



A survey of wood anatomical characters in the tribe Crotalariaeae (Fabaceae)



A.A. Oskolski^{a,b,*}, A.V. Stepanova^{a,b}, J.S. Boatwright^c, P.M. Tilney^a, B.-E. Van Wyk^a

^a Department of Botany and Plant Biotechnology, University of Johannesburg, P.O. Box 524, Auckland Park 2006, Johannesburg, South Africa

^b Komarov Botanical Institute of the Russian Academy of Science, Prof. Popov Str. 2, 197376 St. Petersburg, Russia

^c Department of Biodiversity and Conservation Biology, University of the Western Cape, Modderdam Road, 7535 Bellville, South Africa

ARTICLE INFO

Article history:

Received 19 January 2014

Received in revised form 9 June 2014

Accepted 10 June 2014

Available online 12 July 2014

Edited by JC Manning

Keywords:

Crotalariaeae

Fabaceae

Fynbos

Grouped vessels

Helical thickenings

Shrubs

Wood anatomy

ABSTRACT

Wood anatomical data is presented for 29 southern African shrubby species representing eight genera (*Aspalathus*, *Calobota*, *Crotalaria*, *Leobordea*, *Lotononis*, *Rafnia*, *Wiborgia*, *Wiborgiella*) of the predominantly African tribe Crotalariaeae (Fabaceae). The taxa examined share short vessel elements, exclusively simple perforation plates and vested intervessel pits, i.e. the wood traits that are typical for many other genera of Papilionoideae. The loss of helical thickenings may be considered as a synapomorphy for Crotalariaeae, with a reversal to this character state within *Lotononis*. Generally, the pattern of wood structure diversity within the Crotalariaeae is related more to the growth habits of the plants and probably to environmental factors than to their taxonomy or phylogenetic relationships. All genera (except *Crotalaria*) and practically all species studied showed diagonal to dendritic arrangement of vessel groups, up to their fusion into large dendritic aggregations in *Calobota* species from arid (non-fynbos) regions. Some species from karroid scrubs (*Calobota angustifolia*, *Calobota cytisoides*) and fynbos (*Aspalathus excelsa*, *Aspalathus linearis*, *Aspalathus nigra*) show no dendritic vessel pattern, however. The banded axial parenchyma appears independently in three lineages of Crotalariaeae, i.e. in *Aspalathus* + *Wiborgia* + *Wiborgiella*, *Rafnia*, and in crown species of *Calobota*. *Lotononis* s.str. and *Leobordea* show unbranched or weakly branched coarse vestures in their intervessel pits, whereas other taxa examined share the presence of vestures, appearing as strongly branched fine protuberances. Micromorphological characters of vested intervessel pits are likely to be useful for the systematics of Crotalariaeae.

© 2014 SAAB. Published by Elsevier B.V. All rights reserved.

1. Introduction

The tribe Crotalariaeae comprises 16 genera and 1227 species of papilionoid shrubs and herbs. Known for its intricate generic relationships and high incidence of convergent morphological patterns, the group is subendemic to the African continent with the majority of genera and species confined to the Cape Floristic Region of South Africa (Van Wyk and Schutte, 1995; Van Wyk, 2005). Morphological, chemotaxonomic and cytological studies over the last three decades have resulted not only in several taxonomic revisions of genera but also in a much better understanding of tribal and generic circumscriptions. Further insights into phylogenetic relationships resulted from molecular systematic studies (Boatwright et al., 2008a), which showed the need for some modifications to the classification system.

Currently the tribe includes *Aspalathus* L. [282 species endemic to South Africa (Dahlgren, 1988)]; *Bolusia* Benth. [6 species endemic to south tropical Africa (Van Wyk et al., 2010)]; *Calobota* Eckl. & Zeyh. [16 species – 15 in southern Africa and one in North Africa

(Boatwright et al., 2009)]; *Crotalaria* L. [702 species worldwide in tropical regions, with 497 species endemic to Africa (Polhill, 1968, 1982; Le Roux et al., 2013; Le Roux and Van Wyk, 2013)]; *Euchlora* Eckl. & Zeyh. [one species endemic to the Cape region (Boatwright et al., 2011)]; *Ezoloba* B.-E.van Wyk & Boatwr. [1 species endemic to the Cape region (Boatwright et al., 2011)]; *Lebeckia* Thunb. [14 species endemic to the Cape region (Le Roux and Van Wyk, 2007, 2008, 2009)]; *Leobordea* Del. [51 species, with 45 in sub-Saharan Africa and the remainder in North Africa and Europe to Pakistan (Van Wyk, 1991; Boatwright et al., 2011)]; *Listia* E.Mey. [7 species in south tropical Africa (Van Wyk, 1991; Boatwright et al., 2011)]; *Lotononis* (DC.) Eckl. & Zeyh. [91 species, all in sub-Saharan Africa but mostly southern Africa (Van Wyk, 1991; Boatwright et al., 2011)]; *Pearsonia* Dümmer [13 species – 12 in Africa and one on Madagascar (Polhill, 1974)]; *Rafnia* Thunb. [20 species, all endemic to the Cape region (Campbell and Van Wyk, 2001)]; *Robynsiophyton* R. Wilczek [one species in tropical Africa (Boatwright and Van Wyk, 2009)]; *Rothia* Pers. [two species – one in Africa and one widespread in Asia to Australia (Boatwright et al., 2008b)]; *Wiborgia* Thunb. [10 species, all endemic to the Cape region (Dahlgren, 1975; Boatwright et al., 2009)] and *Wiborgiella* Boatwr. & B.-E.van Wyk [10 species, all endemic to the Cape region (Boatwright et al., 2009)].

* Corresponding author at: Komarov Botanical Institute of the Russian Academy of Science, Prof. Popov Str. 2, 197376 St. Petersburg, Russia.
E-mail address: aoskolski@gmail.com (A.A. Oskolski).

In the Leguminosae, systematic wood anatomy has thus far focussed mostly on trees (e.g. Baretta-Kuipers, 1981) but studies of the tribe Podalyrieae (closely related to Crotalariaeae) included several shrubby members and showed that taxonomically useful information may be obtained (Van Wyk and Schutte, 1995; Schutte and Van Wyk, 1998; Stepanova et al., 2013). The wood structure of the tribe Crotalariaeae has remained unstudied and undescribed despite the potential value of wood anatomical data in exploring the phylogenetic and systematic relationships of legumes. Crotalariaeae genera with at least some woody members (i.e. shrubs or shrublets with perennial branches) include *Aspalathus*, *Calobota*, *Leobordea*, *Lotononis*, *Pearsonia*, *Rafnia*, *Wiborgia* and *Wiborgiella*, while the remaining genera (*Bolusia*, *Euchlora*, *Ezoloba*, *Lebeckia*, *Robynsiophyton* and *Rothia*) comprise annuals and/or perennial herbs with short-lived above-ground parts.

This exploratory paper evaluates, for the first time, the taxonomic value of wood anatomy in the tribe Crotalariaeae. The aim was not only to provide high quality data for comparisons at tribal level but also to consider the feasibility of more detailed studies within and amongst some of the closely related genera.

2. Material and methods

A total of 35 wood specimens were examined, representing 29 different species. Most of the samples were collected by the second and third authors during field studies in South Africa in 2006–2009. Voucher specimens are deposited at JRAU, and various other institutions (Table 1). The samples were taken mostly from stems with a secondary xylem radius of more than 5 mm, so that the wood structure may be considered mature. General vegetation types were based on personal observations, labels from herbarium specimens (whenever available) or on regional floristic accounts for South Africa (Goldblatt and Manning, 2000; Manning and Goldblatt, 2012).

Evolutionary pathways for wood anatomical features were reconstructed by mapping their character states on a subsample of the majority-rule consensus tree recovered from the parsimony and Bayesian analyses of a data set combining two nuclear markers (*nrITS* and *rbCL*) for species of Crotalariaeae (Boatwright et al., 2011). Character optimization along tree branches was visualized using the parsimony

Table 1
Material of the tribe Crotalariaeae used for wood anatomical studies. Voucher specimen abbreviations: AS = A. Stepanova; ALS = A. Schutte; BEVW = B.-E. Van Wyk; JSB = J.S. Boatwright; KK = E.L. Kotina; TP = T. Phago. Abbreviations for provinces: EC = Eastern Cape Province; FS = Free State Province; GA = Gauteng Province; KZN = KwaZulu-Natal Province; LIM = Limpopo Province; MP = Mpumalanga Province; NC = Northern Cape Province; WC = Western Cape Province.

Genera, species and samples	Voucher specimens (all in JRAU)	Locality	Habitat
<i>Aspalathus</i> L.			
<i>A. excelsa</i> R.Dahlgren	AS & BEVW 168	Caledon district, WC	Fynbos
<i>A. linearis</i> (Burm.f.) R.Dahlgren (grey form)	KK 48-11	Elandskloof, Citrusdal, WC	Fynbos
<i>A. linearis</i> (Burm.f.) R.Dahlgren (commercial form)	KK 50-11	Aggenbagskraal, Citrusdal, WC	Fynbos (cultivated)
<i>A. linearis</i> (Burm.f.) R.Dahlgren (black form)	KK 51-11	Aggenbagskraal, Citrusdal, WC	Fynbos
<i>A. linearis</i> (Burm.f.) R.Dahlgren (prostrate form)	KK 56-11	Pakhuis Pass, Clanwilliam, WC	Fynbos
<i>A. nigra</i> L.	AS & BEVW 167	Caledon district, WC	Fynbos
<i>A. nivea</i> Thunb.	KK 45-11	Gamtoos River, WC	Renosterveld
<i>A. vulnerans</i> Thunb.	KK 49-11	Elandskloof, Citrusdal, WC	Fynbos
<i>Calobota</i> Eckl. & Zeyh.			
<i>C. cinerea</i> (E.Mey.) Boatwr. & B.-E.van Wyk	JSB et al. 150	Between Steinkopf and Port Nolloth, NC	Succulent karoo
<i>C. cinerea</i> (E.Mey.) Boatwr. & B.-E.van Wyk	JSB et al. 138	Clanwilliam, WC	Succulent karoo (dunes)
<i>C. cuspidata</i> (Burch.) Boatwr. & B.-E.van Wyk	BEVW 2534	Griekwastad, NC	Nama karoo
<i>C. cytisoides</i> Eckl. & Zeyh.	JSB et al. 114	WC	Renosterveld
<i>C. lotononoides</i> (Schltr.) Boatwr. & B.-E.van Wyk	JSB et al. 142	Roodeheuwel Farm, Hondeklipbaai, NC	Succulent karoo (dunes)
<i>C. psiloloba</i> (E.Mey.) Boatwr. & B.-E.van Wyk	JSB et al. 107	Redhouse, Port Elizabeth, EC	
<i>C. pungens</i> (Thunb.) Boatwr. & B.-E.van Wyk	JSB et al. 106	Meiringspoort, Oudtshoorn, WC	Nama karoo
<i>C. thunbergii</i> Boatwr. & B.-E. van Wyk	JSB et al. 151	NC	Renosterveld
<i>C. sericea</i> (Aiton) Boatwr. & B.E.van Wyk	JSB 138	WC	Succulent karoo
<i>C. spinescens</i> (Harv.) Boatwr. & B.-E. van Wyk	JSB et al. 158	Between Springbok and Pofadder, NC	Nama karoo
<i>C. spinescens</i> (Harv.) Boatwr. & B.-E.van Wyk	BEVW 2849	39 km north of Britstown, NC	Nama karoo
<i>Crotalaria</i> L.			
<i>C. agatiflora</i> Schweinf.	TP s.n.	Colbyn, Pretoria (naturalised), GA	–
<i>C. capensis</i> Jacq.	KK 40-11	Bushman's River, Alexandria, EC	Subtropical thicket
<i>C. pallida</i> Aiton	BEVW 5883	St. Lucia, KZN	Coastal dunes
<i>Leobordea</i> Del.			
<i>L. adpressa</i> (N.E.Br.) B.-E.van Wyk & Boatwr.	BEVW 1916	Clarens, FS	Grassland
<i>L. decumbens</i> (Thunb.) B.-E.van Wyk & Boatwr.	BEVW 2508	Volksrust, MP	Grassland
<i>L. mollis</i> (E.Mey.) B.-E.van Wyk & Boatwr.	BEVW 3105	Kamiesberg, NC	Renosterveld
<i>Lotononis</i> (DC.) Eckl. & Zeyh.			
<i>L. divaricata</i> (Eckl. & Zeyh.) Benth.	BEVW s.n.	Cradock, EC	Arid grassland
<i>L. rigida</i> (E.Mey.) Benth.	ALS & BEVW 165	Worcester, WC	Renosterveld
<i>L. sericophylla</i> Benth.	KK 36-11	Clarens, FS	Grassland
<i>Rafnia</i> Thunb.			
<i>R. amplexicaulis</i> Thunb.	KK 55-11	Pakhuis Pass, Clanwilliam, WC	Fynbos
<i>R. angulata</i> Thunb. ssp. <i>angulata</i>	KK 59-11	Gifberg, WC	Fynbos
<i>Wiborgia</i> Thunb.			
<i>W. monoptera</i> E.Mey.	JSB et al. 152	Kamiesberg, NC	Renosterveld
<i>W. obcordata</i> (P.J. Bergius) Thunb.	KK 52-11	Aggenbagskraal, Citrusdal, WC	Fynbos
<i>Wiborgiella</i> Boatwr. & B.-E.van Wyk			
<i>W. bowiana</i> (Benth.) Boatwr. & B.-E.van Wyk	BEVW 2106	Bredasdorp, WC	Renosterveld
<i>W. leipoldtiana</i> Boatwr. & B.-E. van Wyk	JSB et al. 123	Oorlogskloof, Nieuwoudtville, NC	Renosterveld

Table 2

Wood anatomical characters of the Crotalariaeae. 1: radius of wood sample (mm). 2: length of vessel elements (average/min–max, μm). 3: vessel frequency (per mm^2). 4: tangential diameter of vessels (average/min–max, μm). 5: average and the greatest number of vessels in a vessel group. 6: solitary vessels (%). 7: average length of libriform fibres (average/min–max, μm). 8: fibre to vessel element length ratio. 9: vertical size of intervessel pits (average/min–max, μm). 10: width of multiseriate rays (average and max, μm). 11: width of multiseriate rays (maximum, cells). 12: height of multiseriate rays (average and max, μm). 13: number of multiseriate rays per 1 mm. 15: number of uniseriate rays per 1 mm. 15: total number of rays per 1 mm. Voucher specimen numbers are abbreviated as in Table 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Aspalathus excelsa</i> AS + BEVV 168	3	250 ± 38.5 66–788	83.0	24 ± 2.6 13.1–48	2.5/9	15	680 ± 20.7 418–860	2.7	4.2 ± 0.11 3.0–5.3	53/75	4	392/750	4.6	1.8	6.4
<i>Aspalathus linearis</i> KK-48	6	117 ± 4.1 70–165	208.7	22 ± 1.4 9.9–38	11.2/38	6	573 ± 17.1 390–732	4.9	3.9 ± 0.11 3.0–5.0	45/88	10	392/675	7.8	4.6	12.4
<i>Aspalathus linearis</i> KK-50	7	138 ± 6.2 74–253	44.2	15 ± 1.8 4.8–43	5.8/19	10	647 ± 18.5 454–819	4.7	3.1 ± 0.09 2.4–3.9	58/99	10	427/1665	6.2	5.2	11.4
<i>Aspalathus linearis</i> KK-51	5	147 ± 5.1 81–195	437.9	27 ± 2.7 8.8–67	8.5/35	2	609 ± 19.7 442–823	4.1	3.8 ± 0.45 2.9–4.6	50/84	10	818/1710	9.0	3.5	12.5
<i>Aspalathus linearis</i> KK-56	6	109 ± 3.9 67–147	118.8	22 ± 2.5 9.0–57	4.8/20	22	679 ± 18.2 119–537	6.2	3.9 ± 0.11 2.8–5.2	159/493	18	1295/2860	6.2	4.1	10.3
<i>Aspalathus nivea</i> KK 45-11	5	284 ± 7.7 215–356	60.0	35 ± 3.2 15.2–69	3.0/12	11	1063 ± 39.5 742–1437	3.7	3.6 ± 0.10 3.0–4.6	47/80	5	290/690	5.7	3.2	8.9
<i>Aspalathus nigra</i> AS + BEVV 167	3	125 ± 5.7 71–176	266.0	11 ± 0.8 5.3–19	4.3/31	9	432 ± 16.5 270–624	3.5	3.1 ± 0.08 2.3–4.0	18/24	4	255/600	11.3	9.2	20.5
<i>Aspalathus vulnerans</i> KK 49-11	9	140 ± 6.7 73–239	122.0	24 ± 2.7 6.1–65	3.1/11	10	494 ± 17.4 296–665	3.5	4.4 ± 0.11 3.1–5.5	45/68	4	307/830	3.9	2.9	6.8
<i>Calobota cinerea</i> JSB 136	4	117 ± 4.2 79–173	82.9	32 ± 1.8 20–55	2.1/11	20	491 ± 17.1 205–705	4.2	3.1 ± 0.12 2.5–4.2	40/57	4	456/1490	4.2	1.7	5.9
<i>Calobota cinerea</i> JSB 150	3	117 ± 4.6 65–193	113.7	27 ± 1.4 16–46	2.2/15	25	496 ± 15.0 325–664	4.2	4.7 ± 0.14 3.5–5.5	30/58	4	368/720	3.6	2.2	5.8
<i>Calobota cytoides</i> JSB 114	4	153 ± 6.8 145–229	55.0	29 ± 1.5 16–45	1.7/7	32	461 ± 12.3 338–600	3.0	4.6 ± 0.14 3.4–5.5	33/44	3	353/630	3.2	0.9	4.1
<i>Calobota cuspidosa</i> BEVV 2534	4	177 ± 7.4 116–290	83.5	24 ± 1.2 13–34	2.7/16	15	622 ± 18.5 436–872	3.5	3.8 ± 0.13 3.0–4.9	40/65	4	694/1600	3.7	2.0	5.7
<i>Calobota lotonoides</i> JSB 142	2	167 ± 7.5 67–256	168.7	32 ± 2.6 13–66	4.0/29	6	660 ± 23.8 374–1062	4.0	3.7 ± 0.17 2.6–5.2	53/82	4	520/870	3.9	1.8	5.7
<i>Calobota psiloloba</i> JSB 107	3	116 ± 3.6 74–174	109.8	29 ± 2.2 12–50	2.6/19	16	501 ± 17.3 309–739	4.3	3.8 ± 0.21 2.7–6.9	43/73	8	634/1290	5.2	0.8	6.0
<i>Calobota pungens</i> JSB 106	4	143 ± 6.5 99–228	157.0	23 ± 1.8 9–40	5.5/28	7	491 ± 15.4 302–697	3.4	4.3 ± 0.17 3.1–6.1	40/63	5	381/980	3.2	0.9	4.1
<i>Calobota sericea</i> JSB 138	4	112 ± 3.5 84–176	57.2	27 ± 1.9 10–41	2.1/10	19	511 ± 12.7 348–743	4.6	3.8 ± 0.11 2.9–4.5	25/44	3	514/1280	7.6	3.6	11.2
<i>Calobota spinescens</i> JSB 158	3	155 ± 5.9 99–263	99.2	24 ± 1.3 15–40	3.0/19	11	624 ± 22.2 349–873	4.0	3.5 ± 0.11 3.0–4.8	31/56	4	616/1600	3.6	1.5	5.1
<i>Calobota spinescens</i> BEVV 2849	3	101 ± 2.6 78–128	151.2	24 ± 1.9 11–53	3.0/15	9	403 ± 12.1 248–543	4.0	3.7 ± 0.11 3.2–5.3	37/62	4	738/1380	4.2	0.7	4.9
<i>Calobota thunbergii</i> JSB 151	7	108 ± 3.1 75–143	43.5	32 ± 2.3 11–55	2.1/6	23	467 ± 13.7 307–741	4.3	4.6 ± 0.16 3.5–6.0	30/53	5	308/570	4.2	1.1	4.3
<i>Crotalaria agatiflora</i> TP s.n.	6	172 ± 6.1 128–57	199.0	58 ± 3.1 22.8–95	2.8/15	11	695 ± 30.5 435–1163	4.0	3.6 ± 0.15 2.8–4.4	27/39	4	291/520	9.6	1.8	11.4
<i>Crotalaria capensis</i> KK 40-11	5	203 ± 7.3 98–310	129.0	34 ± 3.1 10.2–71	2.6/12	14	637 ± 21.6 499–848	3.1	3.8 ± 0.07 3.2–5.1	30/52	4	424/972	5.2	3.2	8.4
<i>Crotalaria pallida</i> BEVV 5883	5	247 ± 9.6 169–361	193.0	64 ± 3.2 21.8–94	2.1/10	22	720 ± 21.3 449–1072	2.9	3.2 ± 0.11 2.5–3.9	35/45	4	834/1800	8.9	1.4	10.3
<i>Leobordea adpressa</i> BEVV 1916	4	108 ± 3.1 81–158	334.0	17 ± 0.8 8.8–26	2.9/14	11	515 ± 13.9 371–686	4.7	2.9 ± 0.14 1.8–4.1	37/63	8	426/970	7.5	3.7	11.2
<i>Leobordea decumbens</i> BEVV 2508	3	100 ± 2.7 71–143	334.0	17 ± 0.8 11.1–28	2.2/18	26	552 ± 24.7 367–926	5.5	2.5 ± 0.11 1.9–3.1	107/200	14	574/1140	6.6	1.1	7.7
<i>Leobordea mollis</i> BEVV 3105	10	102 ± 3.1 68–142	68.0	29 ± 1.9 12.2–49	3.9/21	9	595 ± 24.6 354–897	5.8	3.8 ± 0.11 2.8–5.1	54/92	14	290/470	4.8	2.7	7.5
<i>Lotononis divaricata</i> BEVV s.n.	7	123 ± 6.0 56–185	351.0	21 ± 1.4 7–43	3.0/26	15	470 ± 21.9 336–699	3.8	3.7 ± 0.12 2.4–4.6	88/147	12	882/1830	4.1	4.7	8.8
<i>Lotononis rigida</i> ALS + BEVV 165	2	153 ± 5.5 74–227	614.0	13 ± 0.6 6.1–23	5.1/26	5	612 ± 16.1 341–770	4.0	3.9 ± 0.09 3.1–4.6	9/15	2	189/490	2.8	12.3	15.1
<i>Lotononis sericophylla</i> KK 36-11	6	161 ± 8 105–304	337.0	21 ± 2.0 7–42	5.5/43	4	517 ± 16.7 285–647	3.2	3.5 ± 0.11 2.6–4.8	92/115	12	1390/3030	3.2	3.9	7.1
<i>Rafnia amplexicaulis</i> KK 55-11	7	147 ± 5.3 87–196	62.0	47 ± 3.2 19–132	2.6/11	15	744 ± 25.7 364–1040	5.1	4.0 ± 0.10 3.0–5.2	147/207	12	1061/2530	4.7	0.7	5.4
<i>Rafnia angulata</i> ssp. <i>angulata</i> KK 59-11	8	174 ± 7.3 123–312	59.5	51 ± 3.7 19.6–88	2.5/9	14	726 ± 18.9 427–1054	4.2	4.6 ± 0.11 3.3–6.0	143/243	14	1660/3470	4.7	2.0	6.7
<i>Wiborgia monaptera</i> JSB 152	3	100 ± 3.8 70–130	119.9	25 ± 0.4 5–46	3.4/21	6	342 ± 10.2 255–409	3.4	3.9 ± 0.18 2.4–5.8	26/45	4	311/600	2.7	1.0	3.7
<i>Wiborgia obcordatum</i> KK 52-11	4	123 ± 3.7 57–150	52.8	34 ± 2.9 14–92	1.9/8	25	657 ± 16.9 491–853	5.3	2.1 ± 0.10 1.8–3.0	37/48	5	364/826	6.8	2.1	8.9
<i>Wiborgiella bowieana</i> BEVV 2106	2	139 ± 4.3 98–218	158.5	24 ± 1.4 10–42	2.7/10	12	439 ± 17.4 268–768	3.1	3.8 ± 0.13 2.7–4.9	29/41	3	327/530	2.6	1.2	3.8
<i>Wiborgiella leipoldtiana</i> JSB 123	8	99 ± 2.6 81–156	218.2	26 ± 1.2 11–35	3.4/24	8	347 ± 8.8 264–511	3.8	3.7 ± 0.17 2.2–5.2	28/38	5	422/770	3.9	1.0	4.9

reconstruction method with the Character History Tracing option in the computer package Mesquite 2.0 (Maddison and Maddison, 2011).

Transverse, radial and tangential sections were made on rotary microtomes (Ernst Leitz GMBH, Wetzlar, Germany and Jung AG Heidelberg, Germany) and stained with a 1:1 alcian blue/safranin mixture (35/65, v/v). Macerations were made using Jeffrey's solution (Johansen, 1940). The method of Carlquist (1982) to soften very hard woods with ethylenediamine was used, followed by soaking in 15% glycerol in ethanol or boiling in 10% glycerol solution. Descriptive terminology follows IAWA Committee (1989).

3. Results

3.1. Wood structure

The results are summarized in Table 2 and important wood anatomical characters are shown in Figs. 1–5.

3.1.1. *Aspalathus*

Material studied: *Aspalathus linearis* [KK 48-11, KK 50-11, KK 51-11, KK 56-11], *Aspalathus excelsa* [AS + BEVV 168], *Aspalathus nivea* (KK 45-11), *Aspalathus nigra* [AS + BEVV 167], and *Aspalathus vulnerans* [KK 49-11].

Growth rings absent (*A. excelsa*) [AS 168], *A. vulnerans* (Fig. 1A), *A. linearis* [KK 51-11], and *A. nivea* (Fig. 1B), indistinctly marked by 1–5-seriate bands of marginal axial parenchyma with 1 or 2 lines of

flattened axial parenchyma strands and fibres (*A. linearis* [KK 48-11 (Fig. 1C), KK 50-11, KK 56-11 (Fig. 1D)]), or distinct, marked by differences in diameter and frequency of vessels and vascular tracheids between late- and earlywood (*A. nigra*). Wood diffuse-porous. Storied vessel elements, fusiform cells and strands of axial parenchyma occur in *A. excelsa*, *A. vulnerans* (Fig. 1F), *A. nivea* (Fig. 1G), and *A. linearis* [KK 48-11, KK 51-11, KK 56-11 (Fig. 1H)].

Vessels rounded, sometimes angular in outline, narrow to slightly wider (average tangential diameter 10–35 μm). Vessel frequency from 44 per mm^2 in *A. linearis* [KK 50-11] to 438 per mm^2 in *A. linearis* [KK 51-11]. Vessels solitary, in clusters and radial multiples of 2–4 (up to 12 in *A. nivea*), or mostly in large radial multiples in *A. linearis* [KK 56-11] and up to 31 in *A. nigra*. Vessels and vessel groups arranged in tangential rows (*A. vulnerans*), in indistinct diagonal to dendritic pattern (*A. nivea*), or show no clear arrangement in other samples. Vessel walls 2–5 μm thick in *A. nigra*, and 2–7 μm thick in other samples. Tyloses and brownish deposits in vessels in *A. excelsa*. Vascular tracheids absent.

Vessel elements (70–) 109–147 (–253) μm long in *A. excelsa*, *A. linearis* and *A. nigra*, but longer (66–) 250–284 (–788) μm in *A. vulnerans* and *A. nivea*. Perforation plates simple. Intervessel pits vestured, alternate (rarely scalariform in *A. excelsa*), small to medium [3–7 (–8) μm in vertical size], with rounded or oval margins. Vestures scanty, adjacent to the inner pit apertures in *A. linearis* [KK 50-11] (Fig. 5B), or numerous, filling the pit chambers in *A. nivea* (Fig. 5C), vary from simple and unforked warts to strongly branched fine protuberances (only

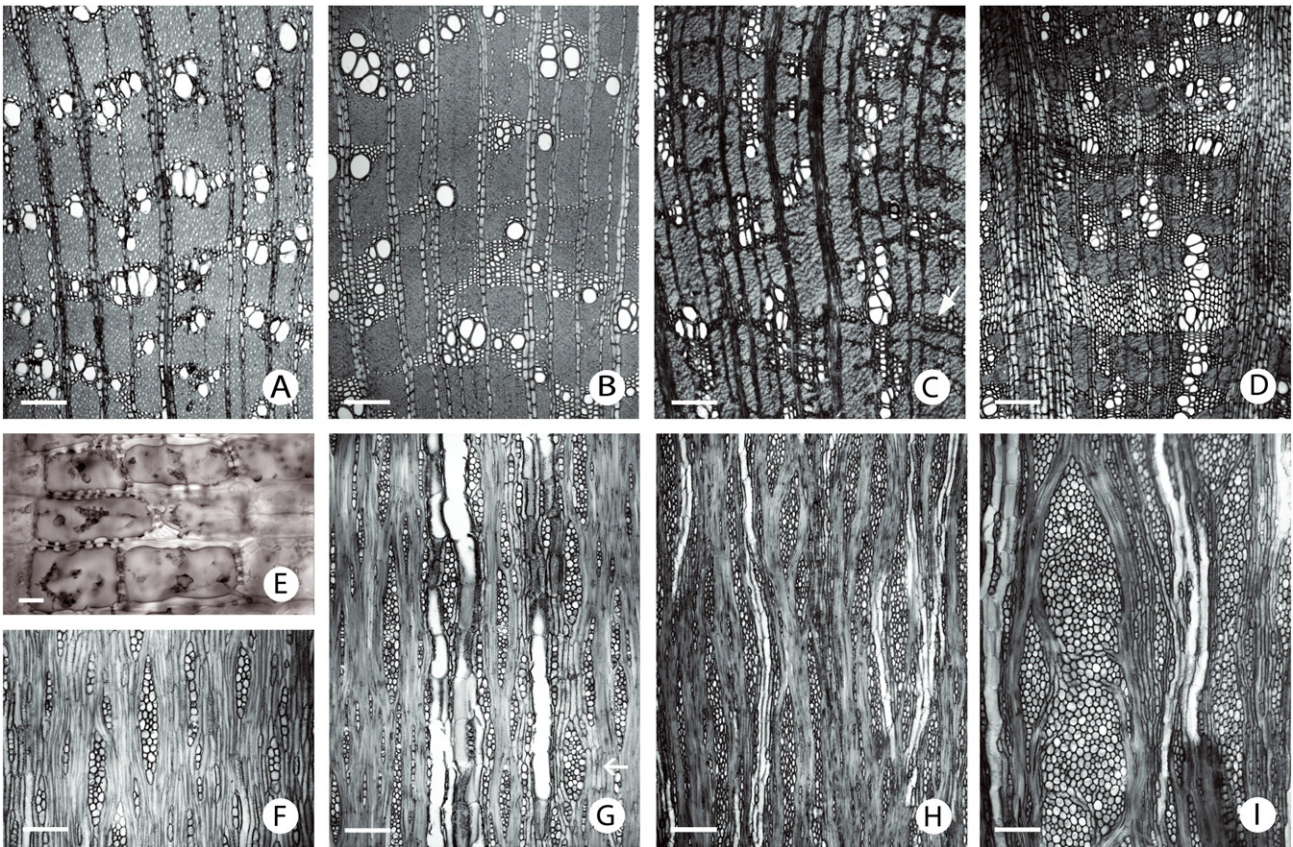


Fig. 1. Wood structure of *Aspalathus*, LM. (A) *A. vulnerans* [KK 49-11], growth rings absent, vessels arranged in tangential rows, vascentric axial parenchyma, TS; (B) *A. nivea* [KK 45-11], growth rings absent, tendency towards diagonal vessel arrangement, vascentric and confluent axial parenchyma, TS; (C) *A. linearis* [KK 48-11], upright form, indistinct growth rings bordered by marginal axial parenchyma (arrow), absence of vessel arrangement pattern, diffuse and diffuse-in-aggregates axial parenchyma, very thick-walled fibres, TS; (D) *A. linearis* [KK 56-11], decumbent form, indistinct growth rings bordered by radially-flattened fibres, very wide bands of axial parenchyma, TS; (E) *A. nigra* [AS + BEVV 167], procumbent ray cells with silica bodies, RLS; (F) *A. vulnerans* [KK 49-11], 1–5-seriate rays mostly of procumbent cells with 1–5 marginal rows of square cells, storied axial parenchyma (arrow), TLS; (G) *A. nivea* [KK 45-11], 1–4-seriate rays mostly of procumbent cells with 1 or 2 marginal rows of square cells, storied fusiform axial parenchyma (arrow), TLS; (H) *A. linearis* [KK 48-11], upright growth form, 1–8-seriate rays mostly of procumbent cells with square and upright cells in a few marginal rows and in incomplete sheaths, TLS; (I) *A. linearis* [KK 46-11], decumbent growth form, very wide (up to 18-seriate) rays mostly of procumbent cells with square and upright cells in a few marginal rows, storied fusiform axial parenchyma, TLS. Scale bars = 100 μm for A–D and F–I, 10 μm for E.

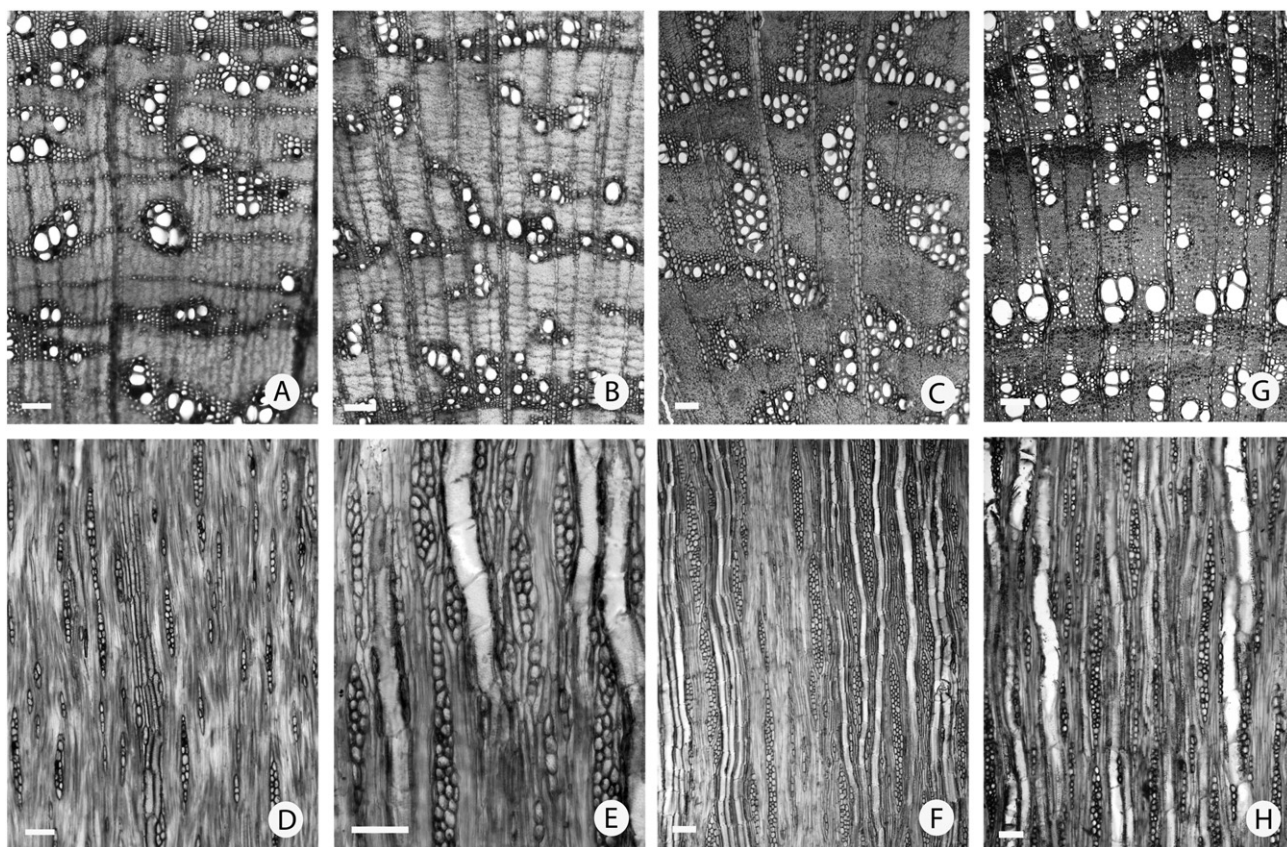


Fig. 2. Wood structure of *Calobota* and *Crotalaria*. (A) *Calobota cytisoides* [JSB 114], vessel groups scattered without a distinct pattern, vascentric, confluent and banded axial parenchyma, TS; (B) *Calobota cinerea* [JSB 136], growth rings bordered by a wide band of marginal axial parenchyma, tendency towards a diagonal vessel arrangement, vascentric and confluent axial parenchyma, TS; (C) *Calobota pungens* [JSB 106], distinct growth ring bordered by vessels, vessel groups tend to fuse into dendritic aggregations, vascentric and confluent axial parenchyma, TS; (D) *Calobota cytisoides* [JSB 114], 1–3-seriate rays mostly of procumbent cells with square cells in 1 or 2 marginal rows, storied axial parenchyma, TLS; (E) *Calobota cinerea* [JSB 136], 1–4-seriate rays of procumbent and square cells mixed throughout the ray, TLS; (F) *Calobota pungens* [JSB 106], 1–4-seriate rays mostly or exclusively of procumbent cells, storied vessel elements, TLS; (G) *Crotalaria capensis* [KK 44–11], distinct growth rings bordered by radially-flattened fibres and by differences in wall thickness, vessel groups scattered without a distinct pattern, scanty paratracheal axial parenchyma, TS; (H) *Crotalaria capensis* [KK 44–11], 1–3-seriate rays mostly of procumbent cells, sometimes with a few marginal rows of square cells, TLS. Scale bars = 200 μ m.

A. linearis [KK 50–11] and *A. nivea* were examined by SEM). Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, narrow to distinctly bordered. Helical thickenings absent throughout the genus.

Fibres libriform, non-septate, mostly moderately thick-walled (*A. vulnerans*), moderately to very thick-walled (*A. nivea*, *A. nigra*), or mostly thick-walled, fibre walls 2–6 μ m thick, with simple to minutely bordered pits. Gelatinous fibre walls occur in all species except *A. vulnerans*.

Axial parenchyma mostly fusiform, rarely in strands of 2–3 cells, vascentric, aliform to confluent, in complete (rarely incomplete) 1–3-seriate sheaths near vessels (Fig. 1A), banded in interrupted 1–3-seriate [*A. nivea* (Fig. 2)] to 1–5-seriate (*A. excelsa*, *A. linearis* [KK 48–11 (Fig. 3), KK 50–11, KK 51–11]) and 1–8-seriate (*A. linearis* [KK 56–11] (Fig. 1D)) bands, or in 1–5-seriate marginal bands (*A. vulnerans*, *A. linearis* [KK 48–11, KK 50–11, KK 56–11]), and diffuse (diffuse-in-aggregates in *A. linearis* [KK 48–11] (Fig. 1C)).

Rays 1–3(4)-seriate in *A. excelsa*, *A. nivea* (Fig. 1G) and *A. nigra*, up to 5-seriate in *A. vulnerans* (Fig. 1F), and distinctly wider in *A. linearis* (up to 10-seriate in KK 48–11 (Fig. 1H), KK 50–11, KK 51–11, and up to 18-seriate in KK 56–11 (Fig. 1I)), of procumbent and square cells mixed throughout the ray (*A. nigra*), or mostly of procumbent cells with square and upright cells in 1–3 (7) marginal rows or as solitary sheath cells in other species (incomplete sheaths occur in *A. excelsa*, *A. linearis* [KK 48–11, KK 50–11, KK 51–11]). Uniseriate rays mostly of procumbent and square cells. Crystals

absent. Silica bodies occur in ray and axial parenchyma cells of *A. nigra* (Fig. 1E) and *A. vulnerans*.

3.1.2. *Calobota*

Material studied: *Calobota angustifolia* [JSB 138], *Calobota cinerea* [JSB 136; JSB 150], *Calobota cytisoides* [JSB 114], *Calobota lotononoides* [JSB 142], *Calobota sericea* [JSB 151], *Calobota spinescens* [JSB 158; BEVV 2849], *Calobota cuspidosa* [BEVV 2534], *Calobota psiloloba* [JSB 107] and *Calobota pungens* [JSB 106].

Growth rings distinct, marked by tangential bands of marginal parenchyma [*C. cuspidosa*, *C. cytisoides* (Fig. 2A), *C. sericea*, *C. angustifolia*, *C. cinerea* (Fig. 2B), *C. spinescens*], by differences in frequency of vessels in early- and late wood (*C. cinerea*, *C. cuspidosa*, *C. lotononoides*, *C. psiloloba*, *C. spinescens*), by vessel arrangement [*C. cinerea*, *C. cuspidosa*, *C. cytisoides*, *C. pungens* (Fig. 2C), *C. sericea*, *C. lotononoides*, *C. spinescens*, *C. psiloloba*] and also rows of radially-flattened fibres (*C. cuspidosa*). Wood diffuse-porous (*C. angustifolia*, *C. cinerea* [JSB 150], *Calobota cytisoides*), or tending to be semi-ring-porous in all other species examined. Storied vessel elements, fusiform cells and strands of axial parenchyma occur in *C. cytisoides* (Fig. 2D), *C. lotononoides*, *C. psiloloba*, *C. pungens* (Fig. 2F) and *C. spinescens*.

Vessels rounded, sometimes angular in outline, narrow to slightly wider (average tangential diameter 22–33 μ m). Vessel frequency from 43 per mm² in *C. sericea* to 169 per mm² in *C. lotononoides*. Vessels solitary, in clusters and radial multiples of 2–8 (–15) (mostly in radial multiples in *C. cinerea*), or mostly in large aggregations in *C. cuspidosa*,

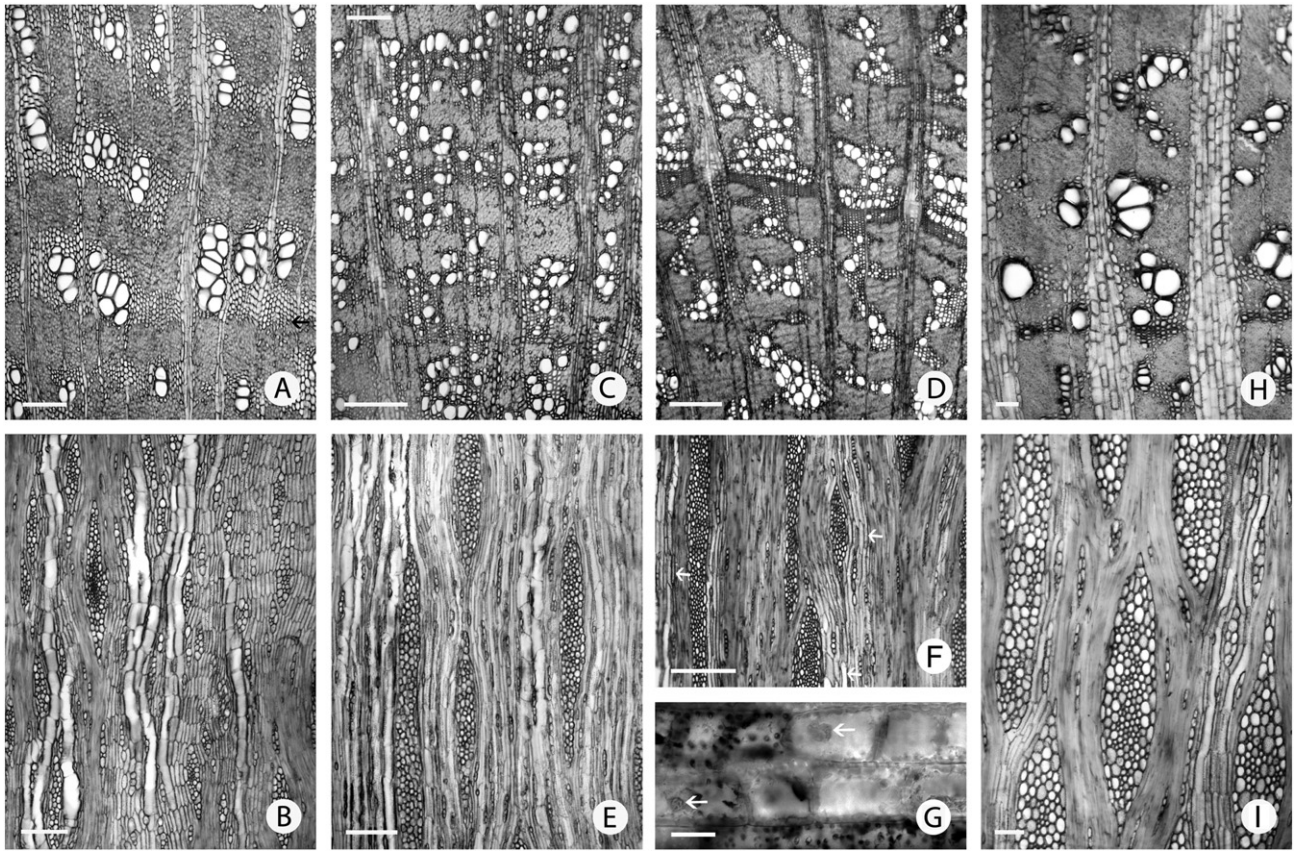


Fig. 3. Wood structure of *Leobordea*, *Lotononis* and *Rafnia*. (A) *Leobordea mollis* [BEVW 3105], growth ring (arrow) bordered by a wide band of marginal axial parenchyma, vessel groups tend to be arranged in diagonal rows, abundant confluent axial parenchyma, TS; (B) *Leobordea mollis* [BEVW 3105], 1–10-seriate rays of procumbent cells with square and upright cells in 1–4 marginal rows and in incomplete sheaths, storied axial parenchyma, TLS; (C) *Lotononis divaricata* [BEVW, s.n.], growth rings absent, diagonal to dendritic pattern of vessel arrangement, vascentric and confluent axial parenchyma, TS; (D) *Lotononis sericophylla* [KK 36-11], growth ring bordered by radially-flattened vessels, vascular tracheids and axial parenchyma cells, diagonal to dendritic pattern of vessel arrangement, vascentric and confluent axial parenchyma, TS; (E) *Lotononis divaricata* [BEVW, s.n.], 1–8-seriate rays of procumbent cells with square and upright cells in 1–3 marginal rows and in incomplete sheaths, storied vessel elements (arrows), TS; (F) *Lotononis sericophylla* [KK 36-11], uniseriate and 5–12-seriate rays of procumbent cells with square and upright cells in 1–3 marginal rows and in incomplete sheaths, storied vessel elements (arrows), TS; (G) *Lotononis sericophylla* [KK 36-11], silica bodies (arrows) in ray cells, RLS; (H) *Rafnia amplexicaulis* [KK 55-11], growth ring marked by band of axial parenchyma and by differences in vessel size, vascentric and unilaterally paratracheal axial parenchyma, TS; (I) *Rafnia amplexicaulis* [KK 55-11], 1–4-seriate and 8–11-seriate rays of procumbent cells with square and upright cells in 1 or 2 marginal rows, storied vessel elements, TLS. Scale bars = 200 μm for A–F, 100 μm for H–I, 20 μm for G.

C. lotononoides, *C. pungens* and *C. spinescens*. Vessels and vessel groups arranged in diagonal or dendritic pattern in *C. cinerea* (Fig. 2B), *C. sericea*, up to continuous diagonal to dendritic aggregations (*C. cuspidosa*, *C. lotononoides*, *C. psiloloba*, *C. pungens* (Fig. 2C), *C. spinescens*). Vessel walls 3–8 μm thick. Tyloses occur in *C. cytisoides* and *C. sericea*. Vascular tracheids absent.

Vessel elements (65–)99–177 (–290) μm long. Perforation plates simple. Intervessel pits vestured, alternate (rarely opposite in *C. pungens*) and small, 3–6 (–7) μm in vertical length with rounded or oval margins, becoming scalariform in some vessels of *Calobota pauciflora*. Vestures in *C. cuspidosa* (Fig. 5D) rather numerous, adjacent to the inner pit apertures, vary from simple and unforked warts to strongly branched fine

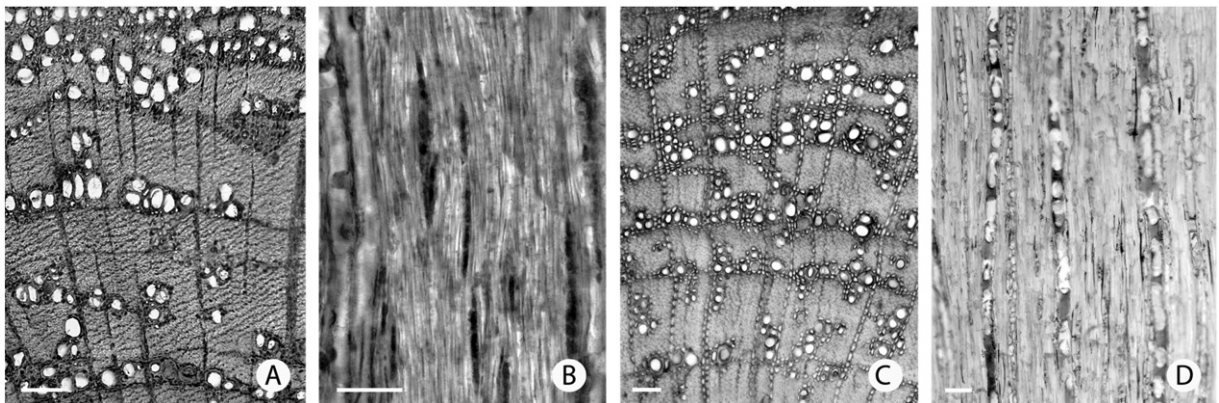


Fig. 4. Wood structure of *Wiborgia* and *Wiborgiella*. (A) *Wiborgia monopectera* [JSB 152], growth rings marked by lines of marginal axial parenchyma and by the vessel arrangement, vessel groups tend to be arranged in a diagonal pattern, vascentric and banded axial parenchyma, TS; (B) *Wiborgia monopectera* [JSB 152], 1–3-seriate rays of upright and square cells, TLS; (C) *Wiborgiella bowieana* [BEVW 2106], growth rings marked by lines of marginal axial parenchyma and by the vessel arrangement, vascentric axial parenchyma, TS; (D) *Wiborgiella bowieana* [BEVW 2106], 1–3-seriate rays of square and procumbent cells with a few rows of upright cells, TLS. Scale bars = 100 μm .

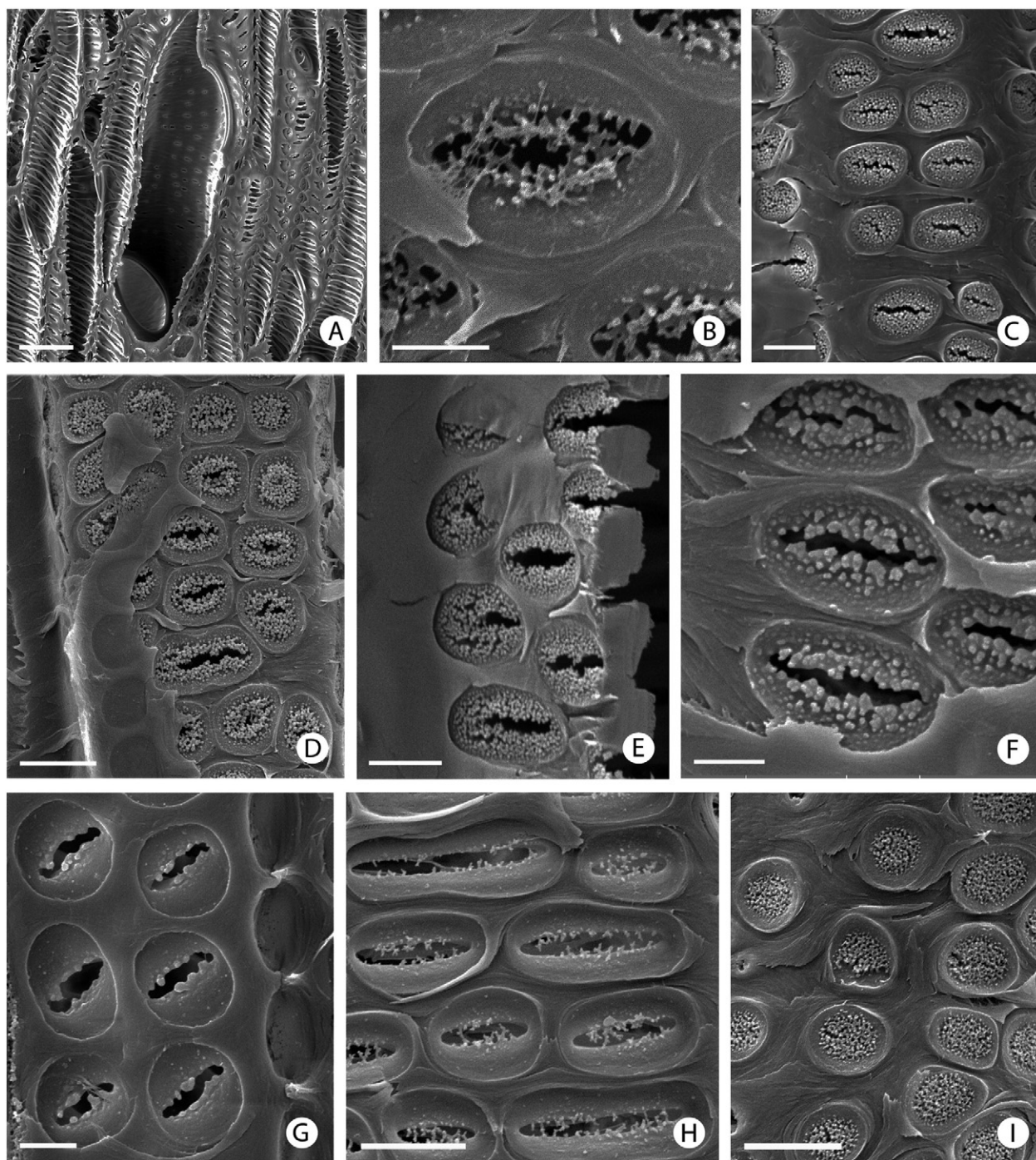


Fig. 5. Wood structural details in selected species of Crotalariaeae, SEM. (A) *Lotononis sericophylla* [KK 36-11], simple perforation plate, alternate intervessel pitting, helical thickenings in narrow vessels, RLS. (B)–(I) Vested interessel pits; (B) *Aspalathus linearis* [KK 50-11], vestures appear as scanty simple warts and branched fine protuberances near the inner pit aperture; (C) *Aspalathus nivea* [KK 45-11], pit chambers filled by vestures appearing as strongly branched fine protuberances; (D) *Calobota cuspidosa* [BEVV 2534], rather numerous vestures appearing as simple warts and strongly branched fine protuberances near the inner pit apertures; (E) *Crotalaria capensis* [KK 44-11], pit chambers filled by vestures appearing as strongly branched fine protuberances; (F) *Leobordea decumbens* [BEVV 2508], rather numerous vestures appearing as simple warts and weakly branched coarse protuberances near the inner pit apertures; (G) *Lotononis sericophylla* [KK 36-11], few vestures appearing as simple warts on the edges of the inner pit apertures; (H) *Rafnia angulata* ssp. *angulata* [KK 59-11], few vestures appearing as tiny, fine, strongly branched protuberances on the edges of the inner pit apertures; (I) *Wiborgia obcordatum* [KK 52-11], rather numerous vestures appearing as simple warts and strongly branched fine protuberances near the inner pit apertures. Scale bars = 2 μm for B, F, G; 5 μm for C, D, E, H, I; 20 μm for A. Note: the mouth-like gaps in C, D and E are apparently artefacts that result from the splitting apart of the vestures due to charging effects under electron beam.

protuberances (only *C. cuspidosa* was examined by SEM). Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, narrow-bordered. Helical thickenings absent.

Fibres libriform, non-septate, very thick-walled, thin to moderately thick-walled in *C. cytisoides*, *C. cuspidosa* and *C. spinescens*; fibre walls 1.5–6.0 (–8.0) μm, with simple to minutely bordered pits.

Axial parenchyma mostly fusiform, sometimes in strands of 2 cells, vasicentric, in complete (rarely incomplete) sheaths near vessels 1–3 (up to 9) cells wide, sometimes confluent [*C. angustifolia*, *C. cytisoides* (Fig. 2A), *C. psiloloba*, *C. pungens* (Fig. 2C)], banded in 1–3-seriate lines (*C. lotononoides*, *C. spinescens*) and also in 2–5-seriate bands (up to 12-seriate in *C. cytisoides* (Fig. 2A) and *C. sericea*), and diffuse (occasionally

diffuse-in-aggregates in *C. angustifolia*, *C. cinerea*, *C. sericea*). Marginal bands of axial parenchyma occur in *C. cuspidosa*, *C. cytisoides* (Fig. 2A), *C. sericea*, *C. angustifolia*, *C. cinerea* (Fig. 2B) and *C. spinescens*.

Rays 1–3(4)-seriate (Fig. 2D, E), up to 5 cells wide in *C. sericea* and *C. pungens* (Fig. 2F), and up to 8 cells wide in *C. psiloloba*, of procumbent and square cells mixed throughout the ray (*C. angustifolia*, *C. cuspidosa*, *C. psiloloba*, *C. cinerea* (Fig. 2E), *C. sericea*), or mostly of procumbent cells with square and upright cells in 1–3 marginal rows and incomplete sheaths as solitary sheath cells [multiseriate rays only of procumbent cells occur in *C. cuspidosa*, *C. psiloloba* and *C. pungens* (Fig. 2F)]. Uniseriate rays mostly of square and upright cells. Prismatic crystals common in ray cells of *C. cinerea*.

3.1.3. *Crotalaria*

Crotalaria agatiflora [Phago s.n.], *Crotalaria capensis* [KK 40-11] and *Crotalaria pallida* [BEVW 5833].

Growth rings absent (*C. agatifolia*, *C. pallida*) or distinct (*C. capensis* (Fig. 2D)), marked by difference in fibre wall thickness between late- and earlywood, and also by 2–6 rows of slightly flattened earlywood fibres. Wood diffuse-porous. Storied vessel elements or axial parenchyma not observed.

Vessels mostly rounded in outline, narrow (average tangential diameter ca. 34 µm), and numerous (vessel frequency 129 per mm²). Vessels mostly in radial to diagonal multiples of 2–6 (*C. pallida*) or 2–8 (–10), sometimes solitary. Vessel walls 3–7 µm thick. Vascular tracheids absent.

Vessel elements (98–) 203 (–301) µm long. Perforation plates are simple. Intervessel pits vested, alternate, small (3–7 µm in vertical size), with rounded or oval margins. Vestures (Fig. 5E) numerous, filled the pit chambers, vary from simple unforked warts to strongly branched fine protuberances (only *C. capensis* was examined by SEM). Vessel-ray and vessel-axial parenchyma pits mostly similar to intervessel pits in size and shape, mostly distinctly bordered. Helical thickenings absent.

Fibres libriform, non-septate, thin-to-thick to very thick-walled, fibre walls 3–9 µm thick, with simple to minutely bordered pits. Gelatinous fibre walls common.

Axial parenchyma in strands of 2–4 cells (also fusiform in *C. pallida*), scanty paratracheal, in incomplete uniseriate sheaths (*C. capensis* (Fig. 2D), *C. pallida*), or vasicentric, in 1–3-seriate sheaths near vessels and vessel groups.

Rays 1–3(4)-seriate, of procumbent and square cells with upright cells in 1–3 marginal rows and in incomplete sheaths (*C. agatifolia*, *C. pallida*), or mostly of procumbent cells, sometimes with few square and upright cells in 1–5 marginal rows and as solitary sheath cells [*C. capensis* (Fig. 2H)]. Crystals absent. Silica bodies common in ray and axial parenchyma cells.

3.1.4. *Leobordea*

Leobordea mollis [BEVW 3105], *Leobordea decumbens* [BEVW 2508], and *Leobordea adpressa* [BEVW 1916].

Growth rings indistinct to distinct, marked by 1–3-seriate bands of marginal axial parenchyma (*L. adpressa*, *L. decumbens*) or by 2–12-seriate ones [*L. mollis* (Fig. 3A)], or by 6–15-seriate bands of radially-flattened narrow vessels, vascular tracheids and axial parenchyma strands, by differences in vessel diameter (*L. mollis*) and also in vessel frequency (*L. decumbens*) between late- and earlywood. Wood diffuse-porous (*L. adpressa*, *L. mollis*) or semi-ring-porous (*L. decumbens*). Storied vessel elements, fusiform cells and strands of axial parenchyma occur (Fig. 3B).

Vessels angular to rounded in outline, very narrow (vessel tangential diameter < 20 µm), and numerous (vessel frequency 68 per mm² in *L. mollis*, and 334 per mm² in the other two species). Vessels solitary, in clusters (up to 6 vessels in *L. decumbens*, and up to 12 in *L. adpressa* and *L. mollis*) and in radial to diagonal multiples [up to 5 vessels in *L. adpressa*, and up to 8 vessels in *L. decumbens* and *L. mollis* (Fig. 3A)]

showing a tendency towards a diagonal or dendritic arrangement. Vessel walls 1.5–3.2 µm thick. Vascular tracheids absent.

Vessel elements (68–) 100–108 (–158) µm. Perforation plates are simple. Intervessel pits vested, alternate (sometimes scalariform in *Lotononis sericophylla* and *Lotononis rigida*), small (3–6 µm in vertical size), with rounded or oval margins. Vestures in *L. decumbens* (Fig. 5F) rather numerous, adjacent to the inner aperture, vary from simple warts to unbranched or weakly branched coarse protuberances (only *L. decumbens* was examined by SEM). Vessel-ray and vessel-axial parenchyma pits mostly similar to intervessel pits in size and shape, narrow to distinctly bordered. Helical thickenings absent.

Fibres libriform, non-septate, very thick-walled, fibre walls 3–5 µm thick, with simple to minutely bordered pits. Gelatinous fibre walls common.

Axial parenchyma mostly fusiform, rarely in strands of 2 cells, vasicentric to confluent in complete (rarely incomplete) 1 or 2-seriate (*L. adpressa*) or 1–5-seriate [*L. decumbens*, *L. mollis* (Fig. 3A)] sheaths near vessels and vessel groups, banded in 1–3-seriate continuous marginal rows (*L. adpressa*, *L. decumbens*) or in 2–14-seriate continuous bands, some of them are marginal [*L. mollis* (Fig. 3A)], and diffuse (also diffuse-in-aggregates in *L. adpressa*).

Rays 1–6(8)-seriate (*L. adpressa*) or 1–10(14)-seriate [*L. decumbens*, *L. mollis* (Fig. 3B)], mostly of procumbent cells with square and upright cells in 1–3 marginal rows or in incomplete sheaths. Uniseriate rays mostly of procumbent and square cells. Crystals and silica bodies absent.

3.1.5. *Lotononis*

L. sericophylla [KK 36-11], *Lotononis divaricata* [BEVW s.n.], and *L. rigida* [AS + BEVW 165].

Growth rings absent in *L. divaricata* (Fig. 3C), or distinct, marked by 1–3-seriate bands of marginal axial parenchyma in *L. rigida*, or by 6–15-seriate bands of radially-flattened narrow vessels, vascular tracheids and axial parenchyma strands, and also by differences in vessel diameter and arrangement between late- and earlywood in *L. sericophylla* (Fig. 3D). Wood diffuse-porous. Storied vessel elements, fusiform cells and strands of axial parenchyma occur in *L. sericophylla* (Fig. 3F).

Vessels angular to rounded in outline, very narrow (average tangential diameter ca. 20 µm), and numerous (vessel frequency ca. 350 per mm² in *L. divaricata* and *L. sericophylla*, and >600 per mm² in *L. rigida*). Vessels solitary, in clusters and diagonal to radial multiples in *L. rigida*, or mostly in large groups (>10 vessels) arranged into diagonal to dendritic pattern (Fig. 3C, D). Vessel walls 1.5–3 µm thick. Vascular tracheids common in *L. sericophylla* and *L. divaricata*, absent in *L. rigida*.

Vessel elements (55–) 123 (–185) µm long in *L. divaricata*, but somewhat longer (74–) 153–161 (–304) µm in *L. sericophylla* and *L. rigida*. Perforation plates simple. Intervessel pits vested, alternate, small (3–6 µm in vertical size), with rounded or oval margins. Vestures in *L. sericophylla* (Fig. 5G) scanty, located at edge of inner aperture, appear as simple rounded warts (only *L. sericophylla* was examined by SEM). Vessel-ray and vessel-axial parenchyma pits mostly similar to intervessel pits in size and shape, narrow to distinctly bordered. Helical thickenings common in narrow vessels of *L. sericophylla* (Fig. 5A) and *L. divaricata*, and absent in *L. rigida*.

Fibres libriform, non-septate, very thick-walled, fibre walls 3–5 µm thick, with simple to minutely bordered pits. Gelatinous fibre walls common.

Axial parenchyma mostly fusiform, rarely in strands of 2 cells (*L. sericophylla*), scanty paratracheal (*L. rigida*) or vasicentric to confluent (*L. divaricata*, *L. sericophylla*) in complete (rarely incomplete) sheaths near vessels and vessel groups (Fig. 3C, D), also banded in 1–3-seriate interrupted to continuous (marginal) rows (*L. rigida*), and diffuse.

Rays 1 or 2-seriate, composed of upright and square cells (*L. rigida*), or 1–10(12)-seriate [*L. divaricata* (Fig. 3E)] mostly of procumbent cells with square and upright cells in 1–3 marginal rows or in

incomplete sheaths (*L. divaricata*, *L. sericophylla*). In *L. sericophylla* rays of two distinct sizes common: uniseriate and 4–12-seriate (Fig. 3F). Uniseriate rays in *L. divaricata* and *L. sericophylla* mostly of procumbent and square cells (*L. divaricata*, *L. sericophylla*), or upright cells (*L. rigida*). Crystals absent. Silica bodies in ray (Fig. 3G) and axial parenchyma cells in all three species examined.

3.1.6. *Rafnia*

Rafnia amplexicaulis [KK 55-11] and *Rafnia angulata* ssp. *angulata* [KK 59-11].

Growth rings absent in *R. angulata* ssp. *angulata*, and indistinctly marked by 1–5-seriate bands of marginal axial parenchyma with 1 or 2 lines of flattened axial parenchyma strands and fibres, and by differences in vessel diameter between late- and earlywood in *R. amplexicaulis* (Fig. 3H). Wood diffuse-porous in *R. angulata* ssp. *angulata* and semi-ring porous in *R. amplexicaulis*. Storied vessel elements, fusiform cells and strands of axial parenchyma occur in *R. amplexicaulis* (Fig. 3I).

Vessels rounded, in *R. angulata* ssp. *angulata* also angular in outline, narrow (average tangential diameter ca. 50 μm). Vessel frequency ca. 60 per mm^2 . Vessels in clusters and radial multiples of 2–6 (up to 11), rarely solitary, tending to be arranged in a tangential to diagonal pattern. Vessel walls 2–5 μm thick. Tyloses and brownish deposits in vessels in *R. angulata* ssp. *angulata*. Vascular tracheids absent.

Vessel elements (87–) 147 (–196) μm long in *R. amplexicaulis*, but somewhat longer (123–) 179 (–312) μm in *R. angulata* ssp. *angulata*. Perforation plates simple. Intervessel pits vested, alternate (rarely scalariform), small (3–6 μm in vertical size), with rounded or oval margins. Vestures in *R. angulata* ssp. *angulata* (Fig. 5H) scanty, located at edge of inner aperture, appear as strongly branched fine protuberances (only *R. angulata* ssp. *angulata* was examined by SEM). Vessel-ray and vessel-axial parenchyma pits mostly similar to intervessel pits in size and shape, narrow to distinctly bordered; vertical ray-vessel pits rare. Helical thickenings absent throughout the genus.

Fibres libriform, non-septate, very thick-walled, fibre walls 3–6 μm thick (up to 8 μm in *R. amplexicaulis*), with simple to minutely bordered pits. Gelatinous fibre walls common.

Axial parenchyma mostly fusiform, rarely in strands of 2 cells, vasicentric and unilaterally paratracheal, in complete (rarely incomplete) sheaths near vessels, and diffuse, also confluent (*R. angulata* ssp. *angulata*), or in 1–5-seriate marginal bands [*R. amplexicaulis* (Fig. 3H)].

Rays 1–8(12)-seriate (up to 14-seriate in *R. angulata* ssp. *angulata*), mostly of procumbent cells with square and upright cells in 1–3 marginal rows as solitary sheath cells (Fig. 3I). Uniseriate rays mostly of procumbent and square cells. Crystals absent. Silica bodies in ray and axial parenchyma cells of *R. amplexicaulis*.

3.1.7. *Wiborgia*

Wiborgia monoptera [JSB 152] and *Wiborgia obcordatum* [KK 52-11].

Growth rings distinct, marked by differences in frequency and diameter of vessels between early- and late wood, by vessel arrangement, also by lines of marginal parenchyma (Fig. 4A). Wood tends to be semi-ring-porous. Storied vessel elements or axial parenchyma not observed.

Vessels rounded, sometimes angular, narrow (up to 50 μm) in *W. monoptera* and moderately wide (up to 92 μm) in *W. obcordatum*. Vessel frequency from 53 per mm^2 in *W. obcordatum* to 112 per mm^2 in *W. monoptera*. Vessels solitary, in clusters and radial multiples of 2–6 (up to 8 in *W. obcordatum*, and up to 21 in *W. monoptera*). Vessels and vessel groups tend to be arranged in a diagonal or dendritic pattern (Fig. 4A). Vessel walls 3–5 μm thick. Brownish deposits in vessels in *W. monoptera*. Vascular tracheids absent.

Vessel elements (57–) 100–123 (–150) μm long. Perforation plates simple. Intervessel pits vested, alternate, small (3–5 μm in vertical size). Vestures in *W. obcordatum* (Fig. 5I) numerous, filling the pit chambers, vary from simple unforked warts to strongly branched fine

protuberances (vestures in *W. monoptera* were not examined by SEM). Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, narrow-bordered. Helical thickenings absent.

Fibres libriform, non-septate, very thick-walled, fibre walls 3–5 μm thick, with simple to minutely bordered pits.

Axial parenchyma mostly fusiform, sometimes in strands of 2 cells, vasicentric, in complete (rarely incomplete) 1 or 2-seriate sheaths near vessels, banded in 1 or 2-seriate lines associated with growth ring boundaries, and diffuse (Fig. 4A).

Rays 1–3(4)-seriate in *W. monoptera* (Fig. 4A), mostly of upright and square cells, with procumbent cells mixed throughout the ray, or 1–5-seriate in *W. obcordatum*, mostly of procumbent cells with square and upright cells in 1–3 marginal rows and as solitary sheath cells. Uniseriate rays mostly of square and upright cells. Crystals absent.

3.1.8. *Wiborgiella*

Wiborgiella bowieana [BEVW 2106] and *Wiborgiella leipoldtiana* [JSB 123].

Growth rings distinct, marked by differences in frequency of vessels in early- and late wood, by vessel arrangement, and in *W. bowieana* also by lines of marginal parenchyma (Fig. 4C). Wood tends to be semi-ring-porous. Storied vessel elements, fusiform cells and strands of axial parenchyma occur in *W. leipoldtiana*.

Vessels rounded, sometimes angular in outline, narrow (tangential diameter up to 42 μm in *W. bowieana*). Vessel frequency 264–268 per mm^2 . Vessels solitary, in clusters and radial multiples of 2–10 (up to 24 in *W. leipoldtiana*). Vessels and vessel groups tend to be arranged in a diagonal or dendritic pattern. Vessel walls 3–5 μm thick. Brownish deposits in vessels (very common in *W. leipoldtiana*). Vascular tracheids absent.

Vessel elements (81–) 99–139 (–218) μm long. Perforation plates simple. Intervessel pits vested, alternate, small (3–5 μm in vertical size). Vessel-ray and vessel-axial parenchyma pits similar to intervessel pits in size and shape, narrow-bordered. Helical thickenings absent.

Fibres libriform, non-septate, very thick-walled, fibre walls 3–5 μm thick, with simple to minutely bordered pits.

Axial parenchyma mostly fusiform, sometimes in strands of 2 cells, vasicentric, in complete (rarely incomplete) 1 or 2-seriate sheaths near vessels, banded in 1–3-seriate lines associated with growth ring boundaries, and diffuse (Fig. 4C).

Rays 1–3-seriate in *W. bowieana* (Fig. 4D), and 1–5-seriate in *W. leipoldtiana*, of square and procumbent cells with numerous upright cells in 1–4 marginal rows and incomplete sheaths. Uniseriate rays of square and upright cells. Crystals absent.

3.1.9. Character evolution within the *Crotalarieae*

Character states for the quantitative wood features listed in Table 2 as well as for some qualitative ones were plotted on a subsample of the majority-rule consensus tree for the combined analysis of nrITS and *rbcL* data for *Crotalarieae* (Boatwright et al., 2011). Patterns of variation for three wood features, viz. vessel arrangement (Fig. 6A), width of axial parenchyma bands (Fig. 6B), and maximum ray width (Fig. 6C) are apparently consistent with the topology of the phylogenetic tree.

4. Discussion

The taxa of the tribe *Crotalarieae* examined in the present study are rather uniform in their wood structure, which is also typical for many other genera of *Papilionoideae* (Metcalf and Chalk, 1950; Baretta-Kuipers, 1981) and characterized by short vessel elements, exclusively simple perforation plates, vested pits, etc. This group, however, can be distinguished from the closely related *genistoid* tribes *Thermopsidae*, *Podalyrieae* and *Genisteae* by the absence of helical thickenings on the vessel walls in all but two species of *Lotononis*. This feature is shared by all the species of these tribes examined to date

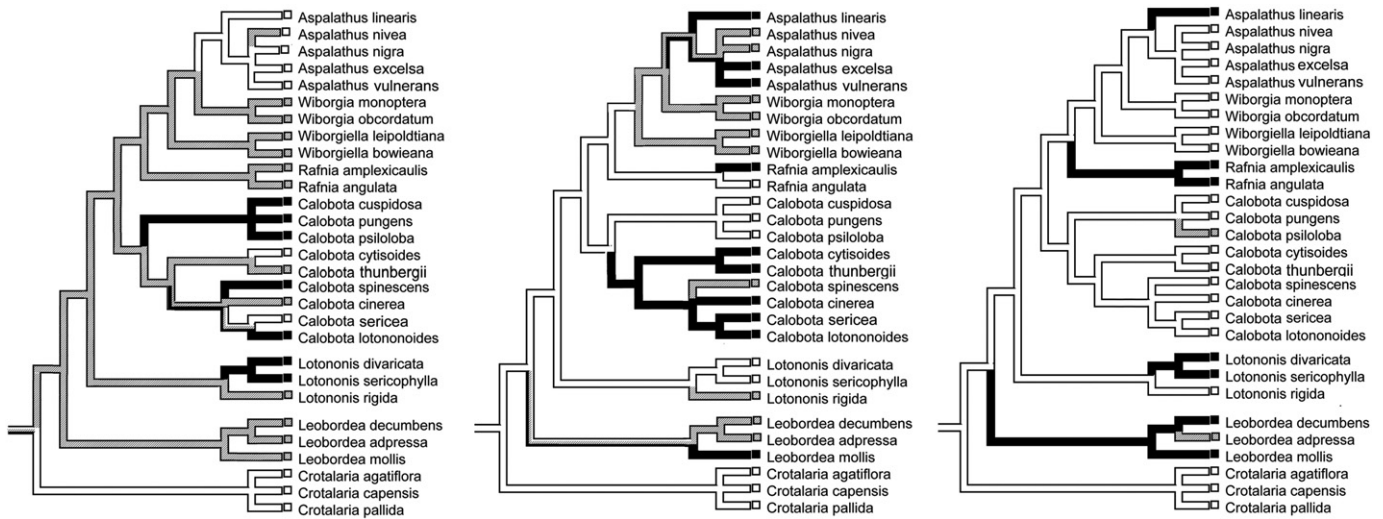


Fig. 6. Distribution of the wood character states mapped onto a subsample of the majority-rule consensus tree for the combined analysis of the nrITS and rbcL data for Crotalariaeae (modified from Boatwright et al., 2011). (A) pattern of vessel arrangement (white – vessels scattered without distinct pattern; dashed – tangential, diagonal or dendritic vessel arrangement without fusion of vessels and vessel groups into large aggregations; black – vessels and vessel groups fused into tangential, diagonal or dendritic aggregations); (B) width of axial parenchyma bands (white – bands absent; dashed – 1–3-seriate bands; black – >3-seriate bands); (C) maximum width of rays (white – 5-seriate; dashed – 6–10-seriate; black – >10-seriate).

with the exception of *Calpurnia*, *Virgilia* and *Cadia*, the members of Podalyrieae (Metcalf and Chalk, 1950; Yatsenko-Khmelevsky, 1954; Grosser, 1977; Fahn et al., 1986; Schweingruber, 1990; Gasson, 1994; InsideWood, 2004–onwards, Stepanova et al., 2013). Thus, the loss of helical thickenings may be considered as a synapomorphy for Crotalariaeae, with a reversal to this character state within *Lotononis*.

Five major lineages, viz. the *Crotalaria* clade, *Lotononis* s.str., *Leorbordea*, *Listia*, and the “Cape” clade (represented in our material by the genera *Aspalathus*, *Calobota*, *Wiborgia*, *Wiborgiella* and *Rafnia*) have been recognized in Crotalariaeae on the basis of molecular phylogenetics and macromorphology (Boatwright et al., 2008a,b, 2009, 2011). None of these lineages (except the non-woody *Listia* that was not examined in the present study) show any wood anatomical traits that can serve as synapomorphies. Generally, the pattern of wood structure diversity within these groups is related more to the growth habits of the plants and probably to environmental factors than to their taxonomy or phylogenetic relationships. The striking wood anatomical differences between *Lotononis rigida* (section *Aulacanthus*, all from the winter-rainfall region of the Cape) and the closely related species *L. divaricata* and *L. sericophylla* (section *Krebsia*, all from the summer-rainfall grassland region) suggests that a more detailed study of this genus will yield valuable results.

The species of the *Crotalaria* clade share the lack of any pattern of vessel arrangement, the absence of banded axial parenchyma, and narrow rays (up to four cells wide). Each of these character states occurs elsewhere within Crotalariaeae, but their combination is distinctive for the *Crotalaria* clade, which represents the most basally diverged lineage in the tribe. This combination may be considered as the ancestral (symplesiomorphic?) condition for Crotalariaeae (Fig. 6A–C) whereas the crown subclades show shifts to diagonal or dendritic vessel arrangements, to banded axial parenchyma as well as the widening of axial parenchyma bands or/and multiseriate rays. A transition to diagonal vessel arrangement occurred also within *Crotalaria*: this character is reported for *Crotalaria saharae*, a dwarf shrub from sand desert in Libya (Schweingruber et al., 2011).

Although the genera of the “Cape” clade show a rather wide range of wood variation, no diagnostic wood characters were revealed for any of them. Only *Rafnia* appears to be distinctive by the combination of relatively wide vessels (average diameter ca. 50 μm) arranged into a

tangential to diagonal pattern, and the occurrence of wide (more than 10-seriate) rays. *Wiborgiella*, *Wiborgia* and most species of *Calobota* differ from other members of the Cape clade by the more or less distinct dendritic vessel arrangement (Fig. 6A). This feature is common in shrubs from Mediterranean environments (Schweingruber, 1990; Schweingruber et al., 2011), suggesting an adaptation for hydraulic safety in case of water stress during the dry season (Carlquist, 1987, 2001; Baas and Schweingruber, 1987). In our material, the most pronounced vessel arrangement involving fusion of some vessel groups into large dendritic aggregations was also found in the shrubby species growing in temporarily dry habitats, such as *Calobota lotononoides* which grows on sand dunes in coastal fynbos, *C. psiloloba* on the sides of streams in grasslands of the northern and eastern Cape, and a few shrubs occurring in karroid scrubs (*C. cuspidosa*, *C. pungens*, *C. spinescens*). Some species from karroid scrubs (*C. angustifolia*, *C. cytisoides*) and fynbos (*Aspalathus excelsa*, *A. linearis*, *A. nigra*) show no dendritic vessel pattern, however. These species may have adaptations for hydraulic protection other than the formation of vessel aggregations.

The mapping of characters on the molecular tree suggests that the absence of banded axial parenchyma is an ancestral condition for the “Cape” clade (Fig. 6A). This feature appears independently in three lineages, viz. in *Aspalathus* + *Wiborgia* + *Wiborgiella*, *Rafnia*, and in crown species of *Calobota*. The abundance of banded parenchyma varies considerably within the genera and even within a species, as the samples of *A. linearis* show. Decumbent forms of this species (sample KK 56-11) have 5–7-seriate bands of axial parenchyma whereas in upright forms (KK 48-11, KK 50-11, KK 51-11) the band width does not exceed five cells. This feature, in combination with the very wide (up to 18-seriate) rays of the decumbent form, shows a common syndrome occurring in many plants with lianescent and other non-self-supporting habits (Carlquist, 1985; Rowe et al., 2004; Angyalossy et al., 2012).

The genus *Lotononis* s. str., recognized recently as a separate major lineage (Boatwright et al., 2011), is also characterized by a diagonal to dendritic vessel arrangement but without fusion of vessel groups into large aggregations. Moreover, the shrublets *L. sericophylla* and *L. divaricata* are distinctive from other Crotalariaeae species examined by the presence of vascular tracheids and the occurrence of helical thickenings in narrow vessels. These features are complementary to

the dendritic vessel arrangement in the adaptive syndrome of wood characters reported for many shrubs from Mediterranean environments (Baas and Schweingruber, 1987; Schweingruber et al., 2011). It is interesting to note that *L. sericophylla* and *L. divaricata* occur in grassland of the summer rainfall regions (where winters are cold and dry), while *L. rigida* grows in Renosterveld vegetation where winters are wet and summers are dry. *L. rigida* differs by lacking helical thickenings and vascular tracheids, and by having uni- and biseriate rays (in contrast to 1–12-seriate rays in *L. sericophylla* and *L. divaricata*). It is likely that these wood traits of *L. rigida* are related to the dwarf shrubby habit of this plant.

The three *Leobordea* species were formerly classified in the section *Leptis* of *Lotononis* (Van Wyk, 1991; Boatwright et al., 2011). Both genera share the diagonal and dendritic vessel arrangement (less pronounced in *Leobordea* than in *Lotononis*) and wide rays (with the exception of *Lotononis rigida*). *Leobordea* has shorter vessel elements, a distinctly higher F/V ratio and more abundant paratracheal and banded axial parenchyma than *Lotononis*, but this quantitative difference appears too weak for diagnostic and systematic purposes.

Micromorphological characters of vested intervessel pits could probably be useful for the systematics of Crotalariaeae, as has been suggested for other taxa (Jansen et al., 2001). As our data revealed, the species of *Crotalaria* (Fig. 5E) and of the “Cape” clade (Fig. 5C, D, H, I) share the presence of vestures, appearing as strongly branched fine protuberances, whereas *Lotononis* s.str. (Fig. 5G) and *Leobordea* (Fig. 5F) show unbranched or weakly branched coarse vestures. Moreover, *Rafnia* is distinctive from *Crotalaria* and other members of the “Cape” clade by having fewer vestures in the pit chambers, and *Lotononis* can also be distinguished from *Leobordea* by the same character. These suggestions, however, are based on data for only two *Aspalathus* species and a single species of the other genera excluding *Wiborgia*. Additional data on the microstructure of vested pits are needed to evaluate the importance of this character for the systematics and phylogenetics of the Crotalariaeae.

Therefore, our study revealed considerable variation of some wood traits within the South African species of the tribe Crotalariaeae as well as within certain genera. However, there are noteworthy discontinuities in this variation (apparently partly geographical and partly taxonomic), that deserve further exploration using a more complete sampling. Additional studies of these discontinuities may provide a better understanding of the ways in which the secondary xylem of southern African genistoid legumes have adapted to wet winters and summer aridity in the western parts of the subcontinent or to wet summers and winter aridity in the eastern regions.

Acknowledgements

The authors would like to thank the National Research Foundation of South Africa (grant # 84442), the University of Johannesburg (UJ) and the Russian Foundation of Basic Research (grant # 12-04-01684) for funding. We also thank Mrs. Eve Kroukamp of Spectrum (UJ) for her assistance.

References

- Angyalossy, V., Angeles, G., Pace, M.R., Lima, A.C., Dias-Leme, C.L., Lohmann, L.G., Madero-Vega, C., 2012. An overview of the anatomy, development and evolution of the vascular system of lianas. *Plant Ecology and Diversity* 5, 167–182.
- Baas, P., Schweingruber, F.H., 1987. Ecological trends in the wood anatomy of trees, shrubs and climbers from Europe. *IAWA Bulletin* 8, 245–274.
- Baretta-Kuipers, T., 1981. Wood anatomy of Leguminosae: its relevance to taxonomy. In: Polhill, R.M., Raven, P.H. (Eds.), *Advances in Legume Systematics Part 2*. Royal Botanic Gardens, Kew, pp. 677–705.
- Boatwright, J.S., Van Wyk, B.-E., 2009. A revision of the African genus *Robynsiophyton* (Crotalariaeae, Fabaceae). *South African Journal of Botany* 75, 367–370.
- Boatwright, J.S., Le Roux, M.M., Wink, M., Morozova, T., Van Wyk, B.-E., 2008a. Phylogenetic relationships of the tribe Crotalariaeae (Fabaceae) inferred from DNA sequences and morphology. *Systematic Botany* 33, 752–761.
- Boatwright, J.S., Tilney, P.M., Van Wyk, B.-E., 2008b. A taxonomic revision of the genus *Rothia* (Crotalariaeae, Fabaceae). *Australian Systematic Botany* 21, 422–430.
- Boatwright, J.S., Tilney, P.M., Van Wyk, B.-E., 2009. The generic concept of *Lebeckia* (Crotalariaeae, Fabaceae): reinstatement of the genus *Calobota* and the new genus *Wiborgiella*. *South African Journal of Botany* 75, 546–556.
- Boatwright, J.S., Wink, M., Van Wyk, B.-E., 2011. The generic concept of *Lotononis* (Crotalariaeae, Fabaceae): reinstatement of the genera *Euchlora*, *Leobordea* and *Listia* and the new genus *Ezoloba*. *Taxon* 60, 161–177.
- Campbell, G.J., Van Wyk, B.-E., 2001. A taxonomic revision of *Rafnia* (Fabaceae, Crotalariaeae). *South African Journal of Botany* 67, 90–149.
- Carlquist, S., 1982. The use of ethylenediamine in softening hard plant structures for paraffin sectioning. *Stain Technology* 57, 311–317.
- Carlquist, S., 1985. Observations on the functional wood histology of vines and lianas; vessel dimorphism, tracheids, vasicentric tracheids, narrow vessels and parenchyma. *Aliso* 11, 138–157.
- Carlquist, S., 1987. Diagonal and tangential vessel aggregations in wood: function and relation to vasicentric tracheids. *Aliso* 11, 451–462.
- Carlquist, S., 2001. *Comparative Wood Anatomy*, 2nd ed. Springer, Berlin, Heidelberg.
- Dahlgren, 1975. *Studies on Wiborgia* Thunb. and related species of *Lebeckia* Thunb. (Fabaceae). *Opera Botanica* 38, 6–83.
- Dahlgren, R., 1988. Crotalariaeae (*Aspalathus*). *Flora of Southern Africa* 16 (3,6), 1–423.
- Fahn, A., Werker, E., Baas, P., 1986. *Wood Anatomy and Identification of Trees and Shrubs From Israel and Adjacent Regions*. The Israel Academy of Sciences and Humanities, Jerusalem.
- Gasson, P.E., 1994. Wood anatomy of the tribe Sophoreae and related Caesalpinioideae and Papilionoideae. In: Ferguson, I.K., Tucker, S. (Eds.), *Advances in Legume Systematics. Structural Botany*, 6, pp. 165–203.
- Goldblatt, P., Manning, J., 2000. *Cape Plants: A Conspectus of the Cape flora of South Africa*. *Strelitzia* 9. National Botanical Institute, Pretoria.
- Grosser, D., 1977. *Die Hölzer Mitteleuropas*. Ein mikrophotographischer LehratlasSpringer-Verlag, Berlin, Heidelberg, New York.
- IAWA Committee, 1989. *IAWA list of microscopic features for hardwood identification*. *IAWA Bulletin* 10, 221–331.
- InsideWood, 2004. Onwards. Published on the Internet <http://insidewood.lib.ncsu.edu/search> (date of accession: 12.11.2013).
- Jansen, S., Baas, P., Smets, E., 2001. Vested pits: their occurrence and systematic importance in eudicots. *Taxon* 50, 135–167.
- Johansen, D.A., 1940. *Plant Microtechnique*. McGraw-Hill, New York.
- Le Roux, M.M., Van Wyk, B.-E., 2007. A revision of *Lebeckia* sect. *Lebeckia*: the *L. sepiaria* group. *South African Journal of Botany* 73, 118–130.
- Le Roux, M.M., Van Wyk, B.-E., 2008. A revision of *Lebeckia* sect. *Lebeckia*: the *L. plukenetiana* group (Fabaceae, Crotalariaeae). *South African Journal of Botany* 74, 660–676.
- Le Roux, M.M., Van Wyk, B.-E., 2009. A revision of *Lebeckia* sect. *Lebeckia*: the *L. pauciflora* and *L. wrightii* groups (Fabaceae, Crotalariaeae). *South African Journal of Botany* 75, 83–96.
- Le Roux, M.M., Van Wyk, B.-E., 2013. A taxonomic revision of *Amphitrichae*, a new section of *Crotalaria* (Fabaceae). *Systematic Botany* 38, 638–652.
- Le Roux, M.M., Boatwright, J.S., Van Wyk, B.-E., 2013. A global infrageneric classification system for the genus *Crotalaria* (Leguminosae) based on molecular and morphological evidence. *Taxon* 62, 957–971.
- Maddison, W.P., Maddison, D.R., 2011. *Mesquite: a modular system for evolutionary analysis*. Version 2.75 <http://mesquiteproject.org>.
- Manning, J., Goldblatt, P., 2012. *Plants of the Greater Cape Floristic Region 1: The Core Cape Flora*. *Strelitzia* 29. South African National Biodiversity Institute, Pretoria.
- Metcalfe, C.R., Chalk, L., 1950. *Anatomy of the Dicotyledons*. Clarendon Press, Oxford.
- Polhill, R.M., 1968. Miscellaneous notes on African species of *Crotalaria* L. II. *Kew Bulletin* 22, 169–348.
- Polhill, R.M., 1974. A revision of *Pearsonia* (Leguminosae–Papilionoideae). *Kew Bulletin* 29, 383–410.
- Polhill, R.M., 1982. *Crotalaria* in Africa and Madagascar. A.A. Balkema, Rotterdam.
- Rowe, N.P., Isnard, S., Speck, T., 2004. Diversity of mechanical architectures in climbing plants: an evolutionary perspective. *Journal of Plant Growth Regulation* 23, 108–128.
- Schutte, A.L., Van Wyk, B.-E., 1998. Evolutionary relationships in the Podalyriaeae and Lipariaeae (Fabaceae) based on morphological, cytological and chemical evidence. *Plant Systematics and Evolution* 209, 1–31.
- Schweingruber, F.H., 1990. *Anatomy of European Woods*. Verlag Paul Haupt, Berne and Stuttgart Publishers, Stuttgart.
- Schweingruber, F.H., Börner, A., Schulze, E.-D., 2011. *Atlas of Stem Anatomy in Herbs, Shrubs and Trees*, vol. 1. Springer, Heidelberg.
- Stepanova, A.V., Oskolski, A.A., Tilney, P.M., Van Wyk, B.-E., 2013. Wood anatomy of the tribe Podalyriaeae (Fabaceae, Papilionoideae): diversity and evolutionary trends. *South African Journal of Botany* 89, 244–256.
- Van Wyk, B.-E., 1991. A synopsis of the genus *Lotononis* (Fabaceae; Crotalariaeae). Contributions from the Bolus Herbarium 14, 1–292.
- Van Wyk, B.-E., 2005. Tribe Crotalariaeae. In: Lewis, G., Schrire, B., Mackinder, B., Lock, M. (Eds.), *Legumes of the World*. Royal Botanic Gardens, Kew, pp. 273–281.
- Van Wyk, B.-E., Schutte, A.L., 1995. Phylogenetic relationships in the tribes Podalyriaeae, Lipariaeae and Crotalariaeae. In: Crisp, M., Doyle, J.J. (Eds.), *Advances in Legume Systematics* 7. Royal Botanic Gardens, Kew, pp. 283–308.
- Van Wyk, B.-E., Venter, M., Boatwright, J.S., 2010. A revision of the genus *Bolusia* (Fabaceae, Crotalariaeae). *South African Journal of Botany* 76, 86–94.
- Yatsenko-Khmelevsky, A.A., 1954. *Caucasian Woods*, vol. 1. Academy of Sciences of the Armenian Soviet Socialist Republic, Yerevan (in Russian).