WOOD ANATOMY OF TREES AND SHRUBS FROM CHINA. IV. ULMACEAE

by

Y. Zhong 1*, P. Baas 1 and E.A. Wheeler 2

Summary

The wood anatomy of 37 species belonging to the eight genera of Ulmaceae native to China is described. The wood of Chinese Ulmaceae is characterised by mostly simple perforations (sporadic scalariform plates occur in *Hemiptelea* and *Zelkova*); alternate, non-vestured intervessel pits; relatively short vessel elements and fibres; nonseptate fibres with simple to minutely bordered pits confined to the radial walls; mainly paratracheal parenchyma; rays rarely higher than 1 mm. Tanniniferous tubes are reported for the first time in Ulmaceae; they are limited to the genus *Pteroceltis*. Other, sporadically occurring features such as perforated ray and axial parenchyma cells and perforated fibres are also reported for the first time.

Wood structure for the most part supports the placement of genera within the groups Celtidoideae and Ulmoideae suggested by Grudzinska (1967). Celtidoideae are characterised by essentially heterocellular rays, the Ulmoideae by homocellular rays. Wood anatomy supports the traditional placement of *Gironniera cuspidata* and *G. yunnanensis* in the genus *Gironniera*, and not in *Aphananthe*. The Ulmaceae, and in particular the Ulmoideae, should be considered specialised in their wood anatomy.

Ecological trends in the wood anatomy of the Ulmaceae from China largely follow general trends established for the dicotyledons. The taxa from temperate provenances tend to have shorter vessel elements and fibres than those from subtropical to tropical provenances. Tropical and subtropical samples are predominantly diffuse-porous, while temperate samples are almost always ring-porous. Counter to the general trend for storied structure to be more common in tropical dicotyledons than in temperate ones, storied structure is more common in temperate zone Ulmaceae than in tropical Ulmaceae.

*Key words:* Ulmaceae, China, wood identification, systematic wood anatomy, ecological wood anatomy.

Introduction

The family Ulmaceae has 15 extant genera and about 200 species (Soepadmo 1977) of deciduous, semi-deciduous or evergreen trees or shrubs widely distributed in the temperate, subtropical and tropical regions in both the northern and southern hemispheres, and has a fossil record extending back to the Late Cretaceous (Manchester 1989). Many of its members are of economic interest for either their timber (e.g., *Ulmus, Zelkova, Celtis*), their bark (e.g. *Pteroceltis* bark is used for Xuan paper for traditional Chinese painting and calligraphy), or as ornamental trees. Traditionally, the family has been divided into two subfamilies, the Ulmoideae and the Celtidoideae, and recently many authors favour treatment of the Celtidoideae as a separate family, the Celtidaceae, suggesting that the genera in the Celtidoideae are more similar to the Moraceae than they are to the genera in the Ulmoideae group (Grudzinska 1967; Chernik 1975, 1980, 1981, 1982; Oginuma et al. 1990; Takahashi 1989; Terabayashi 1991; Takaso & Tobe 1990). However, no cladistic analysis of these relationships has been done, and there are genera with a mixture of ulmoid and celtoid features, e.g., *Ampelocera* and *Aphananthe* (Giannasi 1978; Zavada 1983; Terabayashi 1991), *Gironniera* (Oginuma et al. 1990; Takaso & Tobe 1990).

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Table 1. Numbers of species of the Chinese Ulmaceae.

<table>
<thead>
<tr>
<th>Subfamily</th>
<th>Genus</th>
<th>World Description</th>
<th>China</th>
<th>Number of species (samples) studied</th>
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<tr>
<td>Celtidoideae</td>
<td>Aphananthe</td>
<td>8 (4–5)</td>
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<td>Gironniera</td>
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<td>Pierocelis</td>
<td>1</td>
<td>1</td>
<td>1 (5)</td>
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<tr>
<td>Celtidoideae</td>
<td>Tremata</td>
<td>50 (10–15)</td>
<td>6 (5)</td>
<td>4 (10)</td>
</tr>
<tr>
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<td>Hemiptelea</td>
<td>1</td>
<td>1</td>
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<tr>
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<td>Ulmus</td>
<td>40 (18)</td>
<td>23 (21)</td>
<td>13 (26)</td>
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<tr>
<td>Ulmoideae</td>
<td>Zelkova</td>
<td>10 (5)</td>
<td>4</td>
<td>4 (10)</td>
</tr>
</tbody>
</table>

1) Number of species for the whole world are based on How (1982) and Mabberley (1987, between brackets).

2) Number of species for China follow How (1982), the Iconographia Cormophytorum Sinicorum, Supplement I (Institute & Botany Academia Sinica 1982), and other Chinese literature sources (Nanjing Forest College 1961 and Cheng et al. 1980).

In this study we use the traditional, broader concept of the Ulmaceae.

Eight genera of Ulmaceae occur in China. The approximate total number of species in China and in the world, and the number of species and samples studied here are listed in Table 1.


This study surveys the wood anatomy of the genera of Ulmaceae native to China and discusses its systematic and ecological signifcance. It is a contribution to the series on the wood anatomy of trees and shrubs from China. Previous papers in the series were on the Oleaceae (Baas & Zhang 1986), Theaceae (Deng & Baas 1990), and Rosaceae (Zhang & Baas 1992).

Material and Methods

More than 100 wood samples were obtained from several institutional wood collections in China (see Acknowledgements). Unfortunately, some samples are not vouchered, or data on herbarium vouchers are not available. For nomenclature we largely follow Iconographia Cormophytorum Sinicorum (Institute of Botany, Academia Sinica 1972, 1982). For each sample, the location is listed first, followed by the wood collection number preceded by a code from Stern’s Index Xylariorum (1988), indicating the source of the sample.

Light microscopic studies of sections and macerations were carried out in the usual manner (cf. Baas & Zhang 1986), followed by SEM observations of selected samples.

Conventions for determining quantitative values and the terminology largely follow previous studies (Baas & Zhang 1986; Baas et al. 1988) and recommendations in the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989).

(text continued on page 428)
Legends to Figures 1–40 (pages 422–427):

Figs. 1–4. TS, × 48. – 1: *Trema orientalis* (CAFw 7267), wood diffuse-porous and growth rings absent. – 2: *Trema angustifolia* (CAFw 11828), wood diffuse-porous with very vague growth ring boundary. – 3: *Trema cannabina* (CAFw 19820) wood semi-ring-porous. – 4: *Aphananthe aspera* (CAFw 17625), wood diffuse-porous; growth rings distinct; parenchyma aliform, vasicentric, and in marginal bands.

Figs. 5–8. TS, × 48. – 5: *Ulmus tonkinensis* (CAFw 146600), wood diffuse-porous and vessels partly in small clusters. – 6: *Celtis pandoveroetiana* (CAFw 17413), wood diffuse-porous and vessels partly in radial multiples. – 7: *Celtis bungeana* (CAFw 17072), wood ring-porous, earlywood vessels in 1 or 2 rows, latewood vessels in wavy tangential to diagonal bands, sclerotic tyloses present (arrow). – 8: *Zelkova serrata* (CAFw 16112), wood ring-porous, earlywood vessels in single rows.

Fig. 9. *Zelkova serrata*, SEM, RLS, × 1950. Multiple perforation plate with two irregular bars. – Fig. 10. *Trema virgata*, SEM, RLS, × 1100. Spiral thickenings distinct in very narrow vessel elements and faint in wider vessel elements, simple perforation present in the narrow vessel element (arrow). – Fig. 11. *Celtis koraiensis*, SEM, RLS, × 1650. Tylosis in the libriform fibre. – Fig. 12. *Zelkova serrata*, SEM, TLS, × 1950. Simple perforations and alternate intervessel pits. – Fig. 13. *Celtis koraiensis*, SEM, RLS, × 2500. Vessel with distinct spiral thickenings. – Fig. 14. *Pteroceltis tatarinowii*, TLS, × 1100. Very faint spiral thickenings on vessel wall. – Fig. 15. *Celtis koraiensis*, SEM, TS, × 1000. Latewood vessels intermixed with vascular tracheids and axial parenchyma cells. – Fig. 16. *Zelkova serrata*, SEM, TLS, × 2500. Slit-like, partly coalescent apertures. – Fig. 17. *Trema virgata*, SEM, RLS, × 3600. Unidentified granular deposits on the vessel wall.

Figs. 18 & 19. TLS, × 120. – 18: *Trema orientalis* (CAFw 7267), alternate, polygonal intervessel pits. – 19: *Pteroceltis tatarinowii* (CAFw 13667), minute intervessel pits. – Figs. 20 & 21. RLS, × 300. – 20: *Gironniera subaequalis* (Guangx For. Coll. w 8), vessel-ray pits simple to half-bordered, of varying size and shape. – 21: *Celtis sinensis* (CAFw 13083), vessel lumen filled with sclerotic, partly crystalliferous, tyloses. – Figs. 22 & 23. TLS, × 120. – 22: *Celtis philippensis*, thin-walled tyloses. – 23: *Ulmus pumila* (CAFw 13822), vascular tracheids intergrading with narrow vessel elements; note also the storied arrangement of narrow vessel elements, vascular tracheids and axial parenchyma, and two distinct ray sizes (narrow rays arrowed).

Figs. 24–26. *Ulmus pumila* (CAFw 13822), simple perforations in libriform fibres (arrows). – 24: TLS, × 300; 25: RLS, × 614; 26: RLS, × 455. – Fig. 27. *Ulmus pumila*, TLS, × 300. Simple perforation in axial parenchyma cell (arrow). – Fig. 28. *Zelkova serrata* (HEFw 001400), RLS, × 614. Perforated ray cell, much smaller than other ray cells. – Fig. 29. *Pteroceltis tatarinowii* (CAFw 16386), TLS, × 818. Simple perforations in tangential wall of ray cells. The perforated ray cells are as large as other ray cells. – Fig. 30. *Celtis koraiensis* (CAFw 549) TLS, × 120. Sheath cells (arrow) and storied arrangement of vessel elements, vascular tracheids, axial parenchyma and small rays. – Fig. 31. *Ulmus tonkinensis* (CAFw 6813), RLS, × 120. Homocellular ray and chambered crystalliferous axial parenchyma. – Fig. 32. *Celtis wightii var. consimilis* (CAFw 6795), RLS, × 182. Rays composed of upright cells only, crystal-containing cells non-chambered.

Fig. 33. *Zelkova sinica* (CAFw 5503), RLS, × 300. Integumented prismatic crystal. – Fig. 34. *Pteroceltis tatarinowii* (CAFw 13667), RLS, × 120. Irregularly shaped tanniferous ray cells. – Fig. 35. *Pteroceltis tatarinowii* (CAFw 16386), TLS, × 120. Storied arrangement of vessel elements, rays and axial parenchyma. – Fig. 36. *Gironniera yunnanensis* (CAFw 11934), TS, × 120. Vitreous silica in the vessel. – Fig. 37. *Gironniera subaequalis* (Guangx For. Coll. w 8), TLS, × 120. Vitreous silica in fibres. – Fig. 38. *Gironniera cuspidata* (CAFw 12148), RLS, × 120. Unidentified granules in heterocellular ray. – Figs. 39 & 40. *Pteroceltis tatarinowii* (CAFw 16386), tanniferous tubes in rays. – 39: TS, × 300; 40: RLS, × 180.
Survey of wood anatomical character states in the Ulmaceae from China

Growth rings (Figs. 1–8)

Growth rings vary considerably in their delimitation from distinct to faint or absent. Growth ring boundaries can be of the following types:

I. In diffuse-porous species:
   a) Growth rings absent to faint and marked by differences in fibre wall thickness (Figs. 1 & 2).
   b) Growth rings distinct, marked by radially flattened fibres (Fig. 3).
   c) Marked by marginal parenchyma and irregular zonate parenchyma bands (then boundaries faint), with or without additional differences in fibre diameter (Figs. 4–6).

II. In ring-porous species:
    Marked mainly by differences in vessel diameter, and also by marginal or seemingly marginal parenchyma, and differences in radial fibre diameter and wall thickness (Figs. 7 & 8), rays often inflated at the boundaries.

Vessels

Porosity — As noted above, diffuse-porosity, semi-ring-porosity, as well as ring-porosity occur in the Ulmaceae. With only a few exceptions, ring-porosity is confined to extra-tropical Ulmaceae, and all ring-porous Chinese Ulmaceae are deciduous. Semi-ring-to diffuse-porosity occurs in evergreen as well as in deciduous species.

Although porosity can be of great diagnostic value, semi-ring-porosity is not always a constant feature at the generic level and sometimes varies within a species or from ring to ring within a single specimen.

Arrangement and groupings (Figs. 1–8) — There are two patterns of vessel arrangement and grouping within the Chinese Ulmaceae: Type 1) Vessels mainly or at least partly solitary, with the remainder mainly in radial multiples of 2–4 (–9), or in clusters of 3–4 (–11) (Figs. 1–6). Type 2) Vessels in the latewood forming a more or less wavy tangential to diagonal pattern as in Hemiptelea, Zelkova, and ring-porous species of Celtis and Ulmus (Figs. 7 & 8).

Vessel arrangement and groupings are of substantial diagnostic and systematic value at and above the genus level. Type 1 characterises all diffuse-porous species and semi-ring-porous species. Type 2 characterises all ring-porous Ulmaceae; this distinct pattern is always associated with vascular tracheids and narrow elements that intergrade between tracheids and normal vessel elements, spiral vessel wall thickenings, locally inflated multiserate rays, and marginal parenchyma bands.

Frequency and element size — Average vessel frequency ranges from 6 to 50/mm² in semi-ring- to diffuse-porous samples. In ring-porous species vessels are of very high frequency in the latewood and it is difficult to distinguish between narrow vessels and vascular tracheids. Consequently, we did not measure frequency or tangential diameter of latewood vessels of ring-porous woods. Average tangential vessel diameter (including the wall) of semi-ring- to diffuse-porous Ulmaceae in China ranges from 70 to 160 µm; in ring-porous Ulmaceae the average tangential diameter of earlywood vessels ranges from 100 to 250 µm. Average vessel element lengths of semi-ring- to diffuse-porous Ulmaceae range from 210 to 720 µm; average vessel element lengths of ring-porous Ulmaceae range from 190 to 380 µm. In some instances, quantitative characters can be useful in distinguishing individual genera or infrageneric taxa. For instance, vessel elements are the longest in Gironniera (on average 700–720 µm), followed by Trema (on average 400–510 µm), while in the other genera the average vessel element length ranges from 190–380 µm.

Perforations (Figs. 9–10, 12) — Almost all Chinese Ulmaceae have exclusively simple perforations (Fig. 12). Only in Hemiptelea and Zelkova scalariform plates with 1 or 2 bar(s) (Fig. 9) and simple perforations with vestigial bars very rarely occur. Simple perforations are also found on side walls of some vessel elements (Fig. 10) in some species.

The inclination of the perforation plates varies from highly oblique to horizontal, largely depending on the diameter of the vessels, the narrower vessel elements having more oblique perforations.
Wall pitting (Figs. 12, 16, 18–20) — Intervessel pits in the Ulmaceae are non-vestured and alternate (Fig. 12). Pit shape is polygonal and/or round (Figs. 12, 18). The apertures are usually slit-like, frequently to occasionally coalescent (Fig. 16) and/or oval to round. Intervessel pit size ranges from 3–10 (2–20) μm. Intervessel pits are minute in *Pteroceltis* (3–4 μm, Fig. 19), and minute to small (3–7 μm) in *Aphananthe* and diffuse-porous *Celtis*. All these species with minute to small intervessel pits are diffuse-porous, and mostly from subtropical to tropical regions.

Vessel-ray and vessel-parenchyma pits range from pits with much reduced borders to simple, or half-bordered pits. In *Aphananthe*, *Pteroceltis*, *Celtis*, *Hemiptelea*, *Ulmus*, and *Zelkova* they are usually similar to or smaller than the intervessel pits, rounded (at times elongate in *Celtis*, *Hemiptelea* and *Zelkova*), sometimes unilaterally compound; in *Gironniera* and *Tremad* they are of varying size and shape: small to large, round to angular or elongate, sometimes unilaterally compound (Fig. 20).

Wall thickness and sculpturing (Figs. 10, 13, 14) — Vessel walls range from 1–6 (–10) μm in thickness for the whole family: 4–7 μm in *Aphananthe* and *Pteroceltis*; 2–5 μm in *Gironniera* and *Tremad*; 2–4 μm in *Hemiptelea* and *Ulmus*; 1–5 (–10) μm in *Celtis* and *Zelkova*.

Spiral thickenings are virtually absent in *Gironniera* and *Tremad*, being very faint and only visible with SEM in *G. yunnanensis* and *T. angustifolia*. They vary from fine (*Aphananthe*, *Pteroceltis*) to distinct (*Celtis*, *Hemiptelea*, *Zelkova*, and *Ulmus*) (Figs. 10, 13, 14); and from present in all vessels (*Aphananthe*, *Pteroceltis*, *Celtis austrosinensis*, *Ulmus changii*, and *U. lanceaefolia*) to confined to narrow vessels only. It should be stressed that presence or absence of spiral thickenings is related to ecological factors. For instance, they are virtually absent in south subtropical to tropical diffuse-porous Ulmaceae, but are well-developed in extra-tropical Ulmaceae with only few exceptions. Ring-porous Ulmaceae with a wavy tangential to diagonal vessel pattern in the latewood invariably have well-developed spiral thickenings in latewood vessel elements.

Tyloses and deposits (Figs. 17, 21, 22) — Tyloses are common to rare or absent in Chinese Ulmaceae; tyloses were observed in all genera studied but not as a constant feature. They are mainly thin-walled (Fig. 22), but in some species sclerotic tyloses are common as well (Fig. 21). Dark deposits (gum-like) are of common occurrence in some species. Irregular unidentified deposits on the vessel walls were observed in *Tremad* (Fig. 17).

Vascular tracheids (Figs. 15, 23)

The presence of vascular tracheids is a characteristic feature of all ring-porous Ulmaceae with a wavy tangential to diagonal pattern. Vascular tracheids are here associated with vessel groups and completely intergrade with normal narrow vessel elements (Figs. 15, 23). Frequency of vascular tracheids varies from abundant to relatively rare; the latter situation prevails in a few specimens where the wood is sometimes semi-ring-porous and the tangential vessel distribution pattern is not very pronounced, and in the diffuse-porous species of *Ulmus*.

Vascular tracheids are absent in semi-ring-to diffuse-porous *Celtis*, and of rare occurrence in diffuse-porous *Ulmus*. As mentioned before, presence of vascular tracheids is apparently closely related to vessel grouping; in semi-ring- to diffuse-porous *Celtis* vessels are mainly in short radial multiples and vascular tracheids are absent, whilst in diffuse-porous *Ulmus* some vessels occur in clusters and vascular tracheids are present.

Fibres (Figs. 2, 11, 24–26)

The ground tissue fibres are typically non-septate libriform fibres, with simple to minutely bordered pits (borders smaller than 3 μm) mainly confined to the radial walls. Fibre wall thickness varies from very thin to thin (*Aphananthe*, *Gironniera* and *Tremad*), or thin to thick, or thick to very thick in other genera. Average fibre length ranges from 690–1720 (330–2070) μm (short to moderately long). The systematic value at the genus level of fibre wall thickness or fibre length is limited.

Two peculiar fibre features of aberrant rather than regular occurrence deserve mentioning: Simple perforations in fibre walls (Figs. 24–26) have been observed in almost all genera studied except *Aphananthe*. These
perforations are probably the result of 'trans-piercing' tip growth of adjoining fibres (Vidal Gomes, Curitiba, Brazil, unpublished data). In a few species of *Celtis* some fibres have tyloses (Fig. 11).

**Axial parenchyma (Figs. 1–8, 13, 27)**

Parenchyma ranges from scanty (in *Trema* and subg. *Gironniera*) to abundant. The following types of parenchyma distribution occur in the Ulmaceae: 1) apotracheally diffuse; 2) scanty paratracheal; 3) vasicentric; 4) aliform; 5) confluent to confluent banded; 6) wavy tangential to diagonal paratracheal bands, intermixed with the vascular tracheids; 7) marginal bands; 8) paratracheal zonate bands or lines. All genera have at least two of the above types. Aptomtracheally diffuse and scanty paratracheal parenchyma is typical for *Trema* (Figs. 1–3). In subg. *Gironniera* (*G. subaequalis*) types 1–3 are present. In the other genera including subg. *Galumpita* of *Gironniera* types 3–7 and sometimes type 8 are present (Figs. 4–8).

Parenchyma strand length varies from 2–8 to 24 cells. *Gironniera* and *Trema* have nearly the same range of parenchyma strand lengths (mostly 3–8, total range 2–12). In *Celtis*, *Ulmus* and *Zelkova* parenchyma strands are most commonly 2–4 cells long.

Simple perforations in axial parenchyma cell walls have been noted in some species or samples of *Celtis*, *Ulmus* and *Zelkova* (Fig. 27).

**Rays (Figs. 23, 24, 28–32, 38, 40)**

Multiseriate rays in *Ulmus* are homocellular (composed of procumbent cells) only (Figs. 23, 31). In *Hemiptelea* and *Zelkova*, both heterocellular and homocellular rays may occur in the same specimen. In the other species studied only heterocellular rays occur. Heterocellular rays in the Ulmaceae are composed of procumbent ray body cells and 1 or 2–4 rows of upright and/or square marginal cells (Figs. 38, 40). Rays in *Gironniera* are markedly heterocellular, rays with more than 4 rows of upright/square marginal cells are common. In *Gironniera* and *Trema* some multiseriate rays are composed entirely of upright and/or square cells. Uniseriate rays are often composed of only upright and/or square cells (Fig. 32), sometimes with procumbent, square and/or upright cells mixed throughout the ray.

Ray frequency ranges from 3–13(−17)/mm, most commonly 4–8 or 8–10(−12)/mm. In almost all semi-ring- to diffuse-porous Ulmaceae (except *C. austrosinensis* and *C. vandervoetiana*) the ranges of ray frequency are very similar and tend to be higher than in ring-porous Ulmaceae.

Ray width ranges from 1–13 cells, most commonly 1–3(−5) cells in semi-ring- to diffuse-porous Ulmaceae or 4–6(−8) cells in ring-porous Ulmaceae. In *Pteroceltis*, *Aphananthe*, *Celtis* and other ring-porous Ulmaceae rays tend to be of two more or less distinct sizes (Figs. 23, 24, 30). Ray height varies from 0.03–3.8 mm, most commonly 0.03–0.8 mm, and maximum ray height rarely exceeds 1 mm (some species of *Gironniera*, *Trema*, *Celtis*, *Hemiptelea*, *Ulmus* and *Zelkova*).

Sheath cells are of common occurrence in *Celtis*, usually well-developed in ring-porous *Celtis* (Fig. 30), but weakly differentiated to absent in semi-ring- to diffuse-porous *Celtis*. In *Gironniera* and *Trema* weakly differentiated sheath cells sometimes occur.

Perforated ray cells occasionally occur in *Celtis*, *Hemiptelea*, *Ulmus* and *Zelkova*. Simple ray perforations are usually in radial walls (Fig. 28), but also occur in tangential walls (Fig. 29). There are two kinds of perforated ray cells in Chinese Ulmaceae; one kind, as occurs in *Celtis*, is radially enlarged, similar to those reported in the literature for other families; the other kind is unusual in that perforated ray cells are not enlarged or even much smaller (in *Zelkova*) than normal ray cells (Fig. 28). Perforated ray cells have not been reported before for the family.

Disjunctive ray parenchyma cell walls are of common occurrence.

**Storied structure (Figs. 23, 30, 35)**

Rays and axial elements are irregularly storied in *Pteroceltis* (Fig. 35). Narrow vessel elements, vascular tracheids and axial parenchyma are sometimes locally storied in *Ulmus*, *Zelkova*, *Hemiptelea*, and ring-porous *Celtis* (Figs. 23, 30). Storied structure is absent in *Gironniera*, *Trema*, and *Aphananthe*.
**Tubes** (Figs. 39, 40)

Tanniferous tube occurs in *Pteroceltis*, extending radially among rays (Figs. 39, 40), and are weakly differentiated to well developed. They occur together and partly intergrade with irregularly shaped tanniferous cells (Fig. 34). This is the first report of tanniferous tubes in the Ulmaceae.

**Mineral inclusions** (Figs. 21, 31–33, 36–38)

In our material crystals are absent in *Gironniera, Hemipitelea* and *Trema*, and are of variable occurrence in the other genera. Druses only occur in some samples of some species of *Celtis*. When present, prismatic crystals are abundant to infrequent, integumented (Fig. 33) or not, usually in non-chambered (sometimes chambered in *Celtis*) square and/or upright ray cells (Fig. 32), less commonly in procumbent ray cells, and/or chambered or non-chambered axial parenchyma cells (Fig. 31), and occasionally in sclerotic tyloses of *C. sinensis* (CAFw 13083) (Fig. 21). Crystal-containing cells are enlarged or not, generally with one, sometimes with 2 or more crystal(s) per cell or chamber.

Vitreous silica occurs in *Gironniera* and *Ulmus lanceaefolia*, mostly in vessels, sometimes also in fibres, rarely in axial parenchyma cells (Figs. 36, 37).

Unbleachable, unidentified granular deposits have been noted only in *Gironniera*, common in both upright cells and procumbent body ray cells (Fig. 38), occasionally in axial parenchyma cells.

**Generic wood anatomical descriptions**

**Subfamily:** Celtidoideae

**Aphanaethe** Planch. (Fig. 4)

Material studied: *A. aspera* Planch.: Guizhou: CAFw 17625; Jiangxi: CAFw 17471; Fujian: CAFw 12664; Guangdong: CAFw 9187; Zhejiang: CAFw 386; Guangxi: CAFw 15878; Jiangsu: CAFw 6987; Hunan: CAFw 9418; Anhui: HEFw 000567.

Deciduous trees from temperate to north tropical regions.

Growth rings distinct, marked by marginal parenchyma bands and differences in fibre wall thickness. Wood diffuse-porous, vessels 6–9 (2–13)/sq.mm, 59–74 (41–88)% solitary, remainder mainly in radial multiples of 2–4, rarely in clusters of 3–4 and oblique pairs, oval or rarely round to weakly angular, tangential diameter 120–160 (70–205) μm, radial diameter up to 270 μm, walls 4–7 μm thick. Vessel element length 240–320 (150–400) μm. Perforations simple in slightly oblique to horizontal end walls. Intervessel pits nonvestured, alternate, mainly polygonal, 4–6 μm in diameter, with slit-like, occasionally coalescent apertures. Vessel-ray and vessel-axial parenchyma pits half-bordered or with much reduced borders to simple, similar to intervessel pits in size, sometimes unilaterally compound. Fine (visible with SEM), closely spaced spiral thickenings present throughout vessel elements. Thin-walled tyloses rarely present in CAFw 12664.

Vascular tracheids absent.

Libriform fibres 1090–1290 (830–1520) μm long, very thin- to thin-walled, with simple to minutely bordered pits (1–2 μm in diameter) mainly confined to the radial walls. Gelatinous fibres common.

Axial parenchyma abundant, mainly aliform to confluent and confluent-banded, with the bands more common in the latter part of the growth ring. Also vasicentric (CAFw 17625) and in 2–4-seriate marginal bands, in strands of 2–8 cells.

Rays 7–10/mm, 1–5(–6) cells wide, in CAFw 17471 rays tend to be of two sizes: 1–2-seriate and 4–5(–6)-seriate, 0.1–0.5 (–0.8) mm high. Multiseriate rays heterocellular, composed of procumbent body cells and 1 (2–3) row of upright marginal cells, uniseriate rays with procumbent, square and upright cells mixed throughout the ray or composed of square and/or upright cells only. Disjunctive ray parenchyma cell walls occasionally present.

Crystals common, prismatic, mostly in upright ray cells, less common in procumbent body ray cells, absent in axial parenchyma cells, integumented or not, usually one (rarely two) crystal(s) per non-enlarged and non-chambered ray cell. Silica absent.

*Note:* Sweitzer (1971) described “uniseriate rays homocellular comprised of procumbent cells” in Japanese *A. aspera*, but in our
study, as well as in the studies of Kanehira (1921b), Sudo (1959), Cheng et al. (1980), Yao (1988) etc., homocellular uniseriate rays were not observed.

*Celtis* L. (Figs. 6, 7, 11, 13, 15, 21, 22, 30, 32; Table 2)

**Group I — Ring-porous species of *Celtis***

Material studied: *C. biondii* Pamp.: Guangdong: CAFw 16906; Anhui: HEFW 003164; Guizhou: CAFw 20264; Jiangxi: CAFw 17407; Guangxi: Guangxi Forestry College, w 9; Fujian: CAFw 19819. — *C. bungeana* Blume: Shaanxi: CAFw 556; Guangdong: CAFw 17072; Henan: CAFw 5511; Sichuan: CAFw 8724; Hebei: CAFw 5537; Zhejiang: CAFw 7047; Jiangxi: CAFw 18124; Guizhou: CAFw 20263; Shanxi: HEF 82cw 591. — *C. koraiensis* Nakai: Shaanxi: CAFw 549. — *C. macrocarpa* Chun.: Guangxi: Guangxi Forestry College, w 5. — *C. philippensis* Blanco: Guangxi: CAFw 16043; Guangxi Forestry College, w 10. — *C. sinensis* Pers.: Fujian: CAFw 13083; Jiangshu: CAFw 6663; Shandong: CAFw 5709; Zhejiang: CAFw 391; Henan: CAFw 5628; Taiwan: CAFw 7214; Hunan: CAFw 9415; Anhui: HEFW 000325; Guangxi: Guangxi Forestry College, w 2; Guangdong: CAFw 16893; Sichuan: CAFw 17552; Jiangxi: CAFw 19157. — *C. yunnanensis* Schneid.: Yunnan: CAFw 11301.

Deciduous trees or rarely shrubs from temperate to tropical regions.

Growth rings distinct, marked by differences in vessel diameter, and mostly by marginal or seemingly marginal parenchyma bands and locally inflated multiseriate rays. Wood ring-porous, semi-ring-porous in some rings in certain samples (see Table 2); earlywood pores in 1–3 continuous rows (only discontinuous in *C. biondii*, CAFw 16906), oval to round, mean tangential diameter of the solitary earlywood vessels 90–200 (60–280) μm, radial diameter up to 300 μm; earlywood to latewood transition generally abrupt, but more gradual in *C. biondii* (CAFW 20264), *C. bungeana* (CAFw 556) and *C. sinensis* (CAFW 5709), latewood vessels predominantly in clusters, in wavy tangential to diagonal bands, walls 1–5(9) μm thick. Vessel element length 220–380 (160–470) μm. Perforations simple in horizontal to oblique end walls. Intervessel pits nonvestured, alternate, mainly polygonal, only round in *C. philippensis*, 5–10 (3–12) μm in diameter, with slit-like (sometimes round to oval), often coalescent apertures. Vessel-ray and vessel-axial parenchyma pits mostly simple or with reduced borders, similar to or smaller than intervessel pits in size, rounded, and horizontally or at times vertically elongate in some species, sometimes unilaterally compound. Spiral thickenings present, distinct in narrow vessel elements, faint to absent in wide vessel elements. Both thin-walled and sclerotic tyloses present in most samples (see Table 2).

Vascular tracheids, intergrading with narrow vessel elements, abundant in latewood (only rare in one semi-ring-porous sample of *C. biondii*, CAFw 20264), associated with the vessel-axial parenchyma groups, with distinct spiral thickenings.

Libriform fibres 890–1410 (620–1750) μm long; thin- to thick-walled, or thick- to very thick-walled, with simple to minutely bordered pits confined to the radial walls. Simple perforations occasionally occur in *C. bungeana* (CAFw 17072) and *C. koraiensis*. Tyloses rarely observed, but present in *C. koraiensis* and *C. sinensis* (CAFw 13083).

Axial parenchyma abundant, mainly paramural: vasicentric, confluent, aliform, and in narrow (1–3-seriate) to broad (4–7-seriate) wavy tangential to diagonal paratracheal bands, intermixed with the vascular tracheids; and in marginal (including seemingly marginal) 1–2-seriate bands (see Table 2), in strands of 2–4(10) cells. Simple perforations occasionally occur in tangential walls of some species. Storied arrangement of narrow vessel elements, vascular tracheids and parenchyma very rarely occurs locally and in but a few samples.

Rays 4–12/mm, usually of two sizes: 1–2 (4–seriate) and 5–8(12)-seriate, 0.06–0.8 (0.03–1.3) mm high. Rays mostly heterocellular, composed of procumbent body ray cells and 1–2(5) rows of square to upright marginal cells, also homocellular (all ray cells procumbent) in *C. koraiensis*; some uniseriate rays composed of square and/or upright cells, generally low (rarely over 10 cells high). Sheath cells usually present (see Table 2).
Disjunctive ray parenchyma cell walls present in all species. Perforated ray cells occasionally occur (see Table 2).

Prismatic crystals present in all species, integumented or not, abundant to infrequent, mostly in non-chambered upright and square ray cells (sometimes chambered in some samples) and as viewed in tangential sections crystals often in sheath cells, less common in procumbent ray cells, infrequent in non-chambered axial parenchyma cells in *C. koraiensis*, occasionally in sclerotic tyloses (one sample of *C. sinensis*, CAFw 13083); crystal-containing cells enlarged or not, generally with one, sometimes with 2 or 3, crystal(s) per cell. Druses occur in some species or samples (see Table 2). Silica absent.

*Group II* – Semi-ring-porous to diffuse-porous species of *Celtis*


Deciduous or evergreen trees from subtropical to tropical regions.

Growth rings faint to distinct, marked by marginal or seemingly marginal parenchyma bands and locally inflated multiserate rays, and moderate differences in vessel diameter. Wood semi-ring-porous to diffuse-porous, vessels 10–23 sq. mm, 30–58% solitary, remainder mainly in radial or oblique pairs or multiples of 3(–9), and in clusters of 3–4 (–11), oval to round, tangential diameter 70–105 (50–200) μm, radial diameter up to 270 μm, only up to 95 μm in *C. wightii* var. *consimilis*, walls 1–7 μm thick. Vessel element length 290–360 (140–490) μm. Perforations simple in horizontal to oblique end walls. Intervessel pits nonvestured, alternate, round in *C. austrosinensis*, mainly polygonal in the other two species, 3–10 μm in diameter, with slit-like, often coalescent apertures. Vessel-ray and vessel–axial parenchyma pits simple or with reduced borders, rounded or horizontally elongate, and unilaterally compound in *C. austrosinensis* and *C. vandervoetiana* (CAFw 17624); partly half-bordered in *C. austrosinensis*. Spiral thickenings present, distinct in narrow vessels and usually faint to absent in wide vessels; in *C. austrosinensis* thickenings also distinct in wide vessels. Thin-walled and sclerotic tyloses present (see Table 2). Unbleachable dark materials present in *C. vandervoetiana*.

Vascular tracheids absent.

Libriform fibres 1050–1270 (700–1950) μm long, thin- to thick-walled (but thick- to very thick-walled in *C. wightii* var. *consimilis*), with simple to minutely bordered pits confined to the radial walls. Simple perforations occasionally present in *C. vandervoetiana*.

Axial parenchyma abundant, mainly para-tracheal: vasicentric, confluent, aliform, and slightly wavy tangential paratracheal bands of 4–8 (2–10, occasionally up to 22) cells; and in 1–2-seriate, marginal bands (see Table 2), in strands of 2–4(–10) cells. Simple perforations present in *C. vandervoetiana*.

Rays 5–8(–12) or 12–17/mm, 1–5(–8) cells wide (see Table 2), usually of two sizes: 1–2-seriate and 3–5(–8)-seriate, 0.03–0.5 (1.7) mm high. Multiserate rays heterocellular, composed of procumbent body ray cells and 1–3(–7) rows of square and/or upright marginal cells, in *C. wightii* var. *consimilis*, uniseriate rays mostly with procumbent, square and upright cells mixed throughout the ray. Weakly differentiated sheath cells rare to absent. Disjunctive ray parenchyma cell walls only present in *C. austrosinensis*. Perforated ray cells present (see Table 2).

Prismatic crystals integumented, mostly in upright and square ray cells, less common in procumbent ray cells, sometimes in axial parenchyma cells. Crystal containing cells unenlarged and non-chambered, generally with 1(–2), sometimes with 3–5 or fragmented crystal(s) per cell. Druses occur in *C. vandervoetiana*. Silica absent.

Notes: 1. *Celtis philippensis* was described as diffuse-porous by Kaehira (1921), Sudo (1963), Sweitzer (1971) and Ho (1985). The identity of our material has been confirmed by three collectors, although Tang Yan-cheng, the taxonomist of Chinese Ulmaceae, thought that our material might have been misidentified (personal correspondence). According to Cheng et al. (1985), *C. philippen-
Table 2. Wood anatomical diversity in *Celtis*.

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1. Porosity; S = semi-ring-porous; R = ring-porous; D = diffuse-porous.
2. Average tangential vessel diameter (μm); in ring-porous samples only calculated for earlywood pores; in semi-ring-porous and diffuse-porous samples calculated for the whole growth ring.
3. Average vessel element length (μm).
4. Intervessel pit size (μm).
5. Average fibre length (μm).
6. Parenchyma distribution; V = vasicentric; C = confluent; C-B = confluent-banded; A = aliform; M = marginal parenchyma bands; D = diffuse.
7. Ray frequency (/mm).
8. Ray width (number of cells).
9. Number of rows of square to upright marginal cells.
10. Sheath cells; ± = weakly differentiated sheath cells present in some rays; (±) = very weakly differentiated and rarely present.
11. Perforated ray cells.
12. Prismatic crystals; U = present in upright/square ray cells; P = in procumbent cells; A = in axial parenchyma cells; S = in sclerotic tyloses; a = abundant; e = enlarged; c = chambered.

( ) = of sporadic occurrence.
sis and Ulmus tonkinensis are ring-porous when growing in northern temperate regions, but diffuse-porous in Hainan. It is possible that C. philippensis also becomes ring-porous in Guangxi (subtropical region). Sweitzer (1971) earlier found that wood of Planera aquatica varied from diffuse-porous to ring-porous. Wheeler et al. (1989) also noted a similar variation in C. laevigata.

2. According to Tang Yancheng, our C. austrosinensis Chun. may represent an unpublished new species in China, and the samples we have of C. bungeana (CAFw 17072, Guangdong) might be misidentified since this species is not very likely to occur in Guangdong. He referred C. wightii Planch. var. consimilis (Blume) Gagnep to C. collinsae Craib (personal correspondence).

3. Cox (1941), Grumbles (1941), Sweitzer (1971) and Wheeler et al. (1989) found that evergreen species of Celtis are diffuse-porous and deciduous species are ring-porous. However, the deciduous C. vanderveetiana is semi-ring-porous to diffuse-porous.

4. The wood structure of C. biodii is variable. Most rings in sample CAFw 20264 look semi-ring-porous, and vascular tracheids are rare. The earlywood vessels are widely spaced in CAFw 16906, and crystals occur in both procumbent and upright/square ray parenchyma cells of HEFw 003164.

5. Luo (1989) noted crystals in axial parenchyma cells and tyloses in C. yunnanensis. and reported spiral thickening to be absent in C. wightii.

6. None of the previous wood anatomical descriptions of Celtis in China mentioned marginal parenchyma bands.

7. We did not notice perforations with vestigial bars in our material as Sweitzer (1971) did in the ring-porous species he studied.

Gironniera Gaudich. (Figs. 20, 36, 37, 38; Table 3)
Evergreen trees or shrubs from south subtropical to tropical regions.

Subgenus Galumpita Blume

Growth rings faint, marked by differences in fibre wall thickness and diameter, and very limited marginal parenchyma bands. Wood diffuse-porous, vessels 8–9 (4–13)/sq.mm, 38–51% solitary, remainder mainly in radial multiples of 2–4(–7), sometimes in clusters of 3–4(–5) and oblique pairs, round to oval, or weakly angular, tangential diameter 130–140 (85–190) μm, radial diameter up to 205 μm, walls 2–5 μm thick. Vessel element length 700–710 (300–1240) μm. Perforations simple in oblique to horizontal end walls. Intervessel pits nonvestured, alternate, mainly polygonal, 7–15(–20) μm in diameter, with oval to slit-like, sometimes coalescent apertures. Vessel-ray and vessel-axial parenchyma pits simple to half-bordered, of varying size and shape: small to large, round and angular to horizontally elongate, some with pointed ends, sometimes unilaterally compound. Spiral thickenings virtually absent, but in G. yunnanensis very faint spiral thickenings present throughout some narrow vessel elements. Thin-walled tyloses common.

Vascular tracheids absent.
Libriform fibres 1500–1580 (550–2080) μm long, thin to thick-walled, with simple to minutely bordered pits confined to the radial walls. Simple perforations occasionally occur in G. cuspidata and G. yunnanensis. Gelatinous fibres common.

Axial parenchyma predominantly paratracheal (vasicentric, aliform, occasionally confluent and confluent-banded), in 1–4(–9) uniseriate bands or lines, and in very limited 1-seriate marginal lines, rarely diffuse (see Table 4), in strands of 3–8 (2–13) cells.

Rays 9–12(–13)/mm, 1–4(–5) cells wide, 0.15–1.0(–1.8) mm high. Heterocellular rays composed of procumbent body ray cells and 1–4(–7) rows of upright marginal cells, sometimes with procumbent and square cells mixed throughout the ray; uniseriate rays as high as multiseriate rays and composed of upright cells only. Weakly differentiated sheath cells common (see Table 3). Disjunctive ray parenchyma cell walls present.

Crystals absent. Vitreous silica common in vessels and fibres. Unbleachable, unidentified granular contents common in ray cells, occasionally in axial parenchyma cells.
Table 3. Wood anatomical diversity in *Gironniera*.

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<tr>
<td><em>G. cuspidata</em></td>
<td>F</td>
<td>8</td>
<td>51</td>
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<td>710</td>
<td>8–15</td>
<td>1580</td>
<td>BACVSM(D)</td>
<td>7–11</td>
<td>±</td>
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</tr>
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<td>F</td>
<td>9</td>
<td>38</td>
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<td>700</td>
<td>7–14</td>
<td>1500</td>
<td>BACVSM</td>
<td>9–13</td>
<td>±</td>
<td>1.8</td>
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<td>720</td>
<td>8–13</td>
<td>1260</td>
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<tr>
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<td>A</td>
<td>10</td>
<td>132</td>
<td>–</td>
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<td>–</td>
<td>SV(D)</td>
<td>5–11</td>
<td>–</td>
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</tbody>
</table>

1. Growth rings boundaries; A = absent, F = faint.
2. Vessel frequency (per sq. mm).
3. Solitary vessels (%).
4. Average tangential vessel diameter (μm).
5. Average vessel member length (μm).
6. Intervessel pit size (μm).
7. Average fibre length (μm).
8. Parenchyma distribution; A = aliform; B = banded; C = confluent; D = diffuse; M = marginal; S = scanty paratracheal; V = vasicentric.
9. Ray frequency (/mm).
10. Sheath cells; ± = weakly differentiated; – = absent.
11. Maximum ray height (mm).

**Subgenus Gironniera Planch.** (*Subgenus Neomatostigma*)

Material studied: *G. subaequalis* Planch.: Guangxi: Guangxi Forestry College, w 8; Guangdong: CAFw 17005; Hainan: CAFw 9596; Yunnan: CAFw 11758.

Growth rings absent. Wood diffuse-porous, vessels 10 (5–20)/sq. mm, 43% solitary, remainder mainly in radial multiples of 2–4(–9), sometimes in clusters of 3–4(–5) and oblique pairs, round to oval, or weakly angular, tangential diameter 120–132 (85–180) μm, radial diameter up to 210 μm, walls 2–5 μm thick. Vessel element length 720 (300–1000) μm. Perforations simple in oblique to horizontal end walls. Intervessel pits nonvestured, alternate, mainly polygonal, 8–13(–20) μm in diameter, with oval to slit-like, sometimes coalescent apertures. Vessel-ray and vessels-axial parenchyma pits simple to half-bordered, of varying size and shape: small to large, round and angular to horizontally elongate, some with pointed ends, sometimes unilaterally compound. Spiral thickenings absent. Thin-walled tyloses common. Vascular tracheids absent. Libriform fibres 1260 (870–1670) μm long, thin- to thick-walled, with simple to minutely bordered pits confined to the radial walls. Perforations absent. Axial parenchyma less abundant than in subgenus *Galumpita*, scanty paratracheal and vasicentric, rarely diffuse, in strands of 4–8 (2–11) cells. Rays 5–12(–13)/mm, 1–5 cells wide, 0.15–1.2(–3.8) μm, most frequently over 1 mm high. Heterocellular rays composed of procumbent body ray cells and 1–4(–7) rows of upright marginal cells, sometimes with procumbent and square cells mixed throughout the ray; uniseriate rays composed of upright cells only. Weakly differentiated sheath cells sometimes present (see Table 3). Disjunctive ray parenchyma cell walls absent. Crystals absent. Vitreous silica common in vessels and fibres, occasionally in axial parenchyma cells. Unbleachable, unidentified.
granular contents common in ray cells, occasionally in axial parenchyma cells.

Notes: 1. Sweitzer (1971) observed prismatic crystals in ray cells and axial parenchyma cells of *G. cuspidata*, and Cheng et al. (1979, 1985) noted prismatic crystals in axial parenchyma cells of *G. cuspidata*, *G. subaequalis* and *G. yunnanensis*. Only unbleachable granular contents were observed in the species we studied. Absence of crystals in *G. subaequalis* was also reported by Cheng et al. (1980).

2. Sweitzer (1971) did not observe silica in the 9 samples (belonging to 5 species, including *G. cuspidata* and *G. subaequalis*) he studied. Cheng et al. (1979, 1985) noted silica in axial parenchyma cells and ray cells of *G. cuspidata* and *G. yunnanensis*, and in axial parenchyma cells, ray cells and fibres of *G. subaequalis*; Cheng et al. (1980) noted silica common in ray cells and occasionally in axial parenchyma cells and fibres of *G. subaequalis* (CAFw 9596 etc.). We only observed vitreous silica in vessels, fibres and occasionally in axial parenchyma cells in this genus.

3. Rays are very markedly heterocellular in this genus with the multiseriate rays having high upright marginal cells and the uniseriate rays having all upright cells.

4. Intercellular canals were reported by Den Berger and Bianchi in the rays of *Gironniera* (Metcalfe & Chalk 1950), but we did not find such canals in our material.

*Pteroceltis* Maxim. (Figs. 14, 19, 29, 34, 35, 39, 40; Table 4)


Deciduous trees from temperate to subtropical regions, native to China, also cultivated.

Growth rings faint, marked by marginal parenchyma bands, locally inflated multiseriate rays and differences in fibre wall thickness. Wood diffuse-porous, vessels 19–24 (12–39)/sq.mm, 73–75 (52–100)% solitary, remainder mainly in radial multiples of 2–4, sometimes in clusters of 3–4(--5) and oblique multiples of 2–3, oval to round, tangential diameter 85–110 (70–145) µm, radial diameter up to 185 µm, walls 4–7 µm thick. Vessel element length 230–295 (180–390) µm. Perforations simple in oblique to horizontal end walls. Intervessel pits nonvestured, alternate, polygonal, 3–4 µm in diameter, with oval to slit-like, often coalescent, apertures. Vessel-ray pits half-bordered or with much reduced borders to apparently simple, small, rounded, sometimes unilaterally compound. Vessel-axial parenchyma pits half-bordered, similar to intervessel pits in shape and size. Fine spiral thickenings present throughout vessel elements visible with SEM. Both thin-walled and sclerotic (medium thick-walled) tyloses common in *P. tatarinowii* var. *pubescens* only.

Vascular tracheids absent.

Librofibres 1035–1280 (590–1400) µm long, thick- to very thick-walled, with simple to minutely bordered pits confined to the radial walls. Simple perforations fairly common in both tangential and radial walls.

Axial parenchyma abundant, mainly aliform to confluent and confluent-banded, and in 2–4(--8)-seriate marginal bands, also vasicentric and less commonly scanty paratracheal, in strands of 5–8 (2–9) cells.

Rays 8–12(--13)/mm, of 2 more or less distinct sizes: 1(--2)-seriate and 3–5(--6)-seriate, 0.15–0.75 mm high. Rays heterocellular, composed of procumbent body ray cells and 1–3(--8) rows of upright marginal cells, uniseriate rays with procumbent, square and upright cells mixed throughout the ray; and at times composed of square and/or upright cells only. Disjunctive ray parenchyma cell walls present. Irregular tanniferous cells with pointed outgrowths present.

Rays and axial elements irregularly storied (CAFw 16386) or non-storied (CAFw 16171).

Prismatic crystals present (see Table 4), mostly in upright cells, sometimes in 2-chambered ray cells, less commonly in procumbent cells, sporadic or absent in axial parenchyma cells; cells mostly enlarged, chambered or not, usually one integumented crystal per cell or chamber. Silica absent. Reddish-brown tannins present in ray cells (and tanniferous tubes), occasionally in axial parenchyma cells.

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Table 4: Wood anatomical diversity in *Pteroceltis*.

<table>
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<tr>
<th>Material</th>
<th>1</th>
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<tbody>
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<tr>
<td>CAFw 13667</td>
<td>24</td>
<td>85</td>
<td>260</td>
<td>1280</td>
<td>3–8</td>
<td>nm</td>
<td>(s)</td>
</tr>
<tr>
<td>CAFw 16386</td>
<td>20</td>
<td>110</td>
<td>295</td>
<td>1035</td>
<td>2–8</td>
<td>(c) a</td>
<td>als</td>
</tr>
<tr>
<td><em>P. tatarinowii</em> var. pubescens</td>
<td>19</td>
<td>85</td>
<td>230</td>
<td>1065</td>
<td>2–4</td>
<td>(c) a</td>
<td>(s)</td>
</tr>
</tbody>
</table>

1. Vessel frequency (per sq. mm).
2. Average tangential vessel diameter (μm).
3. Average vessel member length (μm).
4. Average fibre length (μm).
5. Width (number of cells) of marginal parenchyma.
6. Crystals; n = in non-chambered ray cells; (c) = chambered; a = abundant; m = moderately common.
7. Tanniniferous tubes; a = abundant; l = long; s = short.

Tanniniferous tubes common in *P. tatarinowii* (CAFw 16386), extending radially among rays, weakly differentiated to well developed, up to 400 μm long or longer (sometimes difficult to measure), 7–20 μm high, rare and weakly differentiated in the other two samples.

*Notes*: 1. Vessels are mainly in oblique or radial multiples according to Cheng *et al.* (1985) and Ho (1985), but in our and Sweitzer’s material (1971) 73–75% of the vessels are solitary. Spiral thickenings in vessels were not reported by the authors mentioned above, but such thickenings are visible with the SEM.
2. Sweitzer (1971) referred to uniseriate rays as homocellular with procumbent cells, but we, as well as other authors, only observed heterocellular rays.
3. Tanniniferous tubes have not been reported in the Ulmaceae before. To verify tube contents, we stained unbleached radial sections of two samples of CAFw 16386 with a FeCl₃.5H₂O solution and compared them with unstained ones. The tube contents of the stained sections are obviously darker than those of the unstained ones.

*Trema* Lour. (Figs. 1–3, 10, 17, 18; Table 5)


Evergreen or deciduous small trees or shrubs from south subtropical to tropical regions.

Growth rings faint to intermediate, and distinct in *T. cannabina* and *T. virgata* (CAFW 13472), marked by differences in fibre wall thickness and diameter, in *T. cannabina* and *T. virgata* (CAFW 13472) also by differences in vessel diameter. Wood mostly diffuse-porous, but semi-ring-porous in *T. cannabina* and *T. virgata* (CAFW 13472), vessels 9–26 (6–49)/sq mm, 23–66 % solitary, remaining mainly in radial multiples of 2–3(–7), rarely in clusters of 3–4(–11) and oblique pairs, oval to round, or weakly angular, tangential diameter 90–140 (65–165) μm, radial diameter up to 230 μm, walls 2–6 μm thick. Vessel element length 400–510 (190–850) μm. Perforations simple in oblique to horizontal end walls. Intervessel pits nonvestured, alternate, polygonal or round, 4–8 (4–14) μm in diameter, with oval to round or slit-like, sometimes coalescent apertures. Vessel-ray and vessel-axial parenchyma pits with much reduced borders to simple, or half-bor-
Table 5. Wood anatomical diversity in *Trema*.

<table>
<thead>
<tr>
<th>Material</th>
<th>1</th>
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<tbody>
<tr>
<td><em>T. angustifolia</em></td>
<td>F</td>
<td>D</td>
<td>15</td>
<td>66</td>
<td>130</td>
<td>440</td>
<td>4–11</td>
<td>890</td>
<td>9–13</td>
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<tr>
<td><em>T. cannabina</em></td>
<td>D</td>
<td>S</td>
<td>20</td>
<td>36</td>
<td>90</td>
<td>400</td>
<td>4–10</td>
<td>695</td>
<td>9–15</td>
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<td>F</td>
<td>D</td>
<td>14</td>
<td>44</td>
<td>128</td>
<td>–</td>
<td>8–14</td>
<td>–</td>
</tr>
<tr>
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<td>F</td>
<td>D</td>
<td>9</td>
<td>65</td>
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<td>460</td>
<td>7–11</td>
<td>915</td>
<td>7–13</td>
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<td><em>T. virgata</em></td>
<td>CAFw 11805</td>
<td>F</td>
<td>D</td>
<td>10</td>
<td>55</td>
<td>90</td>
<td>510</td>
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<td>23</td>
<td>115</td>
<td>410</td>
<td>5–10</td>
<td>1115</td>
<td>9–12</td>
</tr>
</tbody>
</table>

1. Growth rings boundaries; D = distinct; F = faint.
2. Porosity; D = diffuse; S = semi-ring-porous.
3. Vessel frequency (per sq. mm).
4. Solitary vessels (%).
5. Average tangential vessel diameter (μm).
6. Average vessel element length (μm).
7. Intervessel pit size (μm).
8. Average ray frequency (/mm).
9. Ray frequency (/mm).

Notes: 1. Spiral thickenings have not been reported before for *T. angustifolia* and *T. virgata* (CAFw 6215). In our material, very faint spiral thickenings occur in narrow vessel elements. The occurrence of helical thickenings in *T. angustifolia*, a wood without distinct growth rings, is unusual.

2. Cheng *et al.* (1980) and Luo (1989) referred to fibres in *T. angustifolia* and *T. orientalis* as fibre-tracheids with distinctly bordered pits (3.2–4.0 μm in diameter). Yang and Huang-Yang (1987) also reported fibre-tracheids in *T. orientalis*. But we only observed libriform fibres with simple to minutely bordered pits.

3. Yang and Huang-Yang (1987) described intervessel pitting as opposite in *T. orientalis*, but we, as well as Cheng *et al.* (1985) and Luo (1989) only observed alternate intervessel pits.

4. Sweitzer (1971) referred to uniseriate rays as homocellular with procumbent cells in *T. orientalis*. However, in our and others’ studies, only heterocellular rays were observed.

5. Cheng *et al.* (1980) and Luo (1989) reported that crystals are occasionally present in axial parenchyma cells of *T. angustifolia* and *T. orientalis*. Cheng *et al.* (1985) describ-
ed that silica sometimes occurs in the ray cells of these two species. We, as well as Sweitzer (1971) and Yang and Huang-Yang (1987) did not find crystals or silica.

**Subfamily: Ulmoideae**

*Hemiptelea* Planch.

Material studied: *H. davidii* (Hance) Planch.: Liaoning, w 1.

Deciduous small trees or shrubs from temperate to subtropical regions.

Growth rings distinct, marked by differences in vessel diameter, marginal parenchyma bands and locally inflated multiseriate rays. Wood ring-porous and sometimes semi-ring-porous, earlywood pores in 2–3 discontinuous rows, round to oval, mean tangential diameters of the solitary earlywood vessels 70 (30–135) μm, radial diameter up to 150 μm, latewood vessels predominantly in clusters, in wavy tangential to diagonal bands, walls 1.5–4 μm thick. Vessel element length 210 (150–300) μm. Perforations simple, rarely scalariform with 1 bar, and simple with vestigial bars, in oblique to horizontal end walls. Intervessel pits nonvestured, alternate, polygonal and round, 5–7 μm in diameter, with round to oval and slit-like, sometimes coalescent apertures. Vessel-ray and vessel-axial parenchyma pits with much reduced borders to simple, rounded, and horizontally elongate, smaller than intervessel pits. Spiral thickenings present, distinct in narrow vessels, faint to absent in wider vessels.

Vascular tracheids, intergrading with narrow vessel elements, associated with the vessel–axial parenchyma groups, with distinct spiral thickenings.

Libriform fibres 1120 (710–1400) μm long, thick- to very thick-walled, with simple to minutely bordered pits confined to the radial walls.

Axial parenchyma abundant, vasicentric, in latewood intermixed with the vascular tracheids and surrounding the vessels, confluent to confluent-banded, and in marginal 1–3-seriate bands; in strands of 2–4 cells.

Rays 6–8/mm, 1–9 cells wide, tending to be of two distinct sizes: 1–2(−3)-seriate and 4–9-seriate, 0.05–0.8(1.5) mm high. Rays sometimes homocellular, but mainly heterocellular, composed of procumbent body ray cells and 1–4 rows of upright to square cells, sometimes with all ray cells square and/ or upright, and at times with procumbent, square and upright cells mixed throughout the ray. Perforated ray cells infrequently present.

Locally storied arrangement of vessels, vascular tracheids and axial parenchyma sometimes occurs.

Crystals and silica absent.

**Notes:** 1. Sweitzer (1971) observed some septate fibres and prismatic crystals in ray parenchyma, however, we did not find these features in our material, nor did Minaki et al. (1988) who examined seven specimens of *H. davidii*.

2. The specimens of *H. davidii* examined by Minaki et al. (1988) were all ring-porous with an abrupt transition from earlywood to latewood and the mean tangential diameter (142 μm) and mean radial diameter (174 μm) of the earlywood vessels in their material were larger.

**Ulmus** Linn. (Figs. 5, 23–27, 31; Table 6)

**Group I — Ring-porous species of Ulmus.**


Deciduous trees or rarely shrubs from temperate to subtropical (rarely tropical) regions.

Growth rings distinct, marked by differences in vessel diameter and marginal paren-
Table 6. Wood anatomical diversity in *Ulmus*.

<table>
<thead>
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<tr>
<td>(Ring-porous)</td>
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<td><em>U. changii</em></td>
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<td>200</td>
<td>245</td>
<td>5–12</td>
<td>1505</td>
<td>4–7</td>
<td>1–5</td>
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<td>A (P) (e)</td>
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<td><em>U. davidiana</em></td>
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<td>1–6</td>
<td>+</td>
<td>(Pe)</td>
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<td>270</td>
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<td>1–6</td>
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<td>1–2 c</td>
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<td>5–7</td>
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<td>(A)</td>
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<td>–</td>
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<td>1–6</td>
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<td>A (P) e</td>
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<td>–</td>
<td>A (P) e</td>
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<td><em>U. propinqua</em></td>
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<td>1 dc</td>
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<td>A (P) (e)</td>
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<td><em>U. pumila</em></td>
<td></td>
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<td></td>
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<tr>
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<td>mc</td>
<td>140</td>
<td>210</td>
<td>5–9</td>
<td>1090</td>
<td>4–8</td>
<td>1–7</td>
<td>+</td>
<td>–</td>
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<tr>
<td>CAFW 13822</td>
<td>mc</td>
<td>161</td>
<td>6–10</td>
<td>–</td>
<td>4–7</td>
<td>1–7</td>
<td>+</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>U. uyematsui</em></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>1 d</td>
<td>190</td>
<td>290</td>
<td>8–10</td>
<td>1600</td>
<td>4–6</td>
<td>1–5</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><em>U. wilsoniana</em></td>
<td></td>
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<td></td>
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<td></td>
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<tr>
<td>1 (2) d</td>
<td>240</td>
<td>235</td>
<td>8–13</td>
<td>1545</td>
<td>4–6</td>
<td>1–5</td>
<td>–</td>
<td>A (P) ea</td>
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</table>

| Group II         |   |   |   |   |   |   |   |   |   |
| (Diffuse-porous) |   |   |   |   |   |   |   |   |   |
| *U. lanceaeofolia* | – | 135 | 310 | 7–9 | 1680 | 5–9 | 1–8 | + | Aa |
| *U. tonkinensis* |   |   |   |   |   |   |   |   |   |
| CAFw 146600      | – | 100 | 295 | 2–4 | 1500 | 9–12 | 1–4 | – | A (P) a |
| CAFW 6813        | – | 115 | 290 | 8–10 | 1420 | 8–10 | 1–4 | – | A (P) |

1. Number of rows of earlywood pores; m = many rows; c = continuous; d = discontinuous; cd = continuous to discontinuous. (for ring-porous woods, Group I).
2. Average tangential vessel diameter (μm); in ring-porous samples only calculated for earlywood pores; in diffuse-porous samples calculated for the whole growth ring.
3. Average vessel element length (μm).
4. Intervessel pit size (μm).
5. Average fibre length (μm).
6. Ray frequency (/mm).
7. Most common ray width (number of cells).
8. Perforated ray cells.
9. Crystals; A = in chambered axial parenchyma cells; P = in procumbent ray cells; e = enlarged; a = abundant.
chyma bands and locally inflated multiseriate rays. Wood mostly ring-porous, earlywood pores mainly in 1–2 continuous or discontinuous rows but in 3–10 continuous rows in *U. pumila* and some samples of *U. davidiana*, round to oval, mean tangential diameters of the solitary earlywood vessels 145–240 μm, radial diameter up to 350 μm, earlywood to latewood transition generally abrupt but gradual in wide rings of *U. davidiana* (HEFw 82cw844), *U. lasiophylla*, *U. macrocarpa* (CAFw 554), *U. multi nervis*, *U. propinqu a* and *U. pumila* (HEF w2134), latewood vessels predominantly in clusters, in wavy tangential to diagonal bands, walls 2–4 (1–6) μm thick. Vessel element lengths 190–290 (110–350) μm. Perforations simple in horizontal to oblique end walls, occasionally in side walls. Intervessel pits nonvestured, alternate, round to oval and sometimes polygonal, 5–10(–14) μm in diameter, with oval to round and/or slit-like, sometimes coalescent apertures. Vessel-ray and vessel-axial parenchyma pits simple or with reduced borders, small, rounded, and at times unilaterally compound. Spiral thickenings present, distinct in narrow vessel elements, faint to absent in wide vessel elements, but in *U. changii* distinct spiral thickenings throughout the body of all vessel elements. Thin-walled tyloses present in most samples (see Table 6). Unbleachable dark contents present in some samples.

Vascular tracheids, intergrading with narrow vessel elements, associated with the vessel-axial parenchyma groups, with distinct spiral thickenings.

Libriform fibres 965–1600 (400–1900) μm long; thin- to thick-walled, or thick- to very thick-walled, with simple to minutely bordered pits confined to the radial walls. Simple fibre perforations observed in *U. pumila*. Gelatinous fibres common.

Axial parenchyma mainly paratracheal: vasicentric, scanty paratracheal, and intermixed with the vascular tracheids and surrounding the vessels; and in marginal 1–2 (–3)-seriate bands; rarely diffuse (see Table 6), in strands of 2–4 cells if not containing crystals, crystal-containing strands generally of 2–8(–15) cells. Simple perforations observed in *U. lasiophylla* and *U. pumila*. Storied arrangement of narrow vessels, vascular tracheids and parenchyma sometimes occurs locally.

Rays 4–10 (3–12)/mm, 1–3(–7) cells wide and up to 13 cells wide in *U. macrocarpa* (CAFw 5321), in *U. davidiana* (HEFw 82cw 844) of two more or less distinct sizes: 1–2 (–3)-seriate (rarely more than 10 cells high) and 4–6(–13)-seriate, 0.04–0.6 (0.03–1.1) mm high. Rays essentially homocellular with all cells procumbent, upright marginal cells occur sporadically. Disjunctive ray parenchyma cell walls present in some species. Perforated ray cells occasionally occur (see Table 6). Irregular cells with pointed outgrowths present.

Prismatic crystals present or absent (see Table 6), integumented or not, abundant to infrequent, mostly in chambered, occasionally non-chambered, axial parenchyma cells, less common to absent in procumbent ray cells. Crystal-containing cells mostly enlarged, generally with one, sometimes with 2 crystal(s) per cell. Bleachable dark contents abundant in parenchyma and ray cells, sometimes in fibres. Silica bodies absent.

**Group II — Diffuse-porous species of *Ulmus***


Evergreen or deciduous trees from subtropical to tropical regions.

Growth rings distinct in *U. lanceaefolia* and *U. tonkinensis* (CAFw 6813), marked by marginal parenchyma bands and locally inflated multiseriate rays. Vessels diffuse, 36–50 (12–71)/sq.mm, 20 (3–39) % solitary, remainder mainly in clusters of 3–4 (–11), and in radial pairs or multiples of 3(–9) and oblique pairs, round to oval, tangential diameter 100–135 (75–200) μm, radial diameter up to 180 μm, walls 3–7 μm thick. Vessel element length 290–310 (170–440) μm. Perforations simple in horizontal to slightly oblique end walls. Intervessel pits nonvestured, alternate, round to oval, and polygonal in *U. tonkinensis* (CAFw 6813), 7–9(–10) μm in diameter (see Table 6), with round to oval and slit-like, often coalescent
apertures. Vessel-ray and vessel-axial parenchyma pits simple or with reduced borders, small, rounded, sometimes horizontally elongate and unilaterally compound in *U. tonkinensis* (CAFw 6813). Spiral thickenings present, distinct in narrow vessels, faint to absent in wide vessel elements, but in *U. lanceaeefolia* such thickenings present throughout body of all vessel elements. Thin-walled and sclerotic tyloses present (see Table 6). Unbleachable dark materials present in *U. tonkinensis* (CAFw 6813).

Vascular tracheids very rare to absent.

Libriform fibres 1420–1680 (850–2010) μm long, thick- to very thick-walled, with simple to minutely bordered pits confined to the radial walls. Simple perforations present in all species, especially common in *U. tonkinensis* (CAFw 6813).

Axial parenchyma vasicentric, scanty paratraceal, and in 1–2-seriate (in *U. lanceaeefolia* up to 10-seriate) marginal bands, rarely diffuse (see Table 6), in strands of 2–4 cells if not containing crystals, crystalliferous chains of 2–8(−24) chambers. Simple perforations observed in *U. tonkinensis* (CAFw 6813). Sometimes local storying of narrow vessels, vascular tracheids and parenchyma.

Rays 8–10 (5–12)/mm, 1–4(−8) cells wide, 0.03–0.8 mm high. Rays essentially homocellular with all cells procumbent, marginal upright cells occur sporadically. Disjunctive ray parenchyma cell walls present in *U. tonkinensis*. Non-enlarged perforated ray cells occasionally occur in *U. lanceaeefolia*. Irregular cells with pointed outgrowths present.

Prismatic crystals present (see Table 6), integumented or not, abundant, mostly in chambered axial parenchyma cells, crystalliferous chains of up to 24 chambers, less common to absent in procumbent ray cells. Crystal containing cells often enlarged, generally with one, sometimes with 2 crystal(s) per cell. Bleachable dark contents abundant in parenchyma and ray cells, sometimes in fibres. Vitreous silica present in some small vessel elements, rarely in fibres of *U. lanceaeefolia*.

**Notes:** 1. According to Fu Liguo (personal communication), the identifications of our two samples of *U. propinqua* (Jiangxi) and *U. wilsoniana* (Guangxi) are questionable because there have been no reports of these species in Jiangxi / Guangxi. However, Xie Fuhui (personal communication) suggested that the flora of Guangxi is not completely known and these samples may represent new and legitimate records.

2. Marginal parenchyma was not reported in Chinese publications about *Ulrmus*. In agreement with our observations, Sweitzer (1971) and Wheeler et al. (1989) mentioned that most species of *Ulmus* have marginal parenchyma bands.

3. Cheng et al. (1980) described druses in *U. pumila*, and noted that druses and prismatic crystals are only present in axial parenchyma cells. However, in our two samples neither druses nor prismatic crystals occur.

4. In contrast with our observations, Sweitzer (1971) described that in *U. macrocarpa* and *U. pumila* there are vestigial bars on the perforation plates of narrow vessels and that there are no radial multiples, that in *U. macrocarpa* tyloses are absent and intervessel pitting is opposite, and in *U. uyemat­sui* crystals are present.

Zelkova Spach (Figs. 8, 9, 12, 16, 28, 33; Table 7)


Deciduous trees from temperate to tropical regions.

Growth rings distinct, marked by differences in vessel diameter, and mostly by marginal or seemingly marginal parenchyma bands and locally inflated multiseries rays as well. Wood ring-porous, earlywood pores in 1–2 discontinuous rows, round to oval, mean tangential diameter of the solitary earlywood vessels 170–245 (60–320) μm, radial diam-
Table 7. Wood anatomical diversity in *Zelkova*.

<table>
<thead>
<tr>
<th>Material</th>
<th>1</th>
<th>2</th>
<th>3</th>
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<th>5</th>
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<tbody>
<tr>
<td><em>Z. formosana</em></td>
<td>190</td>
<td>195</td>
<td>5–7</td>
<td>T</td>
<td>1425</td>
<td>5–9</td>
<td>1–6</td>
<td>0.7</td>
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<td>SPA a</td>
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<tr>
<td><em>Z. schneideriana</em></td>
<td>195</td>
<td>220</td>
<td>8–13</td>
<td>TS</td>
<td>1715</td>
<td>4–8</td>
<td>1–10</td>
<td>0.8</td>
<td>+</td>
<td>SPA a</td>
</tr>
<tr>
<td>CAFw 13685</td>
<td>245</td>
<td>245</td>
<td>–</td>
<td>TS</td>
<td>1565</td>
<td>3–6</td>
<td>1–9</td>
<td>0.8</td>
<td>–</td>
<td>SA a</td>
</tr>
<tr>
<td><em>Z. serrata</em></td>
<td>220</td>
<td>200</td>
<td>6–10</td>
<td>–</td>
<td>1600</td>
<td>3–6</td>
<td>1–8</td>
<td>0.9</td>
<td>–</td>
<td>P (SA)</td>
</tr>
<tr>
<td>CAFw 5710</td>
<td>210</td>
<td>170</td>
<td>6–8</td>
<td>TS</td>
<td>1620</td>
<td>3–7</td>
<td>1–9</td>
<td>0.5</td>
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<td>P (SA)</td>
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</tr>
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<td>+</td>
<td>S (P)</td>
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<td>5–9</td>
<td>1–6</td>
<td>0.6</td>
<td>–</td>
<td>S (P)</td>
</tr>
</tbody>
</table>

1. Average tangential vessel diameter (μm) of earlywood vessels.
2. Average vessel element length (μm).
3. Intervessel pit size (μm).
4. Tyloses; T = thin-walled tyloses; S = sclerotic tyloses.
5. Average fibre length (μm).
6. Ray frequency (/mm).
7. Ray width (number of cells).
8. Maximum ray height (mm).
10. Crystals; S = in square and/or upright marginal parenchyma cells; P = in procumbent body ray cells; A = in axial parenchyma cells; a = abundant; ( ) = rarely present or variable.

Vascular tracheids, intergrading with narrow vessel elements, associated with the vessel-axial parenchyma groups, with distinct spiral thickenings.

Libriform fibres 880–1715 (600–2070) μm long, thin- to thick-walled or thick- to very thick-walled, with simple to minutely bordered pits confined to the radial walls. Simple perforations occasionally occur (see Table 7). Gelatinous fibres present in *Z. formosana*.

Axial parenchyma abundant, mainly paratracheal, vasicentric, confluent, scanty paratracheal in earlywood, in latewood intermixed with the vascular tracheids and surrounding the vessels, and in 1–3-seriate marginal bands (see Table 7); in strands of 2–4 cells, simple perforations occasionally occur (see Table 7). Local storied arrangement of narrow vessels, vascular tracheids and axial parenchyma sometimes present.

Rays 3–9/mm, 1–6(–10) cells wide, tending to be of two sizes in some samples: 1–2(–3)-seriate and 4–6(–10)-seriate, 0.07–
Table 8. Selected wood anatomical features of the Ulmaceae from China.

**Celtidoideae**

<table>
<thead>
<tr>
<th></th>
<th>1</th>
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<td><em>Trema</em></td>
<td>D</td>
<td>-</td>
<td>He</td>
<td>400-510</td>
<td>4-14</td>
<td>Vrh (an)</td>
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<td>-</td>
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<td>D</td>
<td>-</td>
<td>He</td>
<td>700-720</td>
<td>7-15</td>
<td>Vrh (an)</td>
<td>+/-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td><em>Aphananthe</em></td>
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<td>-</td>
<td>He</td>
<td>240-315</td>
<td>4-6</td>
<td>Shr iw</td>
<td>+</td>
<td>-</td>
<td>UP</td>
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<td><em>Pteroecelis</em></td>
<td>D</td>
<td>-</td>
<td>He</td>
<td>230-295</td>
<td>3-4</td>
<td>Shr iw</td>
<td>+</td>
<td>RE</td>
<td>UP(A)</td>
<td>-</td>
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<tr>
<td><strong>Celtis</strong></td>
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<tr>
<td>Group II</td>
<td>D</td>
<td>-</td>
<td>He</td>
<td>290-360</td>
<td>3-10</td>
<td>Sr(h) daw</td>
<td>+</td>
<td>-</td>
<td>USP(A)</td>
<td>±</td>
<td>+/-</td>
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<td>-</td>
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<tr>
<td>Group I</td>
<td>R(S)</td>
<td>+</td>
<td>He*</td>
<td>220-380</td>
<td>3-12</td>
<td>Sr dn</td>
<td>+</td>
<td>VTA</td>
<td>USP(A)</td>
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<td>+/-</td>
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**Ulmoidae**

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<td>Sr</td>
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<td>VTA</td>
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<td>-</td>
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<tr>
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<td>+</td>
<td>Ho</td>
<td>190-290</td>
<td>5-14</td>
<td>Sr</td>
<td>daw</td>
<td>+</td>
<td>VTA</td>
<td>A(P)</td>
<td>+/-</td>
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<td>-</td>
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<tr>
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<td>daw</td>
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<td>VTA</td>
<td>A(P)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Legends: + = character present, - = character absent, ± or () = character variable and/or intermediate between two contrasting character states. The order indicates relative abundance of a character.

1. Porosity; R = ring-porous, D = diffuse-porous, S = semi-ring-porous.
2. Latewood vessels in a wavy tangential to diagonal pattern.
4. Ray type; He = heterocellular, Ho = homocellular. * Homocellular rays occur in *C. koraiensis*.
5. Average vessel element lengths (μm).
6. Intervessel pit size (μm).
7. Vessel-ray and vessel-parenchyma pits; S = similar to the intervessel pits in size and/or smaller than the intervessel pits, V = of varying shape and size, r = with much reduced borders to simple, h = half-bordered.
8. Spiral thickenings in vessels; a = very faint, i = fine, d = distinct, w = present in all vessels, n = confined to narrow vessels.
10. Storied structure; RE = rays and axial elements irregularly storied, VTA = narrow vessel elements, vascular tracheids and axial parenchyma sometimes locally storied.
11. Crystal location; U = in upright ray cells, S = in square ray cells, P = in procumbent ray cells, A = in axial parenchyma cells.
12. Sheath cells.

0.8 (0.04–1.1) mm high. Rays both heterocellular and homocellular, heterocellular rays composed of procumbent body ray cells and 1–2(–3) row(s) of square to upright marginal cells; in *Z. serrata* mostly homocellular with all ray cells procumbent. Disjunctive parenchyma cell walls present in *Z. formosana* and *Z. sinica*. Very small perforated ray cells occasionally occur (see Table 7).

Crystals present in all species, integumented and prismatic, infrequent to abundant, usually in non-chambered upright and square ray cells, and/or procumbent ray cells, and/or chambered axial parenchyma cells (in
chains of up to 8 chambers) (see Table 7); crystal-containing cells mostly enlarged, with one crystal per cell. Silica bodies absent.

Notes: 1. Sweitzer (1971) noted only fibre-tracheids (fibres with bordered pits) in his material. We observed only libriform fibres as did Cheng et al. (1985).

2. The above description of ray type agrees closely with that of Japanese Zelkova by Sweitzer (1971), however, not with that of Chinese Zelkova by Cheng et al. (1985). The latter authors refer to ray type as heterocellular III (with one row of square to upright marginal cells). Kanehira (1921a, 1921b) referred to the ray type as predominantly homocellular.

3. Yang and Huang-Yang (1987) noted sheath cells and half-bordered vessel-ray pits in their material. Metcalfe and Chalk (1950) also described rays with sheath cells in some species of Zelkova.

4. Marginal parenchyma bands have never been reported in Zelkova before.

Discussion

Taxonomic and phylogenetic implications

Although the Ulmaceae as a family are diverse in wood anatomy, there are many characters pervading the entire group. These include mostly exclusively simple perforations; alternate, nonvestured intervessel pits; relatively short vessel elements and fibres; non-septate fibres with simple to minutely bordered pits confined to the radial walls; mainly paratracheal parenchyma; rays rarely higher than 1 mm. However, two subfamilies, the Ulmoideae and the Celtidoideae, can be distinguished on the basis of differences in wood anatomy, mainly in ray structure (Table 8). Genera in the Ulmoideae have exclusively homocellular rays or a mixture of homocellular rays and heterocellular rays, while genera in the Celtidoideae have heterocellular rays. Sheath cells are absent from the Ulmoideae, but are present in some Celtidoideae, particularly in the wider rays. All Ulmoideae have vessel-ray parenchyma pits similar in size and shape to or slightly smaller than the intervessel pits, while some Celtidoideae have vessel-ray parenchyma pits of varying size and shape. However, the promotion of the two subfamilies to family level as suggested by Grudzinskaya (1967) and Chernik (1975, 1980, 1981, 1982) is not supported by wood anatomy, because of the many anatomical characters common to both subfamilies. Moreover, there are transitional forms between Celtidoideae and Ulmoideae: Zelkova and Hemi­pitelea have both homocellular and heterocellular rays and resemble ring-porous species of Celtis; C. koraiensis has some homocellular rays. In some non-wood anatomical characters Ampelocera and Aphananthe are inter­mediate between the Celtidoideae and Ulmoideae.

Our study provides some support for the placement of genera by Grudzinskaya (1967). She placed Hemi­pitelea and Zelkova in the ulmoid group, whilst Hutchinson (1967) placed them in the Celtidoideae. There is similarity between ring-porous Celtis species and Hemi­pitelea and Zelkova, but homocellular rays regularly occur in the former two genera and their wide rays lack sheath cells, characters which we suggest ally them with the Ulmoideae, rather than with Celtidoideae.

The Ulmaceae, and in particular the Ulmoideae, should be considered specialised in their wood anatomy. Derived characters, in the Baileyan sense, include the mostly simple perforation plates, alternate intervessel pits, relatively short vessel elements and fibres, rays with a tendency to homogeneity, axial parenchyma occurring in groups (alliform, confluent, confluent-banded, marginal bands); vessels in a wavy tangential to diagonal pattern and associated with vascular tracheids in many species; and storied structure in some species. Wood anatomy does not support Giannassi’s (1986) suggestion, based on flavenoid chemistry, that Ulmoideae are primitive relative to Celtidoideae. Gironniera and Trema (Celtidoideae) have the most primitive wood anatomy of any of the Ulmaceae; their rays are markedly heterocellular, conforming to Kribs heterogeneous type I in Gironniera, and they have the longest vessel elements.

This study supports the generally accepted placement of the Ulmaceae in the order Urticales. The Ulmaceae, especially the Celtidoideae, resemble Moraceae in their wood anat-
omy, the features listed above as characteristic of the Ulmaceae also occur in the Moraceae (Tippo 1938; Metcalfe & Chalk 1950).

The genus *Gironniera* — Traditionally, the genus *Gironniera* contains two subgenera: 1) *Gironniera* (*Nematostigma* Planch.) with *G. cuspidata* and 2) *Galumpita* Blume with *G. yunnanensis* (Bentham & Hooker 1862; Engler & Prantl 1893). However, *G. cuspidata* (Blume) Planch. ex Kurz and *G. yunnanensis* H.H. Hu have been transferred to the genus *Aphananthe* as *A. cuspidata* (Blume) Planch. and *A. yunnanensis* (H.H. Hu) Phuphat. (Phuphathanaphong 1975; Soepadmo 1977). Our study supports the traditional classification because wood anatomically subg. *Galumpita* is more similar to subg. *Gironniera* than to *Aphananthe* (see Table 8). Our material of subg. *Galumpita* differs from *Aphananthe* in vessel element length, intervessel pit size, vessel-ray and vessel-parenchyma pitting, spiral thickenings, tyloses, fibre length, ray height and composition, and mineral inclusions (crystals present in *Aphananthe*, silica present in subg. *Galumpita*.) Wood anatomically *Gironniera* is more similar to *Trema* than to *Aphananthe*. The relationships of *Gironniera* can be resolved only after the study of more material of *Aphananthe*, *Gironniera*, and *Trema*. Karyomorphological and palynological features, vernation patterns and seed coat morphology all suggest that *Gironniera* may have a key role in the understanding of the evolutionary relationships between the celtoids and ulmoids (Oginuma *et al.* 1990; Takahashi 1989; Tera-bayashi 1991; Takaso & Tobe 1990; Zavada 1983). Its wood anatomy clearly allies it with the Celtidoideae.

**Ecological trends in the wood anatomy of the Ulmaceae from China**

The Ulmaceae are widely distributed in the tropics, subtropics, and temperate regions in China, as far south as 19° and as far north as 50°, from sea-level up to 2500 m, varying from evergreen to deciduous and from tall trees to small shrubs. The Chinese Ulmaceae are therefore an attractive group to test general hypotheses on ecological trends in wood structure as proposed by Baas (1986), Carlquist (1975, 1980), and others. However, because of the well-known paucity of field notes on labels accompanying wood samples in institutional wood collections, the scanty ecological information in most floristic literature on the Chinese Ulmaceae, and the relatively small number of specimens studied which may be insufficient to eliminate ‘noise’ variation due to sampling diversity, only two different ecological categories were recognised in this study for the Ulmaceae from China: 1) Subtropical to tropical (19°–32° N latitude); this group includes all diffuse-porous (and a few semi-ring-porous) samples and part of the ring-porous samples studied. 2) Temperate (above 32° N latitude); this group has only ring-porous samples.

In Figures 41–43, frequency diagrams are given for vessel element length and fibre length classes. It appears that in the temperate material vessel elements and fibres tend to be shorter than in the subtropical to tropical material. Such trends can also be retraced within individual genera in China such as *Celtis, Ulmus* and *Zelkova*, or even within individual species like *Z. sinica*, and are in full agreement with the well-established general trends (Baas 1986; Carlquist 1975, 1980).

Although vessel diameter and vessel frequency are crucial parameters for the hydraulic conductivity of wood, we can hardly analyse their ecological trends here. All diffuse-porous (including semi-ring-porous) samples studied belong to the subtropical to tropical group. In ring-porous samples with a wavy tangential to diagonal pattern and vascular tracheids in latewood, it is too difficult, as well as meaningless, to calculate the average vessel diameter and vessel frequency of whole growth rings. Figure 43 shows that in both groups the average tangential vessel diameter of earlywood pores tends to have a similar frequency distribution.

Some qualitative characters tend to differ between tropical and subtropical material. As mentioned above, in the temperate samples, wood is almost always ring-porous; in the tropical samples, ring-porosity is rare. Diffuse-porosity is nearly confined to the tropical to subtropical samples. Some species, such as *C. philippensis*, can be either diffuse-porous (in tropical regions) or ring-porous (in a more seasonal environment). This in-
terspecific variation in porosity has been observed in other species, such as Planera aquatica (Ulmaceae, Sweitzer 1971). However, Aphananthe aspera is diffuse-porous in both temperate and subtropical regions, and Celtis yunnanensis and Zelkova formosana are ring-porous even though they grow in southern subtropical regions. Wavy tangential to diagonal vessel patterns in combination with vascular tracheids are also confined to extratropical latitudes. Spiral vessel wall thickenings are virtually absent in the tropical to south subtropical genera Gironniera and Trema, and well-developed in extratropical genera, being especially distinct in ring-porous Ulmaceae. Parenchyma distribution and abundance show a similar trend: marginal parenchyma is rare in Gironniera, absent in Trema, but is always abundant in ring-porous Ulmaceae. Storied structure is only absent in Gironniera and Trema and diffuse-porous Celtis (also tropical to south subtropical), while it is always present in ring-porous samples. This runs counter to the general trend for storied structure to be more common in tropical dicotyledons than in temperate ones. Related to ring-porosity to some extent, growth rings are less distinct in tropical to subtropical samples than in the temperate samples. Some of these ecological trends in qualitative wood anatomical characters (ring-

Fig. 41. Vessel element length in different latitudinal zones. Hatched = subtropical to tropical; black = temperate.

Fig. 42. Fibre length in different latitudinal zones. Hatched = subtropical to tropical; black = temperate.

Fig. 43. Earlywood vessel diameter in different latitudinal zones. Hatched = subtropical to tropical; black = temperate.

porosity; tangential to diagonal vessel pattern, vascular tracheids, and vasicentric and marginal parenchyma; storied structure; and growth rings) are also traceable within some genera in China such as Celtis, and are in basic agreement with general trends (e.g., Baas et al. 1984).

Gilbert (1940), Tippo (1938), Metcalfe and Chalk (1950) and Sweitzer (1971) have suggested that the ring-porous condition is a response to a temperate (seasonal) environment and that resulting evolution has given impetus to development of other so-called ‘advanced’
characters, such as spiral vessel wall thickenings, relatively short vessel elements and fibres. The fossil record supports these suggestions as the incidence of these characters is higher in the Late Tertiary than in the Early Tertiary (Wheeler & Baas 1991). Our study of Ulmaceae wood also tends to support this contention. In the Chinese Ulmaceae it is especially striking that all ring-porous woods possess many specialised characters such as a wavy tangential to diagonal vessel pattern, vascular tracheids, spiral vessel wall thickenings, abundant marginal parenchyma, relatively shorter vessel elements and fibres and storied structure, and are always restricted to extratropical latitudes, or seasonal environments. However, ring-porous Ulmaceae have very infrequent scalariform perforation plates with 1–2 bars and simple perforation plates with vestigial bars in some narrow vessels, while diffuse-porous woods invariably have exclusively simple perforations.

**Generic wood anatomical key to Chinese Ulmaceae**

1. Wood ring-porous or semi-ring-porous, latewood vessels in wavy tangential to diagonal bands ............... 2
2. Wood diffuse-porous to semi-ring-porous, latewood vessels not in wavy tangential to diagonal bands .............. 6
3. Rays both homocellular and heterocellular in one sample ............... 3
4. Rays either heterocellular or homocellular ....................... 5
5. Sheath cells and druses present, crystals mostly in chambered axial parenchyma cells ........... *Celtis koraiensis*
6. Spiral thickenings in vessels very fine to absent, rays markedly heterocellular with distinctly upright marginal cells, crystals mostly in upright ray cells or absent .......................... 7
7. Vessel–ray pits similar to intervessel pits in shape and size, crystals present, marginal parenchyma bands obvious .................. 8
8. Growth rings faint, vessels 12–39/mm², tangential vessel diameter smaller than 110 μm, rays and axial elements irregularly storied, crystal containing cells mostly enlarged, tanniniferous tubes sometimes present ........... *Pteroceltis*
9. Growth rings distinct, vessels 2–13/mm², tangential vessel diameter larger than 120 μm, storied arrangement absent, crystal containing cells non-enlarged, tanniniferous tubes absent ........ *Aphananthe*
10. Axial parenchyma vasicentric, aliform, confluent-banded and in apotracheal bands and limited marginal lines, rays 1–4–(5)-seriate ............... *Gironniera*
11. Axial parenchyma scanty paratracheal and diffuse, rays 1–2–(4)-seriate ........ *Trema*
12. Rays heterocellular, sheath cells usually present ........... *Celtis* (Group II)
13. Rays essentially homocellular, sheath cells absent ........ *Ulmus* (Group II)

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Zhong, Baas & Wheeler — Wood anatomy of Ulmaceae from China


