* and *Mildbraediodendron,* but the wood anatomy suggests that *Aldina* is more similar to *Cordyla* and *Mildbraediodendron* than to *Swartzia.* Although we did not include *Amburana,* our personal observations suggest that it is rightly placed in the aldinoid clade. The swartzioid clade contains *Swartzia* and *Bocoa* which we studied, and *Bobgunnia* (former African *Swartzia), Ateleia,* and *Cyathostegia,* which we have not examined. *Swartzia* and *Bocoa* are similar except for *B. alterna* , which we discussed earlier. Gasson (1994) and Gasson and Wray (2001) described *Ateleia* and *Cyathostegia,* respectively. In a recent paper Gasson (2000) states that *Swartzia* (including *Bobgunnia)* and *Ateleia* "could be more closely related than originally thought." In their paper on *Cyathostegia,* Gasson and Wray (2001) conclude that "*Ateleia, Cyathostegia, Swartzia, Bocoa,* and perhaps a few more genera could reconstitute a redefined Swartzieae."

CONCLUSIONS

The weighted cluster analysis based on wood anatomical characters shows seven distinct groups within the Brazilian species of *Swartzia* and eight other genera of the tribe Swartzieae. *Bocoa viridiflora, B. prouacensis, Candolleodendron brachysta-*

chium, *Exostyles venusta*, *Lecointea amazonica*, and *Zollernia paraensis* are similar to each other and similar to *Swartzia*. *Bocoa alterna* is different from the other two species of Bocioa and different from *Swartzia*. The wood anatomy supports the transfer of this species to the genus *Trischidium*. *Aldina*, *Cordyla* and *Mildbraediodendron* are similar to each other and *Swartzia* but differ in the abundance of lozenge-type aliform to confluent parenchyma with shorter and broader axial parenchyma cells. This supports the recent cladistic analysis, which groups these three genera together, but not closely to *Swartzia*. Our cluster analysis compares favourably to some clades within cladistic analysis using pollen and morphology. However, the species groupings of *Swartzia* using wood, pollen, and morphology must be reexamined using a large number of species and specimens. Only then can a comprehensive cladistic analysis help clarify the polyphyletic position of *Swartzia* and Swartzieae.

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APPENDIX

Wood specimens examined. Specimens in bold are cited by Cowan (1967)

Swartzia *acutifolia* Vogel var. *parvipetala* Cowan: Krukoff 2061, Brazil, NY, MADw 18904. - *S. apetala* Raddi var. *apetala:* Irwin et al. 18040, Brazil, NY, MADw 36597. - *S. aptera* A.DC.: **Pires & Cavalcante 52589,** Brazil, NY & US, MADw 22709; **Pires & Cavalcante 52616,** Brazil, NY & US, MADw 22714. - *S. arborescens* (Aubl.) Pittier: **Krukoff 5085,** Brazil, NY, MADw 18975; **LI. Williams 3873,** Peru, F, MADw 15920; **LI. Williams 3768,** Peru, F, MADw 31331; **Pires & Cavalcante 52314,** Brazil, **NY & US,** MADw 22692. - *S. argentea* Spruce ex Benth. var. *flavescens* (Suesseng.) Cowan: Amaral et al. 578, Brazil, NY, MADw 45236. - *S. benthamiana* Miq. var. *benthamiana:* Maguire 24823, Suriname, NY & U, MADw 12126; Stahel 369, Suriname, NY & U, MADw 19875; Irwin et al. 55306, Suriname, NY & US, MADw 22847; Cid s.n., Brazil, MADw 46521. - *S. brachyrachis* Harms var. *brachyrachis:* **Pires & Cavalcante 52062,** Brazil, NY & US, MADw 22671. - *S. brachyrachis* Harms var. *colombiana* Cowan: **Cuatrecasas 19947,** Colombia, F & US, MADw 17619; **Cuatrecasas 15910,** Colombia, F & US, MADw 31330. –*S. brachyrachis* Harms var. *glabrata* Cowan: **Maguire 24306,** Suriname, NY & U, MADw 11978; **A.C. Smith 2993,** Guyana, NY & U, SJRw 35768. - *S. brachyrachis* Harms var. *peruviana* Cowan: **Lao Majiin 55 & 70,** Peru, NY & US, MADw 22282. - *S. cardiosperma* Spruce ex Benth.: **Ll. Williams 14442,** Venezuela, NY & US, MADw 31329; **Krukoff 7150,** Brazil, U, SJRw 37109. - *S. conferta* Spruce ex Benth. var. *conferta:* **Wurdack & Adderley 43175,** Venezuela, NY & US, SJRw 54376. - *S. corrugata* Benth.: **Ducke 84,** Brazil, A & F, SJRw 21343; Limla & Chagas, Brazil, INPA, INPAw 1621. –*S. cuspidata* Spruce ex Benth.: **Ll Williams 14479,** Venezuela, G & US, MADw 3 1326; **Krukoff 1443,** Brazil, U, MADw 31327. - *S. dipetala* Willd. ex Vogel: **A.C. Smith 3321,** Guyana, NY & U, SJRw 35902; **A.C. Smith 2424,** Guyana, NY & U, SJRw 35551. - *S. euxylophora* Rizzini & Mattos: Mattos s.n., Brazil, SBG, BCTw 11544; Mattos s.n., Brazil, SBG, BCTw 11543. - *S. fasciata* Rizzini & Mattos; Mattos s.n., Brazil, SBG, BCTw 5466. - *S. flaemingii* Raddi var. *flaemingii:* Forest Service 2827, Brazil, MADw 13358. - *S. flaemingii* Raddi var. *psilonema* (Harms) Cowan: Pires 3574, Brazil, IAN, BCTw 15558. - *S. grandifolia* Bongard ex Benth.: British Guiana Forest Dept. 2280, Guyana, SJRw 43605; **Irwin et al. 55080,** Suriname, NY, MADw 22807. - *S. ingaefolia* Ducke: **Ducke 94,** Brazil, NY & F, SJRw 21353; INPA SF-42, Brazil, CTFw 30309; Coelho & Menezes, Brazil, BCTw 17562. - *S. krukovii* Cowan: **Krukoff 8743,** Brazil, NY, MADw 31323. - *S. laevicarpa* Amshoff. **Krukoff 7247,** Brazil, U, SJRw 37175; **Ducke 380,** Brazil, NY & US, SJRw 40111; **Irwin et al. 55555,** Suriname, NY & US, MADw 22891. - *S. lamellata* Ducke var. *lamellata:* Rodrigues & Loureiro, Brazil, INPA, INPAw 3628. - *S. langsdorfii* Raddi: Kuhlmann, Brazil, BCTw 4433; Forest Service 3589, Brazil, MADw 13 189. - *S. latifolia* Benth. var. sylvestris Cowan: **A.C. Smith 3495,** Guyana, NY & U, SJRw 35959; **A.C. Smith 3115,** Guyana, NY & U, SJRw 35810; **A.C. Smith 2431,** Guyana, NY & U, SJRw 35554. - *S. laurifolia* Benth.: **Krukoff 1411,** Brazil, NY & U, MADw 31321. –*S. laxiflora* Bongard ex Benth.: **Capucho 424,** Brazil, F, MADw 30352; **Ducke 130,** Brazil, MAD, MADw 31320; **Black 47-1140,** Brazil, NY & U, SJRw 45552. - *S. leptopetala* Benth.: **Capucho 403,** Brazil, F, MADw 3 1317. –*S. lucida* Cowan : **Krukoff 1413,** Brazil, NY & U, MADw

31314. - *S. multijuga* Vogel: Bittencourt, Brazil, BCTw 13288. - *S. myrtifolia* J.E. Smith var. *elegans* Cowan: **Irwin 2179,** Brazil, NY & US, SJRw 53077. - *S. myrtifolia* J.E. Smith var. *peruviana* Cowan: **Ll. Williams 5313,** Peru, F, MADw 15918. - *S. myrtifolia* J.E. Smith var. *standleyi* (Britt. & Rose) Cowan: **Kinloch 46,** Honduras, F, SJRw 21500. - *S. oblanceolata* Sandwith: **Capucho 545,** Brazil, F, MADw 31308; **Persuad 73,** Guyana, NY, MADw 31306; British Guiana Forest Dept. 3117, Guyana, NY, MADw 5623. - *S. panacoco* (Aubl.) Cowan var. *panacoco:* Kook 1086, Suriname, SJRw 49792; French Guiana, SJRw 12749; Jari 156, Brazil, BCTw 16572. - *S. panacoco* (Aubl.) Cowan var. *polyanthera* (Steud.) Cowan: **Stahel 25,** Suriname, MAD, MADw 19553; **Suriname Forest Bureau 24A,** Suriname, U, SJRw 2927. - *S. panacoco* (Aubl.) Cowan var. *sagotii* (Sandwith) Cowan: Fouquet 1482, Belize, Uw 31658; Fouquet 1435, Belize, Uw 31632; Thiel 222, French Guiana, CTFw 23400. - *S. pendula* Spruce ex Benth.: **Ll. Williams 1875,** Peru, F, MADw 31311; **Ll. Williams 2175,** Peru, F & US, MADw 31312. - *S. polyphylla* A.DC.: **Wurdack & Adderley 43374,** Venezuela, NY & US, SJRw 54119; **Maguire & Wurdack 42554,** Venezuela, NY & US, SJRw 52623; **Krukoff 6646,** Brazil, F & U, MADw 12588. **–** *S. racemosa* Benth. var. *racemosa:* Pires et al. 51785, Brazil, NY, MADw 21478. - *S. recurva* Poeppig: **Krukoff 8011,** Brazil, U & US, MADw 31309; **Capucho 486,** Brazil, F, MADw 31310; **Krukoff 6648,** Brazil, NY & U, MADw 12590. - *S. reticulata* Ducke: **Irwin et al. 55589,** Suriname, NY & US, MADw 22904; Rodrigues, Brazil, INPA, INPAw 2039. - *S. schomburgkii* Benth. var. *schomburgkii:* British Guiana Forest Dept. 2294, Guyana, NY & US, MADw 5624; Florschutz 3134, Suriname, Uw 11141; Schulz 8841, Suriname, Uw 6884. - *S. sericea* Vogel var. *sericea:* **Maguire et al. 41828,** Venezuela, NY & US, SJRw 52410; Prance 11605, Brazil, INPA, INPAw 4351. - *S. simplex* (Sw.) Sprengel var. *continentalis* Urban: **Cooper 650,** Panama, SJRw 12283; **Stern et al. 203,** Panama, US, SJRw 54679; **Ll. Williams 694,** Peru, F, MADw 31307. - *S. simplex* (Sw.) Sprengel var. *grandifiora* Cowan: Pittier 3800, Panama, F, MADw 4830; Serviço Florestal, Brazil, BCTw 2527; Mattos Filho s.n., Brazil, JBRJ, BCTw 18236. - *S. simplex* (Sw.) Sprengel var. *simplex:* **Ll. Williams 5295,** Peru, F, MADw 31302; **Ll. Williams 6550,** Peru, F, MADw 31303; **LI. Williams 4017,** Peru, F, MADw 31304. - *S. tessmannii* Harms: Lima et al. 2768, Brazil, NY & INPA, MADw 46437. - *S. tomentifera* (Ducke) Ducke: **Krukoff 6882,** Brazil, NY, MADw 12711. - *S. ulei* Harms, INPA, Brazil, INPA, BCTw 9198.

Aldina *insignis* (Benth.) End.: British Guiana Forest Dept, Guyana, MADw 1012. **–** *A. petiolulata* Cowan: Maguire & Wurdack 42555, Venezuela, NY, SJRw 52624.

Bocoa *alterna* Benth.: A.C. Smith 2772, Guyana, U, SJRw 35695; Krukoff 7944, Brazil, NY, MADw 31334; Zarucchi et al. 2850, Brazil, NY & INPA, MADw 46482. - *B. prouacensis* Aubl.: Stahel 69, Suriname, U, MADw 19596. - *B. viridiflora* Ducke: Ducke 185, Brazil, INPA, SJRw 23647.

Candolleodendron *brachystachium* (DC.) Cowan: Oldeman 2297, French Guiana, NY.

Cordyla *africana Lour.:* Schlieben 366, Tanganyika, B, SJRw 29961; Dept. of Forests, Rhodesia, SJRw 47353; Lab. Hist. Tecn. Maderas, Guinea, SJRw 49830.

Exostyles *venusta* Sprengel: Mattos Filho s.n., Brazil, JBRJ, BCTw 13301; Andrade Lima s.n., Brazil, BCTw 13328.

Lecointea *amazonica* Ducke: Ducke 30, Brazil, INPA, SJRw 20711; Standley, Honduras, SJRw 16174.

Mildbraediodendron *excelsum* Harms: FHOw 8284, Uganda, SJRw 32110; Inst. Nat. Agronomique, Belgian Congo, MADw 17296.

Zollernia *paraensis* Huber: Brazil SJRw 5952.