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多心皮類、とくにセンリョウ科の木部組織の解剖学的研究

Anatomical Studies of Xylem of the Polycarpicae,
Especially of the Chloranthaceae

高橋 晃

Akira TAKAHASHI

要 旨

はじめに

多心皮類はモクレン目・クスノキ目・ヤマグルマ目・キンポウゲ目などからなり、最も原始的な被子植物と考えられている一群である。この中にはシキミモドキ科やヤマグルマ科などのいわゆる無道管双子葉植物が含まれている。センリョウ科は4属からなる小さな科で、そのうちのセンリョウ属は無道管双子葉類の一員とされている (Swamy & Bailey 1950)。センリョウ科はコショウ科などとの外見上の類似からしばしばコショウ目に入れられるが (Melchior 1964)、Swamy (1953) によって多隙性の節をもつコショウ目から離されて以来、一隙性の節をもつクスノキ目に入れられることが多い (Takhtajan 1980)。木部組織の形態は被子植物の系統分類を考察するうえに有用で、これまで多くの科で解剖学的研究が行われてきた。しかし、多心皮類全体での比較解剖学的研究は少なく、とくにセンリョウ科を含めた比較解剖はほとんどない。また、無道管双子葉類の木部構造は被子植物の道管進化の最初の段階を解明するのに重要な手がかりを与えるものと思われる。とくにセンリョウ属の仮道管は道管要素と仮道管との中間形であるという見方 (Carlquist 1975) もあり注目に値するが、それについての形態学的証拠は Swamy (1953) 以来ほとんど提出されていない。本研究では、センリョウ科の系統分類と被子植物における道管進化を考察するうえに必要な解剖学的知見を得ることを目的として、センリョウ科を含めた多心皮類の木部組織の比較解剖と、センリョウ属の木部の形態を調べた。本論文は5章からなり、第一章には木本性多心皮類の、第二章には草本性多心皮類の、第三章にはセンリョウ科のそれぞれ比較材解剖を、第四章には多心皮類における管状要素のサイズの比較とその進化傾向について、そして第五章にはセンリョウの茎の一次および二次木部の解剖と管状要素の形態学的・発生学的観察を取りまとめたものである。

結 果

第一章 木本性多心皮類の比較材解剖

(論文 I) Akira TAKAHASHI: Wood anatomical studies of Polycarpicae
I. Magnoliales

まず広義のモクレン目に属する24科のうち、14科36種について材解剖学的記載を行ない、それら科間における解剖学的特徴の異同を論じた。記載に先立ち茎の太さ(年令)による解剖学的特徴の変異をいくつかの種で調べ、以後の研究の参考にした。これらの科の材はすべて散孔材で、道管要素は階段状穿孔と階段状壁孔を有し、放射組織は異性型、木部柔組織は独立型、繊維細胞は繊維状仮道管であるなどの原始的特徴を多数もつが、単一穿孔の短い道管要素や随伴型柔組織、真正木繊維などの特殊化した特徴もかなりみられた。この観察をもとにして広義のモクレン目に含まれる科のグルーピングを試みた。それらを従来の木本性多心皮類の分類による4グループ:モクレン科グループ・シキミ科グループ・ヤマグルマ科グループ・クスノキ科グループと比較したところ、木部柔組織型によるグルーピングが最もよく一致し、各グループに独特の配列パターンがあるように思われた。すなわち、モクレン科グループにおいては独立帯状柔組織とターミナル柔組織;シキミ科グループにおいては随伴散在柔組織とターミナル柔組織;ヤマグルマ科グループにおいては短接線型柔組織とターミナル柔組織;クスノキ科グループにおいては随伴型柔組織が主である。

第二章 草本性多心皮類の比較材解剖

(論文 II) Akira TAKAHASHI: Wood anatomical studies of Polycarpicae
II. Ranunculales

次にキンポウゲ目の3科11種と、現在ではキンポウゲ目とは別目とされるボタン科の1種について材解剖学的記載を行ない、それら間および第一章に述べた木本性多心皮類の科との解剖学的特徴の異同を論じた。キンポウゲ科、メギ科、アケビ科の材解剖は全体として均一で、ほとんどすべての種が単一穿孔と交互状壁孔を有する短い道管要素、単壁孔を有する短い繊維細胞、さらには同性放射組織などの特殊化した構造をもち、木本性のメンバーとは大きく異

なっていた。ボタン科の材解剖は階段状穿孔の道管要素や異性放射組織など特異なもので、他3科とは異なっていた。

第三章 センリョウ科の比較材解剖

(論文 III) Akira TAKAHASHI: Wood anatomy of Hedyosmum orientale Merr. et Chun (Chloranthaceae)

(論文 IV) Akira TAKAHASHI: Comparative wood anatomy of Chloranthaceae

センリョウ科の4属5種について材解剖を行い、それらの間および第一章・第二章に述べた多心皮類の他の科と木部構造を比較した。センリョウ属以外の道管要素はいずれも階段状穿孔と階段状壁孔を有する細長い道管要素である。アスカリナ属とヒトリシズカ属の繊維細胞は繊維状仮道管であるが、ヘディオスムム属には真正木繊維をもつ種がある。木部柔組織はセンリョウ属とヒトリシズカ属では少量の柔細胞が散在しているが、後者は随伴型の傾向を示す。アスカリナ属では独立散在型および短接線型と随伴散在型で、ヘディオスムム属では随伴散在型柔組織である。このようにセンリョウ科の解剖学的特徴は属ごとに異なる傾向があるが、全般に原始的なものが多い。この結果を他の多心皮類の木部構造と比較したところ、特に木部柔組織型から、クスノキ科を中心とするグループとセンリョウ科との関係が示唆された。なかでもモニミア科およびその近縁の科(アンボレラ科・アウストロバイレヤ科・ゴモルテガ科など)とは道管要素や繊維細胞の形態・大きさおよび放射組織の形態に多くの類似点を有することがわかった。

第四章 管状要素の比較

(論文 V) Akira TAKAHASHI & Michio TAMURA: An evolutionary trend in dimension of the tracheary elements of the woody Polycarpicae

木部管状要素の長さや直径に注目し、それらにおける進化傾向を明らかにしようとした。材料として木本性多心皮類13科24種と草本性多心皮類4科8種とセンリョウ科の4属5種を用いた。木本性多心皮類のうち原始的とされて

いる種では道管要素と繊維はともに長く両者の差は小さいが、特殊化しているとされる種ではそれらは短く、差が大きいという傾向が認められる。道管要素の直径が太くなれば繊維の直径との差が大きくなる傾向はみられるが、これに従わない場合も多い。直径と長さに関連づけてみると、一般に道管要素は長さが短くなると直径が大きくなるが、繊維は長さが短くなっても直径はそれほど大きくなる。従って、道管要素が短くなるにつれ道管要素と繊維との差が大きくなるという傾向がみられることになる。裸子植物および他の被子植物との比較から、多くの木本性多心皮類の道管要素と繊維は長さや直径に関する植からみて原始的状态にあると考えられる。特にセンリョウ科の管状要素は、仮道管から道管要素と繊維とに至る移行段階にあることがわかった。一方、草本性多心皮類の道管要素は木本性のものに比べて長さが短い、道管要素と繊維との長さの差は小さく、またそれらの直径の差も小さい。そして他の被子植物との比較から、これらの要素は短いけれどもそれほど特殊化していないと思われた。

第五章 センリョウの木部組織の形態

(論文 VI) Akira TAKAHASHI: Morphology and ontogeny of stem xylem elements in *Sarcandra glabra* (Thunb.) Nakai: Additional evidence for occurrence of vessels

(論文 VII) Akira TAKAHASHI & Michio TAMURA: Occurrence of vessel elements in the stem of *Sarcandra glabra*

センリョウの茎における木部の詳細な解剖と管状要素の形態学的・発生学的観察を行った。後生木部要素は一般に他の部分の管状要素より太く、末端壁に階段状壁孔をもっている。それらの個体発生を調べたところ、分化の過程で細胞質が分解・消失したのち、少なくともいくつかの要素において末端壁の壁孔膜が消失し道管穿孔となることがわかった。またセンリョウ属に近縁なヒトリシズカ属のチャランの道管要素には穿孔部に膜が残るため不完全な穿孔板が生じることがわかった。したがって、道管要素と仮道管の間には明確な形態学的境界がなく、センリョウ科に見られるような最も原始的な道管要素は容易に仮道管へと移行するものと思われる。つぎに、道管が茎のどの部分にあるのか走

査型電顕を用いて一層詳しく調べた。茎には横断面でみると広い維管束と狭い維管束がある。広い維管束の後生木部要素と初期二次木部要素の階段状壁孔には壁孔膜がないが、後期二次木部要素の円形壁孔には壁孔膜がある。すなわち道管要素は階段状穿孔をもち、広い維管束の後生木部と初期二次木部に存在することがわかった。また壁孔膜の有無と管状要素の直径との相互関係を調べたところ、少なくともセンリョウでは壁孔膜の消失すなわち道管形成と管状要素の太さには明らかな関係のないことがわかった。これらの道管は生長中の若い植物体の水分通導に大きな役割を果たしているものと思われる。以上のように、センリョウの木部は以前から言われてきたような無道管ではなく、道管を有することがわかった。

考 察

解剖学的研究を進めるにあたってまず考慮しなければならないのは、種々の要因による解剖学的特徴の変異についてである。最もよく知られているのは材料の年令あるいは茎の太さによる影響である。年令が増すに従って、管状要素の長さや直径が次第に増大する、単位面積当たりの道管数が減少する、木部柔組織の量が増える、単位長当たりの放射組織数が減少する、放射組織の構成細胞に平伏細胞が増えるなどの変化があることは従来から知られている。本研究においても、まず最初に年令による影響を多心皮類のいくつかの種で調べて同様の結果を得ており（第一章）、それを参考にしてその後の研究を続けてきた。次に考えられるのは生態的要因による影響である。材解剖学についての最近の報告には、たとえば緯度や高度による変異を示す結果が組み込まれるようになってきた（Oever et al. 1981, Baas et al. 1988, etc.）。しかし報告数が極めて少なく、このことは材解剖学にとって今後の重要な課題である。筆者は喬木・灌木・蔓などの樹形が解剖学的特徴に及ぼす影響に興味があり、この方面の研究を進めている。

センリョウ科はコシヨウ科などとの外見上の類似からしばしばコシヨウ目に入れられるが（Melchior 1964）、Swamy（1953）が主に節の構造によってセンリョウ科を多隙性の節をもつコシヨウ目から離して以来、今では一隙性の節をもつクスノキ目に入れられることが多い（Takhtajan 1980）。本研究の結果は

木部解剖学の立場から後者の見解を支持するものである。第四章に示したように、コシヨウ科の一種の管状要素はセンリヨウ科のものと大きく異なっていた。コシヨウ科の木部組織の解剖については近い将来報告するつもりである。

被子植物は最初無道管であり、道管は後に獲得したというのが被子植物における道管の起源についての一般的な見方である (Thompson & Bailey 1916, Cronquist 1968, Carlquist 1987, etc.)。それによると、現生の無道管双子葉類であるシキミモドキ科などの無道管木部は原始的な状態である。本研究で得られた結果はこの見解を支持する新しい知見である。多心皮類における比較材解剖 (第一章～第三章) と管状要素の解析 (第四章) とからセンリヨウ科の管状要素は道管進化の最初の段階にあることが示された。従って、センリヨウの木部で見いだされた道管要素 (第五章) は、最も原始的な道管要素すなわち仮道管から生じたばかりの道管要素の形態を示すものといえる。

双子葉植物の茎における道管の位置について、系統発生的に道管はまず二次木部に現れ、一次木部には遅れて出現する傾向があるとされている (Bailey 1944)。そして、道管要素が一次木部に存在すれば、二次木部の要素は必ず道管要素であるということが多数の種で実証されている (Bierhorst & Zamora 1965)。第五章で述べたセンリヨウの木部構造はこの一般的な傾向に合わないものである。現段階ではこの構造がどのような系統学的意味をもつのかわからないが、Baileyらの言う一般的傾向の普遍性には問題がある。また第五章にも記したように、センリヨウの道管は生長中の若い植物体の水分通導と関係していると考えられるので、そのような生理学的観点からの追求がこの問題解決に新しい手がかりを与えるものと思う。

センリヨウ属は Swamy & Bailey (1950) による初期の観察以来ずっと無道管であるとされてきた。しかしその二次木部の横断面は不均質で、Carlquist (1975) もセンリヨウの仮道管が道管要素と他の無道管双子葉類の仮道管との中間的形態をもっていると指摘したが、当時はただちに道管の発見には結びつかなかった。その後、道管を有する種で、走査型電顕による道管要素の発生学的観察が行われるようになり、無道管植物の仮道管を調べるのが可能となってきた。筆者は、仮道管の壁孔膜を調べるには走査型電顕による表面観察だけでなく、これまで行われたことの無い樹脂包埋による切片での観察が有効であ

ると考え、その手法を用いてセンリョウの道管を見いだした。センリョウに道管が存在するということは管状要素の進化を考察するうえに重要な知見である。今後、形態の比較だけでなく、壁孔膜の発生に伴う生理的変化についてもセンリョウの道管要素と仮道管を比較することが必要である。また他の無道管双子葉類でも同様の方法を用いた研究が必要で、まずヤマグルマとテトラセントロンにおいて、一次木部の仮道管の構造を調べ比較しようと思う。

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Chapter 1.

Comparative Wood Anatomy
of Woody Polycarpicae

Wood Anatomical Studies of Polycarpicae

I. Magnoliales

Synopsis

The wood structure of 30 species belonging to 24 genera of 14 families of the Magnoliales (*sensu lato*) were examined and described. Photographs were shown for 26 species. Although the wood anatomy of the Magnoliales shows a wide variety, it seems that each family of the order has its own wood structure. The Magnoliales is generally divided into 4 groups of families and each group has considerable diversity in wood anatomy. Then it seems that the structure of the tracheary elements or the ray tissues can not characterize the groups, but the distribution patterns of the axial parenchyma are characteristic of each group.

Introduction

The Polycarpicae is considered to have many primitive characteristics, such as indistinguishable petals and sepals, many free carpels and laminar stamens arranged helically on an elongated floral axis. The Polycarpicae is an interesting group for considering the phylogeny of the angiosperms. HUTCHINSON¹⁾ divided dicotyledons into a woody group and a herbaceous one. The Polycarpicae was also divided into two groups. Although separation based on habit is an artificial classification, the woody and herbaceous groups in the Polycarpicae are regarded as natural groups. Most of the woody families have ethereal oil cells and monocolpate pollens, on the other hand, oil cells are absent and pollen grains are tricolpate in the many herbaceous families. In general the families of woody Polycarpicae are collectively in the order Magnoliales²⁾, although TAKHTAJAN^{3, 4)} subdivided it into 6 orders, i.e. Magnoliales, Illiciales, Laurales, Trochodendrales, Cercidiphyllales, and Eupteleales. In his Laurales, the Chloranthaceae and Lactoridaceae, which were classified in the Piperales by MELCHIOR⁵⁾, are included. TAMURA⁶⁾ makes these 6 orders into the Magnoliales. In this paper wood

anatomical investigations are carried out within the Magnoliales *sensu* TAMURA, which consists of 24 families.

With respect to the wood anatomy of the Magnoliales, many studies have been carried out in each family. It is known that there are many features which are generally considered to be primitive on the basis of the general trends of structural evolution of dicotyledonous woods⁷⁻¹³): for example, the vesselless woods of the Winteraceae, Trochodendraceae, and so on, the slender vessels with scalariform perforation plates, the fiber-tracheids with conspicuously bordered pits, and the ray tissues of KRIBS's Heterogeneous Type I¹¹). On the other hand, some families of the order have vessels with simple perforation plates, fibers with simple pits, or homogeneous rays. These are the advanced features according to the above stated general trends of structural evolution. Thus, the Magnoliales (*sensu lato*) shows a considerable diversity in the wood anatomy. Although some wood anatomical studies cover many families in this group¹⁴⁻¹⁶), further work is necessary.

In the present study, the descriptions and photographs of the woods of many species of the Magnoliales are shown and some of the anatomical features are compared within and between the families. Moreover, relation between the anatomical features and the thickness of stem is briefly investigated in several species.

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Materials and Methods

A total of 41 wood samples representing 30 species belonging to 24 genera of 14 families of the Magnoliales were examined. The wood samples were prepared from material which was collected in the field or obtained from cultivated plants or herbarium specimens. All the samples were boiled and stocked in glycerin water.

Three dimensional sections were cut on a sliding microtome. Macerations were prepared with JEFFREY's fluid. Sections and macerations were stained with safranin or safranin-fastgreen combination.

Source and stem diameter of each wood sample examined were recorded in each of the descriptions. Quantitative data, such as length, diameter, and wall thickness of imperforate

and perforate tracheary elements, ray sizes, etc. are based on 30 measurements per feature. Number of pores per sq. mm and number of rays per mm are based on 10 measurements per feature. Measurements of element length were obtained from macerated materials.

Results

Descriptions of wood of species

WINTERACEAE

Belliolum sp.

Habit: Small tree

Material: 14 mm in diameter, twig collected by M. TAMURA in New Caledonia (Tamura 27303). (Figs. 1-6)

Wood non-porous. Growth rings indistinct. Tracheids arranged in regular, sometimes irregular, radial rows; square or polygonal in cross section; 10-50 μm in tangential and radial diameters; walls 2.5-4.5 μm thick; 1850-3700 (mean 2847) μm long. Bordered pits circular, 5-7 μm in diameter; arranged in uni- or biseriate rows; with oblique lenticular apertures. Helical thickenings invisible. Axial parenchyma sparse; diffuse and in concentric bands of 1-2 cells wide. Rays heterogeneous, uniseriate and multiseriate; 10-16 rays per mm. Uniseriate rays about 15 μm wide and 1-25 cells (250-3000 μm) high. Multiseriate rays 2-7 cells (40-150 μm) wide and mostly 1-3 mm, sometimes up to 5 mm high; with 1-8, sometimes up to 20 marginal rows of upright cells. Uni- and biseriate rays composed entirely of upright cells. Multiseriate parts composed mostly of square, sometimes procumbent cells; usually upright cells sheathing the central core. Often oil cells present.

Drimys winteri Forst.

Habit: Small tree

Material: 30 mm in diameter, stem collected by KASHIWADANI in Chile. (Figs. 7-10)

Wood non-porous. Growth rings faintly distinct. Tracheids arranged in regular, sometimes irregular, radial rows; square to polygonal in cross section; 15-50 μm and 15-60 μm in tangential and radial diameters, respectively; walls 2-4 μm thick; 1680-3250 (mean 2500) μm

long. Bordered pits circular, 7-8 μm in diameter; arranged in uni- or biseriate rows; occasionally triseriate on the overlapping end walls; with oblique lenticular apertures. Helical thickenings invisible. Axial parenchyma sparse; terminal. Rays heterogeneous, uniseriate and multiseriate; 6-10 rays per mm. Uniseriate rays 12-17 μm wide and 1-15 cells (80-1000 μm), rarely up to 30 cells (2100 μm) high; composed of upright and square cells. Multiseriate rays 2-8 cells, mostly 3-7 cells (50-150 μm) wide and 1-3.5 mm, rarely up to 5.5 mm high; with 1-18, rarely up to 30 marginal rows of upright and square cells; multiseriate parts composed of square and procumbent cells; sheathed with upright cells.

Tasmannia piperita (Hook. f.) Miers

Habit: Small tree

Material: 40 mm in diameter, stem collected by M. TAMURA in Tasmania. (Figs. 11-15)

Wood non-porous. Growth rings indistinct. Tracheids regularly arranged in radial rows; square to polygonal in cross section; 20-45 μm and 15-55 μm in tangential and radial diameters, respectively; walls 5-8 μm thick; 1600-4520 (mean 3364) μm long. Bordered pits circular, 7-10 μm in diameter; arranged in uni- or biseriate rows; with oblique lenticular apertures. Occasionally bordered pits horizontally or vertically elongated on the overlapping end walls. Helical thickenings invisible. Axial parenchyma invisible. Rays heterogeneous, uniseriate and multiseriate; 11-14 rays per mm. Uniseriate rays about 15 μm wide and 1-15 cells (200-2500 μm) high, composed usually of upright cells. Multiseriate rays 2-5 cells (40-100 μm) wide and 1.5-6.6 mm high; with 1-12, rarely up to 30 marginal rows of upright cells; multiseriate parts composed of square and procumbent cells.

DEGENERIACEAE

Degeneria vitiensis I. W. Bailey et A. C. Smith

Habit: Small tree

Material: Diameter unknown. Wood collection of MBG 731362, collected in Fiji. (Figs. 16-20)

Wood diffuse porous. Growth rings indistinct. Pores evenly distributed, 12-24 pores per sq. mm; solitary and in radial multiples of 2-3; solitary pores angular in outline; 50-120 μm in tangential diameter; walls 3-5 μm thick. Vessel members 410-1060 (mean 780) μm long; end walls moderately oblique; perforation plates exclusively scalariform with 17-32 bars. Inter-

vessel pittings predominantly scalariform. Pits to rays scalariform to transitional; unilaterally compound. Helical thickenings invisible. **Fibers** 12-44 μm in diameter; walls 3-7 μm thick; 740-2280 (mean 1533) μm long; pit borders minute or absent; pit apertures oblique slit-like; non-septate. Helical thickenings invisible. **Axial parenchyma** abundant; apotracheal bands of 1-4 cells wide. **Rays** heterogeneous, predominantly multiseriate; 3-5 rays per mm. Multiseriate rays mostly 4-6 cells (150-210 μm), sometimes up to 10 cells (350 μm) wide and mostly 300-800 μm , rarely up to 2 mm high; with 1-2 marginal rows of upright and square cells; multiseriate parts composed of both square and procumbent cells.

EUPOMATIACEAE

Eupomatia laurina R. Br.

Habit: Shrub

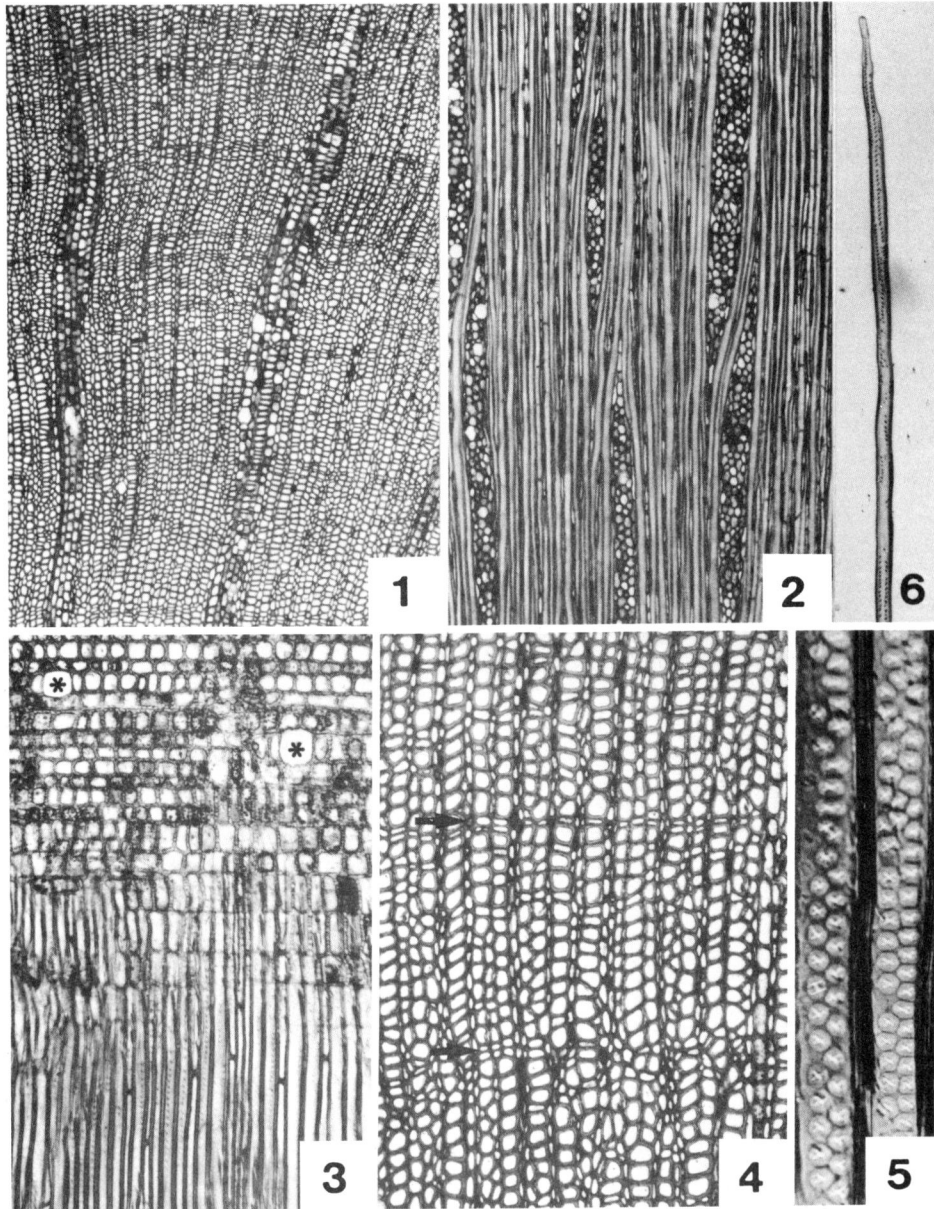
Material: 35 mm in diameter, stem collected by M. TAMURA in Australia. (Figs. 21-27)

Wood diffuse porous. Growth rings indistinct. Pores evenly distributed, 45-66 pores per sq. mm; solitary and in radial multiples of 2-4; solitary pores angular in outline; 35-65 μm in tangential diameter; walls 1.5-3.5 μm thick. **Vessel members** 680-1640 (mean 1229) μm long; end walls steeply oblique; perforation plates scalariform with 40-120 bars, occasionally anastomosing. Intervessel pits transitional to opposite. Pits to rays scalariform to opposite; unilaterally compound. Helical thickenings invisible. **Fibers** 12-40 μm in diameter; walls 4-7 μm thick; 890-2250 (mean 1572) μm long; often septate, 3-6 septa per fiber. Pits bordered, minute, 1.5-2 μm in diameter, with oblique slit-like apertures. Helical thickenings invisible. **Axial parenchyma** moderately abundant; diffuse and scanty paratracheal. **Rays** heterogeneous, uniseriate and multiseriate; 5-8 rays per mm. Uniseriate rays about 15 μm wide and 1-10 cells (150-1200 μm) high, composed of upright cells. Multiseriate rays 2-10 cells, mostly 5-8 cells (90-150 μm) wide and extremely high, 4-15 mm or more high; with 1-10 marginal rows of upright cells; multiseriate parts composed mostly of square cells, sometimes procumbent and upright cells intermingled; also upright cells sheathing the central core. Occasionally oil cells present.

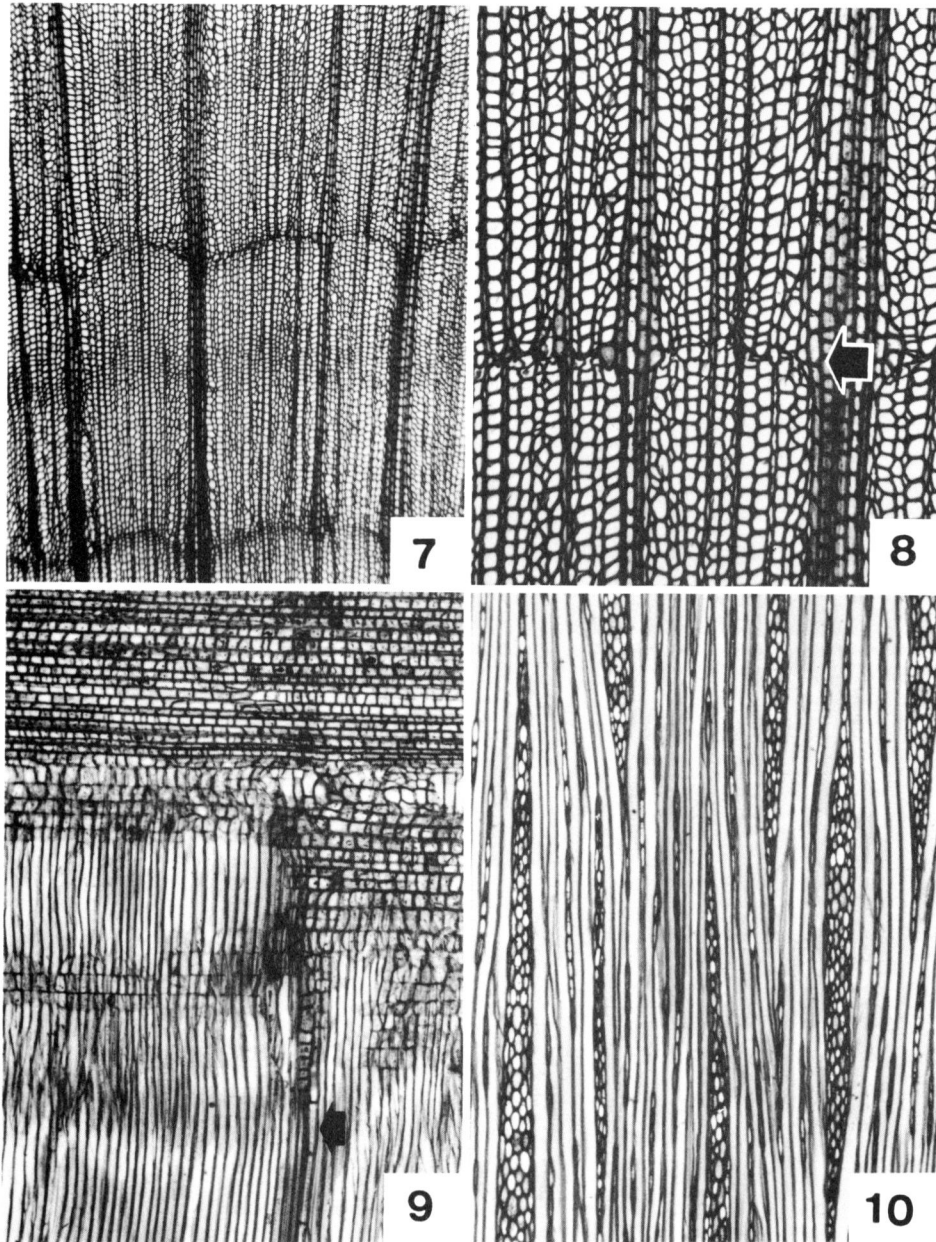
MAGNOLIACEAE

Liriodendron tulipifera L.

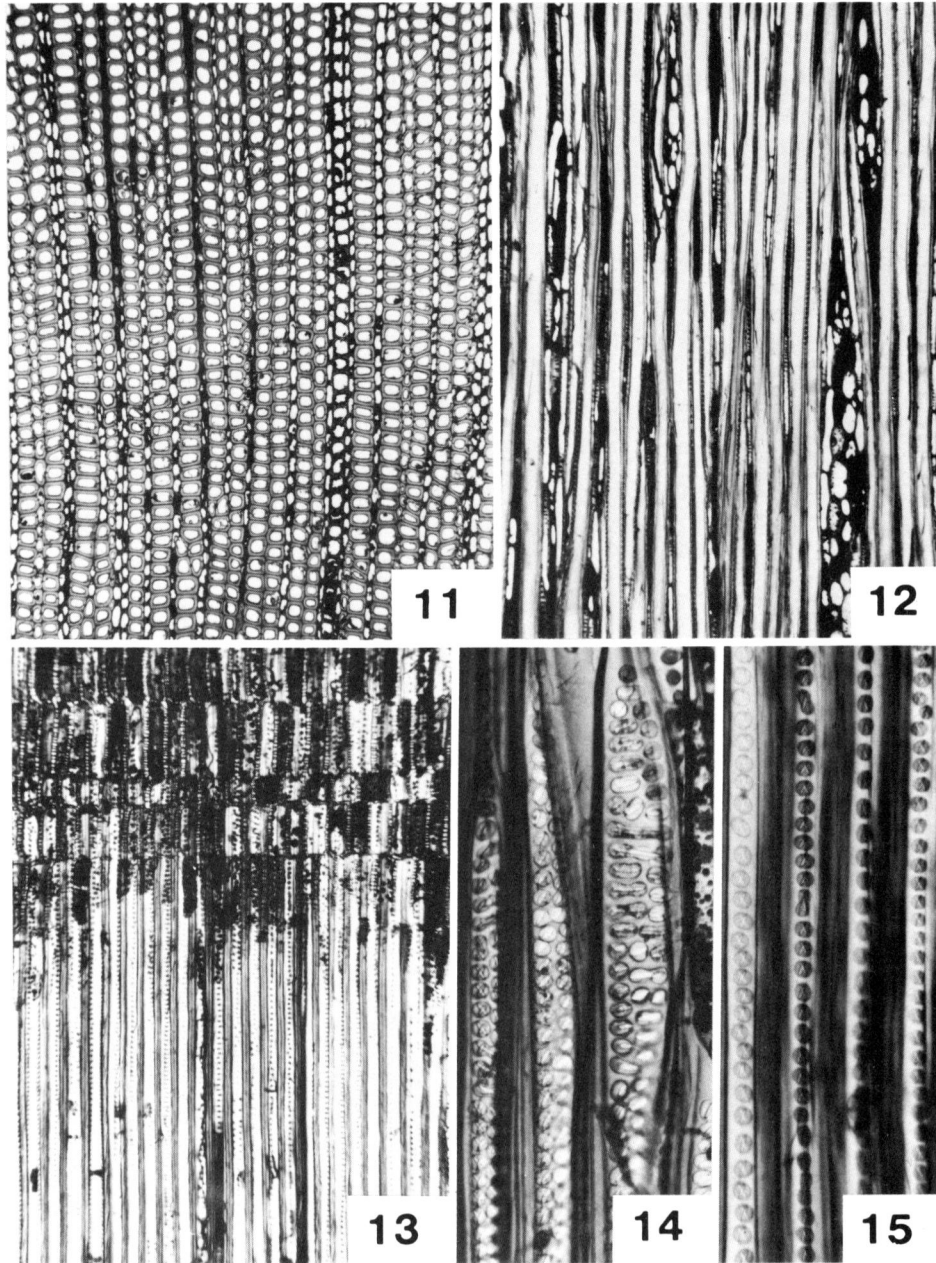
Habit: Tree



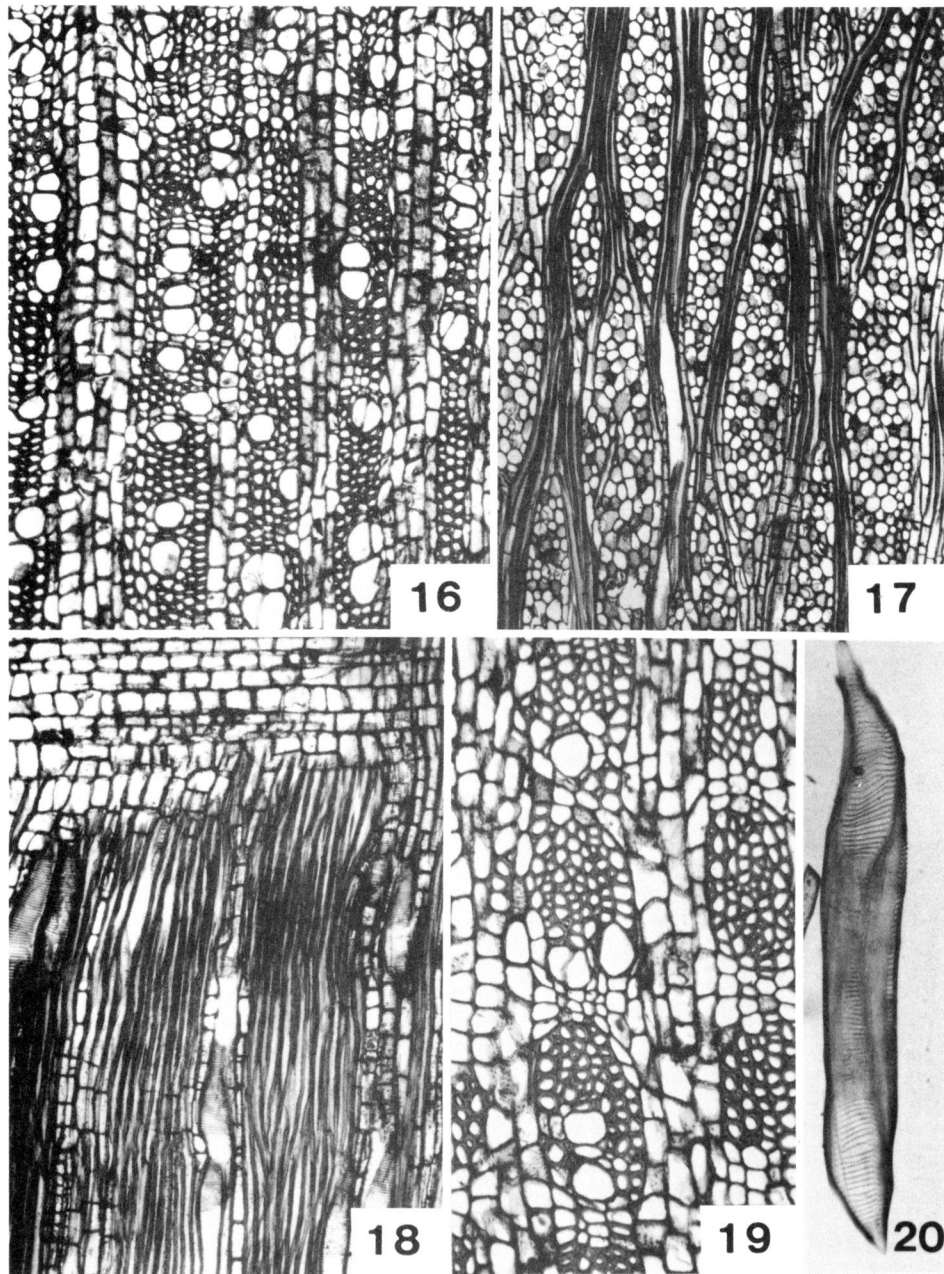
Figs. 1-6. *Belliolum* sp. 1: 1: Cross section, x40. 2: Tangential section, x40. 3: Radial section, showing two oil cells (*) in ray, x75. 4: Cross section. Arrows show concentric bands of one or two layers of axial parenchyma cells, x100. 5: Radial section, showing side wall pits of tracheids, x300. 6: Part of a macerated tracheid, x50.



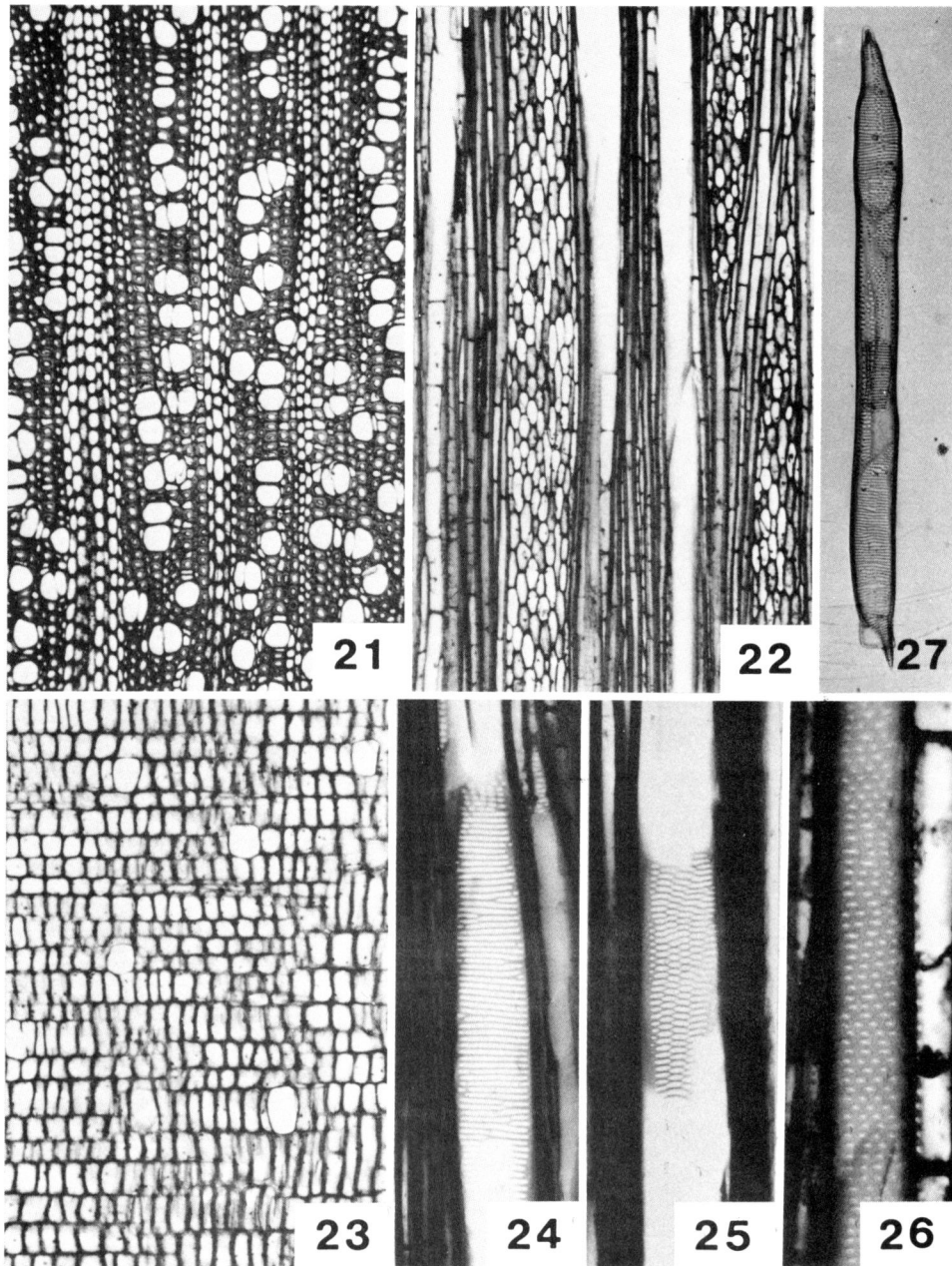
Figs. 7-10. *Drimys winteri*. 7: Cross section through three growth rings. x30. 8: Cross section. An arrow shows growth ring boundary. x75. 9: Radial section. An arrow shows axial parenchyma strand at growth ring boundary. x40. 10: Tangential section. x50.



Figs. 11-15. *Tasmannia piperita*. 11: Cross section, x75. 12: Tangential section, x75. 13: Radial section, x75. 14: Overlapping end walls of tracheids, x300. 15: Side wall pits of tracheids, x300.



Figs. 16-20. *Degeneria vitiensis*. 16: Cross section. x50. 17: Tangential section. x40. 18: Radial section. x50. 19: Cross section, showing banded parenchyma. x75. 20: Macerated vessel member. x100.



Figs. 21-27. *Eupomatia laurina*. 21: Cross section, x75. 22: Tangential section, x75. 23: Ray in radial section, showing occasional occurrence of large square cells, x75. 24: Scalariform perforation plate, x200. 25: Scalariform perforation with anastomosing bars, x200. 26: Opposite intervessel pits, x300. 27: Macerated vessel member, x100.

Material: 80 mm in diameter, stem from plant cultivated in Osaka Univ. (Figs. 28-32)

Wood diffuse porous. Growth rings distinct, delineated by several layers of radially flattened elements. **Pores** evenly distributed, 47-117 pores per sq. mm; solitary, in radial multiples of 2-5, and in clusters of 4-8; solitary pores angular in outline; 25-80 μm in tangential diameter; walls 2-3 μm thick. **Vessel members** 360-780 (mean 558) μm long; end walls moderately oblique; perforation plates scalariform with 2-8 bars. Intervessel pits transitional to opposite. Pits to rays similar to intervessel pits; often unilaterally compound. Helical thickenings invisible. **Fibers** 10-30 μm in diameter; walls 3-6 μm thick; 700-1380 (mean 998) μm long; non-septate. Pits bordered, circular in outline, 2.5-5 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. **Axial parenchyma** sparse; terminal parenchyma 2-5 cells wide. **Rays** heterogeneous, usually multiseriate, rarely uniseriate; 6-10 rays per mm. Uniseriate rays 10-20 μm wide and 2-12 cells (50-300 μm), mostly 3-7 cells (70-170 μm) high; composed of upright and procumbent cells. Multiseriate rays 2-3 cells (20-35 μm), rarely up to 5 cells (60 μm) wide and less than 1 mm, mostly 200-600 μm high; with usually 1-2, rarely up to 5 marginal rows of upright and square cells; multiseriate parts composed entirely of procumbent cells.

Magnolia salicifolia (Sieb. et Zucc.) Maxim.

Habit: Small tree

Material: 70 mm in diameter, stem collected by K. UEDA in Nagano Pref. (Figs. 33-37)

Wood diffuse porous. Growth rings distinct, delineated by several layers of terminal parenchyma. **Pores** evenly distributed, 77-96 pores per sq. mm; solitary, in radial multiples of 2-5, and in clusters of 4-8; solitary pores angular in outline; 30-70 μm in tangential diameter; walls 1.5-2.5 μm thick. **Vessel members** 330-820 (mean 593) μm long; end walls moderately oblique; perforation plates mostly simple, occasionally scalariform with 1-5 bars. Intervessel pits scalariform to transitional, rarely opposite. Pits to rays similar to intervessel pits; often unilaterally compound. Helical thickenings visible. **Fibers** 12-32 μm in diameter; walls 3.5-7 μm thick; 560-1820 (mean 1078) μm long; non-septate. Pits bordered, circular in outline, minute, 2-3 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. **Axial parenchyma** sparse; diffuse and terminal parenchyma 2-3 cells wide. **Rays** heterogeneous, mostly biseriate, sometimes uniseriate; 6-8 rays per mm. Uniseriate rays 15-20 μm wide and 2-12 cells (50-230 μm) high, composed of procumbent and upright cells. Biseriate rays 20-30 μm wide and less than 1 mm, mostly 250-600 μm high; with 1-4, rarely up to 7 marginal rows of upright and square cells; biseriate parts composed almost entirely of

procumbent cells.

Magnolia sieboldii K. Koch

Habit: Shrub

Material: 30 mm in diameter, stem from plant cultivated in Tokyo (kindly sent from Dr. T. YAMAZAKI). (Figs. 38-44)

Wood diffuse porous. Growth rings distinct. Pores evenly distributed, 56-90 pores per sq. mm; solitary, in radial multiples of 2-5, and in clusters of 4-8; solitary pores angular in outline; 30-70 μm in tangential diameter; walls 1.5-3 μm thick. Vessel members 200-860 (mean 528) μm long; end walls moderately oblique; perforation plates mostly scalariform with 4-16 bars, sometimes simple. Intervessel pits scalariform to opposite. Pits to rays similar to intervessel pits; often unilaterally compound. Helical thickenings visible. Fibers 12-35 μm in diameter; walls 2.5-4.5 μm thick; 430-1430 (mean 934) μm long; non-septate. Pits bordered, circular in outline, 2-4 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. Axial parenchyma sparse; diffuse, terminal parenchyma 2-4 cells wide. Rays heterogeneous, mostly multiseriate, sometimes uniseriate; 6-10 rays per mm. Uniseriate rays 15-25 μm wide and 2-10 cells (50-250 μm) high, composed of procumbent and upright cells. Multiseriate rays 2-3 cells (25-40 μm) wide and less than 1 mm, usually 200-500 μm high; with 1-3, rarely up to 10 marginal rows of upright and square cells; multiseriate parts composed entirely of procumbent cells.

Magnolia obovata Thunb.

Habit: Tree

Material: 15 mm in diameter, twig from plant cultivated in Osaka Univ. (Figs. 46-51)

Pores 103-127 per sq. mm; 20-55 μm in tangential diameter; walls 2-3 μm thick. Vessel members 200-600 (mean 424) μm long; perforation plates simple and scalariform with 1-8 bars. Fibers 10-30 μm in diameter; walls 2.5-4 μm thick; 540-1150 (mean 822) μm long. Rays heterogeneous, uniseriate and multiseriate; 5-10 rays per mm. Uniseriate rays up to 13 cells (270 μm) high. Multiseriate rays usually 2 cells (45 μm) wide and less than 1 mm, mostly 150-300 μm high; with up to 10 marginal rows. Otherwise similar to *Mag. sieboldii*.

Magnolia kobus DC

Habit: Small tree

Material: 10 mm in diameter, twig from plant cultivate in Osaka Univ. (Figs. 45, 52)

Pores 88-116 per sq. mm; 20-50 μm in tangential diameter; walls 1-2 μm thick. **Vessel members** 220-600 (mean 351) μm long; perforation plates mostly simple, sometimes scalariform with 1-5 bars. **Fibers** 10-30 μm in diameter; walls 3-4 μm thick; 360-960 μm long. **Rays** heterogeneous, uniseriate and multiseriate; 7-11 rays per mm. Uniseriate rays up to 10 cells (200 μm) high. Multiseriate rays 2-4 cells (40-80 μm) wide and mostly 200-400 μm high; with up to 10 marginal cells. Otherwise similar to *Mag. sieboldii*.

ILLICIACEAE

Illicium anisatum L.

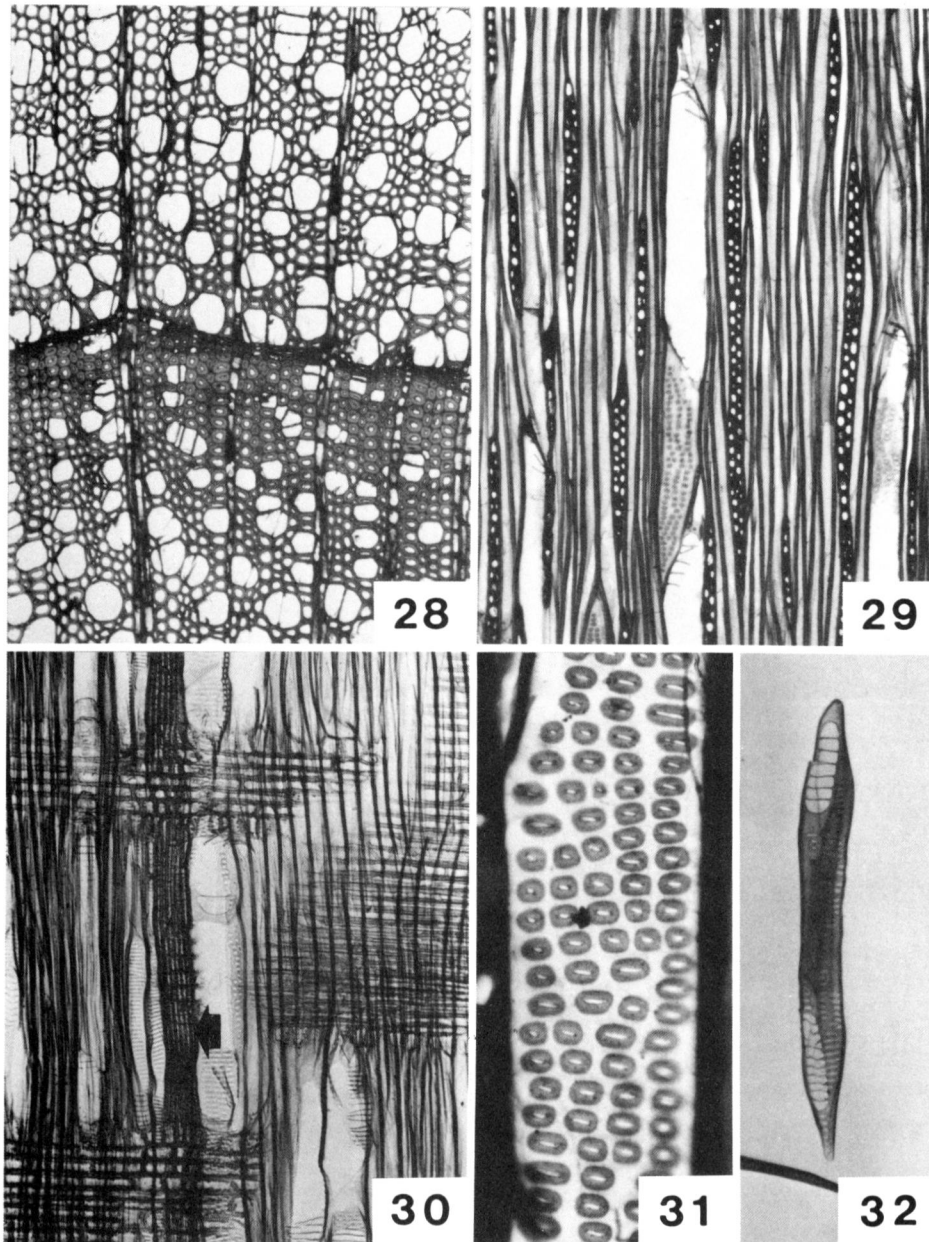
Habit: Small tree

Material: 34 mm in diameter, stem collected by K. KOSUGE in Kyoto Pref. (Figs. 53-57)

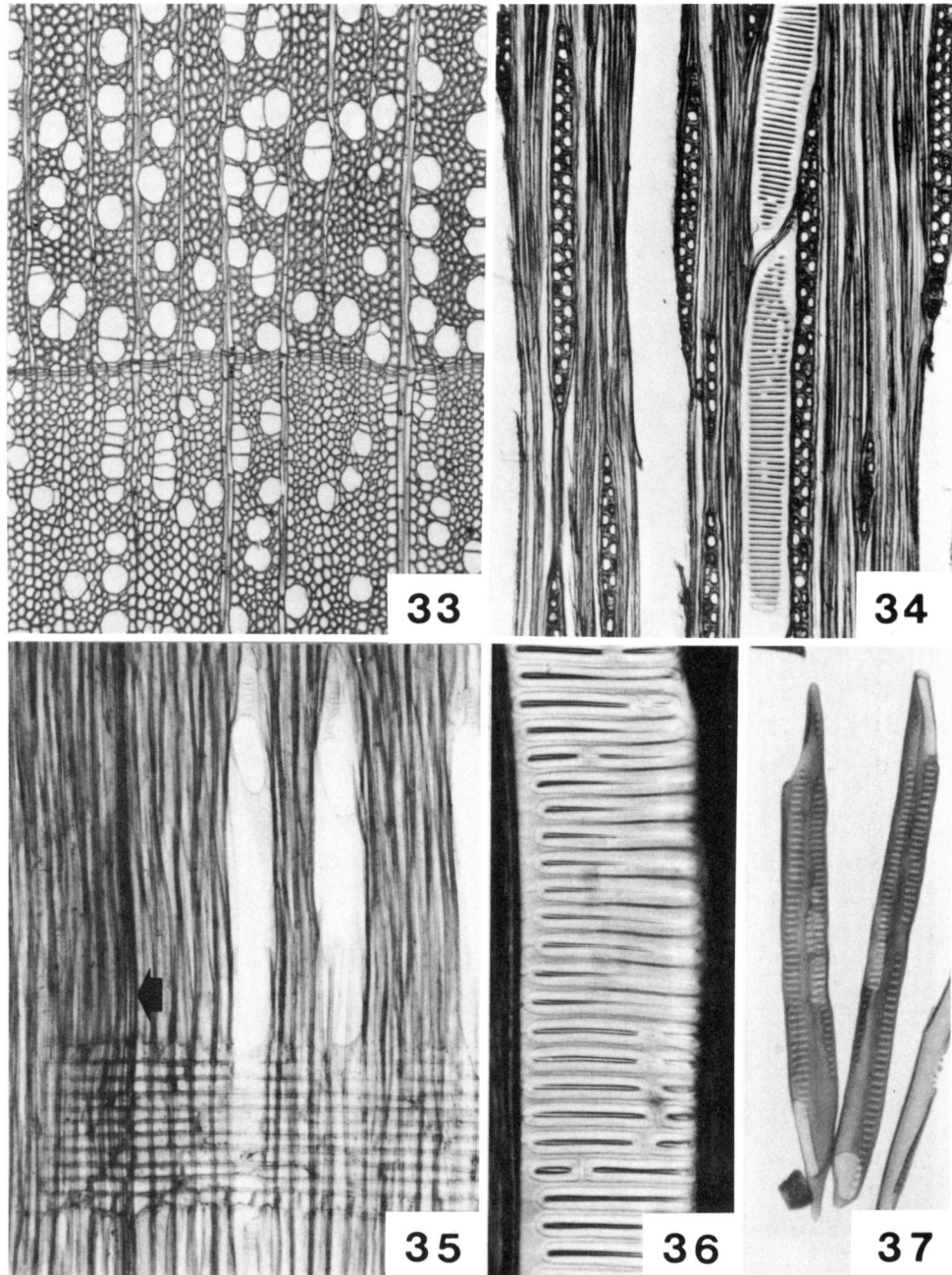
Wood diffuse porous. Growth rings distinct, delineated by 2-3 layers of radially flattened elements. **Pores** evenly distributed, 170-285 pores per sq. mm; exclusively solitary; angular in outline; 17-40 μm in tangential diameter; walls 2-3 μm thick. **Vessel members** 580-1660 (mean 1205) μm long; end walls steeply oblique; perforation plates scalariform with 35-120 bars, occasionally anastomosing. Intervessel pits rarely observed, scalariform. Pits to rays and axial parenchyma scalariform to transitional; often unilaterally compound. Helical thickenings visible, but weak. **Fibers** 12-30 μm in diameter; walls 2-6 μm thick; 600-1800 (mean 1351) μm long; non-septate. Pits bordered, circular in outline, 4-6 μm diameter; with oblique slit-like apertures. Helical thickenings invisible. **Axial parenchyma** sparse; diffuse and scanty paratracheal, with a tendency of abaxial. **Rays** heterogeneous, uniseriate and biseriate; 6-12 ray per mm. Uniseriate rays 20-25 μm wide and 1-5 cells (100-500 μm), rarely up to 10 cells (900 μm) high, composed of upright and square cells. Biseriate rays 35-45 μm wide and mostly 300-800 μm , sometimes up to 1.3 mm high; with 1-7 marginal rows of upright and square cells; biseriate parts mostly 100-350 μm high, composed almost entirely of procumbent cells.

SCHISANDRACEAE

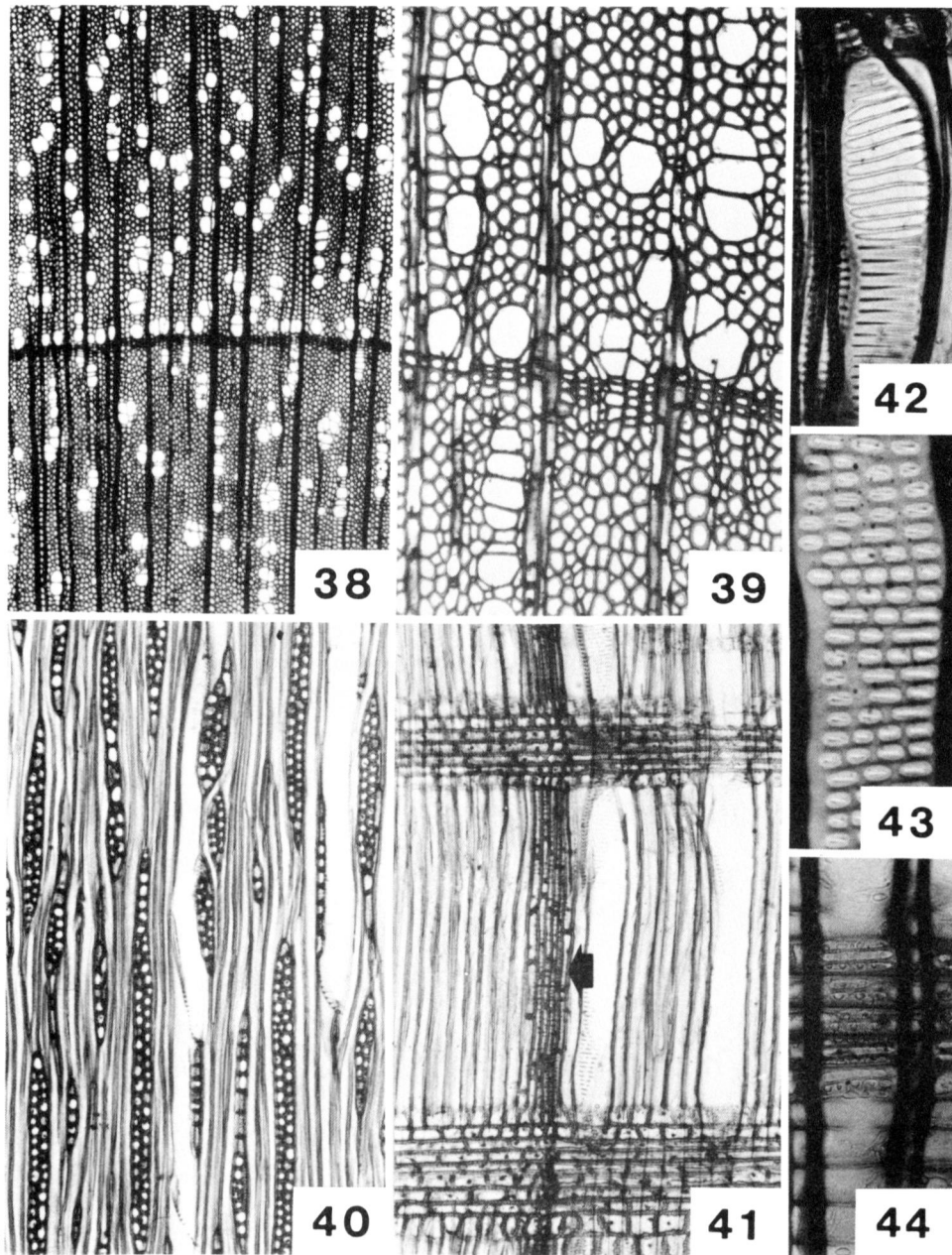
Kadsura japonica (L.) Dunal



Figs. 28-32. *Liriodendron tulipifera*. 28: Cross section through two growth rings, x100. 29: Tangential section, x100. 30: Radial section, Arrow shows terminal parenchyma, x100. 31: Opposite intervessel pits, x500. 32: Macerated vessel member, x150.



Figs. 33-37. *Magnolia salicifolia*. 33: Cross section through two growth rings. x75. 34: Tangential section. x130. 35: Radial section. Arrow shows terminal parenchyma. x100. 36: Scalariform intervessel pits. x500. 37: Macerated vessel members. x150.



Figs. 38-44. *Magnolia sieboldii*. 38: Cross section through two growth rings. x35. 39: Cross section through two growth rings. x130. 40: Tangential section. x110. 41: Radial section. Arrow shows terminal parenchyma. x110. 42: Scalariform perforation plate. x350. 43: Opposite intervessel pits. x500. 44: Vessel-ray pits; unilaterally compound. x350.

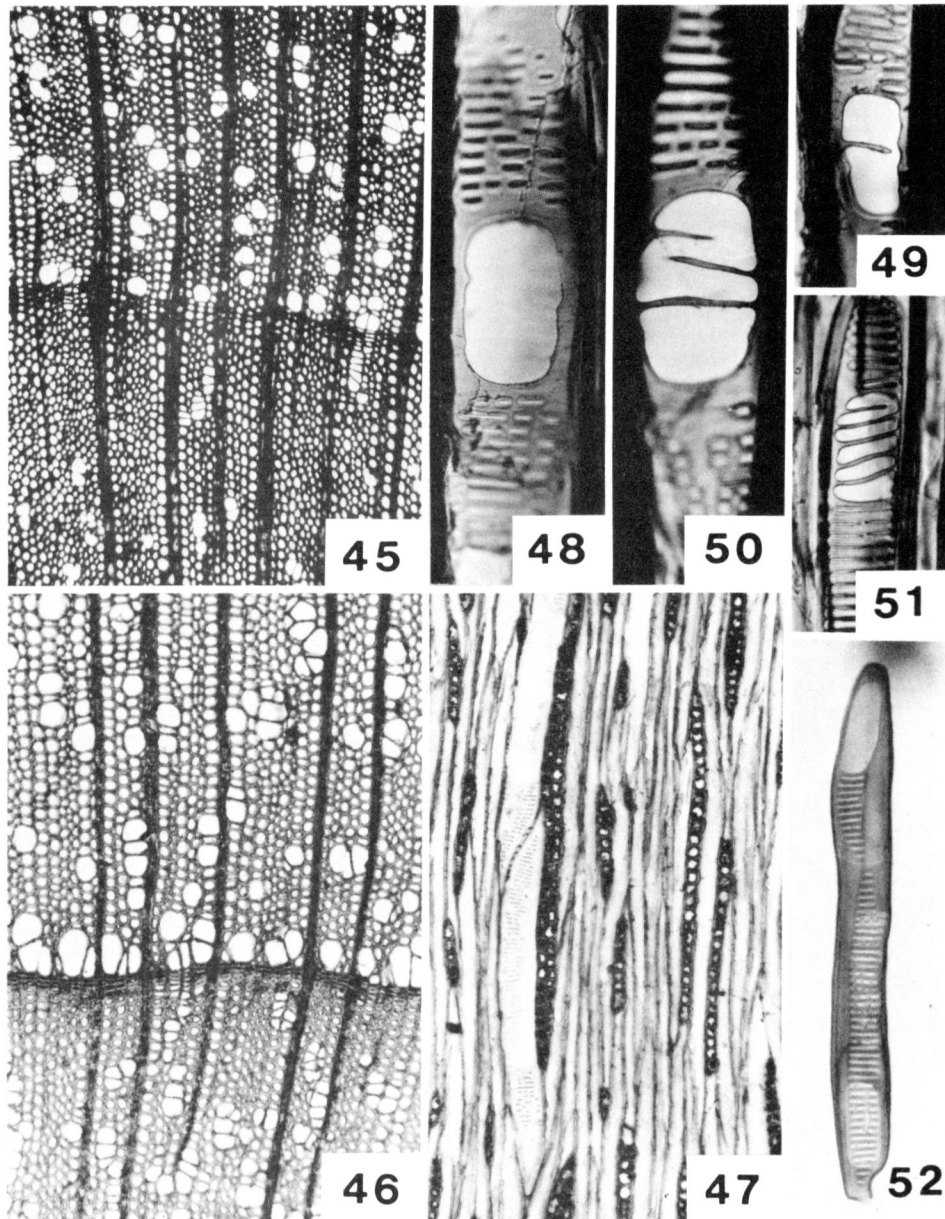
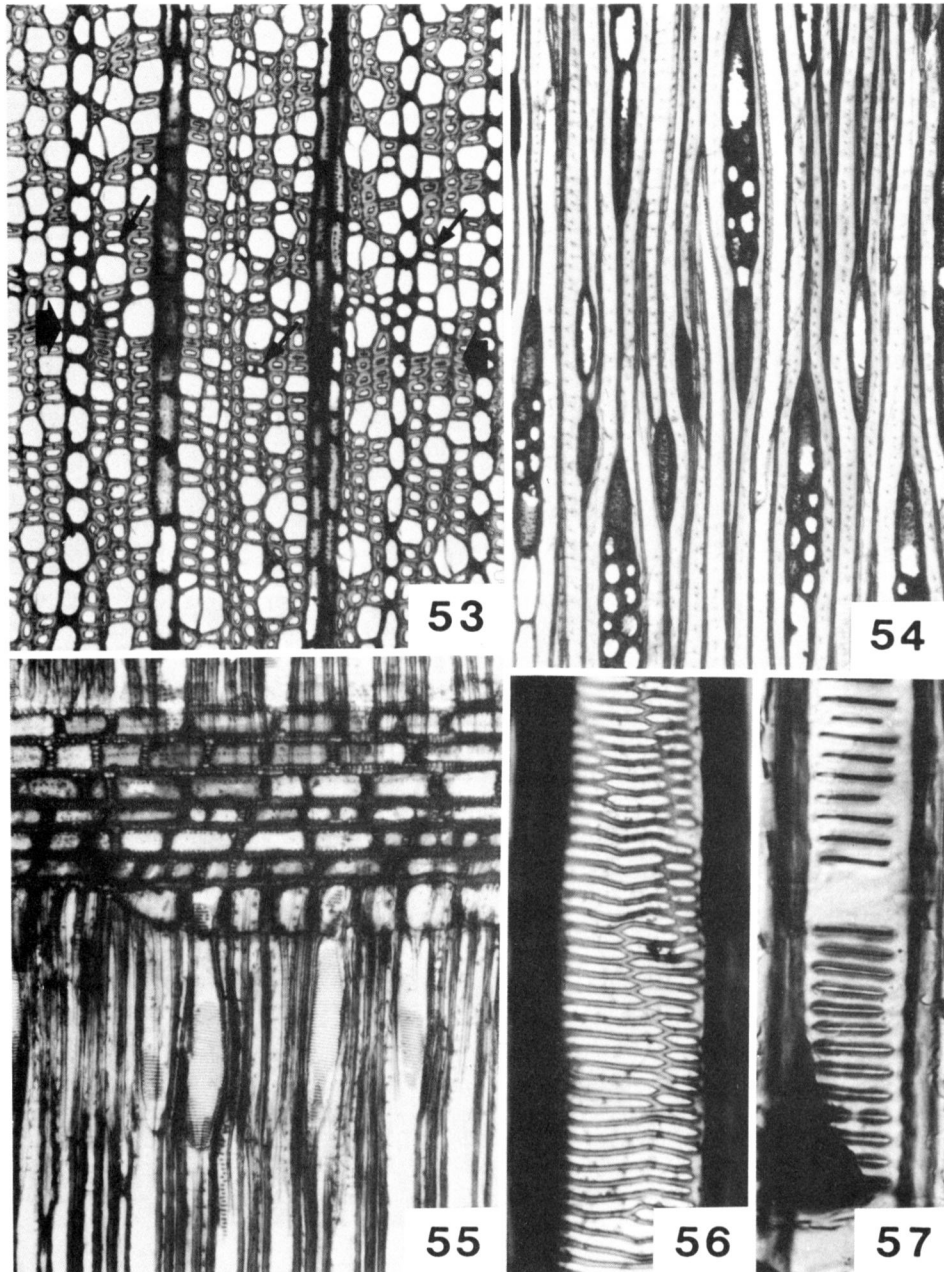


Fig. 45. Cross section of *Magnolia kobus*. x75. Figs. 46-51. *Magnolia obovata*. 46: Cross section through two growth rings. x85. 47: Tangential section. x110. 48: Simple perforation plate. x350. 49-51: Scalariform perforation plates with a few bars. x350. Fig. 52 Macerated vessel member of *Magnolia kobus*. x150.



Figs. 53-57. *Illicium anisatum*. 53: Cross section through two growth rings. Large arrows show a growth ring boundary. Small arrows show axial parenchyma cells in touch with vessels. x130. 54: Tangential section. x130. 55: Radial section. x130. 56: Scalariform perforation with anastomosing bars. x600. 57: Vessel-ray pits. x600.

Habit: Woody vine

Material: 7 mm in diameter, from herbarium specimen (Okada 412). (Figs. 58-63)

Wood diffuse porous. Growth rings invisible. Pores evenly distributed, 43-90 pores per sq. mm; predominantly solitary; angular in outline; 22-60 μm in tangential diameter; walls 1.5-2.5 μm thick. Vessel members 490-1020 (mean 738) μm long; end walls moderately to steeply oblique; perforation plates both simple and scalariform, scalariform plates with 1-25 bars. Intervessel pits rarely observed; scalariform to opposite. Pits to rays and axial parenchyma scalariform to transitional. Helical thickenings invisible. Fibers 10-30 μm in diameter; walls 3-5.5 μm thick; 570-1350 (mean 1004) μm long; non-septate. Pits bordered, circular in outline, 5-7 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. Axial parenchyma sparse; scanty paratracheal, with a tendency of abaxial. Rays heterogeneous, uniseriate and multiseriate; 11-16 rays per mm. Uniseriate rays about 15 μm wide and 1-10 cells (150-1200 μm) or more high; composed entirely of upright cells. Multiseriate rays 2-5 cells (30-60 μm) wide and mostly less than 1 mm, sometimes up to 1.5 mm high; with 1-5 marginal rows of upright cells; multiseriate parts composed of upright and square cells.

Schisandra repanda (Sieb. et Zucc.) Redlk.

Habit: Woody vine

Material: 7 mm in diameter, from herbarium specimen (Okada, Ejima & Hamada 1465). (Figs. 64-69)

Pores 40-70 per sq. mm; 30-80 μm in tangential diameter; walls 3-4.5 μm thick. Vessel members 470-1010 (mean 775) μm long. Fibers 10-20 μm in diameter; walls 5-7 μm thick; 580-1400 (mean 962) μm long; bordered pits 4-5 μm in diameter. Rays heterogeneous, uniseriate and multiseriate; 15-22 rays per mm. Multiseriate rays 2-3 cells (30-50 μm) wide and 2-3 mm or more high; with 1-10 or more marginal cells. Otherwise similar to *Kadsura japonica*.

TROCHODENDRACEAE

Trochodendron aralioides Sieb. et Zucc.

Habit: Tree

Material: 24 mm in diameter, twig collected in Shizuoka Pref. (Takahashi 287). (Figs. 70-

Wood non-porous. Growth rings distinct. **Tracheids** regularly arranged in radial rows; square in cross section in the early wood and radially flattened in the late wood; in the early wood, 12-30 μm and 12-25 μm in tangential and radial diameters, respectively; in the late wood, 12-30 μm and 8-23 μm in tangential and radial diameters, respectively; walls 1-1.5 μm and 3-5 μm thick in the early and late wood, respectively; 2000-3130 (mean 2580) μm long. In the early wood, bordered pits horizontally elongated and scalariform in arrangement; in the late wood, bordered pits circular, 5-7 μm in diameter, with oblique lenticular apertures and arranged in uni- or biseriate rows. Helical thickenings invisible. **Axial parenchyma** sparse and restricted in the late wood; diffuse and diffuse-in-aggregate. **Rays** heterogeneous, uniseriate and multiseriate; 6-11 rays per mm. Uniseriate rays 15-20 μm wide and 1-20 cells (120-1500 μm), mostly 2-12 cells (250-800 μm) high, composed of upright and procumbent cells. Multiseriate rays 2-6 cells (40-120 μm) wide and mostly 600-1500 μm , sometimes up to 2 mm high; with 1-10, rarely up to 20 marginal rows of upright and procumbent cells; multiseriate parts composed of procumbent cells; upright cells partially sheathing the central core.

CERCIDIPHYLLACEAE

Cercidiphyllum japonicum Sieb. et Zucc.

Habit: Tree

Material: 16 mm in diameter, twig from plant cultivated in Osaka Univ. (Figs. 74-79)

Wood diffuse porous. Growth rings distinct, delineated by several layers of radially flattened elements. **Pores** evenly distributed, 270-336 pores per sq. mm; exclusively solitary; angular in outline; 15-60 μm in tangential diameter; walls 1 μm thick. **Vessel members** 260-1250 (mean 850) μm long; end walls steeply oblique; perforation plates scalariform with 25-40 bars. Intervessel pits rarely observed; scalariform. Pits to rays scalariform to transitional; often unilaterally compound. Coarse helical thickenings present on both ligulated ends. **Fibers** 12-20 μm in diameter; walls 2-3 μm thick; 620-1500 (mean 970) μm long; non-septate. Pits bordered, circular in outline, 4-6 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. **Axial parenchyma** sparse; diffuse, terminal parenchyma 2-4 cells wide; diffuse cells often in touch with vessels. **Rays** heterogeneous, mostly biseriate, sometimes uniseriate; 13-19 rays per mm. Uniseriate rays 10-17 μm wide and 2-10 cells (80-300 μm) high, composed of upright and square cells. Biseriate rays 20-25 μm wide and less than 1 mm, mostly 200-500 μm high; often with two or more biseriate parts separated

by uniseriate upright cells; each biseriate part mostly 3-5 cells high, composed almost entirely of procumbent cells; with 1-5, rarely up to 10 marginal rows of upright and square cells. Occasionally crystals present in upright cells.

EUPTELEACEAE

Euptelea polyandra Sieb. et Zucc.

Habit: Small tree

Material: 14 mm in diameter, twig from plant cultivated in Osaka Univ. (Figs. 80-84)

Wood diffuse porous. Growth rings distinct, delineated by one or two layers of radially flattened elements. Pores evenly distributed, 96-140 pores per sq. mm; mostly solitary, occasionally clusters in the late wood; solitary pores angular to round in outline; 20-55 μm in tangential diameter; walls 2 μm thick. Vessel members 470-930 (mean 669) μm long; end walls steeply oblique; perforation plates scalariform with 20-75 bars. Intervessel pits transitional to opposite, rarely alternate. Pits to rays scalariform to transitional; often unilaterally compound. Helical thickenings invisible. Fibers 7-20 μm in diameter; walls 3-5 μm thick; 670-1160 (mean 932) μm long; non-septate. Pits bordered, circular in outline, about 3 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. Axial parenchyma sparse; diffuse and diffuse-in-aggregate. Rays heterogeneous, uniseriate and multiseriate; 5-9 rays per mm. Uniseriate rays 8-10 μm wide and 1-14 cells (50-700 μm), mostly 3-8 cells (150-400 μm) high; composed of upright, square, and procumbent cells. Multiseriate rays 2-5 cells (20-50 μm) wide and 200-1000 μm , rarely up to 2 mm high; with 1-4, rarely up to 10 marginal rows of upright and square cells; multiseriate parts composed of procumbent and square cells; partly sheathed with upright cells.

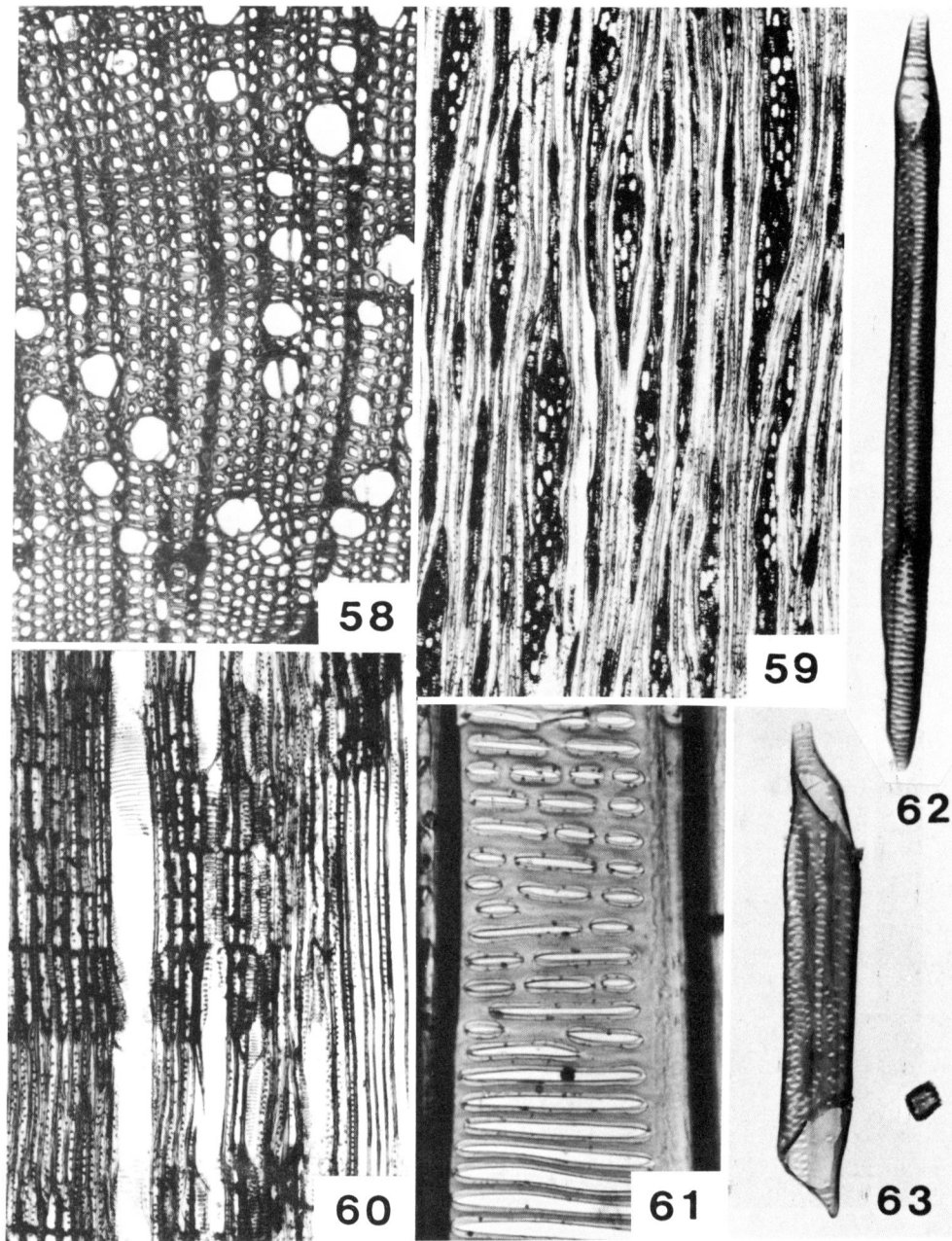
AUSTROBAILEYACEAE

Austrobaileya maculata C. T. White

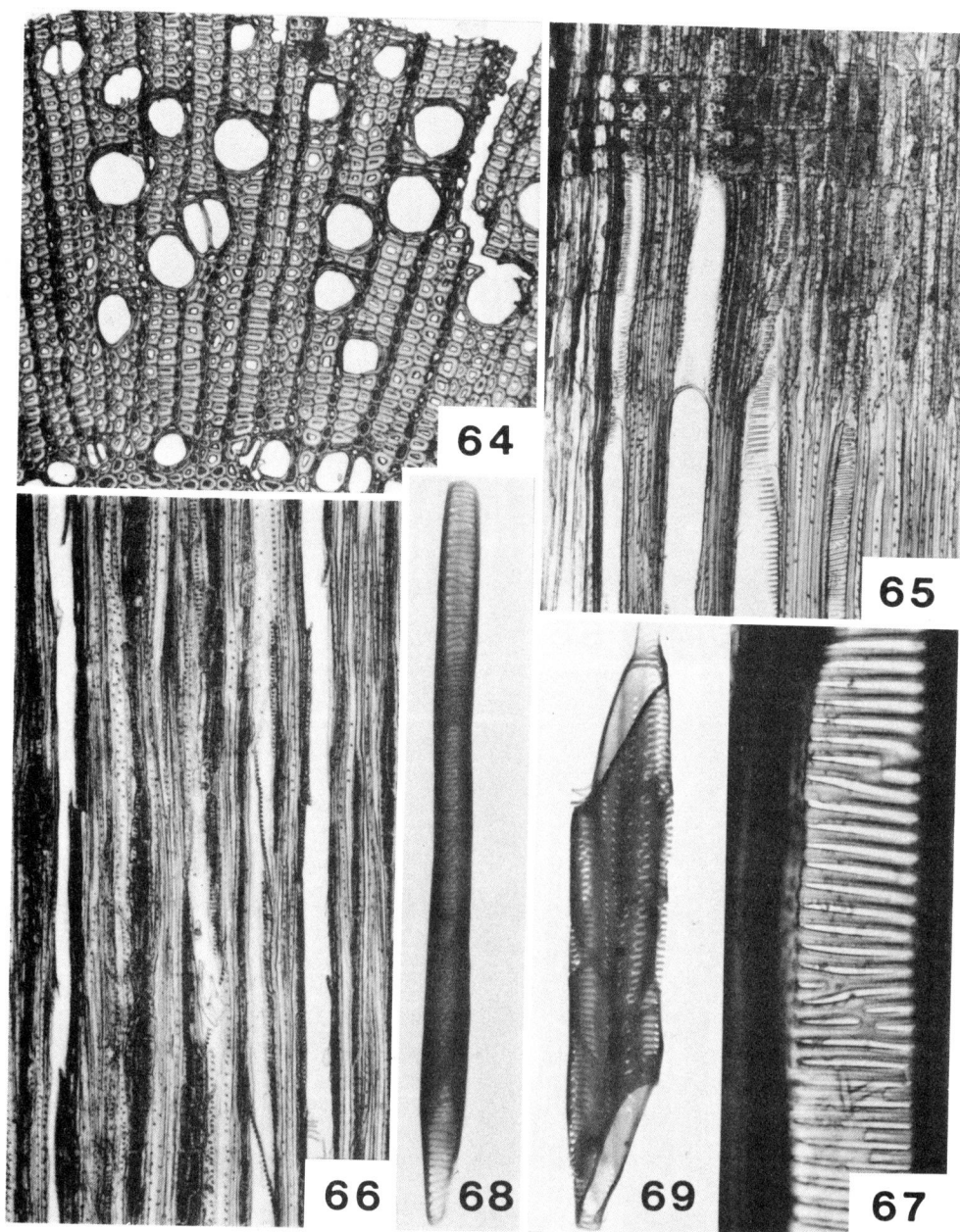
Habit: Liana

Material: 9 mm in diameter, stem collected by M. TAMURA in Queensland, Australia. (Figs. 85-89)

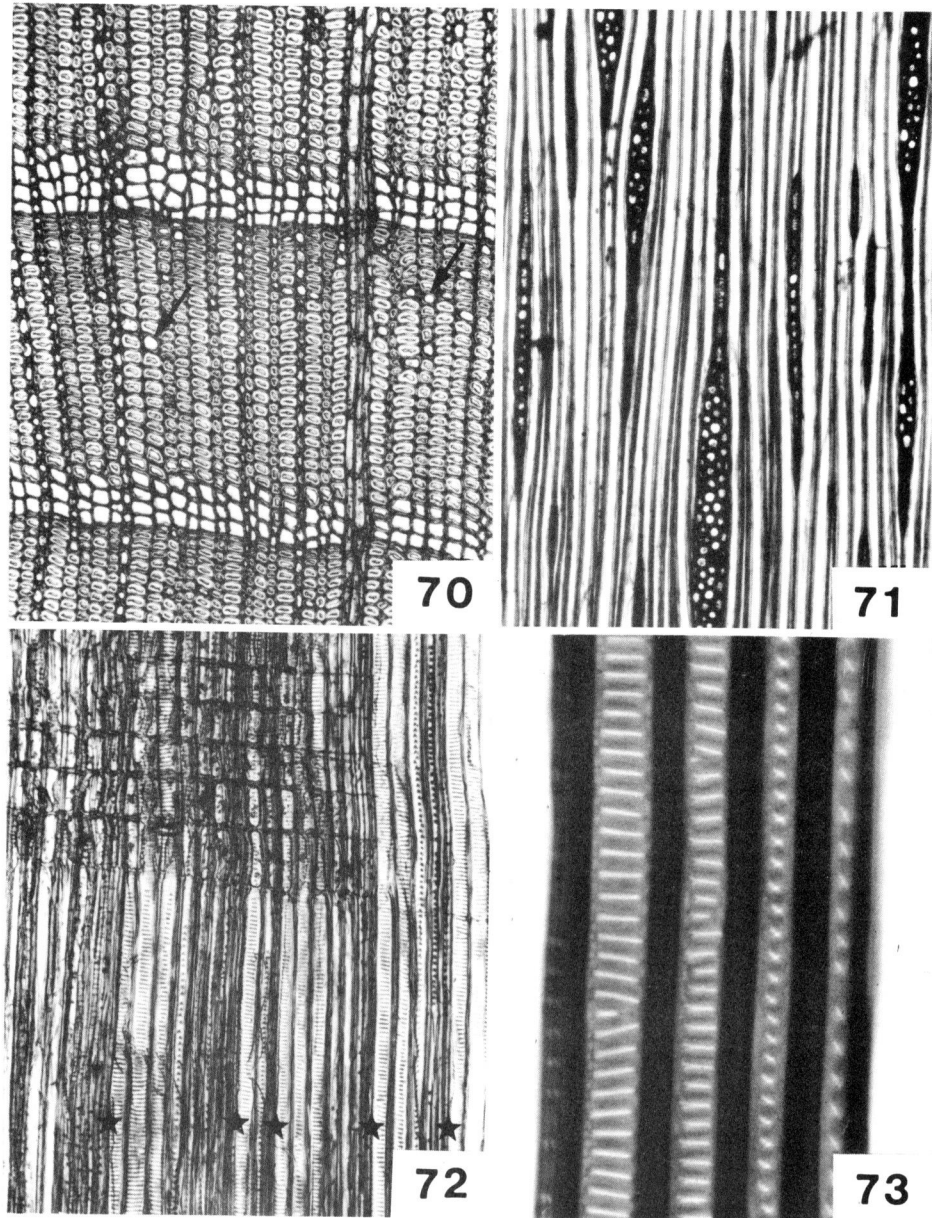
Wood diffuse porous. Growth rings indistinct. Pores evenly distributed, 22-30 pores per sq. mm; exclusively solitary; angular in outline; 32-110 μm in tangential diameter; walls 3-4 μm



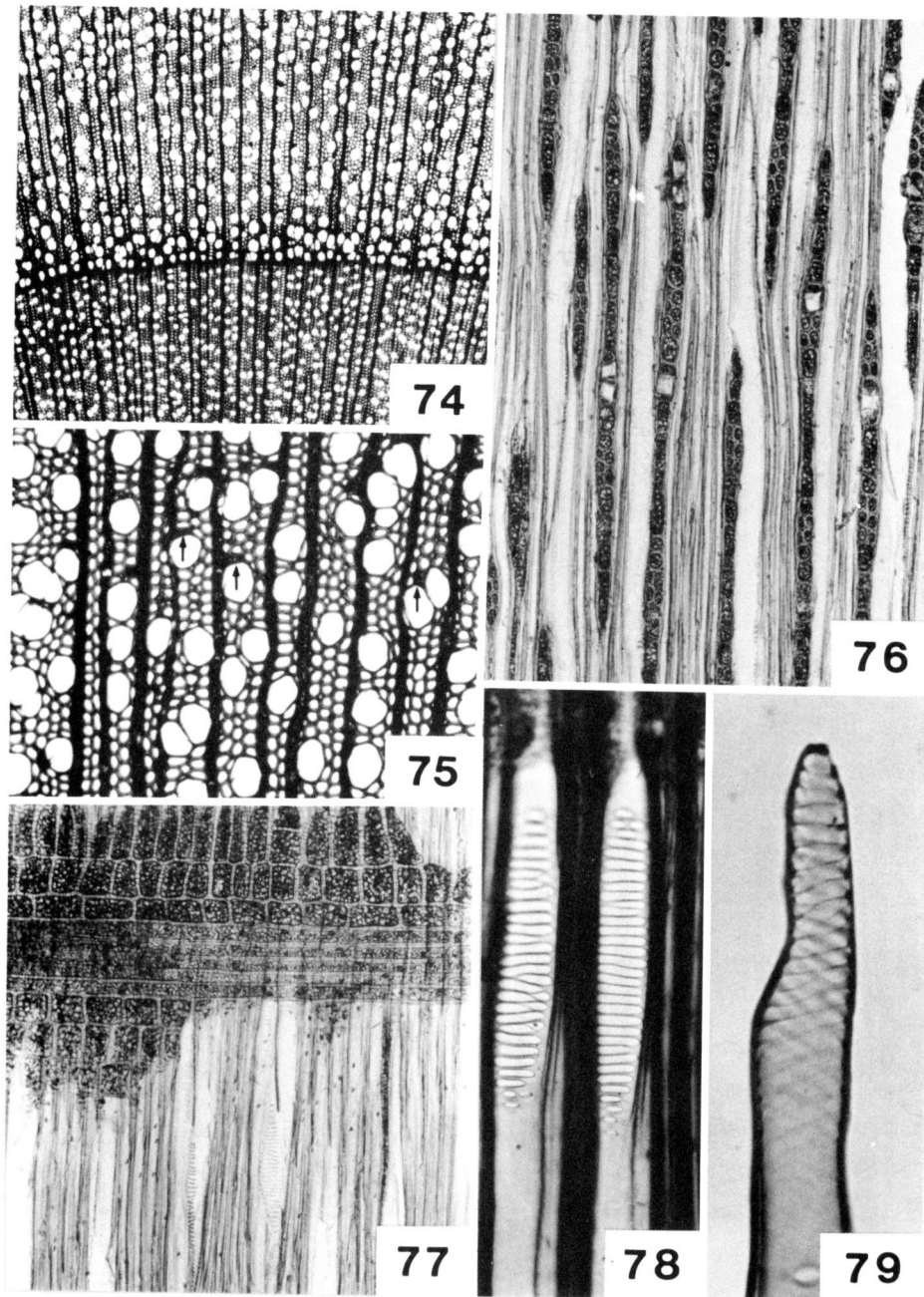
Figs. 58-63. *Kadsura japonica*. 58: Cross section. x130. 59: Tangential section. x85. 60: Radial section. x100. 61: Scalariform to opposite intervessel pits. x600. 62: Macerated vessel member; narrow. x150. 63: Macerated vessel member; large. x150.



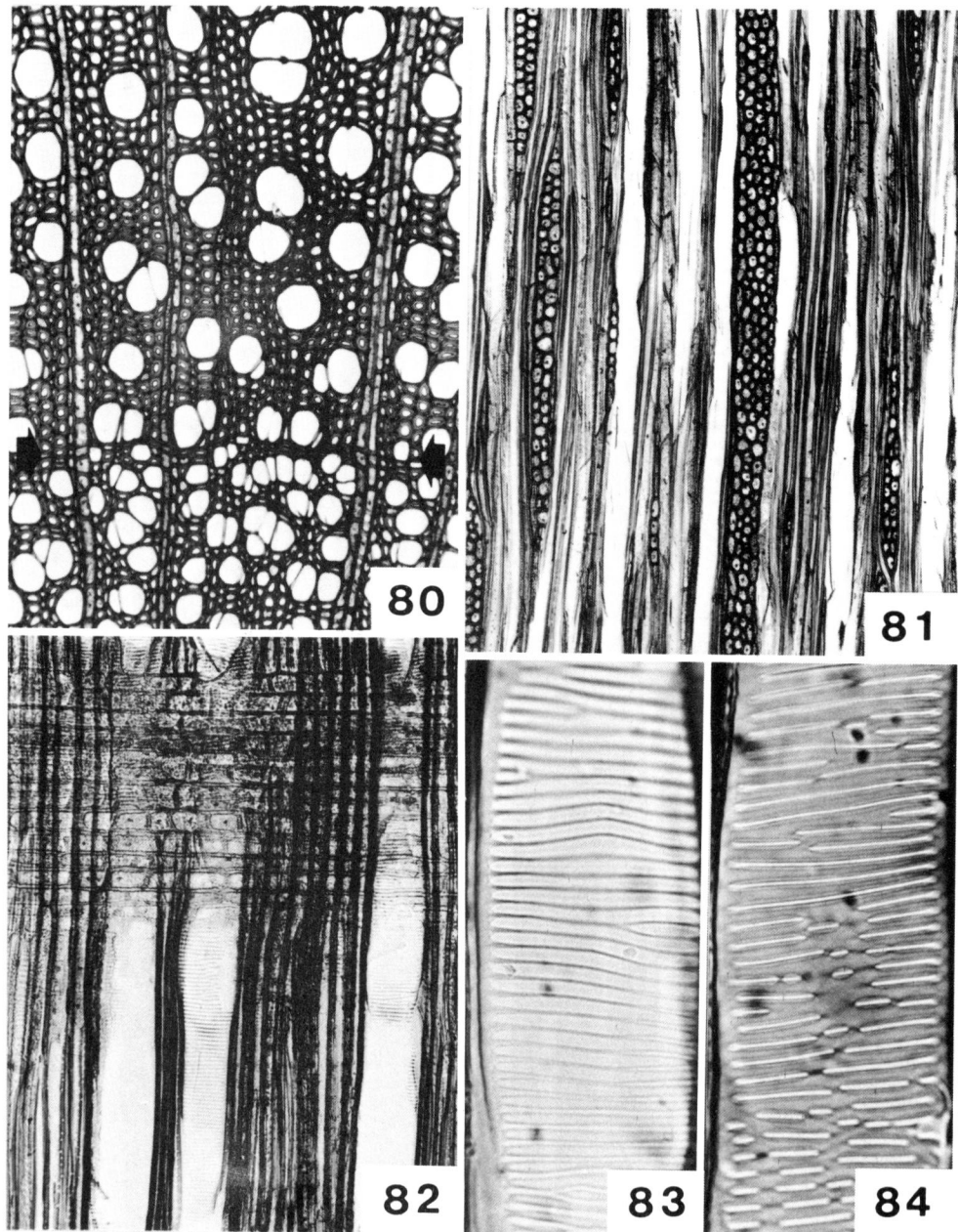
Figs. 64-69. *Schisandra repanda*. 64: Cross section. x130. 65: Radial section. x130. 66: Tangential section. x100. 67: Scalariform intervessel pits. x600. 68: Macerated vessel member; narrow. x150. 69: Macerated vessel member; large. x150.



Figs. 70-73. *Trochodendron aralioides*. 70: Cross section through three growth rings. Arrows show axial parenchyma cells scattered in the late wood. x130. 71: Tangential section. x100. 72: Radial section through six growth rings. Stars show growth ring boundaries. x130. 73: Part of Macerated tracheids, showing circular bordered pits (right) and scalariformly arranged, horizontally elongated pits (left). x600.



Figs. 74-79. *Cercidiphyllum japonicum*. 74: Cross section through two growth rings. x40. 75: Cross section. Arrows show axial parenchyma cells in touch with vessels. x130. 76: Tangential section, showing some crystals in ray cells. x170. 77: Radial section. x170. 78: Scalariform perforation plates. x350. 79: Tail of a macerated vessel member, showing helical thickenings. x600.



Figs. 80-84. *Euptelea polyandra*. 80: Cross section through two growth rings. Arrows show growth ring boundary. x130. 81: Tangential section. x100. 82: Radial section. x130. 83: Scalariform perforation plate. x500. 84: Transitional intervessel pits. x500.

thick. Vessel members 640-1200 (mean 926) μm long; end walls moderately oblique; perforation plates scalariform with 13-20 bars. Intervessel pits invisible. Helical thickenings invisible. Fibers 12-35 μm in diameter; walls 3.5-7 μm thick; 720-1640 (mean 1256) μm long; non-septate. Pits bordered, circular in outline, about 5 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. Axial parenchyma sparse; scanty paratracheal, with a tendency of abaxial. Rays heterogeneous, mostly multiseriate, sometimes uniseriate; 5-8 rays per mm. Uniseriate rays about 15 μm wide and 1-5 cells (200-2000 μm) or more high; composed of very tall upright cells. Multiseriate rays 4-8 cells (100-200 μm) wide and 2-5 mm or more high; with 1-5 or more marginal rows of very tall upright cells; multiseriate parts composed of square and upright cells, sheathed with very tall upright cells.

AMBORELLACEAE

Amborella trichopoda Baill.

Habit: Shrub

Material: 20 mm in diameter, stem collected by M. TAMURA in New Caledonia (Tamura 27301). (Figs. 90-94)

Wood non-porous. Growth rings distinct, delineated by 2-3 layers of radially flattened elements. Tracheids regularly arranged in radial rows; usually square in cross section; 15-50 μm and 10-40 μm in tangential and radial diameters, respectively; walls 3-5 μm thick; 1520-3320 (mean 2630) μm long. Bordered pits circular, 7-9 μm in diameter, or sometimes horizontally elongated, up to 20 μm ; pit apertures oblique lenticular; pits to rays smaller, 5-6 μm in diameter. Helical thickenings invisible. Axial parenchyma scarce and diffuse. Rays heterogeneous, uniseriate and multiseriate; 15-18 rays per mm. Uniseriate rays 1-30 cells (200-3300 μm) high, sometimes extremely high, up to 80 cells (8.5 mm); composed of upright cells. Multiseriate rays 2-5 cells (50-100 μm) wide and 2-7 mm high; multiseriate parts composed of upright, square, and procumbent cells; with 1-10, rarely up to 50 marginal rows of upright cells.

LAURACEAE

Cinnamomum camphora (L.) Presl

Habit: Tree

Material: 140 mm in diameter, stem from plant cultivated in Osaka Univ. (Figs. 95-98)

Wood diffuse porous. Growth rings distinct, delineated by several layers of radially flattened elements. **Pores** evenly distributed, 9-23 pores per sq. mm; solitary and in radial multiples of 2-4; solitary pores round to oval in outline; 60-140 μm in tangential diameter; walls 2-4.5 μm thick. **Vessel members** 200-530 (mean 364) μm long; end walls slightly to moderately oblique; perforation plates usually simple, rarely scalariform with a few bars. Intervessel pits alternate; each pit about 8 μm in diameter; apertures often coalescent. Pits to rays and axial parenchyma large, sometimes unilaterally compound. Helical thickenings visible or invisible. **Fibers** 12-25 μm in diameter; walls 2-4 μm thick; 350-900 (mean 618) μm long; non-septate; with simple pits. Helical thickenings invisible. **Axial parenchyma** abundant; vasicentric and aliform to confluent; occasionally oil cells present. **Rays** heterogeneous, usually multiseriate, rarely uniseriate; 5-7 rays per mm. Uniseriate rays 15-20 μm wide and 1-7 cells (40-200 μm), mostly 2-5 cells high, composed of upright and square cells. Multiseriate rays 2-3 cells (30-60 μm) wide and 100-500 μm , mostly 200-400 μm high; multiseriate parts composed almost entirely of procumbent cells; with 1-2, rarely up to 5 marginal rows of upright and square cells. Often large oil cells present at margin of rays.

Cinnamomum insularimontanum Hayata

Habit: Tree

Material: 6 mm in diameter, twig from herbarium specimen (Okada 1330).

Pores 85-120 distributed per sq. mm; 30-60 μm in diameter; walls 2-4 μm thick. **Vessel members** 260-460 (mean 376) μm long. Intervessel pits alternate; each pit about 5 μm in diameter. **Fibers** 7-25 μm in diameter; walls 1-3 μm thick; 320-640 (mean 498) μm long. **Axial parenchyma** sparse; scanty paratracheal and vasicentric. **Rays** heterogeneous, mostly multiseriate, sometimes uniseriate; 7-10 rays per mm. Uniseriate rays up to 10 cells (400 μm) high. Multiseriate rays 2 cells (30 μm) wide and up to 600 μm high. Otherwise similar to *Cinnamomum camphora*.

Lindera praecox (Sieb. et Zucc.) Blume

Habit: Small tree

Material: 6 mm in diameter, twig from herbarium specimen (Tamura & Okada 26365).

Pores 76-110 distributed per sq. mm; 25-55 μm in diameter; walls 1.5-3 μm thick. **Vessel members** 200-480 (mean 366) μm long. **Fibers** 10-30 μm in diameter; walls 2-3.5 μm thick; 350-680 (mean 497) μm long. **Rays** heterogeneous, 7-11 distributed per mm. Uniseriate rays

up to 8 cells (250 μm) high. Multiseriate rays 2-3 cells (20-30 μm) wide and up to 800 μm high. Otherwise similar to *Cinnamomum insularimontanum*.

Lindera umbellata Thunb.

Habit: Small tree

Material: 4 mm in diameter, twig from herbarium specimen (Okada, Ejima & Hamada 1450).

Pores 20-50 μm in diameter; walls 1-4 μm thick. Vessel members 240-490 (mean 381) μm long. Fibers 5-15 μm diameter; walls 1-3 μm thick; 320-650 (mean 478) μm long. Rays heterogeneous, 7-11 distributed per mm. Uniseriate rays up to 26 cells (900 μm) high. Multiseriate rays 2 cells (25 μm) wide and up to 800 μm high. Otherwise similar to *C. insularimontanum*.

Litsea cubeba (Lour.) Pers.

Habit: Small tree

Material: 8 mm in diameter, twig from herbarium specimen (Tamura & Okada 26450).
(Figs. 99-102)

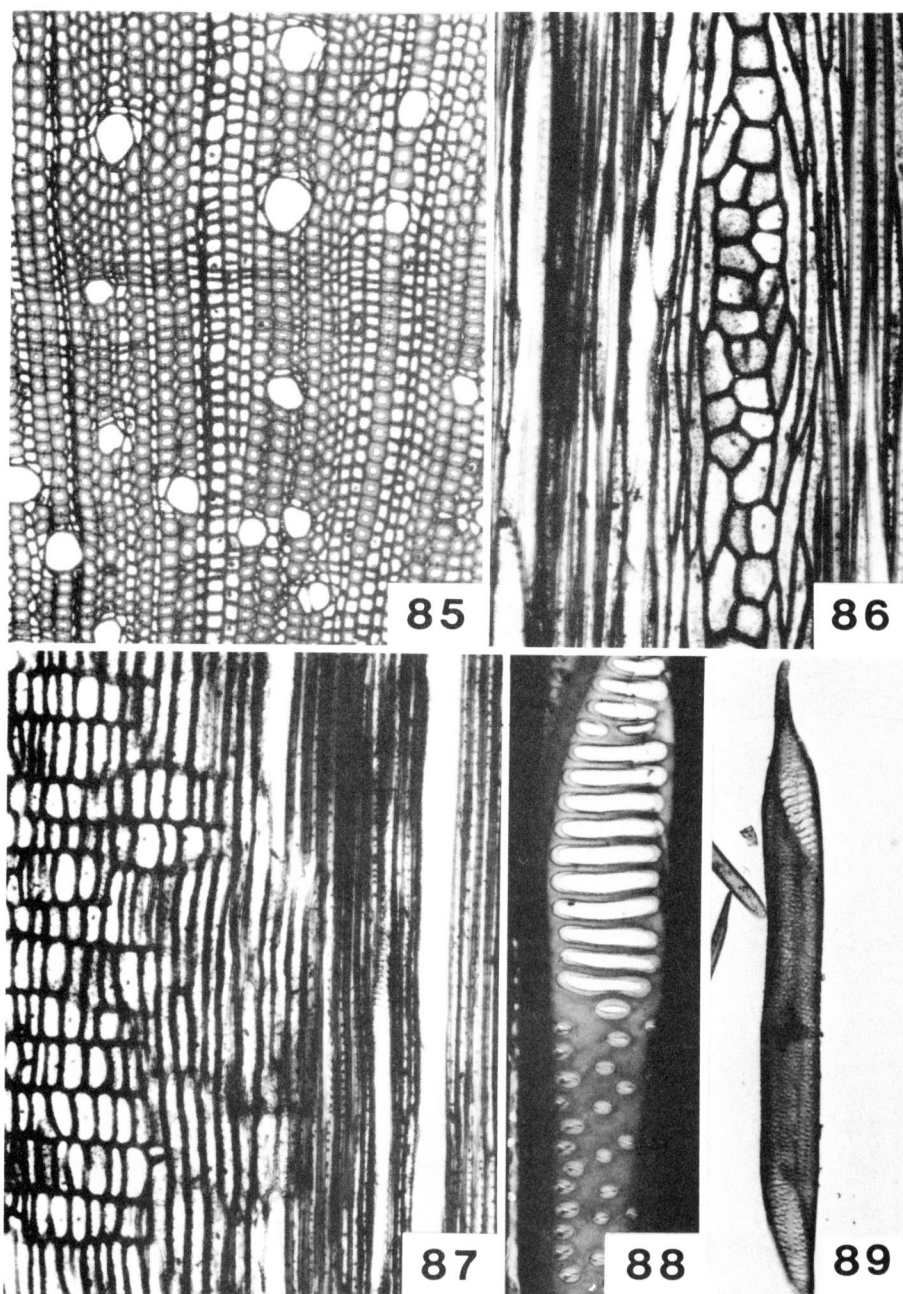
Pores 50-75 distributed per sq. mm; 40-70 μm in diameter. Vessel members 260-530 (mean 407) μm long. Fibers 10-22 μm in diameter; walls 1.5-3 μm thick; 370-750 (mean 526) μm long. Rays heterogeneous, 5-9 distributed per mm. Uniseriate rays up to 15 cells (500 μm) high. Multiseriate rays 2-3 cells (20-30 μm) wide and up to 850 μm high. Otherwise similar to *C. insularimontanum*.

Neolitsea sericea (Bl.) Koidzumi

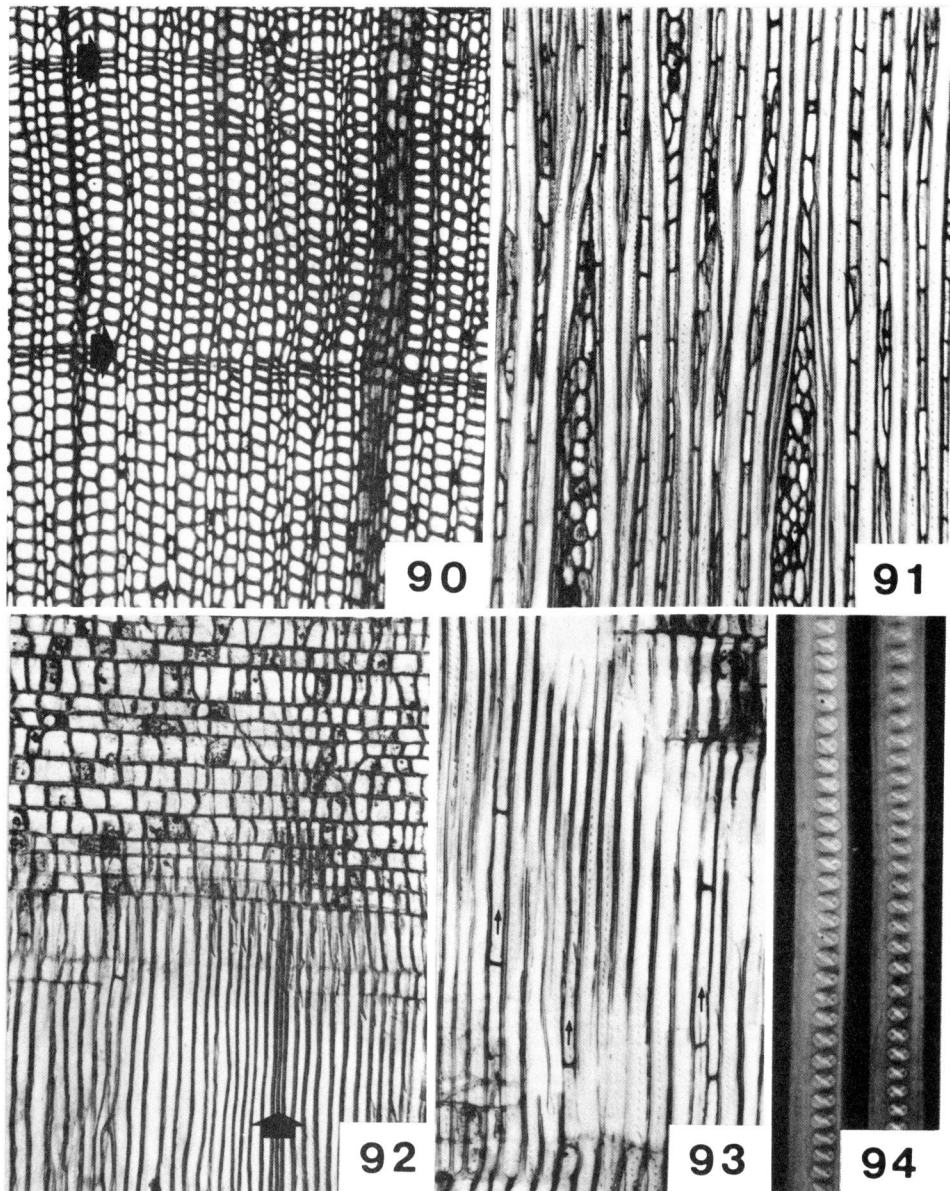
Habit: Tree

Material: 7 mm in diameter, twig from herbarium specimen (Tamura 9690). (Figs. 103-106)

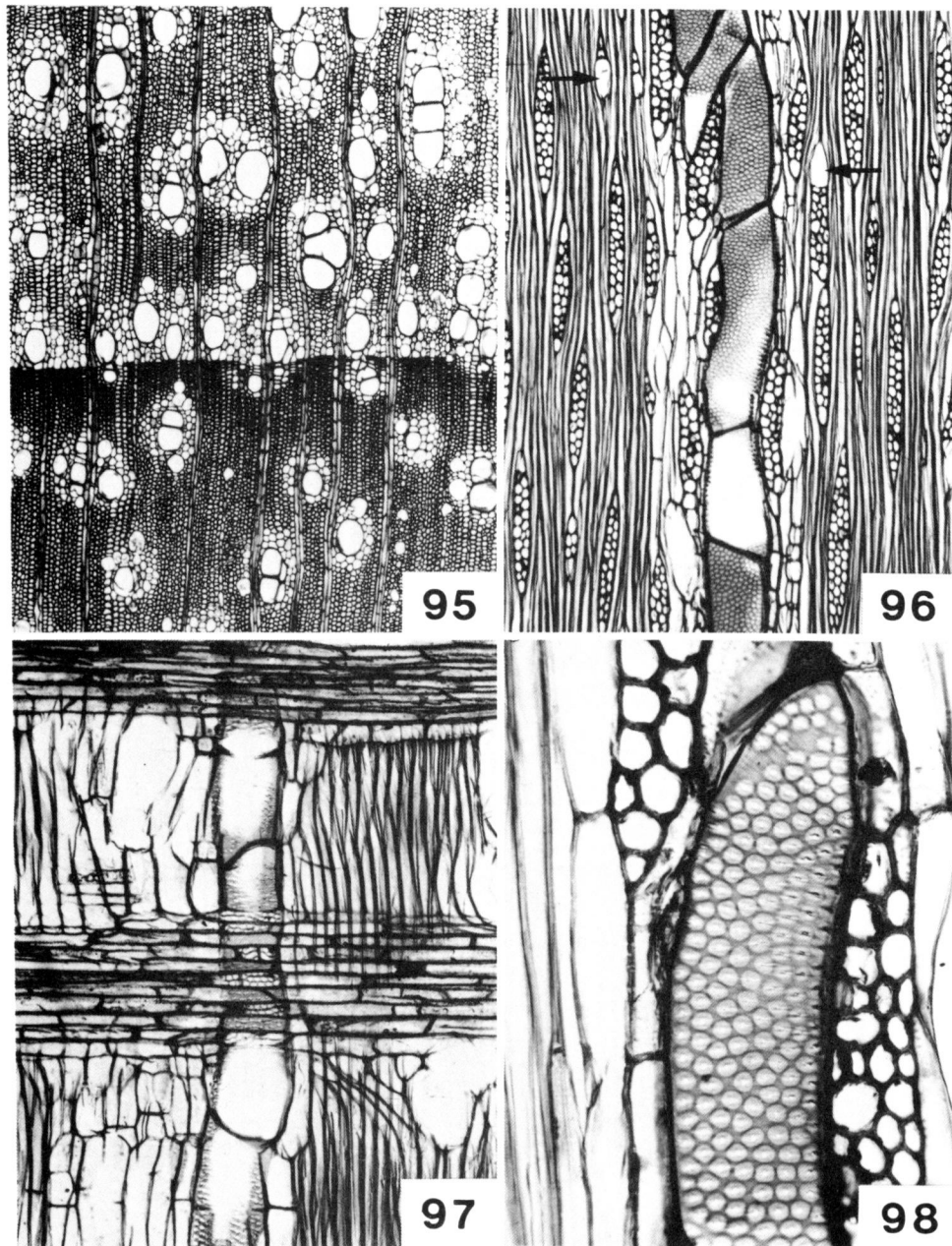
Pores 30-70 μm in diameter; walls 1.5-3 μm thick. Vessel members 260-450 (mean 346) μm long. Fibers 12-30 μm in diameter; walls 1-2.5 μm thick; 220-580 (mean 427) μm long. Rays heterogeneous, 7-12 distributed per mm. Uniseriate rays up to 10 cells (250 μm) high. Multiseriate rays 2-4 cells (20-40 μm) wide and usually less than 800 μm , rarely up to 1300 μm high. Otherwise similar to *C. insularimontanum*.



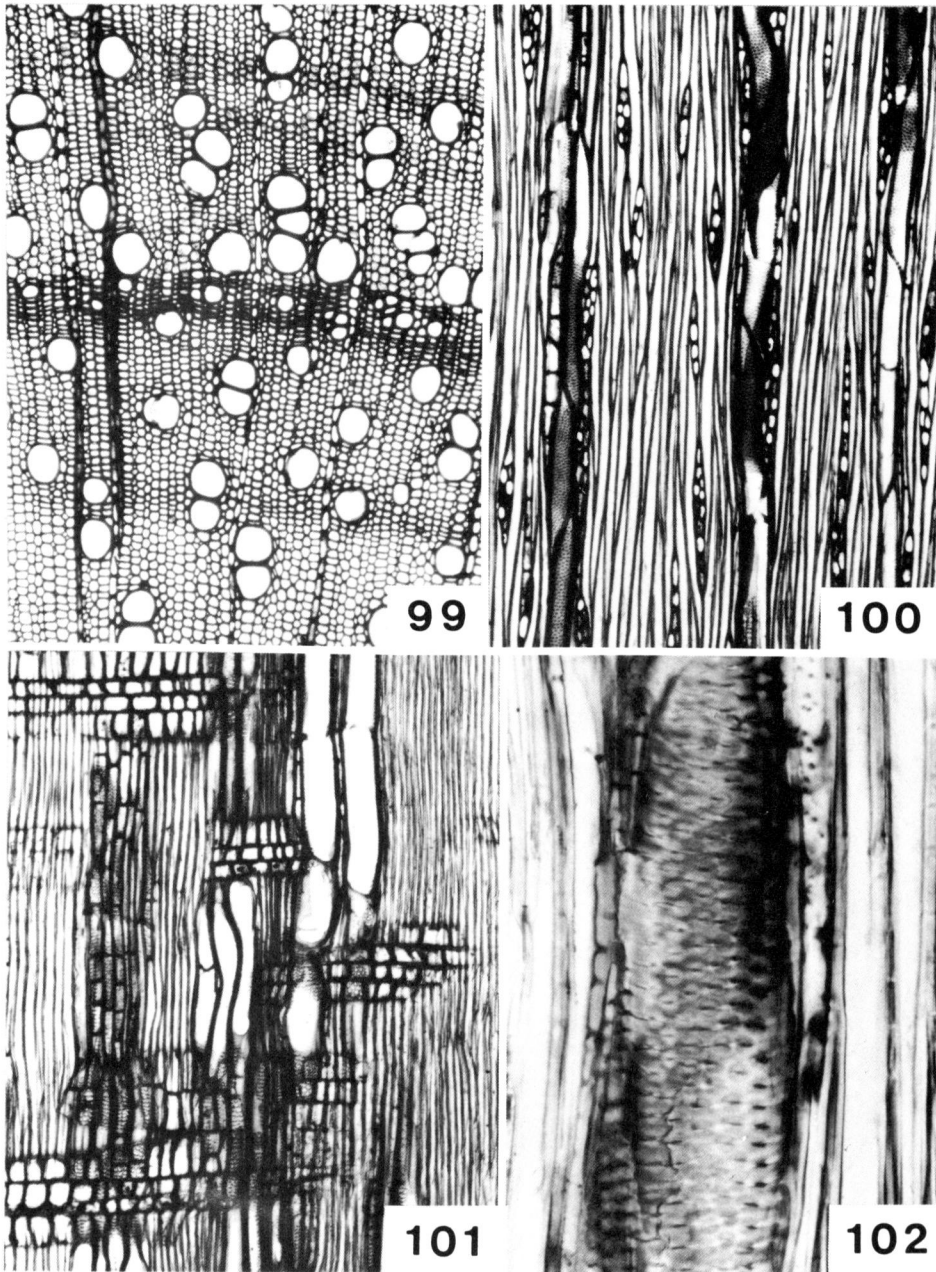
Figs. 85-89. *Austrobaileya maculata*. 85: Cross section, showing incomplete vasicentric parenchyma. x100. 86: Tangential section. x100. 87: Radial section. x100. 88: Scalariform perforation plate and side wall pits of a vessel member. x400. 89: Macerated vessel member. x100.



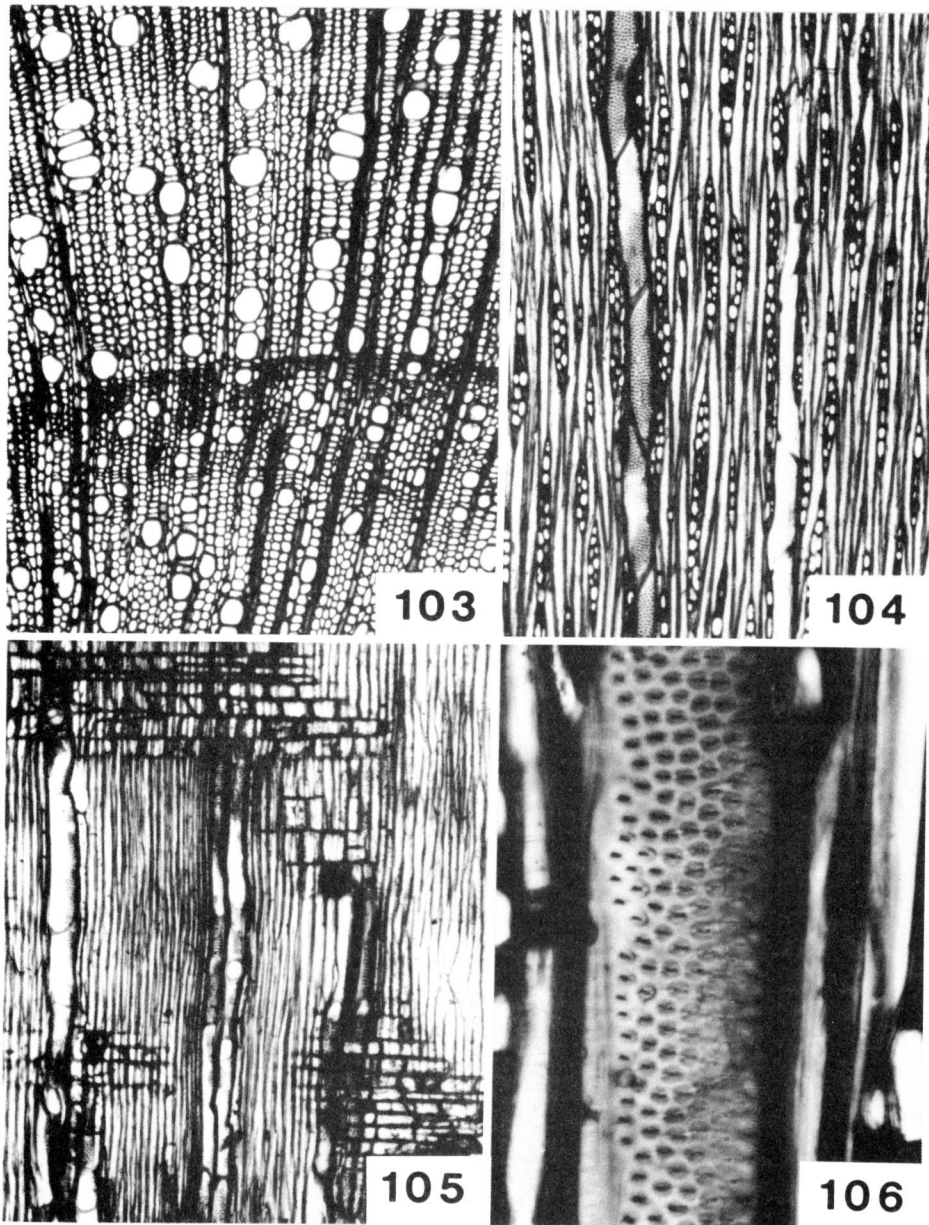
Figs. 90-94 *Amborella trichopoda*. 90: Cross section through three growth rings. Arrows show growth ring boundaries. x100. 91: Tangential section. x75. 92: Radial section. Arrow shows growth ring boundary. x75. 93: Radial section, showing some axial parenchyma strands (small arrows). x85. 94: Side wall pits of tracheids. x300.



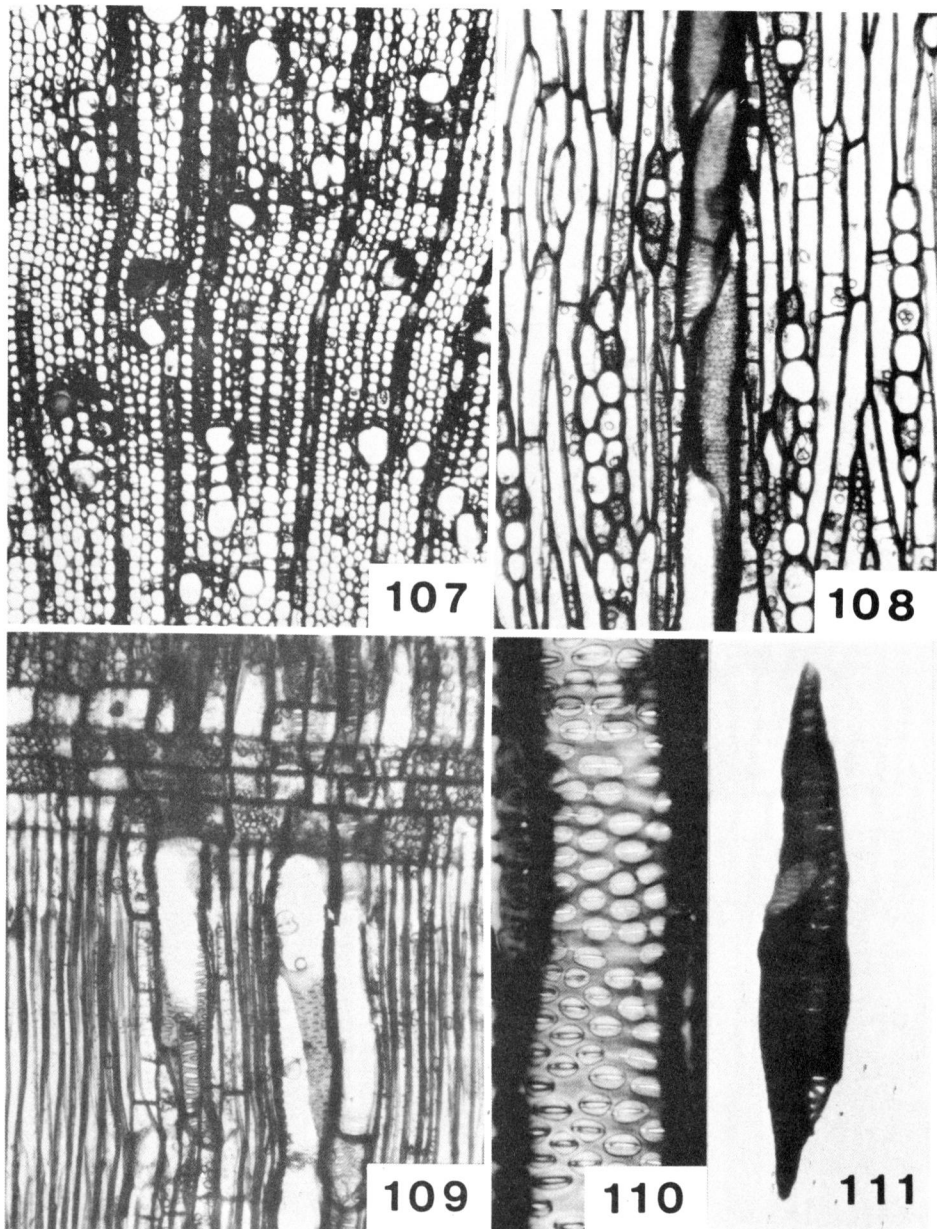
Figs. 95-98. *Cinnamomum camphora*. 95: Cross section through two growth rings, showing well developed paratracheal parenchyma. x40. 96: Tangential section. Arrows show oil cells in rays. x75. 97: Radial section, x100. 98: Tangential section, showing alternate intervessel pits. x300.



Figs. 99-102. *Litsea cubeba*. 99: Cross section through two growth rings. x100. 100: Tangential section. x100. 101: Radial section. x100. 102: Tangential section, showing alternate intervessel pits. x600.



Figs. 103-106. *Neolitsea sericea*. 103: Cross section through two growth rings. x100. 104: Tangential section. x100. 105: Radial section. x100. 106: Tangential section, showing alternate intervessel pits. x600.



Figs. 107-111. *Hernandia nymphaefolia*. 107: Cross section. x100. 108: Tangential section. x130. 109: Radial section. x130. 110: Alternate intervessel pits. x500. 111: Macerated vessel member. x150.

Persea thunbergii (Sieb. et Zucc.) Kostermans

Habit: Tree

Material: 7 mm in diameter, twig from herbarium specimen (Okada 524).

Pores 60-100 distributed per sq. mm; 30-60 μm in diameter; walls 2.5-5 μm thick. Vessel members 190-600 (mean 351) μm long. Fibers 10-20 μm in diameter; walls 1.5-3 μm thick; 330-680 (mean 499) μm long. Rays heterogeneous, 9-13 distributed per mm. Uniseriate rays up to 8 cells (300 μm) high. Multiseriate rays 2-3 cells (25-40 μm) wide and usually less than 800 μm , rarely up to 1500 μm high. Otherwise similar to *C. insularimontanum*.

HERNANDIACEAE

Hernandia nymphaefolia (Presl) Kubitzki

Habit: Tree

Material: 8 mm in diameter, twig from plant cultivated in Osaka Univ. (Figs. 107-111)

Wood diffuse porous. Growth rings distinct. Pores evenly distributed, 19-34 pores per sq. mm; solitary and in radial multiples of 2-4; solitary pores round to oval in outline; 20-80 μm in tangential diameter; walls 3-5 μm thick. Vessel members 170-530 (mean 404) μm long; end walls moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; pits large, about 10 μm in diameter, with long elliptical apertures. Pits to rays and axial parenchyma scalariform to transitional; often unilaterally compound. Helical thickenings invisible. Fibers 10-32 μm in diameter; walls 1.5-2.5 μm thick; 530-890 (mean 671) μm long; non-septate; with simple pits. Helical thickenings invisible. Axial parenchyma moderately abundant; vasicentric and aliform to confluent. Rays heterogeneous, uni- or biseriate; 5-8 rays per mm. Uniseriate rays 25-35 μm wide and 2-16 cells (70-550 μm) high, composed of upright, square, and procumbent cells. Biseriate rays 200-800 μm , sometimes up to 2 mm high, composed of upright, square, and procumbent cells; with 3-12 (130-500 μm), up to 25 (1 mm) marginal rows of upright, square, and procumbent cells.

CHLORANTHACEAE

Ascarina philippinensis C. B. Robinson

Habit: Tree

Material: 10 cm or more in diameter, stem collected by M. TAMURA in Borneo. (Figs. 112-117)

Wood diffuse porous. Growth rings indistinct. Pores evenly distributed, 40-60 pores per sq. mm; solitary and in radial multiples of 2-4; solitary pores angular in outline; 50-150 μm in tangential diameter; walls 2.5-4 μm thick. Vessel members 1990-3130 (mean 2587) μm long; end walls steeply oblique; perforation plates scalariform with 90-200 bars. Intervessel pits scalariform to transitional; pits large, 7-30 μm in horizontal diameter. Pits to rays and axial parenchyma scalariform to opposite. Helical thickenings invisible. Fibers 12-70 μm in diameter; walls 5-10 μm thick; 1390-4160 (mean 2790) μm long; non-septate. Pits conspicuously bordered, circular in outline, 7-10 μm in diameter; with oblique slit-like apertures. Helical thickenings invisible. Axial parenchyma abundant; diffuse, diffuse-in-aggregate, and also scanty paratracheal. Rays heterogeneous, uniseriate and multiseriate; 6-9 rays per mm. Uniseriate rays about 25 μm wide and 1-10 cells (200-2000 μm) high. Multiseriate rays 2-8 cells (50-300 μm), mostly 4-6 cells (150-240 μm) wide and mostly 2.5-5 mm, up to 6 mm high; with 1-10 marginal rows of upright cells. Uni- and biseriate rays composed entirely of tall upright cells. Multiseriate parts composed of square and procumbent cells; partly sheathed with upright cells.

Ascarina rubricaulis Solms

Habit: Tree

Material: 40 mm in diameter, twig collected by M. TAMURA in New Caledonia. (Figs. 118-124)

Pores 45-100 μm in tangential diameter. Vessel members 1270-2180 (mean 1693) μm long. Fibers 15- 60 μm in diameter; walls 4-7 μm thick; 1370-2580 (mean 2023) μm long; pits 5-7 μm in diameter. Rays heterogeneous; uniseriate rays 15-25 μm wide and 1-13 cells (150-1500 μm) high; multiseriate rays 2-10 cells, mostly 4-7 cells (80-150 μm) wide and mostly 1.5-4 mm, up to 5 mm high; with 1-13 marginal cells. Otherwise similar to *Ascarina philippinensis*.

Chloranthus spicatus (Thunb.) Maxim.

Habit: Shrub

Material: 6 mm in diameter, stem from plant cultivated in Osaka Univ. (Figs. 125-128)

Wood diffuse porous. Growth rings faintly distinct. Pores evenly distributed; exclusively solitary; angular in outline; 17-37 μm in tangential diameter; walls 2-4 μm thick. Vessel members 540-1500 (mean 1081) μm long; end walls steeply oblique; perforation plates scalariform with 30-80 bars. Intervessel pits not observed. Pits to rays and axial parenchyma scalariform. Helical thickenings invisible. Fibers 10-25 μm in diameter; walls 3-6 μm thick; 640-1540 (mean 1062) μm long; occasionally septate. Pits bordered, circular in outline, 4-5 μm in diameter; with oblique lenticular apertures. Helical thickenings invisible. Axial parenchyma scarce; diffuse; diffuse cells often in touch with vessels. Rays typically high, more than 3 mm; heterogeneous, mostly multiseriate, sometimes uniseriate. Multiseriate rays 3-7 cells (70-150 μm) wide. All the component cells upright, 100-200 μm tall.

Sarcandra glabra (Thunb.) Nakai

Habit: Shrub

Material: 10 mm in diameter, stem collected in Iriomote Isl., Ryukyu, Japan. (Figs. 129-133).

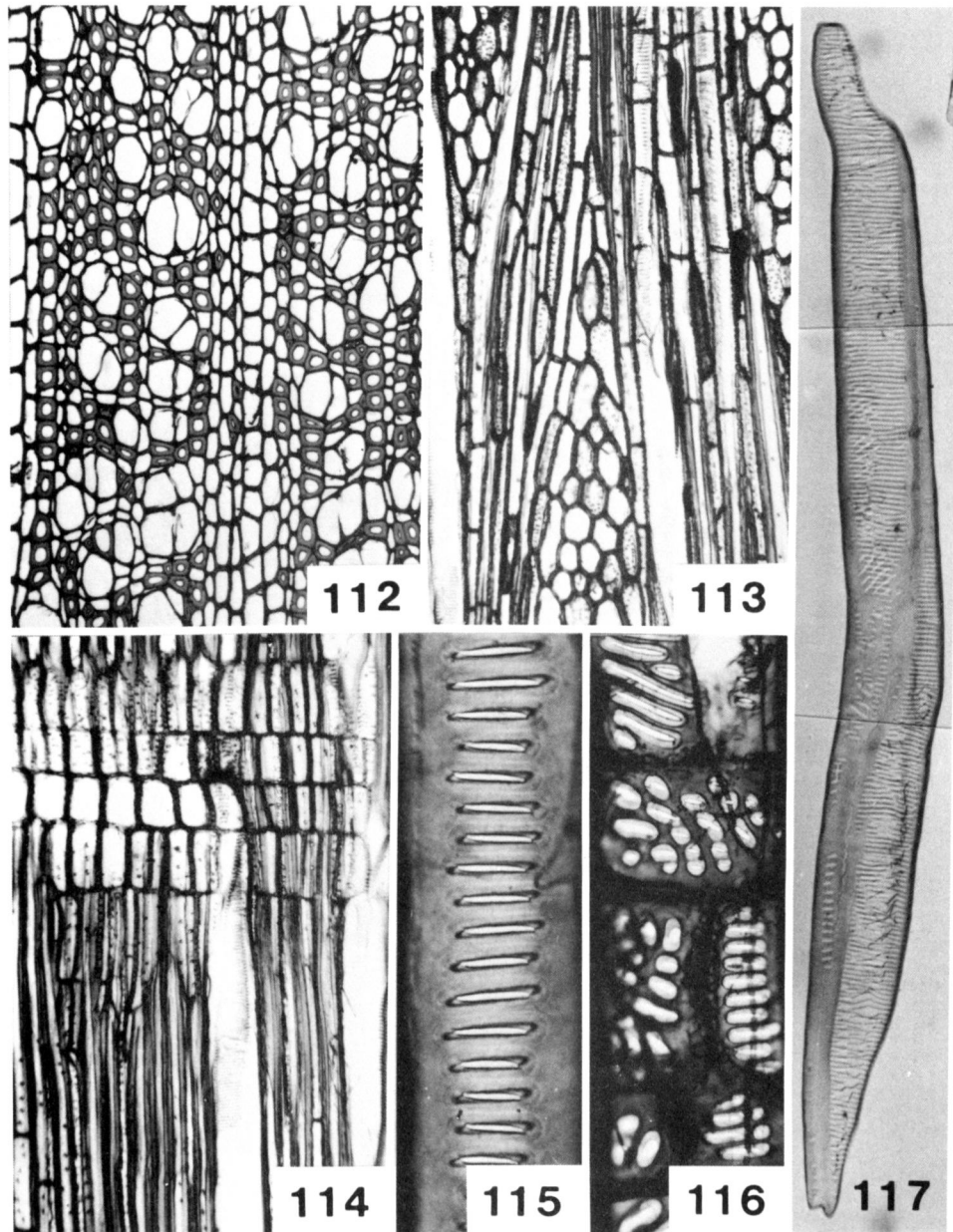
Wood non-porous. Growth rings distinct. Tracheids arranged in regular, sometimes irregular radial rows; square to polygonal in cross section; 12-32 μm and 10-30 μm in tangential and radial diameters, respectively; walls 2.5-5.5 μm thick; 620-2080 (mean 1497) μm long. Bordered pits circular, 5-7 μm in diameter; arranged in uniseriate rows; with oblique lenticular apertures. Often pits horizontally elongated and scalariform in arrangement on both overlapping end walls. Helical thickenings invisible. Axial parenchyma sparse; diffuse. Rays heterogeneous, multiseriate and uniseriate. Uniseriate rays about 15 μm wide and more than 3 mm high. Multiseriate rays 3-10 cells (80-260 μm) wide and more than 10 mm high; with high marginal wings. All the component cells upright, 100-250 μm tall.

Relation between anatomical features and thickness of stem

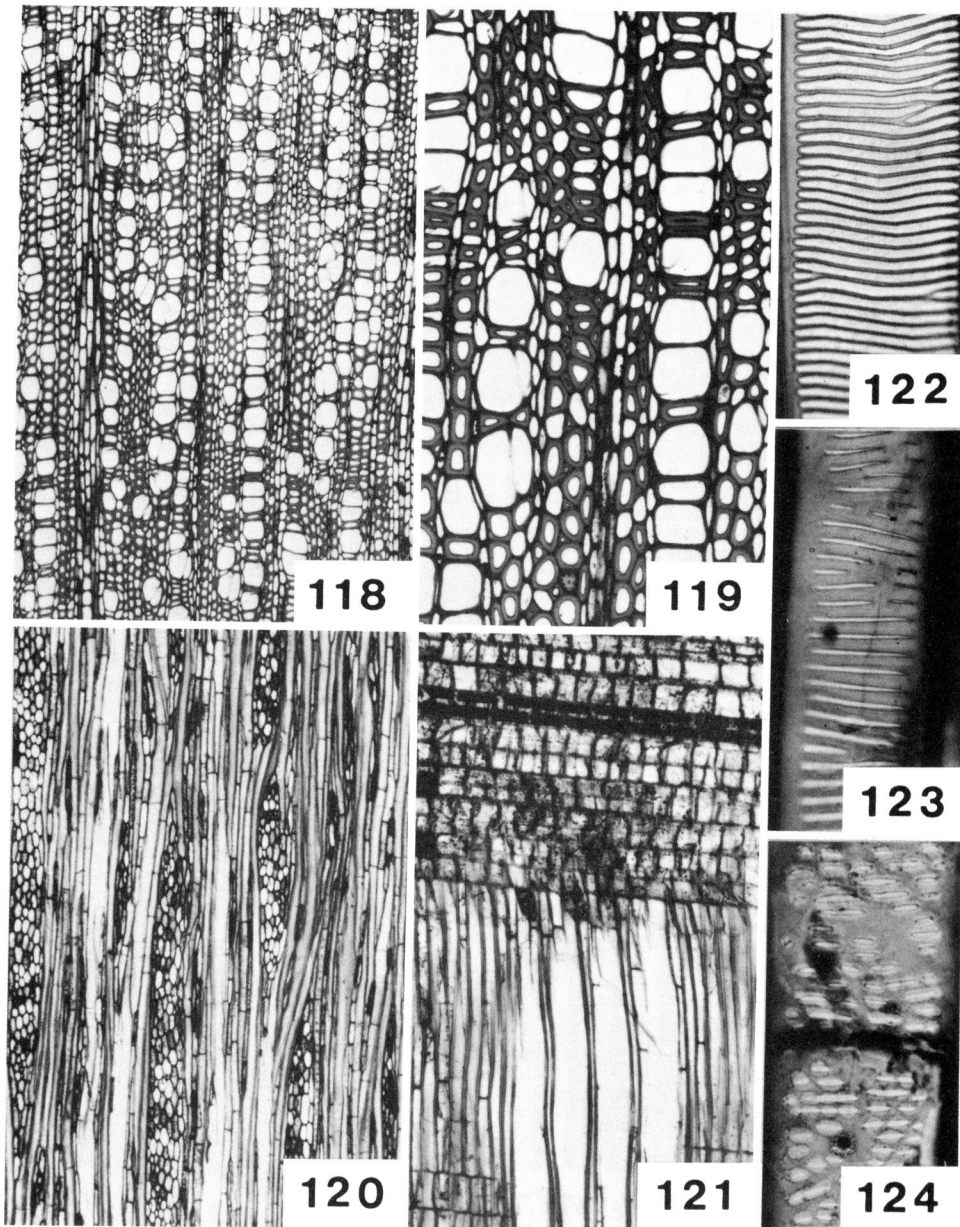
The anatomical features of thick and thin stems of five species were shown in the following Tables 1-5. Differences between the thick and thin stems are as follows:

The length of vessel members, fibers, and tracheids, the diameter of vessels, and the quantity of axial parenchyma were greater in the thick stems rather than in the thin ones in all species examined. In contrast, the pore number per sq. mm, the ray number per mm, and the ray height were smaller in the thick stems rather than in the thin ones.

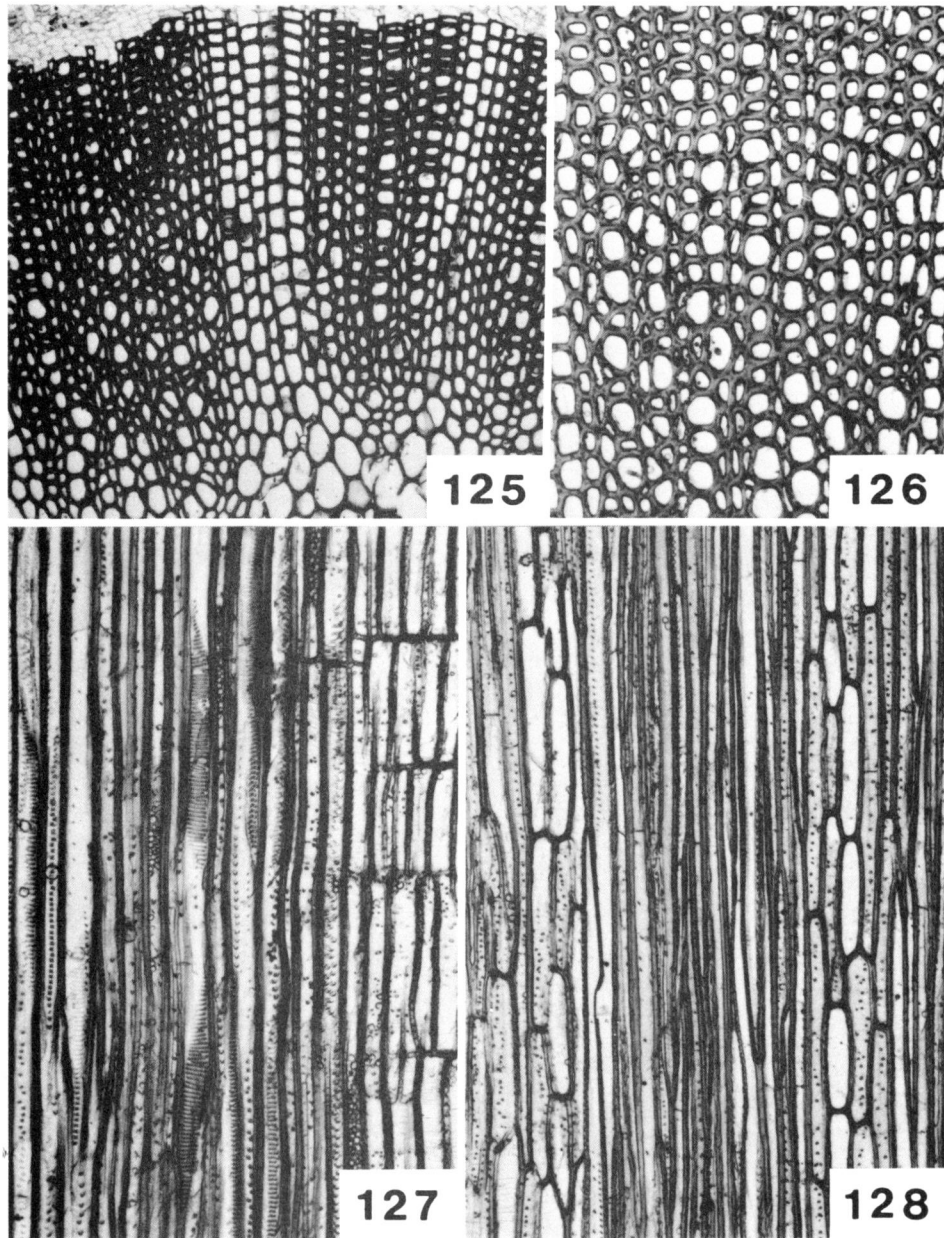
The proportions of the three kinds of cells constituting the rays varied with the thickness of stem, i.e. the ratio of procumbent cells to square and upright cells was higher in the thick stems rather than in the thin ones. Although percentage of uni- or multiseriate rays varied with the thickness of stem, the proportion of uniseriate rays to multiseriate rays was



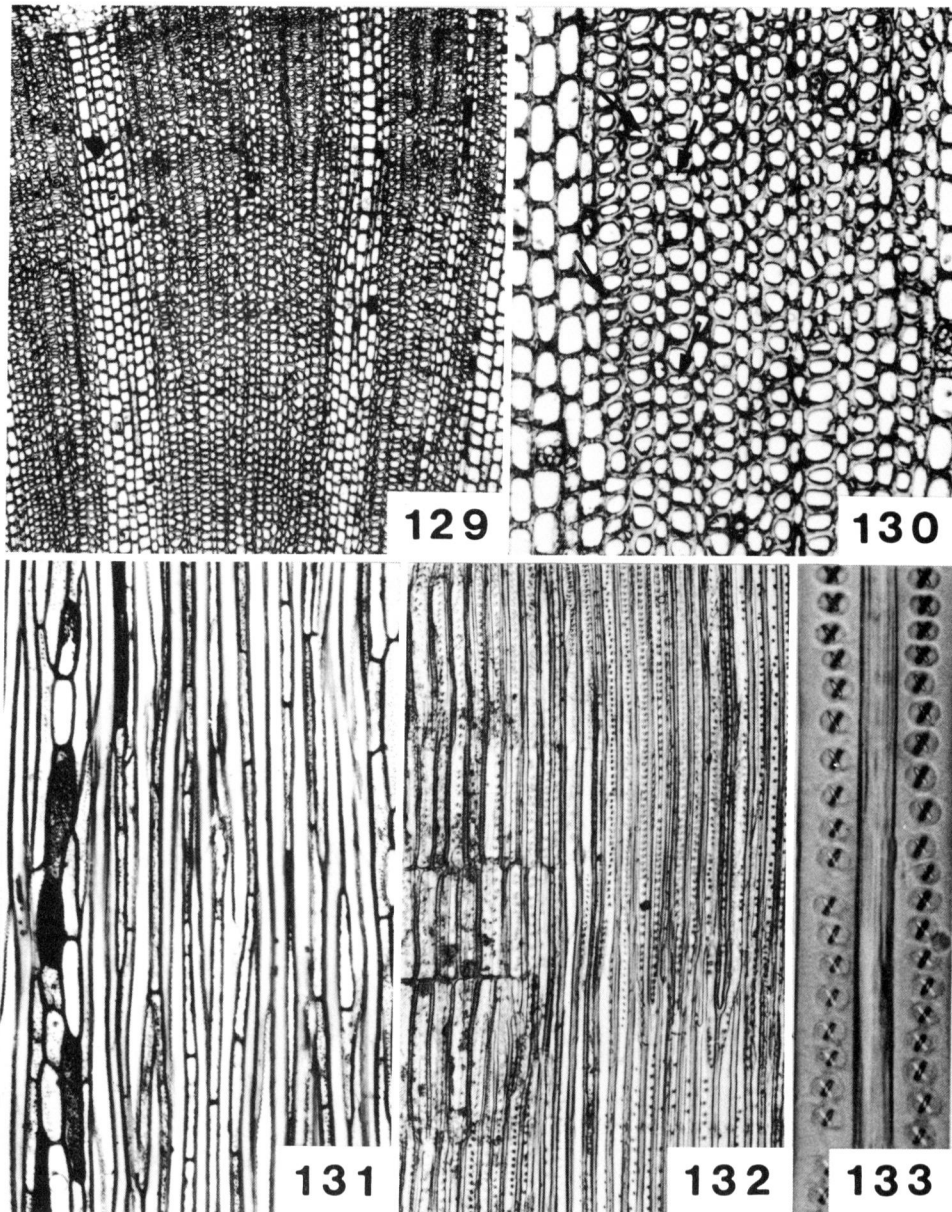
Figs. 112-117. *Ascarina philippinensis*. 112: Cross section. Radial or oblique lines within vessel area represent cross sectional view of overlapping end walls. x75. 113: Tangential section. x75. 114: Radial section. x75. 115: Scalariform intervessel pits. x600. 116: Vessel-ray pits. x300. 117: Macerated vessel member. x150.



Figs. 118-124. *Ascarina rubricaulis*. 118: Cross section, x40. 119: Cross section, x100. 120: Tangential section, x40. 121: Radial section, x50. 122: Scalariform perforation plate, x400. 123: Scalariform intervessel pits, x400. 124: Vessel-ray pits, x400.



Figs.125-128. *Chloranthus spicatus*. 125: Cross section, x140. 126: Cross section, x220. 127: Radial section, x130. 128: Tangential section, x160.



Figs. 129-133. *Sarcandra glabra*. 129: Cross section, x70. 130: Cross section. Arrows show scattered parenchyma cells, x160. 131: Tangential section, x130. 132: Radial section, x130. 133: Side wall pits of tracheids, x700.

not very different between the thick and thin stems, except of *Magnolia sieboldii* in which the proportion was reversed.

In *Cinnamomum camphora* and two species of *Magnolia*, which have two types of perforation plate present at the same time, the scalariform plates more frequently occurred in the thin stems rather than in the thick ones.

The difference between the lengths of the tracheary elements of the thick and thin stems was smaller in *Liriodendron tulipifera* and *Cinnamomum camphora* than the other three species.

In order to know how element length changes as the stem increases in diameter, element length was examined in some species, at three regions in the secondary xylem of the stem (i.e. adjacent to the pith, 1 cm from the pith, and outermost part of the secondary xylem). The results were shown in Table 6. In all species examined, any kind of element was longer at the outer region than at the inner region of the secondary xylem, and element length changed much more between the region nearest the pith and that region 1 cm distant from the pith rather than at the outer region.

Discussion

The influence of thickness of stem on anatomical features

By comparing the wood anatomy of thick and thin stems in several species, it was found that several features varied with the thickness of stem. These features are probably important in wood identification. Most features are quantitative features such as size and number of tracheary elements or rays. The features which are directly correlated with stem diameter are: the length of tracheary elements, the diameter of vessels, and the quantity of axial parenchyma. Features which are inversely correlated to stem diameter are: the number of pores per sq. mm, the number of rays per mm, and the height of rays. In the case of simultaneous occurrence of simple and scalariform perforation plates in the same body, as in some species of *Magnolia*, the scalariform plates are less frequent in the thick stems than in the thin ones. The simultaneous occurrence of both types of perforation plates seems not to be largely influenced by thickness of stem. Moreover, the proportion of component cells of rays varies with thickness of stem, i.e. it seems, in any species examined, that upright and square cells become fewer and procumbent cells become more as stems increase in diameter.

The value of quantitative features seems to change in a complex way as stems increase in diameter. For example, as BAILEY and TUPPER⁷⁾ revealed in various plants, average length of tracheary elements is shortest at a position near the pith and becomes longer toward the outside in the secondary xylem. However, this increase in length is not linear. In all cases the

average length of tracheary elements increases more rapidly in the region near the pith rather than near the outer region of the secondary xylem. At a greater distance from the pith in the secondary xylem tracheary element length increases slowly. Other quantitative features also seem to change conspicuously in the innermost region of the secondary xylem.

In contrast with the features mentioned above, it seems that distribution (or grouping) of pores, types of intervessel pittings or perforation plates, types of pits of fibers, and distribution patterns of axial parenchyma are less influenced by the thickness of stems, however this is not always true in very thin stems obtained from herbarium specimens.

In conclusion, if species which only deposit a small amount of secondary xylem in the stem and stems which are very thin are avoided, material worthy of description can probably be obtained.

Wood anatomy within the families

Some of the plants examined are included in small families, including monotypic families. Each of them is uniform in its own wood anatomy. The following families are relatively large and are worthy of discussion.

WINTERACEAE: The wood of this family is vesselless. There is similarity in the structure of tracheids and rays among the three species examined (this is similar to other members of this family). The tracheids are very long with numerous, conspicuously bordered pits arranged in uni- or biseriate rows on the walls. The rays are typically heterogeneous (KRIBS's Heterogeneous Type I). The pattern of distribution of axial parenchyma is slightly different among the three species. However METCALFE and CHALK¹⁷⁾ and CARLQUIST¹⁸⁻²⁰⁾ describe the common patterns of axial parenchyma in the Winteraceae as diffuse and narrowly banded (terminal parenchyma also present in the species with growth rings), as observed in *Belliolum* sp.

MAGNOLIACEAE: The woods examined of *Liriodendron tulipifera* and *Magnolia* spp. have many characteristics similar to each other except for perforation plates and intervessel pitting. The intervessel pitting is typically opposite in *L. tulipifera* and usually scalariform in *Magnolia*, although in *M. sieboldii* opposite pitting occurs frequently. Perforation plates are exclusively scalariform in *L. tulipifera*, while in *Magnolia* they are mostly simple and occasionally scalariform. The simple perforation plates of *Magnolia*, however, seem not to be a major characteristic of the genus. According to CANRIGHT²²⁾, simple perforation plates occur in some temperate species of *Magnolia*, and generally the perforation plates of *Magnolia* are scalariform, like those of *Liriodendron*. In order to ascertain this, it is necessary to examine tropical species of *Magnolia*. Overall the other main wood anatomical features of *Magnolia* seem to be similar to those of other genera^{14, 17, 22)}.

LAURACEAE: The woods of all the species examined are very similar to each other.

They have many common features such as: pores solitary and small radial multiples; vessel members of short to medium length; perforation plates typically simple, occasionally scalariform; intervessel pitting alternate; fibers with simple pits; paratracheal parenchyma; occurrence of oil cells; etc. These are also common in the family^{17, 23)}. Thus the Lauraceae are markedly uniform in the wood anatomy.

HERNANDIACEAE: The wood of *Hernandia nymphaefolia* differed from the description of METCALFE and CHALK¹⁷⁾ in size of vessels, structure of rays, and others. These are the features which are influenced by the thickness of stem. It seems that these differences are due to the small size of the material examined.

CHLORANTHACEAE: This family is relatively small, but it shows a rather wide diversity in the wood anatomy among the genera. The genus *Sarcandra* is distinct from other genera in lacking vessels. But *Chloranthus spicatus* and *S. glabra* are very similar when transverse and longitudinal section of the woods are compared (with the exception of vessels in *C. spicatus*). *Ascarina* and *Chloranthus* have some features in common, i.e. long vessel members with scalariform perforation plates with numerous bars and the fibers with conspicuously bordered pits, but the two genera differ in the sizes of tracheary elements and the structure of rays. Another genus *Hedyosmum*, according to METCALFE and CHALK¹⁷⁾ and SWAMY²⁴⁾, differs from *Ascarina* in having fibers with simple pits, paratracheal axial parenchyma, and rays which are usually multiseriate and consist of tall upright cells. However, vessel members seem similar between the two genera. The rays of *Hedyosmum* seem to be comparable to those of *Chloranthus*. Previous descriptions for axial parenchyma have reported that only apotracheal parenchyma occurs in *Ascarina* and *Chloranthus*, but both types of parenchyma, apotracheal and paratracheal, seem to be present in these two genera. Thus anatomically these genera are slightly different and the Chloranthaceae are not as uniform in their wood anatomy.

Comparison of wood structures among the families

The Magnoliaceae, Degeneriaceae, and Himantandraceae are considered to have close relations²⁵⁻²⁷⁾. Wood of *Degeneria* did not closely resemble that of the observed species of Magnoliaceae, but many features seem to be common within the Magnoliaceae as a whole, i.e. vessel members are of medium length, with scalariform perforation plates on the oblique end walls, and with scalariform intervessel pittings, pores are solitary and small radial multiples, fibers have small bordered pits, and axial parenchyma is banded apotracheal. BAILEY and SMITH²⁵⁾ pointed out the close similarities in the wood anatomy between *Degeneria* and tropical species of the Magnoliaceae.

BAILEY and NAST²⁸⁾ considered that the Winteraceae have a certain affinity with other ranalian families, but are not closely related to any family. THORNE²⁹⁾ and TAKHTAJAN⁴⁾

separated the Winteraceae from families around the Magnoliaceae into suborder Winterineae, but the last author considers a probable relation of the family to the Degeneriaceae. Because of its vesselless nature, the wood of the Winteraceae has few features in common with that of the Degeneriaceae or the Magnoliaceae, but the pattern of distribution of the axial parenchyma (diffuse and narrowly banded, or terminal) are similar to those of both families.

There are different kinds of opinions on the affinity of Eupomatiaceae. Relations to the Himantandraceae^{4, 29, 30}), the Annonaceae³¹), the Lauraceae³²) are considered, but TAMURA⁶) suggests that there is no family with close relation to the Eupomatiaceae. The wood is less similar to that of any other family observed with the exception of *Ascarina* (Chloranthaceae) in the cross-sectional view.

The Trochodendraceae, Tetracentraceae, Eupteleaceae, and Cercidiphyllaceae are often made into one group, but, as TAKHTAJAN⁴) separated them into three orders, they are considered not to have close relationships with each other. *Trochodendron* has vesselless wood which is easily distinguished in the cross-sectional view from the other dicotyledonous vesselless wood, such as that of the Winteraceae, because of the differences in the sizes of tracheids and the distribution patterns of axial parenchyma between the early wood and the late wood. *Tetracentron*, which is often considered to be closely related to *Trochodendron*, is another vesselless genus of dicotyledons. According to MCLAUGHLIN¹⁴) and METCALFE and CHALK¹⁷), the woods of these two genera resemble each other except for the occurrence of vascular tracheids in *Tetracentron*. BAILEY and NAST³³) state the difficulty of discriminating between the two woods. *Euptelea* is similar to *Trochodendron* in the ray structure and the axial parenchyma patterns, but as NAST and BAILEY³⁴) pointed out, it seems that the structural similarities are neutralized by the wide evolutionary gap between the vesselless wood of *Trochodendron* and the vessel-bearing wood of *Euptelea*. In the meantime, there are many similarities between the woods of *Euptelea* and *Cercidiphyllum*, but also there are some differences in the grouping of pores, intervessel pitting, pits of fibers, ray structure, and patterns of distribution of axial parenchyma. Thus these taxa are not very uniform in their wood anatomy except between *Trochodendron* and *Tetracentron*. These four families are generally considered to be related to the Hamamelidales, and have many similarities with the Hamamelidaceae in their wood anatomy, as MCLAUGHLIN¹⁴) has already indicated. The helical thickenings on both ends of the vessel members shown in *Cercidiphyllum* are characteristic of some species of the Hamamelidaceae³⁵).

The Illiciaceae and Schisandraceae were placed in the Ranunculidae as the Illiciales by TAKHTAJAN³), but later he⁴) transferred it into the Magnoliidae next to the Magnoliales. Thus these families are generally considered to be related to magnoliaceous families, but are not so similar to the Magnoliaceae in wood anatomy. The Illiciaceae and Schisandraceae are different from each other in the structure of the vessel members. The vessel members of the

Schisandraceae are huge and with simplified perforation plates. BAILEY and NAST³⁶⁾ attributed the characteristics of them to the vining habit of the Schisandraceae, and then CARLQUIST³⁷⁾ stated that there is no basic divergence between woods in the two families. But it appears that the two families have no close similarity in the wood structures. The vessel members of *Illicium* are very similar to those of *Eupomatia*, and *Illicium* is also similar to *Cercidiphyllum* and *Euptelea* in cross-sectional view. This is so much so that MCLAUGHLIN¹⁴⁾ proposed to transfer these three genera from the Magnoliales to the Hamamelidales. However, the Illiciaceae and Schisandraceae differ from the Cercidiphylaceae and Eupteleaceae in the rays and the axial parenchyma, for instance the axial parenchyma is apotracheal in the last two families but paratracheal in the former two.

The Lauraceae are generally considered to be closely related to the Hernandiaceae, and there are many similarities between the wood anatomy of the two families. Among the similarities, the presence of oil cells, the occasional occurrence of septate fibers, and the paratracheal nature of the axial parenchyma are regarded by GARRATT³⁸⁾ as the features which indicate affinity between the Hernandiaceae and the Lauraceae. As GOTTWALD¹⁶⁾ divided the ancient dicotyledons into six structural groups by the distribution of their axial parenchyma and vessels in the woods, it seems likely that the paratracheal nature of the axial parenchyma is an important feature on the consideration of the relationships between the two families or with other families.

The Austrobaileyaceae and Amborellaceae are not similar to each other in wood anatomy, and have no similarities to the Lauraceae and Hernandiaceae except for the paratracheal nature of the axial parenchyma in *Austrobaileya*. The Austrobaileyaceae and Amborellaceae are generally considered to be closely related to the Monimiaceae, as BAILEY and SWAMY^{39, 40)} suggested that if the concept of Monimiaceae is to be broadened, *Austrobaileya* and *Amborella* are also included in the family. Moreover, it is generally considered that the Monimiaceae are related to the Lauraceae. The wood of the Monimiaceae has a wide diversity of anatomical features as described by GARRATT⁴¹⁾ and METCALFE and CHALK¹⁷⁾. Therefore the wood anatomy of the Monimiaceae probably plays an important role in the consideration of the relationships not only between the monimiaceous families, but also with the Lauraceae.

The Chloranthaceae are variously treated in the taxonomy. The family has been classified in the Piperales⁵⁾ according to similarities in floral morphology among members of the order. But since SWAMY²⁴⁾ suggested that the non-perispermous seeds and the unilacunar nodes of the Chloranthaceae justify the distinction of the family from the members of the Piperales, the Chloranthaceae are usually classified in the Magnoliales and generally included in families associated with the Lauraceae^{3, 4, 6, 29)}. TAKHTAJAN⁴⁾ regarded the Chloranthaceae as a family near the Austrobaileyaceae, Trimeniaceae, and Lactoridaceae. It is likely

that the Lactoridaceae are closely related to the Chloranthaceae, as MELCHIOR⁵⁾ classified the Lactoridaceae together with the Chloranthaceae in the Piperales.

MCLAUGHLIN¹⁴⁾, in his paper of the wood anatomy of the Magnoliales, suggested transferring the Lactoridaceae from the Magnoliales to the Piperales. This is due to his agreement with the system of BENTHAM and HOOKER⁴²⁾ as opposed to that of HUTCHINSON¹⁾, and so affinity of the Lactoridaceae to any lauracean families is not denied. According to his description, wood features of the Lactoridaceae have a great deal in common with those of the Lauraceae, and to a lesser extent with the Chloranthaceae. Moreover, it has been already indicated that the Piperaceae are not similar to the Chloranthaceae in wood anatomy^{17, 43)}. On the other hand, the woods of the Chloranthaceae and Austrobaileyaceae have some features in common. STERN⁴⁴⁾, in the wood anatomy of the Gomortegaceae, pointed out similarities of the Gomortegaceae to some Monimiaceae and Chloranthaceae. Thus it seems that the wood of the Chloranthaceae is most comparable to that of the Monimiaceae and allied families. However the anatomical evidence is not sufficient to fully explain the relationships, and further study of the wood anatomy of the Monimiaceae is still important.

As mentioned above, there is a wide variety in the wood anatomy of the Magnoliales. If the Magnoliales is divided into four groups of families, they are as follows: Magnoliaceae group, Trochodendraceae group, Illiciaceae group, and Lauraceae group. These groups are equal to the suborders of TAMURA⁶⁾ except that the Chloranthaceae (suborder Chloranthineae) are included in the Lauraceae group. There is also a considerable diversity of the anatomical features in each group of families. With respect to the tracheary elements, most of the families in each group have long and slender vessels with scalariform perforation plates. Moreover, there are vesselless families, tracheids of which are morphologically similar to each other, in three groups except for the Illiciaceae group. Thus each group is not characterized by the tracheary elements. Similarly the rays can not characterize the groups. However with regard to the axial parenchyma it seems that particular patterns are conspicuous in each group as follows: banded apotracheal and terminal (if growth rings present) in the Magnoliaceae group; scanty paratracheal and terminal in the Illiciaceae group; diffuse-in-aggregate and terminal in the Trochodendraceae group; scanty paratracheal and vasicentric in the Lauraceae group.

Table 1. The wood anatomical features of thick stem and thin stem of *Liriodendron tulipifera*.

Diameter of material (mm) (growth rings)	80 (6)	18 (4)
Pores Outline Grouping* Distribution number per sq. mm	Angular Sol, Rad (2-5), Clu (4-8) 47-117	Angular Sol, Rad (2-5), Clu (4-8) 136-198
Vessel members Length** (μm) Diameter** (μm) Wall thickness (μm) Perforation Intervessel pits	280-820 (558) 25-77 (47) 2-3 Scalariform (2-8 bars) Transitional to opposite	220-650 (493) 20-57 (42) 1.5-2.5 Scalariform (2-7 bars) Transitional to opposite
Fibers Length** (μm) Diameter** (μm) Wall thickness (μm) Pits	590-1510 (990) 10-30 (19) 3-6 Bordered, 2-5 μm in diam.	530-1350 (936) 10-30 (19) 2.5-6 Bordered, 2-4 μm in diam.
Axial parenchyma	Sparse; terminal (2-5 cells wide)	Sparse; terminal (2-4 cells wide)
Rays Distribution number per mm Proportion of uni- and multiseriate rays Uniseriate*** Height (cells) (μm) Multiseriate*** Width (cells) Height (μm) Wing (cells) Component cells	6-10 Uniseriate 7% Multiseriate 93% 3-10 70-250 2-5 200-600-(900) 1-2-(4) Mostly procumbent, sometimes upright	8-12 Uniseriate 26% Multiseriate 74% 3-10-(20) 80-200-(360) 2-4 200-600-(800) 1-4-(15) Mostly procumbent, sometimes upright

*: Sol = solitary; Rad (2-5) = radial multiples of 2-5; Clu (4-8) = clusters of 4-8.

** : Showing usually observed range, () shows mathematical mean.

***: Showing usually observed range, () shows rarely observed values.

Table 2. The wood anatomical features of thick stem and thin stem of *Magnolia salicifolia*.

Diameter of material (mm) (growth rings)	70 (43)	5 (5)
Pores Outline Grouping* Distribution number per sq. mm	Angular Sol, Rad (2-5), Clu (4-8) 77-96	Angular Sol, Rad (2-5), Clu (4-8) 225-272
Vessel members Length** (μm) Diameter** (μm) Wall thickness (μm) Perforation Intervessel pits	330-860 (659) 28-70 (51) 1.5-2.5 Usually simple, rarely scalariform Scalariform to transitional	300-590 (454) 20-40 (29) 1-2 Mostly simple, sometimes scalariform Scalariform to transitional
Fibers Length** (μm) Diameter** (μm) Wall thickness (μm) Pits	560-1820 (1103) 12-32 (21) 3.5-7 Bordered, 2-3 μm in diam.	370-900 (617) 10-22 (14) 2.5-4.5 Bordered, 2 μm in diam.
Axial parenchyma	Sparse; diffuse and terminal (2-3 cells wide)	Sparse; terminal (1-3 cells wide)
Rays Distribution number per mm Proportion of uni- and multiseriate rays Uniseriate*** Height (cells) (μm) Multiseriate*** Width (cells) Height (μm) Wing (cells) Component cells	6-8 Uniseriate 18% Multiseriate 82% 2-10 50-200 2 200-600-(1000) 1-4-(7) Mostly procumbent, sometimes square, rarely upright	7-10 Uniseriate 29% Multiseriate 71% 2-10-(20) 60-300-(550) 2-3 300-800-(1700) 1-5-(15) Mostly procumbent, sometimes square and upright

*, **, and *** represent the same as in Table 1.

Table 3. The wood anatomical features of thick stem and thin stem of *Magnolia sieboldii*.

Diameter of material (mm) (growth rings)	30 (7)	8 (5)
Pores Outline	Angular	Angular
Grouping*	Sol, Rad (2-5), Clu (4-8)	Sol, Rad (2-5), Clu (4-8)
Distribution number per sq. mm	56-90	150-220
Vessel members		
Length** (μm)	200-860 (528)	280-630 (460)
Diameter** (μm)	30-70 (49)	20-65 (40)
Wall thickness (μm)	1.5-3	1.5-2.5
Perforation	Mostly scalariform, sometimes simple	Usually scalariform, rarely simple
Intervessel pits	Scalariform to opposite	Scalariform to opposite
Fibers Length** (μm)	430-1430 (934)	410-840 (623)
Diameter** (μm)	12-35 (21)	12-30 (20)
Wall thickness (μm)	2.5-4.5	3-4
Pits	Bordered, 2-4 μm in diam.	Bordered, 2-3 μm in diam.
Axial parenchyma	Sparse; diffuse and terminal (2-4 cells wide)	Sparse; terminal (1-2 cells wide)
Rays Distribution number per mm	6-10	9-12
Proportion of uni- and multiseriate rays	Uniseriate 21% Multiseriate 79%	Uniseriate 62% Multiseriate 38%
Uniseriate***		
Height (cells)	2-10	2-16-(30)
(μm)	50-250	50-340-(600)
Multiseriate***		
Width (cells)	2-3	2-3
Height (μm)	200-500-(800)	200-1500 or more
Wing (cells)	1-3-(10)	1-10-(16)
Component cells	Mostly procumbent, sometimes square and upright	Mostly procumbent and square, sometimes upright

*, **, and *** represent the same as in Table 1.

Table 4. The wood anatomical features of thick stem and thin stem of *Cinnamomum camphora*.

Diameter of material (mm) (growth rings)	130 (8)	14 (4)
Pores Outline Grouping*	Oval Sol, Rad (2-4)	Oval Sol, Rad (2-4)
Distribution number per sq. mm	9-23	28-40
Vessel members		
Length** (μm)	200-530 (364)	260-430 (358)
Diameter** (μm)	60-140 (100)	35-80 (56)
Wall thickness (μm)	2-4.5	1.5-3
Perforation	Usually simple, very rarely scalariform	Usually simple, rarely scalariform
Intervessel pits	Alternate	Alternate
Fibers Length** (μm)	350-900 (618)	300-770 (538)
Diameter** (μm)	12-25 (18)	10-27 (15)
Wall thickness (μm)	2-4	2-5
Pits	Simple	Simple
Axial parenchyma	Very abundant; vasicentric to confluent	Abundant; scanty paratracheal and vasicentric
Rays Distribution number per mm	5-7	7-11
Proportion of uni- and multiseriate rays	Uniseriate 5% Multiseriate 95%	Uniseriate 16% Multiseriate 84%
Uniseriate***		
Height (cells)	1-7	1-6
(μm)	50-200	30-150
Multiseriate***		
Width (cells)	2-3	2
Height (μm)	200-400	100-300
Wing (cells)	1-2-(5)	1-2-(5)
Component cells	Mostly procumbent, sometimes square, rarely upright	Mostly procumbent, sometimes square and upright

*, **, and *** represent the same as in Table 1.

Table 5. The wood anatomical features of thick stem and thin stem of *Drimys winteri*.

Diameter of material (mm) (growth rings)	30 (14)	6 (3)
Tracheids		
Length** (μm)	1670–3250 (2500)	1600–2420 (1990)
Diameter** (μm)	23–48 (32)	12–25 (19)
Wall thickness (μm)	3–4	3–6
Bordered pits	Circular, 7-8 μm in diam.	Circular, 6-7 μm in diam.
Pit arrangement	Uni- or biseriate, sometimes triseriate	Uni- or biseriate
Axial parenchyma	Sparse; terminal	Invisible
Rays		
Distribution number per mm	6–10	12–16
Proportion of uni- and multiseriate rays	Uniseriate 57% Multiseriate 43%	Uniseriate 58% Multiseriate 42%
Uniseriate***		
Height (cells)	1–15–(30)	1–30 or more
(μm)	100–1000–(2000)	100–2300 or more
Multiseriate***		
Width (cells)	2–8	2–3
Height (μm)	500–4000	More than 2800
Wing (cells)	1–10–(35)	1–20 or more
Component cells	Upright, square, and procumbent intermingled	Usually upright and square, rarely procumbent

** and *** represent the same as in Table 1.

Table 6. Tracheary element length at the different positions in the secondary xylem of the stem in five species.

Species	Stem diameter (mm)	Elements	Element length at the different position (μm)		
			Near to pith	1 cm distant from pith	Outermost
			Range (Mean)	Range (Mean)	Range (Mean)
<i>Liriodendron tulipifera</i>	80	Vessel	160– 730 (488)	150– 800 (555)	280– 820 (558)
		Fiber	460–1080 (743)	460–1430 (981)	590–1510 (990)
<i>Magnolia salicifolia</i>	70	Vessel	360– 710 (576)	240– 810 (659)	330– 860 (659)
		Fiber	450–1120 (841)	580–1620 (1044)	560–1820 (1103)
<i>Magnolia sieboldii</i>	30	Vessel	150– 660 (429)	280– 700 (519)	200– 860 (528)
		Fiber	270– 830 (540)	410–1320 (908)	430–1430 (934)
<i>Illicium anisatum</i>	30	Vessel	400–1330 (839)	510–1540 (1103)	590–1660 (1205)
		Fiber	470–1370 (1030)	600–1810 (1310)	600–1810 (1351)
<i>Tasmania piperita</i>	40	Tracheid	1680–3900 (2800)	1800–4050 (3111)	1600–4520 (3364)

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Chapter 2.

Comparative Wood Anatomy
of Herbaceous Polycarpicae

Wood Anatomical Studies of Polycarpicae II. Ranunculales

Synopsis

The secondary xylem of the stems of 12 species belonging to 4 families — Ranunculaceae, Berberidaceae, Lardizabalaceae, and Paeoniaceae — were examined and represented by the descriptions and the photographs. The anatomical features were compared within and among the families.

Introduction

The Polycarpicae is considered to have many primitive characteristics and within the angiosperms it is an interesting group for phylogenetic consideration. It is usually divided into two groups, a woody group and a herbaceous one. In general the woody Polycarpicae is made into the Magnoliales, and the herbaceous one is the Ranunculales. The wood anatomy of the Magnoliales, as reported in the previous paper¹⁾, shows a considerable diversity of characters. On the other hand, the Ranunculales seems to be uniform in its wood anatomy. According to METCALFE and CHALK²⁾, most of the families have short vessel members with simple perforation plates, short fibers with simple pits, and wide rays in the secondary xylem. However, wood anatomical investigations in the order have not been carried out often because most of the members of the order develop secondary xylem poorly. Therefore the wood structure of many species still remains to be observed.

In this paper, the secondary xylem of several species of the Ranunculales and one species of *Paeonia*, which is now not included in the order, are described and the anatomical features are compared with each other. They are also briefly compared with the Magnoliales.

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Materials and Methods

The secondary xylem of the stems of 12 species belonging to 4 families — Ranunculaceae, Berberidaceae, Lardizabalaceae, and Paeoniaceae — were examined and the anatomical features of each species were described. The stems were collected in the field or obtained from cultivated plants or herbarium specimens. Source and stem diameter of each wood sample examined were recorded in each of the descriptions.

Samples were sectioned according to the usual techniques. Macerations were prepared with JEFFREY's fluid. Sections and macerations were stained with safranin or safranin-fastgreen combination. Quantitative data such as length, diameter, and wall thickness of tracheary elements, ray sizes, etc. are based on 30 measurements per feature. Number of pores per sq. mm of transverse section and number of rays per mm of tangential section are based on 10 measurements per feature. Measurements of element length were obtained from macerated materials.

Anatomical Descriptions

RANUNCULACEAE

Clematis patens Morr. et Decne.

Habit: Woody vine

Material: 3 mm in diameter, stem from plant cultivated in Osaka Univ. (Figs. 1-5)

Wood ring porous. Growth rings distinct. Pores decreasing abruptly in size from early to late wood. In the early wood, large pores arranged in one or two layers; solitary and in tangential multiples of 2-5; solitary pores round in outline; up to 100 μ m in tangential diameter; walls 2-4 μ m thick. In the late wood, pores mostly solitary; round to angular in outline; 12 μ m in

minimum diameter; walls 2-3 μm thick. Vessel members 110-330 (mean 221) μm long; end walls horizontal to moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 4-8 μm in diameter; with oblique slit-like apertures. Pits to axial parenchyma similar to intervessel pits. Helical thickenings fairly distinct in narrow vessels, but faintly seen in wide ones. Vascular tracheids present. Fibers 8-25 μm in diameter; walls 4-8 μm thick; 150-340 (mean 256) μm long; non-septate; with simple pits. Helical thickenings invisible. Axial parenchyma few; scanty paratracheal and vasicentric. Rays limited to wide and high primary rays.

Clematis stans Sieb. et Zucc.

Habit: Woody herb

Material: 4 mm in diameter, stem collected in Osaka Pref. (Figs. 6-10)

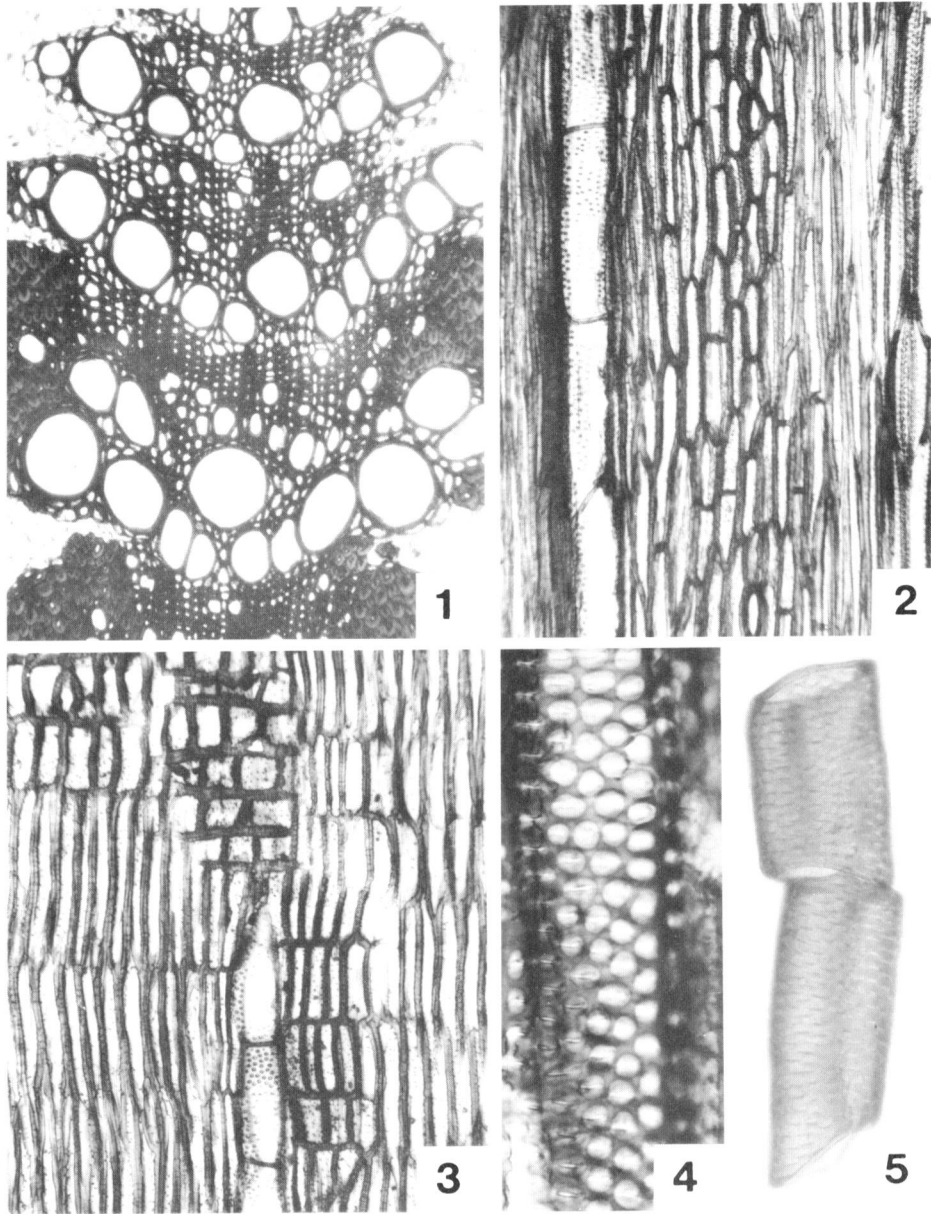
Pores decreasing in size more or less abruptly from early to late wood. In the early wood, pores arranged in one layer; solitary and in tangential multiples of 2-4; solitary pores round in outline; up to 120 μm in tangential diameter; walls 3-5 μm thick. In the late wood, pores mostly solitary; round to angular in outline; 15 μm in minimum diameter; walls 2-4 μm thick. Vessel members 150-360 (mean 255) μm long; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 5-8 μm in diameter. Fibers 7-22 μm in diameter; walls 3-5 μm thick; 200-500 (mean 348) μm long. Otherwise similar to *Clematis patens*.

Clematis sp.

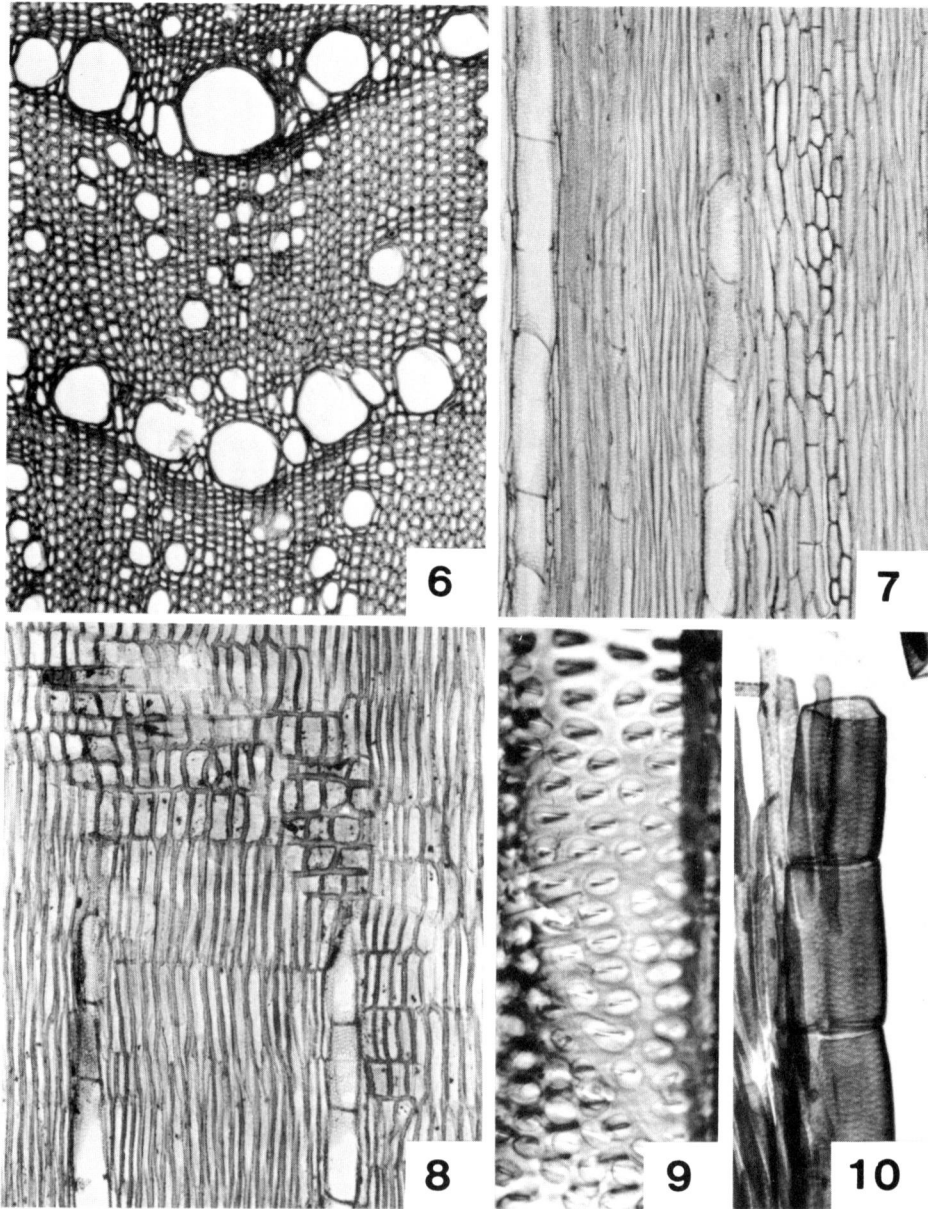
Habit: Woody vine

Material: 10 mm in diameter, stem collected by M. TAMURA in New Caledonia (Tamura 27296). (Figs. 11-16)

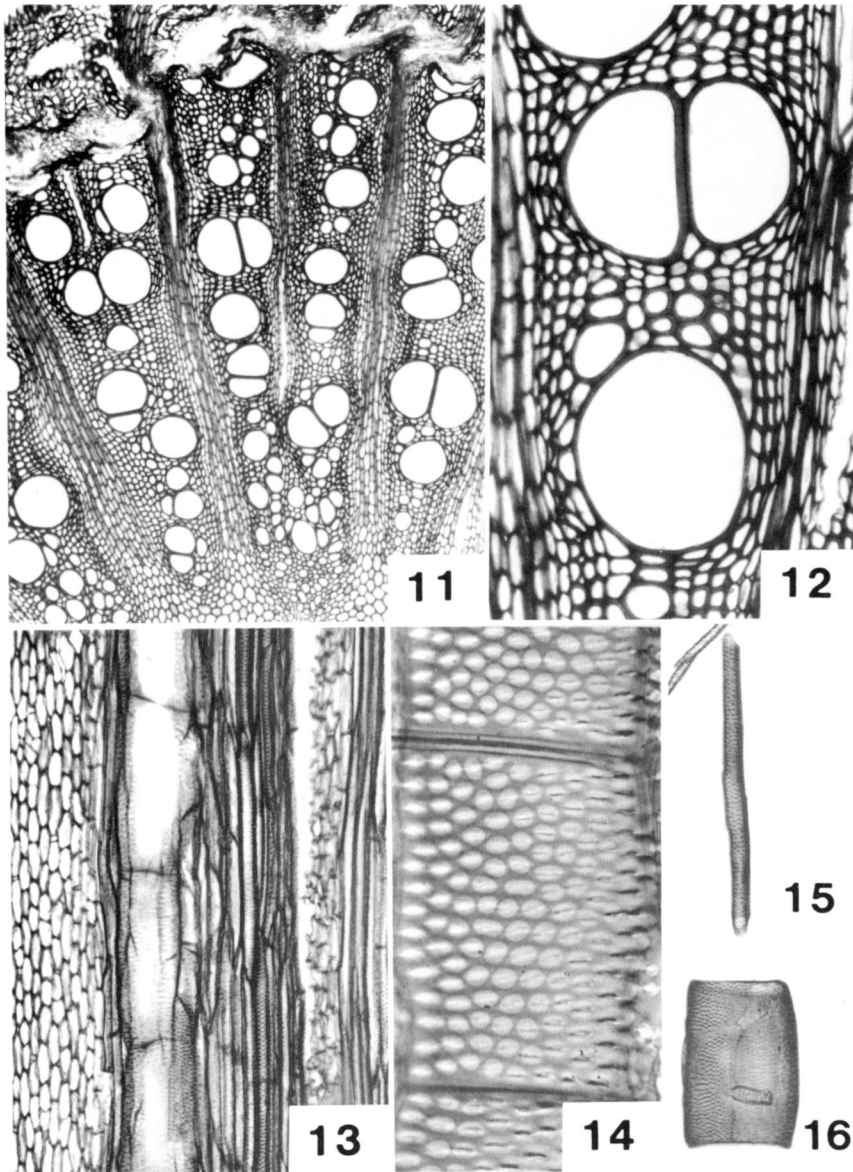
Wood diffuse porous. Growth rings indistinct. Pores evenly distributed, 30-40 per sq. mm; solitary, in radial multiples of 2-3, in tangential multiples of 2-3, and also in clusters of 3-6; solitary pores round in outline; 40-250 μm in tangential diameter; walls 4.5-8.5 μm thick. Vessel members 200-630 (mean 320) μm long; end walls horizontal to moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 6-8 μm in diameter; with oblique lenticular apertures. Pits to ray and axial parenchyma similar to intervessel pits. Helical thickenings invisible. Fibers 15-32 μm in diameter; walls 2.5-5 μm thick; 380-830 (mean 561) μm long; non-septate; with simple pits. Helical thickenings



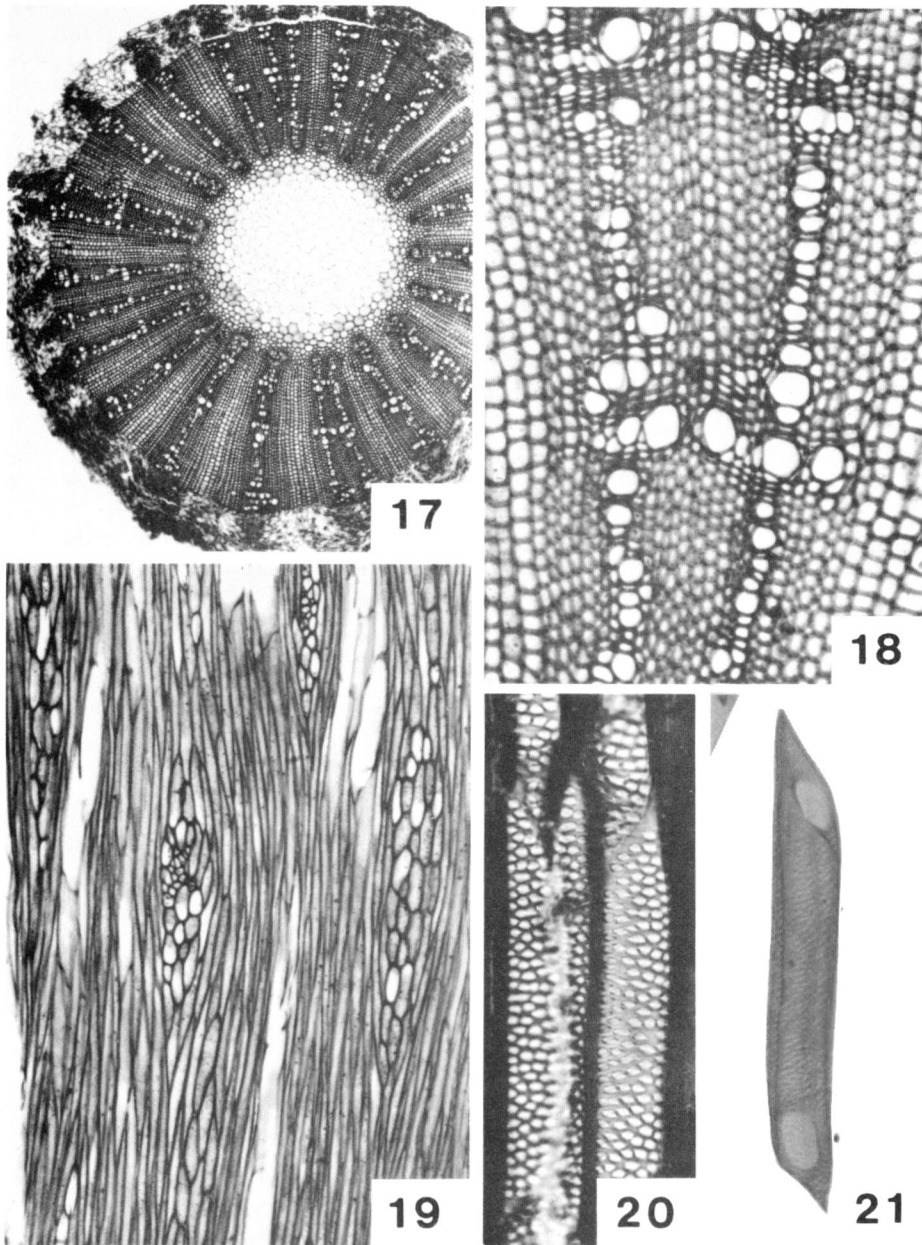
Figs. 1-5. *Clematis patens*. 1: Cross section, x130. 2: Tangential section, x130. 3: Radial section, x130. 4: Side wall pits of a vessel, x600. 5: Macerated vessel members, x300.



Figs. 6-10. *Clematis stans*. 6: Cross section. x110. 7: Tangential section. x100. 8: Radial section. x110. 9: Side wall pits of a vessel. x600. 10: Macerated vessel members and fibers. x150.



Figs. 11-16. *Clematis* sp. 11: Cross section. x40. 12: Cross section, showing vasicentric parenchyma. x110. 13: Tangential section. x75. 14: Side wall pits of vessels. x100. 15: Macerated vessel member; narrow. x75. 16: Macerated vessel member; large. x75.



Figs. 17-21. *Xanthorrhiza apiifolia*. 17: Cross section of stem, x30. 18: Cross section, x170. 19: Tangential section, x110. 20: Side walls of vessels, x600. 21: Macerated vessel member, x300.

invisible. Axial parenchyma slightly abundant; scanty paratracheal and vasicentric. Rays typically wide and high; 5-10 cells (80-150 μm) wide and more than 1 cm high.

Xanthorrhiza apiifolia L'Herit.

Habit: Shrub

Material: 3 mm in diameter, stem from plant cultivated in Osaka Univ. (Figs. 17-21)

Wood semi-ring porous. Growth rings distinct. Pores decreasing in size gradually from early to late wood. In the early wood, pores arranged in one or two layers; solitary and in tangential multiples of 2-5; solitary pores angular in outline; up to 40 μm in tangential diameter; walls 1-2 μm thick. In the late wood, pores solitary and in radial multiples of 2-5; solitary pores angular in outline; about 10 μm in minimum diameter; walls 1-2 μm thick. Vessel members 120-350 (mean 224) μm long; end walls slightly to moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; minute, 2-3 μm in diameter; with oblique slit-like apertures. Pits to axial parenchyma similar to intervessel pits. Helical thickenings faintly seen. Vascular tracheids present. Fibers 8-15 μm in diameter; walls 2-3 μm thick; 170-330 (mean 250) μm long; non-septate; with simple pits. Helical thickenings invisible. Axial parenchyma few; scanty paratracheal. Rays limited to primary, multiseriate rays; 3-8 cells (up to 150 μm) wide and 800-3000 μm or more high; composed of upright and square cells.

BERBERIDACEAE

Berberis amurensis Rupr.

Habit: Shrub

Material: 7 mm in diameter, twig from herbarium specimen (Tamura 3443). (Figs. 22-27)

Wood ring porous. Growth rings distinct, delineated by ring porosity. Pores decreasing abruptly in size from early to late wood. In the early wood, pores arranged in one layer; mostly in tangential multiples of 2-5, sometimes in clusters; pores angular to round in outline; 30-75 μm in tangential diameter; walls 1-1.5 μm thick. In the late wood, pores arranged in flame-like pattern; solitary and in multiples of radial, tangential, and oblique series; solitary pores angular in outline; about 15 μm in minimum diameter; walls 1-1.5 μm thick. Vessel members 150-300 (mean 198) μm long; end walls slightly to moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 3-5 μm in diameter; with oblique or horizontal slit-like apertures. Pits to rays similar to

intervessel pits. Helical thickenings distinct. Vascular tracheids present. **Fibers** 7-20 μm in diameter; walls 2.5-4 μm thick; 150-520 (mean 336) μm long; with simple pits; non-septate. Helical thickenings invisible. Axial parenchyma absent. **Rays** heterogeneous, mostly multiseriate, sometimes uniseriate; 4-5 rays per mm. Uniseriate rays 10-15 μm wide and 3-15 cells (60-300 μm) high; composed of upright and procumbent cells. Multiseriate rays 2-4 cells (25-50 μm) wide and mostly 200-1000 μm , sometimes more than 2 mm high; with 1-6, rarely up to 15 marginal rows of upright and procumbent cells; multiseriate parts composed usually of procumbent cells.

Berberis thunbergii DC.

Habit: Shrub

Material: 6 mm in diameter, twig from herbarium specimen (Tamura 9965). (Figs. 28-33)

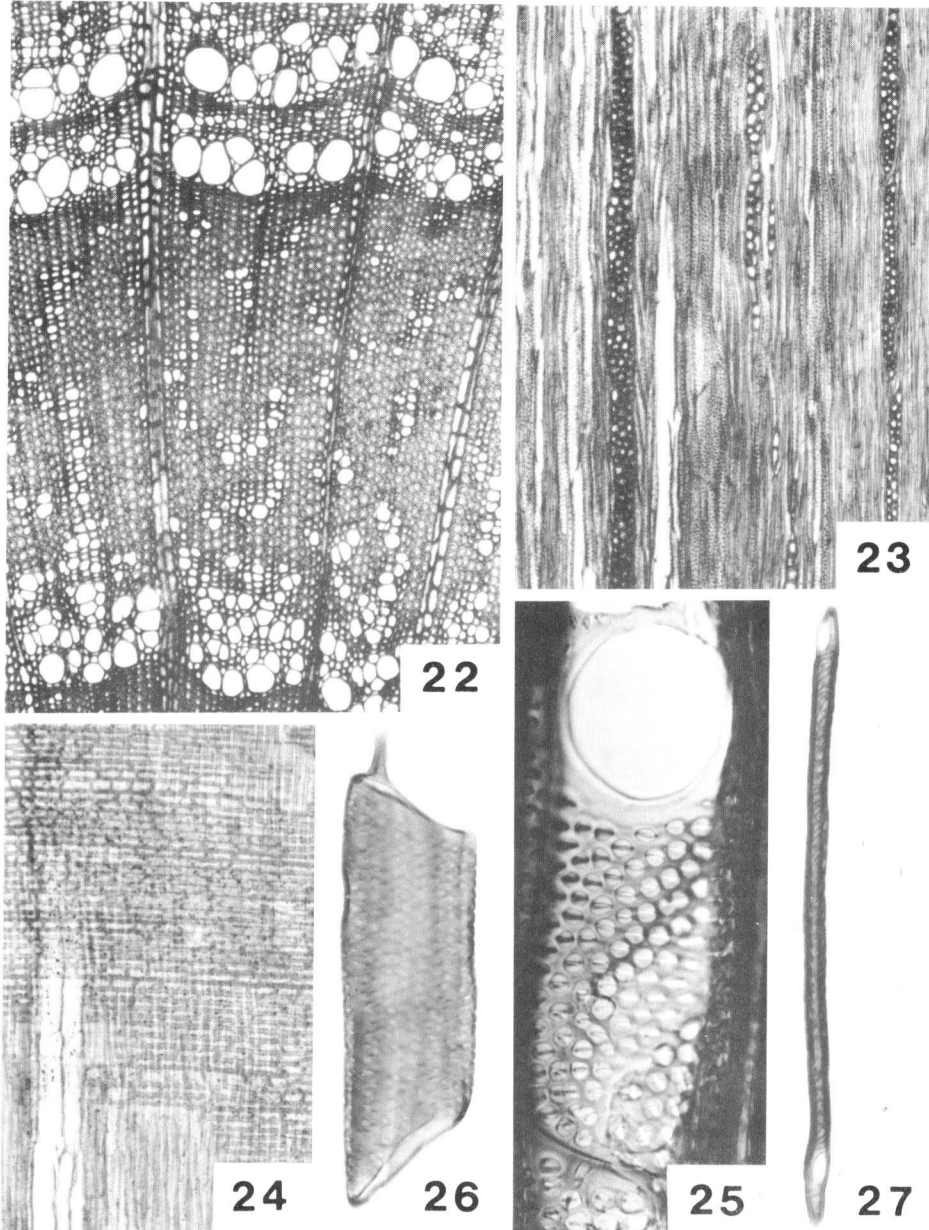
Pores 15-50 μm in diameter. **Vessel members** 150-350 (mean 243) μm long. **Fibers** 150-600 (mean 352) μm long. **Rays** usually multiseriate. Multiseriate rays mostly more than 1 mm high. Otherwise similar to *Berberis amurensis*.

Mahonia japonica (Thunb.) DC.

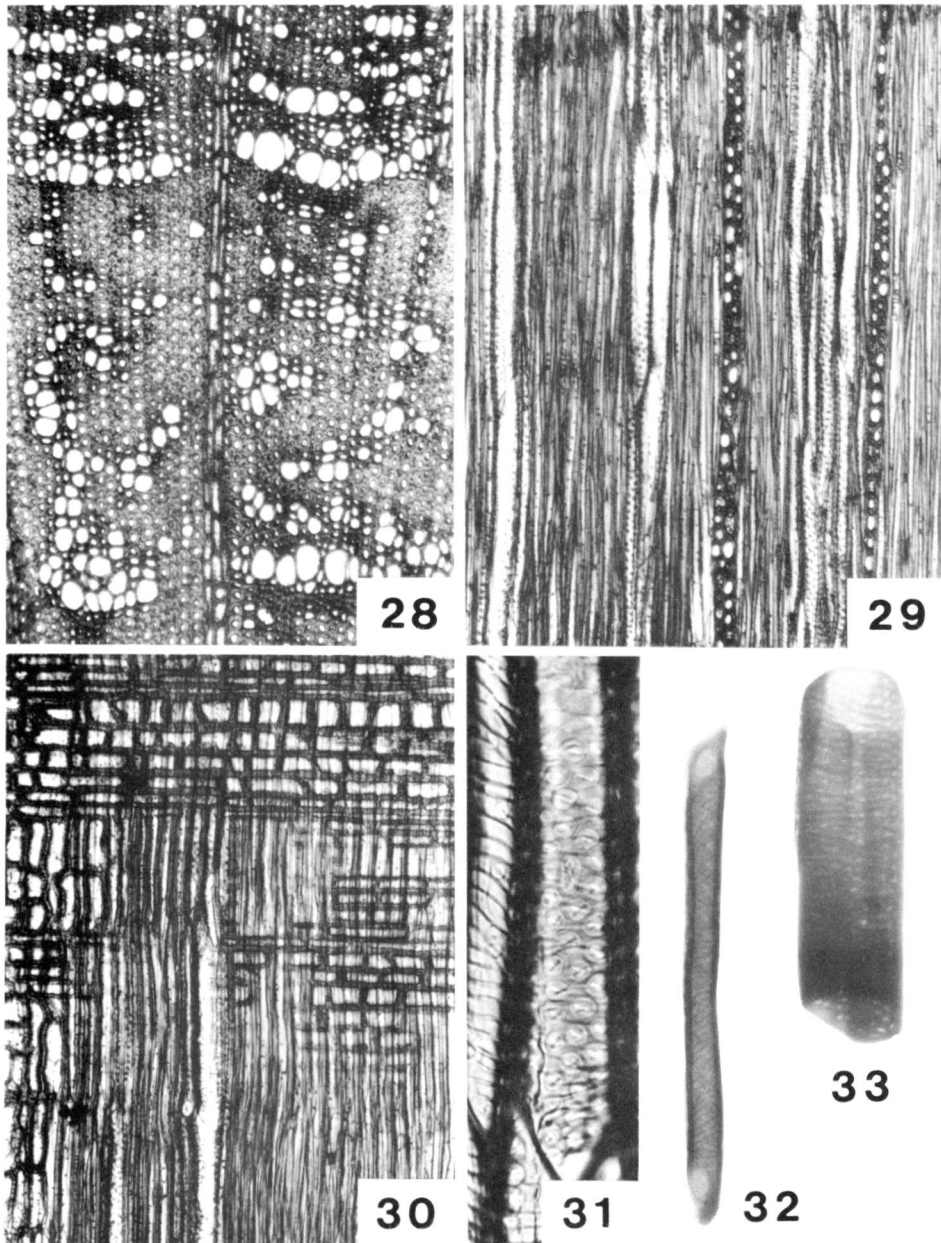
Habit: Shrub

Material: 10 mm in diameter, stem from plant cultivated in Osaka Pref. (Figs. 34-38)

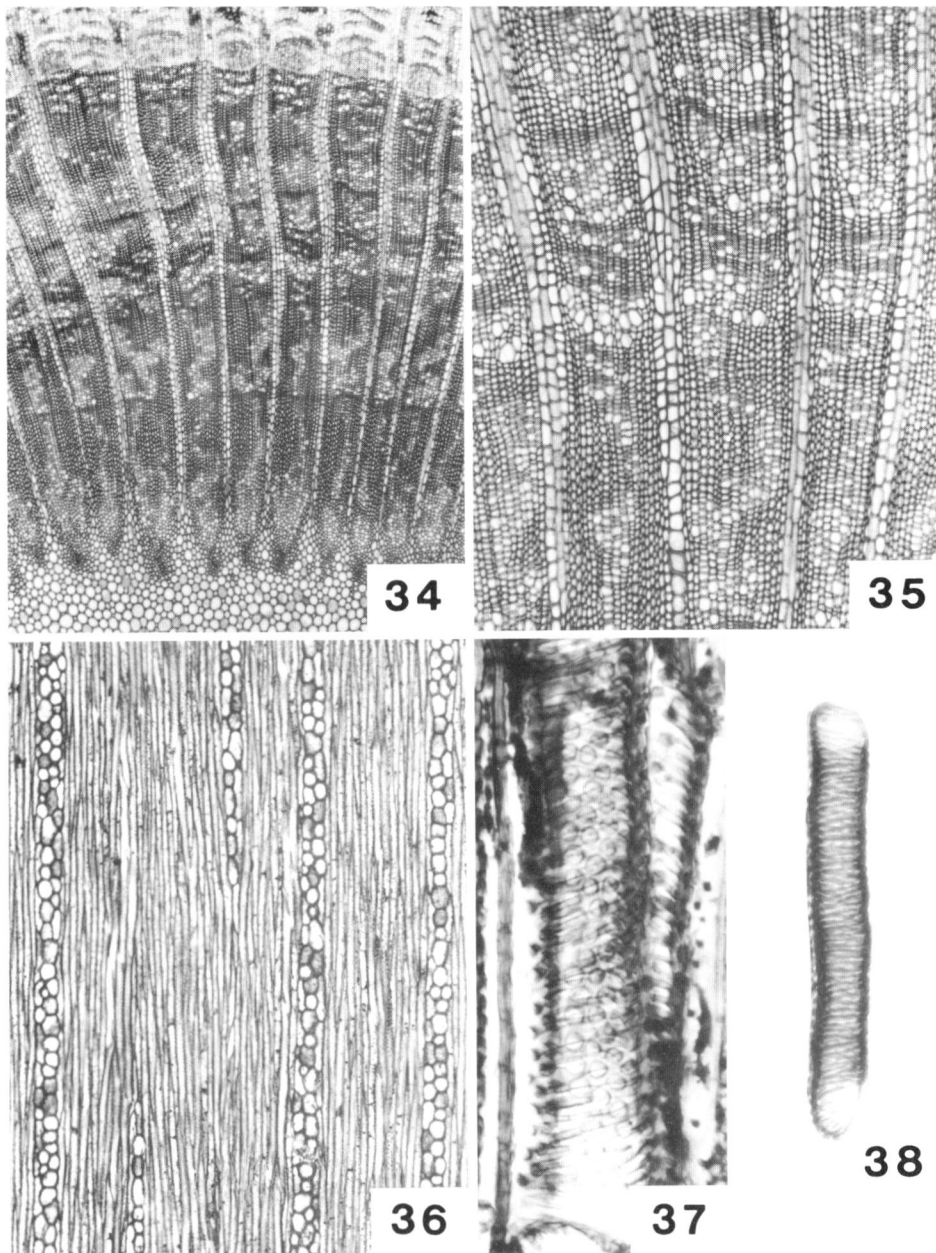
Wood semi-ring porous. Growth rings distinct. **Pores** decreasing in size gradually from early to late wood. In the early wood, pores arranged in one layer; solitary and in tangential multiples of 2-5; solitary pores angular in outline; about 30 μm in tangential diameter; walls 1-2 μm thick. In the late wood, pores arranged in flame-like pattern; solitary and in multiples of tangential, radial, and oblique series; solitary pores angular in outline; about 10 μm in minimum diameter; walls 1-2 μm thick. **Vessel members** 150-380 (mean 248) μm long; end walls slightly to moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 3-5 μm in diameter; with oblique slit-like apertures. Pits to rays similar to intervessel pits. Helical thickenings distinct. Vascular tracheids present. **Fibers** 7-15 μm in diameter; walls 2-3 μm thick; 170-470 (mean 310) μm long; with simple pits; non-septate. Helical thickenings invisible. Axial parenchyma absent. **Rays** heterogeneous, mostly multiseriate, sometimes uniseriate; 4-6 rays per mm. Uniseriate rays 20-25 μm wide and 4-10 cells (200-300 μm) high; composed of upright and square cells. Multiseriate rays 2-5 cells (40-100 μm) wide and often more than 3 mm high; with 1-8 marginal rows of



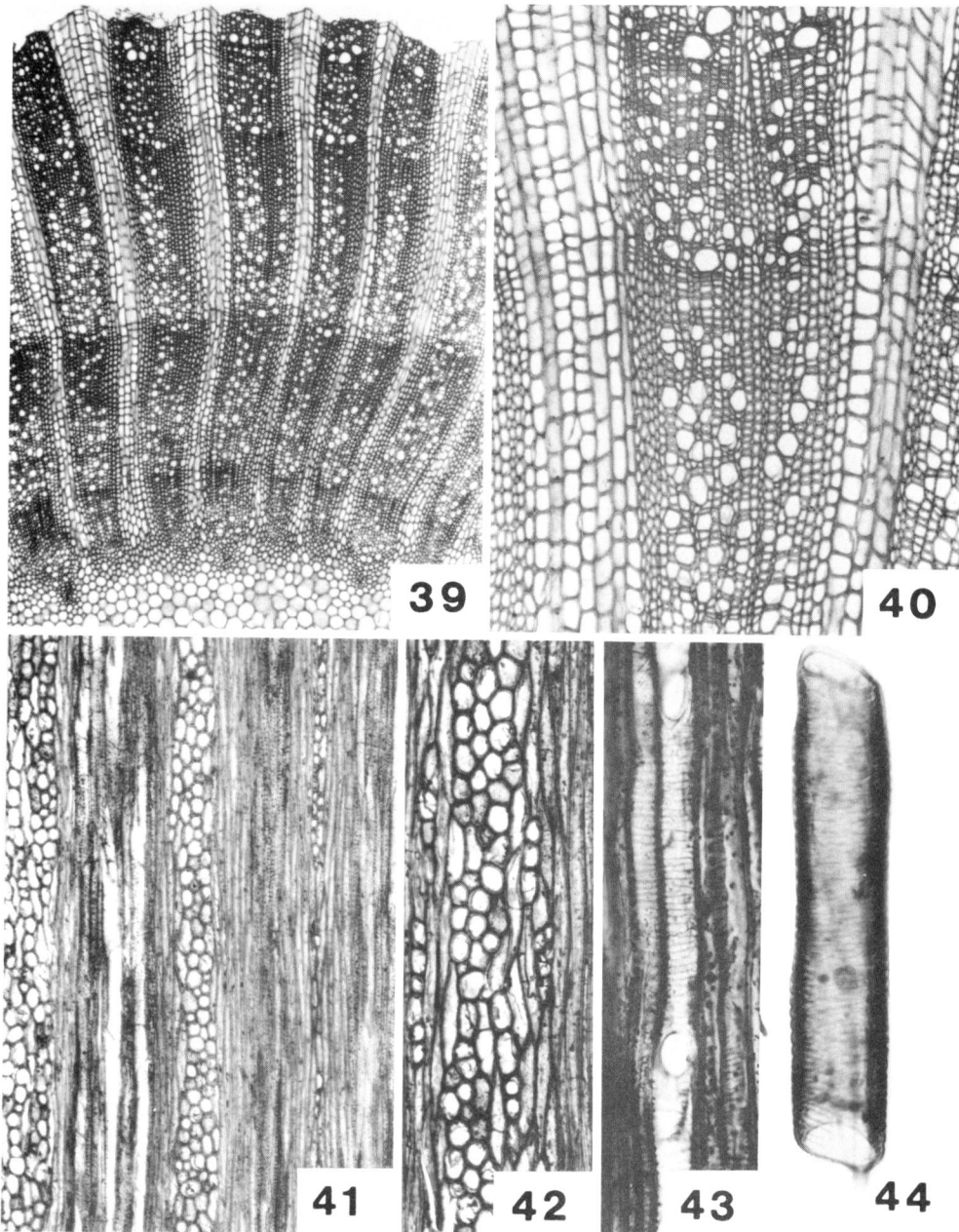
Figs. 22-27. *Berberis amurensis*. 22: Cross section, x100. 23: Tangential section, x100. 24: Ray in radial section, x110. 25: Side wall pits and simple perforation plate of a vessel, x600. 26: Macerated vessel member; large, x300. 27: Macerated vessel member; narrow, x300.



Figs. 28-33. *Berberis thunbergii*. 28: Cross section. x130. 29: Tangential section. x150. 30: Radial section. x150. 31: Side wall pits of vessels, showing helical thickenings. x600. 32: Macerated vessel member; narrow. x300. 33: Macerated vessel member; large. x300.



Figs. 34-38. *Mahonia japonica*. 34: Cross section. x35. 35: Cross section. x85. 36: Tangential section. x110. 37: Side wall pits of a vessel, showing helical thickenings. x600. 38: Macerated vessel member. x300.



Figs. 39-44. *Nandina domestica*. 39: Cross section, x45. 40: Cross section, x110. 41: Tangential section, x110. 42: Ray in tangential section, x170. 43: Vessels in radial section, showing helical thickenings and simple perforation plates, x350. 44: Macerated vessel member, x300.

upright, square, and procumbent cells; multiseriate parts composed of square and procumbent cells.

Nandina domestica Thunb.

Habit: Shrub

Material: 7 mm in diameter, stem from plant cultivated in Osaka Pref. (Figs. 39-44)

Wood diffuse porous. Growth rings distinct. Pores decreasing in size very gradually from early to late wood; mostly solitary, sometimes in clusters; solitary pores angular in outline; 10-35 μm in tangential diameter; walls 1-1.5 μm thick. Vessel members 140-410 (mean 270) μm long; end walls slightly to moderately oblique; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 3-4 μm in diameter; with oblique slit-like apertures. Pits to rays similar to intervessel pits. Helical thickenings distinct. Vascular tracheids present. Fibers 7-15 μm in diameter; walls 2-4 μm thick; 120-460 (mean 275) μm long; with simple pits; non-septate. Helical thickenings invisible. Axial parenchyma absent. Rays typically wide and high; 3-10 cells (60-180 μm) wide and more than 6 mm high; tall rays occasionally subdivided into smaller units; uni- or biseriate rays very few; 3-4 rays per mm. Component cells mostly procumbent and square, sometimes tall upright cells intermingled.

LARDIZABALACEAE

Akebia trifoliata (Thunb.) Koidzumi

Habit: Woody vine

Material: 15 mm in diameter, stem collected by K. KOSUGE in Toyama Pref. (Figs. 45-50)

Wood diffuse porous. Growth rings distinct. Pores distributed in tangential series; 80-100 pores per sq. mm; solitary and in tangential multiples of 2-4; solitary pores round to angular in outline; of two distinct sizes present, large pores 70-200 μm in tangential diameter and smaller ones about 20 μm in minimum diameter; walls 1.5-4 μm thick. Vessel members 200-510 (mean 388) μm long; end walls nearly horizontal to moderately oblique; perforation plates predominantly simple. Intervessel pits alternate; circular in outline, 5-7 μm in diameter; apertures often coalescent. Pits to axial parenchyma similar to intervessel pits. Helical thickenings present. Fibers 15-25 μm in diameter; walls 2-5 μm thick; 210-660 (mean 482) μm long; non-septate. Pits bordered, circular in outline, 5-8 μm in diameter;

with oblique slit-like apertures. Helical thickenings present. Axial parenchyma sparse; scanty paratracheal and vasicentric. Rays of two distinct sizes present, uniseriate and multiseriate. Uniseriate rays up to 8 cells (600 μm) high; composed entirely of upright cells; regular arrangement of ray cells often interrupted by large vessels. Multiseriate rays typically wide and high; 10-20 cells (180-350 μm) or more wide and more than 1 cm high; composed usually of procumbent cells, unligified towards the outside of the stem.

Decaisnea fargesii Franch.

Habit: Shrub

Material: 18 mm in diameter, plant cultivated in Kyoto Univ. (kindly sent by Dr. S. TERABAYASHI). (Figs. 51-55)

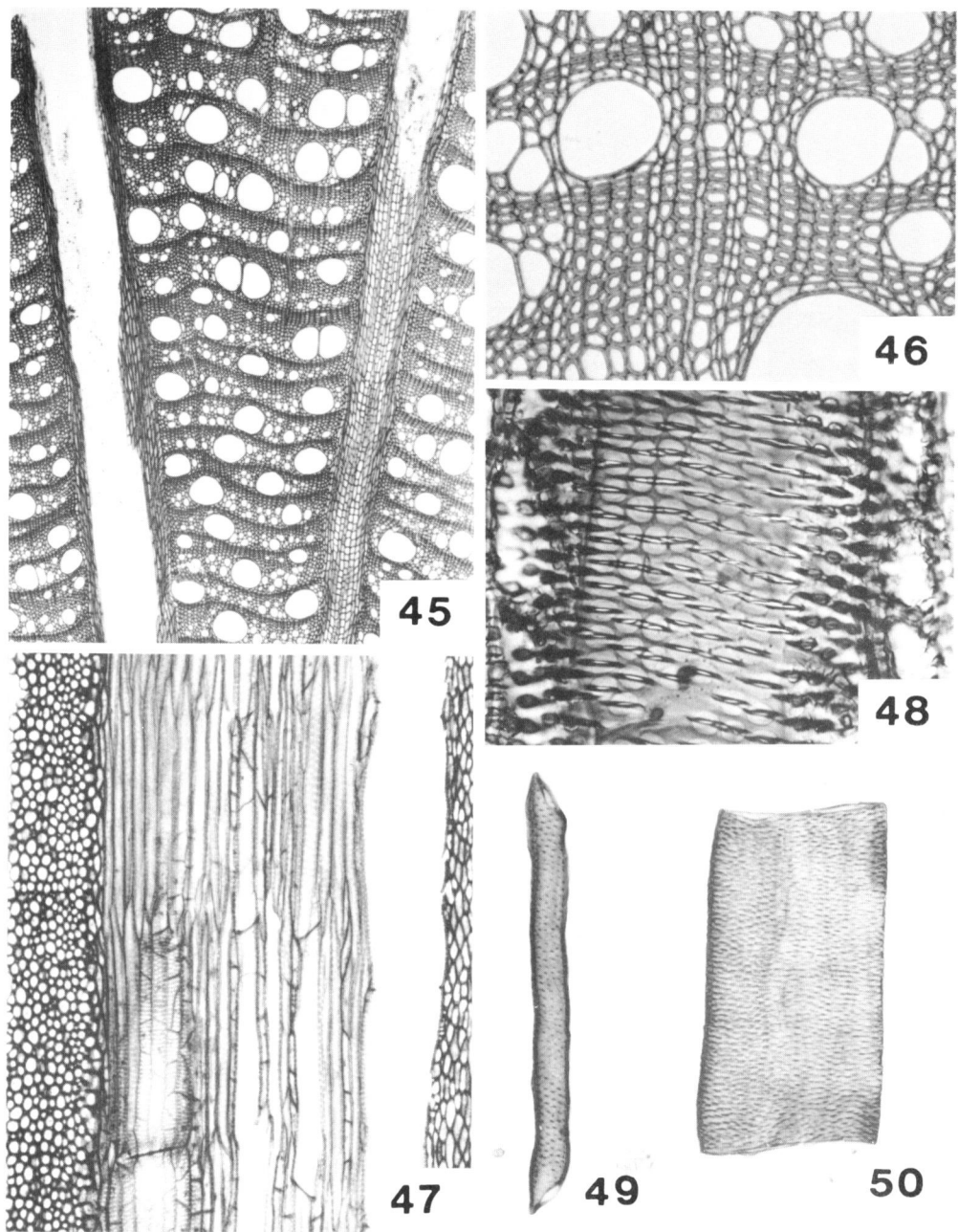
Wood diffuse porous. Growth rings distinct, delineated by 2-5 layers of radially flattened elements. Pores evenly distributed, 90-130 pores per sq. mm; solitary and in radial multiples of 2-4, sometimes in clusters; solitary pores angular in outline; 20-70 μm in tangential diameter; walls 2-3 μm thick. Vessel members 170-460 (mean 327) μm long; end walls moderately oblique; perforation plates predominantly scalariform with 8-18 bars. Intervessel pits scalariform to opposite. Pits to rays transitional to opposite; sometimes unilaterally compound. Helical thickenings invisible. Fibers 7-22 μm in diameter; walls 3-6 μm thick; 220-660 (mean 398) μm long; occasionally septate. Pit borders minute or absent; pit apertures oblique slit-like. Helical thickenings invisible. Axial parenchyma sparse; diffuse and scanty paratracheal. Rays heterogeneous, mostly multiseriate, sometimes uniseriate; 5-8 rays per mm. Uniseriate rays 15-17 μm wide and mostly 3-8 cells (70-200 μm), rarely up to 18 cells (380 μm) high; composed of upright, square, and procumbent cells. Multiseriate rays 2-7 cells (30-100 μm), mostly 3-5 cells wide and mostly 400-1200 μm , rarely up to 2 mm high; with 1-5, rarely up to 15 marginal rows of upright and square cells; multiseriate parts composed mostly of procumbent cells, rarely square cells intermingled.

Stauntonia hexaphylla (Thunb.) Decne.

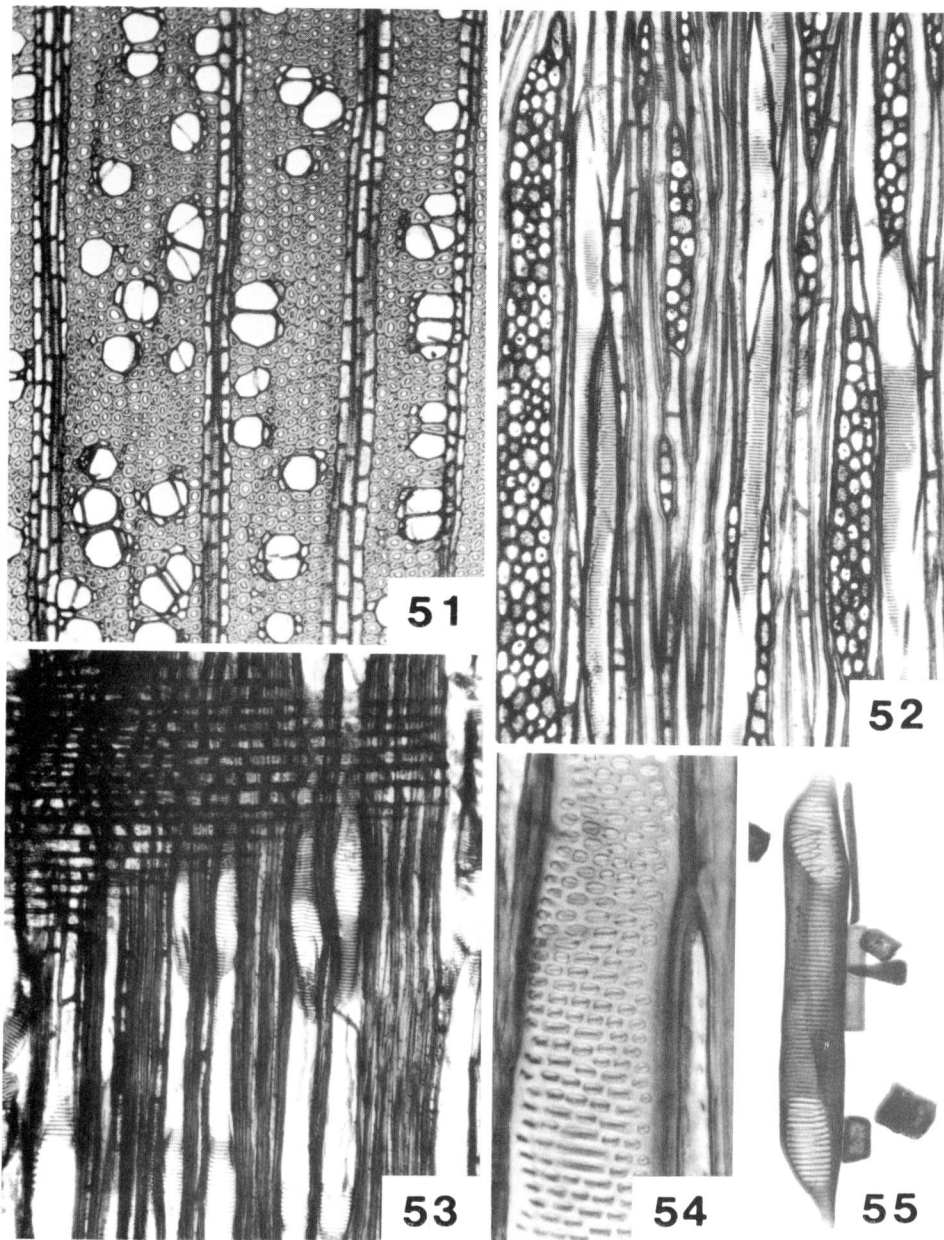
Habit: Woody vine

Material: 7 mm in diameter, stem from herbarium specimen (Kosuge & Tanaka 330). (Figs. 56-62)

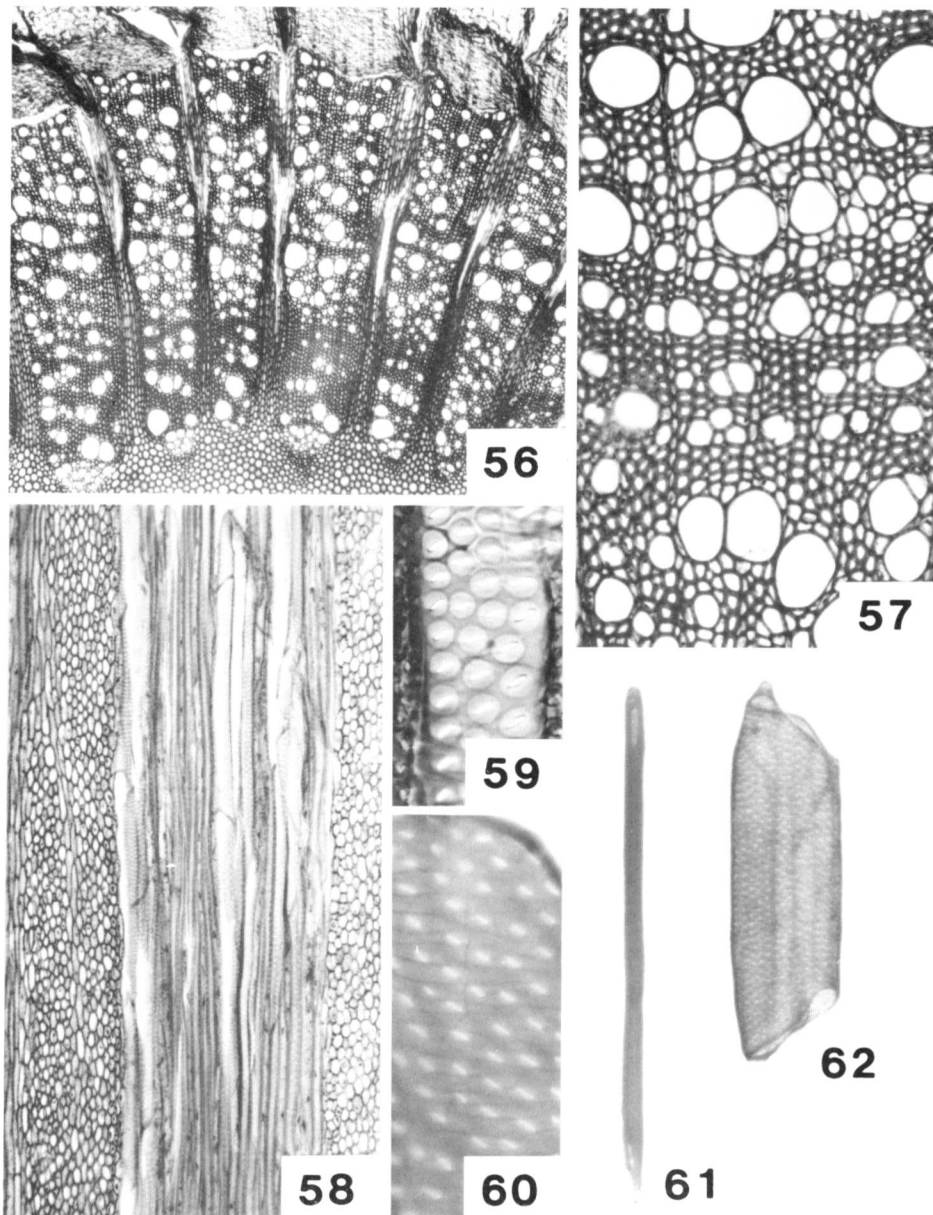
Wood diffuse porous. Growth rings distinct. Pores distributed in tangential or oblique series; solitary, in tangential multiples of 2-4, and in clusters; solitary pores round to angular



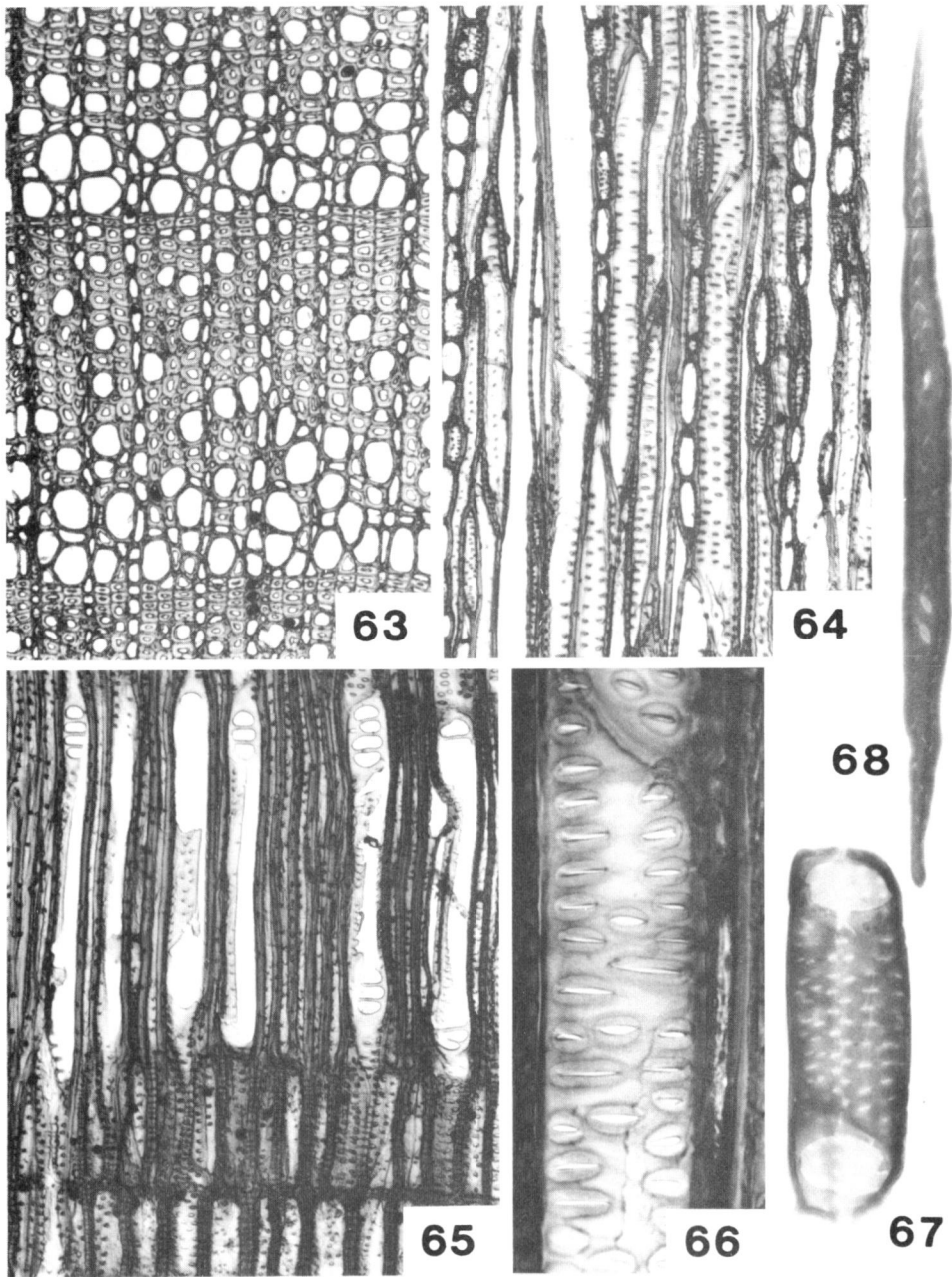
Figs. 45-50. *Akebia trifoliata*. 45: Cross section. x30. 46: Cross section, showing vasicentric parenchyma and some uniseriate rays. x150. 47: Tangential section. x100. 48: Side wall of a vessel. Pit apertures are coalescent. x500. 49: Macerated vessel member; narrow. x130. 50: Macerated vessel member; large. x130.



Figs. 51-55. *Decaisnea fargesii*. 51: Cross section. x100. 52: Tangential section. x130. 53: Radial section. x130. 54: Side wall pits of a vessel. x500. 55: Macerated vessel member and some parenchyma cells. x150.



Figs. 56-62. *Stauntonia hexaphylla*. 56: Cross section. x40. 57: Cross section. x150. 58: Tangential section. x100. 59: Side wall pits of a vessel. x600. 60: Side wall of a vessel, showing helical thickenings. x600. 61: Macerated vessel member; narrow. x150. 62: Macerated vessel member; large. x150.



Figs. 63-68. *Paeonia suffruticosa*. 63: Cross section. x150. 64: Tangential section. x150. 65: Radial section. x150. 66: Side wall pits of a vessel. x600. 67: Macerated vessel member; large. x300. 68: Macerated vessel member, showing three small perforations. x300.

in outline; of two distinct sizes present, large pores 50-120 μm in tangential diameter and smaller ones about 15 μm in minimum diameter; walls 1.5-3 μm thick. Vessel members 240-560 (mean 392) μm long; end walls moderately oblique to nearly horizontal; perforation plates exclusively simple. Intervessel pits alternate; circular in outline, 5-7 μm in diameter. Pits to rays and axial parenchyma similar to intervessel pits. Helical thickenings present. Fibers 10-25 μm in diameter; walls 3-6 μm thick; 290-740 (mean 543) μm long; non-septate. Pits bordered, circular in outline, 3-5 μm in diameter; with oblique lenticular apertures. Helical thickenings present. Axial parenchyma sparse; scanty paratracheal and vasicentric. Rays of two distinct sizes present; uniseriate and multiseriate. Uniseriate rays rather few; up to 8 cells (400 μm) high; composed entirely of upright cells. Multiseriate rays typically wide and high; 10-15 cells (100-150 μm) wide and more than 4 mm high; composed usually of procumbent cells.

PAEONIACEAE

Paeonia suffruticosa Andr.

Habit: Shrub

Material: 7 mm in diameter, stem from plant cultivated in Osaka Pref. (Figs. 63-68)

Wood ring porous. Growth rings distinct. Pores decreasing gradually in size from early to late wood. In the early wood, pores arranged in 2-3 layers; solitary and in tangential or radial couples; solitary pores angular in outline; 30-50 μm in tangential diameter; walls 2-4 μm thick. In the late wood, pores predominantly solitary; angular in outline; about 15 μm in minimum diameter; walls about 3 μm thick. Vessel members 110-660 (mean 334) μm long; end walls slightly to steeply oblique; perforation plates mostly scalariform with 1-6 thick bars, sometimes simple. Intervessel pits transitional to opposite; pits of large vessels horizontally elongated; pits of narrow vessels circular, 7-10 μm in diameter, with oblique slit-like apertures. Pits to rays similar to intervessel pits. Helical thickenings present in narrow vessels. Fibers 8-20 μm in diameter; walls 3.5-6 μm thick; 250-610 (mean 391) μm long; pits bordered, circular in outline, 3-6 μm in diameter; with oblique slit-like apertures; non-septate. Helical thickenings visible. Axial parenchyma sparse and diffuse. Rays heterogeneous, uniseriate and multiseriate; 6-12 rays per mm. Uniseriate rays about 25 μm wide; 1-15 cells (100-800 μm), rarely up to 30 cells (1200 μm) high; composed of upright and square cells. Multiseriate rays 2-3 cells (30-50 μm) wide and mostly 400-1000 μm , rarely 1500 μm high; multiseriate parts composed of upright and square, rarely procumbent cells; with 1-13, rarely up to 20 (800 μm) marginal rows of upright and square cells.

Discussion

Wood anatomy within the families

RANUNCULACEAE: This is a large family, but most of the members are herbaceous. Only two genera *Clematis* and *Xanthorrhiza* more or less develop secondary xylem. Although METCALFE and CHALK²⁾ described ring-porous wood in *Clematis*, the tropical species does not show ring porosity because the wood has no growth rings. Most of the other anatomical features of the tropical species are similar to those of Japanese species of *Clematis*. Moreover, the wood of *Clematis* and *Xanthorrhiza* are similar to each other, although the vessel members of *X. apiifolia*, compared with *Clematis* spp., show some slight differences, i.e. smaller diameter, smaller pits, thinner walls, more oblique end walls, etc.

BERBERIDACEAE: This family contains many herbaceous genera, but only *Berberis*, *Mahonia*, and *Nandina* have a woody structure. *Berberis* and *Mahonia* have ring-porous or semi-ring-porous woods, and *Nandina* has diffuse-porous wood. Rays are very high and composed of upright, square, and procumbent cells in *Nandina*. In *Berberis* and *Mahonia*, rays are often separated vertically into lower units and composed mostly of procumbent cells, and so these rays are more homogeneous than those of *Nandina*. Thus the wood of *Nandina* differs from that of *Berberis* and *Mahonia*. SHEN³⁾ has been already pointed out a distinct difference between them. In comparison with other families, however, these three genera seem to resemble each other in the wood anatomy.

LARDIZABALACEAE: The observed woods of *Akebia* and *Stauntonia* are similar to each other, but *Decaisnea fargesii* is completely different from them. The vessel members of *D. fargesii* are distinctive in having scalariform perforation plates and scalariform to opposite intervessel pittings. According to METCALFE and CHALK²⁾ and CARLQUIST⁴⁾, it is the usual case in the Lardizabalaceae that the vessel members of the secondary xylem have simple perforation plates and alternate intervessel pittings, although SOLEREDER⁵⁾ described a few *Holboellia* vessels with scalariform plates with a few bars. Therefore *D. fargesii* seems to be an exceptional case in the family. It is possible that wood of *D. fargesii* has some ancestral characteristics of the family, because it is not a climber like the members of *Akebia* or *Stauntonia* but an erect shrub. Therefore it is interesting to compare the wood with that of other families. With respect to the rays, occurrence of the uniseriate rays in *A. trifoliata* is a new finding which cannot be found in the former descriptions, which stated that the rays of *Akebia* are limited to broad, primary rays.

PAEONIACEAE: This family consists of one genus *Paeonia*. The observed wood of *P. suffruticosa* has features much the same that of *Paeonia* wood described by METCALFE and CHALK²⁾ except for the perforation plates of the vessels. They reported only scalariform plates with 2-5 thick bars in *Paeonia* vessels. However, in addition to the scalariform

plates, simple perforation plates are commonly observed in *P. suffruticosa*, as AVITA and INAMDAR⁶⁾ reported simultaneous occurrence of both types of perforation plate in six species of *Paeonia*, including *P. suffruticosa*. Although they stated that vessels with ephedroid perforation plates are common in *P. suffruticosa* and three other species of *Paeonia*, the ephedroid perforation was not used as a descriptive term in this paper because the distinction from scalariform perforation was not clearly defined. In *P. suffruticosa* narrow vessel members often have only small perforations like slits. Such vessel members are very similar to fibers (fiber-tracheids) in size and shape except for the presence of perforations. Therefore careful observation is necessary for correct description.

Comparison of wood structure among the families

The Ranunculaceae, Lardizabalaceae, and Berberidaceae are ordinarily included together in the Ranunculales⁷⁻¹⁰⁾ or in the Berberidales¹¹⁾. Vessel members of every observed species of these three families, except for those of *Decaisnea fargesii*, are similar to each other in many characters, e.g. the size, shape, perforation plate, intervessel pitting, and helical thickening. But each family has its own distinct features with the exception of the vessels: wood is mainly ring-porous in the Ranunculaceae and Berberidaceae, but diffuse-porous in the Lardizabalaceae, axial parenchyma is paratracheal in the Ranunculaceae and Lardizabalaceae, but absent in the Berberidaceae, rays are mainly broad and high, primary rays in the Ranunculaceae and Lardizabalaceae, but commonly narrow and low, secondary rays in the Berberidaceae. *Clematis*, *Akebia*, and *Stauntonia* have common features, i.e. wide and high ray structure and vessels of two distinct sizes. These similarities are likely due to the climbing habit^{2,4)}.

Although the Magnoliales, as was reported in the previous paper¹⁾, shows a considerable diversity of wood structure, the three families of the Ranunculales are relatively uniform in wood anatomy. According to the general trends of structural evolution in dicotyledonous woods¹²⁻¹⁷⁾, the Magnoliales has primitive wood structures, such as long and slender vessel members with scalariform perforation plates and scalariform intervessel pitting, fibers with conspicuously bordered pits, typically heterogeneous ray tissues. On the other hand, short vessel members with simple perforation plates and alternate intervessel pits, short fibers with simple pits, and homogeneous ray tissues shown in the observed species of the Ranunculales are regarded as specialized structures. Observed species of these three families are not similar to any one of the Magnoliales in their wood anatomy, except for *Decaisnea fargesii*, which is comparable to *Degeneria* and *Liriodendron* in relation to vessel members, to *Illicium*, *Schisandra*, *Kadsura*, and *Eupomatia* in axial parenchyma, and to *Illicium*, *Euptelea*, and some Magnoliaceae in rays.

Paeonia was once regarded as a member of the Ranunculaceae, but it is now generally

considered to constitute a distinct family Paeoniaceae. The vessel members of *Paeonia* are similar to those of the Ranunculaceae in size and shape, but decidedly different in their perforation plates which are scalariform with a few thick bars. Also *Paeonia* differs in ray structure and axial parenchyma from the members of the Ranunculaceae. KUMAZAWA¹⁸⁾ considered that wood anatomical characteristics of *Paeonia* such as the occurrence of the secondary rays and scalariform perforation plates of the vessels are of phylogenetic significance. He suggested that *Paeonia* represents a distinct family Paeoniaceae which has closer affinities to the Magnoliaceae than to the Ranunculaceae. Those characteristics of *Paeonia* are likely to have some phylogenetic significance, but it seems that the affinity of the Paeoniaceae to the Magnoliaceae is due to overestimation of vessel perforation. Based on their relationships, the most reliable opinion is that the Paeoniaceae are near to the Dilleniaceae^{8, 9, 19, 20)}. The wood of *Paeonia*, however, is different from that of the Dilleniaceae in some features, i.e. ring porosity of wood, short vessel members, reduction in the number of bars in the scalariform perforation plates, reduced ray structure. In spite of these features, DICKISON²¹⁾ states that wood anatomy does not negate the possible position of *Paeonia* as allied to, yet more highly advanced than, the Dilleniaceae. Further investigations may be necessary on the subject of the relationships between the Paeoniaceae and the Dilleniaceae.

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Chapter 3.

Comparative Wood Anatomy
of Chloranthaceae

Akira TAKAHASHI* : Wood Anatomy of *Hedyosmum orientale* MERR. et CHUN (Chloranthaceae)

高橋 晃* : *Hedyosmum orientale* MERR. et CHUN (センリョウ科) の材解剖

Hedyosmum orientale MERR. et CHUN is a shrub of the Chloranthaceae with a unique distribution in SE. Asia (S. China, Sumatra, Borneo and Central Celebes), in contrast to other members of this genus (about 35 spp.) which are distributed in the New World from Mexico to Peru and Brazil and the West Indies (VERDCOURT, 1986). Anatomical features of the wood of several species of *Hedyosmum* are known to be rather advanced for this family (SWAMY, 1953; METCALFE, 1987), but further information concerning the wood anatomy is needed. In this paper, the wood anatomy of *H. orientale* is described and anatomical differences and relationships with other members of this family are discussed.

Material

The specimen of *Hedyosmum orientale* was collected in Padang, West Sumatra, on Aug. 17, 1984 (voucher specimen No. HOTTA et al. 414). The stem is 15 mm in diameter, of which 4 mm is wood.

Description

Wood diffuse porous. Growth rings invisible. Pores evenly distributed; 35-65 pores per square mm; usually solitary, occasionally in couple or triple radial series; solitary pores polygonal in outline; 30-80 and 30-90 μm in tangential and radial diameters, respectively; thin-walled, 1.5-3 μm thick. Vessel elements 1100-2200 (mean 1713) μm long; end walls steeply inclined; perforation plates scalariform with more than 80, up to 200 or more bars; spiral thickenings invisible. Intervessel pits rarely observed, scalariform to transitional; pits of lateral walls circular bordered, 4-7 μm in diameter, with oblique lenticular apertures.

Wood fibers 1000-2100 (mean 1715) μm long; polygonal in cross section, 15-55 μm in diameter;

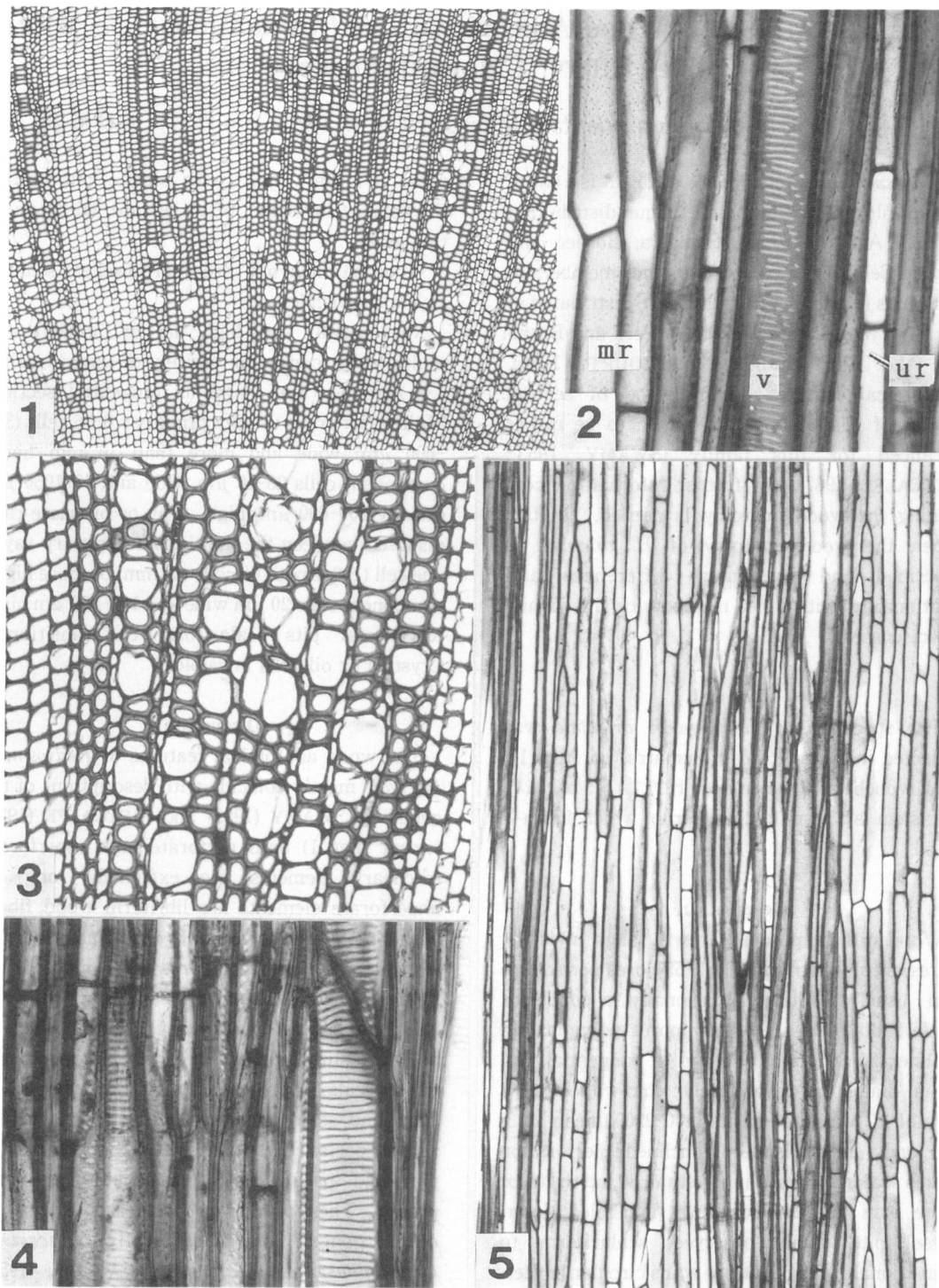
walls 3-7 μm thick; with simple pits; spiral thickenings invisible; often septate, with one or two septa.

Wood parenchyma rare; paratracheal scanty; crystals invisible.

Rays usually very high, uni- or biseriate and multiseriate, consisting entirely of upright cells; 4-8 rays per mm length in tangential section. Multiseriate rays usually primary; 8-16 cells (300-600 μm) wide and more than 10 mm high; component cells 25-40 μm wide and 80-1050 μm (mostly 200-600 μm) high. Uni- or biseriate rays disposed between the multiseriate primary rays; one cell (100 μm) to 60 cells (10 mm) or more high; component cells 20 μm wide and 100-450 μm high. Ray-Vessel pits scalariform to transitional. Crystals or oil cells invisible.

Discussion

The wood anatomical features of *Hedyosmum orientale* mostly coincide with descriptions of the genus by SWAMY (1953) and METCALFE (1987) except that 1) both perforate and imperforate tracheary elements are extremely long, 2) imperforate elements are libriform wood fibers with simple pits, 3) not only uniseriate rays but also biseriate rays are present, and 4) multiseriate rays and the component cells are very high. The wood has rather primitive characters such as angular solitary pores, long vessel elements and fibers, scalariform perforation plates with many bars, and scalariform intervessel pits, whereas rather specialized ones such as fibers with simple pits and paratracheal parenchyma are also present. These primitive characters are shared by other genera of this family, *Ascarina*, *Chloranthus*, and *Sarcandra* (SWAMY, 1953; TAKAHASHI, 1984; METCALFE, 1987), although *Sarcandra* can not be compared with others because it is vesselless (SWAMY and BAILEY, 1950). The imperforate tracheary elements of this



Figs. 1-5. Wood of *Hedyosmum orientale*. 1: Cross section ($\times 40$) showing wide multiseriate rays and diffuse pore distribution. 2: Tangential section ($\times 170$) showing a vessel (v) with scalariform intervessel pits, uniseriate rays (ur), and a multiseriate ray (mr). 3: Cross section ($\times 120$) showing angular solitary pores with thin walls and fibers with thick walls. 4: Radial section ($\times 190$) showing scalariform perforation plates (right side) and scalariform ray-vessel pits (left side). 5: Tangential section ($\times 50$) showing two multiseriate rays.

species are most advanced ones in *Hedyosmum*, which usually has fiber-tracheids with reduced bordered pits, while those of other genera are tracheids or fiber-tracheids with distinctly bordered pits (SWAMY, 1953; METCALFE, 1987). Wood parenchyma is predominantly paratracheal in *Hedyosmum* in contrast with apotracheal parenchyma in other genera (SWAMY, 1953; METCALFE, 1987), although a tendency towards paratracheal parenchyma in *Ascarina* and *Chloranthus* is pointed out by TAKAHASHI (1984, 1985). The ray system of this species may be classified into Heterogeneous Type I (KRIBS, 1935) based on the form and the component cells, as stated by SWAMY (1953). The multiseriate rays, however, are typically wide and high primary rays, which are also characteristic of other shrubby genera *Chloranthus* and *Sarcandra* (METCALFE, 1987) and different from those of arborescent species of *Ascarina* (PATEL, 1975; TAKAHASHI, 1985). It seems that the form of the rays is related to the shrubby habit, as in *Chloranthus* or *Sarcandra*, and the rays are rather specialized, differing from the KRIBS' Heterogeneous Type I. From the view point of wood anatomy, *Hedyosmum* is the most advanced genus in the family and this species has more specialized features than other members of the genus.

Acknowledgments

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摘要

Hedyosmum orientale MERR. et CHUN (センリョウ科) の材解剖学的記載を行ない、この科の他属との相違や関係について論じた。

この種の材は、管孔は角ばり、通常単独配列である。道管要素は 1,713 μm と長く、多数の横線のある階段状穿孔と階段状の道管間壁孔を有する。繊維細胞は単壁孔を有する真性木繊維で、平均 1,715 μm と長い。木部柔組織は少ないが随伴散在型である。放射組織は単列または二列のものと多列のものがあり、いずれも高い直立細胞からなる。多列放射組織は通常、幅広くて高さの非常に高い一次放射組織である、などの特徴をもつことがわかった。これらのほとんどの特徴はこの属の従来に記載に一致するが、管状要素が極めて長いこと、繊維細胞が真性木繊維であること、放射組織には二列のものがあること、多列放射組織とその構成細胞が極めて高いことが異なっている。

長い管状要素や、階段状穿孔と階段状の道管間壁孔を有する道管要素などの原始的な特徴は、センリョウ科の他属においても共通して見られるものである。真性繊維あるいは退化した有縁壁孔を有する繊維状仮道管と、随伴散在型柔組織とは *Hedyosmum* 属の特徴であり、他属のそれらが仮道管か顕著な有縁壁孔を有する繊維状仮道管および、独立柔組織であるのに対して進んだ特徴である。極めて高い多列放射組織はセンリョウ属やヒトリシズカ属と同様の形態で、灌木であることとの関係で特殊化したものと思われる。

材解剖学的見地から、*Hedyosmum* 属は原始的特徴を数多くもつセンリョウ科のなかでも最も進んだ属であり、その中でこの種はより多くの特殊化した特徴をもっていると言える。

(Received Dec. 19, 1987)

Comparative Wood Anatomy of Chloranthaceae

The members of the Chloranthaceae are herbs, shrubs, and trees which are distributed in tropical and temperate zone, including Japan. The family consists of four genera, i.e. Ascarina, Chloranthus, Hedyosmum, and Sarcandra, and has been classified in the Piperales (Melchior, 1964) according to the similarities in the floral morphology among the members of the order. Since Swamy (1953) indicated the difference in the nodal anatomy between this family and the members of the Piperales, the Chloranthaceae are usually classified in the Magnoliales (sensu lato), especially associated with families around the Lauraceae (Thorne, 1974; Tamura, 1974; Takhtajan, 1980).

From the view points of the wood anatomy, the Chloranthaceae are regarded as one of the primitive families in the dicotyledons, because a member of the family, *Sarcandra* lacks vessels and the other members have narrow and slender vessels with scalariform perforation plates with many bars. In the Magnoliales, there are slender vessels with scalariform perforation plates in the Magnoliaceae, Eupomatiaceae, Cercidiphyllaceae, etc. and also vesselless woods in the Winteraceae and Trochodendraceae (Metcalfe and Chalk, 1950). It is taxonomically interesting to compare the woods of these families with those of the Chloranthaceae.

The members of the Magnoliales are generally divided into four groups, i.e. group of families around the Magnoliaceae,

group of the Illiciaceae and Schisandraceae, group consisting of the Trochodendraceae, Tetracentraceae, Cercidiphyllaceae, and Eupteleaceae, and group of families associated with the Lauraceae. In the present investigation, some anatomical features of the wood of the Chloranthaceae are compared with those of the families of these groups.

MATERIALS AND METHODS

Observations were made on 6 wood specimens of four species of three genera in the Chloranthaceae : Ascarina philippinensis, A. rubricaulis, Chloranthus spicatus, and Sarcandra glabra. Also observations were made on 45 wood specimens of 35 species of 29 genera of 17 families in the Magnoliales. In addition to the present observation, anatomical data are supplied from literature. On the woods of the four families which were not obtained, all anatomical data are based on literature.

Wood specimens were sectioned according to the usual techniques. Macerations were prepared with Jeffrey's fluid. Sections and macerations were stained with safranin.

RESULTS AND DISCUSSION

I. A brief description of wood structure of the Chloranthaceae.

Sarcandra is vesselless and the other three genera have vessels. Most of the tracheids in Sarcandra have circular bordered pits arranged in uniseriate rows on the radial walls, and a few tracheids have horizontally long, bordered pits arranged in scalariform pattern on the overlapping end walls. The vessel members of the other genera are narrow, long, and with scalariform perforation plates with many bars. The intervessel pits are scalariform.

Both multiseriate and uniseriate rays are present in Sar-

candra and Ascarina, but in Chloranthus and Hedyosmum, the rays are mostly multiseriate and the uniseriate rays are rather few. The multiseriate rays of all the genera are wide and high. Constituent cells of the rays are usually upright, but square and procumbent cells also occur in older secondary xylem of Ascarina.

The axial parenchyma is scarce and diffuse in Sarcandra and Chloranthus, but Chloranthus shows a tendency to be paratracheal. Ascarina has diffuse, diffuse-in-aggregate, and scanty paratracheal parenchyma. Hedyosmum has scanty paratracheal parenchyma (Metcalf and Chalk, 1950; Swamy, 1953).

II. Comparison on certain anatomical features of the Chloranthaceae with those of the families of the Magnoliales.

1. Tracheary elements

The Winteraceae, Trochodendraceae, Tetracentraceae, and Amborellaceae are all vesselless and other families are long and narrow, with scalariform perforation plates with many bars, and with scalariform intervessel pits. Rather few families have short vessel members with simple perforation plates and alternate intervessel pits. These different kinds of tracheary elements, tracheids in vesselless woods and short or long vessel members, are present together in each group of the families. The vesselless condition or narrow and long vessel members like those of the Chloranthaceae are shown in the members of every groups, consequently the tracheary elements may not evidence an affinity of the Chloranthaceae to a certain family, or families.

2. Axial parenchyma

The distribution patterns of the axial parenchyma in each group are summarized as follow ;

Magnolial group : absent, diffuse, banded apotracheal, terminal

Illicial group : scanty paratracheal, terminal

Trochodendral group : diffuse, diffuse-in-aggregate, terminal

Laural group : absent, diffuse, diffuse-in-aggregate, scanty
paratracheal, vasicentric, confluent

According to Kribs (1937) and Carlquist (1961), who demonstrate the evolutionary specialization of distribution patterns of the axial parenchyma in dicotyledons, diffuse parenchyma is a primitive type, and terminal or vasicentric parenchyma is a specialized one. It seems that there are two course of specialization of the distribution pattern of the axial parenchyma in the groups of the Magnoliales families, i.e. from the basic type, to terminal parenchyma in the Magnolial group and to vasicentric or confluent parenchyma in the Laural group. The occurrence of terminal parenchyma in the Illicial and Trochodendral groups suggests the relationships between these groups and the Magnolial group. Also the axial parenchyma of the Chloranthaceae — diffuse, diffuse-in-aggregate, and scanty paratracheal — suggests the relation of the family to the Laural group. Thus the distribution patterns of the axial parenchyma seems to have an importance for grouping the families in the Magnoliales. The taxonomical importance of the distribution patterns of the axial parenchyma in these plants is also suggested by Gottwald (1977).

CONCLUSION

The possible relation of the Chloranthaceae to the Laural group was indicated. In the Lauraceae, Hernandiaceae, and Lactoridaceae, however, the wood structures are highly specialized and show little similarity to those of the Chloranthaceae. In the Laural group, Monimiaceae and the allied families — Amborellaceae, Austrobaileyaceae, Gomortegaceae —, which are once included in Monimiaceae, have many similarities to the Chloranthaceae in the wood anatomy.

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Chapter 4.

A Comparison
of Tracheary Elements

Akira TAKAHASHI * & Michio TAMURA **: An Evolutional Trend in Dimension of the Tracheary Elements of the Woody Polycarpicae

高橋 晃* ・田村道夫** : 木本性多心皮類の木部管状要素の長さ
と直径における進化傾向

The Polycarpicae are generally regarded as the most primitive group of the angiosperms containing Magnoliales, Illiciales, Laurales, Piperales, Trochodendrales, Ranunculales and so on. In the woody group, vesselless families such as Winteraceae, Trochodendraceae, Tetracentraceae, and Amborellaceae are included. It was already known that morphological features of the vessel elements and imperforate tracheary elements or "fibers" in the Polycarpicae vary considerably (Metcalf and Chalk 1950, Takahashi 1985a, b, Metcalfe 1987). Some vessel elements have scalariform perforations at the steeply inclined ends and scalariform intervessel pits on the lateral walls, whereas some others have simple perforations at the nearly horizontal ends and alternate intervessel pits on the lateral walls. Some fibers have conspicuously bordered circular pits and some others have simple ones. According to the general trends of the vessel evolution, primitive vessel elements are very long and narrow, and as they advance, the length becomes shorter and the diameter wider (Bailey and Tupper 1918, Frost 1930, Bailey

1944). On the other hand, fibers become more or less shorter but not so much wider as they advance. Thus the difference between the length and the width of vessel elements and those of fibers becomes greater. In this study, we attempted to show evolutionary trends in the tracheary elements, based on their length and diameter, in woody species and also in several herbaceous ones of the Polycarpicae.

Materials and Methods

In this study 29 species of 17 families in the woody Polycarpicae, including 6 vesselless species, and 8 species of 4 families in the herbaceous Polycarpicae were examined (Tab. 1). The wood samples used in this study were more than 2 cm in stem diameter except for small shrubs. The materials were sectioned and macerated by the methods used by Takahashi (1985a). In every species examined, length of more than 50 macerated elements was measured. Diameter was obtained from more than 50 measurements of tangential diameter in the cross sections. From the values obtained, mean, standard deviation, F/V ratio (ratio of mean fiber length to mean vessel element length), and L/D ratio (ratio of mean length to mean diameter) were calculated. The values of L/D ratio were transformed to their natural logarithm ($\ln(L/D)$).

Results

Length of tracheary elements

The minimal, maximal and mean lengths, and the standard deviations of the vessel elements and fibers are given in Tab. 2 and plotted in Fig. 1. The values of F/V ratio were plotted against the mean length of fibers in Fig. 2. In the figure,

F/V ratio of the vesselless species was expressed as 1.0. The vessel element and fiber were derived from tracheid, and then the difference between vessel element and fiber is smaller, the value of F/V ratio is closer to 1.0.

As shown in Fig. 1, five species of the vesselless dicotyledons (No. 1-5) have long tracheids of more than 2500 μm in mean length. Tracheids of Sarcandra glabra (No. 6, about 1500 μm in mean length) are considerably shorter than those of the other vesselless species. Vessel elements and fibers of Ascarina (No. 7, 9) and Hedyosmum (No. 8) are very longer than those of the other vessel-bearing families. Chloranthus spicatus (No. 13) has the shortest tracheary elements in this family, but the vessel elements are long in comparison with those of the other vessel-bearing families. In those four species of the Chloranthaceae, the vessel element length and fiber length are not so much different. In eleven species from No. 10 (Illicium anisatum) to No. 20 (Euptelea polyandra), vessel elements are 700-1200 μm and fibers are 1000-1800 μm in mean length. The range of vessel element length and that of fiber length overlap each other in the species in the case of longer vessel elements, e.g., Illicium anisatum (No. 10), and the overlapping becomes smaller as vessel elements become shorter. In five species of the Magnoliaceae (No. 21-25), vessel elements are 500-650 μm and fibers are 900-1100 μm in mean length, and there is a gap between the range of standard deviation of vessel element and that of fiber. In Cinnamomum camphora (No. 26), Litsea citriodora (No. 27), Hernandia nymphaefolia (No. 28), and Piper aduncum (No. 29), vessel elements are about 400 μm and fibers are 600-700 μm in mean length, and there is a gap

between the ranges of their standard deviations. In eight species of the herbaceous Polycarpicae (No. 30-37), tracheary elements are shorter than those of the woody species, except two species of the Lardizabalaceae (No. 30, 31). The range of vessel element and that of fiber overlap in those eight species.

F/V ratio of all 37 species examined shows the values under 2.0. The species are divided into four groups on the basis of relation of F/V ratio to mean fiber length, as shown in Fig. 2. The first group consists of vesselless plants (No. 1-5) whose tracheids are very long, more than 2500 μm in mean length, and values of F/V ratio are 1.0. The second group consists of five species of the Chloranthaceae (No. 6-9, 13), Illicium anisatum (No. 10), Eupomatia laurina (No. 12), Cercidiphyllum japonicum (No. 14), Galbulimima belgraveana (No. 15), Austrobaileya maculata (No. 16), two species of the Schisandraceae (No. 17, 18) and Euptelea polyandra (No. 20) whose fibers are more than about 1000 μm in mean length and values of F/V ratio are under 1.4. Sarcandra glabra (No. 6) is vesselless in the secondary xylem, but it is separated from the first group because its tracheids are distinctly shorter than those of the other vesselless species. The species of the Chloranthaceae (No. 6-9, 13) are situated nearer to the first group as compared with the other members of the second group. The third group consists of Trimenia papuana (No. 11), Degeneria vitiensis (No. 19), five species of the Magnoliaceae (No. 21-25), two species of the Lauraceae (No. 26, 27), Hernandia nymphaefolia (No. 28) and Piper aduncum (No. 29) whose fibers are 600-1200 μm in mean length and values of F/V ratio are over 1.5. Fibers of Trimenia papuana (No. 11) are

distinctly longer than those of the other members of this group, though F/V ratio is nearly the same. The fourth group consists of eight herbaceous species (No. 30-37) whose fibers are short, under 600 μm in mean length, and values of F/V ratio are under 1.5.

Diameter of tracheary elements and its relation with the length

The minimal, maximal and mean diameters, and the standard deviations of the vessel elements and fibers are given in Tab. 3 and plotted in Fig. 3. The values of $\ln(L/D)$ of the vessel elements and fibers are given in Tab. 3 and Fig. 4.

As shown in Fig. 3, mean diameter of fibers varies slightly (9.2 to 32.1 μm), while that of vessel elements varies remarkably (17.3 to 92.5 μm). In the vessel-bearing woody species (No. 7 to 29), the difference between diameter of vessel elements and that of fibers is smaller in the lower numbered species and larger in the higher numbered species. In some species, whose mean diameter of vessel elements are less than 45 μm , i. e., Chloranthus spicatus (No. 13), Illicium anisatum (No. 10), Cercidiphyllum japonicum (No. 14), Schisandra repanda (No. 17), Kadsura japonica (No. 18) and Euptelea polyandra (No. 20), the range of diameter of vessel elements and that of fibers overlap each other. In Degeneria vitiensis (No. 19), five species of the Magnoliaceae (No. 21-25), two species of the Lauraceae (No. 26, 27), Hernandia nymphaefolia (No. 28) and Piper aduncum (No. 29) whose mean diameters of vessel elements are more than 50 μm , the range of diameter of vessel elements and that of fibers do not overlap. But in two species of Ascarina (No. 7, 9), Hedyosmum orientale

(No. 8), Trimenia papuana (No. 11), Eupomatia laurina (No. 12) and Austrobaileya maculata (No. 16) whose mean diameter of vessel elements is also more than 50 μm , the ranges more or less overlap each other. In the herbaceous species (No. 30-37), diameters of vessel elements widely vary from 17 to 180 μm . In most species, the mean diameters are markedly lower than the middle of the ranges. The ranges between vessel elements and fibers more or less overlap each other.

In the woody species (No. 1-29), as shown in Fig. 4, values of $\ln(L/D)$ of fibers are arranged in a nearly straight line from maximum 4.93 (No. 4, Trochodendron aralioides) to minimum 3.73 (No. 28, Hernandia nymphaefolia), and those of vessel elements are also arranged in a nearly straight line from maximum 3.74 (No. 13, Chloranthus spicatus) to minimum 1.48 (No. 29, Piper aduncum). The gap between the value of $\ln(L/D)$ of vessel element and that of fiber becomes larger as the species number becomes higher. In the herbaceous species (No. 30-37), values of $\ln(L/D)$ of fibers vary from maximum 3.61 (No. 35, Berberis thunbergii) to minimum 3.00 (No. 37, Clematis patens), and those of vessel elements vary from maximum 2.69 (No. 33, Nandina domestica) to minimum 1.63 (No. 37, Clematis patens). The gap between the value of $\ln(L/D)$ of vessel element and that of fiber is small in Paeonia suffruticosa (No. 32) and three species of the Berberidaceae (No. 33-35), but slightly larger in the species of the Lardizabalaceae (No. 30, 31) and Ranunculaceae (No. 36, 37).

Discussion

The tracheary elements of the woody Polycarpicae observed in this study vary in length which suggests that the group

includes the elements on various evolutionary stages. In the Austrobaileyaceae, Chloranthaceae, Eupomatiaceae, Illiciaceae, Trimeniaceae, etc., which are regarded as primitive members of the woody Polycarpicae, the vessel elements and fibers are long and not so much different from each other in length and the F/V ratio is low. On the other hand, in the Hernandiaceae, Lauraceae and Piperaceae, which are considered to be advanced, the tracheary elements are short. The fibers are distinctly longer than the vessel elements and a gap is recognized between them, and F/V ratio is high.

In gymnosperms, the lengths of tracheary elements of Chamaecyparis, Cryptomeria and Ephedra were measured and compared with those of the Polycarpicae. The tracheids of Chamaecyparis obtusa (2490 μm in mean length) and Cryptomeria japonica (3113 μm in mean length) are nearly the same in length with those of the vesselless dicotyledons. The tracheary elements of Ephedra pachyclada, as will be mentioned later, are closer in length to those of the herbaceous Polycarpicae than to the woody ones. In non-polycarpicean angiosperms, such as Aquifoliaceae, Compositae, Fagaceae, Rosaceae, Styracaceae, etc., the lengths of tracheary elements were measured. The tracheary elements of these families are not so long, fibers are less than 1 mm and vessel elements are less than 600 μm in mean length. In most species, values of F/V ratio are between 1.5 to 2.0, but in Artemisia stelleriana (Compositae), Prunus yedoensis (Rosaceae) and Quercus glauca (Fagaceae), values of F/V ratio are high, more than 2.0, while in some species of Ilex (Aquifoliaceae), the values are low, about 1.3. If those values are plotted in Fig. 2, they fall into the area of the third group of the Polycarpicae (fiber

length is less than 1 mm and F/V ratio is more than 1.5). According to Carlquist (1988), F/V ratio of the angiosperms is about 2.0 in general. But in many species of the woody Polycarpicae examined in this study, values of F/V ratio are remarkably low (1.1 in Ascarina philippinensis, Hedyosmum orientale and Illicium anisatum, 1.2 in Ascarina rubricaulis, Cercidiphyllum japonicum and Galbulimima belgraveana, 1.3 in Austrobaileya maculata, Eupomatia laurina, Kadsura japonica and Schisandra repanda), and they are considered to be in the primitive stages.

In the woody Polycarpicae, a tendency is recognized that as the vessel elements become thicker, the differences between the diameters of vessel elements and those of fibers become greater. But there are some exceptional cases. Comparing Ascarina with Magnolia, the diameter of vessel elements is more in the former but their difference from the diameter of fibers is apparently greater in the latter. In general, as tracheary elements become shorter, the diameter of vessel elements becomes wider, but the diameter of fibers does not become so wider as in the vessel elements. Carlquist (1988) pointed out that "vessel widening, while apparently operative at the outset of vessel evolution, should not be considered as a measuring-stick of wood evolution." As far as examined in the woody Polycarpicae, however, the diameter of vessel elements can be a measuring-stick of wood evolution to a certain extent when combined with the length.

In Sarcandra glabra, the tracheids are distinctly shorter than those of the vesselless dicotyledons and close to the vessel elements. S. glabra had been regarded as a member of the vesselless dicotyledons (Swamy & Bailey 1950, Swamy 1953),

but recently vessels were detected in the xylem (Carlquist 1987, Takahashi 1988). The vessel elements of the other genera of Chloranthaceae are not so different from the tracheids of S. glabra and the vesselless dicotyledons in length, F/V ratio and ratio of length to diameter ($\ln(L/D)$). The tracheary elements of Chloranthaceae may show the transition from tracheids to vessel elements and fibers.

The vessel elements of the herbaceous Polycarpicae are generally shorter than those of the woody ones. On the contrary to the woody Polycarpicae with short vessel elements such as Hernandiaceae, Lauraceae and Piperaceae, the length of vessel elements and that of fibers of the herbaceous Polycarpicae more or less overlap each other and F/V ratio is low, and their diameters also overlap. As mentioned above, in a gymnospermous species, Ephedra pachyclada, the vessel elements and fibers are moderately short (658 μm and 713 μm in mean length) and F/V ratio is very low (1.08), somewhat similar to those of the herbaceous Polycarpicae. The low F/V ratio in the herbaceous Polycarpicae may suggest that their tracheary elements are short but not so specialized. In the short vessel elements of herbaceous Polycarpicae, e.g., in Decaisnea (Takahashi 1985b), the scalariform perforations are reported, and sometimes in Ranunculaceae (Avita & Inamdar 1981).

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* * * *

木本性多心皮類14科29種と草本性多心皮類4科8種において、木部管状要素の長さや直径を計測し、それらにおける進化傾向を明らかにしようと試みた。長さに関して、木本性多心皮類のうち原始的とされている種では道管要素と繊維は共に長く、両者の差が小さいが、特殊化しているとされる種ではそれらは短く、差も大きいという傾向が認められる。道管要素の直径が大きくなれば繊維の直径との差が大きくなる傾向はみられるが、これに従わない場合も多い。直径と長さに関連づけてみると、一般に道管要素は長さが短くなると直径が大きくなるが、繊維は長さが短くなってもそれほど直径が大きくなる。従って、道管要素が短くなるにつれ道管要素と繊維との差が大きくなるという傾向がみられる。裸子植物および他の被子植物と比較すると、多くの木本性多心皮類の道管要素と繊維は長さや直径に関する値からみて原始的状態にあると思われる。とくにセンリョウ科の管状要素は、仮道管から道管要素と繊維とに至る移行段階を示していると思われる。一方、草本性多心皮類の道管要素は、木本群のものに比べて長さが短い、道管要素と繊維の長さは差が小さく、またそれらの直径の差も小さい。そして、これらの要素は短いけれどもそれほど特殊化していないことが示唆された。

Tab. 1. List of species examined.

No	Species	Families	Localities
1	<u>Tasmannia piperita</u> (Hook.f.) Miers	Winteraceae	Mt.Kinabalu, North Borneo
2	<u>Belliolum crassifolium</u> Tieghem	Winteraceae	Plateau de Degny, New Caledonia
3	<u>Amborella trichopoda</u> Baillon	Amborellaceae	Plateau de Degny, New Caledonia
4	<u>Trochodendron aralioides</u> Sieb. & Zucc.	Trochodendraceae	Mt.Ashitaka, Shizuoka Pref.
5	<u>Drimys winteri</u> Forst.	Winteraceae	Puerto Montt, Chile
6	<u>Sarcandra glabra</u> (Thunb.) Nakai	Chloranthaceae	Isl.Iriomote, Okinawa Pref.
7	<u>Ascarina philippinensis</u> C.Robinson	Chloranthaceae	Mt.Kinabalu, North Borneo
8	<u>Hedyosmum orientale</u> Merr. & Chun	Chloranthaceae	Padang, West Sumatra
9	<u>Ascarina rubricaulis</u> Solms	Chloranthaceae	Mont Dzumac, New Caledonia
10	<u>Illicium anisatum</u> L.	Illiciaceae	Kibune, Kyoto Pref.
11	<u>Trimenia papuana</u> Ridley	Trimeniaceae	Mt.Kaindi, Papua New Guinea
12	<u>Eupomatia laurina</u> R.Br.	Eupomatiaceae	Atherton Tableland, Queensland
13	<u>Chloranthus spicatus</u> (Thunb.) Maxim.	Chloranthaceae	Cult., in Osaka
14	<u>Cercidiphyllum japonicum</u> Sieb. & Zucc.	Cercidiphyllaceae	Hakone, Kanagawa Pref.
15	<u>Galbulimima belgraveana</u> (F.v.Muell.) Sprague	Himantandraceae	Mt.Kaindi, Papua New Guinea
16	<u>Austrobaileya maculata</u> C.White	Austrobaileyaceae	Atherton Tableland, Queensland
17	<u>Schisandra repanda</u> (Sieb. & Zucc.) Radlk.	Schisandraceae	Mt.Omine, Nara Pref.
18	<u>Kadsura japonica</u> (L.) Dunal	Schisandraceae	Mt.Omine, Nara Pref.
19	<u>Degeneria vitiensis</u> I.Bailey & A.C. Smith	Degeneriaceae	Near Suva, Fiji
20	<u>Euptelea polyandra</u> Sieb. & Zucc.	Eupteleaceae	Hakone, Kanagawa Pref.
21	<u>Elmerrillia mollis</u> Dandy	Magnoliaceae	Gunung Buduk Rakik, Kalimantan
22	<u>Magnolia salicifolia</u> (Sieb. & Zucc.) Maxim.	Magnoliaceae	Otaki, Nagano Pref.
23	<u>Liriodendron tulipifera</u> L.	Magnoliaceae	Cult., in Osaka
24	<u>Magnolia sieboldii</u> K.Koch	Magnoliaceae	Cult., in Tokyo
25	<u>Magnolia hypoleuca</u> Sieb. & Zucc.	Magnoliaceae	Hakone, Kanagawa Pref.
26	<u>Cinnamomum camphora</u> (L.) Presl	Lauraceae	Cult., in Osaka
27	<u>Litsea citriodora</u> (Sieb. & Zucc.) Hatus.	Lauraceae	Isl.Yaku, Kagoshima Pref.
28	<u>Hernandia nymphaefolia</u> (Presl) Kubitzki	Hernandiaceae	Isl.Ishigaki, Okinawa Pref.
29	<u>Piper aduncum</u> L.	Piperaceae	Mt.Kaindi, Papua New Guinea
30	<u>Akebia trifoliata</u> (Thunb.) Koidz.	Lardizabalaceae	Mt.Iousen, Toyama Pref.
31	<u>Decaisnea fargesii</u> Franch.	Lardizabalaceae	Cult., Washinton Arboretum
32	<u>Paeonia suffruticosa</u> Andrews	Paeoniaceae	Cult., in Osaka
33	<u>Nandina domestica</u> Thunb.	Berberidaceae	Cult., in Osaka
34	<u>Mahonia japonica</u> (Thunb.) DC.	Berberidaceae	Cult., in Osaka
35	<u>Berberis thunbergii</u> DC.	Berberidaceae	Mt.Tsurugi, Tokushima Pref.
36	<u>Clematis stans</u> Sieb. & Zucc.	Ranunculaceae	Mt.Kongo, Osaka Pref.
37	<u>Clematis patens</u> Morr. & Decne.	Ranunculaceae	Sanda, Hyogo Pref.

1-6. Vesselless: Species are arranged according to mean tracheid length. 7-29. Woody; 30-37. Herbaceous: Species are arranged according to mean vessel element length.

Tab. 2. Length of vessel elements and fibers, and F/V ratio.

Species	Length (μm)								F/V Ratio
	Vessel				Fiber				
	Min.	Max.	Mean.	S.D.	Min.	Max.	Mean.	S.D.	
1 <u>Tasmannia piperita</u>	-	-	-	-	1600	4520	3364	607	1.0
2 <u>Belliolum crassifolium</u>	-	-	-	-	1850	3700	2847	457	1.0
3 <u>Amborella trichopoda</u>	-	-	-	-	1520	3320	2630	463	1.0
4 <u>Trochodendron aralioides</u>	-	-	-	-	2000	3130	2580	469	1.0
5 <u>Drimys winteri</u>	-	-	-	-	1470	3400	2560	479	1.0
6 <u>Sarcandra glabra</u>	-	-	-	-	740	2080	1582	219	1.0
7 <u>Ascarina philippinensis</u>	1720	3450	2467	343	1180	3600	2667	538	1.08
8 <u>Hedyosmum orientale</u>	920	2800	1909	446	1270	3100	2165	451	1.13
9 <u>Ascarina rubricaulis</u>	1020	2350	1636	340	1200	2630	1951	358	1.19
10 <u>Illicium anisatum</u>	580	1670	1191	226	660	1860	1329	228	1.11
11 <u>Trimenia papuana</u>	700	1750	1188	227	1175	2600	1878	302	1.58
12 <u>Eupomatia laurina</u>	530	1700	1166	245	780	2130	1572	328	1.34
13 <u>Chloranthus spicatus</u>	580	1630	1160	190	650	1780	1141	256	0.98
14 <u>Cercidiphyllum japonicum</u>	580	1330	1018	166	710	1650	1245	235	1.22
15 <u>Galbulimima belgraveana</u>	500	1410	1016	217	660	1740	1225	253	1.20
16 <u>Austrobaileya maculata</u>	580	1210	922	146	710	1600	1196	230	1.29
17 <u>Schisandra repanda</u>	390	1170	776	154	580	1410	996	168	1.28
18 <u>Kadsura japonica</u>	430	1020	731	158	570	1350	977	175	1.33
19 <u>Degeneria vitiensis</u>	410	1020	719	150	670	1680	1297	263	1.80
20 <u>Euptelea polyandra</u>	430	930	670	131	520	1310	921	154	1.37
21 <u>Elmerrillia mollis</u>	420	1000	654	128	550	1600	1077	254	1.64
22 <u>Magnolia salicifolia</u>	390	810	650	98	580	1520	1112	239	1.71
23 <u>Liriodendron tulipifera</u>	380	780	551	93	690	1400	1036	168	1.88
24 <u>Magnolia sieboldii</u>	340	740	514	104	440	1350	923	191	1.79
25 <u>Magnolia hypoleuca</u>	240	670	494	101	520	1220	936	164	1.89
26 <u>Cinnamomum camphora</u>	190	530	402	75	350	1100	738	180	1.83
27 <u>Litsea citriodora</u>	250	510	389	65	370	810	612	100	1.57
28 <u>Hernandia nymphaefolia</u>	170	530	385	89	340	900	661	120	1.71
29 <u>Piper aduncum</u>	170	510	379	58	350	950	684	145	1.80
30 <u>Akebia trifoliata</u>	340	680	447	75	340	850	600	132	1.34
31 <u>Decaisnea fargesii</u>	140	680	378	114	220	970	547	226	1.44
32 <u>Paeonia suffruticosa</u>	150	520	348	86	180	600	407	100	1.16
33 <u>Nandina domestica</u>	140	370	270	53	150	460	308	74	1.14
34 <u>Mahonia japonica</u>	150	380	248	42	170	470	321	62	1.29
35 <u>Berberis thunbergii</u>	140	370	243	51	140	640	352	100	1.44
36 <u>Clematis stans</u>	140	360	232	42	160	460	317	71	1.36
37 <u>Clematis patens</u>	110	360	228	58	160	470	266	63	1.16

Arrangement of species is the same as Tab. 1.

Tab. 3. Diameter of vessel elements and fibers, and their ln(L/D).

Species	Diameter (μm)								ln(L/D)	
	Vessel				Fiber				Ves.	Fib.
	Min.	Max.	Mean.	S.D.	Min.	Max.	Mean.	S.D.		
1 <i>Tasmannia piperita</i>	-	-	-	-	12	48	26.3	7.8	-	4.85
2 <i>Belliolum crassifolium</i>	-	-	-	-	15	38	26.2	7.3	-	4.69
3 <i>Amborella trichopoda</i>	-	-	-	-	12	43	28.6	7.7	-	4.52
4 <i>Trochodendron aralioides</i>	-	-	-	-	8	30	18.7	6.1	-	4.93
5 <i>Drimys winteri</i>	-	-	-	-	13	43	27.0	7.5	-	4.55
6 <i>Sarcandra glabra</i>	-	-	-	-	7	35	20.8	7.0	-	4.33
7 <i>Ascarina philippinensis</i>	45	95	69.1	13.1	12	58	32.1	11.3	3.58	4.45
8 <i>Hedyosmum orientale</i>	42	90	56.6	11.1	8	53	29.6	11.0	3.52	4.29
9 <i>Ascarina rubricaulis</i>	45	93	67.1	13.6	12	55	30.3	12.1	3.19	4.16
10 <i>Illicium anisatum</i>	22	50	34.0	6.3	7	30	16.6	6.0	3.56	4.38
11 <i>Trimenia papuana</i>	40	90	69.4	11.2	8	60	23.3	11.6	2.84	4.39
12 <i>Eupomatia laurina</i>	35	65	49.3	7.2	8	43	20.2	9.1	3.16	4.35
13 <i>Chloranthus spicatus</i>	20	38	27.6	5.7	6	28	16.5	6.1	3.74	4.24
14 <i>Cercidiphyllum japonicum</i>	20	66	45.6	10.8	8	28	17.3	6.4	3.11	4.28
15 <i>Galbulimima belgraveana</i>	37	95	63.3	13.4	7	40	22.2	8.2	2.78	4.01
16 <i>Austrobaileya maculata</i>	30	105	55.6	20.6	8	33	20.1	6.1	2.81	4.09
17 <i>Schisandra repanda</i>	20	70	45.4	10.4	7	30	17.5	5.6	2.84	4.04
18 <i>Kadsura japonica</i>	22	75	40.9	11.3	7	30	16.6	5.7	2.88	4.07
19 <i>Degeneria vitiensis</i>	55	110	74.3	12.7	12	50	25.8	9.1	2.27	3.92
20 <i>Euptelea polyandra</i>	20	63	41.8	10.3	7	25	16.2	5.4	2.77	4.04
21 <i>Elmerrillia mollis</i>	42	140	92.5	24.0	7	45	20.4	8.6	1.96	3.97
22 <i>Magnolia salicifolia</i>	30	65	48.5	8.2	8	30	18.8	5.7	2.60	4.08
23 <i>Liriodendron tulipifera</i>	30	83	51.9	10.9	7	30	17.3	6.5	2.36	4.09
24 <i>Magnolia sieboldii</i>	35	70	49.7	8.4	8	32	17.4	6.0	2.34	3.97
25 <i>Magnolia hypoleuca</i>	32	68	49.4	9.4	9	32	19.9	6.6	2.30	3.85
26 <i>Cinnamomum camphora</i>	40	130	72.4	21.8	6	30	16.4	5.7	1.71	3.81
27 <i>Litsea citriodora</i>	32	70	53.9	8.7	6	23	14.6	4.7	1.98	3.74
28 <i>Hernandia nymphaefolia</i>	40	85	62.8	13.7	6	28	15.9	6.6	1.81	3.73
29 <i>Piper aduncum</i>	47	110	85.9	17.3	6	23	13.7	4.9	1.48	3.91
30 <i>Akebia trifoliata</i>	20	180	61.6	41.3	6	28	19.1	6.2	1.98	3.45
31 <i>Decaisnea fargesii</i>	20	68	46.3	13.3	5	28	15.2	5.5	2.10	3.58
32 <i>Paeonia suffruticosa</i>	15	50	30.3	10.7	6	22	13.6	4.5	2.44	3.40
33 <i>Nandina domestica</i>	10	55	18.4	7.7	5	17	9.2	3.2	2.69	3.51
34 <i>Mahonia japonica</i>	10	35	17.3	4.8	5	15	9.4	2.7	2.66	3.53
35 <i>Berberis thunbergii</i>	12	53	22.1	9.5	5	15	9.5	2.9	2.40	3.61
36 <i>Clematis stans</i>	18	128	43.8	25.5	5	23	13.2	3.8	1.67	3.18
37 <i>Clematis patens</i>	20	100	44.7	19.6	5	22	13.3	4.2	1.63	3.00

Arrangement of species is the same as Tab. 1.

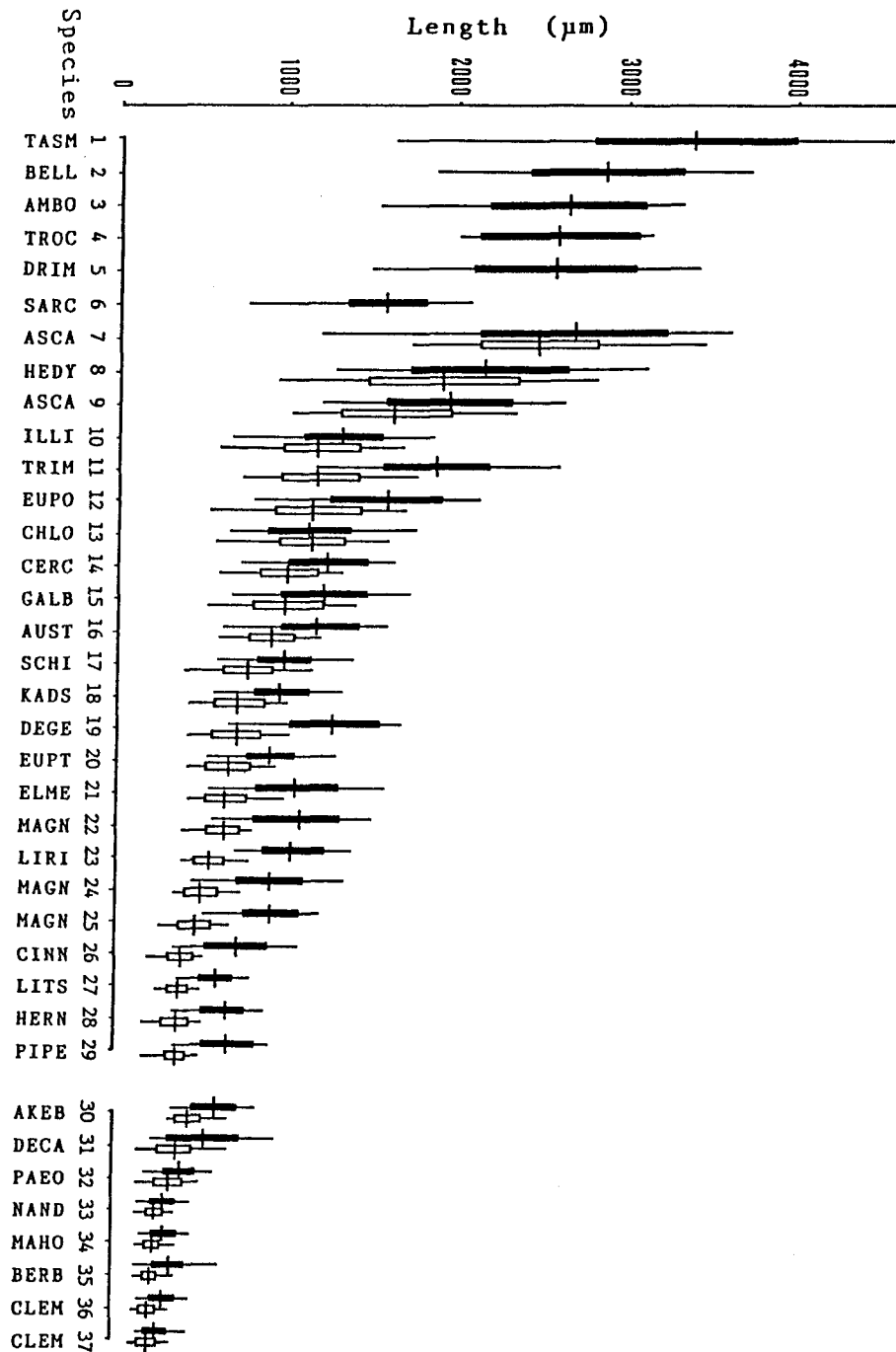


Fig. 1. Tracheary element length. Ranges, means and standard deviations shown by vertical lines, horizontal bars and rectangles, respectively. Solid rectangles: values of imperforate tracheary elements. Empty rectangles: values of vessel elements. Species are shown by the same numbers used in Tab. 1 and the first four letters of generic name.

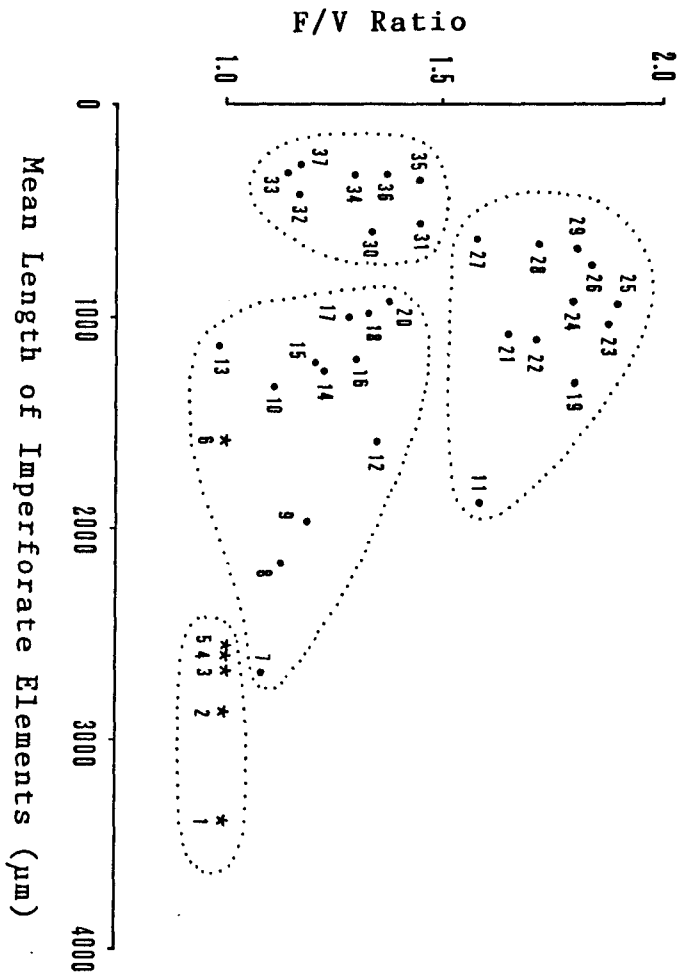


Fig. 2. Relation between vessel element length and fiber length. Values of F/V ratio plotted against mean length of imperforate tracheary elements. Stars show vesselless species. Species are shown by the same numbers used in Tab. 1.

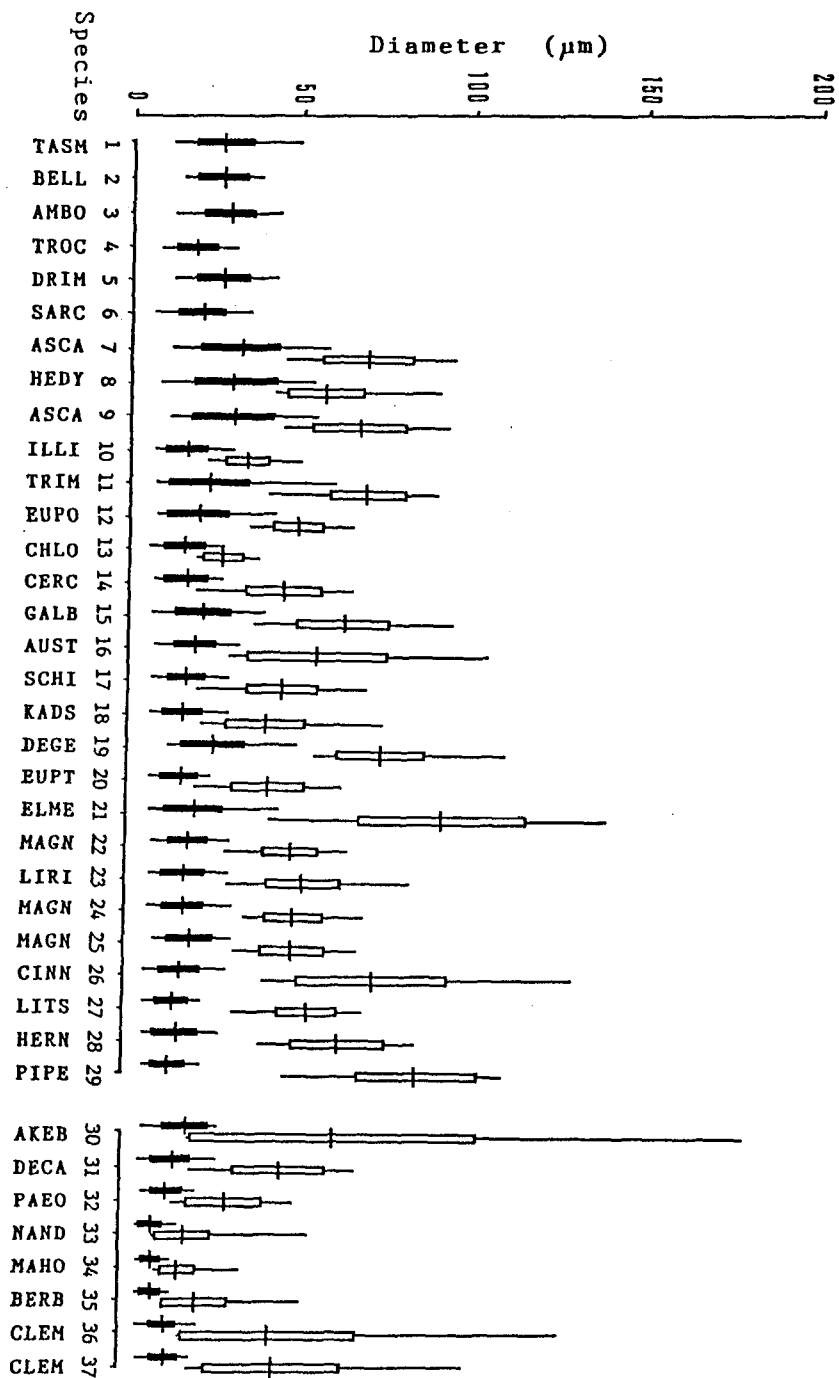


Fig. 3. Tracheary element diameter. Ranges, means and standard deviations shown by vertical lines, horizontal bars and rectangles, respectively. Solid rectangles: values of imperforate tracheary elements. Empty rectangles: values of vessel elements. Species are shown by the same numbers used in Tab. 1 and the first four letters of generic name.

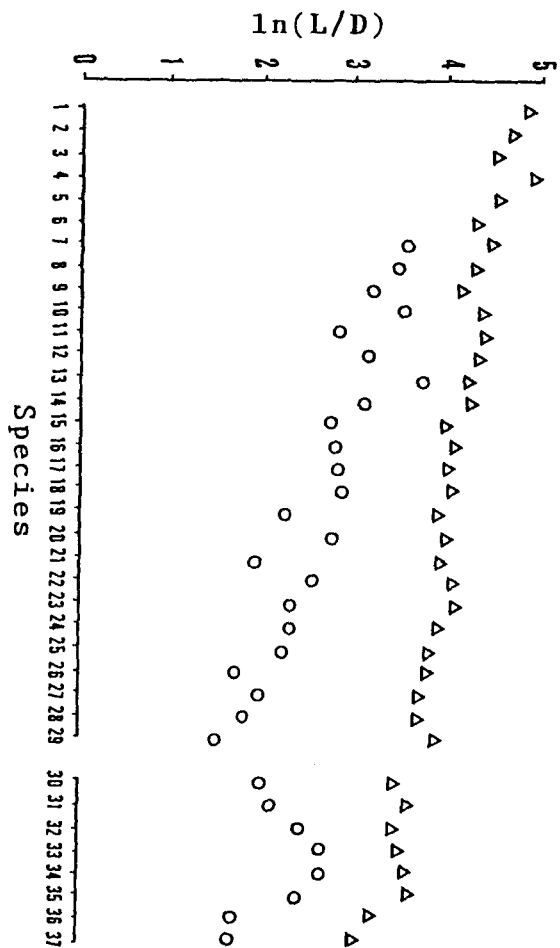


Fig. 4. Relation between length and diameter of tracheary elements. Triangles: values of imperforate tracheary elements. Circles: values of vessel elements. Species are shown by the same numbers used in Tab. 1.

Chapter 5.

Morphology of Xylem
of *Sarcandra*

Morphology and Ontogeny of Stem Xylem Elements in *Sarcandra glabra* (Thunb.) Nakai (Chloranthaceae): Additional Evidence for the Occurrence of Vessels

Very recently *Sarcandra*, which had long been known as the only vesselless genus in Chloranthaceae, was found by Carlquist to have vessels in root secondary xylem. The present study further shows on the basis of observations of the xylem ontogeny that vessels occur in stem metaxylem of *Sarcandra glabra* as well, thus offering additional evidence for the occurrence of vessels in the genus, virtually in all Chloranthaceae. Metaxylem elements of the stem are thicker than the other tracheary elements in general and have scalariform pittings at the end wall, and their ontogeny indicates that, as the surrounding cytoplasm disintegrates, pit membranes at the end wall disappear at least in some elements, resulting in a perforated end wall, i.e., vessel perforation. The present study further shows that *Chloranthus spicatus*, which is closely related to *Sarcandra*, may have an incomplete perforation plate because of retaining membranes at places on the plate. An evolutionary state of the "vesselless" condition in Chloranthaceae is discussed.

Key words: Chloranthaceae — *Sarcandra* — Vesselless dicotyledons — Wood anatomy.

Sarcandra, comprising three species distributed in southeastern Asia to Indomalaysia (Airy Shaw, 1973), has been well known as the only vesselless genus of Chloranthaceae (e.g., Swamy and Bailey, 1950; Swamy, 1953a, b; Melchior, 1964; Young, 1981). Very recently, however, Carlquist (1987) reported the occurrence of vessels for the first time in the secondary xylem of root of *Sarcandra glabra*. On the other hand, in the course of my earlier studies on the wood anatomy of primitive dicotyledons (Takahashi, 1985a, b, 1988), I had noticed probable occurrence of vessels in the stem wood of *Sarcandra glabra*, and the later ontogenetic studies have convinced me of the presence of vessels in *Sarcandra*. Carlquist's paper appeared just before my manuscript was submitted. His work was primarily based on mature root xylem, and vessels were not found in stem xylem. My work, however, has confirmed the vessel occurrence in stem as well on the basis of ontogenetic observations of xylem elements. In view of the phylogenetic significance of the vesselless condition in angiosperms (see Carlquist, 1987, for most recent review and discussions), it seems important to show a rather ubiquitous occurrence of vessels in *Sarcandra* and to document how vessels (and tracheary elements) develop in the genus. The latter might show the "vesselless"

condition in *Sarcandra* in turn.

The present paper thus offers an additional piece of evidence for the vessel occurrence in *Sarcandra*, and also provides the stem xylem anatomy of *Sarcandra glabra* emphasizing the metaxylem ontogeny (i.e., vessel development). For comparison, the morphology of vessel elements of *Chloranthus spicatus* (as one of the closest relatives with vessels) will also be presented.

Materials and Methods

Stem samples of *Sarcandra glabra* were collected in Iriomote Island of Okinawa, Japan (vouchers: *Okada et al.* 206, 207, 250, 271 in Herbarium of Kobe University) and from cultivated plants in the campus of Osaka University (no vouchers); stem samples of *Chloranthus spicatus* were from cultivated plants in the campus of Osaka University (no vouchers).

For light-microscopic observations of mature tracheary elements, xylem was sectioned at 10 μm thicknesses using standard paraffin methods, and macerated by Jeffrey's fluid. For scanning electron microscopic observations of the wood, small cuboidal xylem blocks were dehydrated through an ethyl alcohol-amyl acetate series, and treated with critical point drying by solvent-substituted liquid CO_2 .

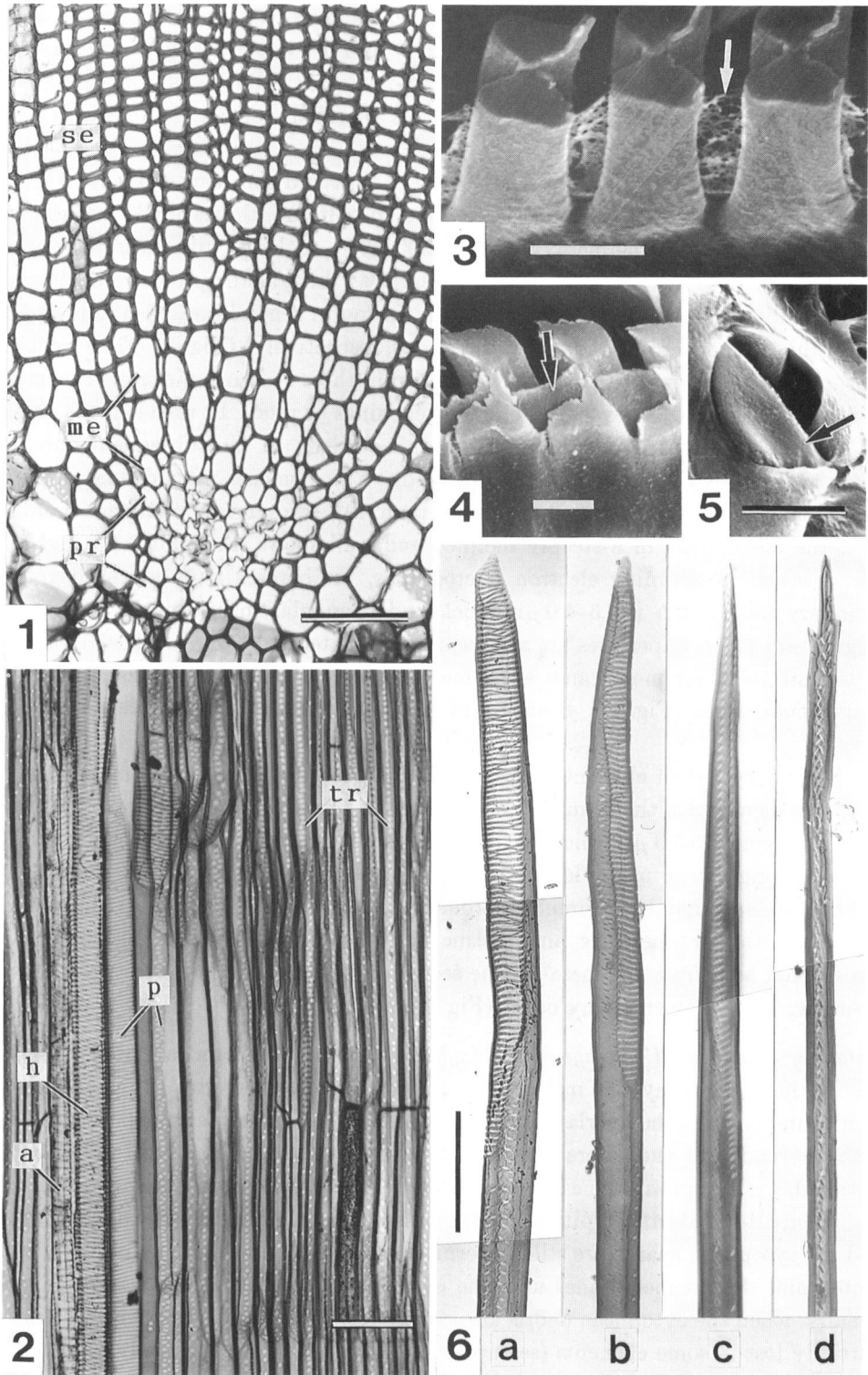
For observations of the ontogeny of tracheary elements, small cuboidal blocks about 2×2 mm square containing the primary and/or the secondary xylem were obtained from growing stems and at various stem levels. Materials were fixed in Karnovsky's fixative (0.1 M phosphate buffer solution of 5% glutar-aldehyde and 4% paraform-aldehyde), dehydrated through an ethyl alcohol-propylene oxide series and then embedded in epoxy resin for microtoming. Tangential sections were cut at about 0.5 μm thicknesses by glass knives and stained with 1% toluidine blue solution.

Observations

Morphology of tracheary elements of Sarcandra glabra

The mature stem is 10–15 mm in diameter, and its cross section shows 20–30

Figs. 1–6. *Sarcandra glabra*. 1: Cross section of stem, showing protoxylem (pr), metaxylem (me), and secondary xylem (se) in a fascicular region. 2: Radial longitudinal section of primary (left side) and secondary xylem (right side), showing annular (a), helical (h), and pitted (p) thickenings in the primary xylem and tracheids (tr) in the secondary xylem. 3–5: Scanning electron micrographs. 3, 4: Sections of overlapping end walls of two adjacent tracheids in metaxylem, showing pit membranes with many small pores (arrow) in Fig. 3 and intact pit membranes (arrow) in Fig. 4. 5: Section of a circular bordered pit-pair of tracheids in secondary xylem, showing a part of pit membrane (arrow). Note lenticular aperture behind the membrane. 6: Macerated tracheary elements; a, an element with scalariform pits in metaxylem; b, a tracheid with scalariform pits in early formed secondary xylem; c, a tracheid with slightly elongated pits in later formed secondary xylem; d, a tracheid with circular bordered pits in later formed secondary xylem. Bar = 100 μm in Figs. 1, 2, and 6, and 4 μm in Figs. 3–5.



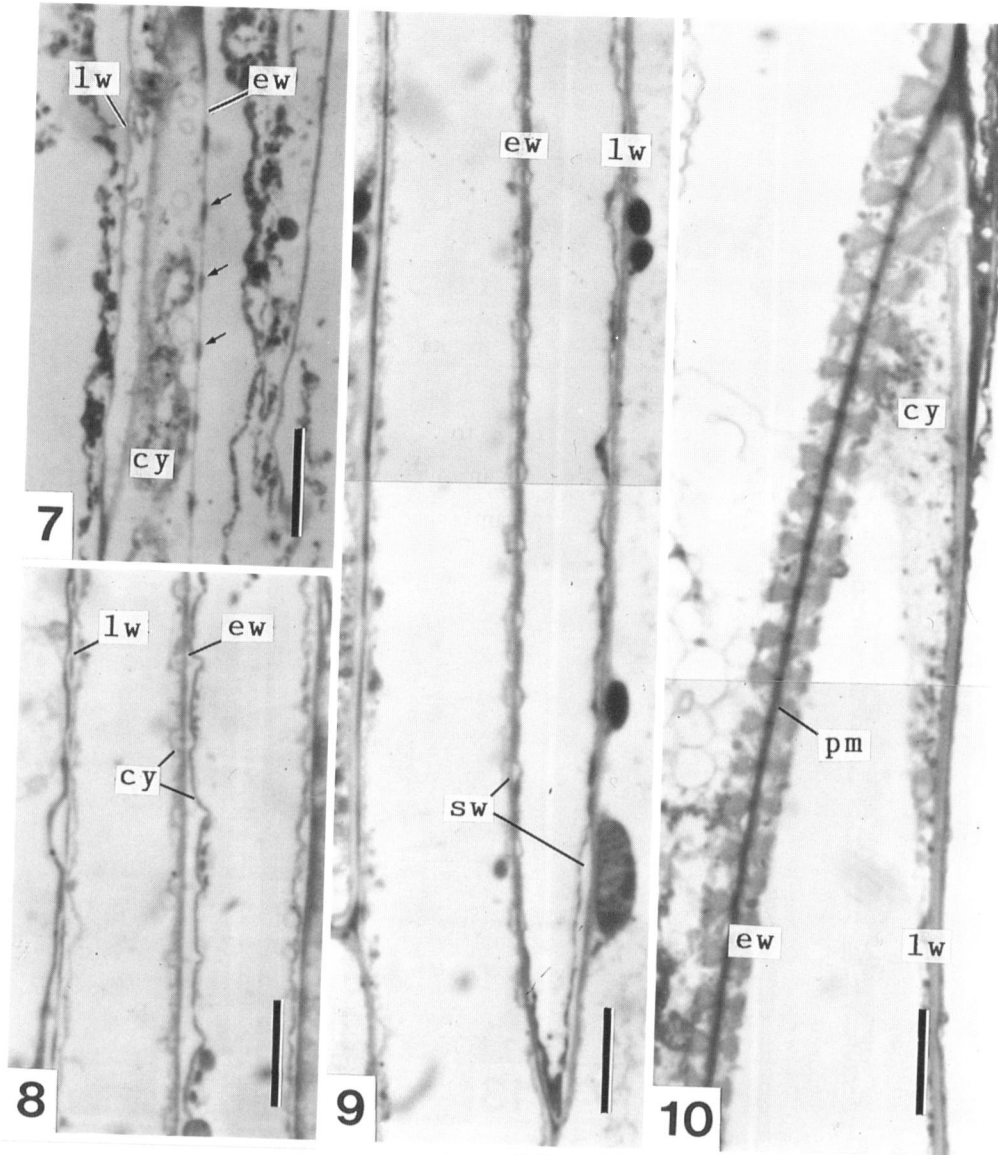
vascular bundles arranged in a ring. Xylem in each vascular bundle is composed of a primary xylem wedge and secondary xylem of 1.5–2.5 mm depth. Tracheary elements of the secondary xylem is mainly formed by fascicular cambium, and not by interfascicular cambium which mostly produces sclerified parenchyma cells developing into multiseriate rays.

Tracheary elements of the protoxylem are thin and sometimes crushed (Fig. 1), and have annular thickenings (Fig. 2); the annuli are thin-walled and oblique. Tracheary elements of the metaxylem are 2500–4000 μm long (with mean length 2964 μm). Those close to the protoxylem are nearly as thick as the protoxylem elements, and those distant from the protoxylem much thicker in general (i.e., 15–35 μm and 30–55 μm thick in tangential and radial directions, respectively) (Fig. 1). The tracheary elements of the metaxylem are mostly arranged in three or four radial rows continuing to secondary xylem. They have helical thickenings or pits. In the elements close to the protoxylem the helices are fewer and thin-walled; in the subsequent outer elements the helices are dense and thick-walled. The elements most distant from the protoxylem have numerous (usually more than 40), transversely elongated bordered pits; the radial facet of a steeply inclined end wall shows scalariform pittings (Fig. 6a). Viewed in scanning electron micrographs, pit borders have a well-developed secondary wall which is 3.5–4.0 μm thick and triangular in outline in cross section (Figs. 3 and 4); pit apertures are narrow, approximately 1.2–1.8 $\mu\text{m} \times 20\text{--}30 \mu\text{m}$ wide. In the pit-pairs, pit membranes are almost smooth (Fig. 4) and are sometimes with many small pores (Fig. 3). Scalariform pit-pairs without membranes are also observed.

Secondary xylem elements are radially flattened and therefore thinner than the tracheary elements of the primary xylem (Fig. 1); in case of later developed secondary xylem, they are 15–30 μm thick in the radial direction. Tracheary elements are 750–2100 μm long (with mean length 1554 μm) and much shorter than those of the metaxylem, and they have circular bordered pits (about 5.5–7.5 μm in diameter) with oblique lenticular apertures and distinct pit membranes (Figs. 5 and 6d). At a transitional area from the meta- to the secondary xylem, intermediate types between their respective elements may occur (Fig. 6b, c).

Ontogeny of end wall pittings in metaxylem elements of Sarcandra glabra

Early in ontogeny, the metaxylem elements have primary wall thickenings with regular intervals at the overlapping end wall (Fig. 7); a cytoplasm is positioned near both the end and the lateral wall (Fig. 8). As the secondary wall deposition is initiated, the cytoplasm comes to be restricted to the thickenings of the end wall (Fig. 9). Soon after scalariform pittings are completed, both pit membranes at the end wall and the cytoplasm near it are still discernible (Fig. 10). Later, the cytoplasm disintegrates, and the pit membranes near the cytoplasm debris becomes obscure (Fig. 11). Finally, when the cytoplasm debris also completely disappears, the pit membranes are partially lost in some elements (see upper part in Fig. 12) or completely lost in others (Fig. 13). The elements destitute of pit membranes at the end wall are evidently



Figs. 7-10. *Sarcandra glabra*. Tangential longitudinal sections of metaxylem elements showing the process of secondary wall deposition. 7: Youngest stage. Note that cytoplasm spreads over the cell and that thick deposition of the primary wall (small arrows) occurs at regular intervals on the end wall. 8: Later stage than Fig. 7, showing cytoplasm disposition on the end and lateral walls. 9: Later stage in which secondary wall deposition is initiated at regular intervals on the end wall. 10: Nearly mature stage in which secondary wall deposition is almost finished. Note the presence of pit membranes and intact cytoplasm. cy, cytoplasm; ew, end wall; lw, lateral wall; pm, pit membrane; sw, secondary wall. All bars = 10 μ m.

vessels.

Vessel elements of Chloranthus spicatus

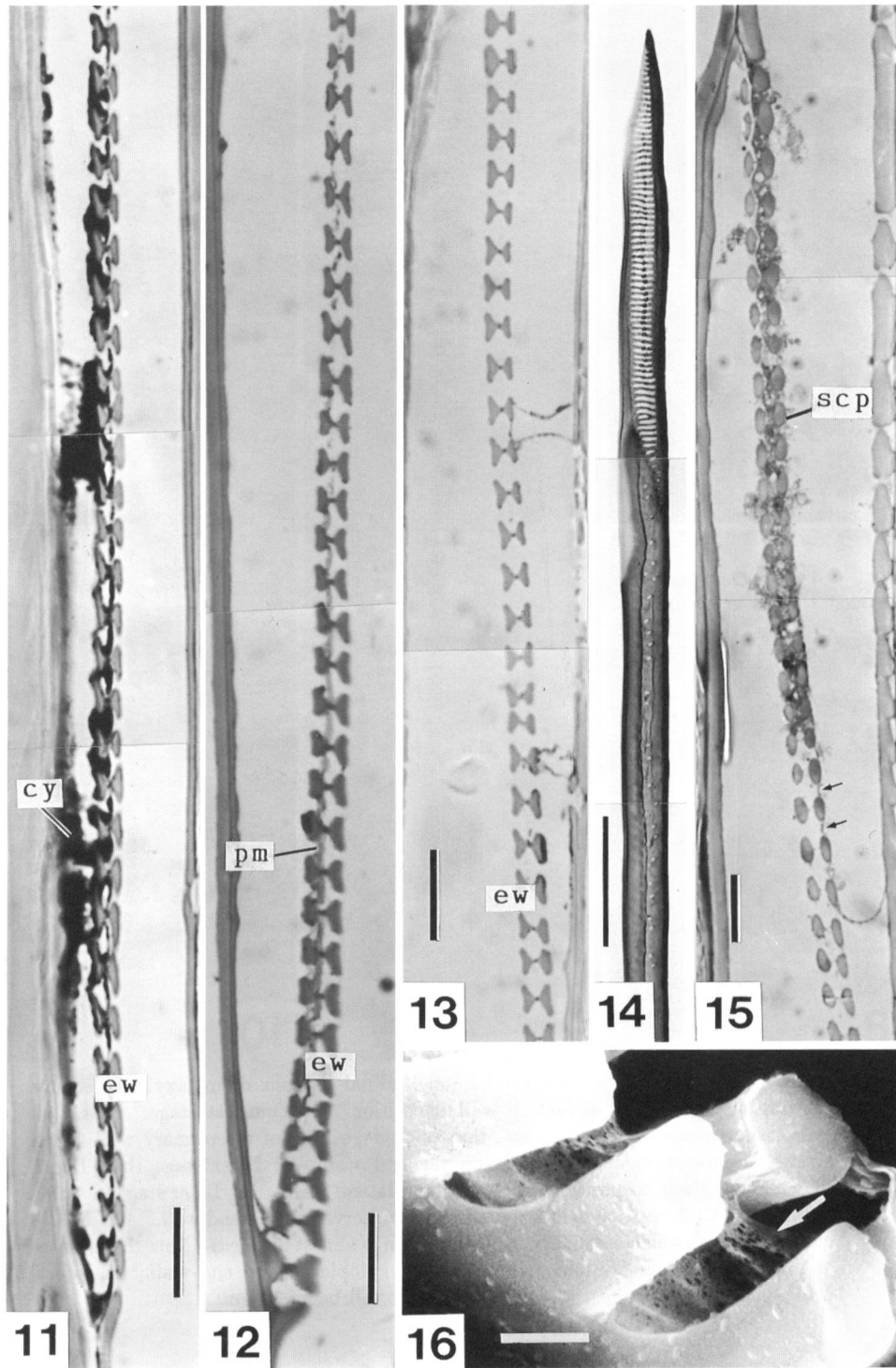
Vessel elements of *Chloranthus spicatus* (Fig. 14) apparently resemble the tracheary elements of *Sarcandra glabra* which have scalariform pittings. According to my own observations, most of the vessel elements, later in ontogeny, lost membranes from the perforation plates (Fig. 15), but some elements retain membranes which have many small pores (Fig. 16).

Discussion

Since the earlier observations by Swamy and Bailey (1950) and Swamy (1953b), *Sarcandra glabra* has been described as "vesselless" in many later publications (e.g., Metcalfe, 1987) with the only exception being that Carlquist (1987) detected vessels in the secondary xylem of root. As presented above, I have confirmed that *Sarcandra glabra* certainly has many tracheids in stem xylem; those tracheids have circular bordered pits, in the later formed secondary xylem, and scalariform pittings at the end wall, in the early formed secondary xylem as well as in the metaxylem, as described by Swamy and Bailey (1950) and Swamy (1953b). The species, however, often has metaxylem elements lacking pit membranes at the end wall, a condition which doubtless agrees with that of the vessel. Thus vessels were confirmed to occur in the stem as well. The earlier workers on the stem wood anatomy of *Sarcandra* seem to have never doubted the absence of vessels; indeed, the xylem looks very homoxyloous in cross section, and besides most of the secondary xylem elements are certainly typical tracheids. Although the confirmation of the vessel occurrence in *Sarcandra* is limited to *Sarcandra glabra* at the present stage, the above result suggests that the two other species also may have vessels. This must be confirmed in future.

The present study further indicates that the difference between the tracheids and vessels is not a clear-cut one, as suggested by Carlquist (1987). As shown in this study, the "vessel" of both *Sarcandra glabra* and *Chloranthus spicatus* may have an incomplete perforation plate because of retaining membranes at places, as in many other dicotyledons which have primitive vessels (Meylan and Butterfield, 1978).

Figs. 11-16. 11-13: *Sarcandra glabra*. Section of end walls of metaxylem elements after secondary wall deposition. 11: Stage of cytoplasmic disintegration. 12, 13: Stage after cytoplasm has disappeared. Pit membranes are rather thick at lower side and partially disintegrated at upper side in Fig. 12, while almost invisible in Fig. 13. cy, cytoplasmic debris; ew, end wall; pm, pit membrane. All bars = 10 μ m in Figs. 11-13. 14-16: *Chloranthus spicatus*. Photomicrographs and scanning electron micrograph of vessel elements. 14: A macerated vessel element with scalariform perforation plate. 15: Section of scalariform perforation plate (scp). Membranes of the perforation openings are disintegrating at upper side and faintly seen (small arrows) or already removed at lower side. 16: Section of a part of scalariform perforation plate, showing membranes with many small pores (arrow) in the perforation openings. Bar = 100 μ m, 10 μ m, and 2 μ m in Figs. 14, 15, and 16, respectively.



Generally the perforation plate of dicotyledons is considered to be formed by a disintegration of perforation plate membranes due to the activity of hydrolytic enzyme in the cytoplasm and by the subsequent removal of disintegrating membranes by transpiration stream (Yata *et al.*, 1970; Butterfield and Meylan, 1972; Meylan and Butterfield, 1972; Esau, 1977). In the case of *Sarcandra glabra* or in Chloranthaceae, failure or success of the removal of the disintegrating membranes, which may rely on the strength of the transpiration stream, seems to result easily in a vesselless or vesseled condition.

In terms of locations of vessels in stem, *Sarcandra* seems outstanding within woody dicotyledons. Vessels in woody dicotyledons are believed to have first originated in the secondary xylem and then have been extended into primary xylem; this trend is documented in large number of dicotyledonous taxa (Bierhorst and Zamora, 1965). Even ontogenetically, the trends of tracheary specialization in the primary xylem of dicotyledons tend to lag behind those that occur in the secondary xylem (Bailey, 1944). In contrast, *Sarcandra glabra* has vessels in the primary xylem of stems (and in roots) and lacks them in the secondary xylem, as in monocotyledons. Wood anatomy of *Sarcandra* probably represents an exceptional case with respect to vessel feature, but may require particular attention for considering vessel evolution in angiosperms.

I wish to express my cordial thanks to Prof. Dr. M. Tamura, Kobe University, for his valuable guidance and encouragement throughout this study, and to Prof. Dr. K. Yashika, Osaka University, for his technical advice and help. I am also grateful to Dr. H. Tobe, Kyoto University, for his suggestions in completing the manuscript.

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Xylem Elements of *Sarcandra glabra*

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Akira Takahashi * & Michio Tamura ** : Occurrence of vessel elements in the stem of *Sarcandra glabra*

高橋 晃* ・ 田村道夫** : センリョウの茎における道管要素の分布

Sarcandra glabra has long been known as a member of vesselless dicotyledons (Swamy & Bailey 1950, Swamy 1953). Recently, however, Carlquist (1987) reported the presence of vessels in the secondary xylem of root. Takahashi (1988) also detected the vessels in the metaxylem of stem. In this paper, we will report at what part of the stem the vessel elements are formed, which was studied by means of scanning electron microscopy.

Materials and Methods

The stems of Sarcandra glabra (Thunb.) Nakai were collected from Iriomote Isl., Okinawa Pref. (vouchers: Okada et al. 206, 207, 250, 271, in Herbarium of Kobe University) and immediately fixed in FAA. Methods for light and scanning electron microscopy were the same as those used by Takahashi (1988).

Results and Discussion

The stem is 10-15 mm in diameter, and in the cross section, 30-40 vascular bundles are arranged in a ring. Each vascular bundle is composed of secondary xylem of 2-3 mm thickness and a small amount of primary xylem. Fascicular

cambia produce tracheary elements, while interfascicular cambia produce sclerified parenchyma cells which develop into multiseriate rays. The width of the vascular bundles varies from 100 to 700 μm and the number of cells in tangential direction varies from 5 to 40. The width of each vascular bundle and the number of cells do not increase greatly during the secondary growth.

In radial section, the inner elements of the primary xylem have helical thickenings, and the outer elements have scalariform pits at the end walls. In the secondary xylem, early formed innermost elements have scalariform pits, which are shorter than those in the primary xylem. Later formed elements have circular bordered pits with oblique apertures. The tracheary elements are generally the thickest in the metaxylem and become narrower toward the outside.

In the broad vascular bundles (Fig. 2), the pit membranes are not always present in the tracheary elements. The membranes are not observed in scalariform pits of metaxylem elements (Fig. 5) and in scalariform (Fig. 6) and circular pits (Fig. 3) of early formed secondary xylem elements. In later formed secondary xylem, however, the membranes are present in circular pits of its elements (Fig. 4). Occasionally, granular or thread-like substances are observed in the scalariform and circular pits (Figs. 7-9). These substances seem to be the debris of disintegrated membranes. The metaxylem elements are 26-50 μm in radial diameter with the scalariform pits whose apertures are 14-38 μm \times 1.0-2.3 μm and regarded as vessel elements because of the absence of pit membranes. The elements of early formed secondary xylem are 19-34 μm in radial diameter with the scalariform pits whose apertures are 5-18 μm \times 1.0-1.8 μm and also regarded as

vessel elements. The elements of later formed secondary xylem are 10-28 μm in radial diameter with the circular pits whose apertures are 3-5 μm \times 1.0-1.4 μm and regarded as tracheids because of the presence of pit membranes.

In the narrow vascular bundles (Fig. 10), the membranes are always observed in the scalariform pits of metaxylem elements (Fig. 12) and in those of secondary xylem elements (Fig. 11). The metaxylem elements are 20-43 μm in radial diameter with the scalariform pits whose apertures are 12-36 μm \times 1.0-2.0 μm . The elements of early formed secondary xylem are 16-36 μm in radial diameter with the scalariform pits whose apertures are 4-12 μm \times 1.0-1.8 μm . The elements of later formed secondary xylem are 12-30 μm in radial diameter with the circular bordered pits whose apertures are 3-5 μm \times 1.0-1.3 μm . These elements are regarded as tracheids because of the presence of pit membranes.

The above descriptions show that in the broad vascular bundles, the elements of metaxylem and early formed secondary xylem are 19 to 50 μm in radial diameter and have no pit membranes, while in the narrow vascular bundles, the metaxylem elements have pit membranes even if they are as thick as 40 μm . The loss of the pit membrane (i.e., vessel formation) is not affected by the thickness of tracheary elements at least in Sarcandra. In this genus, the vessel elements occur in the early formed secondary xylem, as well as in the metaxylem. Those vessel elements seem to play a major role in water conduction of the growing young plants.

We are very grateful to Prof. Dr. K. Yashika, Osaka University, for his encouragement throughout this study.

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無道管双子葉植物の一員とされてきたセンリョウ科センリョウにおいて、最近、根と莖の木部から道管が見いだされた。本研究では、道管が莖のどの部分にあるのか一層詳しく知るために走査型電顕を用いて調べた。後生木部要素は他部分の要素よりいくぶん太く、末端に階段状壁孔を有している。二次木部のうち初期に形成された要素は階段状壁孔を有しているが、後期に形成された要素は円形壁孔を有している。莖には横断面でみると広い維管束と狭い維管束がある。広い維管束の後生木部要素と初期二次木部要素の階段状壁孔には壁孔膜がないが、後期二次木部要素の円形壁孔には壁孔膜が観察された。また狭い維管束のすべての要素には壁孔膜が観察された。すなわちセンリョウの道管要素は階段状穿孔をもち、広い維管束の後生木部と初期二次木部に存在することがわかった。また壁孔膜の有無と管状要素の太さとの相互関係を調べたところ、壁孔膜の消失すなわち道管形成と管状要素の直径には明らかな関係のないことがわかった。これらの道管は生長中の若い植物体の水分通導に大きな役割を果たしているものと思われる。

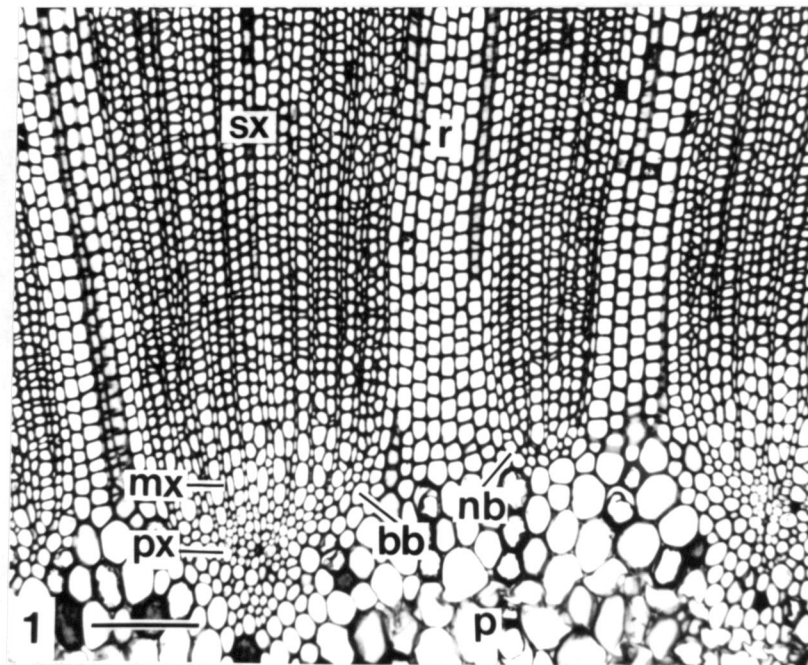
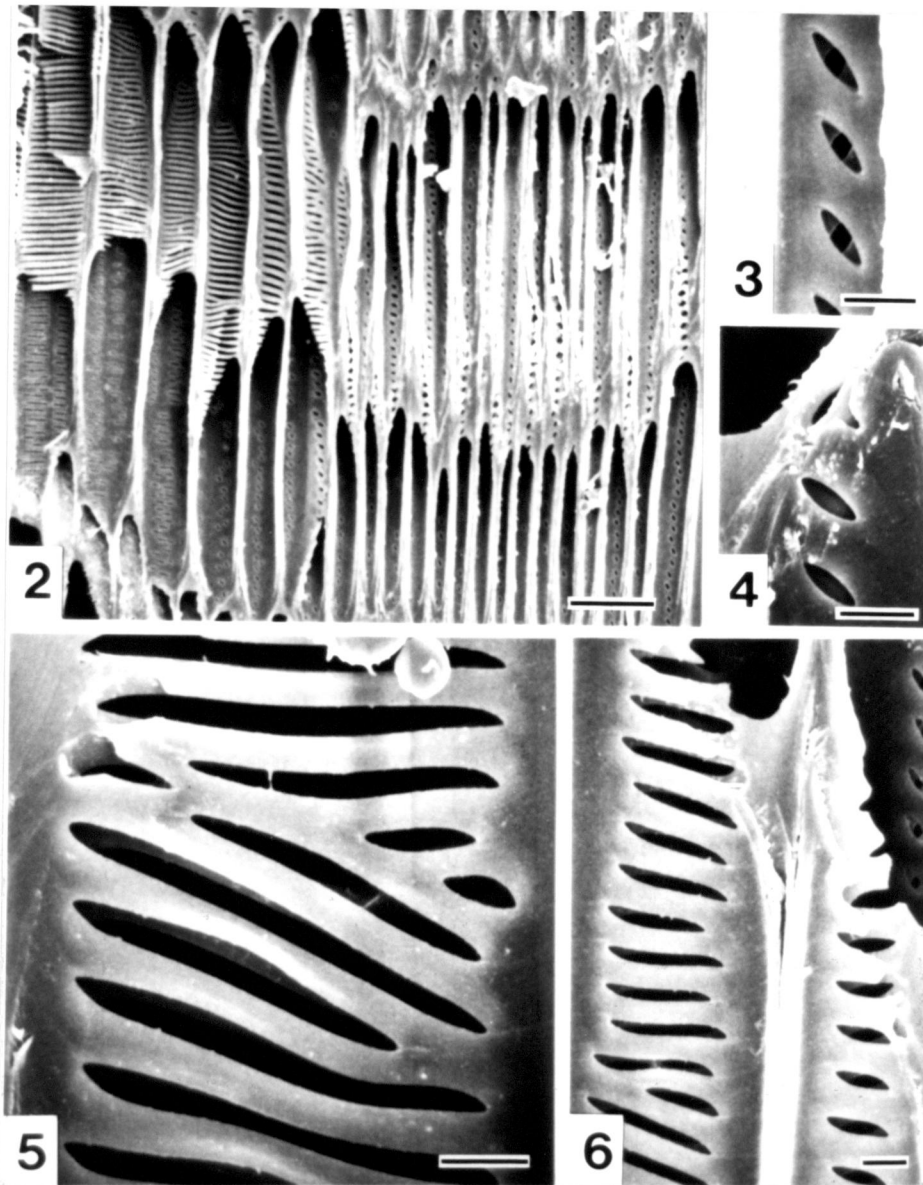
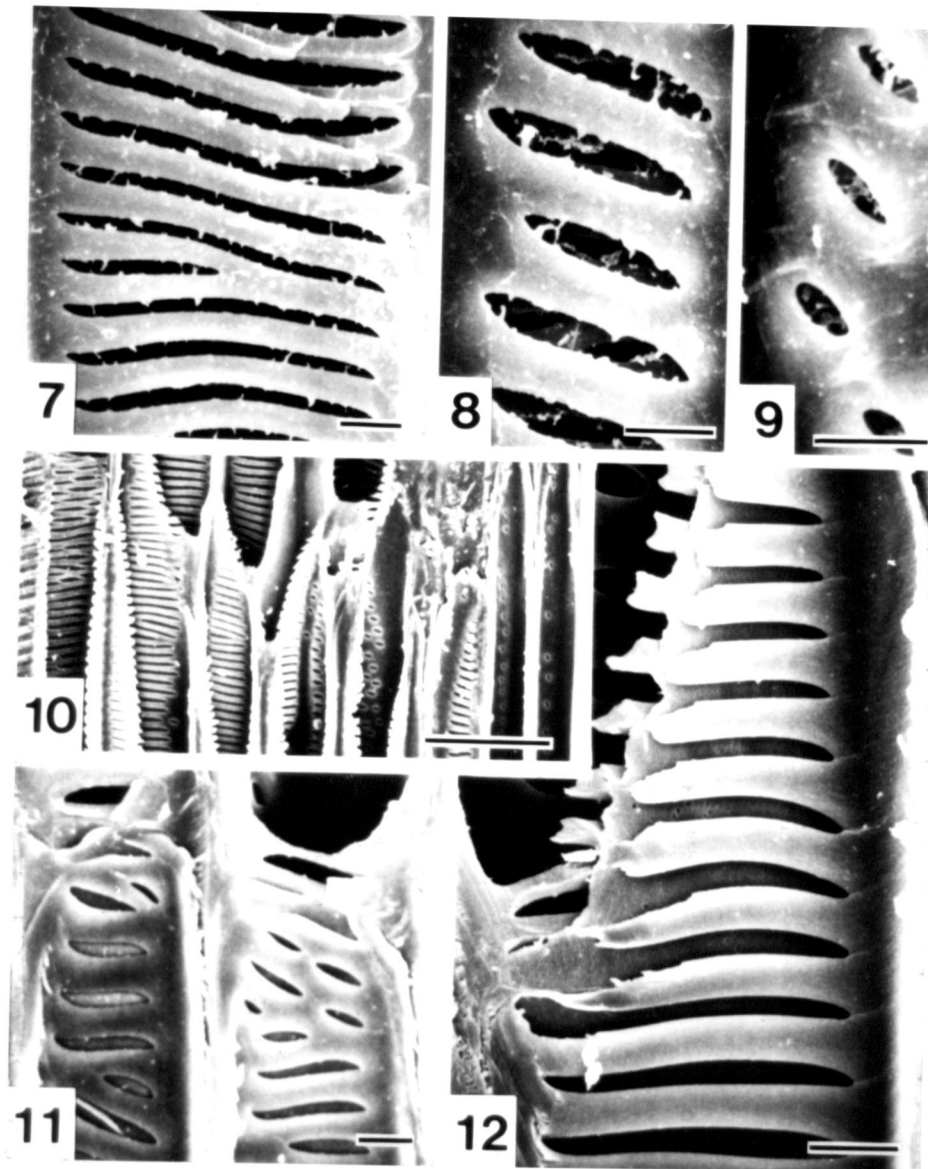


Fig. 1. Cross section of stem. bb, broad vascular bundle; mx, metaxylem; nb, narrow vascular bundle; p, pith; px, protoxylem; r, multiseriate ray; sx, secondary xylem. Bar=200 μ m.



Figs. 2-6. Scanning electron micrographs of radial section of broad vascular bundle. 2. Metaxylem (left side) to secondary xylem (right side). 3. Element of early formed secondary xylem, showing circular pits without pit membranes. 4. Element of later formed secondary xylem, showing circular pits with pit membranes. 5. Metaxylem element, showing scalariform pits without pit membranes. 6. Elements of early formed secondary xylem, showing scalariform pits without pit membranes. Bar=50 μm in Fig. 2, and 5 μm in others.



Figs. 7-12. Scanning electron micrographs of radial sections of broad vascular bundle (7-9) and narrow vascular bundle (10-12). 7-9. Elements of metaxylem (7) and secondary xylem (8 & 9), showing granular substances in their pits. 10. Metaxylem (left side) to secondary xylem (right side). 11. Elements of early formed secondary xylem, showing scalariform pits with pit membranes. 12. Metaxylem element, showing scalariform pits with pit membranes. Bar=50 μm in Fig. 10, and 5 μm in others.