

The Wood Anatomy of *Rubiaceae* tribes *Anthospermeae* and *Paederieae*

By

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Key Words: *Rubiaceae*, *Anthospermeae*, *Paederieae*.—Wood anatomy, secondary woodiness.

Abstract: Detailed wood anatomical descriptions are given for the genera *Anthospermum*, *Nenax*, *Phyllis*, *Carpacoce*, *Coprosmia*, *Neogaillonia*, *Crocyllis*, *Plocama* and *Spermadictyon*, and miscellaneous wood anatomical data on the genera *Normandia*, *Pomax*, *Opercularia*, *Leptodermis* and *Aitchisonia*. The wood anatomical variation within the large genus *Anthospermum* is discussed. Secondary woodiness is likely to occur in a number of *Anthospermum* species; other species of the genus have "normal" wood structure or are herbaceous. *Nenax* and *Carpacoce* may also have secondary woodiness. The *Anthospermeae* and the *Paederieae* differ from each other primarily in the fibre type: *Anthospermeae* have fibre tracheids, *Paederieae* libriform fibres. Except for the genus *Phyllis*, wood anatomical features largely support the delimitation of the two tribes and to a certain extent the suggested groupings of genera within the two tribes.

During the preparation of a paper on the delimitation of the tribes *Anthospermeae* and *Paederieae* (PUFF 1982), it became obvious that very few wood anatomical data are available on the genera belonging to these tribes. Aims of this publication are, therefore, (1) to present wood anatomical descriptions of the woody genera and woody species belonging to genera with both woody and herbaceous representatives, (2) to point out wood anatomical variation, and (3) to compare and correlate the obtained wood anatomical data, as an independent data set, with the new classification of the tribes and the ideas on the relationships between genera and tribes as expressed by PUFF (1982).

Yet another target of the wood anatomical studies is to specifically investigate woody species of *Anthospermum* and allied genera in view of possible secondary woodiness. While, on the basis of the commonly

accepted theories of "evolutionary trends", one would expect woody species to be outfitted with characters of which at least some should be "primitive", and herbaceous species with more "derived" features in their character set, the reverse seems to be the case in the large genus *Anthospermum*. Detailed investigations of the genus (PUFF, under preparation) have shown that the (large) shrubby species are characterized by many morphological features which can clearly be considered "derived", while the herbaceous species exhibit more "primitive" traits. Similarly, the genus *Nenax*, on the basis of ample evidence considered to be closely allied to and a "segregate" of *Anthospermum*, is derived in many of its characters but consists, without exception, of (dwarf) shrubs. The occurrence of secondary woodiness could explain this apparent contradiction.

Materials and Methods

Wood samples of 14 genera were studied. Nine of these were investigated in detail; wood anatomical data on the remaining genera are incomplete, mainly because of the very small diameter of the samples. A complete list of specimens studied, including information on growth form and habitat, is given in Table 1.

Sections, 15-25 μm thick, were stained with safranin. Macerations, obtained by treatment with hydrogen peroxide and glacial acetic acid were stained with astra-blue.

Terms are used according to the Multilingual Glossary of Terms used in Wood Anatomy (IAWA 1964) with the exception of the terms "libriform fibre" and "fibre tracheid". Fibre type definitions follow REINDERS (1935), as their use appears preferable for the descriptions of rubiaceaceous woods (KOEK-NOORMAN 1969).

Mean vessel element and fibre lengths were calculated out of 25 measurements and lowest and highest averages are given; minimum and

Table 1. List of

Species	Collector and institution where voucher specimen is housed
<i>Anthospermum herbaceum</i> L. f.	PUFF 800106-1/2 WU
<i>A. randii</i> S. MOORE	PUFF 780208-2/3 WU
	PUFF 790129-2/2 WU
	PUFF 780215-3/1 WU
<i>A. ternatum</i> HIERN	PUFF 781222-1/1 WU

maximum values are given between brackets. Lowest and highest fibre length/vessel element length ratios are also included.

The parenchyma strands were often very scarce. Therefore, neither averages of lengths nor parenchyma strand length/vessel element length—ratios were calculated.

The most frequently observed highest vessel diameters and ray heights per species are taken, and the range of the lowest and highest values within each genus is given. In some species, the rays were so difficult to trace in tangential sections, that no height (in cells or μm) could be established; for this reason, numbers of rays per mm were not counted.

Table 2 summarizes some wood anatomical characters of the species belonging to the nine genera studied in detail; it also includes information on the diameter of the samples.

Tribe *Anthospermeae*

Anthospermum L. (Figs. 1 a-f)

Growth rings absent to present, mostly formed by a zone of radially flattened fibres and less and narrower vessels; sometimes a tangential row of wider vessels in the first-formed wood, or some terminal parenchyma is present.

Vessels nearly exclusively solitary or partly arranged in radial multiples, over 100 per mm^2 , angular to round, diameter up to 30–60 μm (up to 100 μm in *A. herbaceum*), vessel member length 195–620 (148–775) μm . Perforations simple, but a few reticulate plates observed in *A. galpinii*. Intervascular pits alternate, vestured, round to oval, 3–5 μm ; in *A. herbaceum* irregular, oval to elongated. Vessel-ray and vessel-parenchyma pits similar to the intervascular pits. Spiral thickenings in *A. basuticum*. Fibriform vessel members present in many species.

specimens investigated

Locality	Growth form	Habitat wet → moist → dry
SOUTH AFRICA, Natal, Drakensberge, Royal Natal National Park	herb with a \pm woody base	×
MALAWI, Zomba Plateau	as above	×
ZIMBABWE, c. 20 km E of Headlands	as above	×
MALAWI, Dedza Distr., Chongoni Forest Reserve	as above	×
MALAWI, s. foot of Mafingi Mts., on Zambian border	(short-lived) shrubby herb, woody at base	×

Table 1 (continued)

Species	Collector and institution where voucher specimen is housed	
<i>A. streyi</i> PUFF (ined.)	PUFF 790426-3/1	WU
<i>A. dregei</i> SOND.	PUFF 780810-2/1	WU
<i>A. comptonii</i> PUFF (ined.)	PUFF 790914-3/2	WU
<i>A. hirtum</i> CRUSE	PUFF 800918-4/1	WU
<i>A. welwitschii</i> HIERN	PUFF 790210-2/1	WU
	PUFF 790211-2/3	WU
<i>A. usambarensis</i> K. SCHUM.	PUFF 781220-1/13	WU
	PUFF 781223-2/1	WU
<i>A. ammannioides</i> S. MOORE	PUFF 790124-1/1	WU
<i>A. vallicolum</i> S. MOORE	PUFF 790128-1/1	WU
<i>A. emirnense</i> BAK.	PUFF 800729-1/1	WU
	PUFF 800730-2/1	WU
<i>A. ibityense</i> PUFF (ined.)	PUFF 800730-1/1	WU
<i>A. isaloense</i> HOM. ex PUFF (ined.)	PUFF 800814-1/1	WU
<i>A. spathulatum</i> SPRENGEL (= <i>A. tricostatum</i> SOND.)	PUFF 791226-4/1	WU
	PUFF 800924-3/1	WU
<i>A. aethiopicum</i> L.	PUFF 800918-1/4	WU
<i>A. littoreum</i> L. BOLUS	PUFF 790424-1/1	WU
	PUFF 790116-1/1	WU
	PUFF 790304-1/1	WU
<i>A. galpinii</i> SCHLTR.	PUFF 790303-2/1	WU
	PUFF 790415-4/1	WU

Locality	Growth form	Habitat	
		wet → moist	→ dry
SOUTH AFRICA, Natal, South Coast, Paddock Distr., Highlands Farm	cushion-forming dwarf shrub		×
NAMIBIA (SOUTHWEST AFRICA), southern Namib, Farm Kubub	as above		×
SOUTH AFRICA, Cape Prov., Witteberge, S of Matjiesfontein, Farm Fisantekraal	as above		×
SOUTH AFRICA, Cape Prov., S of Elim, on Viljoenshof rd.	straggling dwarf shrub		×
SOUTH AFRICA, Transvaal, The Downs area	(large) shrub	×	
SOUTH AFRICA, Transvaal, Westfalia Estate near Duivelskloof, Piesangkop	as above	×	
MALAWI, Misuku Hills, Willindi Forest Reserve	as above	×	
ZAMBIA, Nyika Plateau	as above	×	
ZIMBABWE, W of Juliasdale, Vukutu Farm	as above	×	
ZIMBABWE, Vumba Mts., Castle Beacon	as above	×	
MADAGASCAR, Lac Tritriva	as above	×	
MADAGASCAR, Col des Tapias, Mt. Ibity	as above	×	
MADAGASCAR, Mt. Ibity	erect dwarf shrub		×
MADAGASCAR, Isalo Massif, W of Ranohira	shrub		×
SOUTH AFRICA, Cape Prov., "Atlantis" development	(large) shrub		×
SOUTH AFRICA, Cape Prov., Witsenberg, Sneegat Peak area	small, stunted shrub	×	
SOUTH AFRICA, Cape Prov., Stanford-Papiesvlei rd., Perdeberg	(large) shrub	×	
SOUTH AFRICA, Cape Prov., Transkei side of Umtamvuna Bridge, Natal border	straggling shrub		×
SOUTH AFRICA, Cape Prov., Gonubie Mouth	as above		×
SOUTH AFRICA, Natal, Richards Bay	as above		×
SOUTH AFRICA, Natal, Nqutu-Qudeni rd., Sigqokwana ridge	shrub	×	
SOUTH AFRICA, Cape Prov., Transkei, above Port St. Johns	as above	×	

Table 1 (continued)

Species	Collector and institution where voucher specimen is housed	
<i>A. basuticum</i> PUFF (ined.)	PUFF 790113-5/3	WU
<i>Nenax dregei</i> L. BOLUS	PUFF 800831-5/1	WU
<i>N. microphylla</i> (SOND.) SALTER	PUFF 790112-4/1	WU
<i>Phyllis nobla</i> L.	MENDOZA-HEUER 75—143	Z
<i>P. viscosa</i> WEBB. & BERTH.	MENDOZA-HEUER s. n.	Z
<i>Carpacoce spermacoea</i> (REICHB.) SOND.	PUFF 791222-3/2	WU
<i>C. heteromorpha</i> (BUEK) L. BOLUS	PUFF 800101-3/1	WU
<i>C. vaginellata</i> SALTER	PUFF 800913-4/3	WU
<i>Coprosma arborea</i> KIRK	FPRL 3838	—
<i>C. montana</i> HILLEBRAND	STERN & HERBST 2981	US
<i>C. pubens</i> A. GRAY	STERN & HERBST 2924	US
	STERN & HERBST 2977	US
<i>Normandia neocalidonica</i> HOOK. f.	SCHLECHTER 14846	W
<i>Pomax umbellata</i> SOLAND.	BAUER s. n.	W
<i>Opercularia spermacoea</i> LABILL.	PRITZEL 417	W
<i>Neogaillonia aucheri</i> (GUILL.) PUFF	LAMOND 139	E
<i>N. eriantha</i> (JAUB. & SPACH) LINCH.	RECHINGER 54589	W
<i>Crocylis anthospermoides</i> E. MEY. ex SCHUMANN	PUFF 780811-1/1	WU
<i>Plocama pendula</i> AIT.	RIDSDALE & BAAS 4	L
<i>Spermadictyon suaveolens</i> ROXB.	VAN STEENIS 21125	L
<i>Leptodermis virgata</i> EDGEW.	DUTHIE 7491 a	WU
<i>L. potaninii</i> BATAL.	HANDEL-MAZZETTI 6251	WU
<i>Aitchisonia rosea</i> HEMSL. ex AITCH.	RECHINGER 29380	W
<i>Paederia verticillata</i> BL.	WARBURG s. n.	U
	ACHMAD 1598	L

Locality	Growth form	Habitat		
		wet	→ moist	→ dry
SOUTH AFRICA, Cape Prov., Drakensberge, Naudes Nek pass	cushion-forming dwarf shrub			×
SOUTH AFRICA, Cape Prov., Calvinia, Akkerendam Nature Reserve	dwarf shrub			×
SOUTH AFRICA, O.F.S., S of Fauresmith	as above			×
CANARY ISLANDS, Hierro, near La Dehesa	shrub	×		
CANARY ISLANDS, Tenerife, between Buenavista and Rocas del Fraile	as above			×
SOUTH AFRICA, Cape Prov., Robinson Pass	dwarf shrub	×		
SOUTH AFRICA, Cape Prov., Kogelberg Forest Reserve	as above			×
SOUTH AFRICA, Cape Prov., N of Porterville, Dasklip pass	as above			×
NEW ZEALAND	(small) tree	?	?	?
HAWAI, Kauai, Alakai Swamp	(large) shrub- (small) tree	×		
HAWAI, Kauai, Wahiawa Bog (Kanele Swamp)	as above	×		
HAWAI, Kauai, Kokee State Park, rd. to Mohihi	as above	×		
NEW CALEDONIA, mts. near Paita	shrub	?	?	?
AUSTRALIA, Port Jackson	± dwarf shrub			×
AUSTRALIA, between the rivers Moore and Murchison	dwarf shrub			×
PAKISTAN, Balouchistan, Chagai, 100-150 km E of Nokkundi	as above			×
IRAN, Balouchistan, Junabad, tow. Taftan vulcano	as above			×
NAMIBIA (SOUTHWEST AFRICA), southern Namib, Farm Namuskluft nr. Rosh Pinah	shrub			×
CANARY ISLANDS, Tenerife	as above			×
INDIA, Mussoorie	as above	?	?	?
INDIA, Mansehra, Hazara	dwarf shrub			×
CHINA, Yunnan Prov., Taohwa-shan Mts.	shrub			×
PAKISTAN, Quetta, Ziarat	dwarf shrub			×
JAVA, Parakantalat	liana	?	?	?
SUMATRA, Simaloer	as above	?	?	?

Fibres non-septate with bordered pits on radial and tangential walls, 3-4 μm ; thin- to moderately thickwalled. Fibre length 260-890 (200-1000) μm . F/V ratio 1.15-1.55.

Rays hardly recognizable to distinct; composed either of upright cells only, or of square and upright cells mixed with (some) rows of procumbent cells; exclusively uniseriate or uni- and 2-4-seriate, up to 10-70 μm wide, and up to 30 cells (1500 μm) high.

Parenchyma mostly diffuse, sometimes also scanty paratracheal or terminal; absent in *A. randii*; 1-4 cells per strand.

Raphids observed in pith, rays, or axial parenchyma cells in many species.

Wood Anatomical Variation in *Anthospermum*

Two or more samples were studied of eight species. A high constancy of features within species was found except for the ray structure in samples of *A. welwitschii*. In PUFF 790211-2/3, the rays were 1-12-seriate, with a relatively high percentage of procumbent cells, and the uniseriate margins were only few cells high. The other sample (PUFF 790210-2/1) fitted in with the generic description. As yet, no explanation has been found for these differences.

Although the species of *Anthospermum* are comparable in many features (vessel arrangement, shape and pitting of the vessel elements, fibre type, parenchyma pattern; see Table 2), a most noteworthy difference is found in the composition of the ray tissue. On the one hand there are "normal" rays, viz. a mixture of uni- and multiseriate rays composed of upright and square cells, sometimes mingled with some rows of procumbent cells (*A. ammannioides*, *A. galpinii*, *A. littoreum*, *A. emirnense*, *A. usambarensense*, *A. welwitschii*, *A. vallicolum*; Fig. 1 d). On the other hand rays are absent or hardly recognizable, exclusively uniseriate and consisting of one to few upright cells (*A. basuticum*, *A. randii*, *A. ternatum*, *A. isaloense*, *A. comptonii*, *A. aethiopicum*, *A. hirtum*; Fig. 1 f). In *A. dregei*, *A. streyi*, *A. ibityense* and *A. spathulatum* the rays are uniseriate, but easily distinguishable from the other secondary xylem elements, which may be due to the presence of (scanty) square ray cells (Fig. 1 e).

Other differences between the samples were found in the quantitative values, the presence or absence of growth rings and fibriform vessel elements, the tissues in which raphids occur, the presence or absence of radial vessel multiples, and the presence of (some) reticulate perforation plates and spiral thickenings of vessel elements. There appears to be a slight correlation between at least some of the varying characters. "Normal" rays are more or less associated

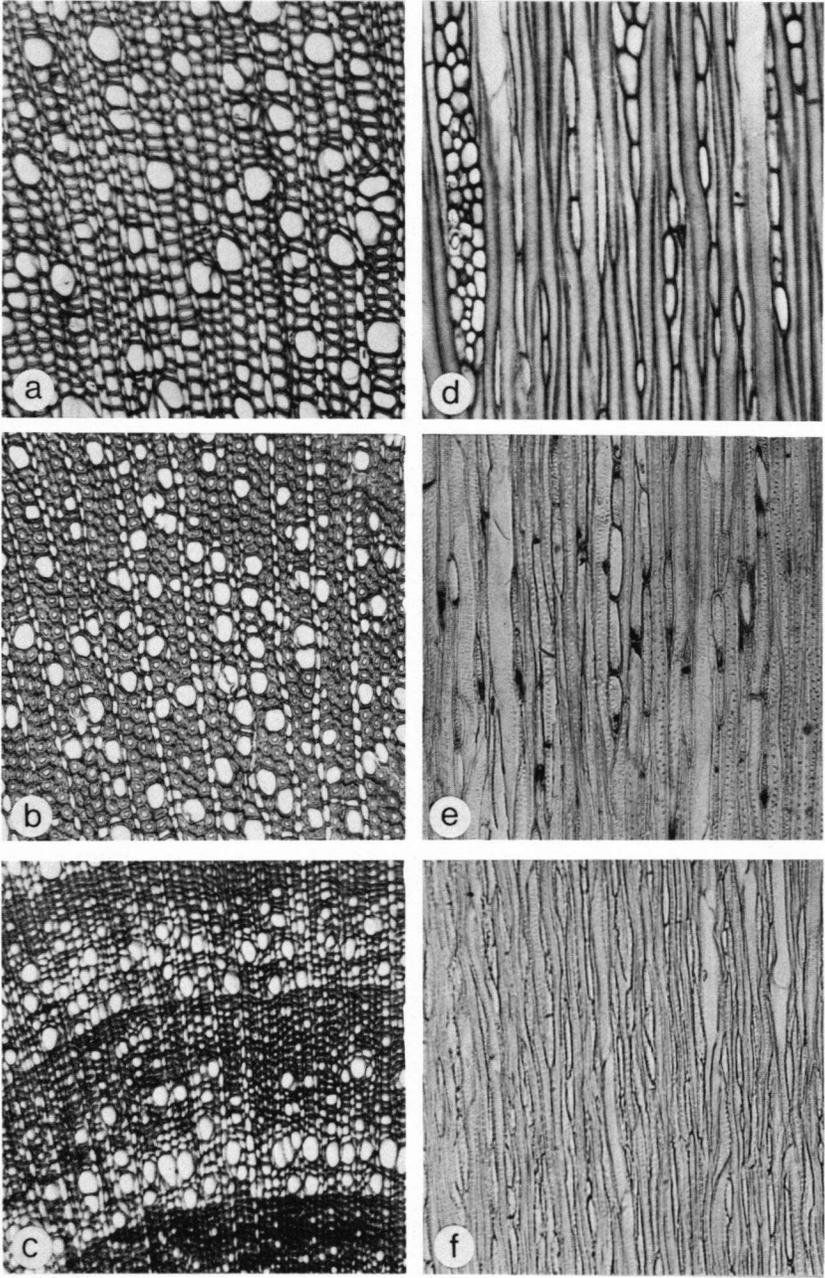


Fig. 1. Wood sections of *Anthospermum* species: a *A. littoreum* (PUFF 790424-1/1), Tr.S.; b *A. isaloense* (PUFF 800814-1/1), Tr.S.; c *A. basuticum* (PUFF 790113-5/3), Tr.S.; d *A. vallicolum* (PUFF 790128-1/1), Tg.S.; e *A. spathulatum* (PUFF 791226-4/1), Tg.S.; f *A. hirtum* (PUFF 800918-4/1), Tg.S.—All $\times 120$

with longer fibres and vessel elements and with slightly wider vessels which are nearly exclusively solitary. "Faint" rays are often found together with shorter fibres and vessel elements, narrower vessels which are partly arranged in radial multiples, and very scanty diffuse parenchyma.

Several wood anatomical features are known to vary according to the diameter of the samples. This requires careful consideration of wood variation, when only tiny stems are available. Variation in vessel arrangement and diameter, for example, may be the result of sample diameter differences. As for the ray composition, however, the smaller samples of *A. galpinii*, *A. littoreum*, *A. usambarensis*, *A. vallicolum*, and *A. welwitschii* show essentially the same structure as the larger samples of these species. Other varying features, apparently not correlated with specimen diameter, are the presence or absence of fibriform vessel elements and growth rings, the length of vessel elements and fibres, and the amount of diffuse parenchyma strands.

It has often been pointed out (e.g. CARLQUIST 1966, 1970 a, BAAS 1975) that woods from dry localities tend to form short, narrow vessels. This phenomenon is found in *A. comptonii*, *A. dregei*, *A. hirtum*, *A. streyi*, and *A. ternatum*, and to a lesser degree in *A. ibityense* and *A. randii*. Exceptions are found in *A. isaloense*, *A. littoreum*, and *A. spathulatum*. The length of the vessel elements of these species, all three occurring in dry localities, are amongst the highest of the genus (Table 2, Fig. 5). Remarkable in this respect is, that the element lengths of *A. spathulatum* (PUFF 800924-3/1) collected in a rather moist locality are found to be notably longer than those of PUFF 791226-4/1 from a dry habitat.

The extreme shortness of the vessel elements of *A. basuticum*, collected at 3 000 m alt., is in accordance with the frequently observed correlation of high altitudes and short element lengths (v. D. OEVER & al. 1981). Although it is tempting to ascribe the spiral thickenings of the vessel walls in *A. basuticum* to the high mountain locality as well, it should be emphasized that in other taxa no significant correlations between spiral thickenings and high (tropical) montane habitats were found (BAAS 1973, v. D. OEVER & al. 1981).

Nenax GAERTN.

Growth rings faint, formed by slightly more and wider vessels, in *N. microphylla* tending to semi-ringporousness combined with some more parenchyma strands.

Vessels diffuse, nearly exclusively solitary, over 100 per mm²,

angular, diameter up to 20-35 μm , vessel member length 260-305 (176-441) μm . Perforations simple. Intervascular pits alternate, vestured, oval to polygonal, 5 μm . Vessel-ray and vessel-parenchyma pits similar to the intervacular pits.

Fibres non-septate with bordered pits on radial and tangential walls, 4 μm ; moderately thickwalled. Fibre length 395-410 (303-500) μm . F/V ratio 1.34-1.54.

Rays composed of upright cells, one cell (15 μm) wide and 1-4 cells (200 μm) high.

Parenchyma (scanty) paratracheal and diffuse; in *N. microphylla* also terminal; probably 1-2 cells per strand.

Raphids observed in parenchyma cells of *N. dregei*.

Phyllis L.

Growth rings absent in *P. viscosa*, present in *P. nobla*, formed by absence of vessels and radially flattened fibres.

Vessels diffuse, mostly solitary or for a large part in radial multiples, over 100 per mm^2 , mostly angular, diameter up to 30-40 μm , vessel member length 420-425 (289-578) μm . Perforations simple. Intervascular pits alternate, vestured, oval, 3-4 μm . Vessel-ray and vessel-parenchyma pits similar to the intervacular pits. Fibriform vessel members present in *P. nobla*.

Fibres non-septate, with simple pits on radial and tangential walls, 4-5 μm ; thin- to moderately thickwalled. Fibre length 675-690 (506-939) μm . F/V-ratio 1.58-1.63.

Rays composed of upright and square cells, 1-2 cells (20 μm) wide and up to 15 cells (1200 μm) high.

Parenchyma scanty to more frequently diffuse; probably 2-3 cells per strand.

Raphids observed in the pith, and in *P. viscosa* also in axial parenchyma cells.

Carpacoce SOND. (Figs. 2 a-d)

Growth rings absent.

Vessels diffuse, nearly exclusively solitary in *C. spermacocea* and *C. vaginellata* and partly in radial multiples in *C. heteromorpha*, over 100 per mm^2 , mostly angular, diameter up to 25 μm , vessel member length 220-400 (168-594) μm . Perforations mostly simple but a few reticulate perforation plates present (relatively frequent in *C. vaginellata*). Intervascular pits alternate, vestured, oval to polygonal, 3-4 μm .

Vessel-ray and vessel-parenchyma pits similar to the intervascular pits. Fibriform vessel members present in all species.

Fibres non-septate with bordered pits on radial and tangential walls, 3-4 μm ; thin- to moderately thickwalled. Fibre length 300-595 (237-673) μm . F/V ratio 1.38-1.50.

Rays composed of upright cells, 1-2 cells (10-30 μm) wide and 10-15 cells high.

Parenchyma scanty to more frequently diffuse; probably 1-2 cells per strand.

Coprosma J. R. & J. G. A. FORST. (Figs. 2 e-f)

Growth rings absent to present, formed by radially flattened fibres, less and narrower vessels, and terminal parenchyma.

Vessels diffuse, mainly solitary or partly in radial multiples and clusters, 20 to over 100 per mm^2 , angular to round, diameter up to 50-80 μm , vessel member length 525-630 (375-800) μm . Perforations simple. Intersvascular pits alternate, vestured, oval, 4-5 μm . Vessel-ray and vessel-parenchyma pits similar to the intervascular pits, but sometimes elongated. Thin spiral thickenings observed in *C. arborea*.

Fibres non-septate with bordered pits on radial and tangential walls, 5-6 μm ; thin- to thickwalled. Fibre length 870-1010 (675-1325) μm . F/V ratio 1.53-1.66.

Rays composed of procumbent, square, and upright cells (procumbent cells lacking in *C. pubens*), up to 5-12 cells (100 to over 300 μm) wide, many cells (2000 to over 7000 μm) high.

Parenchyma paratracheal, terminal and diffuse, tending to short, one cell wide tangential bands; up to 4 cells per strand.

Raphids observed in ray cells of *C. arborea*.

The three species of *Coprosma* studied are quite similar (see Table 2) and their features are in accordance with the scanty published data on the wood anatomy of *Coprosma*. Only the occasionally reticulate perforation plates, described for some species of *Coprosma* by MEYLAN & BUTTERFIELD (1975) could not be confirmed. This seeming contradiction is not disturbing, as they report that 1. in these species the majority of the perforation plates is simple, and 2. in other species the perforation plates are exclusively simple.

The main differences between the samples studied here are found in the percentage of vessels in radial multiples, in the ray width and height, and the abundance of parenchyma strands. Comparable differences have been found in other rubiaceous genera (see, for example, KOEK-NOORMAN 1969, 1972).

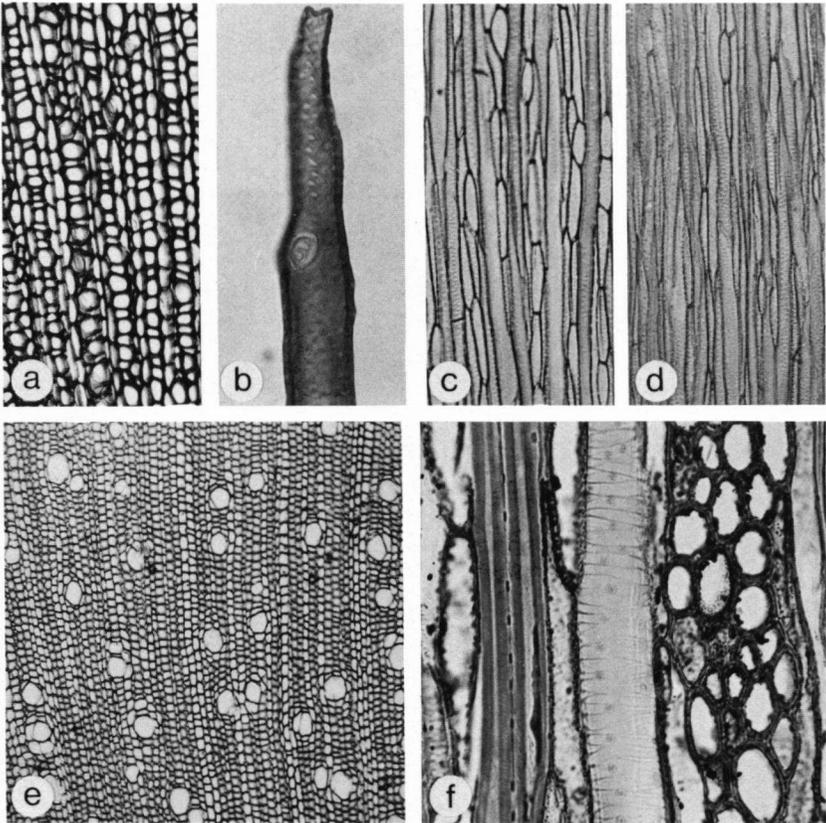


Fig. 2. Wood sections and maceration of *Carpacoe* (a-d) and *Coprosma* (e-f) species: a *C. vaginellata* (PUFF 800913-4/3), Tr.S. ($\times 120$); b *C. heteromorpha* (PUFF 800101-3/1), vessel element with reticulate perforation plate ($\times 450$); c *C. spermacoea* (PUFF 791222-3/2), Tg.S. ($\times 120$); d *C. heteromorpha* (PUFF 800101-3/1), Tg.S. ($\times 120$); e *C. pubens* (STERN & HERBST 2924), Tr.S. ($\times 45$); f *C. arborea* (FPRL 3838), Tg.S. ($\times 450$)

Comparison of the Genera of the *Anthospermeae*

It has already been pointed out that the wood anatomy of *Anthospermum* is very homogeneous. *Anthospermum*, especially those species which have faint uniseriate rays, closely resembles *Nenax*. The quantitative character ranges of the two *Nenax* species fall within the ranges found for *Anthospermum*. The same can almost be said of

Carpacoce. In the three species studied, however, the presence of some reticulate perforation plates (Fig. 2b) proved to be the one differentiating feature. Although only light-microscopical techniques were used, there is little doubt that these reticulate perforation plates closely resemble those found in *Coprosma* (MEYLAN & BUTTERFIELD 1975: SEM-graphs, Figs. 16, 21). Noteworthy in this context is the presence of a few similar plates in *Anthospermum galpinii*. The wood anatomical structure thus indicates a close alliance between the genera *Coprosma*, *Anthospermum*, *Nenax* and *Carpacoce*. It should be noted, that each of these genera of the *Anthospermeae* is characterized by wood containing fibre tracheids.

The available material of *Normandia* (subtribe *Anthosperminae*) and *Pomax* and *Opercularia* (subtribe *Operculariinae*) did not allow elaborate descriptions. It can be said, however, that the fibre tissue consists of fibre tracheids. In *Normandia*, the rays are 1-4-seriate and composed of square upright cells. The insufficient data do not allow any conclusions to be drawn as to their alliance to other genera within tribe, but, at least, the taxonomic position of *Normandia*, *Pomax* and *Opercularia* in the *Anthospermeae* is not contradicted.

Phyllis (subtribe *Anthosperminae*, together with *Anthospermum*, *Nenax* and *Carpacoce*) resembles the above genera in many aspects, but differs from the other *Anthospermeae* studied by the presence of libriform fibres instead of fibre tracheids.

Tribe *Paederieae*

Neogaiilonia LINCH. (Figs. 3 a-b)

One growth ring in both samples, indicated by vessel arrangement (see below).

Vessels mainly arranged in radial and diagonal clusters intermingled with tracheids and parenchyma cells; widest pores (60 μm) in the first-formed zone, gradually becoming narrower (30 μm); vessel member length 220-225 (219-224) μm . Perforations simple. Intervascular pits alternate, vested, 7-8 μm .

Fibres non-septate with pits with small borders on radial walls, 2-3 μm ; moderately thickwalled. Fibre length 420-425 (330-500) μm . F/V ratio 1.88-1.94.

Rays composed of upright and square cells, 1-4 cells (50 μm) wide and up to 20 cells (1000 μm) high.

Parenchyma scanty and difficult to recognize, mainly in the clusters of vessels and tracheids; probably 1-2 cells per strand.

Crocyllis E. MEY. ex HOOK. f. (Figs. 3 c-d)

Growth rings absent.

Vessels partly in radial arrangement; solitary and in radial multiples, over 100 per mm², mostly round, diameter 20-30 μ m, vessel member length 175 (120-264) μ m. Perforations simple. Intervascular pits alternate, vestured, 5 μ m. Vessel-ray pits similar to the intervascular pits.

Fibres non-septate with pits with small borders on radial walls, 2 μ m; moderately thickwalled. Fibre length 330 (228-384) μ m. F/V ratio 1.90.

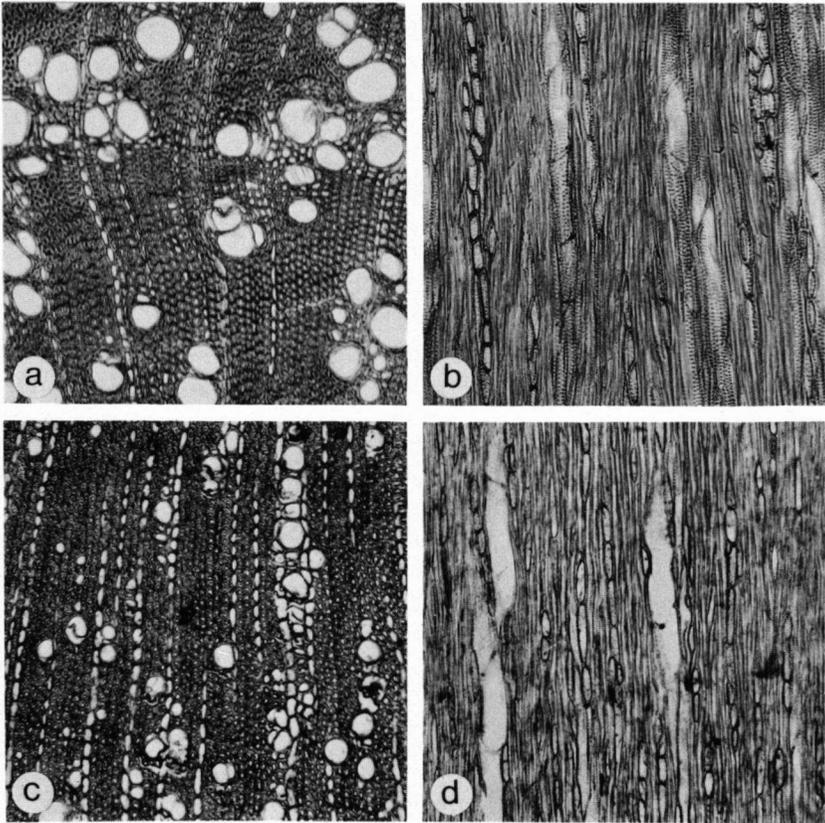


Fig. 3. Wood sections of *Neogailonia* species (a-b) and *Crocyllis* (c-d): a *N. eriantha* (RECHINGER 54589), Tr.S.; b *N. aucheri* (LAMOND 139), Tg.S.; c-d *C. anthospermoides* (PUFF 790811-1/1), Tr.S. and Tg.S.—All $\times 120$

Rays composed of upright and square cells, 1 (2) cells (15 μm) wide and 15 cells (800 μm) high.

Parenchyma absent.

Plocama ART. (Figs. 4 a-b)

Growth rings absent.

Vessels solitary and in short radial multiples, mostly arranged in radial chains, over 100 per mm^2 , round to oval, diameter up to 75 μm , vessel member length 405 (300-500) μm . Perforations simple. Intervascular pits alternate, vested, oval to polygonal, 4-5 μm . Vessel-ray and vessel-parenchyma pits similar to the intervascular pits, but partly unilaterally compound.

Fibres non-septate, with simple pits on radial and tangential walls, 233 μm ; thinwalled. Fibre length 734 (525-1 200) μm . F/V ratio 1.82.

Rays composed of procumbent, square and upright cells, 1-2 (3) cells (15-40 μm) wide and up to 10 cells (800 μm) high.

Parenchyma diffuse and in numerous short, one cell wide tangential bands; probably 1-2 cells per strand.

Raphids observed in axial parenchyma cells.

Spermadictyon ROXB. (Figs. 4 c-d)

Growth rings very faint, only indicated by slightly flattened fibres.

Vessels diffuse, mostly in radial multiples and clusters, up to 40 per mm^2 , angular, diameter 40-60 μm , vessel member length 390 (290-600) μm . Perforations mostly simple but sometimes reticulate. Intervascular pits alternate, vested, oval, 6 μm . Vessel-ray and vessel-parenchyma pits large, reticulate to scalariform.

Fibres septate and non-septate, with pits with small borders (3 μm) on radial walls; thinwalled. Fibre length 655 (420-840) μm . F/V ratio 1.69.

Rays composed of upright and square cells, 1-5 cells (20-150 μm) wide, many cells (over 3 000 μm) high.

Parenchyma paratracheal, often vasicentric, and scanty diffuse, 1-2 cells per strand.

Raphids observed in ray cells.

Comparison of the Genera of the *Paederieae*

The four genera described above have libriform fibres and similar F/V ratios (Fig. 5), but show some differences in other features. *Neogaiilonia* is distinguishable in that the wood contains islands of

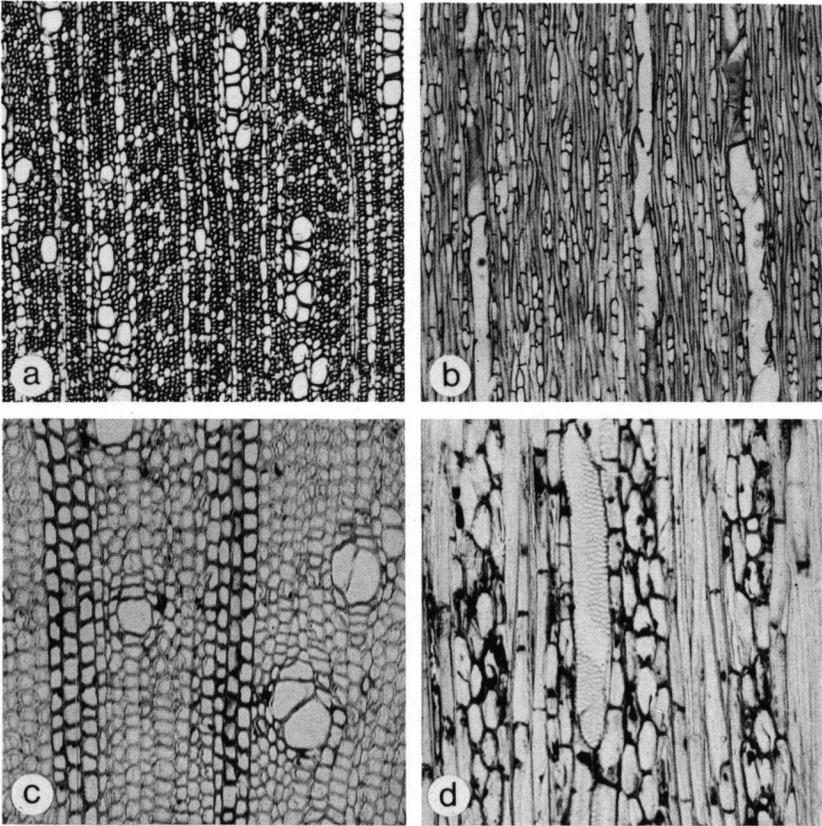


Fig. 4. Wood sections of *Plocama* (a-b) and *Spermadictyon* (c-d): a-b *P. pendula* (RIDS DALE & BAAS 4), Tr.S. and Tg.S. ($\times 30$); c-d *S. suaveolens* (v. STEENIS 21125), Tr.S. and Tg.S. ($\times 120$)

vessels, tracheids, and (some) parenchyma strands (Figs. 3 a-b). In *Crocyllis* axial parenchyma is lacking (Figs. 3 c-d). *Spermadictyon* shows very high 1-5-seriate rays (Fig. 4 d). As far as can be ascertained from the poor samples available, the wood anatomy of *Leptodermis* resembles that of *Spermadictyon* at least in the fibre type and the high, 1-4-seriate rays. The two analysed samples of *Aitchisonia* show a ground tissue composed of libriform fibres with (large) islands of vessels, tracheids and fusiform parenchyma cells, comparable with the structure of *Neogaillonnia*. *Paederia* deviates in having non-lignified ray and parenchyma cells, but in this genus the fibres are, once again, libriform. Although the available samples of *Leptodermis*, *Aitchisonia*, and

Table 2. Some wood anatomical features in species of the *Anthospermeae* and ? = could not be observed with certainty; p = procumbent; s = square; r = round; o = oval; lengths in mean values; absence of sign indicates that the vascular pits and vessel-parenchyma pits oval to oblong, of varying size; 4 = vessels mainly in radial and diagonal clusters, mingled with tracheids and

		Vessels					Fibres			
		rad. or tg. arrangement	rad. multiples present	element length (in μm)	pore diameter	pore shape	reticulate perf. plates	libriform fibres	fibr. vessel members	fibre length (in μm)
<i>Anthospermum herbaceum</i>	(1)	tg	—	?	20-100	a	—	—	?	?
<i>A. randii</i>		—	x	460	20-40	a-r	—	—	x	635
<i>A. ternatum</i>		—	(x)	360	20-40	a	—	—	x	510
<i>A. streyi</i>		tg	—	290	20-30	r	—	—	(x)	410
<i>A. dregei</i>		(tg)	—	310	20-30	r	—	—	(x)	460
<i>A. comptonii</i>		(tg)	—	195	10-20	a	—	—	x	260
<i>A. hirtum</i>		(tg)	(x)	320	15-20	a-o	—	—	x	500
<i>A. welwitschii</i>	(790211-2/3)	—	—	590	25-50	a	—	—	—	720
	(790210-2/1)	—	—	600	25-50	a	—	—	—	790
<i>A. usambarensis</i>		tg	—	660	25-60	a-r	—	—	—	815
<i>A. ammannioides</i>		(tg)	—	570	25-60	a	—	—	—	645
<i>A. vallicolum</i>		—	—	465	25-50	r	—	—	(x)	650
<i>A. emirnense</i>		—	—	630	25-50	a-r	—	—	—	750
<i>A. ibityense</i>		—	—	430	15-30	r	—	—	x	565
<i>A. isaloense</i>		—	x	650	20-40	a	—	—	—	890
<i>A. spathulatum</i>	(800924-3/1)	—	(x)	640	20-30	a	—	—	—	805
	(791226-4/1)	—	(x)	505	20-30	a	—	—	—	705
<i>A. aethiopicum</i>		—	(x)	620	20-30	a-r	—	—	x	790
<i>A. littoreum</i>		—	—	605	25-40	a	—	—	x	805
<i>A. galpinii</i>		—	—	365	25-50	r	(x)	—	x	570
<i>A. basuticum</i>	(2)	tg	—	225	15-25	a-o	—	—	—	295
<i>Nenax dregei</i>		tg	—	260	20	a	—	—	—	395
<i>N. microphylla</i>		tg	—	305	15-35	a	—	—	—	410
<i>Phyllis nobla</i>		—	(x)	425	20-40	a	—	x	x	675
<i>P. viscosa</i>		—	x	420	20-30	a	—	x	—	690
<i>Carpacoce spermacoea</i>		—	—	400	25	a	(x)	—	x	595
<i>C. heteromorpha</i>		—	x	310	25	a	(x)	—	x	460
<i>C. vaginellata</i>		—	—	220	25	a-r	x	—	x	300
<i>Coprosma arborea</i>	(2)	—	(x)	620	25-40	a	—	—	—	1010
<i>C. montana</i>	(3)	—	—	525	20-60	r	—	—	—	870
<i>C. pubens</i>		—	x	630	30-100	a	—	—	—	965
<i>Neogailonia aucheri</i>	(4)	—	—	220	30-60	r	—	x	—	425
<i>N. eriantha</i>	(4)	—	—	225	30-60	r	—	x	—	420
<i>Crocyllis anthospermoides</i>		rad	x	175	20-30	r	—	x	—	330
<i>Plocama pendula</i>	(5)	rad	x	405	30-75	r-o	—	x	—	735
<i>Spermedictyon suaveolens</i>		(rad)	x	390	40-60	a	x	x	—	655

Paederiae. × = present; — = absent; (×) = occasionally present or faint; u = upright; v = vessels; f = fibres; pa = parenchyma; a = angular; character could not be studied.—Notes (following species names): 1 = inter-2 = all vessels with spiral thickenings; 3 = vessel-parenchyma pits partly oval; parenchyma; 5 = vessel-parenchyma pits partly gash-like, oblong to elongated

Rays					Parenchyma			growth rings	diam. of sample (in mm)
width (cells)	width (in μm)	height (cells)	height (in μm)	cell types	diffuse	paratracheal	number of cells/strand		
—	—	—	—	—	×	?		v, pa	4
1	15	8?	?	u	—	—	—	v, f	5
1	20	8?	?	(s), u	?	?	?	v, f, pa	7
1	15	6	300	s, u	(×)	×	1(2)	v, (pa)	4
1	15	7	400	s, u	(×)	×	1(2)	v, p	5
1	10	3?	?	u	(×)	—	1-2	v	5
1	10	3?	300?	u	(×)	—	1	v	5
1-12	130	30	1000	p, s, (u)	(×)	—	2-3	—	40
1-2	25	12	800	s, u	(×)	—	2-3	—	15
1-2(4)	25	9	1500	(p, s), u	(×)	—	2-4	v, f, pa	13
1-2(4)	35	20	1500	p, s, u	(×)	—	1-2	(v, f)	20
1-4	70	30	1500	(p), s, u	×	—	2-4	(v, f)	21
1-3	50	24	1500	p, s, u	×	—	2	—	14
1	15	5	400	u	(×)	—	1-2	(v)	6
1	10	7	700	u	(×)	—	2-3	(v, f)	7
1	20	4	400	s, u	×	—	2	v, f, pa	7
1	20	4	400	s, u	×	—	2	(v)	7
1	10	?	?	u	(×)	—	2-3	v, f	6
1-3	30	10	400	(p), s, u	(×)	—	?	(v, f)	14
1-2	30	10	600	(p, s), u	×	—	2-3	v, f, pa	17
1	10	8	500	(s), u	(×)	—	1-2	v, pa	6
1	15	2(4)	150	u	×	×	2	(v)	8
1	15	2(3)	200	u	(×)	×	—	v, pa	8
1-2	20	15	900	s, u	(×)	—	—	(v, f)	8
1-2	20	12	1200	(s), u	×	—	2-3	—	5
1(2)	30	15	700	u	(×)	—	2	—	5
1	10	10	500?	u	(×)	—	?	—	4
1(2)	20	10	700	u	×	—	?	—	5
1-7	100		2000	p, s, u	×	×	1-3	(v, f, pa)	30
1-12	>300		>7000	p, s, u	×	—	1-4	—	?
1-5	125		>7000	s, u	×	×	—	(f)	20
1-4	50	20	1000	u	(×)	—	2	v (pa)	3
1-4	40	20?	700	s, u	(×)	—	2	v (pa)	4
1(2)	15	15	800	s, u	—	—	—	—	6
1-2	40	10	800	p, s, u	×	—	2	—	28
1-5	150	many mm in height		s, u	(×)	×	2	(f)	8

Paederia were very small, it can be stated with some certainty that, at least for *Aitchisonia* and *Leptodermis*, a close affinity to the other *Paederieae* is supported by the wood anatomy. The presence of libriform fibres in *Paederia* (a genus of lianous species) is particularly noteworthy, as the lianous habit is very often correlated with the presence of fibre tracheids. Their presence may point to and support an affinity to the other genera of the tribe.

Comparison of the *Anthospermeae* and *Paederieae*

The most striking difference between the representatives of both tribes is found in the fibre type: fibre tracheids (fibres with many bordered pits of about the same size as the intervacular pits, on both radial and tangential walls) in the *Anthospermeae*, with the sole exception of *Phyllis*, where, like in the *Paederieae*, libriform fibres (with simple or small, bordered pits occurring predominantly on radial walls) form the ground tissue. Fibre type differences have been shown to be of taxonomic value in distinguishing between a number of rubiaceaceous tribes (KOEK-NOORMAN 1969, 1970, 1972). In some tribes, they can be correlated with certain other wood anatomical characters (KOEK-NOORMAN & HOGEWEG 1974).

A comparison of F/V ratios (Fig. 5), indicating the intrusive growth of the fibres, shows that all values found for the *Anthospermeae* and the *Paederieae* are closely correlated within a narrow range (1.15-1.94). Nevertheless, both tribes can be separated (1.15-1.66 in the *Anthospermeae*, 1.69-1.94 in the *Paederieae*), although the values for *Phyllis*, *Coprosma* and *Spermadictyon* are more or less intermediate (1.58-1.69).

In other character states and ranges (vessels, rays, axial parenchyma), there are some remarkable agreements between the two tribes. The similarity in ray structure of, for example, *Coprosma* and *Spermadictyon* is noteworthy; they deviate in ray width and height from all other genera described here. *Carpacoce*, *Anthospermum galpinii* and *Spermadictyon* are linked to each other (and to *Coprosma*, see MEYLAN & BUTTERFIELD 1975) by the presence of (some) reticulate perforation plates. Parenchyma patterns vary from absent (in *Anthospermum randii* and *Crocyllis*) to rather abundantly diffuse (in species of *Anthospermum* and *Coprosma*, and *Plocama*).

Discussion

Secondary Woodiness in *Anthospermum*? Secondary woodiness is found in groups in which woodiness is phyletically in the process of

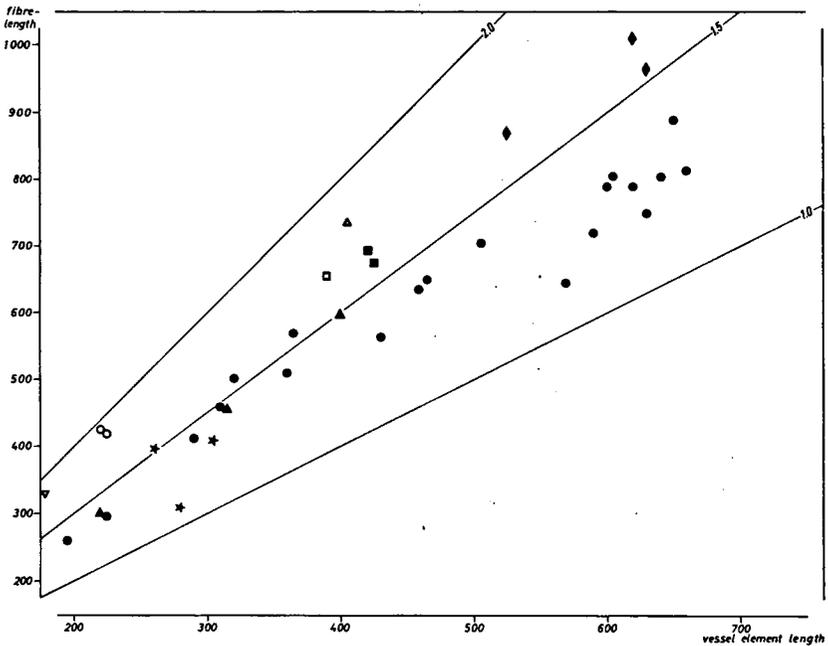


Fig. 5. Fibre length/vessel element length (F/V) ratios of species of the *Anthospermeae* (● *Anthospermum*, * *Nenax*, ▲ *Carpacoce*, ◆ *Coprosma*, ■ *Phyllis*) and the *Paederieae* (○ *Neogaillonnia*, ▽ *Crocylis*, △ *Plocama*, □ *Spermadictyon*). Each symbol represents a different species

increase (rather than decrease), with the herbaceous condition representing the (phyletic) starting point. In a series of papers, CARLQUIST (1962) has put forward that this phenomenon has occurred independently in several, unrelated, plant families. Both, CARLQUIST (1974) and KOEK-NOORMAN (1976) have shown that secondary woodiness is also most likely to occur in at least some herbaceous taxa of the primarily woody *Rubiaceae* (*Sarcopygme*, *Rubia*).

According to CARLQUIST (1975), secondary woodiness can result in secondary xylem showing features deviating from those of truly woody allies. This is due to the process of paedomorphosis, in which the presence of juvenile features from the primary xylem is protracted into the secondary wood. One of the most obvious "juvenilistic" features is the absence of rays, or the presence of uniseriate rays consisting of upright cells only, which is the result of the elongation of ray initials and the failure of these initials to subdivide horizontally (CARLQUIST 1970 b).

Within *Anthospermum*, at least some characters indicative of secondary woodiness are found. In several species, for example, the rays are absent or hardly recognizable. This may be due to the combination of elongated ray initials and short fusiform cambial initials. Such a specialized feature is often found in herbaceous groups and is reflected by the presence of short vessel elements. The combination of absent or faint rays and short vessel elements is found in *A. basuticum*, *A. ternatum*, *A. comptonii*, *A. hirtum*, and more or less in *A. randii*. Exceptions are *A. aethiopicum* and *A. isaloense*, where relatively long vessel elements are found. *A. dregei* and *A. streyi* (and to some extent *A. ibityense*) combine short vessel elements with more defined but still uniseriate rays. In *A. spathulatum*, relatively long vessel elements are found together with uniseriate but well distinguishable rays.

On the other hand, a group of species can be recognized in which the rays are of the "normal" rubiaceous type (1-4-seriate, composed of procumbent, square and upright cells, the multiseriates with long uniseriate margins of upright cells; see a. o. METCALFE & CHALK 1950). These species (*A. ammannioides*, *A. emirnense*, *A. galpinii*, *A. littoreum*, *A. usambarense*, *A. welwitschii*, and *A. vallicolum*) are among those with the longest vessel elements (Table 2, Fig. 5).

For the genus as a whole, it is remarkable that the F/V ratio is very low (Fig. 5) and that only 1-3 (4) cells were counted per parenchyma strand. Both these features indicate a low level of differentiation between the element types as compared to other *Rubiaceae*.

Thus, wood anatomically, the following situation seems to prevail in the large genus *Anthospermum*: there are (1) herbaceous species, (2) "normal" woody species (although with a low differentiation between the wood elements) and (3) species with secondary woodiness.

The ecology of the presumably secondarily woody species casts some doubt on the factors supposedly "favouring" the occurrence of paedomorphosis. CARLQUIST (1975, for example) has repeatedly stated that the occurrence of the phenomenon appears to be associated with milder climatic conditions in which there is no marked annual cessation of growth. Some of the presumed secondarily woody species of *Anthospermum*, however, clearly prefer more xeric conditions and occur in areas with a distinct (short) rainy season and a (rather long) dry season. Similarly, this holds true for the genus *Nenax*; here the tendency towards occupying increasingly drier habitats is even more pronounced. The secondarily woody *Rubia fruticosa* AIT. also is found growing in rather xeric conditions (KOEK-NOORMAN 1976). According to CARLQUIST (personal communication), however, this is not in contradiction to his theories; he emphasizes the mildness of the climate with

respect to frost and puts forward that, despite the marked seasonality in rainfall, the frost-free (or almost frost-free) climate, in which these species occur, permits secondary woodiness.

Phylogenetic Relationships in *Anthospermum*. The species with presumed "primary" woodiness are all clearly related and form a distinct group characterized by dioecy, diploidy and by their occurrence in afro-montane vegetation (except for the two southeast African species *A. galpinii* and *A. littoreum*). The group consists of the largest shrubs within the genus. It occurs from the tropical East African mountains to southeast Africa, with *A. welwitschii* extending across to the highlands of Angola; *A. emirnense* is endemic to the Madagascan mountains. The truly afro-montane species occur only as far South as the northeastern Transvaal; *A. galpinii* occurs at medium altitudes and its close ally, *A. littoreum*, has the same southeast African distribution but is confined to coastal areas (dunes). None of these species—nor any allied species—reach the Cape Floral Kingdom, where the species concentration of *Anthospermum* (and *Anthospermeae*) is highest (PUFF, under preparation).

In contrast, none of the presumed secondarily woody species are found in the afro-montane region. According to our present state of knowledge, these species have the following affinities (PUFF, unpublished): *A. randii*, *A. ternatum*, *A. dregei*, *A. comptonii*, *A. streyi*, and, perhaps, *A. hirtum* belong to the more or less widely distributed group around *A. pumilum* (= *A. rigidum* sensu auct.; little woody and, therefore, not investigated). This group, in turn, appears to be linked with the herbaceous *A. herbaceum*. *A. randii* and *A. ternatum* are very closely allied (not specifically distinct?) and occur in the vast woodlands of South Central Africa and West to Angola. *A. streyi* is narrowly endemic to the sandstone areas on the Natal South Coast (South Africa). *A. dregei*, *A. comptonii*, and *A. hirtum* are centred in the Cape Floral Kingdom, but the (closely allied) first two species show a clear tendency towards inhabiting increasingly drier habitats and localities: *A. dregei* extends as far North as the southern Namib desert (subsp. *dregei*); *A. comptonii* is confined to dry and hot karroid valleys within Capensis. The unusually large average pollen diameters of *A. hirtum* suggest polyploidy; the other species are, as far as it is known to date, diploid. Sex distributions are variable; most common are gynodioecious populations and populations with gynomonocious and purely female individuals next to each other; *A. streyi* may have only hermaphrodite flowers. *A. comptonii* is strictly dioecious. All herbaceous species of this group (*A. herbaceum* and *A. galioides* = *A. ciliare* sensu auct.; both diploid) are polyoecious.

A. ibityense (confined to quartzite hills) and its presumed close ally *A. longisepalum* (confined to sandstone) are isolated Madagascan endemics without any apparent close allies in either Madagascar or on the African mainland. *A. isaloense*, also endemic to Madagascar, appears similarly isolated, although it may have very remote links to the afro-montane species group described above; it is dioecious.

A. aethiopicum is endemic to and *A. spathulatum* is centred in the Cape Floral Kingdom; the latter also extends into the surrounding drier (karroid) areas. This species pair (apparently fairly closely related) is dioecious and consists of large to small shrubs; the former is 2x, the latter 2x, 4x or 6x. The dioecious, high Drakensberg endemic *A. basuticum* appears linked to *A. tricostatum* via *A. monticolum* (not investigated wood anatomically).

Wood anatomical findings, in combination with the information presented above, allow the following speculations as regards to the phylogeny of *Anthospermum*: From a hypothetical "normal" ("primarily") woody ancestor with hermaphrodite flowers which, perhaps, were not yet (fully) adapted to wind pollination, two (unequal) branches could have evolved. One could have remained woody, could have become better adapted to wind pollination (and, in the course of time, have become dioecious) and could have acquired a number of derived features. The other branch could have progressed to herbaceousness, while retaining some fairly primitive characters (polygamy; flowers anemophilous, but still not "perfectly" adapted—e.g. with still distinct, fairly long corolla tubes, such as in *A. herbaceum*, *A. randii* or *A. ternatum*). From this stock, secondarily woody taxa could have evolved which retained, in part, some primitive features (polygamy in some species, for example), but also showed a number of derived characters (polyploidy, for example). The secondarily woody species thus appear to be as "young" as or "younger" than the herbaceous species. It is, in this context, interesting to note that both the "primarily woody" group (*A. usambarense*, etc.) and the herbaceous (but otherwise characterized by many primitive features) *A. herbaceum* occur in afro-montane regions, while the woody species with juvenilistic trends (i.e. "young" species) are centred in the Cape Floral Kingdom or in drier parts of Madagascar. This, perhaps, is an indication that the genus as a whole may have originated somewhere in the African tropics rather than in Capensis. Hence the high concentration of *Anthospermum* species in the Cape Floral Kingdom may not mean that the genus has had its origin there. Similar conclusions were reached by authors dealing with other genera whose distributions and species concentrations are similar to those of

Anthospermum (TAYLOR 1978, p.181, and literature cited there). Similarly, Madagascar—in spite of having the second highest concentration of *Anthospermum* species—is unlikely to be the centre of origin of the genus. A detailed discussion of this problem is under preparation (PUFF).

Phylogenetic Relationships Between the Genera and Tribes; a Cladistic Approach (Fig. 6). Phylogenetic speculations may be based on a phenetic or numerical approach, i.e. on considerations of the extent of similarity or dissimilarity of taxa. In the present study, this approach does not lead to credible suggestions, as the rather faint correlations between features and character states result in a “diffuse” pattern.

In a cladistic approach, one starts by looking for derived features in a data set and by comparing specimens characterized by these features with a “sister group” with less or non-derived (“primitive”) character states (cf. BREMER & WANNTORP 1978). Amongst the material analysed, an obviously derived wood anatomical feature is the presence of islands of vessels, tracheids and some parenchyma strands (*Neogailonia*). This can be coupled with arrangement of vessels (at least partly) in radial multiples and chains (*Crocylis*). This couplet may be linked successively along the pairs: parenchyma absent or diffuse; vessel arrangement radial or diffuse; rays low and perforation plates simple or rays relatively high and perforation plates (at least in part) reticulate (successively *Plocama*, *Phyllis*, *Spermadictyon*).

The hypothetical ancestor of this “branch” would, therefore, be characterized wood anatomically by diffuse vessels, partly in radial multiples, some reticulate perforation plates, non-septate libriform fibres, relatively broad (1-5-seriate?) and high rays and diffuse (and vasicentric) parenchyma.

The phenomenon of juvenilism may provide a second starting point (*Anthospermum* in part, *Nenax*). This may be combined with the absence of juvenilistic trends (*Anthospermum*, in part). A common ancestor, therefore, would be characterized by solitary vessels, ground tissue consisting of fibre tracheids, 1-4-seriate rays and (scanty) diffuse parenchyma. This group may be coupled with the next on the basis of simple or (at least some) reticulate perforation plates (*Coprosma*, *Carpacoce*).

Coprosma and *Carpacoce* are fairly similar. The main difference is found in the ray size. A combination of *Carpacoce* with *Anthospermum* and *Nenax* on the basis of juvenilistic trends seems less likely. Juvenilism in itself does not prove relationship between taxa.

In this concept, all mentioned *Anthospermeae* (with the exception of *Phyllis*) are thought to be derived from an ancestor with the following

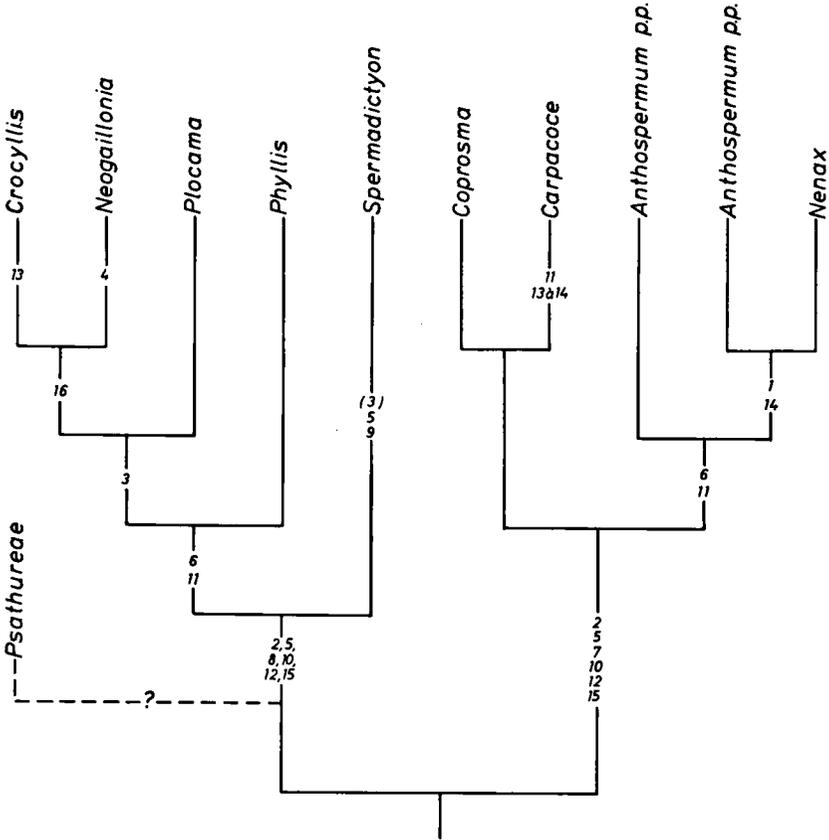


Fig. 6. Cladogram showing wood anatomical relationships between genera of the *Anthospermeae* and *Paederieae*. 1—vessels nearly exclusively solitary; 2—vessels (partly) in radial multiples; 3—vessels (partly) in tangential arrangement; 4—vessels and tracheids intermingled in islands (eventually with some parenchyma strands); 5—(some) reticulate perforation plates; 6—exclusively simple perforation plates; 7—fibre tracheids; 8—non-septate libriform fibres; 9—septate libriform fibres; 10—rays high; 11—rays lower than 1500 μm ; 12—rays multiseriate; 13—rays predominantly uniseriate; 14—rays absent or faint; 15—parenchyma diffuse and in short, one cell wide, tangential bands; 16—parenchyma absent

structure: vessels partly in short radial multiples, perforation plates (at least partly) reticulate, fibre tracheids, high multiseriate rays and diffuse parenchyma (perhaps tending to short, one cell wide, tangential bands).

Although it is also possible to construct an alternative cladogram, in which *Phyllis* is combined with *Anthospermum* and *Nenax* (on the basis

of fibre type differences), there are reasons to believe that the cladogram presented here is the more convincing one (see below).

The main difference between the two halves of the cladogram lies in the fibre type: fibre tracheids vs. libriform fibres. Earlier findings (KOEK-NOORMAN & HOGEWEG 1974; HOGEWEG & KOEK-NOORMAN 1975) not only stress the taxonomic importance of fibre type differences, but also, on the basis of numerical analyses, point to a strong correlation between fibre type (in the definition given by REINDERS 1935) and other wood anatomical features within some rubiaceous tribes. In the present study, there are also some indications of correlations between fibre type and other features which, however, are not used in the composition of the cladogram: there is, for example, a slight difference in the F/V ratio between the two groups (see Fig. 5) and in the group of genera with fibre tracheids, the vessels may be arranged tangentially, contrary to the radial chains in some genera with libriform fibres.

In spite of the known shortcomings of the cladistic method (see, for example, BURGER 1979 and literature cited herein), we shall attempt to compare the cladogram with the newly proposed delimitation of the tribes *Anthospermeae* and *Paederieae* and the subtribal groupings of genera (PUFF 1982) which is further supported by recent pollen morphological investigations (ROBBRECHT 1982):

With the exception of the placement of *Phyllis*, the cladogram supports the delimitation of the *Anthospermeae* and the *Paederieae*: the *Anthospermeae* have wood with fibre tracheids and the *Paederieae* have wood with libriform fibres. While *Phyllis*, on the basis of numerous other characters, clearly belongs to the *Anthospermeae*, it should, on wood anatomical grounds (presence of libriform fibres!) be placed somewhere in the *Paederieae*. Libriform fibres are commonly thought to be more derived than fibre tracheids (*cf.* TIPPO 1946, for example); accepting this assumption it can be speculated that *Phyllis* may, in isolation, have developed this wood anatomical character.

It is, perhaps, interesting to point out that the wood anatomical rating of libriform fibres as "derived" also clashes with the presumed relationships between the tribes. While there are several indications that the *Anthospermeae* may be more derived than the *Paederieae* (PUFF 1982) and that both tribes may be linked to the *Psathureae* (= *Psychotriaceae*), wood anatomical data give a contrasting picture: the *Anthospermeae* would be more "primitive" than the *Paederieae* and the *Psathureae* (also with libriform fibres; KOEK-NOORMAN 1969). The *Paederieae*, furthermore, exhibit other highly derived features (vessel arrangement and vascular tracheids) and the largest wood anatomical variation, whereas the *Anthospermeae*, generally, have a relatively

primitive wood anatomical structure, although the presence of paedomorphosis may be considered a "derived" condition.

Within the *Paederieae*, wood anatomy fully supports the suggested close affinity between *Neogaillonia*, *Crocyllis* and *Plocama*. The occurrence of islands of vessels, tracheids (and parenchyma) in *Aitchisonia* (not included in the cladogram because of lack of complete wood anatomical data), furthermore, is in accordance with the presumed affinity to *Neogaillonia*. Also the relationship between *Spermadictyon* and *Leptodermis* (not included in the cladogram for the same reasons as *Aitchisonia*) can, with some reservations, be supported by wood anatomy.

Within the *Anthospermeae*, wood anatomical data confirm the close relationship between *Anthospermum* and *Nenax*. On wood anatomical grounds, a direct affinity between *Carpacoce* and (an ancestor of) *Anthospermum* seems possible, but another, perhaps better, combination is found with *Coprosma*. This would support the presumed ancient links of *Carpacoce* with a non-African group (PUFF 1982).

In our cladogram, the hypothetical ancestor of the *Anthospermeae* is more or less similar to *Coprosma*, which may indicate that the *Anthospermeae* may have arisen from a *Coprosma*-like ancestor.

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