

WOOD ANATOMY OF THE VANGUERIEAE (IXOROIDEAE–RUBIACEAE), WITH SPECIAL EMPHASIS ON SOME GEOFRUITICES

by

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SUMMARY

The Vanguerieae is a tribe consisting of about 500 species ordered in 27 genera. Although this tribe is mainly represented in Africa and Madagascar, Vanguerieae also occur in tropical Asia, Australia, and the isles of the Pacific Ocean. This study gives a detailed wood anatomical description of 34 species of 15 genera based on LM and SEM observations. The secondary xylem is homogeneous throughout the tribe and fits well into the Ixoroideae s.l. on the basis of fibre-tracheids and diffuse to diffuse-in-aggregates axial parenchyma. The Vanguerieae include numerous geofrutices that are characterised by massive woody branched or unbranched underground parts and slightly ramified unbranched aboveground twigs. The underground structures of geofrutices are not homologous; a central pith is found in three species (*Fadogia schmitzii*, *Pygmaeothamnus zeyheri* and *Tapiphyllum cinerascens* var. *laetum*), while *Fadogiella stigmatoloba* shows central primary xylem which is characteristic of roots. Comparison of underground versus aboveground wood shows anatomical differences in vessel diameter and in the quantity of parenchyma and fibres.

Key words: Vanguerieae, Rubiaceae, systematic wood anatomy, geofrutex.

INTRODUCTION

The Vanguerieae (Ixoroideae–Rubiaceae) is a large tribe consisting of about 500 species and 27 genera. Tropical Africa is the centre of diversity (about 80% of the species are found in Africa and Madagascar), although the tribe is also present in tropical Asia, Australia, and the isles of the Pacific Ocean (Bridson 1987). Most representatives are shrubs, but some are lianas or large trees. The Vanguerieae are morphologically homogeneous and they are characterised by a number of common features which clearly define the tribe from other Rubiaceae, such as the axillary paired inflorescences, a valvate aestivation, secondary pollen presentation, one pendulous ovule per locule, pyrenes with an apical germination slit, and soft oily endosperm with very large embryos (Robbrecht 1988). In the most recent global system of the Rubiaceae (Robbrecht 1988, 1994), the Vanguerieae were placed in the subfamily Antirheoideae,

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i.e. were considered to be related to Alberteae, Guettardeae, Retiniphyllae and Knoxieae. This view corresponds to the classical systems of the Rubiaceae; Schumann (1891) for instance united these tribes in a supertribe "Guettardinae". Recent molecular analyses have proved that the Antirheoideae are polyphyletic and that Vanguerieae and the closely related Alberteae show affinities to the Ixoroideae (Bremer et al. 1995; Andreasen & Bremer 1996; Andreasen et al. 1999; Rova 1999).

The great morphological homogeneity within the Vanguerieae goes hand in hand with major difficulties in the delimitation of the genera. This problem was discussed by Verdcourt (1958, 1987: 123) who emphasised "the poorness of characters used for generic delimitation". According to him, the naturalness of the Vanguerieae should result in reducing the amount of genera. Robyns (1928) was the first taxonomist who revised the tribe, however without treating *Canthium* which is the largest genus. After a revision of the East African representatives of *Canthium* by Bullock (1932), it was Igersheim (1989) and especially Bridson (1992, and literature cited therein) who contributed to the delimitation of this large genus. The latter author divided *Canthium* s.l. into several genera on the basis of morphological characters, a decision which contradicted the ideas of Verdcourt. The division of the large *Canthium* complex was also supported by Tilney et al. (1988) who studied anatomical characters of young stems.

The wood anatomy of the Vanguerieae is poorly known (e.g., Janssonius 1926; Pearson & Brown 1932; Chang 1951; Desch 1954; Lebacqz & Deschamps 1967; Lomibao 1975; Normand & Paquis 1976; Gill & Onuja 1984; Purkayastha 1982; Sosef et al. 1998). These authors described only one or two genera, especially *Canthium* and *Psydrax* sensu Bridson (1992). Koek-Noorman and Hogeweg (1974) give a brief summary of the tribe, based however on 12 species of *Canthium*, *Keetia*, *Meyna*, *Psydrax*, *Rytigynia*, and *Vangueria* only.

The Vanguerieae, especially the genera *Pygmaeothamnus*, *Pachystigma*, *Fadogia*, *Fadogiella*, *Lagynias* and *Tapiphyllum*, are characterised by a relatively large amount of geofrutices or geoxylic shrubs. These are plants with woody massive underground parts and slightly ramified, shortly living aboveground twigs. The geofruticose habit is mainly confined to (sub)tropical savanna regions of Africa, mainly in the Zambesian region where many geofrutices are endemic in the Kalahari desert. A preliminary review of the distribution, ecology and evolution of these "underground forests of Africa" was presented by White (1976). He concluded that this growth form has not evolved in reaction to fire or frost, but as a response to unfavourable edaphic conditions. Because there is, as far as we know, no literature available about underground parts of geofrutices, the Vanguerieae are an interesting group in which to study the wood anatomy of these structures.

The present paper gives a detailed wood anatomical description of selected species of the Vanguerieae, including four geoxylic representatives.

MATERIAL AND METHODS

Wood samples of 34 species of 15 genera were obtained from the wood collection of Tervuren (Tw), Leiden (L), and the herbarium of the National Botanic Garden of Belgium (BR). The material studied is listed below with reference to the origin, collector,

and the diameter of the wood sample (in mm). ‘Large’ indicates mature wood samples although the exact diameter could not be traced. The abbreviation ‘UW’ is used for the four investigated underground wood samples of geofrutices.

Canthium ciliatum (D. Dietr.) Kuntze, South Africa, Farm Rustfontein, H.J. Schlieben 7351 (BR), 5 mm. — *Canthium inerme* (L.f.) Kuntze, Zimbabwe, A.C. Chase 5351 (BR), 7 mm. — *Canthium lactescens* Hiern, Rwanda, Kagera, J. Lebrun 9685 (BR), 10 mm. — *Canthium mundianum* Cham. & Schldtl., South Africa, Forest Research Institute 1641 (Tw 26109), large. — *Canthium parasiebenlistii* Bridson, Tanzania, Iringa region, Mufundi, Penny Pennis Farm, R.K. Brummitt et al. 18165 (BR), 8 mm. — *Canthium setiflorum* Hiern, Ethiopia, Sidamo, J. Ash 2444 (BR), 7 mm. — *Canthium simile* Merr. & Chun, China, Guangdong, Forest Research Institute 266 (Tw 42123), large. — *Cuviera longiflora* Hiern, Congo(-Kinshasa), Yangambi, J. Louis 1255 (Tw 33127), 19 mm. — *Cuviera nigrescens* Wernham, Congo(-Kinshasa), R. Deschamps 640 (Tw 8502), large. — *Fadogia schmitzii* Verdc., Congo(-Kinshasa), Kolwezi, A. Schmitz 2958 (BR), 5 mm, UW 13 mm. — *Fadogiella stigmatoloba* (K. Schum.) Robyns, Congo(-Kinshasa), F. Malaisse (BR), 5 mm, UW 12 mm. — *Keetia cornelia* (Cham. & Schldtl.) Bridson, Senegal, Casamance, J. Dewolf s.n. (Tw 51615), 8 mm. — *Keetia* cf. *gueinzii* (Sond.) Bridson, Congo(-Kinshasa), J. Louis 1198 (Tw 33115), 20 mm. — *Keetia* cf. *hispida* (Benth.) Bridson, Congo(-Kinshasa), J. Louis 1852 (Tw 33301), 22 mm. — *Lagynias pallidiflora* Bullock, Tanzania, H.J. Schlieben 2135 (BR), 5 mm. — *Meyna pubescens* (Kurz) Robyns, Thailand, Chiang Mai, Doi Sutep-Pui N.P., J.F. Maxwell 90-527 (L), 11 mm. — *Meyna spinosa* Roxb. ex Link, India, Maharashtra, Birla Institute of Scientific Research 55140 (Tw 44939), large. — *Pachystigma pygmaeum* (Schltr.) Robyns, Congo(-Kinshasa), Katanga, S. Lisowski 9669 (BR), 5 mm. — *Pachystigma solitariifolia* Verdc., Tanzania, Dodoma district, Ruffo 1164 (BR), 6 mm. — *Psydrax* sp., South India, Pomudi, C.E. Ridsdale 503 (L), large. — *Psydrax horizontalis* (Schumach. & Thonn.) Bridson, Ivory Coast, C. Geerling and J. Bokdam 1035 (BR), 8 mm. — *Psydrax subcordata* (DC.) Bridson var. *subcordata*, Congo(-Kinshasa), De Briey 134 (Tw 68), 10 mm. — *Pygmaeothamnus zeyheri* (Sond.) Robyns, South Africa, C. Puff 2631 (BR), 5 mm, UW 9 mm. — *Pyrostria* sp., Congo(-Kinshasa), J. Louis 2215 (Tw 33410), 16 mm. — *Pyrostria affinis* (Robyns) Bridson, Rwanda, G. Bouxin 784 (Tw 35034), 19 mm. — *Pyrostria madagascariensis* Lecomte, Madagascar, Thouvenot 4053 (Tw 30782), large. — *Rytigynia bagshawei* (S. Moore) Robyns var. *lebrunii* (Robyns) Verdcourt, Rwanda, G. Bouxin 784 (Tw 24176), large. — *Rytigynia umbellata* (Hiern) Robyns, Congo(-Kinshasa), Luiswishi, F. Malaisse 9601 (Tw 35154), large. — *Rytigynia verruculosa* (K. Krause) Robyns, Congo(-Kinshasa), J. Louis 5598 (BR), 10 mm. — *Tapihyllum cinerascens* (Welw. ex Hiern) Robyns var. *laetum* (Robyns) Verdc., Congo (-Kinshasa), Kumanua, F. Malaisse 9658 (BR), 5 mm, UW 35 mm. — *Vangueria* cf. *infausta* Burch., Angola, Cunenc, Roçadas, R. Deschamps et al. 1253 (Tw 28309), 26 mm. — *Vangueria infausta* Burch., Congo(-Kinshasa), Katanga, F. Malaisse 9373 (Tw 31826), 22 mm. — *Vangueriopsis* sp., Congo(-Kinshasa), J. Louis 3379 (Tw 35404), large. — *Vangueriopsis longiflora* (Hiern) Robyns, Congo(-Kinshasa), Katanga, F. Malaisse 9122 (Tw 31257), 20 mm.

Table 1. Summary of the wood anatomical features of the Vanguerieae.
 +: present, -: absent, ±: indistinctly present — AW: aboveground wood, UW: underground wood — S: solitary, RM: radial multiples —
 D: diffuse-in-aggregates, SC: scalariform.

Species	Growth rings	Vessel grouping	Vessel diameter (µm)	Vessels / mm ²	Vessel element length (µm)	Fibre length (µm)	Axial parenchyma	Rays
<i>Canthium ciliatum</i>	+	S	20-(29)-45	52-(123)-180	500-(652)-800	950-(1144)-1300	DA, (SC)	1, 2
<i>Canthium inerme</i>	+	S	25-(41)-60	106-(138)-168	450-(638)-1000	700-(982)-1350	DA	2
<i>Canthium lactescens</i>	+	S, (RM 2-4)	18-(26)-37	193-(204)-275	370-(554)-690	780-(1157)-1375	DA	2
<i>Canthium mundianum</i>	+	S	30-(49)-70	43-(53)-65	400-(656)-900	1400-(1644)-2000	DA	2, 3
<i>Canthium parasiebensisii</i>	+	S	20-(32)-40	184-(219)-252	350-(514)-650	800-(1108)-400	DA, (SC)	2
<i>Canthium setiflorum</i>	+	S	20-(27)-40	166-(206)-240	500-(680)-900	500-(1108)-1500	DA, (SC)	2
<i>Canthium simile</i>	±	RM 2-4, (S)	30-(50)-60	42-(51)-61	500-(748)-1000	1100-(1474)-1800	DA	2, (3)
<i>Civiera longiflora</i>	-	S, (RM 2-3)	30-(50)-82	27-(47)-100	455-(667)-910	1370-(1817)-2100	DA, (SC)	2, 3
<i>Civiera nigrescens</i>	-	S	27-(40)-73	26-(32)-40	825-(1039)-1555	1555-(1811)-2200	DA	2, 3
<i>Fadogia schmitzii</i> (AW)	?	S, (RM 2)	20-(28)-40	?	300-(416)-650	500-(688)-850	DA	1, (2)
<i>Fadogia schmitzii</i> (UW)	+	S, RM 2-4(-6)	35-(46)-55	149-(183)-205	300-(416)-600	600-(848)-1100	DA	2
<i>Fadogiella stigmatoloba</i> (AW)	?	RM 2-6(-8)	30-(45)-60	139-(163)-181	300-(510)-700	700-(988)-1200	D	1, (2)
<i>Fadogiella stigmatoloba</i> (UW)	+	RM 2-4(-7)	40-(55)-75	31-(44)-63	300-(494)-1000	700-(1006)-1300	DA	3, 5
<i>Keetia cornelia</i>	-	S	23-(40)-55	29-(43)-59	550-(758)-915	1000-(1285)-1550	DA	2
<i>Keetia</i> cf. <i>guinezi</i>	-	S, (RM 2-3)	25-(118)-160	4-(13)-21	600-(804)-1000	1150-(1434)-1700	DA	1, 2
<i>Keetia</i> cf. <i>hispidula</i>	-	S	18-(82)-146	12-(30)-55	640-(986)-1280	1190-(1614)-1830	DA	1, (2)

(Table 1 continued)

<i>Lagynias pallidiflora</i>	± S	20-(31)-40	72-(86)-104	400-(592)-900	550-(818)-1000	DA	2
<i>Meyna pubescens</i>	± S	14-(21)-27	81-(110)-184	450-(719)-1000	1000-(1437)-1650	DA, (SC)	2
<i>Meyna spinosa</i>	- S	36-(58)-82	11-(22)-35	550-(726)-1000	1275-(1723)-2100	DA	2, 5
<i>Pachystigma pygmaeum</i>	- S, RM 2-3	25-(38)-50	169-(210)-240	400-(634)-1000	900-(1114)-1300	DA	1, (2)
<i>Pachystigma solitariifolia</i>	± S	30-(41)-55	151-(188)-230	300-(506)-700	600-(908)-1200	DA	1, (2)
<i>Psydrax</i> sp.	- S, (RM 2-3)	18-(25)-32	38-(55)-74	550-(758)-1000	1000-(1435)-1830	DA	2, 3
<i>Psydrax horizontalis</i>	+ S	25-(40)-50	98-(147)-182	500-(770)-1100	650-(1062)-1400	D	1, 2
<i>Psydrax subcordata</i>							
var. <i>subcordata</i>	- RM 2-4(-6), (S)	85-(117)-150	22-(28)-35	350-(948)-1450	950-(1574)-2150	DA, (SC)	3, 4, (5)
<i>Pygmaeoethamnus zeyheri</i> (AW)	± S	20-(29)-40	74-(100)-116	400-(540)-800	450-(842)-1000	DA	2
<i>Pygmaeoethamnus zeyheri</i> (UW)	± S, RM 2(-4)	30-(45)-70	101-(138)-169	350-(488)-700	750-(1074)-1400	DA	2, (3)
<i>Pyrostria</i> sp.	- S	18-(30)-46	77-(133)-256	550-(858)-1000	1200-(1400)-1555	DA	2
<i>Pyrostria affinis</i>	- S	36-(46)-64	42-(57)-73	550-(779)-1000	1100-(1387)-1730	DA	2, (3)
<i>Pyrostria madagascariensis</i>	+ S	40-(53)-65	56-(68)-92	600-(882)-1250	1250-(1716)-2300	D	3
<i>Rygiyenia bagshawei</i>							
var. <i>lebrunii</i>	- S, (RM 2-3)	40-(75)-100	21-(24)-28	600-(984)-1300	1450-(1928)-2450	DA, (SC)	3, 4
<i>Rygiyenia umbellata</i>	+ S, RM 2-3	25-(35)-50	46-(85)-126	250-(576)-900	1050-(1262)-1700	DA, (SC)	1, (2)
<i>Rygiyenia verruculosa</i>	- S, RM 2-4	30-(39)-50	50-(58)-69	600-(738)-950	800-(1066)-1450	DA, (SC)	1, 2
<i>Tapiphyllum cinerascens</i>							
var. <i>laetum</i> (AW)	± S, (RM 2-3)	25-(37)-50	94-(117)-143	250-(372)-500	500-(806)-1000	DA	1, (2)
<i>Tapiphyllum cinerascens</i>							
var. <i>laetum</i> (UW)	+ S, RM 2-4(-7)	25-(36)-55	54-(103)-140	200-(340)-500	500-(756)-1000	DA	2, 3, (4)
<i>Vangueria</i> cf. <i>infausta</i>	+ S, (RM 2-3)	25-(33)-50	106-(137)-194	300-(494)-700	700-(1054)-1400	DA	1, 2, (3)
<i>Vangueria infausta</i>	+ S	23-(36)-50	41-(64)-84	460-(571)-730	1000-(1269)-1555	DA, (SC)	2, 3
<i>Vangueriopsis</i> sp.	- S	47-(78)-119	18-(25)-32	665-(923)-1235	1235-(1834)-2280	DA, (SC)	2, 3
<i>Vangueriopsis longiflora</i>	+ S	25-(32)-45	142-(182)-221	400-(560)-800	800-(1032)-1200	DA, (SC)	2

The preparation of wood for light microscopy (LM) and scanning electron microscopy (SEM) is according to Jansen et al. (1998). Macerations were prepared according to Franklin (1945). The wood anatomical terms are used in accordance with the IAWA Committee (1989). Mean length of vessel elements and fibres and mean vessel diameter were based on 25 measurements; vessels in ten fields of 1×1 mm were counted for vessel frequency. For the definition of fibre-tracheids and libriform fibres, we follow Koek-Noorman (1969).

RESULTS

The measurements for the different vessel and fibre features are always mean values. A summary of the wood anatomical results is listed in Table 1.

Wood anatomy of aboveground stems

Growth rings usually distinct in e.g. *Lagynias* and *Vangueria*; sometimes indistinct in *Canthium simile* (Fig. 1 & 4) or absent in the two species investigated of *Cuviera*.

Wood diffuse-porous. Vessels mainly solitary in *Canthium* (Fig. 3), *Keetia* (Fig. 4) and *Pyrostria*; sometimes in short radial multiples (2–3) in e.g. *Canthium simile* (Fig. 1 & 2). Vessel outline slightly angular to irregular (Fig. 1–6). Perforation plates always simple and oval to circular. Intervessel pits alternate, minute to small, vested (Fig. 14, 15 & 16), and sometimes elongated in e.g. *Vangueriopsis* sp. (Fig. 14) and *Psydrax subcordata* var. *subcordata*. Vessel-ray pits with distinct borders and similar to intervessel pits in size and shape throughout the ray cell. Smallest tangential diameter of vessel lumina 21 μm (*Meyna pubescens*), largest diameter 118 μm in *Keetia* cf. *gueinzii*, on average rather small (48 μm). Lowest vessel density 13 in *Keetia* cf. *gueinzii*, highest value 206 in *Canthium setiflorum*, mean vessel density 87. Vessel element length on average 740 μm , extreme values of 494 μm in *Vangueria* cf. *infausta* and 1039 μm in *Cuviera nigrescens*. Tyloses present in *Keetia* cf. *gueinzii*.

Fibres always with distinctly bordered pits (> 3 μm) common in both radial and tangential walls, sometimes vested. Fibres always non-septate and thin- to thick-walled; fibres very thick-walled in *Pyrostria madagascariensis*. Fibre length on average 1398 μm , shortest fibres in *Canthium inerme* (982 μm), longest fibres in *Pyrostria madagascariensis* (1928 μm).

Apotracheal parenchyma diffuse (Fig. 6) to diffuse-in-aggregates (Fig. 3, 4 & 5); in some species of *Canthium* (Fig. 1 & 2), *Cuviera*, *Rytigynia*, *Meyna*, *Psydrax* and *Vangueriopsis* also a tendency to scalariform parenchyma. Mostly 5–8 cells per parenchyma strand. Pith flecks present in e.g. *Keetia* (Fig. 4).

Rays usually 1- or 2-seriate (Fig. 10); 3-seriate in *Rytigynia bagswahei* var. *lebrunii* (Fig. 9) and in *Pyrostria madagascariensis* (Fig. 11); up to 4- or 5-seriate in *Meyna spinosa* and *Psydrax subcordata* var. *subcordata*. Rays always heterocellular, heterogeneous type I (Kribs 1935); body ray cells procumbent, with > 4 rows of upright and/or square marginal cells (Fig. 13). Perforated ray cells in e.g. *Rytigynia*, *Canthium* and *Vangueria* (Fig. 17); vessel-ray perforations always simple and circular to oval (Fig. 17); in *Fadogiella stigmatoloba*, tangential multiples of 2–5 perforated ray cells

present at the end of the long uniseriate part of a ray (Fig. 12). Rays > 12 per mm and often connected with each other (Fig. 9 & 10). Ray height often > 1 mm.

Crystals absent in the wood. Druses regularly present in the central pith in *Canthium*, *Vangueria* cf. *infausta* (Fig. 19) and *Keetia cornelia*.

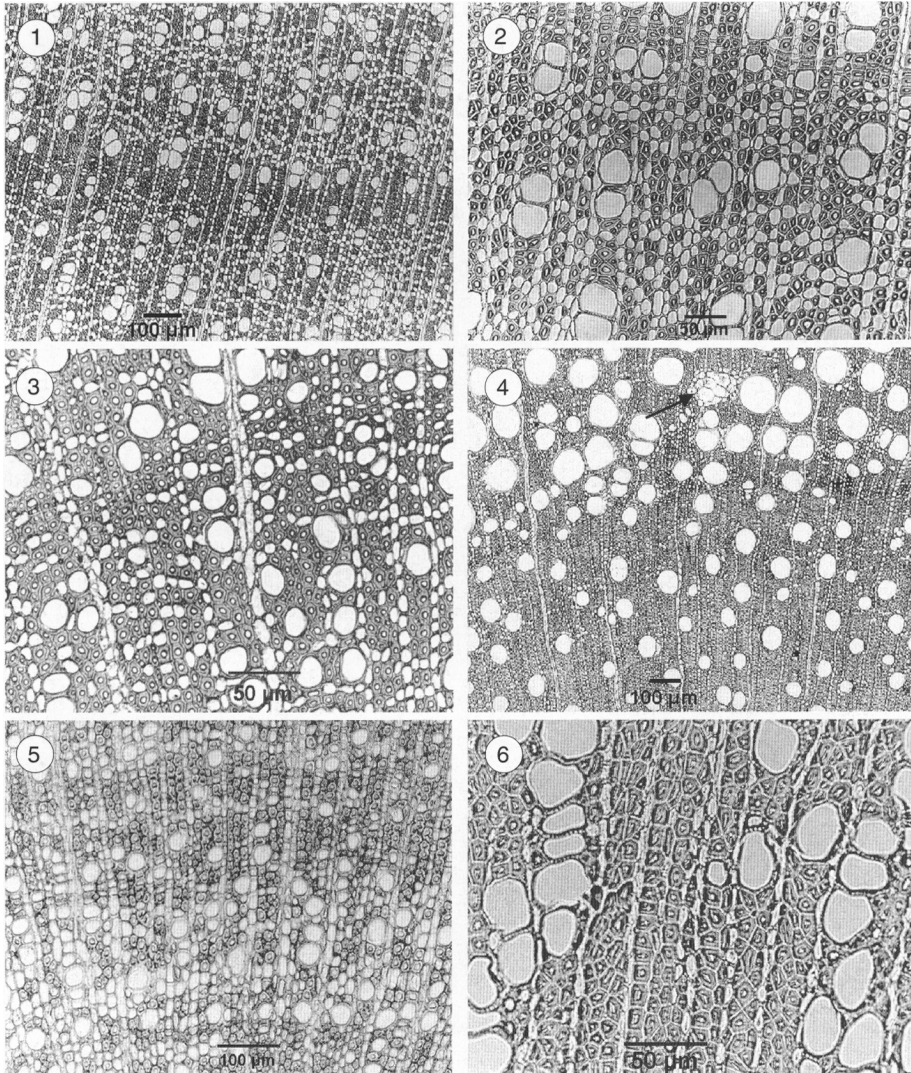


Fig. 1–6. Transverse sections. – 1: *Canthium simile*, vessels in radial multiples of 2–4. – 2: *Canthium simile*, tendency to scalariform axial parenchyma. – 3: *Canthium parasiebenlistii*, vessels solitary and diffuse-in-aggregates axial parenchyma. – 4: *Keetia* cf. *gueinzii*, wide and small solitary vessels, pith fleck present (arrow). – 5: *Pygmaeothamnus zeyheri*, vessels solitary or in small radial multiples, axial parenchyma diffuse-in-aggregates. – 6: Aboveground part of *Fadogiella stigmatoloba*, vessels in radial multiples of 2–6.

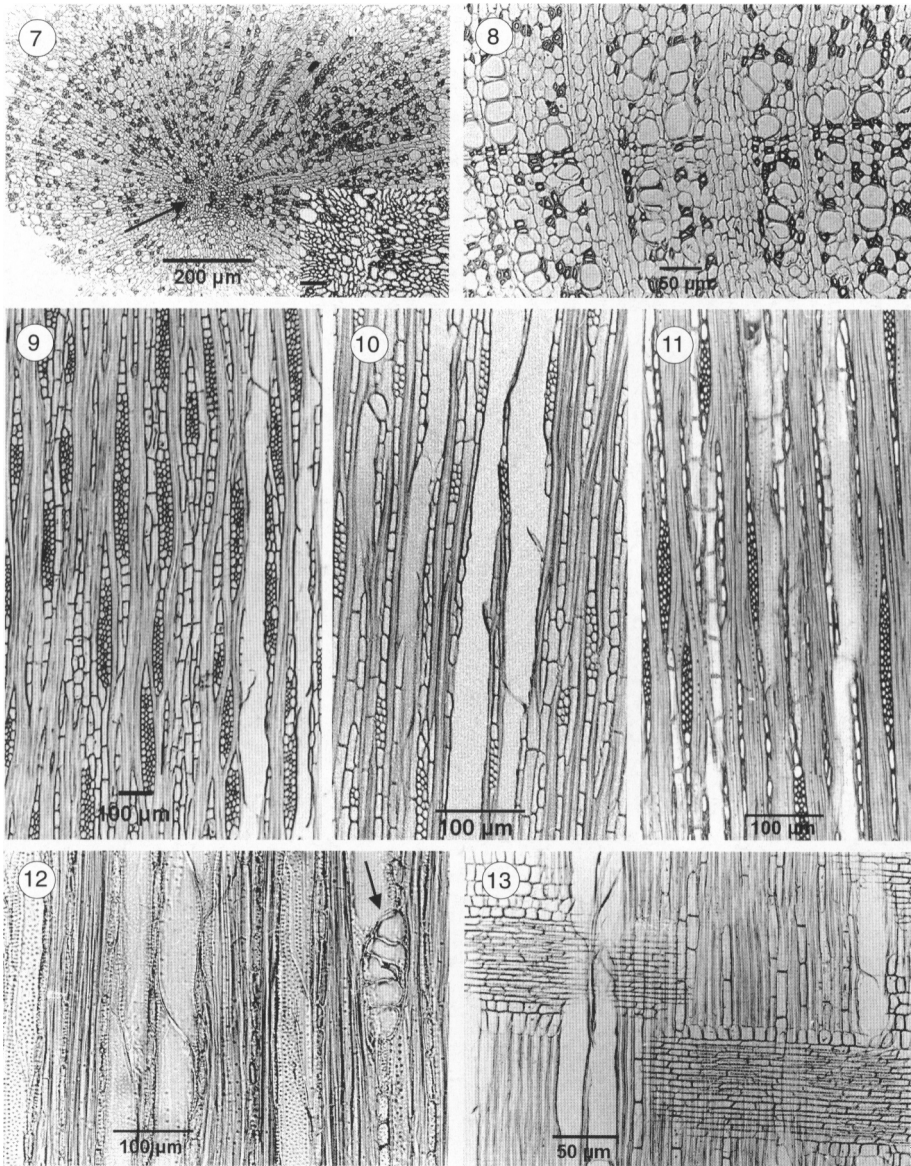


Fig. 7 & 8. Transverse section of the underground part of *Fadogiella stigmatoloba*. – 7: Primary xylem in the centre (arrow), detail of central primary xylem in the right corner (scale bar: 25 μm). – 8: Vessels in radial multiples of 2–4, axial parenchyma abundant, fibres uncommon, wide rays. – Fig. 9–12. Tangential sections. – 9: *Rytigynia bagshawei* var. *lebrunii*, 3- or 4-seriate rays, sometimes connected. – 10: *Canthium simile*: 1- or 2-seriate rays, frequently connected. – 11: *Pyrostria madagascariensis*, 3-seriate rays. – 12: Aboveground part of *Fadogiella stigmatoloba*, vessel-ray multiples of 5 perforated ray cells (arrow). – Fig. 13. *Rytigynia bagshawei* var. *lebrunii*, radial section showing procumbent body ray cells and upright/square marginal ray cells.

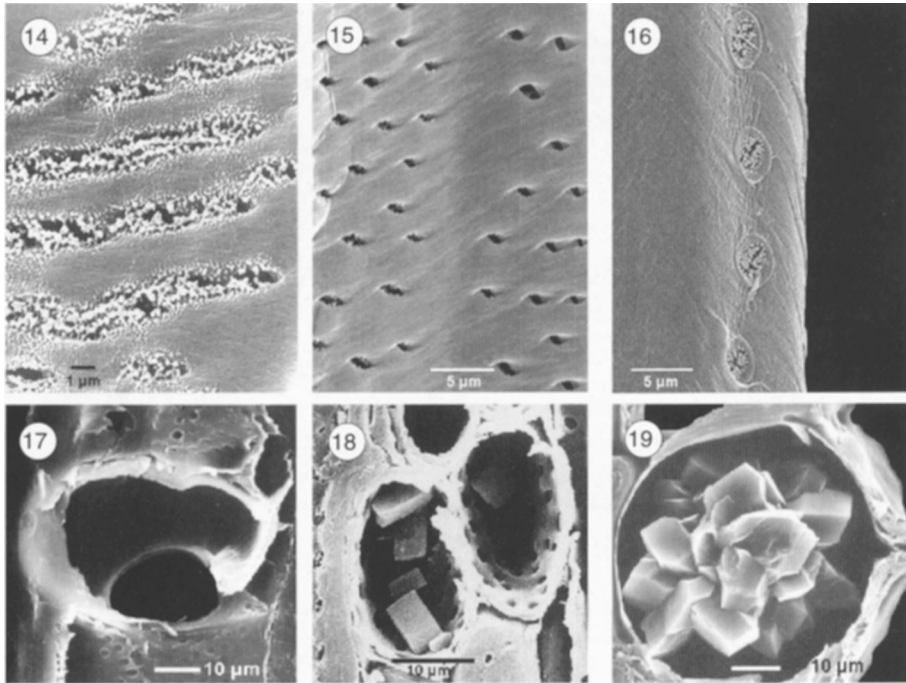


Fig. 14–16. Vestured vessel pits. — 14: *Vangueriopsis longiflora*, vestured pits viewed from the inner side of a vessel. — 15: Aboveground part of *Fadogiella stigmatoloba*, vessel pits viewed from the lumen side, vestures scarcely present near the inner pit aperture. — 16: *Lagynias pallidiflora*, vestured pits viewed from the outer surface of a vessel element, vestures fill up the pit chamber. — Fig. 17. *Vangueria infausta*, simple vessel-ray perforation. — Fig. 18. Underground part of *Fadogia schmitzii*, prismatic crystals in ray cells. — Fig. 19. *Vangueria infausta*, druse in a central pith parenchyma cell.

Underground parts of geofrutices

Several wood anatomical differences between underground and aboveground parts of the same species are found (except for *Pygmaeothamnus zeyheri*). For quantitative features, see Table 1.

In *Fadogia schmitzii*, growth rings are distinct in the underground wood, although absent in its aboveground wood; vessel pits are elongated throughout the length of some vessel members in underground wood, but non-elongated vessel pits in aboveground stems; many small prismatic, elongated, and navicular crystals present in body and marginal ray cells of underground wood (Fig. 18), although no crystals in aboveground stems. In *Tapiphyllum cinerascens* var. *laetum*, up to seven vessels occur in radial multiples of underground wood, but multiples are only up to three cells in aboveground wood. In *Fadogiella stigmatoloba*, presence of primary xylem in the underground part (Fig. 7), but a central pith in its aboveground part; distinct growth rings in the underground part (Fig. 7 & 8), but absent in its aboveground wood; vessels usually in radial multiples, but more distinct in aboveground wood (Fig. 6); pa-

renchyma tissue richly present in underground wood (Fig. 8), although diffuse in the aboveground part (Fig. 6); rays wide (mostly 3-, 4- or 5-seriate or sometimes up to 8-seriate) in underground wood (Fig. 7 & 8), while narrow (uni- or biseriate) in aboveground wood (Fig. 6).

DISCUSSION

Systematic implications

As mentioned in the introduction, the Vanguerieae show a high degree of homogeneity. This is also demonstrated by our observations, which are in agreement with previous qualitative and quantitative wood features of Rubiaceae (Koek-Noorman 1969; Koek-Noorman & Hogeweg 1974; Jansen et al. 1997a, b, 1999). Several wood anatomical features of the tribe are characteristic of Ixoroideae s.l., namely solitary vessels and a low percentage of vessels in small radial multiples, fibre-tracheids, and axial parenchyma diffuse to diffuse-in-aggregates (Koek-Noorman 1972; Jansen et al. 1997a, 1999, unpublished observations).

A transition between solitary vessels and small radial multiples of vessel elements occurs (e.g. in *Canthium*), which was also reported by Koek-Noorman and Hogeweg (1974). As in nearly all Rubiaceae, vessel-vessel and vessel-ray perforations in the study group are simple and circular to oval (Koek-Noorman 1969; Jansen et al. 1997a, b, 1999). Rudall (1982), however, described an unusual type of vessel-ray perforation in *Canthium barbatum* (= now *Cyclophyllum barbatum* – Vanguerieae). Vestures are always present in the Vanguerieae in association with vessel pits; they even appear to characterise all Gentianales (Jansen & Smets 2000). In Vanguerieae, the mean tangential diameter of vessel lumina is generally narrow, but wider in lianas (all examined species of *Keetia* and *Psydrax* subg. *Psydrax*). Wood of the lianescent *Keetia cornelia*, however, has narrow vessels probably because of the thin wood sample studied.

The most common type of axial parenchyma in the Vanguerieae is diffuse to diffuse-in-aggregates. In some species of *Canthium* and *Vangueriopsis* there is even a tendency to scalariform parenchyma. This was also observed by Koek-Noorman and Hogeweg (1974); moreover, they observed bands of axial parenchyma in *Canthium confertum*.

Tangential multiples of perforated ray cells occur in the aboveground twig of *Fadogiella stigmatoloba*. It is known that multiple perforated ray cells have little taxonomic value because the character is not constant even in a single species (Chalk & Chattaway 1932).

Although crystals in the wood of the Vanguerieae are absent, several genera (e.g. *Canthium*) show druses in their central pith. This occurrence cannot be generalised, because the wood samples investigated did not always show a central pith. Moreover, druses are missing in *Pyrostria*, *Vangueriopsis* and *Meyna*. The lack of crystals in the wood of the Vanguerieae, however, distinguishes the tribe from some other tribes of the Ixoroideae s.l. The Coffeae show abundant prismatic crystals in their ray cells (Jansen et al. 1997a), and prismatic crystals in ray cells are also present in some gen-

era of the Aulacocalyceae, Octotropideae, and Gardenieae (S. Jansen: unpublished observations). Moreover, styloids or elongate crystals and crystals in chambered axial parenchyma cells are found in respectively the Ixoreae and the Pavetteae s. s. (Jansen et al. 1999).

Comparison between underground and aboveground parts

Our results of the underground parts of geofrutescient shrubs reveal that they are not so homogeneous as we may suspect. One may clearly define two different types of underground structures. The first type, observed in *Fadogia schmitzii*, *Pygmaeothamnus zeyheri* and *Tapiphyllum cinerascens* var. *laetum*, is characterised by the presence of a central pith. These structures may be called underground stems. A feature specific of the second type of underground parts is the primary xylem situated in the centre. This root structure is only observed in *Fadogiella stigmatoloba*.

The underground stems of geofrutices are very similar to their aboveground stems, despite some quantitative differences. In *Fadogia schmitzii* and *Pygmaeothamnus zeyheri*, for instance, the tangential diameter of the vessels is smaller (mean value of the two species about 30 μm) and the fibre length is shorter (mean value of the two species 765 μm) in the aboveground stems than in their underground stems (respectively 45 μm and 961 μm). On the other hand, the vessel diameter (about 40 μm) and the fibre length (about 750 μm and 800 μm) of the underground and aboveground stem of *Tapiphyllum cinerascens* var. *laetum* are similar. Furthermore, distinct growth rings occur in the underground wood of *Fadogia* (and *Fadogiella*), but they are lacking in the aboveground wood of the same specimens. An obvious explanation for this is the smaller diameter of the aboveground wood samples because aboveground stems of geofrutices may die back towards the base as a result of savanna fires which occur frequently. Moreover, aboveground stems of some geofrutices become moribund after a relatively short period of time, even when no destructive ecological factors occur (White 1976). The underground parts, however, usually stay intact during the whole life time of the plant so that growth rings may be formed. Another difference between underground and aboveground stems is that numerous small prismatic and elongated crystals occur in underground ray cells of *Fadogia schmitzii*, while crystals are absent in the aboveground wood.

When one compares the quantitative characters of underground stems of geofrutices with aboveground stems of non-geofrutices, mainly quantitative differences are found. The vessel density is higher in the three underground stems (on average 141/mm²) compared to aboveground stems of non-geofrutices (on average 87/mm²). Also, the length of the vessel elements (740 μm) and the fibres (1398 μm) in non-geofrutescient stems is generally longer than vessel elements and fibres in underground stems of geofrutices (resp. 415 μm – 893 μm). Besides these quantitative differences, radial multiples of 2–7 vessels are more common in the underground stems.

It is generally known that there are several differences between the secondary xylem of roots and stems. Wider vessel elements with a lower vessel density characteristically occur in roots, and they generally have more parenchyma tissue and less fibres compared to stems (e. g. Cutler 1976; Metcalfe & Chalk 1983). This is confirmed

by our observations on the two types of underground wood. The vessel diameter of rootwood in *Fadogia stigmatoloba* (55 μm) is wider than the mean underground vessel diameter of other geofrutices investigated (on average 42 μm). The vessel density in the underground rootwood of *Fadogia stigmatoloba* is much lower (44/ mm^2) than that of the underground wood in the other geofrutices (on average 141/ mm^2). It is also very obvious that the amount of parenchyma tissue (axial parenchyma as well as ray parenchyma) is much higher in the underground wood of *Fadogiella stigmatoloba* than in the underground stemwood of other geofruticent species.

Apparently, stem characteristics as well as root features can be found in underground parts.

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