

ON THE WOOD ANATOMY OF THE TRIBE “OLMEDIÆAE” (MORACEÆ) AND THE POSITION OF THE GENUS *OLMEDIA* R. & P.

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SUMMARY

The structure of the wood of the genera *Castilla*, *Helicostylis*, *Maquira*, *Naucleopsis*, *Olmedia*, *Perebea* and *Pseudolmedia*, considered to belong in the Olmediæae (cf. BERG 1972) is described. The diversity in anatomical structure between the genera is small, and it is hard to distinguish *Maquira*, *Perebea* and *Pseudolmedia* from each other. *Castilla* can be recognized by its thin-walled and wide-lumined fibres, *Helicostylis* by its parenchyma distribution, *Naucleopsis* (usually) by its more numerous vessels with a smaller diameter. A more marked difference is shown by the monotypic genus *Olmedia* with apotracheal banded parenchyma instead of the paratracheal aliform to confluent-banded parenchyma of the other genera. Septate fibres, which are characteristic for the other genera – some species of *Helicostylis* excepted – are nearly completely absent in *Olmedia*. This structural difference is considered as an argument in favour of the exclusion of *Olmedia* from the tribe Olmediæae (BERG 1977).

1. INTRODUCTION

The structure of the secondary wood of the Moraceæ shows in comparison to that of many other families a rather uniform pattern. This is particularly true for most genera of the tribe Olmediæae. Differences are mainly found in size and number of vessels, absence or presence of septate fibres, and in the distribution and quantity of axial parenchyma. Besides the description of the Moraceæ in METCALFE & CHALK's *Anatomy of the Dicotyledons* (1950), we have TIPPO's (1938) account of the family and a treatment of the American genera by RECORD & HESS (1940). The latter authors pointed out how unreliable their material was, even originating from type trees, because the botanists who proposed the new species were sometimes uncertain as to the genera to which these species should be assigned.

In recent time several taxonomic revisions were published among which BERG's (1972) "Revision of the Neotropical Olmediæae and Brosimeæae." While Berg studied the taxonomy of the Olmediæae, the second author investigated the wood structure of our material of the genera at that time considered to belong to the Olmediæae. It appeared from her study (unpublished doctorate thesis) that differences in wood structure between the species, although small, do enable a certain arrangement into groups. She drew her conclusions from anatomy independantly from Berg's taxonomical results. A subsequent comparison of their respective conclusions showed that the

arrangement of the wood samples agreed remarkably well with the taxonomic arrangement.

It seemed desirable to wait with publication of the results of the anatomical investigation until additional material in genera not or poorly represented up till then would be available. As appears from *table 1* all seven genera which, according to BERG (1972), constitute the tribe Olmedieae are now represented in a most satisfactory way. Among others the genus *Olmedia* is now represented. In a recent paper BERG (1976) points out that the genus *Olmedia* must be excluded from the tribe Olmedieae for various reasons. This necessitated a redefinition of the tribe and a new name for it: Castilleae C. C. Berg. For practical reasons the present paper still refers to the Olmedieae in the former wide sense.

2. MATERIAL AND METHODS

The material is listed in *table 1*. In the table the revised names as well as the scientific names which accompanied the wood specimens received from other institutes are listed. In those cases where the material was very abundant a selection was made of the samples to be sectioned, the other ones being inspected by a $\times 10$ hand lens. All wood specimens are backed by herbarium vouchers which were identified by Berg.

In the usual way sections and macerations were prepared for studying the microscopical characters. For some of the specimens softening in hydrofluoric acid previous to cutting was necessary. Macerations were made by placing wood chips overnight in a mixture of equal parts of acetic acid and hydrogen peroxide at a temperature of 60°C.

In the generic descriptions the averages for the length of vessel members and fibres are calculated from the average values for the species, the lowest and highest averages being placed between brackets. The ranges comprise the lowest and highest values encountered within the species.

3. GENERAL ANATOMICAL CHARACTERS OF THE WOOD

Characteristic for all genera are the scattered vessels with simple perforations and moderate to rather large alternate intervascular pits ranging from 5.5–10 μm ; vessel members with short tips or without tips, and a length of about 400–500 μm . The fibre tissue consists of libriform with small simple pits on the radial walls. Mostly fibres are septate with 1–3 septae per fibre, but in some genera, like *Helicostylis*, only part of the fibres are septate and in *Olmedia* septate fibres are extremely scarce. In a number of the fibres gelatinous walls are nearly always present. The majority shows the long spindle form and ranges from 1000–1700 μm long, but shorter fibres with a wider body and more abruptly ending in bayonet-like tips are also present. In *Castilla* the fibres are wider and thinner-walled than in the other genera; in *Naucleopsis* they tend to be slightly shorter than in the other genera. The ratio of fibre to vessel member

Table 1. List of Material

	Utrecht wood number	Diameter of the tree	Collector(s)	Collection locality	Xylarium number elsewhere	Distributed under the name of:
<i>Castilla</i>						
<i>elastica</i> Cerv.	18026	—	—	Guatemala	MADw 23141	
tunu Hemsl.	7048	—	US 715986	Panama	USw 83	<i>C. fallax</i>
tunu	18808	—	Englesing 97	Nicaragua	SJRw	<i>C. fallax</i>
<i>ulei</i> Warb.	8827	branch, 5 cm	Ellenberg 2949	Peru		
<i>ulei</i>	18427	100 cm	Krukoff 1409	Braz. — Mato Grosso		
<i>ulei</i>	18807	—	Krukoff 5766	Braz. — R. Purus		
<i>ulei</i>	18433	branch, 5 cm	L. Williams	Peru		
<i>ulei</i>	20943	12 cm	Prance, c.s. 19852	Braz. — Mato Grosso		
<i>Helicostylis</i>						
<i>elegans</i> (Macbr.) C. C. Berg	7946	14 cm	Krukoff 6809	Braz. — Amaz.	USw 7946	<i>H. lancifolia</i>
<i>elegans</i>	16159	14 cm	Krukoff 8075	Braz. — Amaz.		<i>Perebea elegans</i>
<i>elegans</i>	16201	8 cm	Krukoff 8521	Braz. — Amaz.		<i>Perebea elegans</i>
<i>elegans</i>	20924	10 cm	Prance, c.s. 18613	Braz. — Mato Grosso		
<i>elegans</i>	20944	11 cm	Prance, c.s. 19868	Braz. — Mato Grosso		
<i>pedunculata</i> R. Ben.	1224	12 cm	Lanj. & Lind. 421	Suriname		
<i>pedunculata</i>	3544	9 cm	Lindeman 3544	Suriname		
<i>pedunculata</i>	5244	over 25 cm	BAFOG 165 M	Fr. Guiana		
<i>pedunculata</i>	5342	over 32 cm	BAFOG 267M	Fr. Guiana		
<i>pedunculata</i>	8956	over 26 cm	Pires 51670	Braz. — Amapa	MGw	
<i>pedunculata</i>	11963	20 cm	van D nselaar 2992	Suriname		
<i>scabra</i> (Macbr.) C. C. Berg	7948	over 16 cm	Krukoff 6811	Braz. — Amaz.	USw 7948	<i>H. asperifolia</i>
<i>scabra</i>	8162	over 8 cm	Krukoff 7081	Braz. — Amaz.	USw 8162	<i>H. asperifolia</i>
<i>scabra</i>	8710	large tree	Ellenberg 2507	Peru		<i>Pseudolmedia scabra</i>
<i>scabra</i>	16222	over 32 cm	Krukoff 8762	Braz. — Amaz.		
<i>scabra</i>	20953	20 cm	Prance, c.s. 17967	Braz. — Amaz.		
<i>tomentosa</i> (P. et E.) Rusby	985	over 24 cm	Fanshawe 148 (F.D. 2757)	Guyana		<i>H. poeppigiana</i>

Table 1 (continued)

	Utrecht wood number	Diameter of the tree	Collector(s)	Collection locality	Xylarium number elsewhere	Distributed under the name of:
tomentosa	3041	2 cm	Lindeman 4076	Suriname		
tomentosa	3267	5 cm	Lindeman 4756	Suriname		
tomentosa	3672	2 cm	Lindeman 5299	Suriname		
tomentosa	3711	3 cm	Lindeman 5356	Suriname		
tomentosa	3712	5 cm	Lindeman 5357	Suriname		
tomentosa	3791	5 cm	Lindeman 5469	Suriname		
tomentosa	4539	5 cm	Lindeman 6712	Suriname		
tomentosa	4924	1 cm	Schulz 7178	Suriname		
tomentosa	6836	14 cm	Schulz 8316	Suriname		
tomentosa	9077	10 cm	Pires 51834 (Maguire)	Braz. - Amapa		
tomentosa	11698	24 cm	LBB (Maas) 10963	Suriname		
tomentosa	16256	13 cm	Krukoff 8859	Braz.		
tomentosa	16775		Maguire c.s. 45735	Guiana		
tomentosa	19122	20 cm	Prance c.s. 15027	Braz. - Amaz.		
tomentosa	19400	over 14 cm	Krukoff 1557	Braz. - Amaz.		
turbinata C. C. Berg	16258	over 18 cm	Krukoff 8832	Braz. - Amaz.		H. pedunculata
Maquira calophylla (P. et E.) C. C. Berg	7655		Krukoff 6347	Braz. - Amaz.	USw 7655	Olmedia calophylla
calophylla	7851		Krukoff 6655	Braz. - Amaz.	USw 7851	(Olmedioperebea caloph.) O. calophylla
calophylla	16208	17 cm	Krukoff 8580	Braz. - Amaz.		O. calophylla
coriacea (Karst) C. C. Berg	7817		Krukoff 6615	Braz. - Amaz.	USw 7817	Olmediophaena (Pseudolmedia) obliqua
coriacea	7886		Krukoff 6705	Braz. - Amaz.	USw 7886	Pseudolmedia obliqua
coriacea	8774		Ellenberg 2823	Peru		
coriacea	11746		Breteler 3726	Venezuela		
coriacea	17149	12 cm	Maguire c.s. (Pires 51743)	Braz. - Amapa	USw 39526	
coriacea	18851			Braz. - Amaz.	INPAw X-3885	

Table 1 (continued)

	Utrecht wood number	Diameter the tree	Collector(s)	Collection locality	Xylarium number elsewhere	Distributed under the name of
costaricana (Stand.) C. C. Berg	16210		Krukoff 8642	Braz. - Amaz.		Olmedia maxima Ducke
guianensis Aubl.	222	over 15 cm	Stahel 222	Suriname		Perebea laurifolia
guianensis	1644	10 cm	Lanjouw & Lindeman 2187	Suriname		
guianensis	1936	14 cm	Lanjouw & Lindeman 2811	Suriname		
guianensis	2318	7 cm	Lindeman 3547	Suriname		
guianensis	3268	5.5 cm	Lindeman 4757	Suriname		
guianensis	8597	5 cm	Daniels & Jonker 1083	Suriname		
guianensis	8855	28 cm	Schulz 8980	Suriname		
guianensis	8949	25 cm	Pires c.s. 51612	Braz. - Amapa	USw 39684	Perebea
guianensis	9634	17 cm	Pires c.s. 51803	Braz. - Amapa	INPAw	Perebea laurifolia
guianensis	11210	10 cm	LBB (Maas) 10795	Suriname		
guianensis	20921	6 cm	Prance c.s. 19609	Braz. - Mato Grosso		
sclerophylla (Ducke)						
C. C. Berg	3424	1 cm	Lindeman 5040	Suriname		
sclerophylla	19224		Krukoff 1133	Braz. - Amaz.		Perebea xinguana
Naucleopsis						
amara Ducke	19340		Krukoff 1406	Braz. - Mato Grosso		Acanthosphaera amara
concinna (Stand.) C. C. Berg	7822	over 8 cm	Krukoff 6620	Braz. - Amaz.	USw 7822	Perebea concinna
concinna	7875	over 10 cm	Krukoff 6687	Braz. - Amaz.	USw 7875	Perebea concinna
glabra Spruce ex Bail.	7549	10 cm	Krukoff 6198	Braz.		
glabra	19277		Krukoff 1300	Braz. - Amaz.		Ogcodeia ulei
glabra	19304		Krukoff 1347	Braz. - Mato Grosso		Og. ternstroemiflora
glabra	19331		Krukoff 1392	Braz. - Mato Grosso		Og. pallescens
glabra	19899	4.5 cm	Krukoff 5323	Braz. - Amaz.		Olmedia caloneura
glabra	20901	5 x 14 cm	Prance c.s. 18241	Braz. - Mato Grosso		
glabra	20938	10 cm	Prance c.s. 19805	Braz. - Mato Grosso		
guianensis (Mildbr.)						
C. C. Berg	2776	3 cm	Lindeman 3790	Suriname		

Table 1 (continued)

	Utrecht wood number	Diameter the tree	Collector(s)	Collection locality	Xylarium number elsewhere	Distributed under the name of:
guianensis	1816	3.5 cm	Lindeman & Lanj. 2544	Suriname		
guianensis	4700	3 cm	Lindeman 4700	Suriname		
guianensis	12167	6 cm	V. Donselaar 3791	Suriname		
guianensis	17042	10.5 cm	Maguire c.s. 51293	Braz.		
imitans (Ducke)	19991	ca. 16 cm	Krukoff 5485	Braz. - Amaz.		
inaequalis (Ducke)	19364	8 cm	Krukoff 1458	Braz. - Mato Grosso		Ogcodeia inaequalis
krukovii (Standl.)	19254		Krukoff 4544	Braz. - Amaz.		Naucleopsis caloneura
macrophylla Miq.	2667		Ducke 232	Braz.	Yale 31959	
macrophylla	20920	13 cm	Prance c.s. 18534	Braz. - Mato Grosso		
mello-barreto (Standl.)	7974		Krukoff 6839	Braz.	USw 7974	Ogcodeia ternstroemiiflora
mello-barreto	19694	big tree	Krukoff 4969	Braz. - Amaz.		
stipularis Ducke	18423	4.5 cm	Ducke 370	Braz. - Amaz.	SJRw 40	Palmolmedia stipularis
stipularis	20939	4.5 cm	Prance c.s. 19807	Braz. - Mato Grosso		
ternstroemiiflora (Mildbr.)	19281	ca. 7 cm	Krukoff 1306	Braz. - Mato Grosso		Ogcodeia ternstroemiiflora
C. C. Berg	20912	4 cm	Prance c.s. 18467	Braz. - Mato Grosso		
ternstroemiiflora	20960	14 cm	Prance c.s. 19881	Braz.		
ternstroemiiflora	16170	14 cm	Krukoff 8271	Braz.		
ulei (Warb.) Ducke	18421	2.5 cm	Cuatrecasas	Colombia	SJRw 16629	Ogcodeia ulei
ulei	18428	5 cm	Ll. Williams 5194	Peru		Og. ulei
ulei	19278	over 14 cm	Krukoff 1301	Braz. - Amaz.		Og. ulei
						Acanthosphaera ulei
Olmedia						
aspera Ruiz. et Pav.	18429	5 cm	Ll. Williams 7082	Peru	MADw	
aspera	18430	5 cm	Ll Williams 6019	Peru	MADw	
aspera	21743	4.5 cm	Dressler 5196	Panama		

Table 1 (continued)

	Utrecht wood number	Diameter the tree	Collector(s)	Collection locality	Xylarium number elsewhere	Distributed under the name of:
<i>Perebea</i>						
<i>guianensis</i> Aublet	8128	4 cm	Krukoff 7041	Braz. - Amaz.	USw 8128	<i>Perebea tessmannii</i>
ssp. <i>guianensis</i>	8241	8 cm	Krukoff 7209	Braz. - Amaz.	USw 8241	<i>Perebea tessmannii</i>
<i>guianensis</i> ssp. <i>guian.</i>	16989	4 cm	Irwin c.s. 48718	Braz.		
<i>guianensis</i> ssp. <i>guian.</i>	20795	5 cm	Prance c.s. 18131	Braz. - Amaz.		
<i>guianensis</i> ssp. <i>intermed.</i>						
between <i>guian.</i> and						
<i>acanthogyne</i>	16183	over 16 cm	Krukoff 8350	Braz.	USw 38402	<i>Perebea pseudopeltata</i>
<i>mollis</i> (P & E.) Huber						
ssp. <i>mollis</i>	2668		Ducke 175	Braz.	SJRw 23637	<i>Noyera mollis</i>
<i>mollis</i> ssp. <i>mollis</i>	8080	shrub	Krukoff 6985	Braz. - Amaz.	USw 8080	<i>Noyera mollis</i>
<i>mollis</i> ssp. <i>mollis</i>	19268		Krukoff 1289	Braz. - Amaz.		<i>Noyera mollis</i>
<i>mollis</i> ssp. <i>mollis</i>	20918	18 cm	Prance, c.s. 18525	Braz. - Mato Grosso		<i>Noyera mollis</i>
<i>mollis</i> ssp. <i>rubra</i> (Tréc.)						
C. C. Berg	211	over 14 cm	Stahel 211	Suriname		
<i>xanthochyma</i> Karsten	18421		Cuatrecasas s.n.	Colombia	SJRw	<i>Ogcodeia ulei?</i>
<i>xanthochyma</i>	18431	7 cm	Ll. Williams 3412	Peru	MADw	<i>Ogcodeia ulei?</i>
<i>Pseudolmedia</i>						
+ <i>laevigata</i> Tréc.	2669		Ducke 359	Braz.	SJRw 40090	<i>Ps. brosimifolia</i>
<i>laevigata</i>	7880		Krukoff 6697	Braz. - Amaz.	USw 7880	
<i>laevigata</i>	8096		Krukoff 7003	Braz. - Amaz.	USw 8096	
<i>laevigata</i>	14465	24 cm	de Bruyn 1063	Colombia		
<i>laevigata</i>	14482	53 cm	de Bruyn 1504.	Colombia		
<i>laevigata</i>	14484	26 cm	de Bruyn 1510	Colombia		
<i>laevigata</i>	14492	26 cm	de Bruyn 1538	Colombia		
<i>laevigata</i>	14493	43 cm	de Bruyn 1543	Colombia		
<i>laevigata</i>	14498	24.5 cm	de Bruyn 1557	Colombia		

Table 1 (continued)

	Utrecht wood number	Diameter the tree	Collector(s)	Collection locality	Xylarium number elsewhere	Distributed under the name of:
laevigata	16186	big tree	Krukoff 8383	Braz.		Ps. mildbreadii
laevigata	20923	10 cm	Prance c.s. 18611	Braz. - Mato Grosso		
laevis (R. et P.) Macbr.	96a	over 12 cm	Stahel 96a	Suriname		
laevis	988		For. Dept. 5378	Guyana		Ps. sagotii
laevis	3421	1 cm	Lindeman 5034	Suriname		
laevis	11817	30 cm	Breteler 3929	Venezuela		
laevis	19815	over 10 cm	Krukoff 5188	Braz. - Amaz.		
laevis	19823	big tree	Krukoff 5217	Braz. - Amaz.		
laevis	19889	big tree	Krukoff 5312	Braz. - Amaz.		
laevis	19916		Krukoff 5440	Braz. - Amaz.		
laevis	20907	14 cm	Prance c.s. 18437	Braz. - Mato Grosso		
laevis	20922	14 cm	Prance c.s. 18610	Braz. - Mato Grosso		
+macrophylla Tréc.	2670		Krukoff 10738	Bolivia	SJRw 39639	Ps. laevis
macrophylla	16202	big tree	Krukoff 8524	Braz.		Ps. laevis
macrophylla	20906	10 cm	Prance c.s. 18376	Braz. - Mato Grosso		
+oxyphyllaria Donn. Sm.	-		Stevenson 119	Br. Honduras	SJRw 14901	
oxyphyllaria	20653	? big tree	Mexico INIF 152	Mexico		
+spuria (Sw.) Griseb.	-		C. S. Brown 35	Br. Honduras		
spuria	18027		-	Guatemala		

+ Sections only

length is moderately high as it ranges between 2–3. In the ray tissue the scarcity of uniseriate rays is characteristic; the multiseriates range from 2–8 cells wide, they mostly consist of numerous rows of low procumbent cells bordered by short uniseriate wings, the highest rays up to 2.6 mm high (165 cells), are often diagonally dissected by one or two fibres. Rays are seldom in contact with the vessels, consequently ray/vessel pitting is rare and restricted to occasional half-bordered round pits in the procumbent cells and larger oval pits in the square and upright cells. Narrow latex tubes occur in the rays of all genera except *Olmedia*. Crystals may be present but usually are not abundant; brown or yellowish contents are generally present. Parenchyma, except in *Olmedia*, is always paratracheal in mostly incomplete, vasicentric, aliform rings, the lateral wings locally confluent or even forming confluent banded parenchyma. A narrow terminal band is occasionally present. Strands of 2–4 (8) cells; in the 2-celled strands the individual cells sometimes with long pointed ends, resembling short fibres. Crystals rather scarce, but abundant in long rows of divided cells in *Pseudolmedia oxyphyllaria*. Brown contents generally present. Pits to vessels large, oval or irregular, mainly in horizontal arrangement. In *Olmedia* the parenchyma distribution is different, the parenchyma occurring in wide, regular, apotracheal bands.

4. KEY TO THE WOOD OF THE OLMEDIÆ

It was not without hesitation that a key to the genera was prepared. In this rather homogeneous group of genera it is extremely difficult to find distinguishing characters which are sufficiently clearly defined to allow someone not familiar with the tribe to identify his material. This difficulty is enhanced by the fact that in large genera represented by much material usually an odd sample is likely to be present that does not correspond to the general picture of the genus. Aberrant features are usually found in the parenchyma distribution and the average vessel number. From a detailed investigation of the material of *Helicostylis tomentosa* (table 2) it appeared that stems and branches with a diameter of less than 5 cm differ a great deal in those features from more mature stems. Therefore samples from such small-sized stems or branches cannot be identified with much certainty.

All this applies to the genera *Helicostylis*, *Maquira*, *Naucleopsis*, *Perebea* and *Pseudolmedia*. The other genera, *Castilla* and *Olmedia*, are easily distinguished, mainly on the basis of general texture, and parenchyma distribution and absence of latex tubes respectively. *Maquira* and *Perebea* are so much alike that they can hardly be distinguished by their wood. Though the absence of dark brown contents in the ray and parenchyma cells is often characteristic for *Maquira*, as it comes true for the majority of specimens, it is not sufficiently distinctive for all samples. Neither is the usually abundant presence of dark brown contents in the parenchymatic cells of *Pseudolmedia* a constant and reliable feature that may be used for diagnostic purposes. Taking into account what is pointed out above, the following tentative key is proposed:

Table 2. A comparison between wood samples of *Helicostylis tomentosa* from trees of various diameter.

Uw	Diameter of the stem	Number of vessels per square mm	Vessel diameter in μm	Size of vascular pits	Number of rays per mm	Parenchyma distribution
6836	14 cm	7 (2-13)	120-150	10	6 (4-7)	vasicentric, and aliform with short wings
9077	c. 12 cm	7 (3-10)	110-150	8-10	6.5 (4-8)	vasicentric, seldom aliform
11698	24 cm	5 (3-7)	120-160	10-12	6.5 (6-8)	incomplete vasicentric rings, and aliform
4539	5 cm	7 (5-13)	100-120	10	6 (4-8)	vasicentric, and short-aliform
3267	5 cm	8 (4-13)	100-120	10	5 (3-6)	vasicentric, and often aliform
3791	5 cm	7 (4-12)	90-120	8-9	6 (3-8)	vasicentric, and often aliform
3711	3 cm	10 (8-13)	85-95	8	6 (4-8)	vasicentric, and aliform with longer wings
3672	2 cm	13 (9-17)	80-95	10	5.5 (4-7)	complete lozenge-shaped rings
3041	2 cm	10 (8-18)	60-80	8.5	7 (5-8)	aliform with rather long wings
4924	1 cm	16 (14-18)	c. 60	8	8	aliform with rather long wings, sometimes confluent

1. Parenchyma in straight, moderately broad, regularly spaced, apotracheal bands; fibres not septate or exceptionally so: latex tubes absent . *Olmedia*
Parenchyma vasicentric, short to long aliform, or locally or generally aliform/confluent to confluent banded 2
2. Wood cream-coloured; weight light, c. 0.40; texture course; fibres thin-walled with a large lumen and a diameter of 20–35 μm *Castilla*
Wood yellowish brown to middle brown, the heartwood sometimes darker brown or with dark streaks; moderately heavy to heavy; fibres thick-walled to moderately thick-walled with a diameter of 15–25 μm 3
3. Vessels moderately numerous to numerous, 20–35 per square mm on the average, diameter 70–100 (120) μm ; fibres all septate with 2–3 septae per fibre *Naucleopsis* p.p.
Vessels less numerous, 5–15 per square mm on the average, diameter 90–150 (200) μm : fibres usually septate but septae often absent in most fibres in *Helicostylis* 4
4. Rays 4–6 per mm; vessels 100–200 μm wide, usually over 140 μm : intervascular pits generally 8–10 μm ; parenchyma in complete, short-aliform rings *Helicostylis*
Rays 6–9 per mm; vessels less wide, intervascular pits 5–8 μm 5
5. Parenchyma generally aliform-confluent, forming wavy tangential bands; rays often diagonally dissected by a few fibres (tg. sections) . *Pseudolmedia*
Parenchyma vasicentric, aliform, only locally confluent or forming interrupted bands (the bands more pronounced in *Perebea mollis* and *Perebea xanthochyma*) *Maquira*, *Perebea*, *Naucleopsis amara*, *N. ulei*

5. DESCRIPTION OF THE GENERA

1. CASTILLA Sessé

plate I, fig. 1, 2

A genus of three species, each represented by one or more wood samples. (table 1).

General characters

According to WILLIAMS (1936), RECORD & MELL (1924), RECORD & HESS (1940, 1944) without clear demarcation between sapwood and heartwood; the sapwood light yellowish brown; texture coarse; straight-grained; rather light, vol. weight c. 0.40.

Microscopical characters

Vessels: Few to moderately few, 3–6 (2–9) per sq. mm, sometimes nearly all solitary, but generally for about 50% in radial multiples of 2–4 or in longer dumb-bell shaped rows or in irregular clusters; fairly regularly distributed; outline oval or rounded, tang. diameter 160–200 (100–300) μm ; perforations simple; intervascular pits 8–10 μm , the border angular; thin or hard tyloses occasionally present; vessel members on the average 420 (200–700) μm long.

Fibres: All or partly septate, in *C. elastica* and *C. tunu* with one or two septae, in the material of *C. ulei* the occurrence of septae variable; diam. 20–28 (35) μm :

walls very thin, 2–3 μm ; length on average 1270 (600–1900) μm ; simple pits on radial walls only. Fibre/vessel member length ratio 3 (2.6–3.7).

Rays: 1 and 2–6 cells wide. The uniseriates comprising c. 25% but scarce in two samples of *C. ulei*; up to 30 cells (650 μm) high, consisting of square and upright cells. The multiseriates generally 2–6 cells wide, but 3 cells wide in one sample of *C. ulei*, the narrow multiseriates usually with long uniseriate wings, in the samples with the widest rays the wings 2–3 cells high, and the individual upright cells less high than in the samples with long uniseriate wings; width from 20–90 μm ; height up to 1 mm or more, if vertically fused, which occurs more frequently in the narrow type of rays, up to 1700 μm ; pits to vessels scarce, round and half-bordered to oval, mainly in the square and upright cells. Latex tubes present in all species, though rather scarce in some samples of *C. ulei*. In one sample of *C. tunu* (Uw 7046) sclerotic ray cells present. Number 4–8 per mm.

Parenchyma: Paratracheal, mostly restricted to narrow vasicentric or short-aliform rings, occasionally confluent into a narrow band, however up to 8 cells wide bands present in *C. elastica*, and in one sample of *C. ulei* nearly all parenschyma banded, the bands 12–20 cells wide (240 μm), concentric, regular and completely enveloping the vessels. Strands of 2–4 (8) cells. Pits to vessel large, oval, and elongated.

Diagnostic characters

All samples share the extremely thin-walled, wide fibres, and the resulting rather light weight of the wood.

Remarks

The variation in distribution of the parenchyma and in structure of the rays shown by the present material, is also apparent from the description given by RECORD & HESS (1940). WILLIAMS (1936) described the parenchyma of the sample collected by him near Loreto as paratracheal and sometimes aliform.

2. HELICOSTYLIS Trécul

plate I, fig. 3, 4; plate III, fig. 1

In BERG's (1972) revision *Helicostylis* comprises seven species. Wood specimens from five of those were available. The type species of the genus *H. tomentosa* (P. et E.) Rusby is by far the most widespread and is also the best represented in our wood collection. Several of the wood specimens studied were originally assigned to other genera like *Pseudolmedia* and *Perebea* as appears from *table 1*.

General characters

Sapwood a golden yellowish brown, c. 7–10 cm wide, the heartwood light brown in *H. pedunculata* to very dark brown in *H. elegans* and *H. scabra*, medium brown in the other species; sometimes with dark brown streaks on the tangential surfaces, in the cross section showing as irregular light and dark concentric zones; the demarcation between sapwood and heartwood generally irregular. Texture moderately fine; straight- or roey-grained; moderately hard and moderately heavy to heavy, vol. weight 0.50–0.86.

Microscopical characters

Vessels: Mostly moderately few, averages ranging from 5–12.5 (2–16) per sq. mm, the highest average of 12.5 occurring in the sample of *H. turbinata* (Uw 16528); mostly solitary, for 10–30% in radial multiples of 2–3(5), scattered, but with a tendency towards a diagonal arrangement. Outline round, diameter 120–160 (200) μm ; perforations simple; intervascular pits 8–10 (12) μm , but in one sample of *H. scabra* (Uw 16222) 4 μm , the borders oval or angular, the slits enclosed or extended and confluent. Thin tyloses often present. Vessel members on average 470 (430–515) μm long, ranging from 300–630 μm .

Fibres: Libriform, partly septate, the number of septate fibres variable for the same species, in some samples of *H. tomentosa* and *H. scabra* nearly all fibres non-septate, diam. 16–20 μm , in *H. pedunculata* 20–30 μm ; walls occasionally gelatinous; pits restricted to the radial walls, small; the average length 1230 (1140–1380) μm , the range 900–1700 μm . Fibre/vessel member length ratio on average 2.6 (2.3–3.0).

Rays: 1- and 2–5 cells wide. The uniseriats scarce, very low, mostly 3–5 (1–10) cells high, consisting of square and upright cells. The multiseriats mostly 3–4 cells (40–50 μm) wide, but in *H. pedunculata* and in *H. turbinata* and in one sample of *H. scabra* 50–80 μm wide; in the other sample of *H. scabra* and in *H. elegans* 2–4 cells (20–40) μm wide; the uniseriate wings generally very low, however, sometimes up to 6 or 8 cells high; vertically fused rays present but not abundant, normally height 300–800 μm , but also rays of 1300–1500 μm (70–90 cells) high present; sheath cells locally. Pits to vessels scarce, large, irregular, or half-bordered and round, mainly restricted to the square and upright cells. Latex tubes present. Crystals occasionally present; brown contents frequent in two samples of *H. scabra*, absent or very scarce in the other species. Number on average 5 (4–7) per mm.

Parenchyma: Paratracheal, usually as a moderately broad ring completely surrounding the pores, and broadened laterally; in *H. turbinata* often confluent and locally forming long uninterrupted bands 7–8 cells wide, in the other species also locally confluent, but the bands narrower and less conspicuous; sometimes a straight narrow band suggesting marginal parenchyma present. Strands of 2–8 cells, mostly 4 cells. Brown contents often present, crystals and sclerotic cells occasionally noticed. Pits to vessels large, irregular to oval, often horizontally arranged.

Diagnostic characters

The medium-sized vessels, the short-aliform vasicentric parenchyma, and the moderately few rays are characteristic for *Helicostylis*.

Remarks

Helicostylis is one of the genera of the Olmedieae which can be recognized moderately well by its anatomical features. At least no great difficulties were encountered in assigning a large number of Moraceous wood samples backed by sterile herbarium twigs to this genus, which identifications were later on confirmed by Berg.

RECORD & MELL (1924) mentioned in their description of the genus the different

distribution of the parenchyma in material of *H. latifolia* Pitt. as compared to *H. poeppigiana*. To them the long and narrow aliform parenchyma of *H. latifolia* is suggestive of the genus *Brosimum*. In Berg's revision *H. latifolia* Pitt. was indeed transferred to *Brosimum alicastrum*.

3. MAQUIRA Aublet

plate III, fig. 3; plate IV, fig. 1

Aublet's genus *Maquira* reestablished by BERG (1972) comprises a.o. *M. guianensis* Aubl. formerly known as *Perebea laurifolia* Tréc., a relatively common tree in the Guyanas. Furthermore Ducke's genera *Olmedioperebea* and *Olmediophaena*, as well as all species of *Olmedia* with the exception of *O. aspera* R. et P., were assigned by Berg to *Maquira*. The genus consists of five species, all of which are represented by wood samples (table 1).

General characters

Without clear demarcation of sapwood and heartwood; straw-coloured or light brown, in one sample of *M. guianensis* with irregular dark patches in the central part of the stem; irregular light and dark concentric zones may be conspicuous on the polished cross surface of a stem. Texture rather fine; straight- or roey-grained; moderately hard; heavy, vol. weight 0.70–0.90.

Microscopical characters

Vessels: Number variable from 6–26 per sq. mm, most numerous in *M. coriacea* but the same value of 11–23 per sq. mm also occurs in some samples of *M. guianensis*; mostly solitary, for 20–40% in radial multiples of 2–3, or in clusters; scattered or rather irregularly distributed without a definite pattern; outline oval to nearly round, tang. diameter 100–160 μm ; perforations simple; intervascular pits on the average 8 (6–11) μm , border angular, slits enclosed; thin tyloses sometimes present; length of vessel members on the average 500 (390–580) μm , range 260–850 μm .

Fibres: Libriform. The fibres septate with one or two septae; diameter 16–26 μm , lumen as wide as or narrower than the breadth of the walls, but in *M. sclerophylla* the lumen wider; occasionally with gelatinous walls; length on the average 1225 (1100–1400) μm , ranging from 800–1700 μm . Fibre/vessel member length ratio 2.6 (2.1–3).

Rays: 1-seriate and (2) 3–5 (8)-seriate. The uniseriates very few, mostly about 7 cells high, sometimes 15–17, consisting of square and upright cells. The multiseriates of variable width even within a species, but generally 3–5 cells (40–70 μm) wide, widest in *M. coriacea* and *M. sclerophylla* (4–8 cells); the uniseriate wings usually 1–3 cells high, occasionally much higher; height variable, mostly 20–60 cells (300–800 μm), but often some rays 100 cells (1200–1400 μm) high present, and those high and wide rays dissected diagonally by one or two fibres; vertically fused rays present but scarce; sheath cells rare. Light brown to brown contents often present, crystals scarce. Pits to vessels scarce, rounded, half bordered, mainly in the square and upright cells. Latex tubes present. Number on the average 6–8 per mm.

Parenchyma: Paratracheal, generally in wide to rather narrow vasicentric,

short-aliform rings, occasionally confluent into narrow bands, sometimes with a tendency to diagonal alignment of the vessels; however, in some specimens of *M. guianensis* wings and bands much better developed. Pits to vessels large and irregular. Crystals rare. Strands of 2–4 (8) cells.

Diagnostic characters

The lozenge-shaped parenchyma, occasionally confluent tangentially or diagonally over a short distance is the only constant feature to distinguish species of *Maquira* from *Pseudolmedia*, which it closely resembles in most characters. Admittedly distinction between individual specimens may prove impossible due to the great variability in the samples of a species, viz. *M. guianensis*. It is even more hazardous to distinguish *Maquira* from *Perebea*, while characters of the species here are often completely overlapping.

Remarks

As the reestablished genus *Maquira* includes so many species formerly assigned to several other genera, no description related to the genus itself nor to the majority of its species could be found in the literature. RECORD & HESS (1940) referred to the aberrant structure of *Perebea calophylla* (Yw 23650 = Ducke 188) now identified as *M. calophylla*, which did not fit either in *Perebea* nor in *Olmedia*, where it also had been placed. Under the paragraphs treating *Olmedia* and *Olmedioperebea* we also find references to species now placed in *Maquira* but since their descriptions are very brief and general a comparison with our data is hardly possible. In any case it is noticeable that they drew attention to the fact that the abundant parenchyma of *O. aspera* is strongly different from that of the other species they treated under *Olmedia*.

4. NAUCLEOPSIS Miquel

plate III, fig. 2

According to BERG's (1972) conception of the genus, *Naucleopsis* comprises the species formerly assigned to *Acanthosphaera*, *Ogcodeia*, *Palmolmedia*, and two species earlier placed in *Perebea*: *P. concinna* and *P. macrophylla*. In the present circumscription there are 18 species in *Naucleopsis*, twelve of which are represented by wood samples.

General characters

Wood uniformly straw-coloured to yellow-brown, heartwood not seen but according to L. WILLIAMS (1936) dark brown in *Ogcodeia tamamuri* (syn. of *N. glabra*). RECORD & HESS (1940) stated that the heartwood is pale brown and not clearly differentiated from the sapwood. Texture moderately fine, straight-grained. Moderately hard and moderately heavy, vol weight c. 0.75.

Microscopical characters

Vessels: Fairly numerous to numerous, on the average 20–35 (16–50) per sq. mm. but less numerous in *N. amara* (Uw 19340) and in *N. ulei* (Uw 18620) with 13 (10–17) per sq. mm.; about 10–20 (40)% in radial rows of 2–4, occasionally in longer rows and then the vessels often of diminishing diameter, or in irregular groups. Outline round to angular, diameter generally 70–100 μm , in *N. amara* up to 140 μm ; intervacular pits 5.5–7.5 μm , in some cases

9 μm and in *N. amara* and *N. ulei* normally 8–10 μm . Thin tyloses seldom present. Vessel members on the average 450 (400–500) μm long, range 300–670 μm .

Fibres: Libriform, nearly all fibres septate, with 2–3 septate per fibre. Diameter (12) 15–20 μm , relatively thin-walled, walls 3–4 μm , but thicker (4–6 μm) in *N. glabra*; gelatinous walls frequent; pits simple, exclusively on the radial walls; length variable within a sample, on the average 950 (800–1060) μm , range 430–1400 μm . Fibre/vessel member length ratio on the average 2.1 (1.6–2.4).

Rays: 1- and 3–4 (6) cells wide. The uniseriates usually scarce, very low, 3–7 (14) cells high, with square and upright cells. The multiseriates in general 3–4 cells wide, the uniseriate wings with square and upright cells mostly not over two cells high, but occasionally much higher in one sample of *N. glabra*, in *N. imitans*, *N. stipularis* and *N. ulei*; width 25–50 μm ; usually 20–60 cells (700–1500 μm) high, but some up to 100 cells (2 mm) or, when vertically fused, even 3 mm high. Pits to vessels scarce, rounded. Cell dimensions of the procumbent cells as seen on a radial section often very irregular. Latex tubes usually present but not abundant. Crystals generally present as well as brown cell contents. Average number 6–8 per mm.

Parenchyma: Paratracheal, vasicentric with narrow and short aliform extensions, occasionally locally confluent over a short distance, the vasicentric ring often incomplete and absent on the adaxial side of the vessels. In one specimen of *N. guianensis* and in *N. macrophylla* marginal parenchyma is present as a one cell wide band; in *N. inaequalis*, *N. ternstroemiiflora* and *N. ulei* growth rings are sometimes indicated by a 3–5 cells wide marginal band. Strands of 4 (2–8) cells. Pits to vessels large and irregular, or oval and in horizontal rows. Brown cell contents usually present; crystals rare.

Diagnostic characters

Fairly numerous and rather narrow to moderately wide vessels, except in one sample of *N. amara* and of *N. ulei* with less numerous vessels of a larger size. Intervascular pits 5.5–7.5 μm , but larger in *N. amara* and *N. ulei*. Parenchyma inconspicuous, vasicentric, aliform, and confluent. Crystals usually present in the rays.

Remarks

L. WILLIAMS (1936) described the general and the lens characters of three species of *Ogcodeia* (*O. tamamuri* Macbr. = *N. glabra* Spruce ex Pitt., *O. tessmannii* Mildbr. = *N. glabra* and *O. ulei* (Warb.) Macbr. = *N. ulei* (Warb.) Ducke). He also recorded the numerous vessels, but his statement that parenchyma occurs both surrounding the pores and in fine, short tangential lines could not be confirmed as far as the lines are concerned. RECORD & HESS (1940) based their description of *Naucleopsis* on one specimen of *N. macrophylla* Miq. The affinity of the wood with that of *Ogcodeia* and *Noyera* was pointed out. Their description of the genus *Ogcodeia*, based on one wood sample of each of 6 species, the names of which were not given, matches the description of *N. macrophylla* quite well indeed, and also agrees with the general description

of *Naucleopsis* sensu Berg given by us. *Noyera mollis* (now *Perebea mollis* (Poepp.) Huber) is different from *Naucleopsis* in the less numerous and wider vessels. LOUREIRO & FREITAS (1968) described the lens characters of *Perebea concinna* (= *N. concinna* (Standl.) C. C. Berg). They mentioned a pore distribution of 7–17 per sq. mm, considerably less than our value.

5. OLMEDIA Ruiz & Pavon

plate II, fig. 3,4; plate IV, 3

BERG (1972) considered the genus as monotypic, *Olmedia aspera* R. & P. being the sole species. Specimens formerly considered to belong in this genus were transferred by him to *Pseudolmedia* and *Helicostylis*. Three samples of *O. aspera* were available for investigation.

General characters

Wood uniformly cream-coloured; texture rather fine, parenchyma clearly visible on cross sections; slightly roey-grained. Moderately heavy, vol. weight 0.78.

Microscopical characters

Vessels: Moderately few, 7.5–10 (4–13) per sq. mm; for about 50% in radial multiples of 2–4, seldom in clusters, fairly regularly distributed. Outline round, diameter generally 100 (70–140) μm ; perforations simple; intervascular pits angular with enclosed slit, 7–10 μm . Vessel members on the average 530 (370–700) μm long.

Fibres: Non-septate, exceptionally one or two septate fibres seen in macerations. Rather irregularly arranged. Diameter 16–22 μm , walls thin, c. 2 μm ; gelatinous walls present in nearly all fibres; pits very small, on radial walls only; length on the average 1050 (640–1400) μm . Fibre/vessel member length ratio 2.– (1.7–2.2).

Rays: 1– and 2–4 (5) cells wide. The uniseriates scarce, consisting of square and upright cells, very low, 2–8 cells high. The multiseriates mostly 2–4 cells wide, the uniseriate wings often restricted to one or two rows of upright cells, but sometimes much longer; sheath cells nearly always present, though not completely enveloping the rays; on tangential section the cell sizes very irregular; rays sometimes vertically fused or diagonally dissected by a fibre; width 30–50 μm ; up to 65 cells (1700 μm) high. Pits to vessels scarce, rounded and half bordered or large and elongated. Latex tubes not observed. Brown cell contents absent, crystals very scarce. Average number 7 (5–8) per mm.

Parenchyma: Apotracheal and paratracheal. Chiefly in regularly spaced, straight or slightly undulating, 5–8 (12) cells wide bands, which occasionally border the vessels or envelop them; paratracheal parenchyma usually present as an incomplete vasicentric ring. Strands of 2–4 cells, on average 530 μm long. No specific cell contents observed.

Diagnostic characters

Regularly spaced, moderately straight, broad bands of apotracheal parenchyma, non-septate fibres and the absence of latex tubes characterize the wood of *Olmedia*.

Discussion

The wood of *Olmedia aspera* was first described by WILLIAMS (1936) based on specimens collected by himself in Peru. The same material was subsequently studied by RECORD & HESS (1940) and by ourselves. Williams mentions trunks of 20–25 cm in diameter, but the material at hand (MADw s.n.) is 5 cm in diameter. Another specimen which we owe to the courtesy of Dr. R. L. Dressler is a piece of a stem of an arching shrub (Uw 21743). It shows the same features as the Williams' samples. Like Record & Hess remarked, the wood by its "lamellated" structure resembles the wood of *Ficus* more than that of the other genera of the Olmediaeae. This different wood structure combined with the absence of a very characteristic type of branch abscission present in all other genera of the Olmediaeae – anatomical details of which are described by KOEK-NOORMAN & TER WELLE (1976) – as well as differences in the floral structure lead BERG (1977) to exclude *Olmedia* from the tribe.

6. PEREBEA Aublet

plate III, fig. 4; plate IV, fig. 2, 4

BERG (1972) widened the concept of the genus to include several species assigned by previous taxonomists to other genera. Among them is the former genus *Noyera* Tréc. which became a section of *Perebea*. Of the eight species only the three most common ones with the widest distribution are represented by wood samples.

General characters

The wood is greyish or yellowish brown without a clear demarcation between sapwood and heartwood; straight-grained, texture moderately fine, moderately light, the vol. weight between 0.70–0.80, much lighter (0.53) in one sample of *P. guianensis*.

Microscopical characters

Vessels: Moderately few, on the average 7–8 (2–14) per sq. mm, slightly more numerous in *P. guianensis* (12–15 per sq. mm); mostly solitary, for about 20–25% in radial multiples of 2–4, fairly regularly distributed with a tendency towards a diagonal arrangement; outline oval or rounded, tang. diameter generally 100–160 (90–200) μm , widest in *P. guianensis*; perforations simple; intervacular pits 7–9 μm ; thin tyloses occasionally present in *P. guianensis* and *P. mollis*; vessel member length on the average 460 (370–560) μm , the total range from 240 to 680 μm .

Fibres: All septate, usually with 2–3 septae; arrangement irregular. Diameter mostly 18–20 (24) μm , walls 3–4 μm thick; length on the average 1260 (1050–1460) μm , range 500–1900 μm ; pits very small, limited to the radial walls. Fibre/vessel member length ratio: 2.6 (2–3.8).

Rays: Uniseriate and 2–5 cells wide. The uniseriates consisting of square and upright cells, rather frequent in *P. guianensis* and *P. xanthochyma*, but nearly absent in *P. mollis*; mostly 4–10 cells high. The multiseriates mostly 2–3 cells (20–40 μm) wide in *P. guianensis*, 4–6 cells (50–70 μm) in *P. mollis* and *P. xanthochyma*, generally with short uniseriate wings, often partly with longer

wings; height usually 600–800 μm , but up to 1000 and 1250 μm (50–68 cells). Pits to vessels scarce, round, half bordered, mostly in the square and upright cells. Latex tubes present. Often brown contents in the cells; crystals scarce, noticed in *P. mollis* and in *P. xanthochyma*. Average number 6.5 (5–8) per mm.

Parenchyma: Paratracheal in generally complete, narrow, aliform vasicentric rings, often confluent in tangential or diagonal direction over a short distance, the sheaths usually widest on the abaxial sides of the vessels, continuous bands rare, though fairly often present in *P. mollis*. Strands of 4 (2–8) cells. Pits to vessels large, irregular, mostly horizontal. Brown cell contents often present; crystals very scarce, noticed only in *P. mollis* p.p. and *P. xanthochyma*.

Diagnostic characters

As already stated before, it is very hard to find characters which are specific for *Perebea*, as *Maquira* and *Perebea* closely resemble each other in nearly all anatomical features, as they also do in morphological characters.

Remarks

RECORD & HESS (1940) described the wood of *Noyera mollis* (at present *P. mollis* ssp. *mollis*) and their description complies very well with our findings, as is to be expected since the specimens studied by them and by us are, at least partly, the same. Under the heading *Perebea* they treated wood samples of 5 species, only 3 of which, viz: *P. castilloides* Pitt. (now *P. guianensis* ssp. *castilloides* (Pittier) C. C. Berg), *P. chimiqua* Macbr. (now *P. xanthochyma* Karsten) and *P. tessmannii* Mildbr. are still considered as *Perebea* species at present. Of the other two *P. concinna* Standl. was transferred by Berg to *Nucleopsis* and *P. laevigata* Standl. from Panama could not be traced. They mentioned the rather aberrant structure of *P. castilloides* with non-septate fibres and the abundant parenchyma often occurring in wide concentric bands next to the more usual short aliform vasicentric rings. This, however, need not be considered as a really disturbing fact, since we found in our material banded parenchyma in a sample of *P. mollis* rather often. The absence of septate fibres in their material is more unusual as this character was always clearly present in our samples. In an earlier publication RECORD & MELL (1924) described a sample of *Perebea* spec. (Yale 4952 = BW 5493) from Suriname. The herbarium voucher of this number has now been identified by Berg as *P. mollis* ssp. *rubra*. In their description they mentioned the high, and up to five cells wide rays and the occasional occurrence of bands of parenchyma apparently limiting growth rings, but otherwise present in wing-like patches about the pores, and the often septate fibres. A description which matches quite well our general description given above.

7. PSEUDOLMEDIÆ Trécul

plate II, fig. 1, 2

In Berg's revision a number of species formerly considered to belong in *Pseudolmedia* were transferred to other genera like *Helicostylis* and *Maquira*, as will be discussed below.

The material investigated consists of 18 samples belonging to 5 species (*table 1*). The genus comprises 9 species.

General characters

Colour yellowish brown, heartwood not different from the sapwood, except, according to RECORD & HESS (1940, 1944), in *P. spuria* with reddish brown heartwood not sharply demarcated from the thick grayish or pinkish brown sapwood. L. WILLIAMS (1936) described the heartwood of a large tree of *P. multinervis* (now *P. laevis*) as pinkish or dark brown. The wood is straight or slightly roey-grained; moderately heavy, vol weight 0.75–0.80, or heavy, like in *P. oxyphyllaria* with a vol. weight of 1.0.

Microscopical characters

Vessels: Number variable, on the average 10–15 per sq. mm, in samples of small-sized trees (Krukoff 6697, 7003) often more numerous: 30 or more per sq. mm and then resembling *Naucleopsis*; usually scattered but sometimes irregularly distributed, for about 30–50% in radial multiples of 2–3(4), multiples less frequent in *P. laevigata*; tang. diam. 100–150 μm ; intervacular pits 6–8 μm ; tyloses often present, generally thin, but occasionally very thick and sclerotic; often with solid white contents in *P. laevigata*, *P. laevis* and *P. oxyphyllaria*; vessel member length 350–500 μm .

Fibre tissue: Nearly all fibres septate, except in one sample of *P. macrophylla*; fibre arrangement irregular. Diameter 15–20 (24) μm , walls 3–5 μm thick, in *P. oxyphyllaria* and *P. spuria* walls 6 μm thick and the lumen narrow, c. 3 μm ; sometimes a gelatinous layer present, pits small, simple, on the radial walls only; average length about 1100 (800–1340) μm . Fibre/vessel member length ratio 2.60, range 2.25–3.10.

Rays: Uniseriates scarce, short, consisting of square and upright cells, sometimes also a few procumbent cells present. The multiseriates mostly 3–4 (2–6) cells wide with uniseriate margins, 1–3 cells high; width 30–50 μm and up to 70 μm ; height variable between 30 and 100 cells or 300 and 800 (1400) μm respectively, the large rays often dissected by one or two diagonal fibres (*plate II, fig. 2*). Pits to vessels large, mainly horizontal. Latex tubes present. Many cells with brown contents, rhombic crystals sometimes present, very numerous in *P. oxyphyllaria* and *P. spuria*. Number on the average 7–8 (5–11) per mm.

Parenchyma: Paratracheal, vasicentric in complete and incomplete rings, often aliform with long wings in *P. laevis* and *P. laevigata* in part of the growth ring, but mostly confluent into irregular, wavy, narrow, 3–6 cells wide, bands; strands of (2)4–8 cells; crystals present in *P. laevigata*, *P. oxyphyllaria* and *P. spuria*.

Diagnostic characters

Paratracheal parenchyma predominantly arranged in wavy irregular bands; rather wide and often high rays, often obliquely crossed by fibres; frequent occurrence of crystals in rays and parenchyma cells.

Discussion

Of *P. macrophylla* two wood samples were available, both collected by Krukoff,

the herbarium vouchers of which were identified by Berg. The wood structure of one of them (Uw 16202 = Krukoff 8524) differs in various characters from the general structure of the genus as described above: the fibres are hardly septate, the rays not over 3 cells wide and not dissected by fibres, the parenchyma is narrow vasicentric instead of aliform confluent.

The most extensive information on the genus to be found in the literature is RECORD & HESS's (1940) description chiefly based on *P. spuria* and *P. oxyphyllaria*. In 3 other species, viz. *P. multinervis*, *P. obliqua* and *P. scabra*, they noted a different parenchyma distribution and a larger fibre width. In Berg's revision *P. multinervis* is placed in synonymy with *P. laevis*. Material of *P. laevis* seen by us, is rather uniform and agrees quite well with the general aspect of *Pseudolmedia*. However, like stated above, individual variations in structure happen to occur occasionally in each genus. *P. obliqua* was transferred by Berg to *Maquira coriacea* and *P. scabra* to *Helicostylis scabra*. This is in accordance with their anatomy as neither in *Maquira* nor in *Helicostylis* (except *H. turbinata*) parenchyma confluent over a long distance occurs.

GENERAL DISCUSSION

From the key and descriptions it becomes clear how much the genera *Helicostylis*, *Maquira*, *Naucleopsis*, *Perebea* and *Pseudolmedia* have in common in their wood structure. As already pointed out in the remarks following each generic description, many of the incongruities signalized by RECORD & HESS (1940) have been eliminated by BERG's (1972) new concepts of the generic circumscriptions. On the other hand some inconsistencies in the general aspect of most of the larger genera still remain. Sometimes it is one out of several samples of the same species that shows a slightly different wood pattern, like *Pseudolmedia macrophylla* (Uw 16202 = Krukoff 8524) resembling a *Helicostylis* or two samples of *Perebea mollis* (Uw 8080, Uw 19268 = Krukoff 6985, Krukoff 1289) the parenchyma distribution of which is more like *Pseudolmedia*. Or in *Naucleopsis*, *N. amara* (Uw 19340 = Krukoff 1406) being different from the other species in its number of vessels. However, these differences are much smaller and of a different nature than those between *Olmedia* and the other genera, *Olmedia* being distinguished by the apotracheal banded parenchyma, the bands being regularly spaced and more or less straight, a type of parenchyma distribution not occurring in any other genus of the Olmediæ, but resembling that in *Ficus*, *Malaisia*, *Pseudomor*, *Sorocea*, *Sparattosyce* and *Trophis*. To the latter genus *Olmedia* seems to be related (BERG 1977). METCALFE & CHALK (1950) also list *Trymatococcus* among the genera with banded non-confluent parenchyma, but this could not be confirmed in our material of the three species of this genus. In *Olmedia* septate fibres are extremely rare, which is another character distinguishing it from the other genera. However, in *Helicostylis* septate fibres are not of a general occurrence and in some specimens like in *H. turbinata* they could not be traced at all. Moreover, in the Anatomy of the Dicotyledons *Helicostylis* is not cited among the genera with septate fibres,

indicating that their presence is not as evident as it is in the other genera. Thus, the parenchyma distribution in particular is an argument in favour of BERG's (1976) recent exclusion of *Olmedia* from the tribe.

TIPPO (1938), in a special paragraph of his general survey of the anatomy of the family, drew attention to the distribution of septate fibres within the Moraceae. From a total of 28 species with septate fibres 25 belong to the subfamily Artocarpoideae; in all Olmedieae septate fibres are present. He also found them in two species of *Olmedia*, but as he did not give names or numbers of collections it is hard to be certain whether the specimens seen by him really belong to what is now considered as *Olmedia* – i.e. *O. aspera* R. & P. only –, or not. Another genus that would fit in well with the Olmedieae is the African genus *Antiaris*, placed by BUREAU (1873) in the Olmedieae, which was followed by BENTHAM (1880) and more recently by CORNER (1962). From other paleotropical genera which Corner tentatively placed in the Olmedieae, *Sparattosyce* would not fit. Of two more genera cited in this context, viz. *Antiaropsis* and *Mesogyne*, no material was available. According to TIPPO (1938) *Mesogyne* possesses septate fibres which fact he stresses as being exceptional in the Dorsteneae, the tribe in which *Mesogyne* was included at that time. As a matter of fact in none of the tribes, beside Olmedieae, septate fibres were found by him, with the exception, however, of *Ficus religiosa* in the Ficeae and *Prainea* in the Conocephaloideae. Thus the septate fibres of *Mesogyne* form a strong argument in favour of Corner's opinion that *Mesogyne* is closely related to *Antiaris*. (The wood of *Prainea* shows a certain resemblance to the Olmedieae not only in the septate fibres, but also in its aliform-vasicentric parenchyma distribution. CORNER (1962) placed *Prainea* in the alliance of *Artocarpus* and *Malaisia*, stressing, however, its own character.) Genera belonging to the tribe Brosimeae show a certain resemblance to the Olmedieae in their parenchyma distribution (LINDEMAN & MENNEGA 1963) but they differ in other characters, a.o. by the complete or almost complete absence of septate fibres.

In general, the structure of the wood of the Olmedieae may be considered as advanced. Features like scalariform vessel perforations, strongly heterogeneous rays, diffuse apotracheal parenchyma (cf. the characters listed by TIPPO 1938), usually considered as primitive structures are not encountered in any of the genera. If septate fibres and a considerable amount of paratracheal parenchyma are an indication of specialization then *Helicostylis* has to be placed at the base of the series and *Castilla* at the top. The other genera are to be placed somewhere in between.

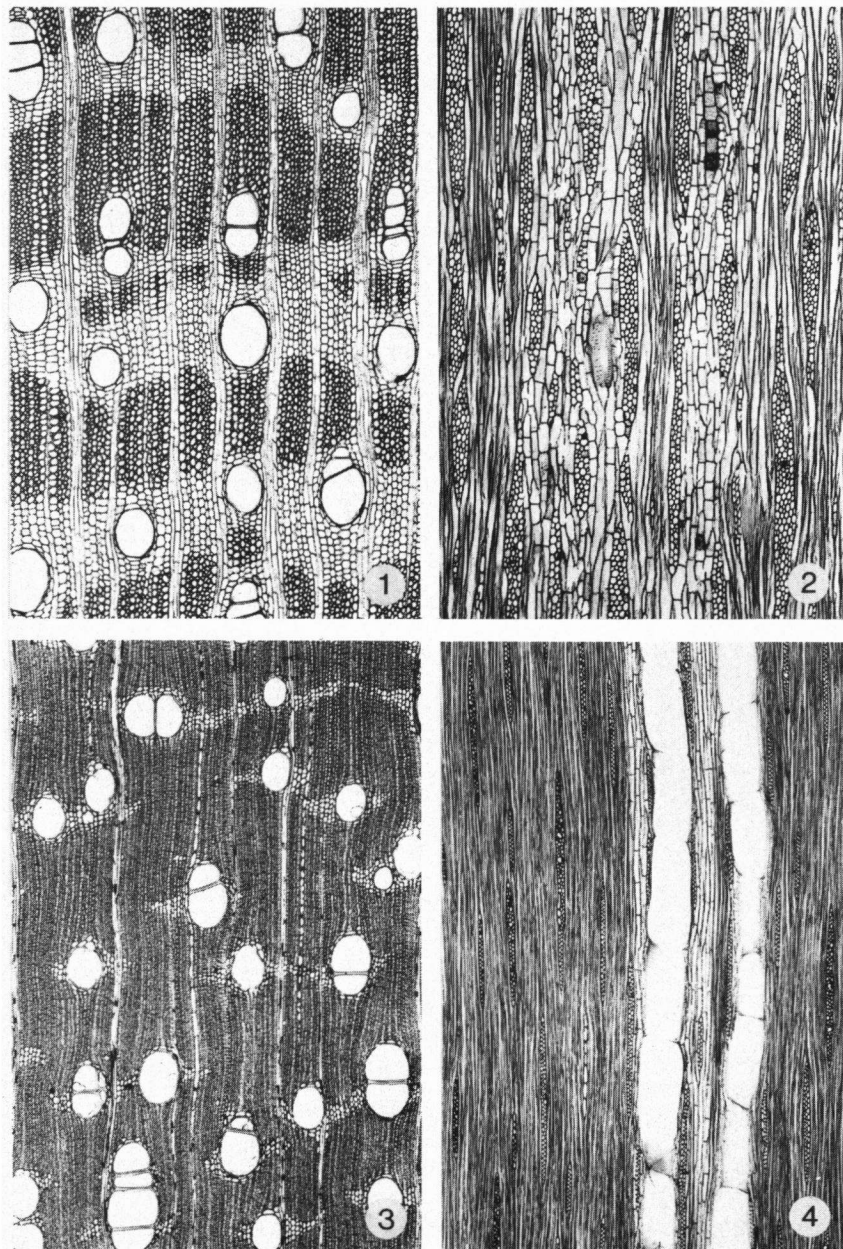


Plate I. Fig. 1, 2: *Castilla ulei* (Uw 8827), cross sect. $\times 36$, tg. sect. $\times 36$; fig. 3, 4: *Helicostylis scabra* (Uw 16222), cross sect. $\times 36$, tg. sect. $\times 36$.

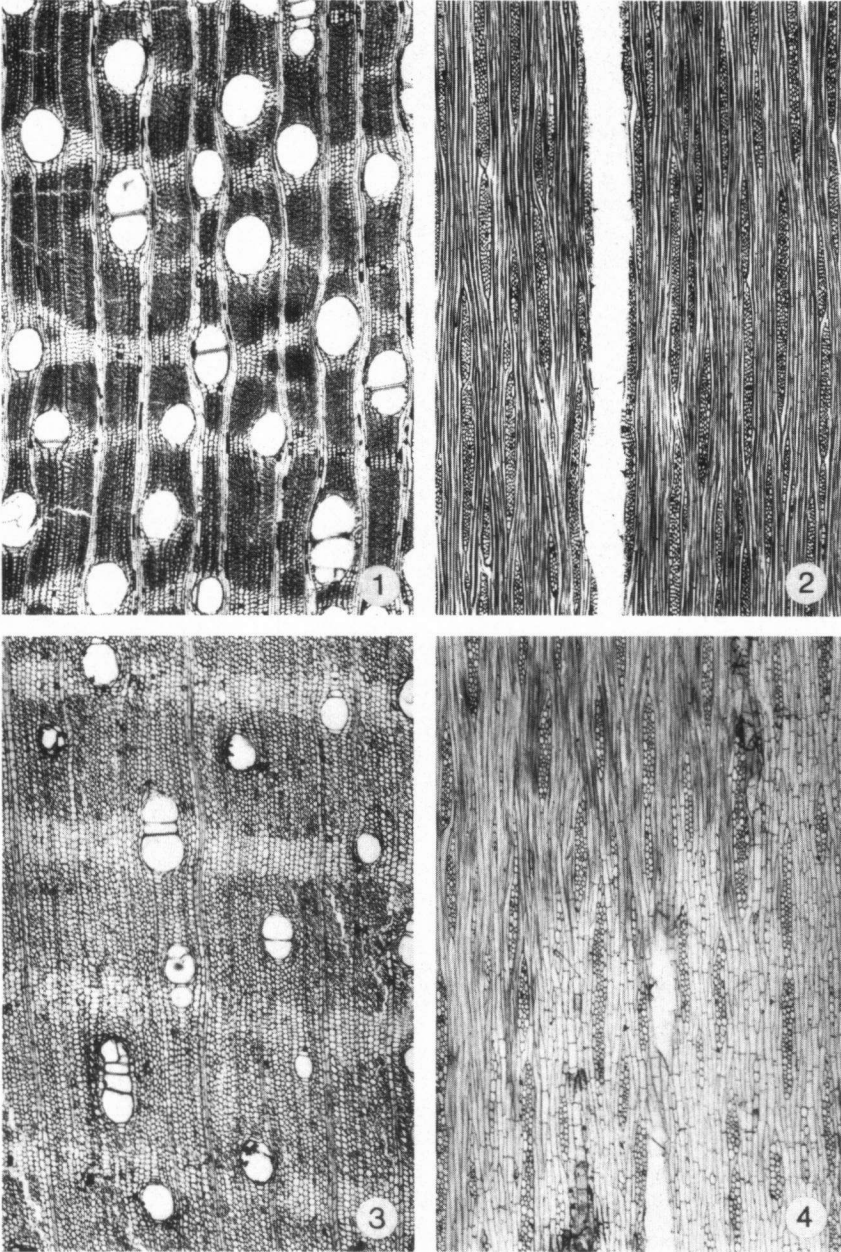


Plate II. Fig. 1, 2: *Pseudolmedia laevis* (Uw 11817), cross sect. $\times 36$, tg. sect. $\times 36$; fig. 3, 4: *Olmedia aspera* (Uw 18429) cross sect. $\times 36$, tg. sect. $\times 36$.

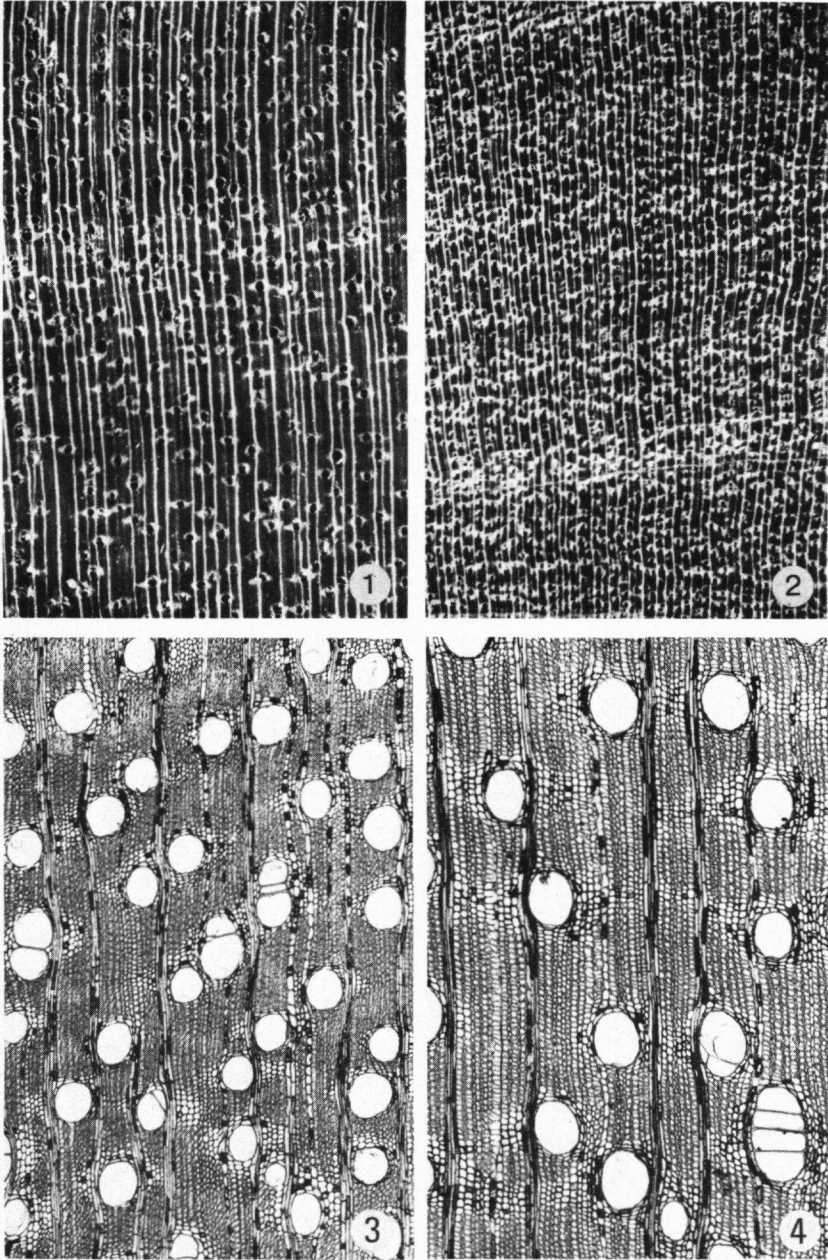


Plate III. Fig. 1: *Heliocostylis tomentosa* (Uw 6836), cross sect. $\times 10$; fig. 2: *Naucleopsis glabra* (Uw 7549), cross sect. $\times 10$; fig. 3: *Maquira coriacea* (Uw 17149) cross sect. $\times 36$; fig. 4: *Perebea guianensis* ssp. indet. (Uw 16183) cross sect. $\times 36$.

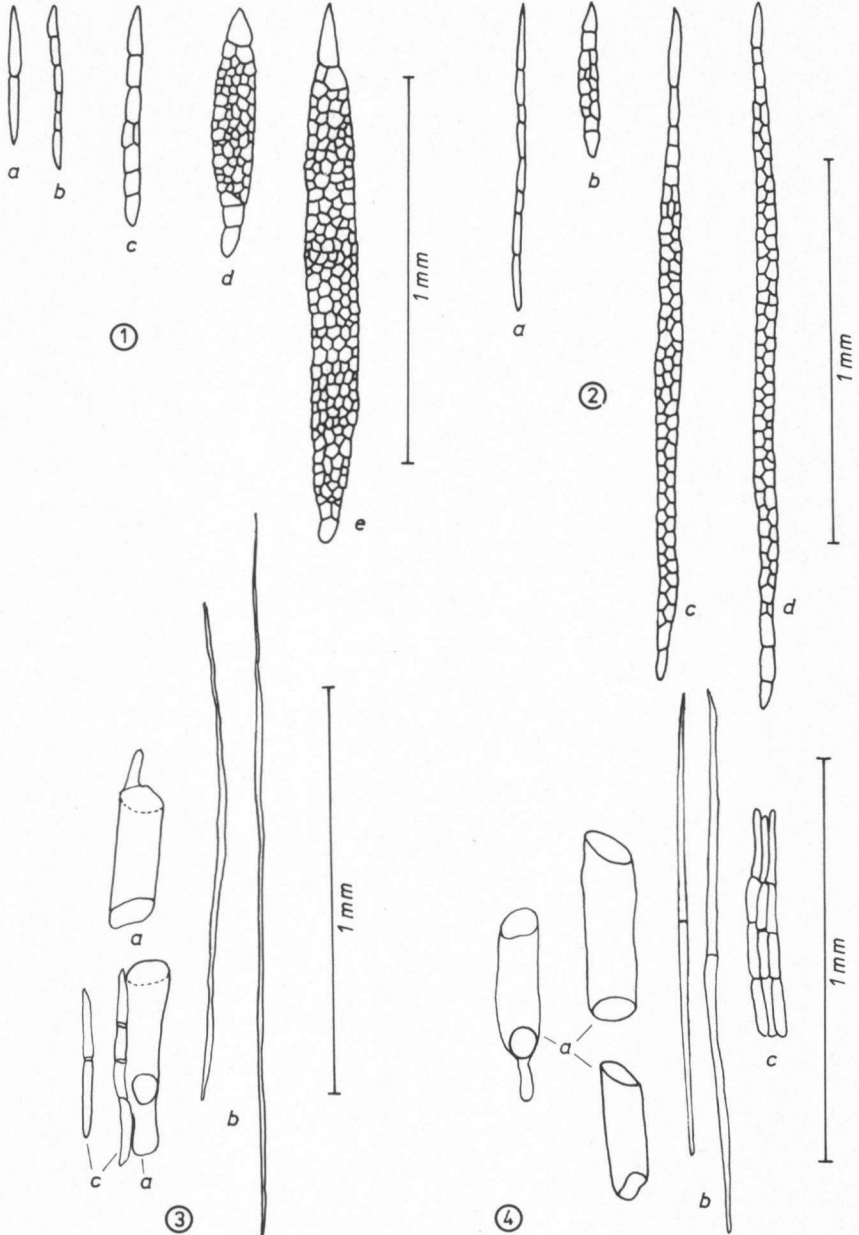


Plate IV, camera lucida drawings. Fig. 1: *Maquira coriacea* (Uw 7886), various ray types, type "e" being the most common one; fig. 2: *Perebea guianensis* ssp. *guianensis* (Uw 8241), types of rays among which types "c" and "d" are the most frequent; fig. 3: *Olmedia aspera* (Uw 21743) elements from macerated wood; fig. 4: *Perebea xanthochyma* (Uw 18431).

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