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THE SECONDARY PHLOEM OF SOME COMBRETACEAE AND THE SYSTEMATIC POSITION OF STREPHONEMA PSEUDOCOLA A. CHEV.

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SUMMARY

The anatomy of the secondary phloem of *Strephonema pseudocola* A. Chev. has been compared with that of some other representatives of the Combretaceae originating from the Ivory Coast, Africa. This is done because there exist different opinions about the systematic position of the genus. Also the anatomical wood properties of the species concerned were investigated and the results compared with those found by others. Although *Strephonema pseudocola* differs fundamentally from the rest of the family, the anatomy of the secondary phloem, may be more so than that of the secondary xylem, leads us to retain the genus in the Combretaceae, but as a distinctly separate subfamily. By its bark and anatomical wood characters, the genus has some claim to be an ancestral type in the Combretaceae.

1. INTRODUCTION

The tribal and generic classification of the Combretaceae is based on ENGLER & DIELS (1899), as modified by EXELL (1931) and EXELL & STACE (1966). In this system the family is divided into two subfamilies Strephonematoideae, containing a single genus *Strephonema*, and Combretoideae, consisting of four tribes:

Combreteae with the genera *Combretum*, *Pteleopsis*, *Quisqualis*, *Guiera*, *Thiloa* and *Calopyxis*;

Terminalieae with the genera *Terminalia*, *Bucida*, *Buchenavia*, *Ramatuella*, *Conocarpus* and *Anogeissus*;

Calycopterideae with the genus *Calycopteris* and

Lagucularieae with the genera *Laguncularia*, *Lumnitzera* and *Macropteranthes*.

There are about 500 species in the family. The classification is based upon morphological characters of the flowers, fruits and vegetative shoot. The geographical range of each genus is stated; all the species belonging to the Combretaceae are tropical or only in a few cases subtropical.

However, the family is a natural and well-defined taxon (EXELL 1954, VERHOEVEN & VAN DER SCHIJFF 1973), only if we exclude *Strephonema* with five species in tropical West-Africa, all trees or shrubs. The genus *Strephonema* differs from the rest of the family in its semi-inferior ovary, and was originally placed in the Lythraceae and later in several other families. Other unique

features of this genus are its revolute domatia, characteristic pattern of epidermal cells, paracytic subsidiary cells and two-armed hairs, none of which is found elsewhere in the family (STACE 1965). Of great importance (STACE 1965) however, is the possession of typical Combretaceous one-armed compartmented hairs by at least two of the five *Strephonema* species. The two-armed hairs of the remaining species can easily be visualized as derivatives of the one-armed type. This indicates the affinity of this genus with the Combretaceae, but because of the above mentioned other unique features only as a separate subfamily (STACE 1965, EXELL & STACE 1966). It was not quite possible for LIBEN (1965) to investigate *Strephonema* in detail, because the amount of herbarium material at his disposal was minute. Also the possibility is not excluded that material was scattered amongst other families, as *Strephonema* possesses large, fleshy fruits which do not resemble in any way the typical winged fruits of the other genera of the family (LIBEN 1965).

The wood anatomy of *Strephonema pseudocola* A. Chev. has been compared with the known members of the Lythraceae and the Combretaceae by VENKATESWARLU & PRAKASA RAO (1970). This comparison shows that the species has little in common with the Lythraceae, but certain xylotomical features point to a relationship between *Strephonema* and a few of the Combretaceae taxa. Nevertheless the distinctiveness of the wood structures merit separation of *Strephonema* from the Combretaceae into a separate monogeneric family, the Strephonemataceae. This family is to be considered allied to Combretaceae (VENKATESWARLU & PRAKASA RAO 1970). So the genus either might constitute a distinct family or belongs to a subfamily of the Combretaceae. This possibility is to be tested using new evidence. A small piece of new evidence is found in the comparison of the secondary phloem of *Strephonema pseudocola* A. Chev. with that of some other representatives of Combretaceae. The secondary xylem was also investigated and the results compared with those of VENKATESWARLU & PRAKASA RAO (1970).

2. MATERIAL AND METHODS

Bark and wood samples used are from the Versteegh and den Outer collection, Ivory Coast, West-Africa (1969). The collection is housed at the Department of Botany, Agricultural University, Wageningen, The Netherlands. All material studied had been vouched. The samples, except those of climbers, were collected from stems at breast height and immediately fixed in FAA.

Anatomical features were studied in transverse, radial and tangential sections and macerations. All sections were embedded in Kaiser's gelatin-glycerin (JOHANSEN 1940). Means and ranges of length of sieve-tube members, vessel-members, fibrous elements and the radial vessel diameter are based on at least twenty individual measurements. Measurements were made with the help of a Wild M20 light-microscope. For our research in tropical wood species we have used the definition of tracheids and libriform fibres given by MOLL & JANSSONIUS (1906–1936), JANSSONIUS (1940) and REINDERS (1935). The ray type desig-

nations employed here are those of KRIBS (1935); the sieve tube-, sieve area- and companion cell-types were classified according to ZAHUR (1959).

3. RESULTS

The results of the comparison of the secondary phloem of *Strephonema pseudocola* A. Chev. with that of some other representatives of the Combretaceae, are given in the following three tables: *table 1*, information on sieve tubes; *table 2*, information on companion cells and mechanical tissue; *table 3*, information on phloem parenchyma and phloem rays.

Fig. 1–6. Combretaceae. Drawings of transverse sections of the conducting secondary phloem near the cambium.

Legends *figs. 1–6* and *tables 1–3*.

+		= present
–		= absent
bast type:	4mr	= orderly sequence in four, multiseriate, regular: PhF (CrC)–PC–ST–PC–PhF (CrC).....
	4mi	= orderly sequence in four, multiseriate, irregular: PhF (CrC)–PC–ST–PC....PhF (CrC)....
	3mi	= orderly sequence in three, multiseriate, irregular: PhF (CrC) – PC–ST....PhF(CrC)....
	s	= sieve tubes scattered
	g	= sieve tubes in groups
CA		= cambium
CC		= companion cell
Cli		= climber

companion-cell type classified according to the method of ZAHUR (1959):

	A	= the companion cells are much shorter than the sieve-tube elements and usually occur singly
	B	= the companion cells are as long as the sieve-tube elements they accompany
	C	= the companion cells are as long as the sieve-tube elements, but are septated to form a strand of cells so that more than one companion cell accompanies each sieve-tube member
CrC		= crystalliferous cell
CSCL		= contact sclereid
dbh		= diameter at breast height
Int		= intercellular space
L		= libriform fibre
obl.; s.		= sieve plate oblique, simple
PC		= parenchyma cell

PhF = phloem fibre

phloem-ray type, classified according to the method of KRIBS (1935):

- He = heterogeneous phloem rays; procumbent and upright cells are present
- Ho = homogeneous phloem rays; only procumbent or only upright cells are present
- I = uniseriate rays and multiseriate rays with long uniseriate tails
- II = uniserate rays and multiseriate rays with short uniseriate tails
- III = only uniseriate rays are present

PhR = phloem ray

PhRPC = phloem-ray parenchyma cell

SCL = sclereid

sieve-area type, classified according to the method of ZAHUR (1959):

- IItg = a small number, rather poorly developed sieve areas on the side walls, unequally spaced or diffuse. Sieve areas mostly on tangential walls
- III = sieve areas on the side walls entirely absent or obscure

sieve-tube type, classified according to the method of ZAHUR (1959):

- I = sieve tubes are essentially long (>500 μm), with very oblique sieve plates with 10 or more sieve areas. When the number of sieve areas is extremely variable, or when the sieve areas are very closely placed, the plate length and the angle of inclination were relied upon as defining features
- II = intermediate between types I and III
- III = sieve tubes are short (100–300 μm), with slightly oblique to transverse, simple sieve plates

ST = sieve tube

T = tracheid

V = wood vessel

vert.; comp. 15–20 s.a. = sieve plate almost vertical, compound, with 15–20 closely placed sieve areas

V + O number = number of the bark sample and corresponding herbarium material of the Versteegh and den Outer collection, Ivory Coast, West-Africa, 1969

WR = wood ray

WRPC = wood-ray parenchyma cell

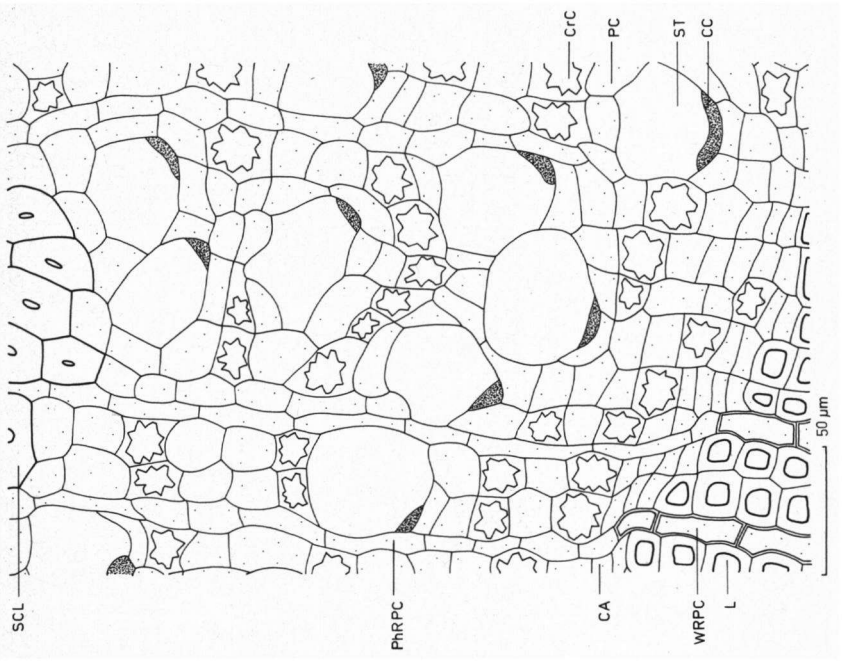

Fig. 2. *Combretum grandiflorum* G. Don (bast-type 4 mr–4 mi).

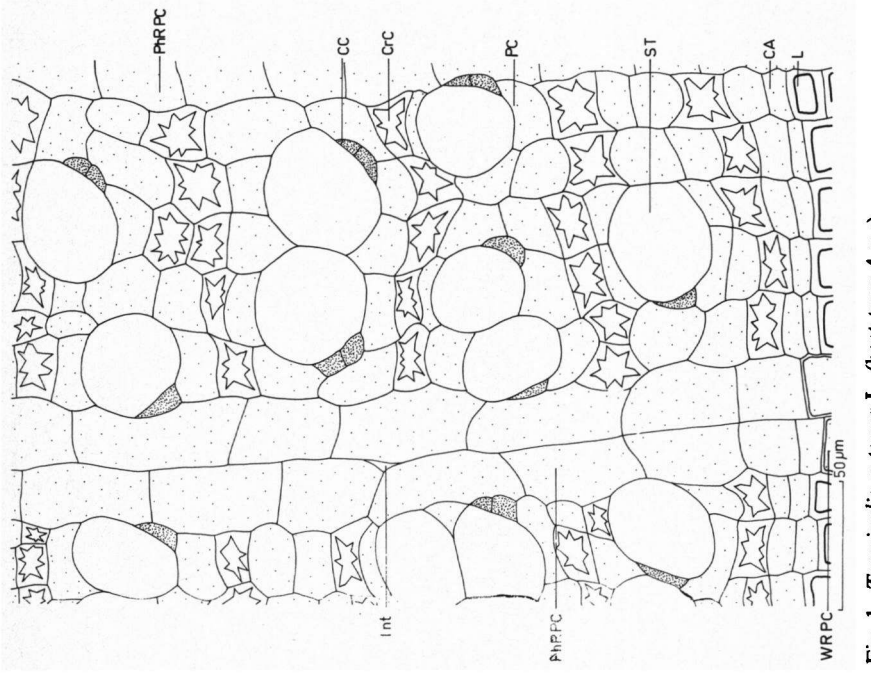

Fig. 1. *Terminalia catappa* L. (bast-type 4 mr).

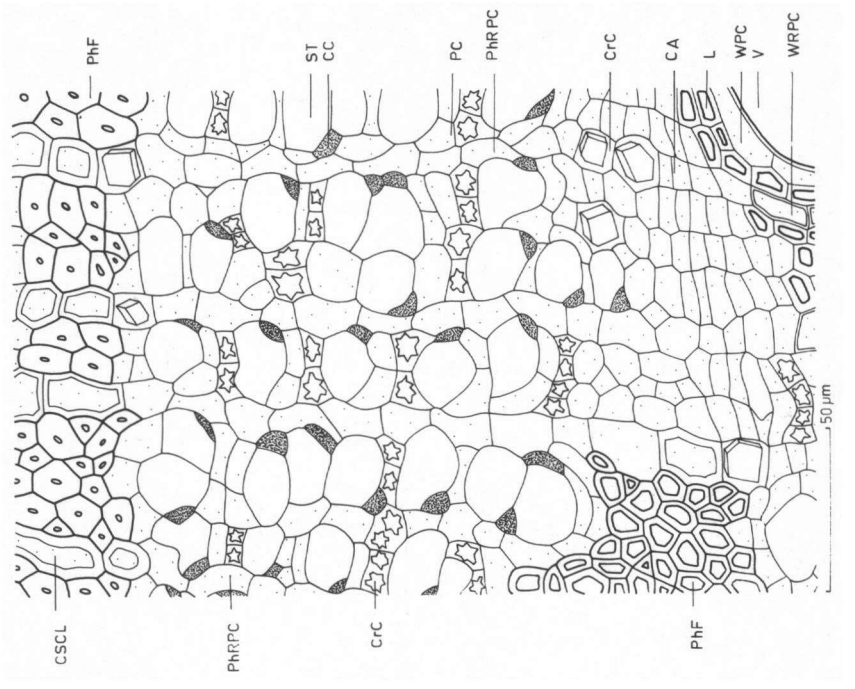

Fig. 4. *Combretum* cf. *smeathmannii* G Don (bast-type 3 mi)

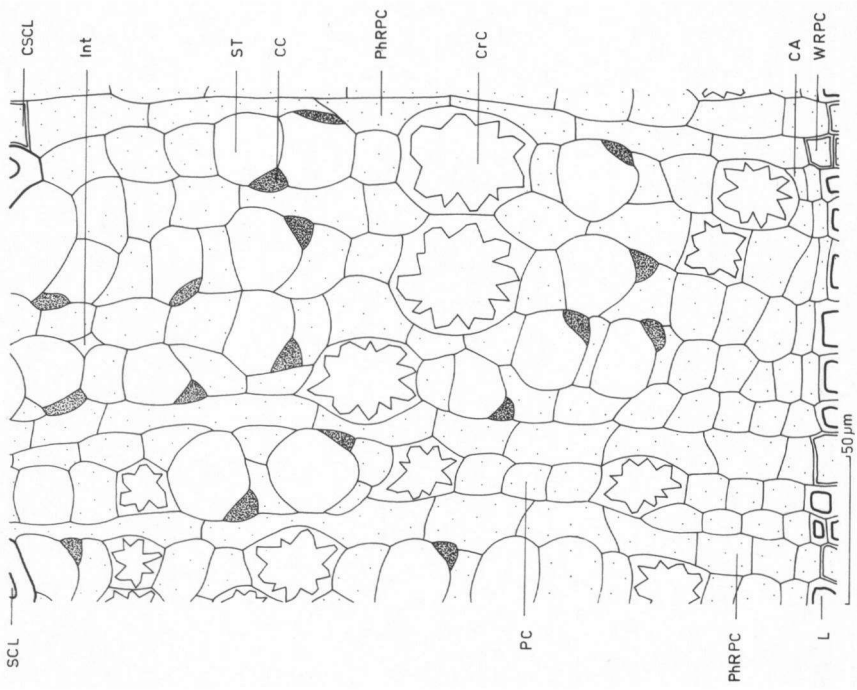

Fig. 3. *Anogeissus leiocarpus* (DC.) Guill. et Perr. (bast-type 4 mi)

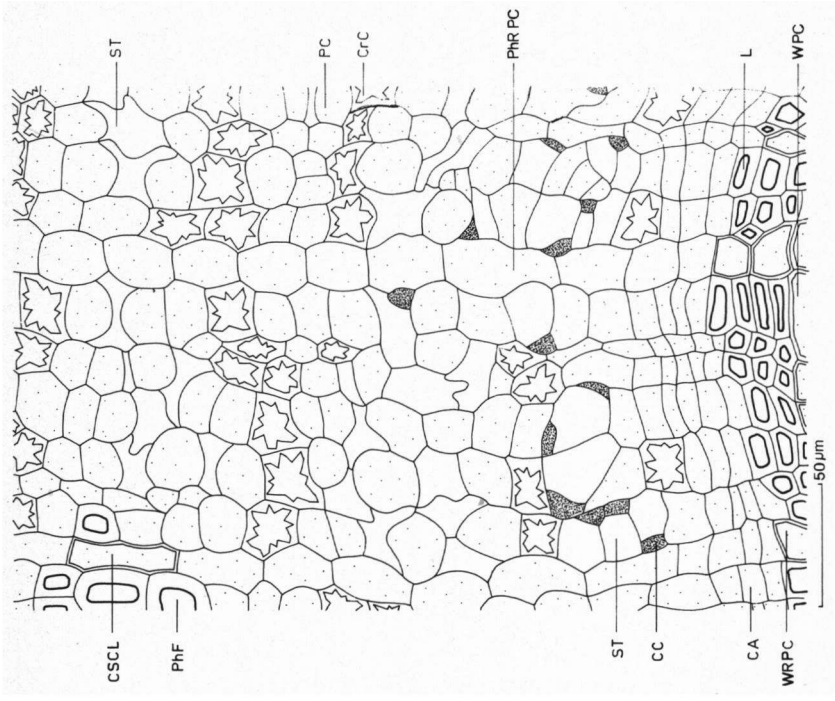

Fig. 6. *Quisqualis indica* L. (bast-type g)

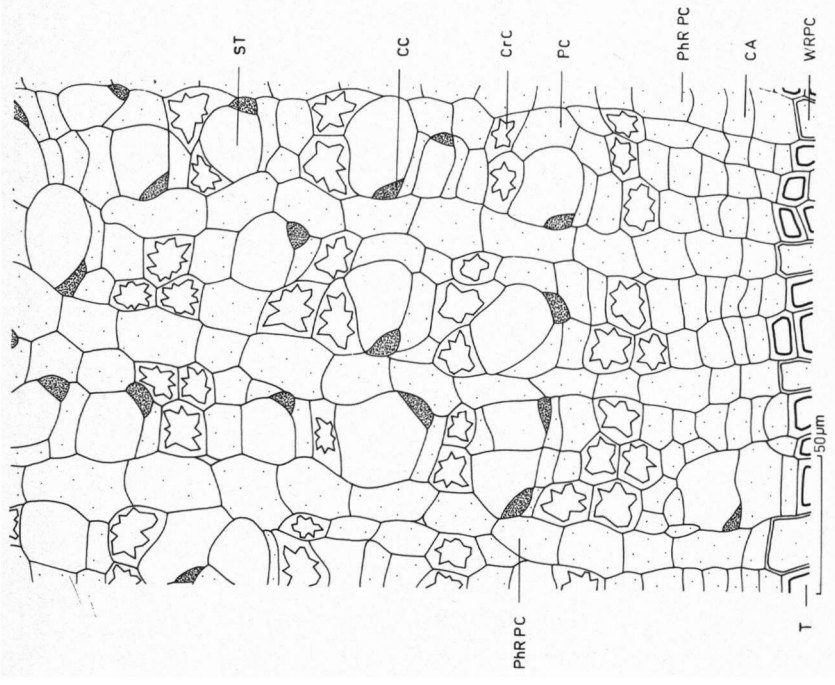

Fig. 5. *Strephonema pseudocola* A. Chev. (bast-type 3 mi)

Table 1
Specimens studied

Specimens studied	V + O number	dbh cm	bast-type				sieve tube	
				type	average member length μm	simple sieve plates, ± horizontal	horizontal diameter of sieve areas on the side walls μm	type sieve area III
Strephonema pseudocola A. Chev.	667 and 808	20 and 30	3mi	I	535	vert.; comp. 15–20 s.a.	35	II tg
Anogeissus leiocarpus (DC.) Guill. et Perr.	357 and 427	25 and 60	4mi	III	290	+	–	+
Combretum binderianum Kotschy	363 and 528	25 and 5	4mi	III	245	+	–	+
Combretum dolichopetalum Engl. et Diels	733 (Cli)	3	4mi	III-II	390	+	–	+
Combretum grandiflorum G. Don	204 (Cli)	3	4mr-4mi	III-II	390	+	–	+
Combretum hypopilinum Diels	529	6	4mi	III	230	+	–	+
Combretum nigricans Lepr. ex Guill. et Perr. var. *elliottii* (Engl. et Diels) Aubrév.	525	7	s	III	130	+	–	+
Combretum cf. *nigricans* Lepr. ex Guill. et Perr. var. *nigricans*	467	10	s-g	III	190	+	–	+
Combretum platypterum (Welw.) Hutch. et J. M. Dalz.	115, 374 and 560	4, 3, and 2	4mi	III	340	obl.; s.	–	+
Combretum cf. *smeathmannii* G. Don	220 (Cli)	3	3mi	III	275	+	–	+
Combretum spec.	769 (Cli)	3	4mi	III	335	+	–	+
Quisqualis indica L.	103 (Cli)	3	g	III	205	+	–	+
Terminalia catappa L.	189	25	4mr	II	405	+ to obl.; comp. < 10 s.a.	15	II tg
Terminalia glaucescens Planch. ex Benth.	300, 310, 422 and 512	30, 25, 20 and 30	4mi	II	360	obl.; comp. 4–5 s.a.	12	II tg
Terminalia ivorensis A. Chev.	617	100	4mi	II	375	obl.; comp. 7 s.a.	12	II tg
Terminalia superba Engl. et Diels	244	30	4mi	III	350	obl., s.	–	+

Table 2

Specimens studied	companion cell type C	companion cell place in corner of sieve tube	average fibre length μm	average fibre-sclereid length μm	mechanical tissue stone cell	average length of crystal cell strand μm	average number of cells per crystal cell strand
Strephonema pseudocola A. Chev.	+	+ to tg. wall	–	–	+	610	30
Anogeissus leiocarpus (DC.) Guill. et Perr.	+	+	–	1020	+	400	15
Combretum binderianum Kotschy	+	+	–	580	+	380	22
Combretum dolichopetalum Engl. et Diels	+	+	2030	–	–	610	30
Combretum grandiflorum G. Don	+	+	–	–	+	500	18
Combretum hypopilinum Diels	+	+	–	725	+	435	24
Combretum nigricans Lepr. ex Guill. et Perr. var. *elliottii* (Engl. et Diels) Aubrév.	+	rd. wall	–	–	+	?	>12
Combretum cf. *nigricans* Lepr. ex Guill. et Perr. var. *nigricans*	+	rd. wall	–	–	+	230	17
Combretum platypterum (Welw.) Hutch. et J. M. Dalz.	+	+	2030	930	–	480	30
Combretum cf. *smeathmannii* G. Don	+	+ to rd. wall	1450	–	–	375	32
Combretum spec.	+	+	1015	–	+	465	36
Quisqualis indica L.	+	rd. wall	1015	+	–	375	21
Terminalia catappa L.	+	+	2030	+	–	495	25
Terminalia glaucescens Planch. ex Benth.	+	+	1115	–	–	420	20
Terminalia ivorensis A. Chev.	+	+	1160	–	–	435	22
Terminalia superba Engl. et Diels	+	+	1510	–	–	550	20

Table 3

Specimens studied	phloem parenchyma cell		phloem ray	
	average length of strand μm	average number of cells per strand	type	further information
Strephonema pseudocola A. Chev.	610	8	He II-He I	rays ⩽ 3-seriate, mostly 2-seriate
Anogeissus leiocarpus (DC.) Guill. et Perr.	380	6	Ho I	rays ⩽ 3-seriate, seldom 3-seriate; ray cells are seldom upright
Combretum binderianum Kotschy	330	5	He III	rays ⩽ 2-seriate, seldom 2-seriate; most ray cells are procumbent
Combretum dolichopetalum Engl. et Diels	520	5	He I	rays ⩽ 2-seriate, mostly uniseriate; most ray cells are upright
Combretum grandiflorum G. Don	465	5	He III	rays ⩽ 2-seriate, seldom 2-seriate; most ray cells are upright
Combretum hypopilinum Diels	375	4	He III	rays ⩽ 2-seriate, seldom 2-seriate
Combretum nigricans Lepr. ex Guill. et Perr. var. *elliottii* (Engl. et Diels) Aubrév.	230	4	He I	rays ⩽ 3-seriate, mostly uniseriate; many large crystals
Combretum cf. *nigricans* Lepr. ex Guill. et Perr. var. *nigricans*	205	5	He I	rays ⩽ 2-seriate, mostly uniseriate; stone cells in tg. layers
Combretum platypterum (Welw.) Hutch. et J. M. Dalz.	425	4	Ho I	rays ⩽ 2-seriate, mostly uniseriate; ray cells are seldom procumbent
Combretum cf. *smeathmannii* G. Don	375	5	Ho III	rays ⩽ 2-seriate, seldom 2-seriate; ray cells are seldom procumbent
Combretum spec.	375	6	He III	rays ⩽ 2-seriate, seldom 2-seriate; most ray cells are upright
Quisqualis indica L.	390	4	He I	rays ⩽ 3-seriate, mostly uniseriate
Terminalia catappa L.	405	5	He II	rays ⩽ 4-seriate, rather often 3-seriate
Terminalia glaucescens Planch. ex Benth.	440	6	He II	rays ⩽ 4-seriate, often 3-seriate
Terminalia ivorensis A. Chev.	495	6	He II-Ho II	rays ⩽ 4-seriate, often 3-seriate; most ray cells are procumbent
Terminalia superba Engl. et Diels	375	6	Ho III	rays ⩽ 2-seriate, seldom 2-seriate; ray cells are seldom upright

The structure of the conducting secondary phloem near the cambium of *Strephonema pseudocola* provides an image which fits quite well within the variation of bast types as they occur in the investigated species of the family *(fig. 1–6)*. Yet *Strephonema pseudocola* is the only species possessing sieve-tube members of type I (ZAHUR 1959). They are much longer than those of the other species, while the almost vertical sieve plates are compound, with more than ten sieve areas. Moreover, the sieve areas in the side walls are clearly visible and large. The companion cells tend to occur against the tangential walls of the sieve-tube member, besides the more general position in the corners. The crystalliferous parenchyma strands and the parenchyma strands are long with many cells per strand. Yet the last phenomenon is also present in *Combretum dolichopetalum* Engl. et Diels. The phloem rays of *Strephonema pseudocola* are in general 2-seriate, whereas those of the other species mostly uniseriate or 3-seriate *(Terminalia)*. We also compared the wood anatomical properties of the species listed in *table 1*. It appears that *Strephonema pseudocola* differs from the other investigated species in the following characteristic features:
the ground tissue consists of tracheids, at least the percentage of tracheids is very much higher than in the other species;
the wood rays are exclusively heterogeneous. while homogeneous rays often occur in the other species;
the number of vessels per square mm in small compared with most other species, except with those of *Combretum dolichopetalum* Engl. et Diels and *Terminalia superba* Engl. et Diels.

4. DISCUSSION

The anatomical wood evidence used by VENKATESWARLU & PRAKASA RAO (1970), to place *Strephonema pseudocola* A. Chev. in a newly constituted monogeneric family, the Strephonemataceae, is not entirely convincing to us.

Although the values of their measurements are somewhat higher in general than ours, there are other points. The differences in number of vessels per square mm between *Lumnitzera*, *Laguncularia* and *Macropteranthes* and the other investigated genera found by the above mentioned authors, are much greater than those between *Strephonema* and the same remaining genera. The cross-sectional diameters of vessel elements of 330–400 μm for *Strephonema* are much greater than the values of 50–160 μm measured by us. The last values fit quite well within the range of the other diameters found. On the other hand Venkateswarlu and Prakasa Rao emphasized the importance of the length of the vessel elements. These elements, like the fibrous elements of the ground tissue of the secondary xylem, of *Strephonema* are long, distinctly separated from the other Combretacean taxa with perhaps the exception of *Pteleopsis* and *Ramatuella*. But also important is the fact, mentioned by us, that *Strephonema pseudocola* is in the possession of a ground tissue mainly composed of tracheids, whereas all the other specimens possess libriform fibres.

Bark anatomy can be used complementary to wood anatomical criteria

(THORENAAR 1925; LAWTON & LAWTON 1971; LAWTON 1972; PARAMESWAREN & LIESSE 1968, 1974). *Strephonema pseudocola* differs clearly from the other genera investigated by the possession of type I sieve-tube members. Like all the elements of the axial system, these sieve-tube members are longer than those of the other genera. Furthermore the companion cells are quite often placed against the tangential walls of the sieve-tube member. Also these companion cells, septated to form a strand of cells, are not as long as the sieve-tube members but often shorter. So a tendency towards ZAHUR's (1954) type A can be noticed.

The arrangement and types of the elements of the secondary phloem of *Strephonema pseudocola* on the other hand, are clearly characteristic for the Combretaceae. For instance the frequently present druses, the orderly sequence of elements and the small width of the rays. MÖLLER's (1882) features for the secondary phloem of the Combretaceae such as phloem rays not wider than 2-seriate; short, wide sieve-tube members with simple sieve plates, sometimes compound with a few sieve areas, will not do for *Strephonema* but neither for *Terminalia*. But of course, one has to bear in mind that we only investigated species of about twenty percent of the genera belonging to the family. The bark and wood anatomical characteristics all plead for a more primitive, less specialized status of *Strephonema* compared with the other investigated genera of the family (ZAHUR 1959, DEN OUTER 1967, CARLQUIST 1975). Also only by its semi-inferior ovary the genus has some claim to be an ancestral type in the Combretaceae (EXELL & STACE, 1966). So the anatomy of the secondary phloem of *Strephonema pseudocola*, may be more than that of the secondary xylem, leads us to retain the genus in the Combretaceae, but as a distinctly separate subfamily. To detach the genus from the rest of the Combretacean taxa and place it in a newly constituted monogeneric family as suggested by VENKATESWARLU & PRAKASA RAO (1970), does not seem entirely justified.

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