

Systematic wood anatomy and affinities of the Urticaceae

By

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With 19 figures and 7 tables in the text

Abstract

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The wood anatomy of all tribes of the Urticaceae, a family of herbs, shrublets, and sometimes shrubs, trees or lianas, has been studied and described in detail. Special attention is given to the interpretation of the characters in terms of taxonomy and phylogeny. A classification, in part deviating from the existing morphological classification, is presented. Finally, the relationship within the Urticaceae, as well as the relationships with the Ulmaceae and Moraceae (including Cecropiaceae) are discussed.

1. Introduction

There is no doubt about the close relationships between the taxa of the Urticales. The main systematic problem is the subdivision of the order into taxa of lower rank. Some taxonomists (BENTHAM & HOOKER 1880) recognize only one family within this order, whereas others (ENGLER 1889, CRONQUIST 1981) prefer the concept of 3 to 5 families (Table 1).

The Cannabaceae have not been studied as the two genera of this family are always herbaceous. The Ulmaceae can easily be separated from the other families by flower and fruit characteristics.

Discriminating characters are less obvious for the group consisting of Moraceae, Cecropiaceae, and Urticaceae. Taxonomic studies of the Moraceae have been carried out most recently by Dr. C. C. BERG, Institute of Systematic Botany, Utrecht, while anatomical studies are conducted in the same Institute by

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Table 1. Classification of the Urticales.

BENTHAM & HOOKER 1880	ENGLER 1889	CRONQUIST 1981
	ULMACEAE	
Ulmeae	Ulmoideae	
Celtideae	Celtoideae	ULMACEAE
	MORACEAE	
Cannabineae	Cannaboideae	CANNABACEAE
Moreae	Moroideae	MORACEAE
Artocarpeae	Artocarpoideae	
Conocephaleae	Conocephaloideae	CECROPIACEAE
Urticeae	URTICACEAE	URTICACEAE

KOEK-NOORMAN, TOPPER and TER WELLE (in press). BERG (1978) separated the Cecropiaceae (6 genera) from the Moraceae. A detailed study of this new family was carried out by BONSEN & TER WELLE (1983). The results obtained from this study justify the exclusion of the genus *Poikilospermum* from the Cecropiaceae. The similarity with some species of the Urticaceae supports its inclusion in this family, although the proper place of *Poikilospermum* within the Urticaceae remained doubtful.

The present paper deals, among others, with the systematic position of this genus in the Urticaceae. At the same time it completes the wood anatomical survey of the Moraceae/Cecropiaceae/Urticaceae complex. The wood anatomy of the Ulmaceae has not been studied. As this family stands beyond dispute within the Urticales, wood anatomical data from the literature will be used to discuss the relationship of Ulmaceae with the other families.

The Urticaceae constitute a family of about 50 genera and 2000 species (HUTCHINSON 1967), mainly consisting of annual or perennial herbs and shrub-

Table 2. Classification of the Urticaceae (ENGLER 1889).
(The woody genera investigated for this study.)

UREREAE	BOEHMERIEAE	
<i>Dendrocnide</i>	<i>Boehmeria</i>	<i>Phenax</i>
<i>Gyrotaenia</i>	<i>Debregeasia</i>	<i>Pipturus</i>
<i>Laportea</i>	<i>Leucosyke</i>	<i>Poikilospermum</i>
<i>Ureia</i>	<i>Maoutia</i>	<i>Ponzolzia</i>
<i>Urtica</i>	<i>Myriocarpa</i>	<i>Touchardia</i>
	<i>Neraudia</i>	<i>Villebrunea</i>
PROCRIDEAE	PARIETARIEAE	FORSSKAOLEEAE
<i>Pilea</i>	<i>Gesnouinia</i>	<i>Forsskaolea</i>
<i>Procris</i>		

lets, sometimes shrubs, trees, or lianas. The geographical distribution is given by ENGLER (1889): 33 % New World, 33 % Asia and Malesian Archipelago, 14 % Africa, 14 % Oceanic Islands, and 3—4 % Europe. A classification of the Urticaceae was given by BENTHAM & HOOKER (1880), and ENGLER (1889), see also Table 2.

In his monographic treatments of the genera *Poikilospermum* (1963), *Laportea* (1969b), and *Dendrocnide* (1969c) CHEW WEE-LEK transferred the woody species of *Laportea* to *Dendrocnide*. The genus *Neraudia* was revised by CO-WAN (1949). Finally, CHEW WEE-LEK described a new genus *Nothocnide* formerly included in *Pipturus* (1969a). Anatomical studies of the Urticaceae were made by BIGALKE (1933) and SOLEREDER (1899, 1908). A comprehensive survey of the literature was published by METCALFE & CHALK (1950).

2. Methods

Sections and macerations were prepared according to standard techniques, and embedded in Canada balsam and in glycerin respectively.

The wood anatomical terminology used is that proposed by the Committee on Nomenclature of the I.A.W.A. (1964).

The quantitative wood data were measured as follows: vessel diameters were measured in tangential directions; averages are based on 25 measurements. The vessel frequency is based on 25 counts of areas of 1 sq. mm. In the descriptions lowest and highest averages per specimen are given, and the minimum and maximum values found in the material studied are given for both characters. The percentage of solitary vessels was calculated after counting at least 100 pores. Clusters and multiples were regarded as 2, 3, 4, etc. vessels, depending on the number of vessels per group. For the intervacular pits the minimum and maximum sizes are given. Vessel member length and fibre length are based on 25 measurements per sample. Averages, minimum and maximum sizes are presented. For the fibres, maximum wall thickness and maximum lumen diameters are given. Multiseriate ray height is presented in micrometers, ray width in micrometers and in number of cells. Both data are related to the average of the 25 highest rays as observed in one section. The number of rays per mm is the average of 25 counts.

3. Materials

This study is based on 85 wood specimens representing 21 genera and 50 species. Information on collectors number and wood collection accession numbers (abbreviations according to STERN 1978), locality and diameter of the samples is provided in Table 3.

4. Results

4.1. Description of the family Urticaceae Juss.

Growth rings faint or absent. Vessels diffuse, round to oval; solitary (20—95 %) and in radial multiples and irregular clusters of 2—4 (20); 2—30 (1—100)

Table 3. Material studied.

Genus/species	Xylarium	Collector	Locality	Habit	♁
<i>Boehmeria caudata</i> Sw.		ex FHOw 9954	unknown	T	6
	Uw 20833	Lindeman 9202	Brazil	T	3
	Uw 23594	Maas et al. 3071	Ecuador	T	3
	Uw 27644	U.P.D. 776	Argentina	T	10
<i>B. vs. cylindrica</i> (L.) Sw.	Uw 23595	Maas et al. 3072	Ecuador	T	3
<i>B. excelsa</i> (Bertero ex Steudel) Wedd.	Uw 15011	Meyer 9597	Juan Fern.	T	8
<i>B. nivea</i> (L.) Gaudich.		Sandwijck s.n.	Neth. Cult.	T	1
<i>B. pavonii</i> Wedd.	Uw 21090	Schunke 4977	Peru	T	10
<i>B. platyphylla-virgata</i> Wedd.	Uw 27817	Grant 4024	Society Isl.	T	3
<i>B. ramiflora</i> Jacq.	Uw 15446	Chambers 2686	Dominica	T	4
<i>B. spec.</i>	Uw 23616	Berg et al. 426	Ecuador	T	—
<i>Debregeasia longifolia</i> Wedd.	Uw 27818	Koorders 8841 B	Indon. Java	T	1.5
	Uw 27819	Koorders 8844 B	Indon. Java	T	1.5
	Uw 27820	Koorders 8845 B	Indon. Java	T	2
	Uw 27821	Koorders 14768 B	Indon. Java	T	3
	Uw 27822	Koorders 26746 B	Indon. Java	T	4
<i>Dendrocniide excelsa</i> (Wedd.) Chew	Uw 27647	U.P.M. 211	Australia	T	5
<i>D. luzonensis</i> (Wedd.) Chew		ex FHOw 5283	unknown	T	—
<i>D. microstigma</i> (Gaudich, ex Wedd.) Chew	Uw 27828	Koorders 40042 B	Indon. Java	T	6
<i>D. moroides</i> (Wedd.) Chew	Uw 27829	BW 7097	Indon. Irian	T	6
	Uw 27830	BW 7519	Indon. Irian	T	4
<i>D. rechingeri</i> (H. Winkler) Chew	Uw 27823	Craven & Schodde 515	Solomon Isl.	T	5
<i>D. stimulans</i> (L.f.) Chew	Uw 27831	Zw. et R. 134	Indon.	T	—
	Uw 27832	ex WIBw 22863	unknown	—	8
<i>D. spec.</i>	Uw 27824	v. Beusekom 4196	Thailand	T	6
<i>Forsskaolea angustifolia</i> Retz	Uw 27825	Haman 130383	Canary Isl.	S	0.6
<i>Gesnouinia arborea</i> (L.f.) Gaudich.		Hortus Bot. 76—577	Neth. Cult.	S.	5
	Uw 27826	Haman 170383	Canary Isl.	S.	1.5
<i>Gyrotaenia microcarpa</i> Fawcett & Rendle	Uw 8357	ex USw 6019	Jamaica	T	5
<i>Leucosyke candidissima</i> Wedd.	Uw 27833	ex WIBw 22532	unknown	—	—
<i>L. capitellata</i> Wedd.	Uw 27834	Koorders 9538 B	Indon. Java	T	8
	Uw 27836	Koorders 14774 B	Indon. Java	T	10
	Uw 27835	Koorders 11152 B	Indon. Java	T	8
<i>Maoutia cf. ambigua</i> Wedd.	Uw 27837	v. Royen 5289	Indon. Irian	S	5
<i>M. diversifolia</i> Wedd.	Uw 27838	Koorders 9525 B	Indon. Java	S	3
<i>Myriocarpa stipitata</i> Benth.	Uw 21084	Schunke 4008	Peru	T	10

Table 3 cont.

Genus/species	Xylarium	Collector	Locality	Habit	ø
<i>M. yzabalensis</i> (J. D. Smith) Killip	Uw 29521	<i>Nee 7146</i>	Panama	S	4
<i>M. spec.</i>	Uw 23574	<i>Maas et al. 2911</i>	Ecuador	T	5
	Uw 23614	<i>Berg 420</i>	Ecuador	T	9
<i>Nerandia kauaiensis</i> (Hillebr.) R. Cowan	Uw 27841	<i>Degener 1511—17459</i>	Hawaii Isl.	S	0.5
<i>N. melastomaefolia</i> Gaudich.	Uw 27843	<i>St. John 080233</i>	Hawaii Isl.	S	1
	Uw 27844	<i>Carlquist 1958</i>	Hawaii Isl.	S	2
	Uw 27845	<i>Forbes 5/23/20</i>	Hawaii Isl.	S.	0.5
<i>Nothocnide discolor</i> (C. Robinson) Chew		<i>Elmer 13859</i>	Philippines	C	—
<i>N. repanda</i> (Blume) Blume	Uw 27857	<i>de Vogel 4410</i>	Indon. Mol.	C	1
	Uw 27858	<i>Koorders 20736B</i>	Indon. Java	C	4
<i>N. spec.</i>	Uw 27860	<i>Jacobs 9133</i>	Papua N.G.	C	2
<i>Phenax angustifolius</i> Kunth Wedd.	Uw 27846	<i>Schunke 3973</i>	Peru	S	1.5
<i>Pilea spec.</i>	Uw 23592	<i>Maas et al. 3059</i>	Ecuador	H	1.2
<i>Pipturus albidus</i> A. Gray ex Mann	Uw 27645	<i>U.P.M. 318</i>	Hawaii Isl.	T	4
<i>P. argenteus</i> (G. Forster) Wedd.	Uw 27848	<i>Grant 4561</i> <i>SFCw R977</i> <i>—239</i>	Society Isl. unknown	T —	2 10
<i>P. incanus</i> Wedd.	Uw 27851	<i>Koorders 9573 B</i>	Indon. Java	T	10
	Uw 27855	<i>ex WIBw 13354</i>	Indon.	T	2
<i>P. spec.</i>	Uw 27859	<i>Hoogland 3382</i>	Indon. Irian	T	3
<i>Poikilospermum amboinense</i> Zipp. ex. Miq.	Uw 26781	<i>Lam 647</i>	Indon. Irian	C	2
<i>P. inaequale</i> Chew	Uw 26780	<i>Docters v. Leeuwen 9671</i>	Indon.	C	1
<i>P. naucleiflorum</i> (Roxb. apud Lindley) Chew	Uw 27519	<i>RTIw 1507</i>	unknown	C	3
<i>P. suaveolens</i> (Blume) Merr.	Uw 27020	<i>Jacobs B 502</i>	unknown	C	4
	Uw 27516	<i>de Vogel 4516</i>	Indon. Mol.	C	2
	Uw 27518	<i>Koorders 35779 B</i>	Indon. Java	C	2
<i>P. spec.</i>	Uw 27517	<i>Jacobs 9575</i>	Papua N.G.	C	2
<i>Pouzolzia siminea</i> Wedd.	Uw 27861	<i>Koorders 26609 B</i>	Indon. Java	S	1
<i>Procris frutescens</i> Blume	Uw 27862	<i>Pleyte 522</i>	Indon. Irian	S	1
<i>P. reticulato-venosa</i> (Hall) Schroeter	Uw 27864	<i>Bünnemeyer 1172</i>	Indon. Sum.	L	1
<i>P. spec.</i>	Uw 27866	<i>Jacobs 8469</i>	Indon. Sum.	L	1
<i>Touchardia latifolia</i> Gaudich.	Uw 18601	<i>Stern & Herbst 518</i>	Hawaii Isl.	S	5
<i>Urera baccifera</i> (L.) Gaudich.	Uw 29522	<i>Nee 7148</i>	Panama	S	3
<i>U. cameroonensis</i> Wedd.	Uw 9332	<i>Breteleur 1500</i>	Cameroun	L	6
	Uw 9443	<i>Breteleur 2037</i>	Cameroun	L	4

Table 3 cont.

Genus/species	Xylarium	Collector	Locality	Habit	Ø
<i>U. caracasana</i> (Jacq.) Griseb.	Uw 25080	<i>Cuatrecasas 14509</i>	Colombia	L	4
	Uw 27650	<i>U. P. D. 784</i>	Argentina	L	3
<i>U. elata</i> (Sw.) Griseb.	Uw 27194	<i>Mathias & Taylor</i> <i>5343</i>	Peru	S	1
<i>U. hypselodendron</i> Wedd.	Uw 15936	<i>Schlieben 1721</i>	East Africa	L	3
	Uw 27404	<i>Berg s.n.</i>	Zimbabwe	L	5
	Uw 27646	<i>Schlieben 4683</i>	East Africa	L	3
<i>U. laciniata</i> Wedd.	Uw 3902	<i>Lindeman 5660</i>	Surinam	T	4
<i>U. cf. myriocarpa</i>	Uw 8662	<i>Ellenberg 2275</i>	Peru	T	3
<i>U. robusta</i> A. Chev.	Uw 27868	<i>Versteegen</i> <i>den Outer 178</i>	Ivory Coast	T	1
<i>Urtica dioica</i> L.	Uw 27869	<i>ter Welle s.n.</i>	France	H	1
		<i>Bonsen s.n.</i>	Nethl.	H	0.5
		<i>Niloufari</i>	Iran	H	1
<i>U. morifolia</i> Poiret	Uw 27871	<i>Haman 160383</i>	Canary Isl.	H	0.5
<i>Villebrunea rubescens</i> Blume	Uw 27880	<i>de Vogel 2545</i>	Indon. Cel.	T	7
<i>V. spec.</i>	Uw 27882	<i>Craven & Schodde</i> <i>983</i>	Papua N.G.	T	6
	Uw 27643	<i>Seibt 38</i>	Indon. Java	T	8

Legenda: Habit: T = tree or treelet; S = shrub; C = climber; L = liana; H = herb; Ø: diameter of the wood sample in cm.

per sq. mm; diameter 40–360 (25–480) µm; vessel member length 195–525 (130–1230) µm. Perforations simple. Intervascular pits alternate, round or polygonal, 6–18 µm, sometimes scalariform. Thin-walled tyloses present or absent.

Fibres 370–1745 (170–2139) µm long; with simple pits in the radial and tangential walls; all non-septate or partly septate, storied in some genera; lumen diameter 9–30 µm; walls 2–7 µm thick; fibre dimorphism sometimes present: short fibres and very long fibres, length 3400–5000 µm.

Uniseriate rays mostly absent or scarce, if present composed of square and upright cells. Multiseriate rays 2–6 (0–8) per mm; sheath cells mostly present; heterogeneous, entirely or almost entirely composed of square and upright cells, up to several mm high or with a central part of procumbent cells and marginal rows of square or upright cells, 600–1940 (420–2850) µm high; 3–10 (15) cells = 45–255 (40–390) µm wide; sometimes containing druses, rhombic crystals, or vitreous silica. In part of the genera with unignified parenchyma (see below) the rays are sometimes partly unignified too.

Vascentric paratracheal parenchyma in strands of 2–4 (8) cells. If apotracheal parenchyma is present, it is unignified, occurring as islands or bands as seen in cross-section; sometimes containing druses, raphides, styloids or vitreous silica.

Specific gravity: 0.25–0.70.

4.2. Descriptions of taxa of the Urticaceae

For this study 21 genera were studied. They can be separated already at first view into two groups, based on the presence or absence of unligified elements. Within these groups A and B, the overlap in wood anatomical characters is considerable. Therefore a description of these two groups is presented, instead of 21 separate generic descriptions.

Group A. *Boehmeria*, *Debregeasia*, *Forsskaolea*, *Gesnouinia*, *Leucosyke*, *Maoutia*, *Neraudia*, *Phenax*, *Pipturus*, *Pouzolzia* and *Villebrunea* (Fig. 4 and 5).

Growth rings faint or absent. Vessels diffuse, round to oval; solitary (35–85 %) and in radial multiples and irregular clusters of 2–4 (6); 3–30 (1–45) per sq. mm; 70–180 (55–230) μm in diameter; vessel member length 240–525 (155–1230) μm . Perforations simple. Intervascular pits alternate, round or polygonal, 6–12 μm . Thin-walled tyloses present or absent.

Fibres 665–1745 (360–2130) μm long; with simple pits in the radial and tangential walls; septate in *Boehmeria* p.p., *Pipturus* p.p. and *Villebrunea* p.p.; non-septate in the other taxa; lumen diameter 15–30 μm ; walls 2–7 μm thick.

Uniseriate rays occur in *Leucosyke* and *Maoutia* and occasionally in *Pipturus*, *Boehmeria*, and *Villebrunea*, and are composed of square and upright cells. Multiseriate rays 3–6 (7) per mm; sheath cells usually present; entirely or almost entirely composed of square and upright cells, up to several mm high; 3–8 (11) cells = 50–150 (45–180) μm wide; containing druses in *Boehmeria* p.p., *Pipturus* p.p., and *Villebrunea* p.p.; rhombic crystals in *Pipturus* p.p. and *Villebrunea* p.p.; vitreous silica in *Leucosyke* p.p.

Parenchyma scarce, paratracheal, vasicentric, in strands of 2–4 (8) cells.

Specific gravity: 0.30–0.70.

Note: The herbs and small shrublets belonging to this group A (*Forsskaolea*, *Gesnouinia*, *Neraudia kauaiensis*) differ from the description given before in the following characters: Vessels solitary (45–95 %), in *N. kauaiensis* 20 %; 20–70 per sq. mm; diameter 45–70 (25–95) μm ; vessel member length 195–275 (130–370) μm . Intervascular pits 6–12 μm , sometimes scalariform. Fibres 425–575 (265–755) μm long; lumen diameter 12–15 μm ; walls 2–4 μm thick. Rays 2–7 (8) per mm; 3–5 (8) cells = 45–60 (40–85) μm wide; containing druses in *Forsskaolea*.

Group B. *Dendrocnide*, *Gyrotaenia*, *Myriocarpa*, *Nothocnide*, *Pilea*, *Poikilospermum*, *Procris*, *Touchardia*, *Urera*, and *Urtica* (Figs. 6, 7 and 11).

Growth rings faint or absent. Vessels diffuse, round to oval; solitary (45–85 %) and in radial multiples and irregular clusters of 2–4 (6); 2–15 (1–25) per sq. mm; diameter 100–270 (120–310) μm ; vessel member length 295–460 (205–540) μm . Perforations simple. Intervascular pits alternate, round and polygonal, 8–15 μm . Thin-walled tyloses present or absent.

Fibres 825—1255 (370—1650) μm long; with simple pits in the radial and tangential walls; non-septate and occasionally septate in *Gyrotaenia*; lumen diameter 12—24 μm ; walls 3—6 μm . Storied fibres in *Dendrocnide*, and sometimes, but less strikingly so in the other genera, except *Gyrotaenia* and *Myriocarpa*.

Uniseriate rays absent. Multiseriate rays 1—4 (0—6) per mm; sheath cells mostly present; heterogeneous, entirely or almost entirely composed of square and upright cells, up to several mm high or with a central part of procumbent cells and marginal rows of square and upright cells, 600—1940 (420—2850) μm high; 3—10 (15) cells = 50—255 (45—390) μm wide; sometimes partly unligified; containing druses in *Gyrotaenia* p.p. and *Urera* p.p., and cystoliths in *Gyrotaenia* p.p.

Paratracheal parenchyma as vasicentric rings, in strands of 2—4 (5) cells. Apotracheal parenchyma unligified, occurring as islands or bands in cross-sections; containing druses in *Gyrotaenia*, *Myriocarpa* and *Urera*; containing raphides in all but one specimen of *Dendrocnide*; styloids in *Dendrocnide* p.p., and vitreous silica in *Dendrocnide moroides*.

Specific gravity: 0.25—0.55.

Notes: The herbs and small shrublets belonging to this group B (*Urtica*, *Procris*, and *Pilea*) differ from the description given before in the following characters: — Vessels 25—100 per sq. mm; diameter 40—85 (25—110) μm ; vessel member length 205—250 (155—310) μm . Intervascular pits 6—9 μm , sometimes scalariform. Fibres 370—435 (170—590) μm long; non-septate; lumen diameter 9—15 μm ; walls 3—5 μm thick; sometimes slightly storied in *Procris* and *Urtica*. — Rays composed of fusiform parenchyma cells in *Procris* and *Urtica*; high rays with upright cells in *Pilea*, and unligified rays in *Procris reticulata-venosa*.

The climbers and scramblers of this group B (*Nothocnide*, *Poikilospermum*, *Urera* p.p.) differ from the description given before in the following characters: Vessels solitary (45—80%) and in radial multiples of 2—4 (20); 5—9 (2—15) per sq. mm; diameter 260—360 (180—480) μm ; vessel member length 270—480 (225—590) μm . Intervascular pits 9—18 μm . Fibre dimorphism present in *Poikilospermum* and *Nothocnide*; short fibres with a lumen diameter of 18—26 μm , walls 2—6 μm thick, and 545—865 (370—1175) μm long, sometimes slightly storied; the other type over 3000 μm long. In *Nothocnide* the short fibres are very scarce and sometimes unligified. — Rays mainly or totally unligified. Apotracheal parenchyma unligified, containing druses in *Poikilospermum*, *Nothocnide*, and *Urera*, rhombic crystals often present in addition.

Although some generic differences and variations occur in the Urticaceae, the family constitute a well-defined group as regards the wood anatomical features. There are no arguments to exclude one of the genera studied here from the family.

5. Discussion

5.1. Discussion of diagnostic, taxonomic, and phylogenetic value of some wood anatomical features

Unlignified elements

The unlignified elements, characterizing all taxa of group B, are sometimes absent or faint in the early stages of secondary growth in the erect or climbing shrubs and trees. The herbaceous species show unlignified bands from the beginning of their secondary growth (Fig. 7). With increasing girth the number as well as the proportion (as percentage of the transverse section) of these unlignified elements increases. The majority of the elements is formed by axial parenchyma and is shown as islands or bands (Fig. 6). The most extreme state of this character is found in *Dendrocnide* where continuous bands occur.

In the secondary xylem of the climbing species the rays are also unlignified, resulting in a typical pattern of isolated islands of vessels surrounded by lignified elements (Fig. 8 and 9). Sometimes, e.g. in *Nothocnide*, part of the fibres and rays also remain unlignified (Fig. 11).

The existence of this feature might well be explained in terms of mechanical strength: it occurs in lianas, climbers, and in the tall erect herbs with stems having a small diameter, like e.g. *Urtica* (Fig. 7). On the other hand, it is hard to see how the above could apply to plants of tree-like habit.

Fibre dimorphism

Species of the climbing genera *Poikilospermum* and *Nothocnide* show fibre dimorphism. The main difference between the two fibre types in *Poikilospermum* and *Nothocnide* is the fibre length. Apart from normal fibres (see hereafter), very long fibres (over 3000 μm) are also found. In transverse section these long fibres are distributed as (small) islands. The short fibres in these genera are comparable to those found elsewhere in the Urticaceae, as is shown in the following comparison:

fibre length in <i>Poikilospermum/Nothocnide</i>	545—865 μm ;
fibre length in other taxa of group B	825—1255 μm ;
fibre length in taxa of group A	665—1745 μm .

Even when most of the short fibres remain unlignified, the long fibres are lignified (Fig. 8). The occurrence of these long fibres might be related to the climbing habit of *Poikilospermum/Nothocnide*. This idea is strengthened by the

results of investigations by A. M. W. MENNEGA (pers. comm.), who compared the wood anatomy of climbing and non-climbing taxa in various families. In general, lianas have longer fibres than tree like species in the same family.

Crystals

Some of the genera possess crystals in the axial parenchyma. Druses are most common, although they sometimes occur in combination with rhombic crystals. Intermediate crystal forms which can neither properly be described as a druse, nor as a rhombic type, sometimes occur in the same parenchyma strands. As a result, the presence of druses and/or rhombic crystals is of limited taxonomic value. However, absence or presence of raphides is very important in terms of taxonomy, as raphides are found in all samples except one of *Dendrocide*, and have not been observed in any other sample of the Urticaceae studied.

Rays

The rays of the Urticaceae show juvenilistic features in their composition: great height and predominantly erect cells (CARLQUIST 1962). Some genera, e.g. *Dendrocide* (Fig. 13) possess rays in the mature secondary xylem where the juvenilistic stage is not immediately recognized. However, in the first formed secondary xylem of these taxa juvenilistic ray composition is clearly visible (Fig. 12).

The rays of the representatives of group A can easily be interpreted as being derived from a juvenile stage of KRIBS's (1935) heterogeneous types I and II (Fig. 16). Uniseriate rays are always found in *Maoutia* and *Leucosyke*, they are sometimes present in *Pipturus*, *Villebrunea* and *Boehmeria*. No uniseriate rays were observed in *Neraudia*, *Debregeasia*, *Pouzolzia*, *Gesnouinia*, *Forsskaolea*, and *Phenax*.

In group B of the Urticaceae a much wider range of ray types occurs. In the first formed secondary xylem two basic ray types can be distinguished: the high and wide rays (Fig. 12) and the high and narrow rays (Fig. 15). The wide rays can be considered as medullary rays (Fig. 10). In the mature secondary xylem these rays tend to become less wider; or they are probably dissected and are composed of more radially elongated (procumbent) ray cells, e.g. *Dendrocide* (Fig. 13), *Poikilospermum*, and *Nothocide*.

In taxa with a restricted secondary growth, i.e. the group of small shrubs and herbs, the rays are either medullary rays (*Pilea*; Fig. 14) or they are mainly composed of fusiform cells (*Urtica*, *Procris*; Fig. 19). In the shrubby genus *Touchardia* the medullary rays are replaced by parenchymatic tissue which is hardly distinct from the fibre tissue (Fig. 18).

The narrow and very high rays are found in species with an almost completely closed cylinder of primary xylem elements. In the mature secondary xylem of *Myriocarpa* and *Gyrotaenia* the rays become dissected and sometimes become wider. Simultaneously, the ray cells are more radially enlarged or procumbent.

The phenomenon of dissected rays does not occur in the climbing species of *Urera*, *Poikilospermum*, and *Nothocnide*. As stated before, with increasing stem diameter more and more ray cells become unligified in these taxa (Fig. 8 and 9).

5.2. Subdivision of the Urticaceae and the position of *Poikilospermum*

The woody Urticaceae, including *Poikilospermum* (BONSEN & TER WELLE 1983) can be separated into two well distinguishable groups using the wood anatomical characters (Table 4). They can be recognized easily by the absence or presence of unligified elements (commonly axial parenchyma).

Table 4. Relevant wood anatomical characters of the shrubs and trees of group A and B of the Urticaceae (see § 4.2).

	Group A	Group B
Vessels per sq. mm	3—30	2—15
Vessel diameter (µm)	70—180	100—270
Uniseriate rays	present or absent	absent
Shape of multiseriate ray cells	upright/square	upright/square and often procumbent (herbs with fusiform parenchyma)
Number of multiseriate rays/mm	3—6	1—4
Apotracheal parenchyma	absent	present, unligified

Group A contains the tribes Forsskaoleae and Parietariae. In group B the tribes Urereae and Procridae are found. Most genera of the tribe Boehmeriae belong to group A (see Table 5), but *Myriocarpa*, *Touchardia*, and *Nothocnide* show all features defining group B. The classification of the family in tribes, mainly based on flower characteristics (see, e.g. WEDDELL 1856), was already disputed by BIGALKE (1933) on the base of leaf anatomical features. For instance the presence of elongated cystoliths and the absence of hooked hairs in *Myriocarpa* and *Touchardia* (*Nothocnide* was not investigated) points towards a position near the Urereae and Procridae. In conclusion, it may be said that both wood anatomy and leaf anatomy thus indicate that the Boehmeriae are a heterogeneous group, and should be re-evaluated.

Poikilospermum (BIGALKE 1933) is said to have elongated cystoliths, while hooked hairs are not reported. BIGALKE's suggestion of similarity of *Poikilospermum* with Urereae and Procridae, again, is in accordance with our findings, which place *Poikilospermum* near group B, rather than in group A. In

fact, the genus *Poikilospermum*, wood anatomically, is not distinguishable from the genus *Nothocnide*, and is very similar to the climbing species of *Urera* (see also Table 6).

Table 5. Relevant wood anatomical characters of individual genera of group A of the Urticaceae (see § 4.2).

	Trees/treelets/shrubs									Herbs	
	<i>Leu.</i>	<i>Mao.</i>	<i>Boe.</i>	<i>Pip.</i>	<i>Vil.</i>	<i>Pou.</i>	<i>Deb.</i>	<i>Ner.</i>	<i>Phe</i>	<i>For.</i>	<i>Ges.</i>
Uniseriate rays	+	+	(+)	(+)	(+)	—	—	—	(+)	—	—
Septate fibres	—	—	(+)	(+)	(+)	—	—	—	—	—	—
Druses	—	—	(+)	(+)	(+)	—	—	—	—	(+)	—
Rhombic crystals	—	—	—	(+)	(+)	—	—	—	—	—	—

Legenda: + = present in all specimens; (+) = present in part of the specimens; — = absent. Only the first three letters of the genera are mentioned.

Table 6. Relevant wood anatomical characters of individual genera of group B of the Urticaceae (see § 4.2).

	Trees/treelets/shrubs					Climbers			Herbs		
	<i>Gyr.</i>	<i>Myr.</i>	<i>Tou.</i>	<i>Ure.</i>	<i>Den.</i>	<i>Not.</i>	<i>Poi.</i>	<i>Ure.</i>	<i>Urt.</i>	<i>Pro.</i>	<i>Pil.</i>
Septate fibres	(+)	—	—	—	—	—	—	—	—	—	—
Druses	+	+	—	+	—	+	+	+	(+)	+	+
Raphides	—	—	—	—	+	—	—	—	—	—	—
Rhombic crystals	—	—	—	—	—	(+)	(+)	(+)	—	—	—
Storied fibres	—	—	(+)	(+)	+	(+)	(+)	(+)	(+)	(+)	(+)

Legenda: see Table 5.

5.3. Phylogeny in the Urticaceae

To clarify the phylogenetic relationships within the Urticaceae some wood anatomical characters can be used. Relevant characters in terms of phylogeny are: ray type and composition, fibres, presence of unligified elements, the occurrence of storied fibres and raphides.

Ray composition

Trends for the specialization of rays have been established by BARGHOORN (1941b). He recognized two trends: the elimination of uniseriate rays, and the

elimination of multiseriate rays. In both trends the composition of the rays changes from square and upright into procumbent ray cells.

The representatives of group A of the Urticaceae possess rays similar to the heterogeneous ray type of KRIBS (1935). Taking into account the trends established by BARGHOORN (1941b), these rays have to be considered as a juvenile form of these heterogeneous rays. This juvenile type is most prominent in *Maoutia* and *Leucosyke*, where both uni- and multiseriate rays are present. The ray patterns found in *Villebrunea*, *Pipturus*, and *Boehmeria* show a reduction of the uniseriate rays. Finally, in *Pouzolzia*, *Debregeasia*, and *Neraudia* uniseriate rays are completely lost (see also Fig. 1). A further reduction of cambial activity results in diminishing proportions of the multiseriate rays, like in e.g. *Phenax*.

The variation as observed in the ray composition of the taxa of group B is much wider and cannot be explained in terms of phylogeny using the trends established by BARGHOORN (1941b). However, the ontogenetic variation in the material studied, and the differences between the various species, agree remarkably well with the theory on paedomorphosis as presented by CARLQUIST (1962). Some of the taxa of group B possess rays which can be considered as descendent from medullary rays: very wide and high rays, which are linked with the pith. In the ontogeny of the secondary xylem new rays are not formed. This pattern of wide medullary rays and completely isolated secondary xylem parts is common in herbs.

The other taxa of group B possess very high, but narrow rays. These rays are linked with the pith, but are bound by primary xylem elements situated close to each other or almost forming a closed ring. These taxa have a stem which is hardly herbaceous anymore. Plants with an irregular, almost closed ring of primary xylem produce both wide and narrow rays (Fig. 17). These narrow rays still have the same height as the medullary rays. This points towards a herbaceous ancestor.

A correlation between both phylogenetic trends in the Urticaceae remains hypothetical. Decreasing cambial activity, mentioned before for group A, would result in a subshrubby or herbaceous habit, like e.g. *Phenax*, and ultimately in herbs. Here, the division of the primary xylem ring leads to isolated vascular bundles, separated by medullary rays. The secondary xylem produced in these herbs does not possess rays originating from primary xylem, but only rays directly linked with the medullary rays, like in e.g. *Urtica* and *Pilea*.

On the other hand, an increasing cambial activity would result in shrubs and trees, e.g. *Dendrocnide*, and sometimes climbers like in e.g. *Poikilospermum* and *Nothocnide*. In these last two taxa medullary rays are still present. Gradual closure of the primary cylinder results in plants with narrower rays in the secondary xylem, like in e.g. *Gyrotaenia*, *Myriocarpa*, and *Urera*. A schematic survey of the possible lines of specialization of the rays in the Urticaceae is presented in Fig. 1.

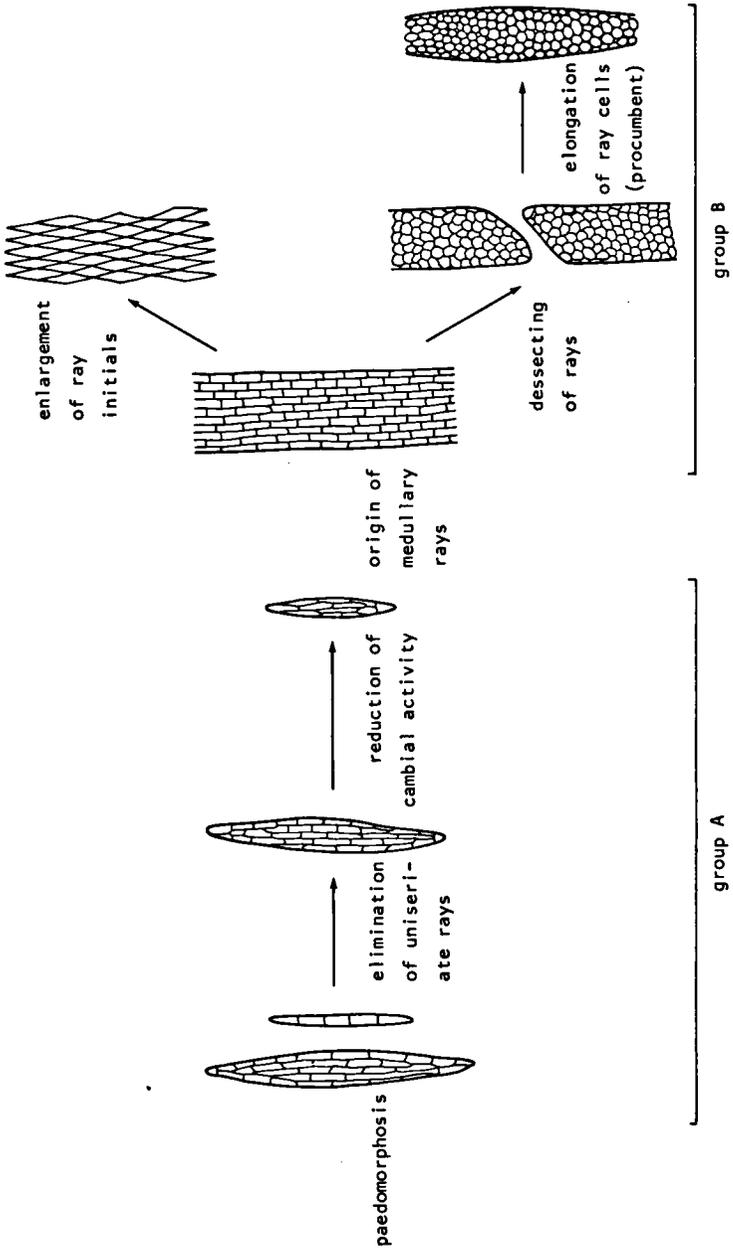


Fig. 1. Possible sequence of ray development in the Urticaceae and the underlying processes.

Fibres

As already mentioned before, fibre dimorphism occurs in *Poikilospermum* and *Nothocnide*. This phenomenon is regarded as a specialization trend within the Urticaceae. The wood anatomy of *Urera* is very similar to that of *Poikilospermum* and *Nothocnide*. However, fibre dimorphism does not occur.

Storied fibres are generally accepted as being a specialization of non-storied fibres (e.g. BAILEY 1920, 1923, JANSSONIUS 1931). Storied fibres are scarce in the Urticaceae, and were only observed in some genera of group B. They occur, although sometimes not very clear, in *Procris*, *Pilea*, *Touchardia*, *Urtica* and the non-climbing species of *Urera*. Storied fibres are very prominent in *Dendrocnide*, *Poikilospermum* (all climbers), *Nothocnide* (all climbers), and the climbing or lianlike *Urera*-species.

Unlignified elements

The occurrence of unlignified elements in the Urticaceae with regard to function has been discussed before. As it is hard to see how these elements could contribute to mechanical strength in plants of tree-like habit, one might suggest that the trees of group B are descendants from herbaceous ancestors.

Habit

The occurrence of paedomorphosis in all Urticaceae and the trends of specialization of the rays point towards a common ancestor with limited cambial activity (CARLQUIST 1962): a small shrub or a herb. The overall presence of rays originating from the pith indicates that the ancestor of group B is a herb. This group is also characterized by the occurrence of unlignified elements. This character, too, points towards a herbaceous origin. A possible habitual pathway of the group is presented in Fig. 2.

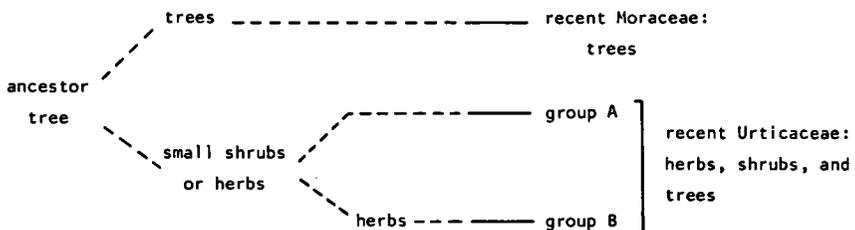


Fig. 2. Possible habitual pathway of the Moraceae and the Urticaceae.

5.4. Phylogeny in the Urticales

Apart from the suggestion to include *Poikilospermum* in the Urticaceae, BONSEN & TER WELLE (1983) proposed to assign the remaining 5 genera of the Cecropiaceae sensu BERG to the Moraceae, based on the fact that neither leaf nor wood anatomical features were found to distinguish the taxa of the two families.

The affinities and a possible phylogeny within the Urticales will be discussed here, based on some wood anatomical features, commonly considered to have phylogenetic value.

The general phylogenetic trend from scalariform to simple perforation plates as established by BAILEY and his students (1920, 1923), is supplemented by CARLQUIST's theory of pedomorphosis (1961, 1983), and CARLQUIST's and BAAS's contributions to ecological wood anatomy (1973). It is, therefore not justified to consider the Ulmaceae as primitive within this order on the base of the occurrence of scalariform perforation plates alone.

In the Urticales septate fibres are found in nearly all Moraceae and in some Urticaceae, but never in the Ulmaceae. METCALFE (1983) suggests that the formation of septa represents some kind of specialization. However, as this character is restricted to some taxonomic groups only, it is impossible to establish a phylogenetic trend for the angiosperms as a whole. TIPPO (1938) concluded from his study of the Moraceae and presumed allies that septate fibres are more specialized than non-septate fibres.

In the Urticales, only libriform fibres are found. The simple pits mainly occur in the radial walls with the exception of the Urticaceae. Here, the simple pits occur in both radial and tangential walls, mostly in equal quantities, but sometimes the pits in the tangential walls outnumber those in the radial walls. We can interpret this phenomenon either as an intermediate structure between fibre-tracheids and libriform fibres, or as a specialized feature derived from the normal libriform fibre type.

As already mentioned before, storied fibres in the Urticales are only found in the tribes Procridae and Urereae of the Urticaceae. Based on this character the Urticaceae must be regarded as the most specialized within the order.

Evolutionary trends in ray types of dicotyledons are given by KRIBS (1935) and BARGHOORN (1940, 1941a, b). Within the Urticales the most important trend is from heterogeneous type I to heterogeneous type IIA and IIB. Rays with increasing length of erect cells are considered to be highly specialized by BARGHOORN; CARLQUIST (1983) considered this feature as an expression of pedomorphosis.

The Ulmaceae show heterogeneous ray types I and IIA, the Moraceae show heterogeneous IIA and IIB. In the Urticaceae juvenilistic rays are common. Besides, a certain specialization is found in some woody taxa which show "islands" of procumbent cells in these rays.

Evolutionary trends of unglified elements are not mentioned in the literature. In the Urticales it occurs only in the Urticaceae p.p.. Therefore the presence of unglified elements is considered as highly specialized within the Urticales.

The phenomenon of fibre dimorphism has already been discussed under the phylogeny of the Urticaceae, and is regarded as a specialization in the Urticaceae.

Table 7. Wood anatomical characters used to show the relationships within the Urticales.

	Ulmaceae	Moraceae	Urticaceae
Perforation plates	(scalariform)/ simple	simple	simple
Fibres	non-septate	(septate)	(septate)
Fibre pit location	radial walls	radial walls	rad. & tang. walls
Ray type	He I/He II A	(He II A)/He II B	juvenile
Unglified elements	absent	absent	(present)
Storied fibres	absent	absent	(present)
Raphides	absent	absent	(present)
Fibre dimorphism	absent	absent	(present)

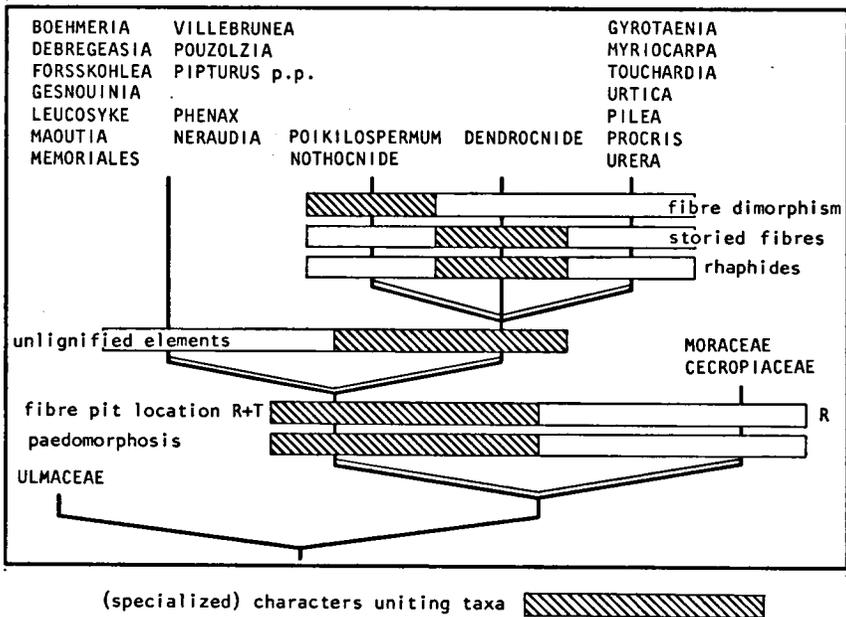


Fig. 3. Schematical arrangement of inferred relationships in the Moraceae, Cecropiaceae, and Urticaceae based on character states given in Table 6.

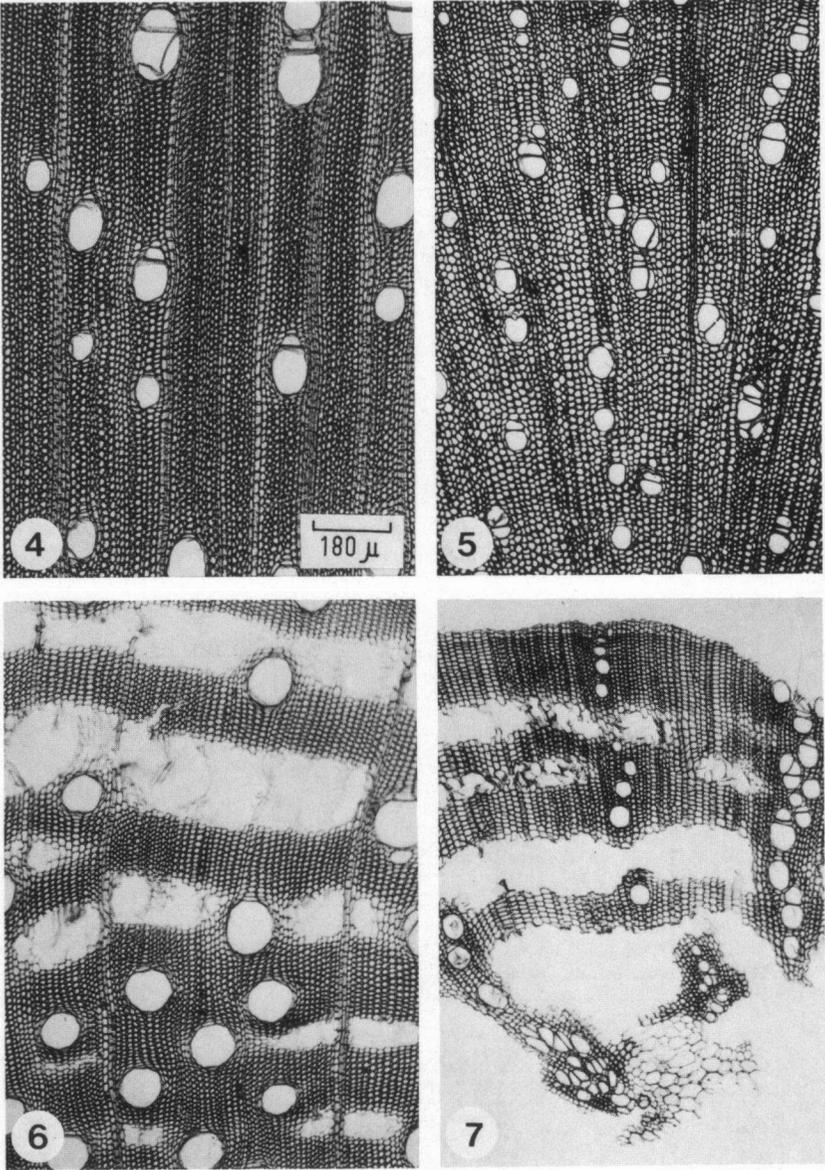


Fig. 4—7. Cross-sections. — 4, *Boehmeria excelsa* (Meyer 9597). — 5, *Gesnouinea arborea* (Haman 170383). — 6, *Urera* cf. *myriocarpa* (Ellenberg 2275). — 7, *Urtica dioica* (Bonsen *s.n.*). Magnification for Fig. 4—19 as indicated in Fig. 4.

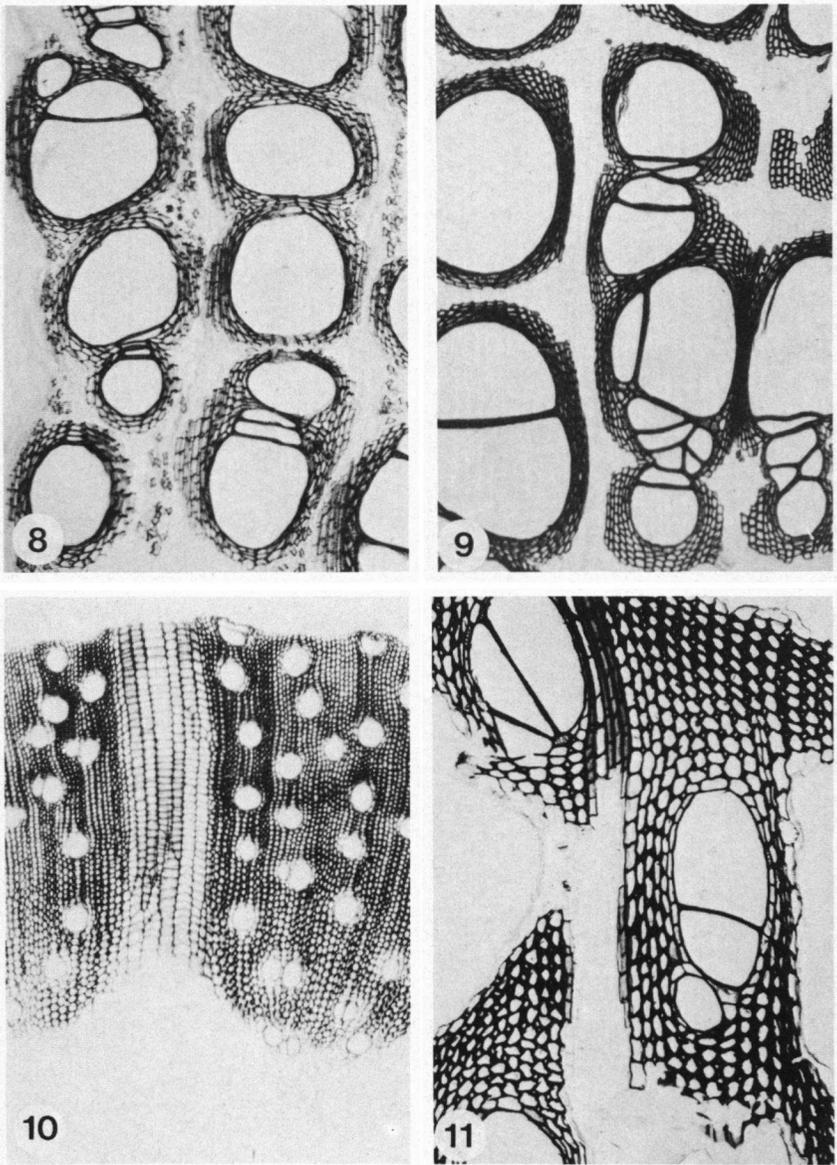


Fig. 8—11. Cross-sections. — 8, *Nothocnide repanda* (de Vogel 4410). — 9, *Urera cameroonensis* (Bretelet 2037). — 10, *Pilea* spec. (Maas et al. 3059). — 11, *Dendrocnide excelsa* (U.P.M. 211).

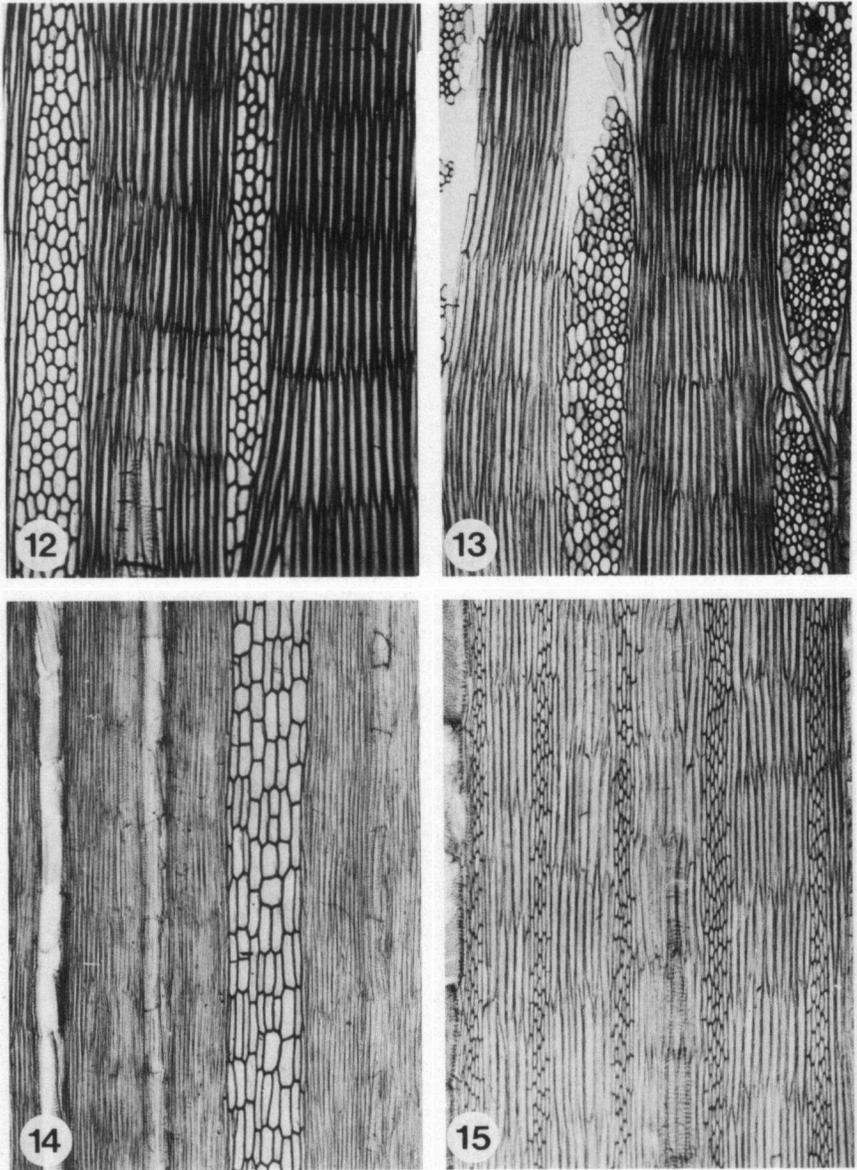


Fig. 12—15. Tangential sections. — 12 and 13, *Dendrocnide stimulans* (Zw. et R. 134).
— 14, *Pilea* spec. (Maas et al. 3059). — 15, *Urera robusta* (V. et O. 178).

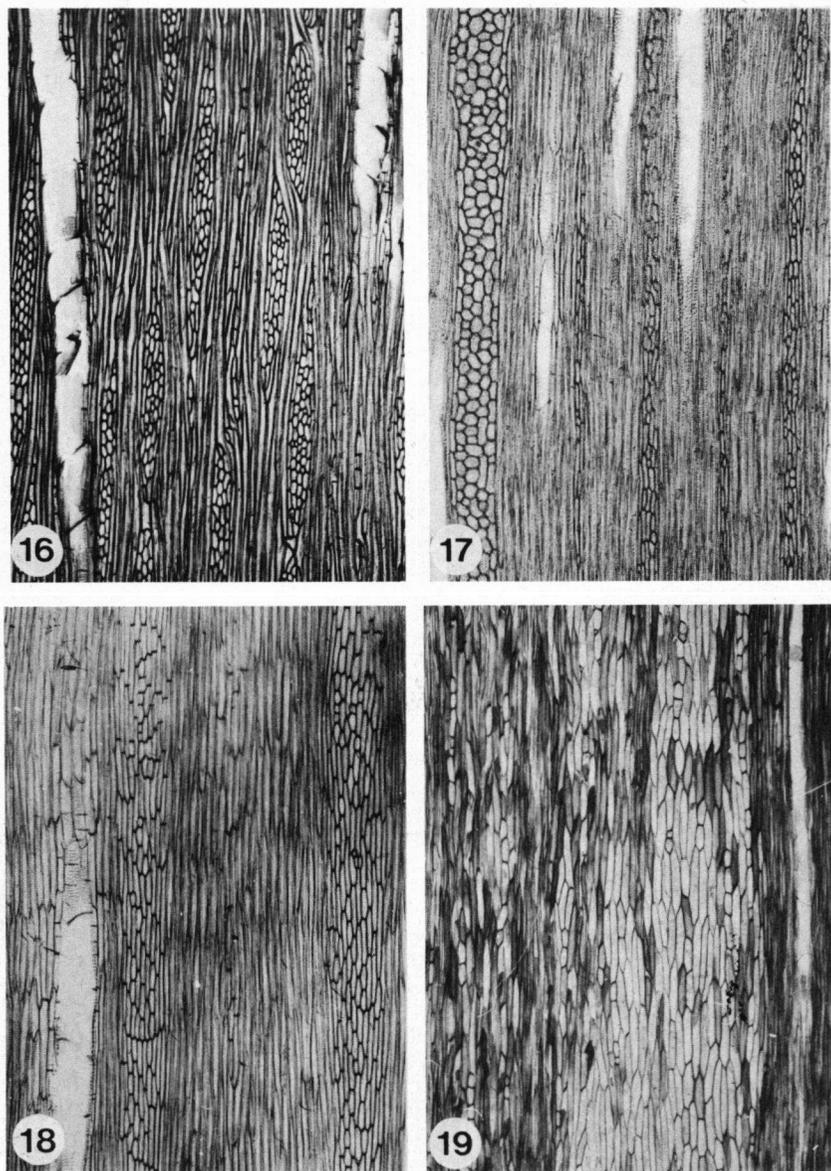


Fig. 16—19. Tangential sections. — 16, *Leucosyke capitellata* (Koorders 11152 B). — 17, *Poikilospermum inaequale* (Uw 26780). — 18, *Touchardia latifolia* (Stern et Herbst 518). — 19, *Urtica dioica* (ter Welle s.n.).

Taking into account the individual interpretation of the relevant wood anatomical characters (see also Table 7), it can be concluded that the Ulmaceae are the most primitive family, and the Urticaceae are the most specialized family in this order. (The position of the Cannabaceae has not been studied).

A schematic arrangement of the phylogenetic relationships is presented in Fig. 3.

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