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THE SECONDARY PHLOEM OF SOME OCHNACEAE AND THE SYSTEMATIC POSITION OF LOPHIRA LANCEOLATA V. TIEGHEM EX KEAY

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SUMMARY

The secondary phloem of *Lophira lanceolata* v. Tieghem *ex* Keay (*Ochnaceae*) has been compared with that of some representatives of the family, especially of the tribe *Ochneae* of the subfamily *Ochnoideae*. The removal of *Lophira* from the subfamily *Ochnoideae* ('*Exalbuminosae*'), as proposed by Kanis (1968), appears to be justified from an anatomical standpoint.

INTRODUCTION

The *Ochnaceae* is a family primarily of shrubs and trees which have centres of distribution in tropical Africa, America, and the East Indies. The family can be divided into two subfamilies and five tribes (Kanis, 1968), viz. the subfamily *Ochnoideae* comprising the tribes *Ochneae* and *Elvasieae* Rchb. and the subfamily *Sauvagesioideae* Lindl. including the tribes *Sauvagesieae*, *Euthemideae* Planch., and *Lophireae* Rchb. The tribe *Ochneae* is subdivided (Kanis, 1968) into the subtribes *Ochninae* and *Ouratinae* (v. Tieghem) Kanis, and the tribe *Sauvagesieae* into the subtribes *Sauvagesiinae* and *Luxemburgiinae* (Planch.) Kanis. The systematic position of the monogeneric African tribe *Lophireae*, however, is questionable. Because of the different opinions existing on this matter, a comparison of the secondary phloem of *Lophira lanceolata* v. Tieghem *ex* Keay with that of some representatives of the *Ochnaceae* seemed worthwhile.

MATERIALS AND METHODS

Bark samples used were from the Versteegh and den Outer collection, Ivory Coast, West-Africa (1969). All the material studied was vouched. The samples were collected from stems of small trees at breast height and from basal parts of shrubs, and immediately fixed in FAA. Only *Lophira lanceolata* is a rather large tree.

Anatomical features were studied in transverse, radial, and tangential sections and macerations. All sections were embedded in Kaiser's gelatin-glycerin after treatment (Johansen, 1940). Means of the length of sieve-tube members, parenchyma strands, and fibre-sclereids are based on at least twenty-five individual measurements. The ray type designations employed here are those of Kribs (1935); the sieve-tube type, sieve-area type, and companion-cell type were classified according to Zahur (1959).

RESULTS

The results are summarized in table 1.

The axial system of the conducting secondary phloem of the investigated *Ochnaceae* species is composed of sieve tubes, companion cells, parenchyma cells, and sometimes fibre-sclereids (see plate I and II).

In *Campylospermum flavum*, *C. dybowskii*, and *C. glaberrimum*, and in *Idertia morsonii*, the main part of the axial system is occupied by parenchyma cells, whereas sieve tubes lie scattered in between this ground tissue (see plate I, 4). The transverse section of the sieve tubes is almost rectangular and rather small: in tangential direction about 15 μm, in radial direction about 9 μm. The sieve tubes of *Campylospermum flavum*, however, are somewhat larger.

Ochna rhizomatosa, *Rhabdophyllum affine*, and *R. calophyllum* constitute a group intermediate between the first mentioned species and *Lophira lanceolata*.

In *Lophira lanceolata* the axial system is composed half of sieve tubes and about half of parenchyma cells. They constitute 1—3 cell wide (mostly one cell wide) irregular tangential bands that alternate regularly (see plate II, 7 and 9).

Besides the characteristics mentioned in table 1, the sieve tubes also differ in size from those species mentioned above; in tangential direction about 32 μm, in radial direction about 26 μm. The transverse section of the sieve tubes is also oval to round rather than rectangular.

Both *Lophira lanceolata* and the species from the intermediate group possess fibre-sclereids with a diameter of about 40 μm (see plate II, 6 and 8). They are somewhat larger in *Ochna rhizomatosa*, viz. about 60 μm (see plate I, 3 and 5). Only in *Lophira lanceolata* these fibres occur in groups, whereas they lie scattered in the species of the intermediate group. While in the intermediate group the fibres occupy about 20 percent of the cross section of the conducting secondary phloem, this is only 5 percent in *Lophira lanceolata*.

The crystals occurring in the bark are isodiametric to somewhat elongated in species of the first group, styloids in species of the intermediate group, and about isodiametric again in *Lophira lanceolata*; but in *Lophira lanceolata* they are much less numerous than in the other species.

Also stone cells occur in the bark of all the investigated species (see plate I, 1 and 2), only in *Lophira lanceolata* they are present in large quantities.

The phloem rays are heterogeneous, often uniseriate but also multiseriate, whereas *Lophira lanceolata* possesses mainly homogeneous phloem rays which are seldom uniseriate.

Both the parenchyma cells of the axial system and those of the phloem rays have brown to red-brown contents, except for *Lophira lanceolata* where only the parenchyma cells of the axial system sometimes possess brown contents.

So the picture produced by the conducting secondary phloem near the cambium of *Lophira lanceolata* differs in a few points from that of the other investigated species of the family.

The arrangement of sieve tubes and axial parenchyma cells is quite often in tangential uniseriate layers, taking into account that layers with sieve tubes alternate with those consisting of parenchyma cells. The sieve tubes of the other investigated species lie scattered within a ground tissue of parenchyma cells. Only *Ochna rhizomatosa* (v. Tieghem) Keay and *Rhabdophyllum affine* (Hook. *f.*) v. Tieghem show a slight tendency towards an irregular tangential layering of the elements of the secondary phloem. Furthermore *Lophira lanceolata* is the only species possessing sieve-tube members of type II with compound sieve plates, large sieve areas in the tangential walls of the sieve-tube members, companion cells of type C, fibre-sclereids in groups, and homogeneous phloem rays consisting of procumbent cells.

DISCUSSION

The structure of the secondary phloem of *Lophira* differs from all the other investigated species. These species all belong to the tribe *Ochneae* (Farron, 1963, 1969). Although the number of investigated species is small, it is obvious from the results of this study that *Lophira* does not quite fit within the tribe *Ochneae* of the subfamily *Ochnoideae*. Whether *Lophira* fits in the subfamily *Sauvagesioideae* as far as the anatomy of its secondary phloem is concerned, is not sufficiently known in the absence of suitable material for study.

Also the secondary xylem of *Lophira* presents several features unique in the family (Decker, 1966), viz. vasicentric tracheids, greater diameter of vessel elements, axial parenchyma in distinctive metatracheal bands, and homogeneous rays. The tribes *Ochneae* and *Elvasieae* on the other hand have heterogeneous rays, diffuse and vasicentric axial parenchyma, and no vasicentric tracheids. Still following Gilg (1925), Decker (1966) placed *Lophira* in the subfamily '*Exalbuminosae*' (*Ochnoideae*) as representing a distinct tribe, because of the presence of vessel elements with vestured pits and the absence of unilaterally compound pitting between vessel and parenchyma like in the other representatives of the '*Exalbuminosae*'. It must be kept in mind that she studied especially the tribe *Sauvagesieae* ('*Luxemburgieae*') of the subfamily '*Albuminosae*' (*Sauvagesioideae*). Also according to Metcalfe and Chalk (1950) the genus *Lophira* differs in wood structure from all the others, particularly in its parenchyma arrangement and its much more highly specialized rays. The parenchyma of the *Ochnaceae* is typically paratracheal and often scanty in the '*Albuminosae*', apotracheal, abundant diffuse in the '*Exalbuminosae*' with a tendency towards abaxial aliform types; however, it occurs in broad metatracheal bands in *Lophira*. If there are affinities of *Lophira* with the family *Ochnaceae* it would appear to be with the '*Exalbuminosae*' rather than with the '*Albuminosae*' (Metcalfe and Chalk, 1950), but its position is rather isolated. This in spite of the fact that *Lophira* lacks 'cristarque' cells that are characteristic for the subfamily '*Exalbuminosae*' (Bailey, 1933).

Kanis (1968) accepted Engler's (1874) main division of the *Ochnaceae* into the '*Exalbuminosae*' and '*Albuminosae*' as two distinct subfamilies, named *Ochnoideae* and *Sauvagesioideae* respectively. The tribe *Lophireae* was not included by Engler. Gilg (1893, 1895, 1925) and Dwyer (1941) placed it in the *Ochnaceae*, more specifically in the '*Exalbuminosae*' because the seeds lack albumen. However, a position in the *Sauvagesioideae* seems more logical (Kanis, 1968) since it shares non-distichous leaves and a 2-carpelled, 1-celled, many-ovuled ovary with that subfamily. Except for the position of the tribe *Lophireae*, the systems of Kanis (1968) and Gilg (1925) are not very different from each other.

The removal of *Lophira* from the *Ochnoideae* appears fully justified, not only because of the evidence used by Kanis (1968) but also because of its anatomy. This goes for the secondary phloem, but may after all also apply to the secondary xylem in spite of Decker's conclusion. Besides this, Metcalfe and Chalk (1950) pointed to the taxonomic importance of the 'cristarque' cells in the genera united in the subfamily *Ochnoideae* and *Lophira* lacks those cells.

Lophira had been placed also in the *Dipterocarpaceae* (Agardh, 1825; Don, 1831) because it shares some features with that family, namely cortical bundles, vestured vessel pits, vasicentric tracheids, metatracheal axial parenchyma, chambered crystalliferous axial parenchyma, and winged exalbuminous seeds. Vestal (1937) and Decker (1966) suggest that there may be a connection between the *Dipterocarpaceae* and the *Ochnaceae* through *Lophira*.

Table 1. A comparison of Lophira lanceolata with some species of the Ochnaceae

Specimen studied	V+O number	dbh cm	bast-type	sieve tube type	average member length µm	sieve plates
1. Lophira lanceolata v. Tieghem *ex* Keay	347	20	2ui	II	465	obl., comp., 7 s.a.
2. Campylospermum flavum (Schum. et Thonn.) Farron	388	3	s	III	220	± horizontal, simple
3. Campylospermum dybowskii v. Tieghem	64	10	s	III	275	± horizontal, simple
4. Campylospermum glaberrimum (P. Beauv.) Farron	146 and 537	4 and 2	s	III	190	± horizontal, simple
5. Idertia morsonii (Hutch. et Dalz.) Farron	798	8	s	III	190	± horizontal, simple
6. Ochna rhizomatosa (v. Tieghem) Keay	450	10	s to 2ui	III	465	± horizontal, simple
7. Rhabdophyllum affine (Hook. *f.*) v. Tieghem	247 and 253	6	s to 2ui	III	260	± horizontal, simple
8. Rhabdophyllum calophyllum (Hook. *f.*) v. Tieghem	785	6	s	III	320	± horizontal, simple

			companion cell	mechanical tissue			phloem-parenchyma cells		phloem rays		further information
Species number	Horizontal diameter of sieve areas on the side walls µm	type sieve area	type	average fibre-sclereid length µm	stone cells	crystals	average length of strand µm	average number of cells per strand	type	maximum number of rows	
1.	12	IItg	C	580 (in groups)	+	±isodiametric	550	5—6	Ho II	4	ray cells procumbent; only a few crystals
2.	6	II	A	—	+	±isodiametric	290	3	He II	7	many ray cells upright
3.	6	II	A	—	+	±isodiametric	375	3	He II	7	most ray cells upright
4.	—	III	A	—	+	±isodiametric	260	3	He II	7	
5.	—	III	A	—	+	±isodiametric	400	4	He I-II	5	
6.	—	III	A	960	+	styloid	610	6	He II	6	
7.	—	III	A	725	+	styloid	580	7	He II	6	
8	—	III	A	930	+	styloid	695	8	He I	6	

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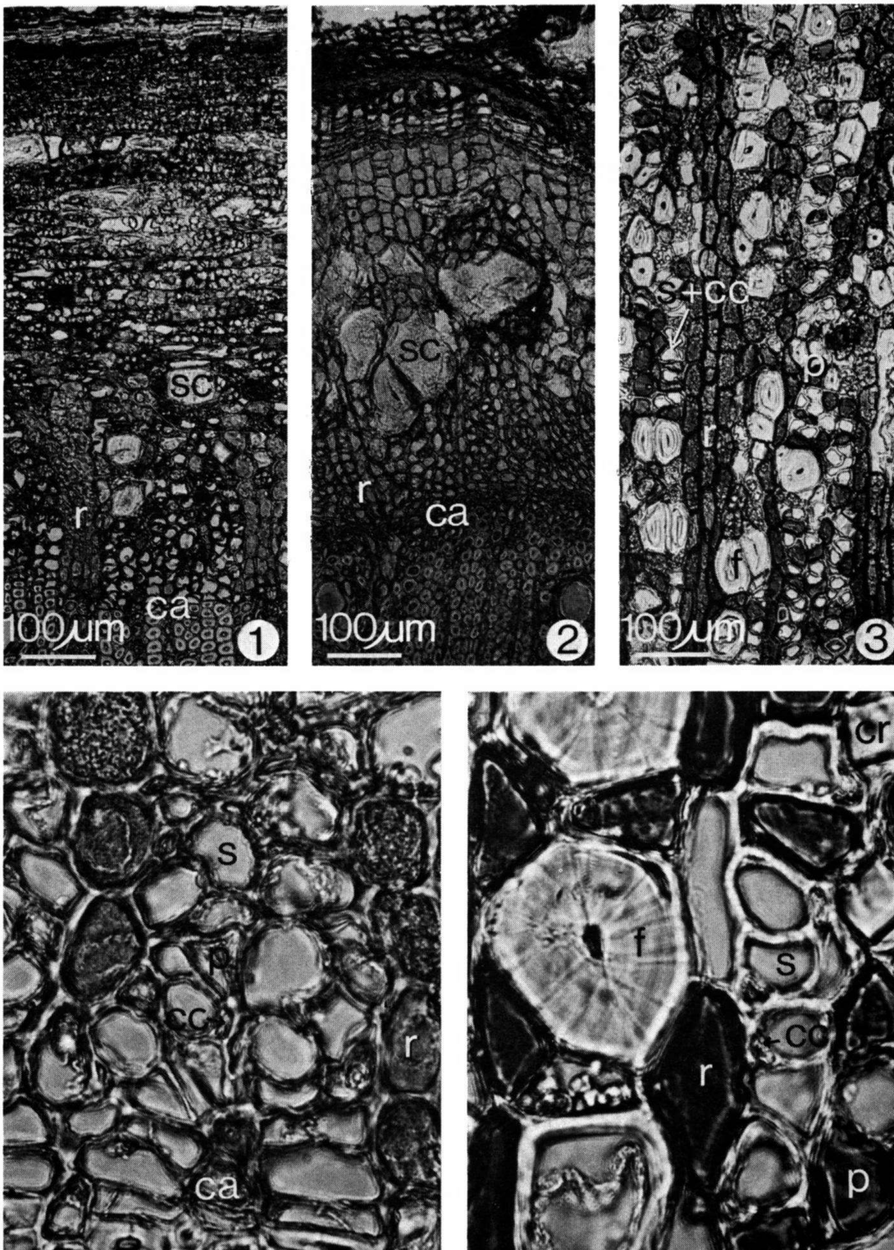
LEGENDS TO THE PLATES

Plate I. *Ochnaceae*. Transverse sections of the secondary phloem. 1 and 4. *Campylospermum dybowskii* v. Tieghem; 2. *Idertia morsonii* (Hutch. et Dalz.) Farron; 3 and 5. *Ochna rhizomatosa* (v. Tieghem) Keay.

Plate II. *Ochnaceae*. Transverse sections of the secondary phloem. 6. *Rhabdophyllum calophyllum* (Hook. *f.*) v. Tieghem; 7 and 9. *Lophira lanceolata* v. Tieghem *ex* Keay; 8. *Rhabdophyllum affine* (Hook. *f.*) v. Tieghem. ca = cambium; cc = companion cell; cr = crystalliferous cell; f = fibre-sclereid; p = phloem-parenchyma cell; r = phloem-ray parenchyma cell; s = sieve tube; sc = stone cell.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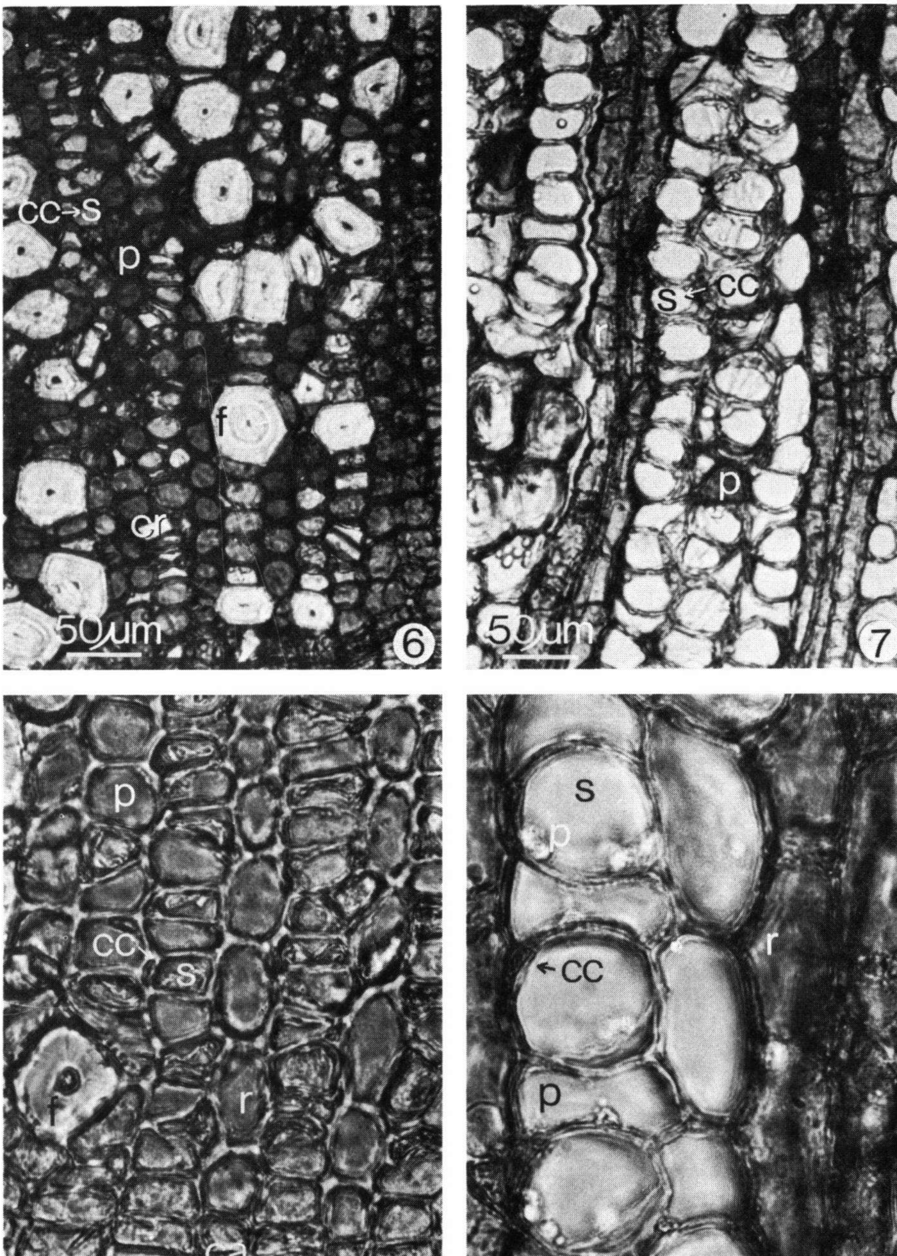
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LEGENDS TO TABLE I

+	= present
—	= absent
V+O number	= number of the bark sample and corresponding herbarium material of the Versteegh and den Outer collection, Ivory Coast, West-Africa, 1969
dbh	= diameter at breast height of small trees, or diameter of basal parts of shrubs
bast type 2ui	= sieve tubes constitute 1—3 cell wide (mostly one cell wide) irregular tangential bands, which alternate regularly with tangential bands of the same width composed of parenchyma cells
s	= sieve tubes scattered in ground tissue of parenchyma cells

sieve-tube type, classified according to 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

obl., comp., 7 s.a. = oblique sieve plate, compound, with 7 closely placed sieve areas

sieve-area type, classified according to Zahur (1959):

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

companion-cell type, classified according to Zahur (1959):

A	= the companion cells are much shorter than the sieve-tube elements and usually occur single
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

phloem-ray type, classified according to Kribs (1935):

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