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Wood anatomy of the tribe Podalyrieae (Fabaceae, Papilionoideae): Diversity and evolutionary trends

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ABSTRACT

Detailed wood anatomical data for 32 species from all nine genera of the tribe Podalyrieae are presented, together with numerical analyses and the mapping of character states onto the latest available molecular phylogeny. It was found that trees (*Cadia*, *Calpurnia* and *Virgilia*) have vessels in small isolated groups, whilst fynbos shrubs (the remaining genera: *Amphithalea*, *Cyclopia*, *Liparia*, *Podalyria*, *Stirtonanthus* and *Xiphotheca*) commonly show highly grouped narrow vessels (frequently in a dendritic pattern), and helical thickening on the vessel walls. Comparisons of the main character state changes with the molecular phylogeny of the tribe show that the wood structure of trees probably represents the basic condition in the tribe; character states present in shrubs appear to have arisen a few times and very likely represent adaptations to seasonal water stress. In general, the wood anatomy is congruent with current subtribal and generic delimitations. Fire-survival strategy is reflected in the rays, with seeders having mostly procumbent cells whilst sprouters have square and upright cells. The close similarity in wood anatomy between *Cadia* and *Calpurnia* is in agreement with the transfer of *Cadia* to the Podalyrieae. A remarkable diversity of crystals was found, including prismatic, acicular and navicular crystals, the last two of which may occur singly or in sheaf-like aggregates.

1. Introduction

The tribe Podalyrieae is subendemic to the Cape Floristic Region of South Africa, with six of the nine genera confined to the Fynbos biome with its cold wet winters and dry summers, namely *Amphithalea* Eckl. & Zeyh. (42 spp.), *Cyclopia* Vent. (23 spp.) (Schutte et al., 1995), *Liparia* L. (20 spp.), *Stirtonanthus* B.-E. Van Wyk & A.L. Schutte (3 spp.), *Xiphotheca* Eckl. & Zeyh. (10 spp.) and *Virgilia* Poir. (2 spp.). *Podalyria* Willd. has 16 of the 17 species endemic to fynbos (one species extends into the grassland region of South Africa) (Schutte-Vlok and Van Wyk, 2011); *Calpurnia* E. Mey. has only one species in the Cape Floristic Region, whilst the other seven species occur in the summer rainfall Grassland biome of South Africa, with one [*C. aurea* (Lam.) Benth.] extending to tropical east Africa and India (Beaumont et al., 1999); *Cadia* Forssk. has one species in tropical Africa and six in Madagascar.

The current tribal and generic classification system (Van Wyk and Schutte, 1995; Schutte and Van Wyk, 1998; Van Wyk, 2005) was based on morphological, chemical and cytological evidence, which closely agreed with later molecular phylogenetic analyses. The molecular studies showed that *Cyclopia* forms an isolated group sister to the remaining genera (Van der Bank et al., 2002) and that the genus *Cadia*, despite its radially symmetrical flowers, should be included in the tribe (Boatwright et al., 2008). In the current classification system, *Amphithalea* and *Xiphotheca* are placed in the monophyletic subtribe Xiphothecinae whilst the remaining genera are placed in the paraphyletic subtribe Podalyriinae, the latter shown to comprise three main clades: *Liparia*/*Podalyria*/*Stirtonanthus*, *Calpurnia*/*Virgilia*, and *Cyclopia* (Boatwright et al., 2008).

Although it has been shown that wood anatomy is useful in exploring the systematics and evolution of Fabaceae (Baretta-Kuipers, 1981; Gasson, 2000), such studies have thus far focussed mainly on groups which consist predominantly of trees. All species of Podalyrieae are woody plants – mostly shrubs or small trees but ranging from tall trees to subshrubs and creeping shrublets – but their wood anatomy has remained largely unknown. Some tree species of *Cadia*, *Virgilia* and *Calpurnia* have been studied in detail (Gasson, 1994; Fujii et al., 1994) but data for the remainder of the tribe are limited to the observations by Van Wyk and Schutte (1995) and Schutte and Van Wyk (1998), who noted and illustrated the diversity of vessel grouping.

This paper describes, for the first time, the wood anatomy of all genera of the tribe Podalyrieae, and attempts to relate the diversity and main discontinuities of wood anatomical characters to the current state of knowledge regarding the systematics and phylogenetics of the group.

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Table 1
Quantitative wood characters of Podalyrieae.

Species and voucher specimens (all in JRAU)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
Cadia purpurea Ait.	24 ± 1.3	145	2.0	7	22.0	3.9	128 ± 4.3	504 ± 19.7	3.9	18 ± 0.8	135 ± 6.7	3.7	5.2	8.9
KK 33-10	12–38	119–165				2.8–5.8	79–178	290–740		12–31	83–244	2.1–6.3	3.2–7.4	5.3–12.6
Calpurnia aurea Baker	35 ± 1.5	73	2.5	11	12.5	3.9	191 ± 8.0	601 ± 21.5	3.2	27 ± 1.4	217 ± 12.9	8.7	2.4	11.2
KK 39-11	18–48	60–91				2.7–5.3	102–287	279–807		14–43	105–396	6.3–11.6	1.1–4.2	9.5–12.6
Calpurnia intrusa E. Mey.	41 ± 2.7	44	1.8	10	29.8	5.7	151 ± 4.5	577 ± 17.3	3.8	24 ± 1.3	216 ± 14.7	7.8	1.9	9.7
BEVW 3249 C	11–61	23–63				4.4–6.7	95–214	396–828		14–41	107–476	5.3–11.6	0.0–3.2	7.4–12.6
Calpurnia sericea Harv.	45 ± 2.6	75	1.8	5	31.0	4.9	150 ± 4.5	453 ± 18.5	3.0	22 ± 0.9	225 ± 30.8	5.8	3.4	9.2
KK 35-11	18–74	49–102				3.8–5.9	106–204	269–760		11–32	88–875	3.2–8.4	0.0–8.4	5.3–12.6
Cyclopia aurescens Kies.	8 ± 0.3	792	160.5	461	0	5.4	228 ± 6.1	63 ± 15.3	2.8	56 ± 2.2	798 ± 67.3	2.9	4.2	7.1
ALS + BEVW 771	3–18	706–877				4.0–7.8	164–323	448–817	39–80		238–v	1.1–5.3	2.1–6.3	5.3–9.5
Cyclopia burtonii Hofmeyr & E. Phillips	13 ± 0.5	658	138.2	476	0	4.5	172 ± 7.0	53216.4	3.1	51 ± 2.2	377 ± 27.9	4.6	2.7	7.4
ALS 641	4–31	486–788				3.6–5.7	87–245	329–673		29–73	141–879	3.2–7.4	1.1–5.3	6.3–8.4
Cyclopia buxifolia (Burm.f.) Kies	19 ± 0.8	228	81.2	407	0.1	5.1	227 ± 8.5	601 ± 19.8	2.6	24 ± 0.7	282 ± 25.0	3.7	4.4	8.1
ALS 544	5–44	110–411				4.0–7.3	132–347	262–814		16–31	121–635	0–6.3	2.1–6.3	5.3–10.5
Cyclopia genistoides (L.) Sieber ex C. Presl	12 ± 0.7	411	14.2	40	0	5.4	322 ± 13.2	709 ± 24.1	2.2	36 ± 1.2	605 ± 77.7	1.6	7.2	8.8
ALS 615	6–22	199–575				4.0–7.8	165–483	422–1019		29–52	137–1421	0.0–4.2	4.2–9.5	5.3–11.6
Cyclopia genistoides	16 ± 1.7	418	29.6	84	0.1	4.9	245 ± 11.6	537 ± 22.9	2.2	88 ± 10.6	331 ± 18.7	2.6	4.2	6.8
ALS 624	7–30	308–610				3.6–6.5	148–393	226–801		38–320	145–577	1.1–4.2	3.2–6.3	5.3–10.5
Cyclopia intermedia E. Mey.	18 ± 1.4	390	44.8	122	0.2	5.0	278 ± 12.7	751 ± 34.2	2.7	42 ± 1.6	729 ± 76.2	6.5	1.2	7.7
ALS 646	7–36	240–637				3.7–6.6	158–405	424–1064		27–59	267–1887	5.3–7.4	0–3.2	6.3–8.4
Cyclopia intermedia	11 ± 0.5	503	118.8	496	0.1	4.5	174 ± 8.5	654 ± 32.7	3.8	44 ± 1.3	453 ± 37.2	7.3	3.3	10.5
ALS 647	3–39	226–706				3.4–5.8	97–298	300–1181		33–59	178–923	5.3–12.6	2.1–5.3	8.4–14.7
Cyclopia maculata (Andrews)	18 ± 1.2	247	61.6	287	0.5	5.0	207 ± 9.0	602 ± 15.8	2.9	40 ± 3.0	418 ± 22.8	4.7	3.3	8.0
KiesALS 636	6–34[a]	192–329				4.0–7.2	12–5324	442–810		19–90	239–765	3.2–7.4	1.1–5.3	6.3–9.5
Cyclopia maculata	31 ± 2.8	143	4.6	18	5.0	5.1	167 ± 6.6	719 ± 22.8	4.3	34 ± 1.5	311 ± 27.7	4.5	3.2	7.7
ALS 528	8–60	121–170				4.1–8.2	109–232	557–866		2–48	116–759	4.2–5.3	2.1–6.3	6.3–10.5
Cyclopia plicata Kies	7 ± 0.4	1615	–[a]	–[a]	–[a]	4.2	161 ± 5.5	542 ± 17.8	3.4	46 ± 2.2	227 ± 18.2	4.8	6.5	11.4
ALS 670a	3–22	1322–2144				3.2–5.6	102–232	346–714		27–86	73–429	3.2–6.3	4.2–9.5	9.5–13.7
Cyclopia subternata Vogel	23 ± 2.1	470	102.4	277	0.04	5.1	249 ± 11.3	744 ± 21.1	3.0	34 ± 1.2	375 ± 27.6	4.5	3.8	8.3
KK 43–11	10–48	384–555				3.1–6.8	154–425	512–983		24–49	173–771	3.2–6.3	1.1–6.3	6.3–10.5
Liparia hirsuta Moench	19 ± 1.0	280	5.4	29	7.4	6.0	217 ± 7.1	495 ± 14.3		44 ± 1.7	233 ± 15.7	4.9	3.1	8.0
JSB 595	11–33	158–356				4.6–11.6	159–313	367–611		18–62	128–456	3.2–7.4	1.1–5.3	6.3–9.5
Liparia myrtifolia Thunb.	22 ± 1.5	545	15.7	84	1.0	4.0	191 ± 6.5	411 ± 37.3	2.2	34 ± 1.7	456 ± 51.602	4.5	2.6	7.1
ALS 727a	10–44	412–688				2.7–4.9	115–266	135–767		19–58	160–13	3.2–6.3	1.1–5.3	5.3–8.4
Liparia racemosa A.L. Schutte	25 ± 1.0	358	18.9	78	1.0	5.6	224 ± 7.5	605 ± 17.5	2.7	52 ± 2.6	304 ± 26.9	5.4 ± 0.4	1.5 ± 0.3	6.9
ALS 642a	16–42	265–574				4.1–7.1	131–323	456–821		29–87	146–656	3.2–7.4	0.0–3.2	5.3–9.5
Liparia splendens (Burm.f.) Bos & de Wit	16 ± 1.0	433	8.0	44	4.0	6.7	198 ± 6.8	757 ± 17.4	3.8	36 ± 1.6	475 ± 38.6	4.0 ± 0.2	7.2 ± 0.3	11.2
BEVW 3147	9–28	229–593				4.8–8.9	125–269	625–952		22–71	106–1182	1.9–5.6	4.6–10.2	9.3–13.9
Podalyria calyptrata (Retz.) Willd.	47 ± 2.5	7156–84	2.1	7	20.0	5.2	216 ± 9.3	602 ± 17.4	2.8	44 ± 1.6	259 ± 19.6	4.9	3.4	8.3
KK 03-10	22–78					4.2–6.3	94–306	381–783		26–60	84–687	3.2–6.3	1.1–5.3	5.3–10.5
Podalyria lanceolata Benth.	26 ± 2.3	199	11.7	54	16.7	5.4	271 ± 11.1	841 ± 23.3	3.1	32 ± 1.1	257 ± 15.5	5.1	1.7	6.7
ALS s.n.	8–61	164–235				4.2–7.2	177–404	654–1085		22–45	123–415	3.2–6.3	0.0–4.2	5.3–8.4
Podalyria myrtifolia D. Dietr.	21 ± 1.2	2250	3.0	26	13.0	5.1	161 ± 7.6	511 ± 16.0343–678	3.2	25 ± 0.8	314 ± 29.4	4.83.2–6.3	2.51.1–6.3	7.45.3–9.5
ALS + BEVW 166	12–36	200–26				3.8–6.8	80–257			15–31	158–515			

(continued on next page)

Table 1 (*continued*)

Species and voucher specimens (all in JRAU)	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
Podalyria rotundifolia (P.J. Bergius) A.L. Schutte	25 ± 2.1	40	3.9	10	16.0	5.4	189 ± 7.3	660 ± 21.0	3.5	30 ± 1.2	286 ± 20.6	6.7	3.1	9.8
ALS s.n.	10–48	13–59				3.5–8.5	108–273	414–846		16–42	107–607	3.2–9.5	1.1–5.3	6.3–13.7
Stirtonanthus insignis (Compton) B.-E.van Wyk & A.L. Schutte	18 ± 1.3	159	4.5	44	6.2	4.2	169 ± 8.1	438 ± 17.7	2.6	24 ± 1.0	342 ± 34.9	3.6	3.4	6.9
BEVW 3331	6–36	97–207				3.6–5	85–267	254–663		14–33	102–658	2.1–6.3	2.1–5.3	5.3–8.4
Stirtonanthus taylorianus (L. Bolus) B.–E.van Wyk & A.L. Schutte	16 ± 1.7	317	17.7	89	1.0	5.8	350 ± 13.5	701 ± 27.1	2.0	25 ± 1.2	181 ± 9.2	4.6	3.4	8.0
BEVW 3169	4–47	286–367				4.4–7.8	228–512	457–1025		16–39	87–325	1.1–6.3	2.1–5.3	5.3–10.5
Virgilia divaricata Adamson	74 ± 3.1	18	1.5	5	40.2	5.8	291 ± 10.3	636 ± 35.2	2.2	28 ± 0.7	244 ± 13.6	4.8	2.2	7.1
AO 16-09	39–108	15–20				4.4–8.2	194–410	306–1016		20–35	130–404	3.2–7.4	0–4.2	5.3–10.5
Virgilia divaricata	69 ± 3.2	17	1.5	5	44.7	6.4	321 ± 9.8	615 ± 39.4	1.9	27 ± 0.9	275 ± 22.4	2.3	2.4	4.7
KK 02-10	35–98	4–19				5.0–8.1	229–484	375–1088		16–36	136–572	1.1–4.2	0.0–4.2	3.2–6.3
Virgilia oroboides subsp. *oroboides* (P.J. Bergius) T.M. Salter	85 ± 3.9	18	1.5	5	39.5	7.3	288 ± 11.5	995 ± 40.8	3.5	31 ± 0.9	386 ± 36.6	4.7	2.3	7.1
BEVW 5722	49–130	13–21				5.2–10.4	153–406	586–1314		22–44	198–1060	2.1–6.3	1.1–3.2	5.3–9.5
Virgilia oroboides subsp. *ferruginea* B.-E.van Wyk	80 ± 3.6	18	1.5	6	38.4	6.2	274 ± 13.3	813 ± 30.9	3	30 ± 0.9	310 ± 19.8	2.8	2.3	5.2
KK 44-11	37–121	15–21				4.6–8.7	120–424	367–1114		20–38	121–537	1.1–5.3	0 – 4.2	4.2–6.3
Amphithalea ericifolia (L.) Eckl. & Zeyh.	14 ± 0.9	294	2.3	18	23.0	3.8	176 ± 7.6	430 ± 13.8	2.4	29 ± 1.0	237 ± 20.8	4.9	5.6	10.6
ALS 617	6–26	240–333				2.9–5.1	118–265	258–586		16–40	78–602	3.7–6.5	3.7–8.4	8.4–13.0
Amphithalea rostrata A.L. Schutte & B.-E.van Wyk	10 ± 0.7	295	3	19	16.0	5.0	175 ± 7.5	546 ± 20.9	3.1	20 ± 1.0	242 ± 24.5	4.4	8.6	13.1
ALS 629	5–18	263–374				3.2–7.7	84–258	256–815		12–32	98–616	2.1–8.4	4.2–13.7	11.6–15.8
Amphitalea vlokii (A.L. Schutte & B.–E.van Wyk) A.L. Schutte	13 ± 1.3	104	2.8	17	23.0	2.5	135 ± 5.3	572 ± 13.7	4.2	22 ± 0.8	276 ± 20.5	6.2	5.2	11.4
ALS 743	4–34	67–163				1.4–4.1	74–187	458–704		16–37	117–511	3.2–8.4	2.1–9.5	9.5–12.6
Xiphotheca canescens (Thunb.) A.L. Schutte & B.-E.van Wyk	16 ± 1.1	281	15.9	174	13.8	4.8	193 ± 8.6	517 ± 15.4	2.7	27 ± 0.9	33 ± 21.5	3.6	3.4	7.1
ALS 595a	6–27	254.5–334.6				3.9–6.1	121–300	348–678		16–40	162–564	1.1–6.3	0.0–10.5	5.3–1.6
Xiphotheca elliptica (DC.) A.L. Schutte & B.-E.van Wyk	17 ± 1.7	134	14.6	38	2.3	5.3	205 ± 9.0	576 ± 20.6	2.8	32 ± 1.5	336 ± 19.2	4.7	3.8	8.6
ALS 600	8–40	124–154				4.0–7.0	111–345	335–813		21–52	157–650	2.8–6.5	1.9–6.5	7.4–10.2
Xiphotheca phylicoides A.L. Schutte & B.–E.van Wyk	13 ± 1.0	275	16.1	51	20.0	5.0	160 ± 10.5	421 ± 11.0	2.6	31 ± 1.1	230 ± 15.9	2.6	8.6	11.2
ALS 648	4–16	259–303				3.6–6.3	112–445	344–571		20–44	103–513	0.9–3.7	6.5–10.2	8.4–13.0
Xiphotheca tecta A.L. Schutte & B.–E.van Wyk	18 ± 1.6	415	16.4	120	2.0	6.7	158 ± 6.1	590 ± 16.1	3.7	29 ± 0.7	336 ± 26.2	3.8	5.1	8.9
ALS 597	6–35	314–581				5.3–8.1	93–229	394–764		22–38	39–670	2.1–6.3	3.2–7.4	6.3–10.5

Legend:
I — Tangential diameter of vessels, μm.
II — Number of vessel lumina per mm^2.
III — Mean number of vessel lumina per group.
IV — Max number of vessel lumina per group.
V — Percent of solitary vessels.
VI —Intervessel pit diameter, μm.
VII — Length of vessel elements, μm.
VIII — Length of fibres, μm.
IX — F/V ratio (Fibre length/Vessel element length ratio).
X — Width of multiseriate rays, μm.
XI — Height of multiseriate rays, μm.
XII — Number of multiseriate rays per mm.
XIII — Number of uniseriate rays per mm.
XIV — Total number of rays per mm.

[a] In *Cyclopia plicata* all vessels are united in one group.

2. Material and methods

We studied the wood anatomy of all nine genera of Podalyrieae, with a representative sample between one and nine species of each genus. The source of material was the collection of FAA-fixed samples, housed in the herbarium of the Department of Botany and Plant Biotechnology at the University of Johannesburg. As shown in Table 1, each sample has a voucher specimen (in the UJ Herbarium, acronym JRAU), collected by A.-L. Schutte (ALS), A.A. Oskolski (AO), A.V. Stepanova (AS), B.-E. van Wyk (BEVW), JSB (J.S. Boatwright) and E.L. Kotina (KK). The taxa studied, collection numbers, and stem diameters are shown in the Results section (in the generic descriptions of the wood anatomy and also in the summary of the results in Table 1). The age of the woody stems or shoots was no less than three years, with diameters ranging from 4 to 55 mm. Transverse, radial, and tangential sections were made on freezing (shoots with a small diameter) or rotary microtomes (Ernst Leitz GMBH, Wetzlar, Germany and Jung AG Heidelberg, Germany), and then stained with a 1:1 alcian blue/safranin mixture (Jansen et al., 2004). Macerations were made using Jeffrey's solution (Johansen, 1940). Where necessary, the wood was softened in ethylenediamine (Carlquist, 1982) followed by soaking in 15% glycerol in ethanol or boiling in 10% glycerol solution (Jansen et al., 1998). The ethylenediamine method for softening very hard woods was first used by Kukachka (1977) and also by Maclachlan and Gasson (2010) but we followed the protocol of Carlquist (1982). The descriptive terminology used is in accordance with that of the IAWA Committee (1989).

A special method was used for counting the number of vessels in wood with a dendritic pattern of vessel arrangement. Since the groups are often very large whilst the vessels are very small, it is difficult to count the number of vessels per group. For every sample, we chose five groups of vessels, measured their size and then counted the number of vessels in each group. The mean ratio of vessel number per unit area

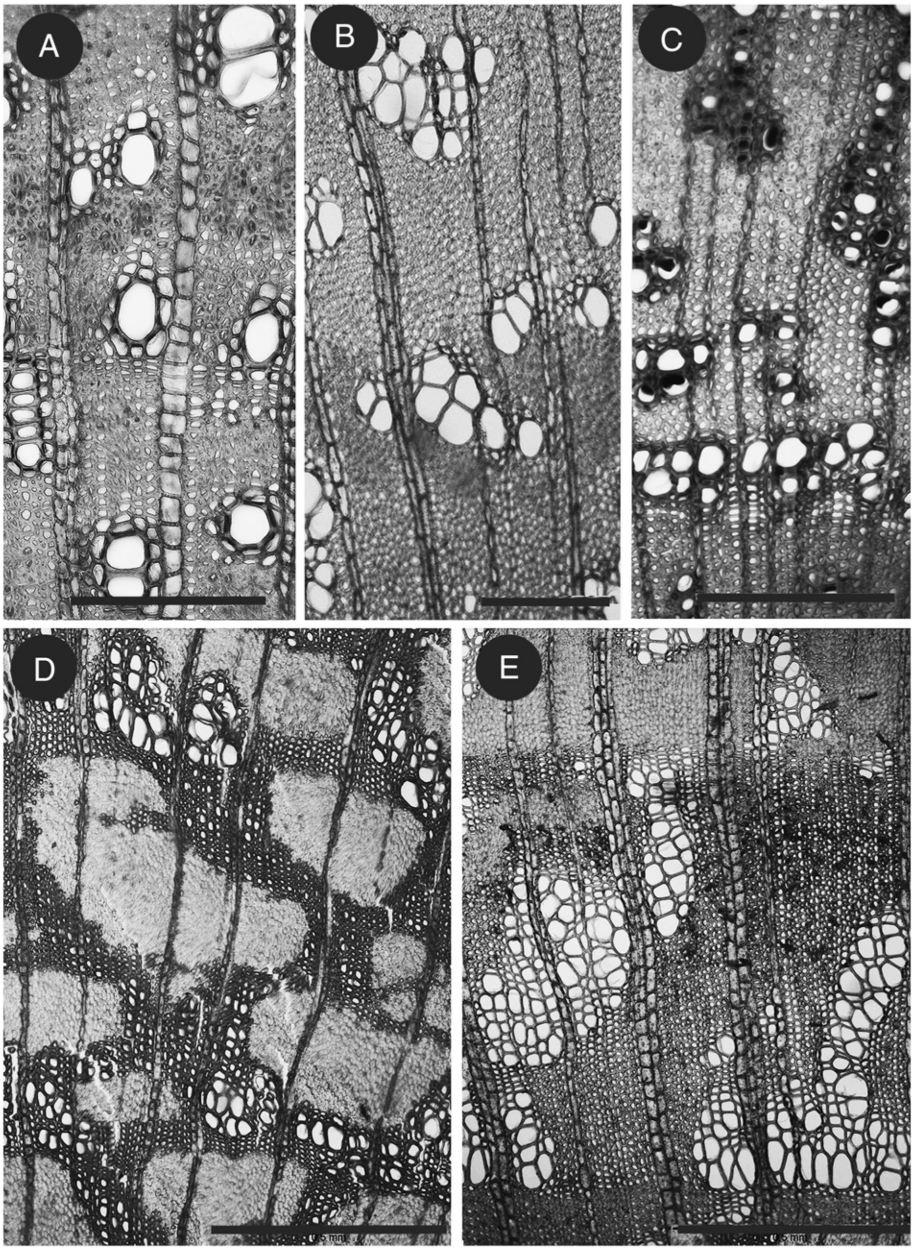

Fig. 1. Wood porosity and vessel arrangement, LM, TS. (A) diffuse-porous wood, vessels solitary and in radial multiples, *Calpurnia sericea*; (B) diffuse-porous wood, vessels in clusters, *Cyclopia maculata*; (C) diffuse-porous wood, tangential multiples at the beginning of growth ring, *Podalyria myrtifolia*; (D) semi-ring-porous wood (weakly so), vessels in a dendritic pattern, *Cyclopia plicata*; (E) diffuse-porous wood, vessels in a dendritic pattern, *Liparia racemosa*. Scale bars: 200 μm.

of the group was then calculated. Using this ratio, we determined the vessel number of 30 groups for each of the samples. Standard methods were used (IAWA Committee, 1989) for all other parameters.

Measurements and photographs were made, respectively, with an Olympus ColorView Soft Imaging System (Olympus Soft Imaging Solutions, Stream Essentials version 1.8). Crystals were studied under polarised light. Scanning electron microscope (SEM) observations and photographs were made on a Tescan Vega TC SEM. Samples for SEM study were first preserved in 96% ethanol and then dried in an Edward Tissue Dryer (ETD 4).

Evolutionary pathways for wood anatomical features were reconstructed by mapping their character states on a subsample of one of the 140 equally most parsimonious trees from the combined molecular analysis of ITS and rbcL data for Podalyrieae taken from Boatwright et al. (2008). Character optimisation along tree branches was visualised using the parsimony reconstruction method with the “Character History Tracing” option in the computer package Mesquite 2.0 (Maddison and Maddison, 2007).

3. Results

3.1. General wood description

Wood mainly diffuse-porous (Fig. 1A–C, F). Semi-ring porosity was observed in some species of *Cyclopia* (Fig. 1D). Growth rings commonly distinct to faint or absent in two species of *Podalyria*, some species of *Cyclopia*, and some specimens of *Virgilia*, *Liparia splendens* and *Amphithalea ericifolia*. Width of growth rings commonly 0.4–1 mm in

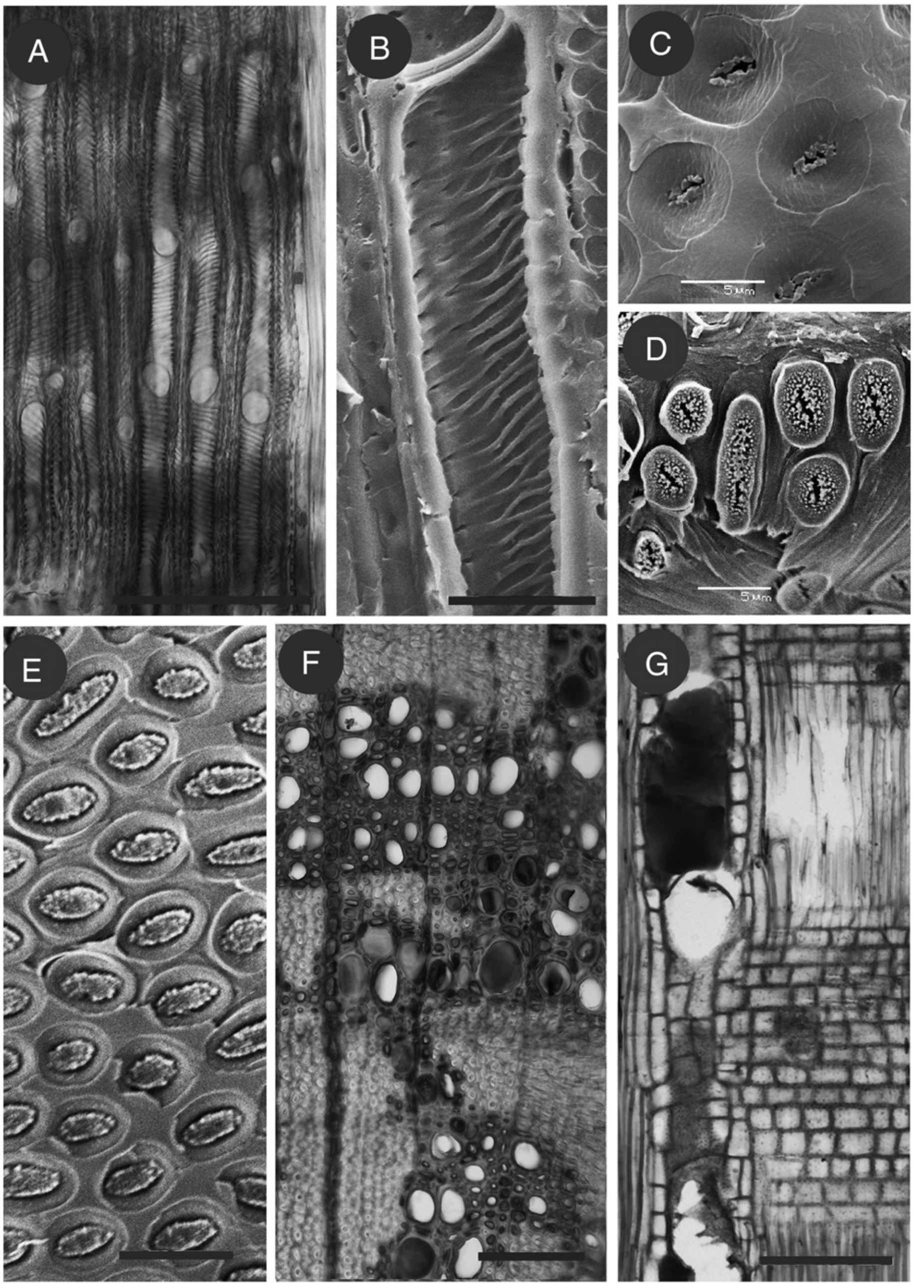

Fig. 2. Vessels characters. (A) Vessels with simple perforation plates and spiral thickening, *Cyclopia plicata*, LM, RS; (B) spiral thickening, *Amphithalea rostrata*, SEM; (C) vestured intervessel pits with scanty vestures located at edge of inner aperture viewed from the outside, appearing as simple rounded and weakly branched warts, *Cyclopia buxifolia*, SEM; (D) vestured intervessel pits with numerous vestures varying from simple and unforked warts to strongly branched fine protuberances viewing from the outside, *Calpurnia sericea*, SEM; (E) vestured intervessel pits with numerous seemingly unbranched vestures near inner pit apertures viewed from the outside, *Virgilia oroboides* subsp. *oroboides*, SEM; (F) deposits inside vessels, *Xiphotheca canescens*, LM, TS; (G) deposit inside vessels, *Virgilia oroboides* subsp. *oroboides*, LM, RS. Scale bars: 100 μm (A, F), 20 μm (B), 5 μm (C, D), 10 μm (E), 200 μm (G).

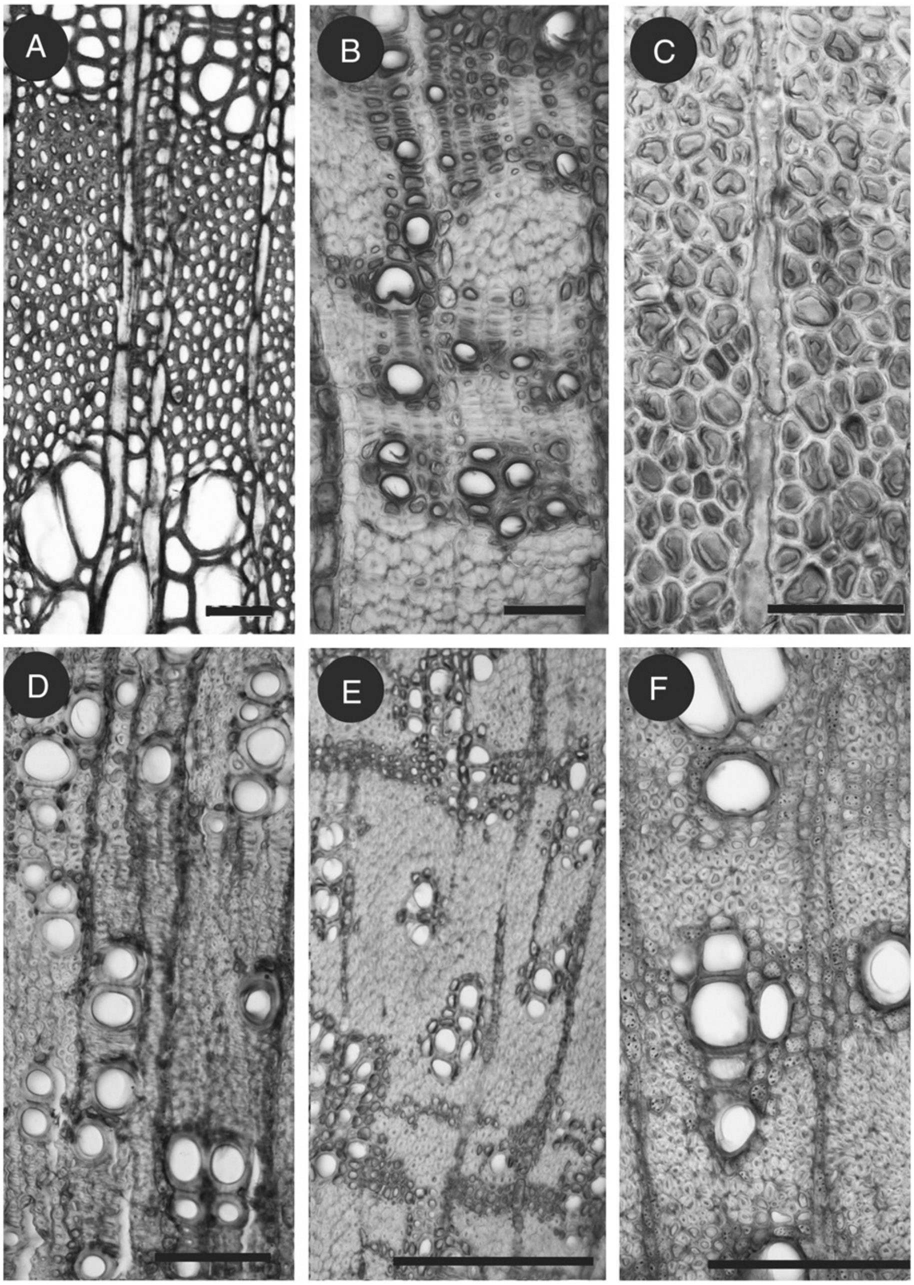

Fig. 3. Fibre wall thickness and axial parenchyma distribution, LM, TS. (A) Thin- to thick-walled fibres, *Stirtonanthus taylorianus*; (B) very thick-walled fibres, *Stirtonanthus insignis*; (C) gelatinous fibres, *Podalyria rotundifolia*; (D) axial parenchyma scanty paratracheal, *Cadia purpurea*; (E), axial parenchyma scanty paratracheal and marginal, (also vasicentric and in narrow bands), *Amphithalea rostrata*; (F) axial parenchyma confluent, *Calpurnia intrusa*. Scale bars: 50 μm (A–C), 100 μm (D), 200 μm (E, F).

shrubs and 1.4–2.5 mm in trees. Boundaries of growth rings may be marked by rows of flattened fibres or flattened vascular tracheids and/or narrow vessels (in species with very thick-walled fibres) and/or by marginal parenchyma. Vessels narrow, round to angular in outline, relatively rare (Fig. 1A) to very numerous (Fig. 1D, F), commonly in dendritic pattern (Fig. 1D, F), less often in radial and oblique multiples and clusters (Fig. 1A, B), or in tangential multiples in *Podalyria*, *Virgilia* and *Xiphotheca* (Fig. 1C). Perforation plates simple (Fig. 2A), intervessel pits alternate, vestured, 3–8 μm in diameter (up to 10 in *Virgilia* spp.), round and oval to polygonal with narrow oval to slit-like apertures (Fig. 2C–E). Vessel-ray pits similar to intervessel ones in size and shape. Helical thickenings in vessels absent in large trees (*Cadia*, *Calpurnia* and *Virgilia*) and in two shrubby species (*Amphithalea rostrata* and *Liparia splendens*), but present in almost all species of shrubby genera (Fig. 2A, B), occurring throughout the bodies of the vessel elements of all diameters (and not only in the tails). Brown to yellowish-brown deposit (Figs. 1C, 2F, J) in vessels, vascular tracheids and adjacent parenchyma cells in all genera examined except *Stirtonanthus.* Vascular tracheids commonly present, more or less numerous in woods with dendritic pattern of vessel arrangement and rare in woods with isolated vessel groups. Fibres nonseptate, thin- to thick-walled (Fig. 3A) or very thick-walled (Fig. 3B, E), with small simple pits, more common on the radial walls; thin- to thick-walled fibres often gelatinous (Fig. 3C). Axial parenchyma scanty paratracheal to vasicentric, rarely confluent (Fig. 3D–F), often also in narrow bands of 1–6 cells wide (Fig. 3E), sometimes marginal, fusiform (Fig. 4C), and in 2, sometimes up to 4 cells per strand (Fig. 4A). Rays commonly 1 or 2- or 1–3-seriate (Fig. 4B–E), rarely broader (up to 6), 1–6 times higher than axial parenchyma strands, composed of procumbent, square and upright cells, perforated ray cells often present (Fig. 4F). Prismatic crystals occur in ray cells in some species of *Calpurnia* and *Amphithalea* (Fig. 5A, B); navicular crystals, often aggregated (Fig. 5C) and crystal sand common for two species

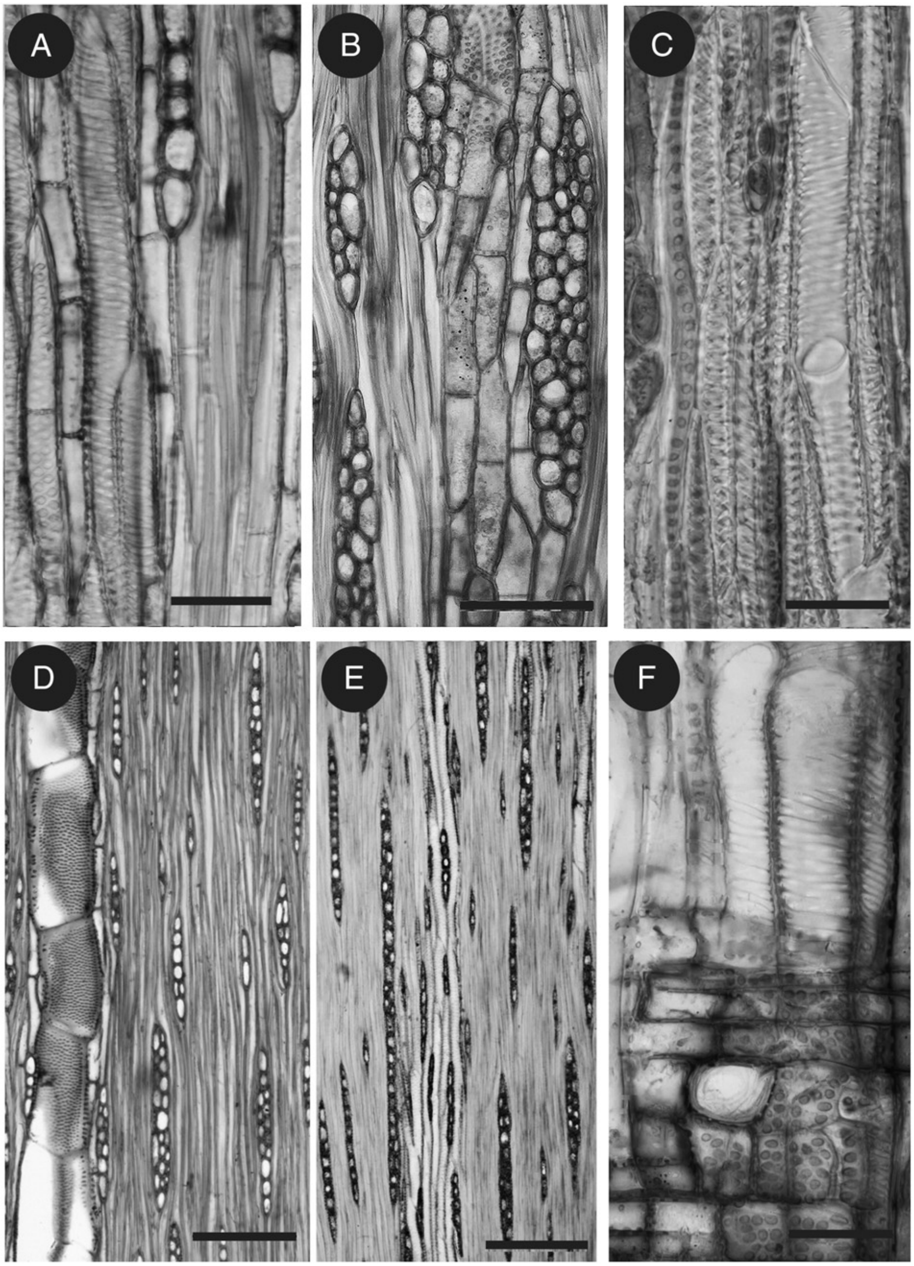

Fig. 4. Axial parenchyma strands and rays. (A) Axial parenchyma strand of 4 cells, *Podalyria lanceolata*, LM, TLS; (B) axial parenchyma in 2 or 3 cells per strand and 2 or 3-seriate rays, *Calpurnia intrusa*, LM, TLS; (C) fusiform axial parenchyma cells, *Xiphotheca canescens*, LM, TLS; (D) 1 or 2-seriate rays, *Virgilia oroboides* subsp. *ferruginea*, LM, TLS; (E) 1 or 2-seriate rays, *Cyclopia buxifolia*, LM, TLS; (F) perforated ray cell, *Stirtonanthus taylorianus*, LM, RLS. Scale bars: 50 μm (A, C, F), 100 μm (B), 200 μm (D, E).

of *Amphithalea*; acicular crystals in sheaf-like aggregates present in almost all species of *Cyclopia* and *Virgilia* (Fig. 5D, E), and also in one species of *Calpurnia*. Silica bodies commonly occur in rays and axial parenchyma cells (Fig. 5F) in almost all genera, but their presence often varies within genera. They are small (up to 3 μm in diameter), spheroidal and yellowish, and usually solitary. Storied structures were not found.

3.2. Generic wood descriptions

3.2.1. Cadia

Material studied: *C. purpurea* Ait. (KK 33–10, 15 mm).

Wood diffuse-porous. Growth rings indistinct, marked by 1–3 layers of radially flattened fibres. Vessels narrow, very thick-walled, rounded in outline, solitary and in short radial multiples of 2–7. Intervessel pits alternate, vestured, with abundant seemingly unbranched vestures filling the pit chambers. Vessel-ray pits with distinct borders. Helical thickenings not found. Vascular tracheids rarely occur. Fibres very thick-walled. Axial parenchyma fusiform and in strands of 2 cells, scanty paratracheal, in solitary strands near vessels, and sometimes diffuse. Rays 1- or 2-seriate, formed mostly by procumbent and square cells; sometimes with 1 or 2 marginal rows of upright cells. Crystals not observed. Silica bodies in ray and axial parenchyma cells. Brown deposits in a few vessels.

3.2.2. Calpurnia

Material studied: *C. aurea* Baker (KK 39–11, 22 mm), *C. intrusa* E. Mey. (BEVW 3249 C, 22 mm), *C. sericea* Harv. (KK 35–11, 16 mm).

Wood diffuse-porous. Growth rings absent in *C. intrusa*, or distinct, marked by flattened latewood fibres and commonly also by marginal axial parenchyma. Vessels narrow, rounded and angular in outline, solitary and in radial multiples of 2–6. Intervessel pits alternate, vestured, in *C. sericea* with rather numerous vestures, adjacent to the

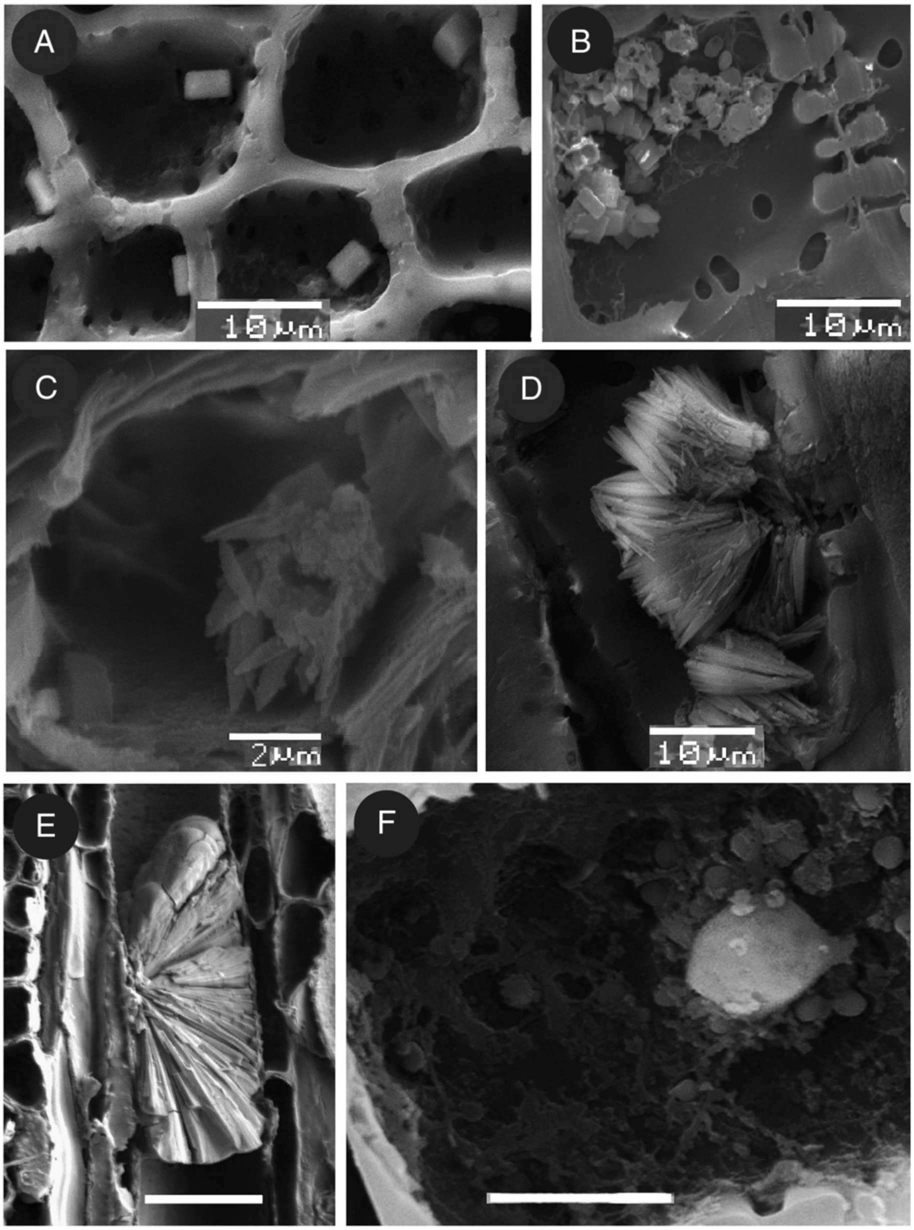

Fig. 5. Inclusions, SEM. (A) Prismatic crystals in ray cells, *Calpurnia aurea*; (B), starch grains and very small prismatic crystals in ray cell, *Amphithalea rostrata*; (C) navicular crystals in aggregates in ray cell, *Amphithalea rostrata*; (D) acicular crystals in sheaf-like aggregates in ray cell, *Cyclopia aurescens*; (E) acicular crystals in sheaf-like aggregates in vessel, *Virgilia oroboides* subsp. *oroboides*; (F) silica body in ray cell, *Cyclopia aurescens*. Scale bars: 10 μm (A, B, D, F), 2 μm (C), 50 μm (E).

inner pit apertures, varying from simple and unforked warts to strongly branched fine protuberances (vestures in *C. aurea* and *C. intrusa* were not examined by SEM). Vessel-ray pits with distinct borders. Helical thickenings not found. Vascular tracheids rare. Fibres very thick-walled (*C. intrusa*) or thin- to thick-walled. Axial parenchyma fusiform or in strands of 2 or 3 cells (*C. sericea*), or of (2–)3–4(−5) cells (*C. aurea* and *C. intrusa*). Axial parenchyma scanty paratracheal, in incomplete uniseriate sheaths near vessels (*C. aurea* and *C. sericea*), or vasicentric, sometimes aliform to confluent (*C. intrusa*), and also banded in 2–8-seriate tangential bands (in *C. aurea* and *C. introsa* also in marginal bands). Rays are 1–2(3)-seriate (*C. sericea*) or 1–3(4)–seriate. Multiseriate rays mostly of square and upright cells with few procumbent cells scattered throughout (*C. aurea* and *C. sericea*), or mostly of procumbent cells with 1 or 2 marginal rows and incomplete sheaths of square and upright cells (*C. intrusa*). Prismatic crystals in ray cells of *C. aurea* and *C. sericea*. Acicular crystals in sheaf-like aggregates in vessels and parenchyma cells of *C. intrusa*. Silica bodies in ray and axial parenchyma cells of *C. intrusa*. Brown deposits in vessels rarely in *C. intrusa* and *C. sericea*.

3.2.3. *Cyclopia*

Material studied: *C. aurescens* Kies. (ALS + BEVW 771, 9 mm), *C. burtonii* Hofmeyr & E. Phillips (ALS 641, 10 mm), *C. buxifolia* (Burm.f.) Kies (ALS 544, 10 mm), *C. genistoides* (L.) Sieber ex C. Presl (ALS 615, 7 mm; ALS 624, 10 mm), *C. intermedia* E. Mey. (ALS 646, 6 mm; ALS 647, 10 mm), *C. maculata* (Andrews) Kies (ALS 636, 9 mm; ALS 528, 14 mm), *C. plicata* Kies (ALS 670, 14 mm), *C. subternata* Vogel (KK 43–11, 22 mm).

Wood semi-ring-porous (at least weakly so) in *C. plicata*, *C. aurescens* and *C. buxifolia*, or diffuse-porous. Growth rings absent (*C. maculata* and *C. subternata*), distinct (*C. aurescens*, *C. burtonii*, *C. buxifolia* and *C. plicata*) or inistinct, marked by 1 or 2 rows of flattened latewood fibres, narrow vessels and vascular tracheids, tangentially extended groups of vessels and vascular tracheids in some species (*C. aurescens*, *C. buxifolia* and *C. plicata*) form more or less distinct rings of wider earlywood vessels; commonly growth ring boundaries also marked by marginal axial parenchyma. Vessels narrow (5–50 μm in diameter) and numerous (>125 per mm^2), in clusters and radial multiples arranged in diagonal rows (*C. maculata* [AL 528]), or mostly in large groups (>10 vessels) arranged in diagonal to dendritic pattern, or in continuous dendritic aggregations (*C. plicata*) or diagonal bands (*C. subternata*) with co-occurrence of a few solitary vessels (no solitary vessels found in *C. aurescens*, *C. genistoides* [AL 615], and *C. plicata*) and groups of 2–8 vessels. Intervessel pits alternate, vestured, with scanty vestures located at edge of inner aperture, appearing as simple rounded (*C. burtoni*, *C. intermedia* and *C. subternata*) and also weakly branched (*C. buxifolia* and *C. genistoides*) warts (vestures in *C. aurescens*, *C. maculata* and *C. plicata* not examined by SEM). Vessel-ray pits with distinct (*C. burtonii*) or reduced borders. Helical thickenings present. Vascular tracheids common. Fibres thin- to thick-walled in *C. maculata*, very thick-walled in other species. Axial parenchyma fusiform (*C. plicata*) or also in strands of 2 cells (up to 3 cells in *C. aurescens* and *C. maculata* [AL 636]), vasicentric (*C. intermedia*, *C. plicata* and *C. subternata*) or scanty paratracheal (mostly as incomplete sheaths near vessel groups), also in 1–3-seriate tangential (sometimes marginal) bands (up to 5-seriate in *C. burtonii*, up to 7-seriate in *C. aurescens* and *C. gentionoides*, up to 12-seriate in *C. plicata*). Rays 1–2(3)-seriate (*C. buxifolia* and *C. genistoides*) or 1–3 (4)-seriate (up to 5-seriate in *C. burtonii* and *C. maculata* [AL 636]), composed mostly of procumbent cells (*C. burtonii*, *C. maculata*, *C. plicata* and *C. subternata*) with square and upright cells in few (up to 5 in *C. maculata*) marginal rows and in incomplete sheaths (*C. maculata* and *C. plicata*), or mostly of square cells with procumbent and upright cells mixed throughout. Acicular crystals in sheaf-like aggregates in vessels and ray cells in all species examined except *C. plicata*. Small bands of acicular crystals in intervessel pits in *C. intermedia*. Silica bodies in ray and axial parenchyma cells. Yellowish-brown deposits common in vessels of *C. intermedia*, rare in *C. maculata* and *C. subternata*.

3.2.4. *Liparia*

Material studied: *L. hirsuta* Moench (JSB 595, 13 mm), *L. myrtifolia* Thunb. (ALS 727, 12 mm), *L. racemosa* A.L. Schutte (ALS 642, 19 mm), *L. splendens* (Burm.f.) Bos & de Wit (BEVW 3147, 11 mm).

Wood diffuse-porous. Growth rings absent (*L. splendens*), indistinct (*L. myrtifolia*) to distinct (*L. hirsuta* and *L. racemosa*), marked by flattened latewood fibres, and also by tangentially extended groups of vessels and vascular tracheids in earlywood, and by difference in vessel diameter between late- and earlywood (*L. hirsuta* and *L. racemosa*). Vessels narrow, rounded and angular in outline, mostly in radial multiples and clusters (*L. splendens*), or in nearly continuous diagonal bands and dendritic patterns, rarely solitary and in small clusters. Intervessel pits alternate, vestured, in *L. splendens* with scanty vestures at edge of inner aperture, appearing as simple warts (vestures in *L. hirsuta*, *L. myrtifolia* and *L. racemosa* not examined by SEM). Vessel-ray pits with reduced borders. Helical thickenings absent (*L. splendens*) or present. Vascular tracheids common. Fibres thin- to thick-walled. Axial parenchyma commonly fusiform, rarely in strands of 2 cells, scanty paratracheal, in incomplete sheaths near vessel groups, and also in 2–6-seriate tangential bands (*L. splendens*). Rays 1 or 2-seriate, of square and upright cells with few procumbent cells (*L. splendens*), or 1–3(4)-seriate (up to 5-seriate in *L. racemosa*), with predominance of procumbent cells in both multi- and uniseriate rays; square and upright cells in 1 or 2 marginal rows and occasionally as solitary sheath cells. Crystals not observed. Silica bodies in ray cells. Brown deposits in a few vessels of *L. myrtifolia*.

3.2.5. *Podalyria*

Material studied: *P. calyptrata* (Retz.) Willd. (KK 03–10, 22 mm), *P. lanceolata* Benth. (ALS s.n., 23 mm), *P. myrtifolia* D. Dietr. (AS + BEVW 166, 7 mm), *P. rotundifolia* (P.J. Bergius) A.L. Schutte (ALS s.n., 24 mm).

Wood diffuse-porous. Growth rings absent (*P. calyptrata* and *P. rotundifolia*), or distinct, marked by flattened latewood fibres, 2–4-seriate bands of marginal axial parenchyma, and by difference in vessel diameter between late- and earlywood. Vessels narrow to moderately wide, rounded in outline, solitary and in clusters and radial multiples of 2–10, tending to form diagonal to dendritic arrangement most distinctive in *P. lanceolata* and *P. myrtifolia*. Intervessel pits alternate, vestured, in *P. rotundifolia* with scanty vestures located at edge of inner aperture, appearing as flattened weakly branched protuberances (vestures in *P. calyptrata*, *P. lanceolata* and *P. myrtifolia* not examined by SEM). Vessel-ray pits with distinct borders. Helical thickening present. Vascular tracheids common. Fibres thin- to thick-walled. Axial parenchyma in strands of 2–4 cells, scanty paratracheal to vasicentric, in incomplete to complete 1–3-seriate sheaths near vessel groups, sometimes aliform and confluent, and also marginal in 1–4-seriate bands (*P. lanceolata* and *P. myrtifolia*). Rays are 1 or 2(3)-seriate (up to 4-seriate in *P. rotundifolia*), composed mostly of square and upright cells (*P. myrtifolia*), or mostly of procumbent cells, with 1–4 marginal rows of square and upright cells. Crystals not observed. Silica bodies in ray cells of *P. lanceolata* and *P. myrtifolia*. Yellowish-brown deposits in a few vessels of *P. myrtifolia*.

3.2.6. *Stirtonanthus*

Material studied: *S. insignis* (Compton) B.-E.van Wyk & A.L. Schutte (BEVW 3331, 14 mm), *S. taylorianus* (L. Bolus) B.-E.van Wyk & A.L. Schutte (BEVW 3169, 28 mm).

Wood diffuse-porous. Growth rings distinct, marked by flattened latewood fibres, and also by marginal axial parenchyma (*S. insignis*) or by difference in vessel diameter between late- and earlywood (*S. taylorianus*). Vessels narrow, rounded to angular in outline, in dendritic pattern. Intervessel pits alternate, vestured, with scanty vestures located at edge of inner aperture, appearing as simple rounded warts. Vessel-ray pits with reduced borders. Helical thickenings present. Vascular tracheids common. Fibres thin- to thick-walled in *S. taylorianus* and very thick-walled in *S. insignis*. Axial parenchyma in strands of 2(3) cells, sometimes fusiform, scanty paratracheal to vasicentric and confluent, in incomplete to complete uniseriate (sometimes up to 3-seriate) sheaths near vessel groups, and also banded, in interrupted tangential (sometimes marginal) 1–3-seriate bands (*S. insignis*). Rays 1–3-seriate, mostly of procumbent cells, sometimes with 1–3 marginal rows of square and upright cells (*S. taylorianus*), or mostly of square cells mixed with procumbent and upright cells throughout ray (*S. insignis*). Crystals not observed. Silica bodies in ray cells. Deposits in vessels not observed.

3.2.7. *Virgilia*

Material studied: *V. divaricata* Adamson (AO 16-09, 43 mm; KK 02-10, 28 mm), *V. oroboides* subsp. *oroboides* (P.J. Bergius) T.M. Salter (BEVW 5722, 55 mm), *V. oroboides* subsp. *ferruginea* B.-E. van Wyk (KK 44-11, 23 mm).

Wood diffuse-porous. Growth rings absent or indistinct, marked by tangential rows of larger vessel groups (*V. divaricata* [AO 16-09]). Vessels narrow to relatively wide, angular to rounded in outline, solitary, in clusters and radial multiples of 2–4(6). Intervessel pits alternate, vestured, in *V. oroboides* subsp. *oroboides* with rather numerous seemingly unbranched vestures near inner apertures (vestures not examined by SEM in *V. divaricata* and *V. oroboides* subsp. *ferruginea*). Vessel-ray pits with distinct borders. Helical thickenings absent. Vascular tracheids rare. Fibres thin- to thick-walled. Axial parenchyma in strands of 2–5 cells, scanty paratracheal to vasicentric, sometimes aliform, in complete or incomplete 1–3-seriate sheaths near vessels and vessel groups. Rays 1–3-seriate. Bi- and triseriate rays of procumbent cells, sometimes with 1–2(4) marginal rows of upright and square cells. Uniseriate rays consist mostly of square and upright cells, with few procumbent cells. Acicular crystals in sheaf-like aggregates in ray and axial parenchyma cells.

Silica bodies in ray cells of *V. divaricata* (AO 16-09). Yellowish-brown deposits in a few vessels.

3.2.8. *Amphithalea*

Material studied: *A. ericifolia* (L.) Eckl. & Zeyh. (ALS 617, 4 mm), *A. rostrata* A.L. Schutte & B.-E. van Wyk (ALS 629, 5 mm), *A. vlokii* (A.L. Schutte & B.-E.van Wyk) A.L. Schutte (ALS 743, 5 mm).

Wood diffuse-porous. Growth rings absent (*A. ericifolia*) or distinct to faint marked by marginal parenchyma. Vessels very narrow (5–18 μm in tangential diameter), mostly rounded in outline, in radial multiples and clusters of 2–10 vessels, rarely solitary, with tendency to dendritic arrangement. Intervessel pits alternate, vestured (vestures not examined by SEM). Helical thickenings on vessel walls common (*A. vlokii*), rare (*A. ericifolia*) or absent (*A. rostrata*). Vessel-ray pits with distinct borders. Vascular tracheids common. Fibres very thick-walled. Axial parenchyma fusiform and in strands of 2 cells (*A. vlokii*) or 2–4 cells (*A. rostrata*), scanty paratracheal (*A. vlokii*) to vasicentric (*A. rostrata*), and marginal, in 1 or 2-seriate tangential rows (*A. vlokii*) or 2–4-seriate bands (*A. rostrata*). Rays 1 or 2(3)-seriate, mostly of square cells mixed with procumbent cells throughout ray. Small prismatic crystals, solitary or aggregated small navicular crystals, and crystal sand in ray cells of *A. rostrata* and *A. vlokii*. Silica bodies common in ray and axial parenchyma cells of *A. rostrata*. Brown deposits in vessels in all studied species.

3.2.9. *Xiphotheca*

Material studied: *X. canescens* (Thunb.) A.L. Schutte & B.-E.van Wyk (ALS 595a, 9 mm), *X. elliptica* (DC.) A.L. Schutte & B.-E.van Wyk. (ALS 600, 8 mm), *X. phylicoides* A.L. Schutte & B.-E.van Wyk (ALS 648, 5 mm), *X. tecta* (Thunb.) A.L. Schutte & B.-E.van Wyk (ALS 597, 11 mm).

Wood diffuse-porous. Growth rings absent (*X. tecta*) or distinct, marked by marginal parenchyma, flattened latewood fibres, and sometimes also by tangential band of vessels and vascular tracheids in earlywood (*X. canescens*). Vessels narrow, rounded to angular in outline, mostly in clusters of 3–6 and large radial multiples (*X. tecta*), or in dendritic pattern (*X. canescens*). Intervessel pits alternate, vestured in *X. tecta* with scanty vestures located at edge of inner aperture, appearing as weakly branched coarse protuberances (vestures not examined by SEM in *X. canescens*, *X. elliptica* and *X. phylicoides*). Vessel-ray pits with reduced to distinct borders. Helical thickenings present. Vascular tracheids common. Fibres very thick-walled. Axial parenchyma fusiform and in 2-celled strands, scanty paratracheal (*X. tecta*) to mostly vasicentric (*X. canescens*), and also in uniseriate marginal rows (*X. canescens*) or in 1–4 seriate tangential bands (*X. tecta*). Rays 1 or 2(3)-seriate, up to 4-seriate in *X. elliptica*. Multiseriate rays mostly of square and upright cells mixed with few (*X. tecta*) or quite numerous (*X. canescens*) procumbent cells throughout ray. Crystals not observed. Silica bodies in ray and axial parenchyma cells. Yellowish-brown deposits in a few vessels of *X. canescens* and *X. tecta*.

3.3. Numerical analysis

The effects of fire-survival strategies on wood structure were assessed by one-way analysis of variance (ANOVA) using the F-test for quantitative wood characters (Table 1), and the Chi-square test for two types of rays (with a predominance of procumbent cells vs square and upright cells). The variability of wood characters was compared amongst and within two groups of samples representing seeders (reseeders) and sprouters (resprouters). As these groups differ greatly in the average size of the wood samples (mean sample radius 10.8 mm for seeders and 5.0 mm for sprouters), the 12 largest samples of both groups (with a radius >9 mm) were excluded from the data matrix to avoid the potential influence of sample size on the results.

A comparison of the wood anatomical data between the two groups revealed a statistically significant effect ($p < 0.0001$) of fire-survival strategy on the ray composition. All the seeder samples included show a predominance of procumbent cells in the rays, whereas the sprouters share rays that consist mostly of square and upright cells.

3.4. Character evolution within the Podalyrieae

Character states of the quantitative wood features listed in Table 1 as well as some qualitative ones were plotted on the tree topology based on the combined simultaneous parsimony analysis of ITS and *rbc*L data for Podalyrieae (Boatwright et al., 2008). Patterns of variation for a few wood features [the occurrence of a dendritic vessel arrangement (Fig. 6A), helical thickenings (Fig. 6B), fibre wall thickness (Fig. 6C) and acicular crystals in sheaf-like aggregates (Fig. 6D)], are apparently consistent with the topology of the phylogenetic tree and support the four main clades in Fig. 6.

4. Discussion

The wood diversity within the tribe Podalyrieae is due mainly to variations in the grouping and arrangement of vessels, as well as in the occurrence of helical thickenings on the vessel walls. Most members of the genera *Amphithalea*, *Cyclopia*, *Liparia*, *Podalyria*, *Stirtonanthus*, and *Xiphotheca* share large vessel grouping, commonly arranged in dendritic or diagonal patterns, and the presence of helical thickenings. In *Cadia*, *Calpurnia* and *Virgilia* as well as in the single species of *Liparia* (*L. splendens*), however, smaller vessel groups (up to 7 vessels), without a distinct arrangement, co-occur with the absence of helical thickenings. An apparent loss of helical thickenings in combination with large vessel grouping is found only in *Amphithalea rostrata*, whereas *Cyclopia maculata* shows relatively small vessel grouping and very prominent helical thickenings.

An increasing degree of vessel grouping — a transition from solitary vessels and small isolated groups to large groups and a dendritic pattern, has been noted in genistoid tribes closely related to Podalyrieae, i.e. in Genisteae, Thermopsideae and Crotalarieae (Metcalfe and Chalk, 1950; Yatsenko-Khmelevsky, 1954; Grosser, 1977; Baretta-Kuipers, 1981; Fahn et al., 1986; Schweingruber, 1990; Van Wyk and Schutte, 1995; InsideWood, 2004–onwards; Schweingruber et al., 2011; and our unpublished observations) as well as in some members of the tribes Sophoreae (Gasson, 1994), Hedysareae (Benkova and Schweingruber, 2004); Galegeae (Fahn et al., 1986), Loteae (Schweingruber et al., 2011) and the subfamily Caesalpinioideae (Cozzo, 1951; Schweingruber et al., 2011). This trend can be postulated to be an adaptation to water stress, because the vessel groups provide the bypass water conduits in the case of an embolism of some vessels (Zimmermann, 1983; Carlquist, 1987; Sperry, 2003). This hypothesis on the adaptive value of vessel grouping was recently demonstrated in experiments (Lens et al., 2011). Helical thickenings are mostly present in shrubs growing in Mediterranean climates. High percentages of species with spiral thickening were noted in Californian chaparral as well as in maquis and batha biomes in Israel (Baas and Carlquist, 1985; Carlquist, 1987). Batha is a secondary vegetation type comprising Mediterranean semi-shrubs that colonise abandoned cultivated lands in Israel.

The shifts in fire-survival strategy between seeders and sprouters are considered by Schnitzler et al. (2011) to be one of the most important factors for the evolutionary diversification of the Podalyrieae. Recently, Pratt et al. (2012) found that sprouters show lower water stress resistance but higher efficiency of xylem transport than seeders. Within Podalyrieae, no significant differences were found in the wood characters related to the safety and efficiency of water transport (vessel diameter, frequency and grouping) between the species with these two strategies. Nevertheless, we found that the rays in seeders consist of numerous procumbent cells whilst those of sprouters have mainly square and upright cells. This difference in ray composition is unlikely to be related to the safety or efficiency of xylem transport. Rather, this character reflects a difference in the rate of radial growth (especially during the

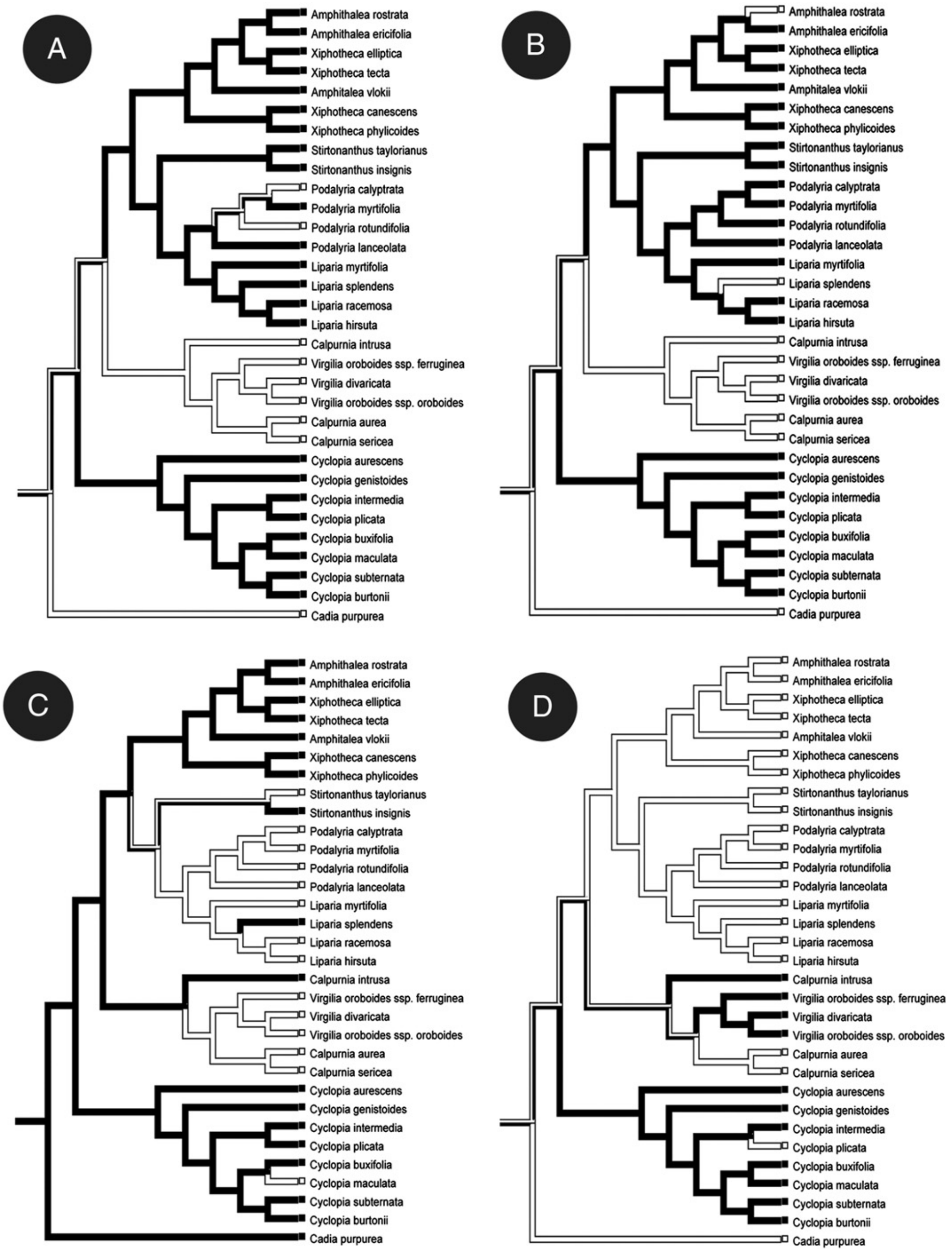

Fig. 6. Distribution of the wood character states reconstructed onto a subsample of the tree based on the combined simultaneous parsimony analysis of ITS and *rbc*L data for Podalyrieae (modified from Boatwright et al., 2008). (A) Occurrence of dendritic vessel arrangement: white — no arrangement, black — diagonal or dendritic arrangement; (B) occurrence of helical thickenings: white — absent, black — present; (C) fibre wall thickness: white — thin or thin to thick, black — very thick; (D) occurrence of acicular crystals in sheaf-like aggregates: white — absent, black — present.

early stages of stem development) that seems to be faster in seeders than in sprouters. This explanation agrees with the difference in habit between these fire-survival strategies. Commonly, seeders form a single, tall and relatively thick stem, whereas sprouters produce numerous thin stems from an underground lignotuber (Schutte et al., 1995).

The wood anatomy of all tree genera is very similar, and also strongly supports the inclusion of *Cadia* in the Podalyrieae (Boatwright et al., 2008). It was shown that *Cadia* should be excluded from the *Cadia* group of Sophoreae s.l. because it has very narrow rays and no crystals (Gasson, 1994). Our study shows that most of the Podalyrieae have 1 or 2- or 1–3-seriate rays. In four genera (*Liparia*, *Podalyria*, *Stirtonanthus* and *Xiphotheca*), crystals were not observed. The similarity in wood anatomy is especially close between *Cadia* and *Calpurnia*, the main difference being the presence of crystals in the latter.

As molecular phylogenetic analysis (Boatwright et al., 2008) suggested, *Cadia* belongs to the basal-most lineage of Podalyrieae. Thereafter the *Cyclopia* clade diverges. Then *Calpurnia* and *Virgilia* form a weakly supported clade that is sister to the rest of Podalyrieae. The members of these basally diverged clades show some common wood features. *Cadia*, *Calpurnia* and *Virgilia* have pits with numerous vestures, vessel-ray pits with distinct borders as well as the absence of helical thickenings and relatively small vessel groups. On the other hand, *Calpurnia Cyclopia* and *Virgilia*, share the very distinctive feature of the occurrence of acicular crystals in sheaf-like aggregates. Although the patterns of variation in these wood characters (Fig. 6A, B and D) are consistent with the topology of the phylogenetic tree (including the monophyly of the *Virgilia*/*Calpurnia* clade) proposed by Boatwright et al. (2008), the wood anatomical data do not contribute to the clarification of relationships between the early diverged lineages of Podalyrieae which remain poorly resolved.

As for the rest of the Podalyrieae, the members of the *Liparia*/*Podalyria*/*Stirtonanthus* subclade have mostly thin- to thick-walled fibres whereas all species of its sister subclade, comprising *Amphithalea* and *Xiphotheca*, show the presence of very thick-walled fibres. As the character mapping suggests, modifications from very thick-walled fibres in Podalyrieae to thinner fibre walls occurred at least three times in the course of its evolution (i.e. in the *Cyclopia*, *Virgilia*/*Calpurnea*, and *Liparia*/*Podalyria*/*Stirtonanthus* clades).

The Podalyrieae show a remarkable diversity of crystals in the axial and radial parenchyma. Amongst its related genistoid tribes Thermopsideae, Genisteae and Crotalarieae, the presence of crystals has thus far been reported only in a single species of *Calobota* belonging to the Crotalarieae (Metcalfe and Chalk, 1950; Yatsenko-Khmelevsky, 1954; Grosser, 1977; Fahn et al., 1986; Schweingruber, 1990; Schweingruber et al., 2011; InsideWood, 2004–onwards; Oskolski et al., in prep.). Prismatic crystals are commonly found in Fabaceae wood (Gasson, 1994), whilst in Podalyrieae we also observed acicular crystals in sheaf-like aggregates, solitary and aggregated navicular crystals, as well as crystal sand. Different types of crystals may be present in the same genus as, for example, in *Calpurnia*. Acicular crystals in sheaf-like aggregates have been described in the bark of *Virgilia* (Kotina et al., 2013-in this issue). It is also noteworthy that in Fabaceae, crystals occur mainly in axial parenchyma cells, commonly in chambered parenchyma and less often in ray cells. In a few well-studied tribes of Papilionoideae, prismatic crystals in ray cells were not found in Dipterygeae, whilst they do occur in Millettieae, Sophoreae, and Swartzieae (Fujii et al., 1994; Gasson, 1994, 2000; Gasson et al., 2004). However, in all these tribes, species with crystals in the rays are much less numerous than those with crystals in chambered axial parenchyma cells. In the species of Podalyrieae, crystals are localised in ray cells but acicular crystals in sheaf-like aggregates are also often found inside vessels. The occurrence of acicular crystals in the intervessel pits of *Cyclopia intermedia* is especially noteworthy. Such crystals are very rare within angiosperms and have been described in detail only in the fern genus *Botrichium* Sw. (Morrow and Dute, 2002).

The common occurrence of silica bodies in the ray and axial parenchyma cells in most species of Podalyrieae (this trait is absent or lost only in particular species of *Amphithalea*, *Calpurnia*, *Podalyria* and *Virgilia*) is rather surprising. Silica bodies occur in several genera of Caesalpinioideae, namely *Apuleia* Gaertn., *Dialium* L., *Dicorynia* Benth., *Distemonanthus* Benth., *Loesenera* Harms., *Sclerolobium* Vogel and *Tachigali* Aubl. but are not found in any Mimosoideae (InsideWood, 2004). They are also absent in all but one species of Papilionoideae investigated (Gasson, 1994; Fujii et al., 1994; Gasson et al., 2004; et al.). The occurrence of silica bodies in ray cells was reported in *Calobota saharae* (Coss. and Dur.) Boatwr. & B.-E.van Wyk (InsideWood, 2004, as *Genista saharae* Coss. & Dur.). This species belongs to the tribe Crotalarieae that is closely related to the Podalyrieae. Thus the occurrence of silica bodies seems to be a shared character state of these two tribes. However, further wood anatomical studies of other genistoid groups are necessary to clarify the distribution and evolutionary trends for this character.

5. Conclusions

Our wood anatomical study of several members of all genera belonging to the tribe Podalyrieae has led to the following new insights: (1) wood anatomical characters allow for the distinction between some genera, especially if unique combinations of characters are taken into account; (2) variation in some wood characters (vessel grouping and arrangement, and occurrence of helical thickenings) is consistent with the idea that their evolution occurred independently in different lineages of Podalyrieae in the course of adaptation to seasonally arid environments; (3) unlike the related genistoid tribes, the Podalyrieae show a remarkable diversity of crystals in the axial and radial parenchyma; (4) the placement of *Cadia* in the Podalyrieae is confirmed by wood anatomical data; (5) the occurrence of sheaf-like crystals and the thickness of fibres are apomorphic features for some subclades of Podalyrieae; and (6) within the Podalyrieae, seeders can be distinguished from sprouters by some ray features related to their habits, but they show no differences in the wood characters related to the safety and efficiency of water transport. Therefore, the observed range of wood diversity related both to habit and habitat, and to the phylogenetic relations within Podalyrieae, provides us with a better understanding of the trends and conditions of plant diversification that have occurred in the Cape region.

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