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WOOD ANATOMY OF THE LYTHRACEAE

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SUMMARY

The wood anatomy of 18 genera belonging to the Lythraceae is described. The diversity in wood structure of extant Lythraceae is hypothesized to be derived from a prototype with scanty paratracheal parenchyma, heterogeneous I uniseriate and multiseriate rays, (septate) libriform fibres with minutely bordered pits, and vessels with simple perforations. These characters still prevail in a number of Lythraceae. Specialization has been very limited in most Lythraceae of shrubby or herbaceous habit: these have juvenilistic rays composed mainly of erect rays and sometimes completely lack axial parenchyma. Ray specialization towards predominantly uniseriate homogeneous rays, concomitant with fibre dimorphism leading to abundant parenchyma differentiation, and with the advent of chambered crystalliferous fibres has been traced in the "series" *Ginoria, Pehria, Lawsonia, Physocalymma* and *Lagerstroemia.* The latter genus has the most specialized wood anatomy in the family and has species with abundant parenchyma as well as species with alternating bands of dimorphous septate fibres. *Pemphis* represents an independent specialization with its vasicentric parenchyma and thick-walled nonseptate fibres.

The affinities of Lythraceae with other Myrtales are discussed. *Punica, Rhynchocalyx, Psiloxylon,* Oliniaceae, *Alzatea,* Sonneratiaceae, Onagraceae and Melastomataceae all resemble Lythraceae in their wood anatomy. The former three genera could even be accommodated in the family without extending its wood anatomical range. Oliniaceae, *Alzatea* and *Sonneratia* only differ in minor details from Lythraceae. In order to facilitate identification of wood samples, tentative keys to the genera or groups of genera of Lythraceae as well as to some species of *Lagerstroemia* are presented.

1. INTRODUCTION

This study forms part of a wood anatomical survey of the families assigned to the order Myrtales. Previous studies carried out at the Rijksherbarium are by VAN VLIET on Crypteroniaceae sensu lato (1975) and on Rhizophoraceae (1976; not truly Myrtalean), and by BRIDGWATER & BAAS (1978) on Punicaceae. Comprehensive publications on Combretaceae (VAN VLIET 1979) and on Melastomataceae (Van Vliet and Koek-Noorman & Ter Welle) are in preparation together with a paper analysing the overall implications of wood anatomy for the classification and affinities of true or putative members of the Myrtales (Van Vliet, in preparation). Other families described wood anatomically in the recent wood anatomical literature are by MUJICA & CUTLER (1974) on Oliniaceae, by CARLQUIST (1975a) on Onagraceae, by CARLQUIST & DEBUHR (1977) on Penaeaceae, and by VENKATESWARLU & RAO (1964) on Sonneratiaceae. Work on Psiloxylaceae and Lecythidaceae (probably out of place in Myrtales) is currently in progress by Dr. Rudolf Schmid (Berkeley, California) and Dr. C. H. de Zeeuw (Syracuse, New York) respectively.

The main aim of this study is to contribute to our understanding of relationship patterns within the family and to facilitate wood identification. In addition it is hoped that a comprehensive survey of Lythraceae wood anatomy will help to clarify the controversial issues of inclusion or exclusion of such enigmatic genera as *Alzatea*, *Rhynchocalyx*, *Heteropyxis* and *Psiloxylon* and of the status of closely related families such as Oliniaceae, Punicaceae, Sonneratiaceae and Crypteroniaceae (pro parte or sensu stricto). Furthermore correlations between the wood anatomy of the individual Lythraceous taxa and their habitat and habit will be searched for. Lythraceae show an interesting range of variation especially in their habit which varies from herbaceous plants to large forest trees.

The older wood anatomical literature is listed and summarized by SOLEREDER (1899 & 1908) and METCALFE & CHALK (1950). These data have been added to by relatively few publications, usually only describing very few species: MCLEAN & RICHARDSON (1973, on vascular ray cells in *Lagerstroemia indica*); PURKAYASTHA et al. (1976, on *Lagerstroemia hypoleuca*); HAYASHI et al. (1973, on *Lagerstroemia ovalifolia* and *L. speciosa*); DAS (1976, on *Lagerstroemia* species); BURGESS (1966, on *Lagerstroemia* from Sabah); DESCH (1957, on Malayan *Lagerstroemia*); PURKAYASTHA (1958, on septate and crystalliferous fibres in *Lagerstroemia*); KRIBS (1968, on *Lagerstroemia piriformis* and *L. speciosa*); OHTANI & ISHIDA (1976, on vestured pits in *Lagerstroemia subcostata*); and GRAHAM & LORENCE (1977, on *Tetrataxis*). Reference to these publications will only be made if relevant for the discussion of our present results on a more comprehensive sample of most woody genera.

Except for a number of genera, of which the taxonomic affinities have been debated over the years, the delimitation of the family Lythraceae has changed little since BENTHAM and HOOKER's Genera Plantarum (1867). KOEHNE (1892) more or less stabilized the generic composition of the family, excluding Bentham and Hooker's "genera anomala" and recognizing a separate family for *Sonneratia* and *Duabanga* (Sonneratiaceae). KOEHNE's system (1892, 1903) for the Lythraceae is summarized for the woody genera in *table 3*. This system has not met with serious opposition from later taxonomists.

The checkered taxonomic history of the genera *Alzatea* and *Rhynchocalyx* has been reviewed by VAN VLIET & BAAS (1975). Although VAN BEUSEKOM-OSINGA & VAN BEUSEKOM (1975) and VAN BEUSEKOM-OSINGA (1977) recently treated these genera in their newly delimited Crypteroniaceae, older literature and also part of the anatomical evidence point to a close affinity of these genera with Lythraceae (SPRAGUE & METCALFE 1937; LOURTEIG 1965; VAN VLIET 1975; VAN VLIET & BAAS 1975). The status of *Crypteronia* as a monogeneric family has been questioned by LOURTEIG (1965), who could not find enough reasons to separate it from Lythraceae. The Oliniaceae, Punicaceae and Sonneratiaceae have likewise been linked with or even included in Lythraceae from time to time (cf. VENKATESWARLU & RAO 1964, THORNE 1976, and BRIDGWATER & BAAS 1978). Thorne is the most recent advocate of a broad family concept of Lythraceae, including Sonneratiaceae, Punicaceae as well as Crypteroniaceae "because of insufficient gaps between them" (l.c. p. 90).

The Lythraceae are mostly restricted to the tropical and subtropical areas of the world. Only some genera have more or less herbaceous representatives in more temperate areas (*Lythrum, Peplis*). *Ammannia, Nesaea* and *Lawsonia* have a pan-tropical distribution. The others are restricted to America or to Asia and Africa. The American genera have their distribution mainly in Central and South America (*Adenaria, Crenea, Cuphea, Diplusodon, Ginoria, Lafoënsia, Pehria* and *Physocalymma*), while some are also represented in North America (e.g. *Decodon* and *Heimia*). *Lagerstroemia, Woodfordia* and *Pemphis* occur only in Asia and Africa. *Tetrataxis* is an endemic of Mauritius.

Although emphasis in this study is on the truly woody members of the Lythraceae, some semi-woody species and stems of perennial herbs were also studied. The number of wood samples available from shrubby species was limited because of the general lack of this important category of woody plants in institutional wood collections. Often we had to use twigs from herbarium specimens. In all, 18 genera were studied; most other genera listed by KOEHNE (1903) or in the Index Kewensis are truly herbaceous. Only of the woody genera *Capuronia* Lourteig, *Galpinia* N.E. Brown, *Haitia* Urb., *Orias* Dode, and *Pleurophora* D. Don no material was studied at all.

Several members of the Lythraceae are of economic importance. Species of *Lafoënsia, Lawsonia* (henna) and *Woodfordia* are used for the preparation of dyes; species of *Lafoënsia, Lagerstroemia* and *Woodfordia* yield commercial timbers; and *Cuphea indica, Lagerstroemia indica* and *Woodfordia* species are cultivated for ornamental purposes.

2. MATERIALS AND METHODS

Wood samples were obtained from several institutional wood collections referred to according to STERN (1978). Herbarium vouchers are listed where known; collection numbers referring only to wood samples are given between brackets; mature samples are listed without special indication but immature samples (less than 5 cm ⌀) have the diameter given. The immature samples were all obtained from herbarium sheets in the Rijksherbarium. Material of *Tetrataxis* and some *Heimia* and *Cuphea* species were received through courtesy of Dr. S. A. Graham. Sections were stained with safranin and haematoxylin or according to a modified method by MAÁCZ & VÁGÁS (1961) with safranin and astrablue. Macerations were obtained using Franklin's method (hydrogen peroxide and glacial acetic acid) and mounted in glycerine jelly.

For each mature sample 25 measurements were made for vessel members length (tails included), vessel diameter, fibre length, fibre diameter and ray height. Ray frequencies are based on 5 counts over a tangential distance of 1 mm each. For quantitative data on immature wood (of twigs or stems of "woody herbs") measurements have been more limited, and mostly extreme values are given only.

Specimens marked with an asterisk were studied with a Cambridge scanning electron microscope. Tangential, transverse and oblique surfaces were cleaned in diluted household bleach and coated with carbon and gold for this purpose.

3. DESCRIPTIVE PART

3.1. Explanatory note

The taxonomic nomenclature follows KOEHNE (1903), and where possible has been brought up to date according to FURTADO & SRISUKO (1969, *Lagerstroemia*), GRAHAM (1975, *Cuphea*), LÉON (1953, *Ginoria*, *Lawsonia*), WALKER (1976, *Pemphis*), and LEMÉE (1953, *Crenea*). In the absence of a recent monograph of the whole family the possibilities for questionable taxonomic delimitation and erroneous identifications are considerable.

In the wood anatomical descriptions absence of a certain character has only been recorded if considered important for identification purposes. Descriptive terms for size classes follow CHATTAWAY (1932), except for fibre wall thickness which is expressed according to VAN VLIET (1976). For terminology and classification of vestured pits recommendations by VAN VLIET (1978) are followed.

For herbaceous species or woody species of which only stems of very restricted diameter were available abbreviated descriptions are given, with a minimum of quantitative data. For stems of 1 cm ⌀ or thicker full descriptions are presented.

3.2. General wood anatomical descriptions of the Lythraceae

Growth rings absent to distinct. Wood diffuse-, or semi-ring-porous to ring-porous. *Vessels* 6–108/mm^2 or up to 250/mm^2 in woody herbs, solitary and in radial multiples of 2–8, round to oval, sometimes ± angular, small to medium-sized (30–220 μm in tangential diameter). Average vessel member length 200–580 μm. Perforations simple in oblique to transverse end walls. Inter-vessel pits crowded, alternate, vestured, round or oval to polygonal, 3–12 μm in diameter, occasionally with coalescent apertures. Vessel–ray and vessel–parenchyma pits usually similar but half-bordered; in some species with strongly reduced borders to simple and in a reticulate pattern. Vestures mostly of Van Vliet's type B form 2, but also of forms 1 or 3 or tending towards type A in a number of taxa. *Vascular tracheids* rarely present. *Fibres* typically libriform, with simple to minutely bordered pits, tending to be confined to the radial walls, short or of medium length (380–1850 μm on average), often septate, sometimes chambered crystalliferous, with thin to thick walls. Fibres in some taxa of two types, one of which is transitional towards axial parenchyma. *Parenchyma* mostly scanty paratracheal to almost absent, rarely also apotracheally diffuse; in some taxa vasicentric to aliform and confluent. Strands of (1–)2–4(–12) cells. *Rays* heterogeneous or more rarely homogeneous; in small shrubs and herbs often exclusively composed of erect cells; mostly uniseriate with occasional biseriate portions, but bi- to triseriate in some taxa. *Crystals*, if present, almost always rhomboidal and in chambered fibres or chambered axial parenchyma strands; very rarely also in ray cells.

3.3. Generic wood anatomical descriptions

Adenaria Kunth

Material studied: *A. floribunda* H.B.K.: Peru, Woytkowski 5506* (= USw 15543, ⌀ 3 cm); Panama, Stern, Chambers, Owyer & Ebinger 20 (= USw 16051, ⌀ 2.5 cm).

Shrub from Central and South America.

Growth rings faint to distinct. *Vessels* diffuse, 45 & 56/mm^2, solitary and in radial multiples of 2–3(–6), rarely clustered, 20% solitary, round to oval, tangential diameter (31–)60 & 81(–135) μm, radial diameter up to 145 μm, walls 2–3 μm thick. Vessel member length (160–)340 & 580(–730) μm. Perforations simple in transverse to oblique end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 4–5 μm in diameter, apertures very rarely coalescent. Vestures of type B form 2. Vessel–ray and vessel–parenchyma pits similar but half-bordered, infrequently elongate and up to 10 μm. Vessel walls densely to sparsely warted; warts globular, but near pit apertures sometimes irregularly shaped. Some vessels with solid amorphous contents. Tyloses absent. *Fibres* (320–)570 & 810(–950) μm long, walls very thin (c. 2 μm) or medium thick to very thick and gelatinous (c. 5 μm), with simple to minutely bordered pits (2 μm) with lenticular to slit-like apertures mainly confined to the radial walls, frequently septate. *Parenchyma* extremely scanty; only occasionally paratracheal or apotracheal cells noted, strands of 2–3 cells. *Rays* heterogeneous I–II, 16–18/mm, mostly uniseriate, rarely with a biseriate portion, entirely composed of erect cells or with central portion of square to weakly procumbent cells and 3–8 rows of marginal erect cells. *Crystals* absent.

Note: WILLIAMS (1936, cited in METCALFE & CHALK 1950) reported abundant parenchyma in *A. floribunda*. Probably this record is based on unreliably named material.

Ammannia L. *(plate I: 1–3)*

Material studied: *A. octandra* L. f.: Java, Houwing 22* (stem from herbarium specimen, ϕ 4 mm).

"Woody" herb from S.E. Asia and Ceylon.

Growth rings distinct. *Vessels* diffuse, solitary and in radial multiples of 2–4, round to oval, diameter up to 45 μm. Vessel member length up to 400 μm. Perforations simple in oblique end walls. Inter-vessel pits alternate, vestured, round to polygonal, 5 μm in diameter. Vestures of type B, intermediate between forms 2 and 3. Vessel–ray and vessel–parenchyma pits similar but half-bordered or elongate and up to 10 μm. Vessel walls infrequently warted. Vessel contents or tyloses absent. *Fibres* up to 550 μm long, walls thin (2–3 μm) with simple to very minutely bordered pits (1–2 μm) mainly confined to the radial walls, not septate. *Parenchyma* extremely scanty; only a few paratracheal cells observed, strands of 2–3 cells. *Rays* uniseriate and entirely composed of erect cells. *Crystals* absent.

Note: According to KOEHNE (1903) and BACKER & BAKHUIZEN VAN DEN BRINK Jr (1963) *A. octandra* is usually an annual herb. The three distinctive growth increments observed in the xylem of the specimen studied by us, are suggestive of a longer life-span for individual plants although the increments cannot of course be equated with annual wood production.

Crenea Aubl. *(plate VI: 1)*

Material studied: *C. maritima* Aubl.: Surinam, Hostmann s.n. = Herb. Leiden 903.322-320, and Splitgerber 344* – *C. repens* G.F.W. Mey. (= *C. surinamensis* Koehne): Colombia, Lehmann B.T. 661*. All material was derived from stems of herbarium specimens, 3–4 mm in diameter.

Herbs and small shrubs from South America.

Growth rings faint. *Vessels* diffuse, solitary and in radial multiples of 2–3, round to oval, diameter up to 35 μm. Vessel member length up to 450 μm. Perforations simple in oblique end walls. Inter-vessel pits alternate, vestured, round to polygonal, 5 μm in diameter, infrequently elongate and up to 8 μm. Vestures of type B form 1. Vessel–ray and vessel–parenchyma pits slightly larger, half-bordered, often elongate and arranged in a reticulate or scalariform pattern leaving on the parenchyma side only space for thin portions for secondary wall deposition, thus creating the impression of helical wall thickenings. Warts not observed. Tyloses and vessel contents absent. *Fibres* up to 650 μm long, walls very thin (1 μm) or thick and gelatinous, with simple pits on both radial and tangential walls, infrequently septate. *Parenchyma* scanty paratracheal, strands of 2–5(–9) cells. *Rays* uniseriate and entirely composed of erect cells. *Crystals* absent.

Cuphea P. Br. *(plate VI: 2)*

Material studied: *C. carthagensis* (Jacq.) Macbr.: Fiji, A.C. Smith 4816*; Paraguay, Hassler 11517* – *C. speciosa* (Anders.) O. Ktze (= *C. melvilla* Lindl.): Venezuela, Wurdack & Adderley 42832* – C. spec.: Mexico, Reveal 4339. All material was derived from stems of herbarium specimens, 3–4 mm in diameter.

Herbs or small shrubs, America.

Growth rings absent to fairly distinct. *Vessels* diffuse, solitary and in radial multiples of 2–4(–10), round to oval, diameter up to 40 μm except in *C. speciosa* in which they measure up to 80 μm. Vessel member length up to 350–450 μm. Perforations simple in oblique end walls; some vestigal scalariform perforation plates observed in first-formed secondary xylem of *C. carthagensis*. Inter-vessel pits alternate, vestured, round to polygonal and 4–6 μm in diameter, or tending to opposite and elongate and up to 10 μm. Vestures of type B form 2 or form 1. vessel–ray pits similar but half-bordered, vessel–parenchyma pits not observed. Warts observed in varying density in vessels of *C. speciosa* only. Tyloses and vessel contents absent. *Fibres* up to 500–650 μm long, walls thin or medium thick, or thick and gelatinous, with simple pits mainly confined to the radial walls, all nonseptate *(C. carthagensis)* or fairly frequently septate (other species). *Parenchyma* very scanty paratracheal or virtually absent, strands of 2 cells. *Rays* uniseriate only *(C. carthagensis)* or uniseriate and biseriate (*C.* spec.) or uni- to 4-seriate *(C. speciosa)*, composed of erect to square cells; occasionally with some weakly procumbent cells in *C. speciosa*. *Crystals* absent.

Note: C. speciosa stands out in the material studied on account of its numerous, wide vessels and broad rays. The vessels are most numerous in the rounded corners of the stem. The anatomy in the specimen studied suggests a scandent or climbing habit, but no data on the herbarium label or in the literature have been found to substantiate this.

Decodon J. F. Gmelin

Material studied: *D. verticillatus* (L.) Ell.: N. America, Pennsylvania, Heller & Halbach s.n.* (April 1893), stem from herbarium specimen, 6 mm in diameter.

Shrub from shallow water or swamps in Eastern North America.

Growth rings distinct. Wood diffuse- to semi-ring-porous. *Vessels* solitary and in radial multiples of 2–5, round to oval or tending to angular, diameter up to 40 μm. Vessel member length up to 480 μm. Perforations simple in oblique end walls. Inter-vessel pits alternate or in an opposite to reticulate pattern, vestured, often with reduced borders round to polygonal or elongate, 4–10(–20) μm. Vestures of type B form 1–2. Vessel–ray and vessel–parenchyma pits similar but half-bordered and sometimes in opposite to scalariform arrangement. Warts not observed. Vessel contents and tyloses absent. *Fibres* up to 700 μm long, walls thin (2 μm) with simple pits mainly confined to the radial walls, infrequently septate. *Parenchyma* scanty paratracheal and very scanty apotracheally diffuse, strands of (1–)2–4 cells. *Rays* heterogeneous, uni- and bi(–tri)-seriate, the latter tall and with short bi(–tri)-seriate portions of weakly procumbent to erect cells and occasionally with sheath cells. Solitary and fragmented (irregular clusters) *crystals* in ray and axial parenchyma cells, especially in first-formed secondary xylem.

Note: The ray cells are relatively large in this species creating a characteristic histology as seen in transverse and tangential section.

Diplusodon Pohl

Material studied: *D. buxifolius* (Cham. et Schlechtd.) DC.: Brazil, Herb. Martii Bras. 865, stem from herbarium specimen, 4 mm in diameter.

Small shrub, South America.

Growth rings absent. *Vessels* diffuse, solitary and in radial multiples of 2–4, round to oval or tending to angular, diameter up to 55 μm. Vessel member length up to 400 μm. Perforations simple in oblique end walls. Inter-vessel pits alternate, vestured, round to polygonal, 5–7 μm. Vestures of type B form 1–2. Vessel–ray pits similar but half-bordered. Warts (or loose particles on the vessel walls?) present in low density. Tyloses and vessel contents absent. *Fibres* up to 700 μm long, walls of medium thickness with simple pits mainly confined to the radial walls, nonseptate. *Parenchyma* absent. *Rays* uniseriate, composed of square to erect cells, rarely with some weakly procumbent cells. *Crystals* absent.

Ginoria Jacq. *(plate V: 3)*

Material studied: *G. americana* Jacq.: Cuba, Herb. d'Alleizette 2902* (twig of 3 mm diameter) – *G. arborea* Britt.: Cuba, (SJRw 16002) – *G. diplusodon* Koehne (= *G. ginorioides* Britt.): Cuba, (SJRw 19998)* and (SJRw 16714, branch of c. 15 mm diameter) – *G. koehneana* Urb.: Cuba, (SJRw 26542).

Trees and shrubs, West Indies.

Growth rings faint to distinct. *Vessels* diffuse, 50–108/mm^2, solitary and in radial multiples of 2–4(–7), longer pore chains interrupted by fibres often present, 11–35% solitary, round to oval, tangential diameter (21–)44–59(–84) μm, radial diameter up to 71–110 μm, walls 3–5 μm thick. Vessel member length (270–)390–420(–610) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 3–5(–6) μm in diameter, apertures rarely coalescent. Vestures of type B form 1–2. Vessel–ray pits similar but half-bordered, rarely elongate or unilaterally compound. Vessel–parenchyma pits very rarely observed, similar. Warts abundant, intergrading with vestures on pit apertures in *G. diplusodon*, not observed in twig of *G. americana*. Tyloses absent. Heartwood vessels with solid, dark brown, amorphous contents. *Fibres* with thin to thick walls with simple pits mainly confined to the radial walls, septate. A varying portion of the fibres chambered and crystalliferous (up to 90% of the fibrous ground tissue), (440–)720–820(–1130) μm long. Noncrystalliferous fibres shorter, sometimes with the appearance of parenchyma strands but with 2 or 3 septae, (340–)510–700(–990) μm long. In some specimens the crystalliferous and noncrystalliferous fibres arranged in alternating tangential bands. *Parenchyma* extremely scanty paratracheal, strands of 3–4 cells. *Rays* heterogeneous II, 11–15/mm, 1–2(–4)-seriate. Uniseriates low and composed of upright cells only; bi(–4)-seriates composed of procumbent cells with 1–3 marginal, square to upright cells. Rays up to 4-seriate in *G. diplusodon* (SJRw 19998) only. Rhomboidal *crystals* abundant in chambered fibres, with or without minute satellite crystals in each chamber. Rhomboidal crystals in procumbent, chambered ray cells observed in *G. diplusodon* (SJRw 19998) and *G. koehneana* only. Crystals absent from twig of *G. americana*, and very rare in sapwood of *G. diplusodon* (SJRw 16714).

Note: In the above description no quantitative data have been included of the immature xylem of *G. americana*. The usually abundant crystalliferous fibres, with a higher average length than the noncrystalliferous fibres constitute a remarkable feature of this genus. The lack of any crystals in the twig specimen of *G. americana*, and the relatively low percentage of fibres with crystals (20) in the branch sample of *G. diplusodon* (SJRw 16714) are suggestive that the maximum frequency of crystalliferous fibres is only attained in mature wood samples. Within Lythraceae, the wood of *Ginoria* is unique because of its distinctive (dark) heartwood formation.

Heimia Link & Otto *(plate I: 3–6; VI: 3, 6 & 7)*

Material studied: *H. myrtifolia* Cham. & Schlechtd.: Java, Cult. hort. Bogor, Boerlage s.n.* – *H. salicifolia* Link: Mexico, Graham 141* – *H.* spec.: Mexico, Anderson & Laskowski 3620*. All specimens from herbarium, 4–8 mm in diameter.

Shrubs, Central and South America.

Growth rings faint to distinct. Wood semi-ring-porous to diffuse-porous. *Vessels* solitary and in radial multiples of 2–6, round to oval or tending to angular, diameter up to 50 μm. Vessel member length up to 350 μm. Perforations simple in oblique end walls. Inter-vessel pits diffuse or crowded and alternate, vestured, round to polygonal, 5(–7) μm in diameter. Vestures of type B form 3, but rather thin. Vessel–ray and vessel–parenchyma pits similar but half-bordered, or with much reduced borders and tending to large and simple. *Vascular tracheids* intergrading with narrow vessels abundant near growth ring boundaries (latewood) and also associated with vessels. Walls of vessels and vascular tracheids with well-developed spiral thickenings which are occasionally branched. Tyloses and vessel contents absent. Warts absent. *Fibres* up to 500 μm long, walls of medium thickness (normal) or very thick (gelatinous) with simple pits mainly confined to the radial walls, septate. *Parenchyma* extremely scanty paratracheal, some strands of 1–2 cells observed only. *Rays* uni(–bi)seriate, composed of erect to square cells. *Crystals* absent.

Note: Heimia stands out from all other Lythraceae studied because of its well-marked spiral thickenings on the vessel walls, and the occurrence of abundant vascular tracheids, which also have wall thickenings.

Lafoënsia Vand. *(plate II: 1–3)*

Material studied: *L. punicifolia* DC.: Peru, (MADw 22448); Panama, Pittier 4763 (= MADw 5792 = USw 58)*.

Trees, Central and South America.

Growth rings faint to distinct. *Vessels* diffuse, 21 & 29/mm², solitary and in radial multiples of 2–3(–4), 15 & 40% solitary, round to oval, tangential diameter (39–)84 & 90(–130) μm, radial diameter up to 185 μm, walls 3–6 μm thick. Vessel member length (220–)320 & 390(–510) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 4–7 μm in diameter, apertures sometimes coalescent. Vestures of type A to B form 1. Vessel–ray and vessel–parenchyma pits similar but half-bordered. Warts densely present in some localized vessel wall areas, intergrading with vestures on pit apertures. Tyloses absent. Solid amorphous contents present in some of the vessels. *Fibres* (540–)890 & 910(–1100) μm long, walls thin to medium thick, rarely gelatinous, with simple to minutely bordered pits, mainly confined to the radial walls, septate. *Parenchyma* scanty paratracheal to vasicentric and very scanty apotracheally diffuse, strands of 2–3(–5) cells. Some strands also containing some septae and strands than intermediate between septate fibres and true parenchyma strands in their morphology. *Rays* heterogeneous II, 14 & 16/mm, uni- and biseriate, both composed of major portions of procumbent cells and 1–2(–4) rows of erect marginal cells. *Crystals* absent.

Lagerstroemia L. *(plate III, IV & VI: 4)*
Material studied: *L. archeriana* Bailey: Queensland, (FPRw 18846) – *L. calyculata* Kurz: Thailand, Royal For. Dept.* (= K-Jw s.n.) – *L. floribunda* Jack: Singapore, Ridley s.n. (= K-Jw s.n.) and (FHOw 1406*) – *L. hypoleuca* Kurz: India, Gamble s.n.* (= FHOw 535) – *L. indica* L.: Cult. Texas, (K-Jw s.n.*) – *L. loudonii* Teysm. et Binn.: Thailand, King 5420 (twig of herbarium specimen, 6 mm in diameter) – *L. macrocarpa* Kurz: Burma, Conserv. of Forests s.n.* (= FPRw 4642) – *L. microcarpa* Wight (= *L. lanceolata* Wall.): India, Gamble s.n. (= FHOw 534) – *L. ovalifolia* Teysm.: Malaya, For. Dept. 0586* (= FHOw 8953) – *L. parviflora* Roxb.: India, Gamble s.n. (= FHOw 528), (FHOw 536), and (FHOw 2357) – *L. piriformis* Koehne: New Guinea, Hoogland & Craven 10552*; Philippines, for. Bur. 6138 TS (= SJRw 29884) and Rojo 194 – *L. reginae* Roxb.: India, (FHOw 538)–*L. speciosa* (L.) Pers.: Malaya, (KEPw 378), (KEPw 1118), (FHOw 953*), and (USw 5419) – *L. subcostata* Koehne: Japan, (FHOw 2529*) – *L. tomentosa* Presl: Burma, (FHOw 1977*) – *L. venusta* Wall.: Burma, (FHOw 5333*) and (FHOw 2340 = *L. collettii*) – *L. villosa* Kurz: India, Cult. hort. Calcutta as *L. apetala* T. Anders. (= K-Jw s.n.).

Trees or shrubs, S.E. Asia, Malesia and Queensland.

Growth rings absent to distinct. Wood diffuse- to semi-ring-porous or ring-porous. *Vessels* 4–52/mm², solitary or in radial multiples of 2–3(–7), 10–80% solitary, round to oval, tangential diameter (30–)60–220(–380) μm, radial diameter up to 440 μm, walls 3–12 μm thick. Vessel member length (110–)220–580(–880) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 5–12 μm in diameter, apertures occasionally to frequently coalescent. Vestures of type B form 1 or 2, sometimes tending to be of type A. Vessel–ray and vessel–parenchyma pits similar but half-bordered, or with strongly reduced borders to simple and then in alternate to reticulate arrangement and frequently unilaterally compound. Normal *fibres* (420–)540–1860(–2180) μm long, with thin to thick walls with simple to minutely bordered pits mainly confined to the radial walls. In some species the fibres are of two types: "normal", including chambered crystalliferous fibres, and "parenchyma-like", including chambered crystalliferous fibres, with thinner walls and much shorter, often of wider diameter and with intercellular spaces between them. The parenchyma-like fibres in regular or irregular paratracheal and/or apotracheal bands (see *table I*); of rare occurrence in some species and then located between the normal axial parenchyma and normal fibres (especially *L. archeriana* and *L. piriformis*). All fibres septate. *Parenchyma* scanty paratracheal to vasicentric in species with abundant thin-walled, short, parenchyma-like fibres; abundant and aliform to confluent or in continuous paratracheal bands in other species. Strands of (1–)2–4(–12) cells; occasionally with thin septae in addition to or instead of ordinary transverse walls; partly chambered and crystalliferous. *Rays* homogeneous, 11–21/mm, almost exclusively uniseriate but in all species infrequent rays with very small biseriate portions present; the latter more frequent in a specimen of *L. speciosa* (KEPw 378) and in *L. reginae* and *L. venusta*. In immature specimen of *L. loudonii* the rays are weakly heterogeneous and contain a high proportion of square to erect cells, especially in the very first-formed secondary xylem. In mature sample of *L. indica* rays also rarely very weakly heterogeneous. Rhomboidal *crystals* infrequent to abundant in chambered axial parenchyma and chambered fibres; very rarely also present in ray cells.

(1969). Sizes given in µm.

	Vessel distribution	Vessel frequency	Percentage of solitary vessels	Average tangential diameter	Average vessel member length	Vessel–ray pit type	Size of inter-vessel pits	Fibre dimorphism	Length of normal fibres	Length of short fibres	Distribution of thin-walled fibres	Parenchyma distribution	Length of parenchyma strands in cells*
Section SIBIA													
L. indica	d.	52	50	60	220	h.b.-r.b.	5–7	+	540	380	irr.pa.ba.	sc.pa.	1–3
L. microcarpa	sr.	12	40	220	400	r.b.-s. (ret.)	10–12	–	1420			al.co.ba.(d.)	2–4
L. parviflora	d.-sr.	8	40	150	380	r.b.-s. (ret.)	7–10	–	1280			al.co.ba.(d.)	3–4
L. venusta	sr.-r.	9	55	130	380	r.b.-s. (ret.)	8–10	–	970			al.co.ba.d.	3–4 (–12)
L. ovalifolia	sr.-r.	7	70	140	350	r.b.-s. ret.	6–9	–	1220			al.co.ba.	4–7
L. piriformis	sr.-r.	5–6	80	150	430	r.b.-s. ret.	8–12	–	1480			al.co.ba.	3–4
L. villosa	d.-sr-	10	60	100	390	r.b.-s. ret.	6–10	–	1170			al.co.(ba.d.)	2–8
Section ADAMBEA													
L. hypoleuca	r.	7	65	185	320	r.b.-s. ret.	8–10	–	1370			al.co.ba.(d.)	2–7
L. reginae	sr.-r.	6	55	140	330	r.b.-s.	8–10	–	910			v.al.co.ba.	2–8
L. speciosa	d.-sr.	6	50	160	340	h.b.-s. (ret.)	7–9	–	1610			al.co.ba.(d.)	4–8
L. macrocarpa	d.-sr.	12	35	150	420	r.b.-s. (ret.)	8–11	–	1860			al.co.ba.	4–8
L. subcostata	d.	21	10	100	370	h.b.-r.b.	6–8	+	890	430	ap./pa.ba.	sc.pa.	2–5
Section TRICHOCARPIDIUM													
L. tomentosa	d.	14	20	110	580	r.b.-s. (ret.)	8–12	+	1120	620	ap./pa.ba.	sc.pa.	2–4
L. archeriana	d.-sr.	20	50	100	440	h.b.-r.b.	6–8	–	1100			al.co.ba.	1–4
L. calyculata	d.-sr.	20	30	120	520	r.b.-s. ret.	6–8	+	1230	550	ap.ba.	sc.pa.(d.)	2–7
L. floribunda	d.	20	35	90	380	r.b.-s. ret.	6–8	+	940	490	ap./pa. irr.ba.	sc.pa.(d.)	2–4
L. loudonii (twig)	d.	98	20	45	–	h.b.-r.b. (ret.)	6–9	±			irr.ba.	(sc.pa.)	4

Legend: al.: aliform, ap.: apotracheal, ap./pa.: intermediate between apotracheal and paratracheal (applies to bands), ba.: banded, co.: confluent, d.: diffuse, h.b.: half bordered, irr.: irregular, pa.: paratracheal, r.: ring-porous, r.b.: with reduced borders, ret.: reticulate, s.: simple, sc.pa.: scanty paratracheal, sr.: semi-ring-porous, v.: vasicentric. A character if placed between brackets is of rare occurrence or poorly developed in its expression.

* Strand length variation may be considerably greater in some species than recorded here, but especially in species with scanty paratracheal parenchyma the number of complete strands observed was very limited.

Note: Additional observations were made on herbarium twigs of *L. indica* and *L. speciosa.* Parenchyma appeared very scanty paratracheal in *L. indica,* but fibre dimorphism was hardly in evidence. In *L. speciosa* twigs, parenchyma was scanty paratracheal to vasicentric, very rarely aliform; fibre dimorphism was absent here as in the mature wood studied.

The distribution of wood anatomical characters over the different species is given in *table 1.* Taxonomic implications and the significance of fibre dimorphism are discussed in subsequent sections of this paper. Previous authors including species with outspoken fibre dimorphism in their studies (e.g. KANEHIRA 1921; PEARSON & BROWN 1932, DESCH 1957) have mistaken the thin-walled, short fibres for parenchyma.

Key to species or groups of species of *Lagerstroemia*

1. Fibre dimorphism well-developed; true axial parenchyma scanty 2
   Fibre dimorphism absent or hardly developed; axial parenchyma abundant 4
2. Vessel–ray pits half-bordered or with slightly reduced borders, not simple and in reticulate pattern . . . . *L. indica, L. subcostata*
   Vessel–ray pits at least partly tending to simple and in reticulate pattern 3
3.* Inter-vessel pits 8–12 μm . . . . *L. tomentosa*
   Inter-vessel pits 6–8 μm . . . . *L. calyculata, L. floribunda (L. loudonii)*
4. Vessel–ray pits mostly half-bordered or with reduced borders, not in reticulate pattern . . 5
   Vessel–ray pits at least partly tending to simple and in reticulate pattern . . . *L. hypoleuca, L. macrocarpa, L. microcarpa, L. ovalifolia, L. parviflora, L. piriformis, L. speciosa, L. venusta, L. villosa*
5.* Inter-vessel pits 8–10 μm . . . . *L. reginae*
   Inter-vessel pits 6–8 μm . . . . *L. archeriana*

* The separation on the basis of inter-vessel pit size may prove unjustified if more material than used for this study would be taken into account.

Lawsonia L. *(plate II: 4 & 5)*
Material studied: *L. inermis* L.: Palestine, (K-Jw s.n.)*.

Erect shrub or small tree, probably native to E. Africa and S.W. Asia; widely cultivated as ornamental or dye-tree.

Growth rings distinct. *Vessels* diffuse, $60/mm^2$, solitary and in radial multiples of 2–5(–9), 20% solitary, round to oval, tangential diameter (28–)50(–67) μm, radial diameter up to 105 μm, walls 4–6 μm thick. Vessel member length (260–)370(–470) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 3–4 μm in diameter, apertures frequently coalescent. Vestures of type B form 1–2. Vessel–ray and vessel–parenchyma pits similar but half-bordered, vessel–parenchyma pits less crowded. Warts present, intergrading with vestures on the pit apertures. Tyloses absent. Solid amorphous contents in some of the vessels. *Fibres* of two types: medium thick-walled fibres, (440–)740(–940) μm long; and thin-walled, parenchyma-like, (200–)400(–570) μm long. both categories partly chambered crystalliferous, and all fibres septate, with simple to minutely bordered pits mainly confined to the radial walls. The thin-walled fibres in a confluent to banded parenchyma-like distribution pattern; some fibres bordering the vessels intergrading morphologically with septate fusiform parenchyma cells. Thin-walled fibres often with small intercellular spaces between them. *Parenchyma* scanty paratracheal and in marginal (terminal) bands. Strands of 1–3 cells; fusiform parenchyma cells bordering the vessels septate and intergrading morphologically with short thin-walled fibres. *Rays* heterogeneous II, 14/mm, 1–3-seriate. Uniseriate rays composed of erect cells; bi- and triseriate rays composed of central portions of procumbent cells and short uniseriate tails of 1–4 square to erect cells. Solitary *crystals* common in chambered fibres.

Lythrum L.
Material studied: *L. virgatum* L.: Japan, Herb. Leiden 908.129-917 (stem of 5 mm diameter from herbarium material*).

Perennial herb with woody stems, Eurasia.

Growth rings faint. *Vessels* diffuse, solitary and in radial multiples of 2–4(–9), round to oval or tending to angular, diameter up to 35 μm. Vessel member length up to 630 μm. Perforations simple in oblique end walls. Inter-vessel pits alternate, vestured, round to oval, 4–5 μm in diameter. Vestures of type B form 1. Vessel–ray and vessel–parenchyma pits similar but half-bordered, occasionally unilaterally compound. Warts, tyloses and vessel contents absent. *Fibres* up to 1050 μm long, walls thin to medium thick with simple pits on both radial and tangential walls, very rarely septate, partly with gelatinous walls. *Parenchyma* very scanty paratracheal, strands of 2–4 cells. *Rays* uniseriate, exclusively composed of erect cells. *Crystals* absent.

Nesaea Comm. *(plate VI: 5)*

Material studied: *N. erecta* Guillem. & Perr.: Africa, Sénégambie, Herb. d'Alleizette s.n. – *N. floribunda* Sond.: South Africa, Herb. Lugd. Bat. 908.128-1529 – *N. sagittifolia* (Sond.) Koehne: South Africa, Wilms 481 (stems, 3–4 mm in diameter from herbarium material).

Annual or perennial herbs, Africa, Australia, North America.

Growth rings absent. *Vessels* diffuse, solitary and in radial multiples of 2–3, round to oval or slightly angular, diameter up to 40–45 μm. Vessel member length up to 300–480 μm. Perforations simple in oblique end walls. Inter-vessel pits (irregularly scalariform to opposite to) alternate, vestured, round to polygonal and 4–6 μm in diameter, or elongate and up to 12 μm. Vestures of type B form 1(–2). Vessel–ray and vessel–parenchyma pits half-bordered, scalariform (especially in *N. erecta*) to opposite or irregularly alternate. Warts absent or infrequently present. Tyloses and vessel contents absent. Fine and faint spiral thickenings usually present. *Fibres* up to 500–700 μm long, with medium thick, often gelatinous, walls with simple to minutely bordered pits on radial and tangential walls, nonseptate. *Parenchyma* very scanty paratracheal, strands of 2–4 cells. *Rays* uniseriate, exclusively composed of erect cells. *Crystals* absent.

Pehria Sprague

Material studied: *P. compacta* (Rusby) Sprague (syn. *Grislea compacta* Rusby and *Grislea secunda* Loefl. non Linn. cf. Sprague, J. Botany 61: 238, 1923): Venezuela, Standen 124 (= MADw 14266)*, Hallier 196* (herbarium twig of 6 mm diameter); Colombia, (SJRw 20982, branch of 1.5 cm diameter).

Shrub, South America.

Growth rings absent to distinct. *Vessels* diffuse, 28 & 29/mm^2, solitary and in radial multiples of 2–4(–5), 25 & 27% solitary, round to oval, tangential diameter (34–)70 & 74(–95) μm, radial diameter up to 120 μm, walls 2–5 μm thick. Vessel member length (130–)300 & 530(–640) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 4–6(–9) μm in diameter, apertures sometimes coalescent. Vestures of type B form 1–2. Vessel–ray pits similar but half-bordered and slightly larger, sometimes unilaterally compound. Vessel–parenchyma pit pairs very rarely observed, similar. Warts present in varying density. Thin-walled tyloses present in SJRw 20982 only. Vessel contents absent. *Fibres* (250–)480 & 710(–890) μm long, walls thin to medium thick (normal) or very thick (gelatinous), with simple pits mainly confined to the radial walls. Part of the fibres chambered and crystalliferous. Crystalliferous fibres shorter than noncrystalliferous fibres in MADw 14266 but of about the same length in SJRw 20982 (see *table 2*). Crystalliferous fibres very infrequent in twig sample (Hallier 196). Noncrystalliferous fibres also partly septate. *Parenchyma* extremely scanty paratracheal; no complete strands observed. *Rays* heterogeneous I–II, 13/mm, 1–2(–3)-seriate. Uniseriates composed of erect cells with small to large portions of square to weakly procumbent cells; biseriates (only present in MADw 14266) with large portions of procumbent cells and 1–2(–3) rows of erect marginal cells. Rhomboidal *crystals* of varying size in chambered fibres; also infrequently present in procumbent, chambered ray cells of MADw 14266. Crystals infrequent in twig sample (Hallier 196).

Note: In the above description no quantitative data have been included of the immature xylem of Hallier 196. It is remarkable that the average values for fusiform element length of the branch wood of SJRw 20882 are much higher than for the mature sample MADw 14266. The latter sample appears more differentiated in its ray structure than the immature samples.

Pemphis J. R. & G. Forst. *(plate V: 1 & 2)*
Material studied: *P. acidula* Forst.: Solomon Isl., Walker 204* (= FHOw 17893); Marshall Isl., Taylor 46-1169 (= USw 12015); Java, For. Res. Inst. Buitenzorg 1174 (= FHOw 11965).

Small trees of shrubs of rocky or sandy shores. Tropical East Africa to Pacific.

Growth rings absent to fairly distinct. Wood diffuse- to semi-ring-porous. *Vessels* 25–37/mm^2, solitary and in radial multiples or clusters of 1–6, 15–43% solitary, round to oval, tangential diameter (23–)53–62(–77) μm, radial diameter up to 98 μm, walls 4–6 μm thick. Vessel member length (150–)250–390(–520) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round or very slightly polygonal, 4–6 μm in diameter, apertures infrequently coalescent. Vestures of type B form 1–2. Vessel–ray and vessel–parenchyma pits similar or elongate, but half-bordered and less crowded. Vessel–ray pits infrequently unilaterally compound. Warts infrequent. Thin-walled tyloses and solid amorphous contents abundant. *Fibres* (340–)560–730(–1020) μm long, walls thick to very thick with simple to minutely bordered pits mainly confined to the radial walls, non-septate. *Parenchyma* vasicentric to aliform, occasionally confluent on growth ring boundaries, and scanty apotracheally diffuse. Strands of 2–4(–6) cells. *Rays* heterogeneous II, 11–16/mm, 1–2(–3)-seriate, composed of erect to procumbent cells. Rays relatively low and occasionally with sheath cells. Biseriates with 2–5 rows of square to erect marginal cells. *Crystals* absent. Ray- and parenchyma cells with dark amorphous contents; fibres occasionally with granular contents.

Note: The combination of non-septate, thick-walled fibres, vasicentric to aliform parenchyma and low heterogeneous rays make this genus outstanding and easily recognizable within the Lythraceae.

Physocalymma Pohl
Material studied: *P. scaberrimum* Pohl: Brazil, Prance 13773 (= Uw 19007), Krukoff 7911* (= USw 19501); Peru, Williams 3882 (= USw 10204 = SJRw 18331).

Trees, tropical South America.

Growth rings faint. *Vessels* diffuse, 16–63/mm^2, solitary and in radial multiples of 2–5, 25–48% solitary, round to oval, tangential diameter (24–)43–91(–113) μm, radial diameter up to 145 μm, walls 3–5 μm thick. Vessel member length (140–)240–330(–460) μm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 3–5 μm in diameter, occasionally to frequently coalescent. Vestures of type A to B form 1. Vessel–ray and vessel–parenchyma pits similar but half-bordered, rarely unilaterally compound. Warts abundant, intergrading with vestures on pit apertures. Thin-walled tyloses and solid amorphous contents noted in Williams 3882 only. *Fibres* of two types of varying distinctness: medium thick-walled to thin-walled "normal" fibres, (320–)460–770(–930) μm long with minute simple pits mainly confined to the radial walls; and thin-walled fibres, often with intercellular spaces between them, (210–)240–400(–540) μm long, with simple usually larger and more numerous simple pits mainly confined to the radial walls. Short, thin-walled fibres in distinct, largely apotracheal, tangential bands in Krukoff 7911 and Prance 13773 (in these specimens the short fibres intergrading in morphology with fusiform, septate or nonseptate parenchyma) or in less clearly defined tangential bands in Williams 3882. Chambered crystalliferous fibres, mainly in zone of thin-walled fibres, present in Williams 3882 only. Many fibres non-septate in Krukoff 7911 (especially the long fibres); most to all fibres septate in other specimens. *Parenchyma* scanty paratracheal. Strands of 2–5 cells. Cells intermediate in morphology between fusiform, septate or non-septate parenchyma and thin-walled fibres present in Prance 13773 and Krukoff 7911. *Rays* heterogeneous II–III or almost homogeneous, 1–2(–4)-seriate. Uniseriate rays composed of erect to procumbent cells; 2–4-seriates with central portion of procumbent cells and 1(–4) rows of square to erect marginal cells. Rays more heterogeneous in Williams 3882 than in other specimens. Rhomboidal to diamond-shaped *crystals* infrequent in chambered fibres of Williams 3882.

Note: Williams 3882 differs fairly strongly in its wood anatomy from the other two specimens studied: beside the deviations recorded in the descriptions this specimen stands out because of its high vessel frequency (63/mm^2) and narrow average vessel diameter (43 μm). In spite of these deviations misidentification is unlikely because of the overall Lythraceous wood anatomy and the fact that within Lythraceae, *Physocalymma* also provides the best wood anatomical match with this specimen.

Tetrataxis Hook. f.
The wood anatomy of this monotypic genus from Mauritius has recently been described by GRAHAM & LORENCE (*Bot. J. Linn. Soc.* **76**: 71–82, 1977). The trees growing in water saturated ground have secondary xylem characterized by the following feature (observations made on twigs up to 9 mm in diameter):

Growth rings faint. *Vessels* diffuse, solitary and in radial multiples of 2–6, round to oval or tending to angular, diameter up to 50 µm. Vessel member length up to 430 µm. Perforations simple in oblique end walls. Inter-vessel pits alternate, vestured, round to polygonal, 4–6 µm in diameter, infrequently elongate and up to 9 µm. Vestures of type B form 2. Vessel–ray and vessel–parenchyma pits half-bordered, similar or with reduced borders and elongate (up to 26 µm) and occasionally unilaterally compound. Warts present, intergrading with vestures on the pit apertures. Tyloses absent. Granular contents present in some of the vessels. *Fibres* up to 810 µm long, thin-walled or thick-walled and gelatinous, with simple to minutely bordered pits mainly confined to the radial walls, septate. *Parenchyma* scanty paratracheal, strands of (2–)4(–6) cells, very rarely septate. *Rays* heterogeneous I–II, 1–3-seriate, composed of erect to procumbent cells. *Crystals* absent.

Note: This description is largely based on Graham & Lorence's account. The data were confirmed, and partly amplified by original observations of a branch from Mauritius, Coode 5073, 9 mm in diameter, of *T. salicifolia* (Thouars ex Tulasne) Baker.

Woodfordia Salisb. *(plate V: 4)*
Material studied: *W. fruticosa* (L.) S. Kurz (= *W. floribunda* Salisb.): India, Indian For. Dept. (KJw s.n.); Java, Koorders 29473* (⌀ 8 mm).

Erect shrubs, Africa, Madagascar, and south Asia.

Growth rings distinct. Wood diffuse- to semi-ring-porous. *Vessels* 75/mm², solitary and in radial multiples of 2–6(–11), 20% of the vessels solitary. "Normal" vessels often associated with *vascular tracheids* and/or very narrow vessels near growth ring boundaries. "Normal" vessels round to oval, tangential diameter (28–)52(–72) µm, radial diameter up to 77 µm. Tangential diameter of very narrow vessels 21–32 µm. Vessel member length (260–)440(–630) µm. Perforations simple in oblique to horizontal end walls. Inter-vessel pits crowded, alternate, vestured, round to polygonal, 3–5 µm in diameter, apertures occasionally coalescent. Vestures of type B form 2(–1). Vessel–ray and vessel–parenchyma pits similar but half-bordered, infrequently elongate (up to 11 µm) and unilaterally compound. Warts not observed. Thin-walled tyloses infrequent; solid amorphous contents abundant. *Fibres* (770–)970(–1200) µm long, thin- to medium thick-walled, with simple pits mainly confined to the radial walls, infrequently septate. *Parenchyma* very scanty paratracheal, strands of 3–4 cells. *Rays* heterogeneous I, 19/mm, 1–2-seriate. Uniseriate rays most common and mainly composed of erect cells, often with central portion of square to weakly procumbent cells. Biseriates with fairly short central portions of procumbent to square cells and tails of square to erect cells. *Crystals* absent. Pith flecks present.

4. DISCUSSION OF THE INDIVIDUAL WOOD ANATOMICAL CHARACTERS WITH COMMENTS ON VARIABILITY AND TAXONOMIC VALUE

4.1. Growth rings and vessel distribution and frequency

Growth ring boundaries occur in most Lythraceae but may vary from absent to faint or distinct. In perennials from the subtropical or temperate regions they are usually well-marked but many warm tropical representatives also show distinctive growth rings (notably many *Lagerstroemia* species). Often the distinctiveness of the growth ring boundaries (as expressed in differences in wall thickness of the fibres and in vessel diameter) is variable below the genus as well as the species level which makes it a rather useless character for diagnostic or taxonomic purposes. Most Lythraceae are diffuse-porous but semi-ring-porosity or ring-porosity occurs in *Decodon* (weak), *Heimia* (weak), *Lagerstroemia* pro parte (the whole range from diffuse-porous to ring-porous), *Pemphis* (weak) and *Woodfordia* (weak). The genera with a weak development of semi-ring-porosity also show diffuse-porous parts in the same wood sample or in other wood samples of the same species, which leaves *Lagerstroemia* as the only genus with well-developed semi-ring-porosity or ring-porosity in part of its species. The occurrence of intermediates between diffuse- and semi-ring-porous and between the latter and ring-porous within *Lagerstroemia* limits the potential use of this character for taxonomic purposes in this genus, however. Possibly the tendencies toward ring-porosity in *Lagerstroemia* are related with alternating dry and wet seasons and a deciduous habit of the species involved. Even within species the habit may vary from evergreen to deciduous (cf. KOORDERS & VALETON 1894 for *L. speciosa*) which may also explain the variability – and hence limited diagnostic value – of the expression of ring-porosity within this genus.

Vessel frequency varies between wide limits in Lythraceae. For the representatives with tree habit or large shrubs the values range from 4–108/mm^2. For stems of small shrubs or perennials and also for twigs of tree species the values range from about 100–250/mm^2. The lowest vessel frequencies are found in *Lagerstroemia* tree species. High values occur in *Ginoria* and *Woodfordia*, small trees or shrubs respectively. There is a considerable overlap between genera in vessel frequency: e.g. 4–52/mm^2 in *Lagerstroemia*, 16–63/mm^2 in *Physocalymma* and 50–108/mm^2 in *Ginoria*. Probably the range in the other genera is quite substantial as well, but this has not been revealed in the very limited number of specimens and species used for this study. Due to this large infrageneric or even infraspecific variation vessel frequency has not been used as a diagnostic or taxonomic character. On the whole there is a clear tendency for vessel frequency to be positively related to plant size. This does not only apply to the family as a whole but also to the species of the genus *Lagerstroemia*, where the shrub *L. indica* shows a much higher value for vessel frequency than the other species of tree habit.

The percentage of solitary vessels varies from 10 to 80. This entire range is exhibited by *Lagerstroemia;* in the other genera it is mostly between 15 and 40, and cannot be used for diagnostic or taxonomic purposes.

4.2. Vessel members and vascular pitting *(plate IV: 4 & 5; V: 1–5)*

Average tangential vessel diameter varies for the mature wood of trees and large shrubs between 43 and 220 μm, roughly in inverse correlation with vessel frequency. For small shrubs, perennial herbs and twigs of trees vessel diameter may be much smaller.

Average vessel member length varies between rather narrow limits between 220 and 580 μm within Lythraceae. This total range occurs in *Lagerstroemia* and all other shrub and tree species are thus within the range of variation of *Lagerstroemia.* Average values below 300 μm are restricted to *Lagerstroemia indica*, *Pemphis* and *Physocalymma.* The short vessel members in *L. indica* and *Pemphis* may be accounted for by their ecologies because the former species was studied using a sample from a subtropical locality where it was cultivated (Texas) and

Pemphis occupies physiologically dry coastal habitats. These two taxa might thus be cited in favour of altitudinal and mesic/xeric trends postulated for vessel member length (BAAS 1973 and 1976; VAN DER GRAAFF & BAAS 1974; CARLQUIST 1975b). The short vessel members of *Physocalymma* remain unaccounted for, however. Vessel members with an average length above 500 μm are found in *Adenaria*, *Pehria* and some *Lagerstroemia* species all from tropical localities. Unfortunately ecological data were too limited to attempt a detailed correlation between fusiform element length and environmental factors. Such an analysis would be especially interesting for the genus *Lagerstroemia*.

For taxonomic and diagnostic purposes vessel element length cannot be used within Lythraceae because of the overlap of *Lagerstroemia* with all other genera. For phylogenetic interpretation the pattern of vessel member length variation is also unsuitable.

It is noteworthy that the vessel members of small twigs or stems of perennial herbs and small shrubs are not very much shorter than those of the mature wood of large shrubs and trees.

The vessel perforations in Lythraceae are invariably simple in mature secondary xylem. Only once vestigal bars were noted in the first formed secondary xylem of *Cuphea carthagensis*. This rare occurrence of a primitive xylem character should in our opinion not be given phylogenetic significance.

Heimia is the only genus with well-developed spiral thickenings on its vessel walls. This small genus has its distribution in subtropical and tropical Central and South America and the consistent occurrence of spiral thickenings in this partly tropical genus is of highly diagnostic and possibly of taxonomic value (cf. BAAS 1973 and 1976, and VAN DER GRAAFF & BAAS 1974, for the occurrence of spirals in different geographical areas). The same may apply to the faint spirals of *Nesaea*.

A warty layer on the vessel walls of varying appearance occurs quite frequently within Lythraceae. Structure and occurrence are, however, too variable (even within a single specimen) to use this character for diagnostic or taxonomic purposes.

Like all "truly" Myrtalean families, Lythraceae have vestures in their bordered vessel pits. Recently VAN VLIET (1978) has proposed an alternative classification for the different types of vesturing which has been adopted here. In VAN VLIET's classification which is mainly based on the range of variation found in Combretaceae and Melastomataceae there are two main types: type A in which branched, thin vestures are attached to all parts of the roof of the pit chamber; and type B where the vestures have a trunk-like base attached to the roof of the pit chamber nearby the pit canal. Depending on the degree of branching of the type B vestures and the relative thickness of trunks and branches Van Vliet recognizes three subtypes or forms: B1 where the bases are only slightly thicker or of the same thickness as the branches resulting in a coarse or fine mat of branch-endings when viewed from the pit floor (thus indistinguishable from type A in that aspect); form B2 where the trunks are thick and branch profusely into thin vestures, again resulting in a mat of vestures, which when viewed from the pit floor is indistinct from type A or form B1; and form B3 where the trunk-like vestures are hardly branched and appear as thick trunk ends bearing knobs when viewed from the pit floot. Of all Lythraceous genera available to us, the type of vesturing was carefully studied with a scanning electron microscope, and the predominating type appeared to be type B, mostly forms 1 and 2.

There is, however, a great tendency for these subtypes to intergrade with each other or with subtype B3 (the latter through "reduction" of terminal vesture branches in *Ammannia* and *Heimia*). In some genera there is also a tendency for the vestures to be attached to a major part of the roof of the pit chamber, thus conforming to Van Vliet's type A (*Lafoënsia* and *Physocalymma*). On the whole the occurrence of intermediates makes Van Vliet's classification difficult to apply in the Lythraceae. This is not so in Combretaceae where no intermediates occur between types A and B and where type B form 1 (closest to type A) is completely absent. another problem concerning the application of Van Vliet's classification is the fact that the B3 subtype of vesturing in Lythraceae seems to be the result of the absence of branches from form B1, whilst in Combretaceae they are more fundamentally different from type B form 1 through the massive development of the trunk-like base of the non-branched vesture (therefore directly to be derived from Van Vliet's subtype B2). The range of variation in type of vesturing has, in our opinion, little or no taxonomic value below the family level in Lythraceae.

Other characters of vascular pitting are fairly constant throughout the family. Inter-vessel pits are almost invariably alternate and round to polygonal with the exception of some of the woody herbs where, in addition, opposite to scalariform or widely spaced diffuse pits may occur (*Cuphea*, *Decodon*, *Heimia* and *Nesaea*). The largest alternate inter-vessel pits occur in some species of *Lagerstroemia* (up to 12 μm); usually they are fairly small (4–6 μm). The vessel–ray and vessel–parenchyma pits are usually half-bordered but resemble the inter-vessel pits in size and arrangement. Exceptions are found in *Crenea*, *Heimia*, *Lagerstroemia* pro parte and *Woodfordia* where these pits tend to differ in shape or in reduction of the pit borders from the inter-vessel pits. The tendency toward large and simple reticulate vessel–ray pits is especially pronounced in the majority of species studied of *Lagerstroemia*. Unilaterally compound vessel-ray pits are of infrequent occurrence throughout the family. The wide range of variation in vascular pit size and in reduction of the borders in the vessel–ray and vessel–parenchyma pits within the genus *Lagerstroemia* make these characters of limited diagnostic or taxonomic value at the genus level within Lythraceae.

4.3. Tracheids *(plate I: 5 & 6)*

True tracheids, i.e. spindle-shaped imperforate cells with conspicuously bordered pits of the same size as on the vessel walls, were only observed in *Heimia* and *Woodfordia*. In both genera they intergrade with narrow vessel elements and they are mostly confined to the growth ring boundaries. It seems appropriate to consider them to be phylogenetically derived from narrow vessels and to classify them as vascular tracheids. Consequently they constitute a specialized character state for the genera in which they occur.

4.4. Fibres, fibre dimorphism and axial parenchyma *(plate I–VI, especially plate II: 4 & 5 and plate III & IV)*

All Lythraceae studied show fibres which can be classified as belonging to the libriform type: almost invariably the pits are simple and largely confined to the radial walls. In those genera where the pits have strongly reduced borders or where the tangential walls also have fairly numerous pits the fibres are still to be classified as libriform fibres because they are a far cry from true fibre-tracheids which should always show distinctly bordered pits. Fibre wall thickness ranges from thin to thick and reaches a maximum in the hard woods of *Ginoria, Pemphis* and in some species of *Lagerstroemia.* Gelatinous fibres are of frequent occurrence throughout the family. Chambered, crystalliferous fibres, of fairly rare occurrence in dicotyledons as a whole are characteristic for *Ginoria, Lagerstroemia, Lawsonia* and *Pehria.* In *Physocalymma* they were only infrequently present in one of the samples studied. Usually the crystalliferous fibres are of the same length as the non-crystalliferous fibres. However, in *Ginoria* the crystalliferous fibres were found to be consistently longer on average than the non-crystalliferous ones, whilst in *Pehria* the reverse tends to be the case (see *table 2*). In *Lagerstroemia* species showing fibre dimorphism (see below), the crystalliferous "normal" and "parenchyma-like" fibres have the same length as the adjoining non-crystalliferous fibres. Septation of the fibres is typical for most Lythraceae with the notable exceptions of *Ammannia, Diplusodon, Nesaea* and *Pemphis.* Species of some other genera may have very scarce septate fibres: *Crenea, Cuphea, Decodon, Lythrum* and *Woodfordia.* In *Cuphea* one species even completely lacks septate fibres. this variation below the genus level and the sporadic occurrence in some genera make it difficult to evaluate septate or non-septate fibres as a taxonomic character, especially for the genera of woody herbs or small shrubs. In *Pemphis* the lack of septate fibres constitutes, in our opinion, another indication of the deviating wood structure of this genus within the family.

Fibre dimorphism of another type than the occurrence of gelatinous or crystalliferous fibres beside normal fibres was found in *Physocalymma, Lawsonia* and in part of the species of *Lagerstroemia* (*L. calyculata, L. floribunda, L. indica,*

Table 2. Length (in μm) of crystalliferous and noncrystalliferous fibres in *Ginoria* and *Pehria.* Vessel member length is also given to enable an estimate of the intrusive growth of the fibres.

Material		Vessel member length	Length of crystalliferous fibres	Length of noncrystalliferous fibres
Ginoria arborea	SJRw 16002	280–390–510	450–720–950	410–620–920
Ginoria koehneana	SJRw 26542	270–400–610	440–730–920	390–510–600
Ginoria ginorioides	SJRw 16714	270–420–560	620–820–1130	340–700–990
Pehria compacta	MADw 14266	130–300–430	250–400–620	360–550–700
Pehria compacta	SJRw 20982	320–530–640	590–710–870	460–720–890

L. loudonii, *L. subcostata* and *L. tomentosa*). Here vague or well-defined bands of fibres occur which are much shorter than the normal fibres and which have thinner walls. Expecially in some specimens of *Physocalymma* and *Lagerstroemia* these fibres very strongly resemble septate fusiform parenchyma cells because the wall pitting approaches the simple pits with round apertures, typical of parenchyma cells whilst the fibres have (crossed) lenticular to slit-like apertures (cf. *plate III: 4 & 5*). Fibre dimorphism of this type has recently also been reported for *Miconia* of the Melastomataceae (TER WELLE & KOEK-NOORMAN 1978). Like in *Miconia*, the short fibres in *Lagerstroemia* and *Physocalymma* often have well-developed intercellular spaces between them. In *Lagerstroemia* these thin-walled short fibres obviously function similarly as the parenchyma bands which are well-developed in the other species. In some of the latter, transitions could be observed between the abundant true parenchyma strands and the normal fibres, similar to the short fibres of the *Lagerstroemia* species showing fibre dimorphism. It is our belief that the morphological series from normal fibre, to short fibre, to fusiform (septate) parenchyma cell, to normal parenchyma strand reflects a phylogenetic specialization trend within Lythraceae. This implies that the well-developed parenchyma bands in the majority of *Lagerstroemia* species are phylogenetically derived from fibres through fibre dimorphism. This view can be supported by the fact that scanty paratracheal parenchyma is the prevailing condition within Lythraceae and its close allies (*Sonneratia*, Punicaceae, most Melastomataceae, *Alzatea*, etc.) and may be considered to be the primitive type for this group. Similar views for other plant families have been put forward by CARLQUIST (1958, 1961, 1978) who considers the parenchyma in some taxa to be phylogenetically derived from fibres through fibre dimorphism. For *Pemphis* which has moderately abundant vasicentric to aliform parenchyma one has to assume a different derivation of axial parenchyma, simply through an increase of primitively scanty paratracheal parenchyma. Criticism to this hypothesis may be put forward by those who wish to visualize the scanty to absent parenchyma of the majority of Lythraceae as a reduction from the character state of abundant parenchyma as in most *Lagerstroemia* species. Such an opposing view could also imply that one has to read the series from normal fibres to short parenchyma-like fibres to parenchyma strands in a different phylogenetic direction. We would find such an interpretation most unlikely since it would mean that normal fibres are derived from parenchyma cells – a derivation leading to absurd consequences if applied rigidly. Within *Lagerstroemia* fibre dimorphism is of good diagnostic value at the species level (as far as can be concluded from the limited number of specimens studied). In view of the presumed primitive nature of fibre dimorphism as opposed to the possession of abundant parenchyma in *Lagerstroemia* this character cannot be too heavily relied on for judging mutual affinities amongst the species. Yet it is noteworthy that there is some correlation between FURTADO & SRISUKO's infrageneric classification (1969) of *Lagerstroemia* and the occurrence of fibre dimorphism: most of the species involved belong to their section *Trichocarpidium*. Since for Lythraceae as a whole fibre dimorphism is presumably an advanced character, and since it seems unlikely that it arose twice in the phylogenetic history of the family, it is tempting to suggest close mutual affinities for *Physocalymma* and *Lagerstroemia* on the basis of this character (see also section on mutual affinities).

Starch grains may be present in axial parenchyma as well as in the fibrous tissue (cf. *plate VI: 7*).

4.5. Rays *(fig. 1)*

Composition and width of the rays in Lythraceae show an interesting range of variation which can be used for diagnostic and taxonomic purposes. Most woody herbs or small shrubs show exclusively uniseriate rays, composed of erect cells only, or of a mixture of erect and square cells (*Ammannia*, *Crenea*, *Cuphea* p.p., *Lythrum*, and *Nesaea*). Similar rays but with occasional biseriate or even triseriate portions occur in *Heimia* and *Cuphea* p.p. This type of ray may be called juvenilistic and resembles that of very young twigs of shrub or tree species studied of *Ginoria* and *Pehria* which form heterogeneous I or II rays in their mature xylem.

Weakly to strongly procumbent cells constitute parts of the rays in the other genera. In *Adenaria*, *Cuphea* p.p., *Decodon*, *Diplusodon*, *Tetrataxis* and *Woodfordia* the narrow uni- and/or biseriate rays have a small central portion of usually weakly procumbent cells and these rays could be classified as heterogeneous type I in Kribs' classification (1968), although they do not show the typical abrupt difference between strongly procumbent and erect cells usually illustrated for this type. These rays intergrade in cellular composition with the rays composed of erect and square cells referred to above. They also intergrade with the heterogeneous type II rays which can be found in the woody genera *Ginoria*, *Lafoënsia*, *Lawsonia*, *Pehria*, *Pemphis*, and *Physocalymma* and *Tetrataxis*. In *Tetrataxis* the rays are in fact intermediate in type, but it is likely that this genus shows exclusively heterogeneous II rays in wood which is more mature than was available for study. In *Physocalymma* the proportion of square to erect cells may be very small, and part of the rays in that genus have therefore to be classified as heterogeneous type III.

The latter type is transitional between the markedly heterogeneous types I and II and the homogeneous rays which are typical and diagnostic for the genus *Lagerstroemia*. Only in *Lagerstroemia indica* the rays occasionally contain some square to erect marginal cells and then also tend to heterogeneous III, although virtually all rays are uniseriate. The homogeneous rays of *Lagerstroemia* pass through a "brief" heterogeneous phase in early ontogeny: in the very first formed secondary xylem of *L. loudonii* the rays contain a high proportion of erect to square cells but become homogeneous at a very short distance from the pith.

The range of variation in rays of Lythraceae lends itself well for phylogenetic interpretation in accordance with generally accepted ideas on ray specialization. The ancestral type is most probably constituted by the 1–3-seriate heterogeneous I rays. The narrow juvenilistic rays of almost exclusively erect cells of the small shrubs and woody herbs can be considered to be an early ontogenetic phase of this type. The lack or paucity of bi- or triseriate rays in these Lythraceae may be considered to be a specialization through reduction. The heterogeneous II to III rays of a number of truly woody Lythraceae can be considered as a moderate advancement from the heterogeneous I condition. *Lagerstroemia*, finally shows the most highly specialized rays of the family: exclusively composed of procumbent cells and predominantly uniseriate through loss of multiseriate rays.

The derivation of the different ray types and their distribution over the genera of Lythraceae is pictured in *fig. 1.* It should be stressed that either the shared possession of a specialized or of a primitive ray type not necessarily indicates close mutual affinity because parallel development in ray specialization must have been extremely common in Dicotyledons as a whole and probably also within individual families. Moreover, one cannot exclude the possibility that the juvenilistic ray type, occurring in many Lythraceae, may also have been phylogenetically derived through ancestors with more specialized rays in their mature secondary xylem. This does not only apply to the typically juvenilistic rays of the woody herbs and small shrubs, but also to Kribs' ray types of different advancement levels (see broken line in *fig. 1*). Since ray ontogeny usually covers (or "recapitulates") several levels of ray specialization this opens up these possibilities of paedomorphosis where a juvenile character state is perpetuated throughout the mature secondary xylem.

5. HABIT AND HABITAT AND THE WOOD ANATOMICAL DIVERSITY IN LYTHRACEAE

In the previous sections some miscellaneous remarks have been made on the correlations of habit and habitat with certain wood anatomical features (vessel member length, spiral thickenings etc.). Unfortunately data on the ecology of the species studied were extremely limited so that an overall analysis of ecological anatomical aspects could not be carried out. It is tempting to consider the rather isolated wood anatomical position of *Pemphis* within Lythraceae in combination with its "extreme" habitats on the shores of the Indian and Pacific Ocean. However, its character complex of very thick-walled fibres, vasicentric to aliform parenchyma and low, narrow rays also occurs in numerous unrelated groups with totally different ecologies. The unusual ecologies of *Tetrataxis* (water saturated soils) and *Decodon* (shallow waters and swamps) do not seem to have left any mark on their wood structure – they are in this respect very similar to a number of other Lythraceae with various different ecologies.

The herbaceous or "semi-woody" habit in Lythraceae is quite strongly associated with a special type of wood anatomy. As would be expected paucity of parenchyma, and predominance of erect cells in the rays, together with a high frequency of vessels are typical for this habit. Within the Lythraceae of this habit the wood anatomical diversity is very limited (spiral thickenings and vascular tracheids in few representatives only), and it should be stressed that the taxonomic significance of wood anatomy in this group of genera (*Ammannia*, *Crenea*, *Cuphea*, *Lythrum*, and *Nesaea*) is very limited. Small shrubs tend to show the

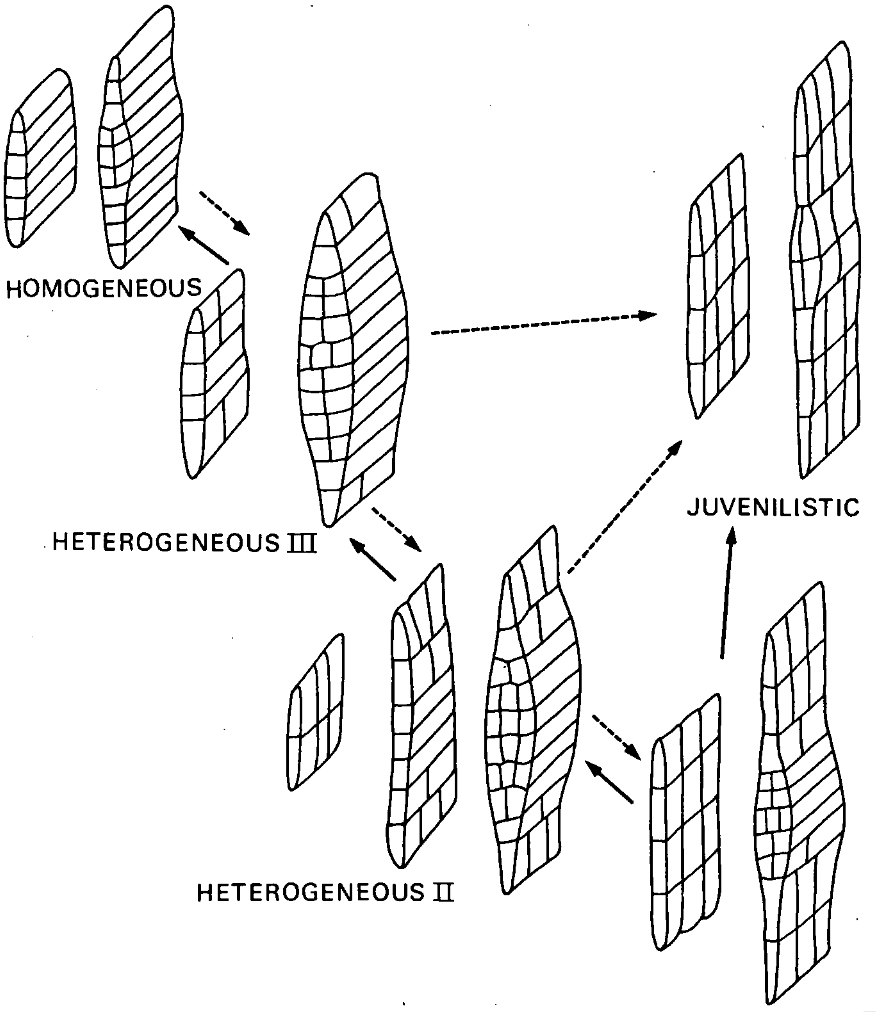

Fig. 1. Ray types of Lythraceae and their putative phylogenetic relationships. Dotted arrows indicate possibilities of reversion of the major specialization trends through paedomorphosis.

same character complex, although their rays may contain a higher proportion of procumbent cells (*Adenaria*, *Decodon*, *Diplusodon*, *Woodfordia*).

These relationships between habit and wood anatomy imply that in the subsequent sections where the affinities within Lythraceae are discussed, the position of these herbaceous and shrubby Lythraceae can hardly be assessed on the basis of their wood structure. The study of more mature wood samples for such genera as *Decodon* and *Diplusodon* might yield a slightly better differentiation than could be obtained with the material at our disposal.

6. WOOD ANATOMY AND AFFINITIES

6.1. Infrageneric classification of Lagerstroemia

The number of specimens and species of *Lagerstroemia* studied is too limited to make optimal use of the wood anatomical diversity within this genus for classification purposes. The following remarks should therefore be considered as tentative suggestions only, to be checked by future studies of more material and more characters. The most recent complete classification of the genus is by FURTADO & SRISUKO (1969) who largely followed KOEHNE's (1903) subdivision. In *table 1* summarizing the wood anatomical diversity of *Lagerstroemia* the species are arranged according to Furtado and Srisuko's sectional subdivision. In general there is little correlation between the occurrence of different wood anatomical characters and this classification. Fibre dimorphism occurs in all three sections, albeit that in section *Trichocarpidium* it is the most common condition, while it occurs in only one species each of the other two sections (*L. indica* of section *Sibia; L. subcostata* of section *Adambea*). As pointed out before, fibre dimorphism within *Lagerstroemia* is probably the primitive (plesiomorphic) condition and its occurrence in all sections is therefore not necessarily in conflict with this subdivision. However, on account of overall wood anatomical similarities *L. indica* and *L. subcostata* should be grouped closer together than in the macromorphological system, in our opinion. For similar reasons *L. archeriana* would seem better placed outside section *Trichocarpidium*, either in section *Adambea* or in section *Sibia*.

6.2. Affinities within Lythraceae

Since KOEHNE's revision of the whole family (1903) no comprehensive classification of the Lythraceae has been proposed. His system is summarized for the genera used in this study in *table 3*. For the subdivision into two tribes Koehne used complete or incomplete septation of the ovary. For seed characters he used presence or absence of wings mainly. The strictly hierarchical application of such a limited number of characters (in both tribes using seed characters subordinated

Table 3. Koehne's system for Lythraceae applied to the genera surveyed in this study.

Tribe	Lythreae	
	Subtribe	Lythrinae
		Series I. Ammannia, Lythrum, Woodfordia
		Series II. Cuphea
	Subtribe	Diplusodontinae
		Series I. Pemphis, Diplusodon
		Series II. Physocalymma, Lafoënsia
Tribe	Nesaeeae	
	Subtribe	Nesaeinae
		Series I. Crenea
		Series II. Nesaea, Heimia, Decodon, Pehria, Adenaria
		Series III. Tetrataxis, Ginoria
	Subtribe	Lagerstroemiinae. Lagerstroemia, Lawsonia

to the ovary character) is immediately suggestive of an artificial rather than a natural classification: if the seed characters were given more weight than the completeness of the septa of the ovary, Koehne's system would be drastically altered.

The wood anatomical pattern of variation also suggests that Koehne's system is artificial. Wood anatomically the subtribes Lythrinae of the Lythreae and Nesaeinae of the Nesaeeae are very close, in fact much closer to each other than to some genera of the other subtribes of their own tribes. Ray type, parenchyma distribution and fibre dimorphism together with more incidental characters like presence of crystalliferous fibres, vascular tracheids, and spiral thickenings to the vessel walls suggest a rather different pattern of relationships within Lythraceae. Based on the hypotheses of ray specialization and parenchyma specialization and/or derivation outlined in the previous chapter an alternative system has been worked out and is presented in *fig. 2* and *3*. This system only reflects wood anatomical diversity and specialization and is therefore incomplete in the sense that the use of additional characters may easily result in further subdivision of the large groups of genera with juvenilistic or otherwise unspecialized wood

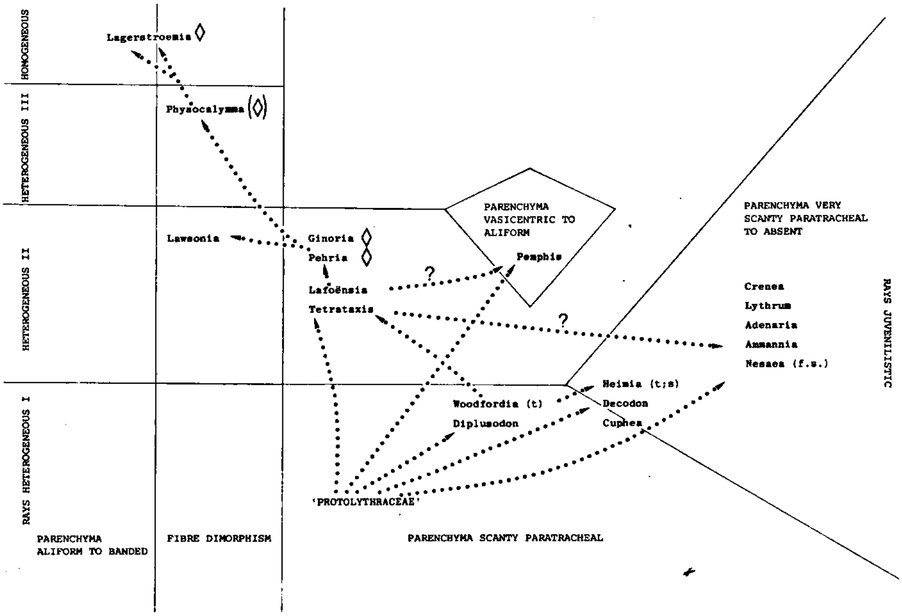

Fig. 2. Wood anatomical patterns of resemblance within Lythraceae. Ray characters are given on the vertical axis; parenchyma characters and fibre dimorphism are indicated on the horizontal axis. Chambered crystalliferous fibres are indicated with diamonds. Arrows indicate possible phylogenetic derivations of the wood anatomical types represented by the individual genera. Arrows involving presumed paedomorphosis or deviations from the main specialization trends are queried. f.s.: faint spiral thickenings present; s: distinct spiral thickenings present; t: vascular tracheids present.

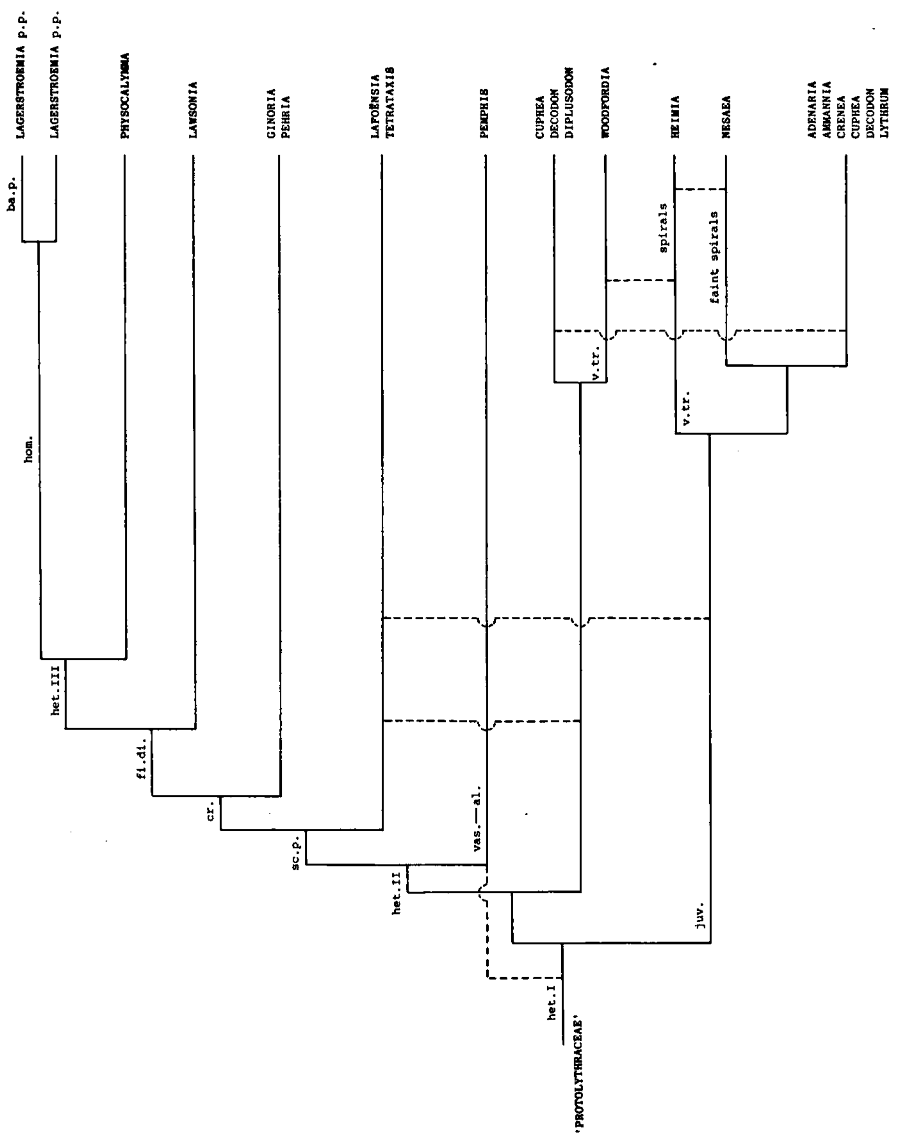

Fig. 3. Cladogram showing phylogenetic relationships of Lythraceae as deduced from wood anatomy only. Broken lines indicate alternatives on the assumption that juvenilistic rays could originate from more derived types through paedomorphosis or that certain specializations developed independently in different groups. The weakness of this approach is demonstrated by the fact that *Cuphea* and *Decodon* appear twice each in this system, because these genera have several and/or transitional ray types. Main specializations (apomorphic character states) are indicated at each bifurcation (the other branch retaining the plesiomorphic character state).

ba.p.: banded or aliform to confluent parenchyma; cr.: crystalliferous fibres present; fi.di.: fibre dimorphism; hom., and het. I–III: rays conforming to Kribs' homogeneous type or heterogeneous types I, II, or III respectively; juv.: rays juvenilistic; sc.p.: parenchyma scanty paratracheal; vas.–al.: parenchyma vasicentric to aliform; v.tr.: vascular tracheids present.

anatomical characters. *Fig. 2* pictures the affinities as based on morphological series. It is noteworthy that the presence of crystalliferous fibres agrees well with the classification which is primarily based on ray type, fibre dimorphism and parenchyma distribution. *Fig. 2* also reflects wood anatomical advancement because the most specialized conditions are found in the upper half of the diagram. Following Hennig's principles (cf. Bremer & Wanntorp 1978) the wood anatomical variation has also been used for constructing a phylogenetic (cladistic) system in *fig. 3*. Note that this system is markedly different from the classical subdivision of the family by Koehne. It would also differ rather markedly from a system based on pollen types and specialization (Muller 1979, in preparation). A great weakness of the application of the methods developed by Hennig to wood anatomical variation patterns as found in the Lythraceae is our lack of knowledge about the monophyletic or polyphyletic origin of specialized character states within Lythraceae. Especially for the ray type it is most likely that parallel development has introduced a certain degree of artificiality in the "phylogenetic system" of *fig. 3*. Moreover it is obviously based on too few characters to be very meaningful. Some aspects of the wood anatomical classification merit special emphasis, however, because they are pertinent to future, comprehensive classifications of Lythraceae. Both ray structure and parenchyma distribution or fibre dimorphism unambiguously point to the advanced level of specialization of the genus *Lagerstroemia*. This is in conflict with the generally held opinion that within Lythraceae *Lagerstroemia* is the most "primitive" representative (cf. Graham & Graham 1971 – also backed by fossil evidence and inference therefrom). To reconcile the wood anatomical facts with this notion one has to assume an early diversification of the microscopic wood structure in the evolutionary history of the Lythraceae. From the ancestral type, characterized by scanty paratracheal parenchyma and heterogeneous I rays the juvenilistic pattern in the majority of perennial woody herbs and small shrubs with narrow rays of erect cells only or with some square cells can be directly derived. Probably the reduction in plant size was incompatible with further xylem specialization or diversification – in spite of the marked specializations occurring in the floral region and other morphological characters of this quite possibly heterogeneous group. Incidental xylem specializations like spiral thickenings (*Heimia* and to a lesser extent *Nesaea*) and vascular tracheids (*Heimia* and *Woodfordia*) in this group of genera are in poor contrast with the macromorphological specializations and diversity. One can also derive (part) of the woody herbs and small shrubs from a more woody ancestral group with heterogeneous II rays, because extant genera with this ray type may also show juvenile rays (i.e. near the pith) of the same type as in these woody herbs. *Pemphis* represents an independent line of wood anatomical specialization which may either have been derived from the moderately advanced level with heterogeneous II rays through parenchyma specialization (i.e. an increase in paratracheal parenchyma) or from the most primitive level with heterogeneous I rays through concomitant ray and parenchyma specialization. *Lawsonia*, *Physocalymma* and *Lagerstroemia* show a different type of specialization in their fibre dimorphism, ultimately culminating in abundant parenchyma in part of the *Lagerstroemia* species. This specialization is remarkably well related with ray specialization which progresses from heterogeneous II to homogeneous in the series *Lawsonia*, *Physocalymma*, *Lagerstroemia*. All these three genera moreover possess crystalliferous fibres in their wood, a character which is shared by two genera from the group with scanty paratracheal parenchyma and heterogeneous II rays, thus confirming natural affinity and possibly monophyletic origin of this character and of the genera exhibiting this character. The affinities of *Lawsonia* with *Lagerstroemia* are compatible with Koehne's classification, where they are together in the subtribe Lagerstroemiinae. Affinities of these paleotropical genera with the neotropical *Physocalymma* as suggested by wood anatomy are, however, in contrast with Koehne's assignment of this genus to a different tribe (Lythreae). Yet these affinities as well as those with *Ginoria* and *Pehria* through the shared crystalliferous fibres should be seriously considered in a future classification of the Lythraceae. As mentioned before, one has to assume a very early wood anatomical diversification in the evolutionary history of the Lythraceae to account for the far-going geographical and macromorphological divergence of these wood anatomically specialized taxa. This is, however, supported by the occurrence of similar characters in isolated, but obviously related genera and small families of the Myrtales as pointed out below.

6.3. Affinities with other Myrtales and the position of *Alzatea*, *Heteropyxis*, *Rhynchocalyx*, and *Psiloxylon*

On account of their macromorphology Lythraceae have been confidently assigned to the Myrtales by students for Angiosperm classification. The Myrtalean alliance is confirmed by the anatomical characters intraxylary phloem and vestured pits in the xylem and also by a very close resemblance of the wood histology with a number of other Myrtalean representatives. THORNE (1976) has recently reopened the debate of family delimitation of Lythraceae by incorporating Sonneratiaceae (*Sonneratia* and *Duabanga*), Punicaceae (*Punica*) and Crypteroniaceae (*Crypteronia* and possibly *Alzatea*, *Axinandra*, *Dactylocladus* and *Rhynchocalyx* if VAN BEUSEKOM-OSINGA & VAN BEUSEKOM's family concept of Crypteroniaceae from 1975 is adopted). Anticipating Van Vliet's future comprehensive paper on the wood anatomical diversity and its taxonomic implications for the Myrtales as a whole, the wood anatomical similarities or dissimilarities with these and other putative relatives will be discussed here.

Sonneratiaceae are wood anatomically very heterogeneous: *Sonneratia* has no axial parenchyma, weakly heterogeneous to homogeneous rays and abundant crystals in the rays; *Duabanga* on the contrary abounds in paratracheal parenchyma containing crystals, and has strongly heterogeneous rays. General affinities with Lythraceae cannot be denied on the grounds of wood anatomy (septate fibres, compatible ray types) but Sonneratiaceae would add somewhat to the heterogeneity of Lythraceae. On balance the wood anatomical evidence is neutral with respect to Thorne's suggestion.

Punicaceae have recently been the subject of a detailed wood anatomical study by BRIDGWATER & BAAS (1978); they would fit admirably well in Lythraceae with their crystalliferous fibres, very scanty paratracheal parenchyma and predominance of square to erect cells in the (narrow) rays. Their wood resembles that of *Pehria* and *Ginoria* and through some degree of fibre dimorphism also that of *Lawsonia*. It should be noted that *Punica* shares a number of derived wood anatomical characters with, in this respect specialized, Lythraceae. Assuming a monophyletic origin of such specializations this would even necessitate the inclusion of *Punica* in Lythraceae, thus supporting Thorne's suggestion.

Crypteronia with its distinctive fibre-tracheids and diffuse and aggregated parenchyma does not show any wood anatomical affinity to Lythraceae. The same applies to *Axinandra* and *Dactylocladus* (see VAN VLIET 1975, VAN VLIET & BAAS 1975, BAAS in VAN BEUSEKOM-OSINGA 1977, and VAN BEUSEKOM-OSINGA & VAN BEUSEKOM 1975 and MULLER 1975 for the debate on the affinities of Crypteroniaceae sensu lato).

Alzatea and *Rhynchocalyx* assigned to Lythraceae by some authors but accommodated in Crypteroniaceae by VAN BEUSEKOM-OSINGA & VAN BEUSEKOM (1975) are anatomically out of place in the latter family (VAN VLIET 1975; VAN VLIET& BAAS 1975) and show more affinity to Lythraceae in their anatomy. *Rhynchocalyx* with its crystalliferous fibres and heterogeneous narrow rays, scanty paratracheal to vasicentric parenchyma surrounded by thin-walled fibres might even be derived from the same Lythraceous ancestors as those of *Ginoria*, *Lawsonia*, *Pehria*, *Physocalymma* and *Lagerstroemia*. Recently mature wood has become available of *Alzatea* (see BAAS 1979, this issue) enabling a more complete comparison with Lythraceae than could be afforded by VAN VLIET (1975). Lythraceous affinities are confirmed. With its markedly heterogeneous rays, extremely scanty paratracheal parenchyma and lack of crystals *Alzatea* can, hypothetically, be derived from the wood anatomically most primitive Lythraceous stock. Through its very coarse elongated, simple vessel–ray pits (a specialization!) *Alzatea* slightly stands apart from the other Lythraceae and shows some affinities with Melastomataceae. As was the case for Sonneratiaceae it remains questionable whether *Alzatea* should be included in Lythraceae or considered as a closely allied monotypic "sister group" derived from a common stock. The disagreement between these views and the broad family concept of Crypteroniaceae of VAN BEUSEKOM-OSINGA & VAN BEUSEKOM (1975) can perhaps best be accounted for by the fact that the latter authors have heavily relied on presumably primitive Myrtalean characters shared by the five genera. As pointed out by several authors such a synplesiomorphy is no indication of close mutual affinity: one can very well imagine that remotely related groups in an ancient Myrtalean matrix gave rise to genera which preserved a number of primitive characters in their flowers and inflorescences while they were in fact more closely linked with different lines of specialization (i.e. Lythraceae or Melastomataceae) than to each other.

Recently Dr. Rudolph Schmid (Berkeley, California) drew our attention to the genus *Psiloxylon* from Mauritius. This genus has been said to show affinities or belong to Myrtaceae or Lythraceae. A wood sample (Lorence 1488) kindly put at our disposal by Dr. Schmid revealed anatomical characters similar to the presumed primitive conditions for Lythraceae: heterogeneous I rays, and scanty paratracheal parenchyma. *Psiloxylon*, however, also has chambered crystalliferous fibres, a presumed specialization. The septate fibres of *Psiloxylon* bear numerous minutely bordered pits on the radial walls, and are in this respect slightly more primitive than the typical Lythraceous fibres. Applying the principle that synapomorphy (the shared crystalliferous fibres) indicates true affinity, *Psiloxylon* would have to be derived from the same stock as *Punica*, *Rhynchocalyx*, *Ginoria*, *Lawsonia*, *Pehria*, *Physocalymma* and *Lagerstroemia* and included in the Lythraceae. However, in view of the strong arguments from floral morphology and leaf anatomy to treat *Psiloxylon* in Myrtaceae (SCHMID 1977 and personal communication) it seems more probable that in this case crystalliferous fibres arose independently. Anyway the wood anatomy of *Psiloxylon* is more suggestive of a Lythraceous than a Myrtaceous alliance (cf. METCALFE & CHALK 1950 and INGLE & DADSWELL 1953 for accounts of Myrtaceae wood anatomy). The solution of CROIZAT (1961) to raise *Psiloxylon* to family rank may after all be the best. The combination of both Myrtaceous characters (flowers and leaves) and Lythraceous characters (wood) is then suggestive of an early derivation from an ancestral Myrtalean stock. Croizat's remark in the formal Latin family validation: "positione geographica bene cum Medusagynaceis (Seychelles), Punicaceis (Socotra) quadrat" is intriguing since it brings to mind the Lythraceous affinity of *Psiloxylon* through Punicaceae alluded to above. Croizat's suggestions of affinities of *Psiloxylon* and other Myrtales with Guttiferae and *Medusogyna* must, however, be refuted on anatomical (and probably also other) grounds.

Heteropyxis from South Africa presents a case similar to that of *Psiloxylon*. Besides suggested affinities with certain groups outside the Myrtales, the genus has been assigned to Lythraceae as well as Myrtaceae. There can be little doubt about the Myrtalean alliance of *Heteropyxis* (cf. STERN & BRIZICKY 1958 and SCHMID 1977) and inclusion in Myrtaceae has been advocated most strongly by the latter authors. A detailed comparison of the wood anatomical description presented by Stern & Brizicky l.c. with the wood anatomy of the Lythraceae yield two points of difference: the distinctly bordered pits of the fibres and crystals in ray cells of *Heteropyxis*. However, its overall wood histology (heterogeneous rays, absence of xylem parenchyma) recalls Lythraceae rather than Myrtaceae. The combination of Lythraceous and Myrtaceous characters in both *Psiloxylon* and *Heteropyxis* may be cited in favour of common ancestry of Lythraceae and Myrtaceae. The further phylogenetic implications of such a suggestion are, however, beyond the scope of this study.

Myrtaceae differ from Lythraceae in a number of wood anatomical tendencies (cf. METCALFE & CHALK 1950 and INGLE & DADSWELL 1953). Distinct fibre-tracheids, vasicentric tracheids and diffuse and/or paratracheal parenchyma occur in most genera, whilst septate fibres are virtually always absent. The exceptions to these trends within Myrtaceae are yet unlike Lythraceae so that wood anatomical links between Myrtaceae and Lythraceae can only be traced through such anomalous genera like *Psiloxylon* and *Heteropyxis* (see above).

Onagraceae, recently studied wood anatomically by CARLQUIST (1975a) witness affinity with Lythraceae in a number of characters: usually septate libriform fibres, scanty paratracheal parenchyma and rays composed largely of erect cells. Other characters (crystal complement, included phloem) of a number of Onagraceae tend to stress diverging specializations within the family "away from the Lythraceous prototype". Carlquist erroneously stressed affinities of Onagraceae with Crypteroniaceae – evidence for such an alliance cannot be derived from wood anatomy.

Oliniaceae (see MUJICA & CUTLER 1974) can also be derived wood anatomically from the Lythraceous prototype with its markedly heterogeneous rays, vasicentric to scanty paratracheal parenchyma and partly septate libriform fibres.

Combretaceae recently treated wood anatomically by VAN VLIET (1979) have been mentioned by Carlquist in the same close alliance with Onagraceae, Punicaceae, Sonneratiaceae, Crypteroniaceae and Lythraceae. The latter family differs rather markedly from Combretaceae, however, in spite of the large wood anatomical ranges, especially in the Combretaceae. Parenchyma is rarely scanty paratracheal only, and crystals of highly specialized types differ in type and/or distribution from those of Lythraceae. Ray- and fibre type in many Combretaceae are, however, compatible with Lythraceous affinities. In our evaluation of the wood anatomical diversity Lythraceae are somewhat closer to Combretaceae than to Myrtaceae but much closer to some other taxa discussed in this section.

Melastomataceae (cf. VAN VLIET in preparation, KOEK-NOORMAN & TER WELLE in preparation, and TER WELLE & KOEK-NOORMAN 1978 and KOEK-NOORMAN et al. 1979) share many wood anatomical tendencies with Lythraceae. Narrow rays of mainly erect cells, septate libriform fibres, scanty paratracheal parenchyma, and different degrees of fibre dimorphism in many genera all recall Lythraceae. The predominance of very coarse vessel–ray and vessel–parenchyma pits provide a wood anatomical distinction between most Melastomataceae and Lythraceae, however. The fibre dimorphism probably also leading to the advent of more abundant parenchyma in some taxa of Melastomataceae must have arisen independently from that in Lythraceae. Yet this strikingly similar tendency may be cited in favour of fairly close relationships between Lythraceae and Melastomataceae.

Penaeaceae (CARLQUIST & DEBUHR 1977), though doubtless members of the Myrtales, differ markedly in their wood structure from Lythraceae on account of their ground tissue of tracheids or fibre-tracheids.

In conclusion, the wood anatomy of Lythraceae points to close affinities with the following Myrtalean taxa (arranged in order of decreasing similarity): *Punica*(ceae), *Rhynchocalyx*, *Psiloxylon*, Oliniaceae, *Alzatea*, Sonneratiaceae, Onagraceae and Melastomataceae. The former three taxa could be accommodated within Lythraceae without significantly extending the present wood anatomical range of the family. *Olinia*, *Alzatea* and *Sonneratia* also are closely similar in their wood to Lythraceae but would slightly extend the wood anatomical range if included.

7. KEY TO THE WOODS OF THE LYTHRACEAE

(*Alzatea*, *Punica* and *Rhynchocalyx* included in the key)

Explanatory note: This key is only intended to facilitate the identification of Lythraceous woods. In view of the limited material studied this key should be considered as a provisional one only.

1\. Rays of procumbent cells only . . . . *Lagerstroemia*
Rays heterogeneous or exclusively composed of erect cells 2
2\. Rays exclusively or almost exclusively uniseriate 11
Rays partly bi- or 3–4-seriate 3
3\. Parenchyma vasicentric 4
Parenchyma scanty paratracheal to (almost) absent 5
4\. Fibres all thick-walled and non-septate . . . . *Pemphis*
Fibres at least partly thin-walled and septate . . . . . . *Rhynchocalyx*
5\. Fibres in alternating bands of short, thin-walled cells and longer, more thick-walled cells 6
Fibres more or less of one type (not considering gelatinous and crystalliferous fibres) 7
6\. Chambered crystalliferous fibres common, Old World . . . . *Lawsonia*
Chambered crystalliferous fibres rare or absent, New World *Physocalymma*
7\. Vessel–ray pits ± similar to inter-vessel pits 8
Vessel–ray pits with strongly reduced borders and much bigger than inter-vessel pits . . . . *Alzatea*
8\. Crystalliferous chambered fibres present . . *Pehria*, *Ginoria*, *Punica* p.p.
Crystalliferous fibres absent 9
9\. Vascular tracheids present, especially near growth ring boundaries *Woodfordia*
Vascular tracheids absent 10
10\. Rays of predominantly erect cells . . . . *Cuphea* p.p., *Decodon*
Rays containing a fairly high proportion of procumbent cells *Tetrataxis*, *Lafoënsia*
11\. Conspicuous spiral thickenings present in the vessels, vascular tracheids present . . . . *Heimia*
Conspicuous spiral thickenings and vascular tracheids absent 12
12\. Fibres all non-septate 13
Fibres at least partly septate 14
13\. Fine and faint spiral thickenings on the vessel walls . . . . . *Nesaea*
Spiral thickenings absent . . . . *Ammannia*, *Diplusodon*
14\. Chambered crystalliferous fibres present . . . . *Punica* p.p.
Crystalliferous fibres absent . *Adenaria*, *Crenea*, *Cuphea* p.p., *Lythrum*

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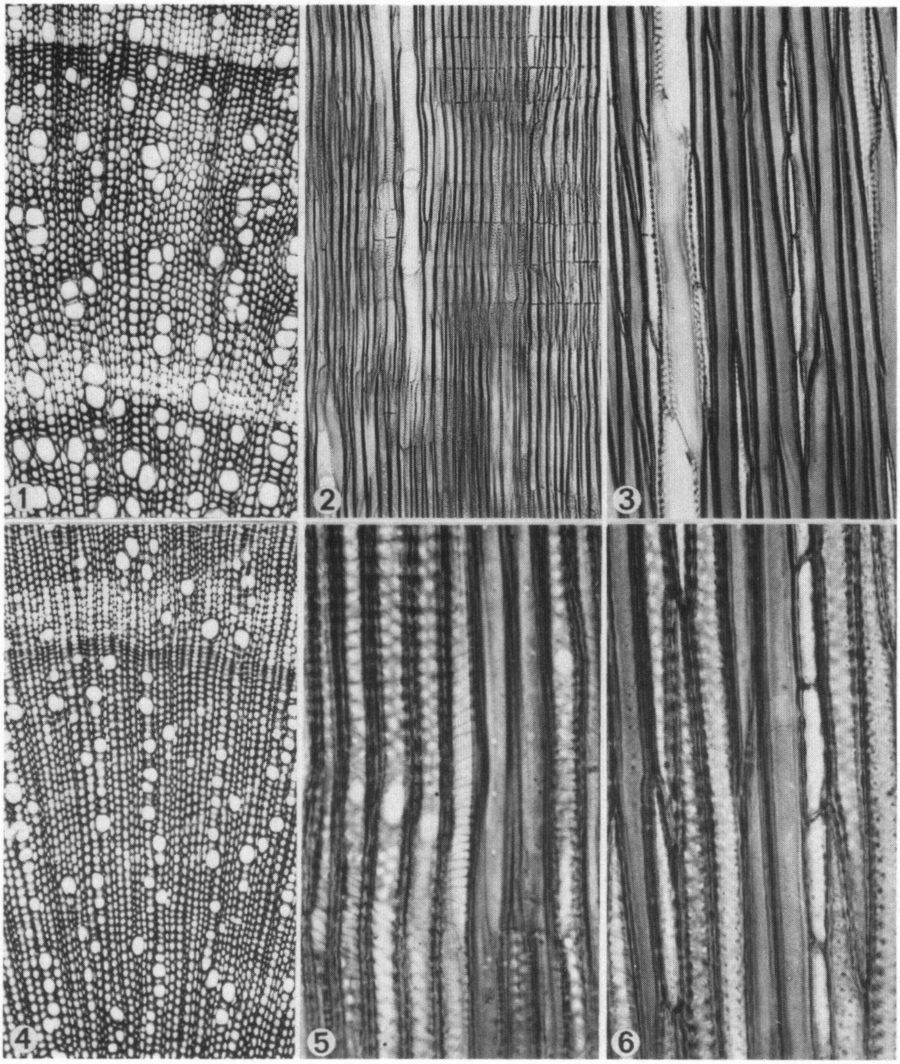

Plate I. 1–3. *Ammannia octandra*, transverse, radial and tangential sections showing juvenilistic type of wood structure; 1 & 2, × 88; 3, × 220. – 4–6. *Heimia myrtifolia*, transverse, radial and tangential sections showing juvenilistic type of wood structure and vessels and vascular tracheids with spiral thickenings; 4, × 88; 5 & 6, × 350.

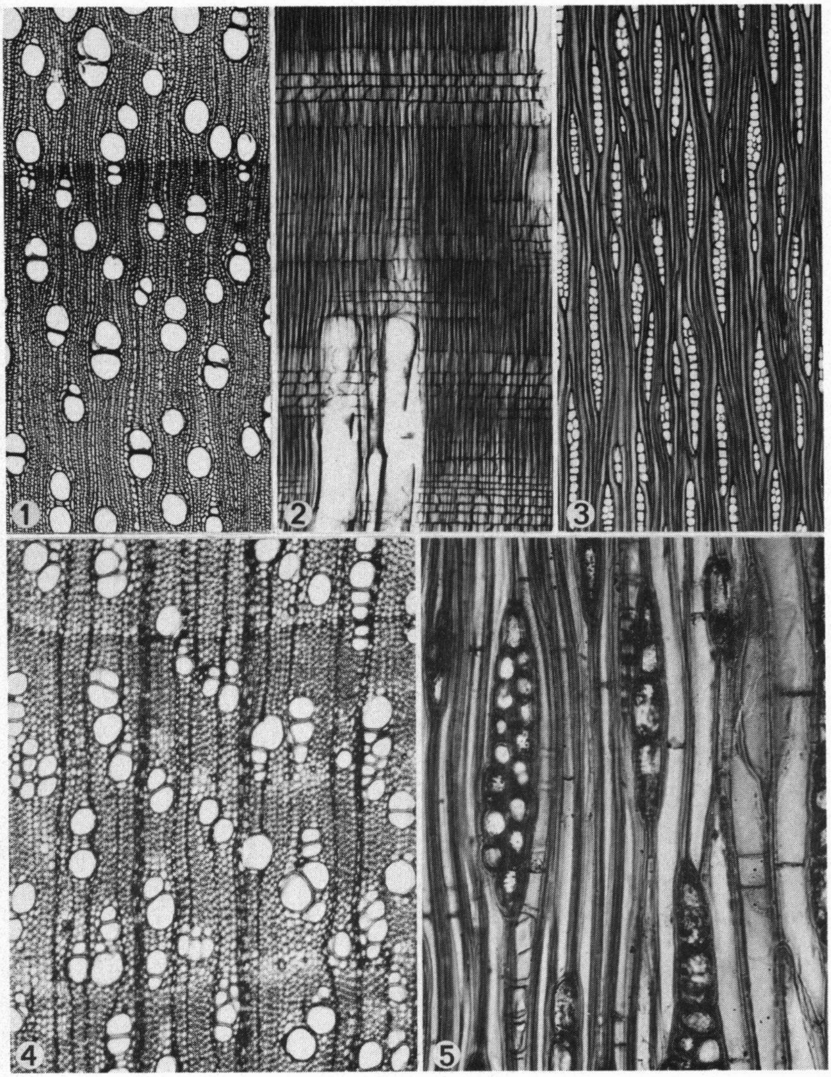

Plate II. 1–3. *Lafoënsia punicifolia*, transverse, radial and tangential sections; 1, × 35; 2 & 3, × 55. – 4 & 5. *Lawsonia inermis*, transverse and tangential sections showing fibre dimorphism; 4, × 35; 5, × 220 (with short, thin-walled fibres on the right and normal fibres and a crystalliferous fibre on the left).

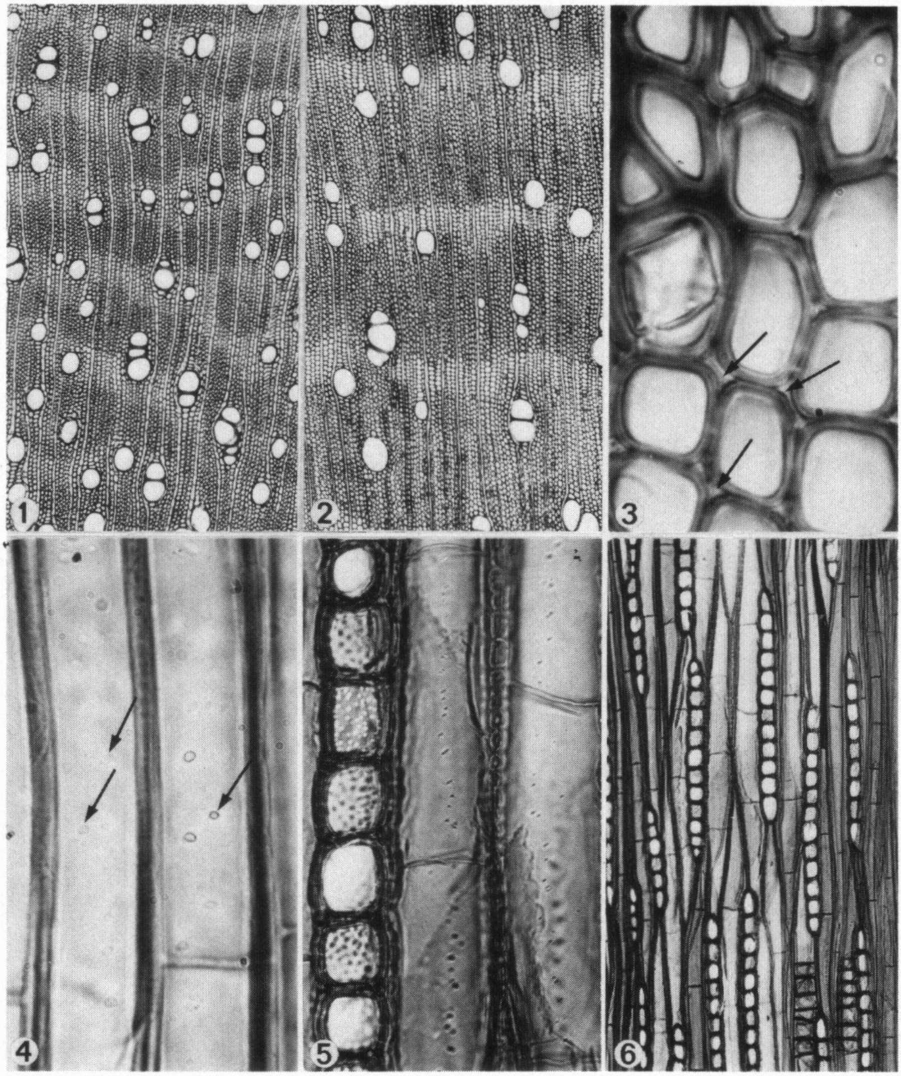

Plate III. *Lagerstroemia* and fibre dimorphism. – 1. *L. indica*, transverse section showing banded pattern of short, thin-walled fibres, × 35. – 2. *L. floribunda*, ibid. – 3. *L. floribunda*, detail of transverse section showing normal fibres (top) and thin-walled fibres with intercellular spaces between them (bottom, arrows), × 880. – 4. *L. floribunda*, radial section showing detail of short, thin-walled, septate fibres with simple pits with round to oval apertures (arrows; partly redrawn), × 880. – 5. *L. calyculata*, tangential section showing detail of short, thin-walled, septate fibres with minute, slit-like apertures, × 880. – 6. Ibid., showing thin-walled fibres in centre and normal fibres on the left and on the right, × 220.

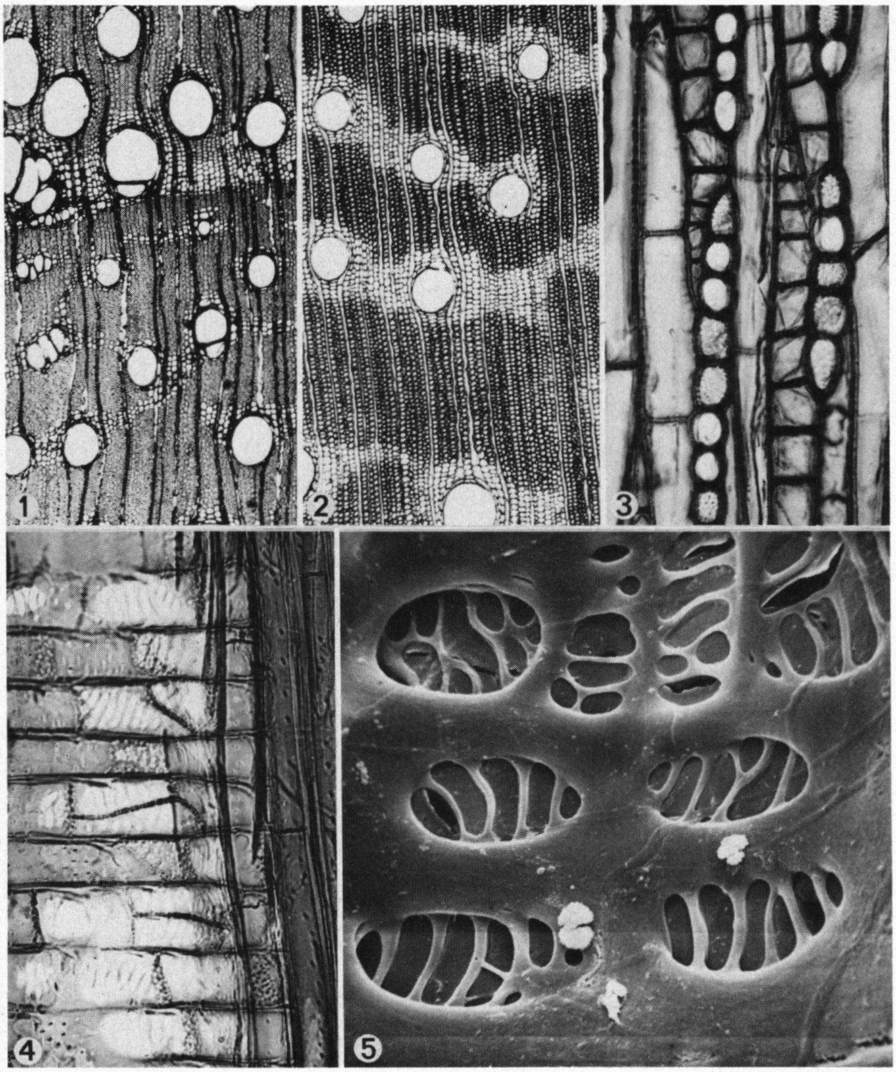

Plate IV. *Lagerstroemia*, miscellaneous features. – 1. *L. parvifolia*, fibres thick-walled, parenchyma aliform and confluent to banded, × 35. – 2. *L. ovalifolia*, fibres thin-walled to medium thick-walled, parenchyma aliform and confluent, × 35. – 3. *L. archeriana*, tangential sections showing axial parenchyma strands (partly chambered, crystalliferous), × 220. – 4. *L. calyculata*, homogeneous ray with large, simple vessel–ray pits, × 220. – 5. *L. tomentosa*, SEM photograph of large vessel–ray pits, × 780.

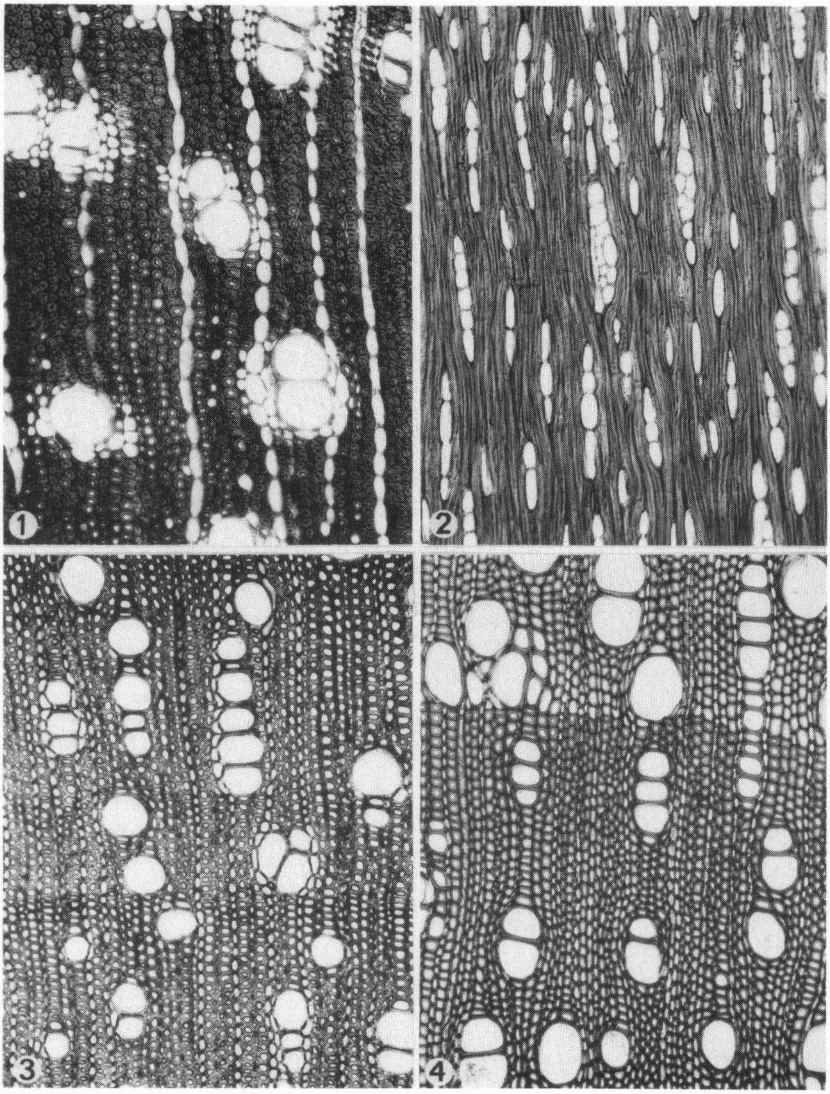

Plate V. All ×88. – 1 & 2. Transverse and tangential section of *Pemphis acidula*. – 3. *Ginoria ginorioides*, transverse section. – 4. *Woodfordia fruticosa*, transverse section.

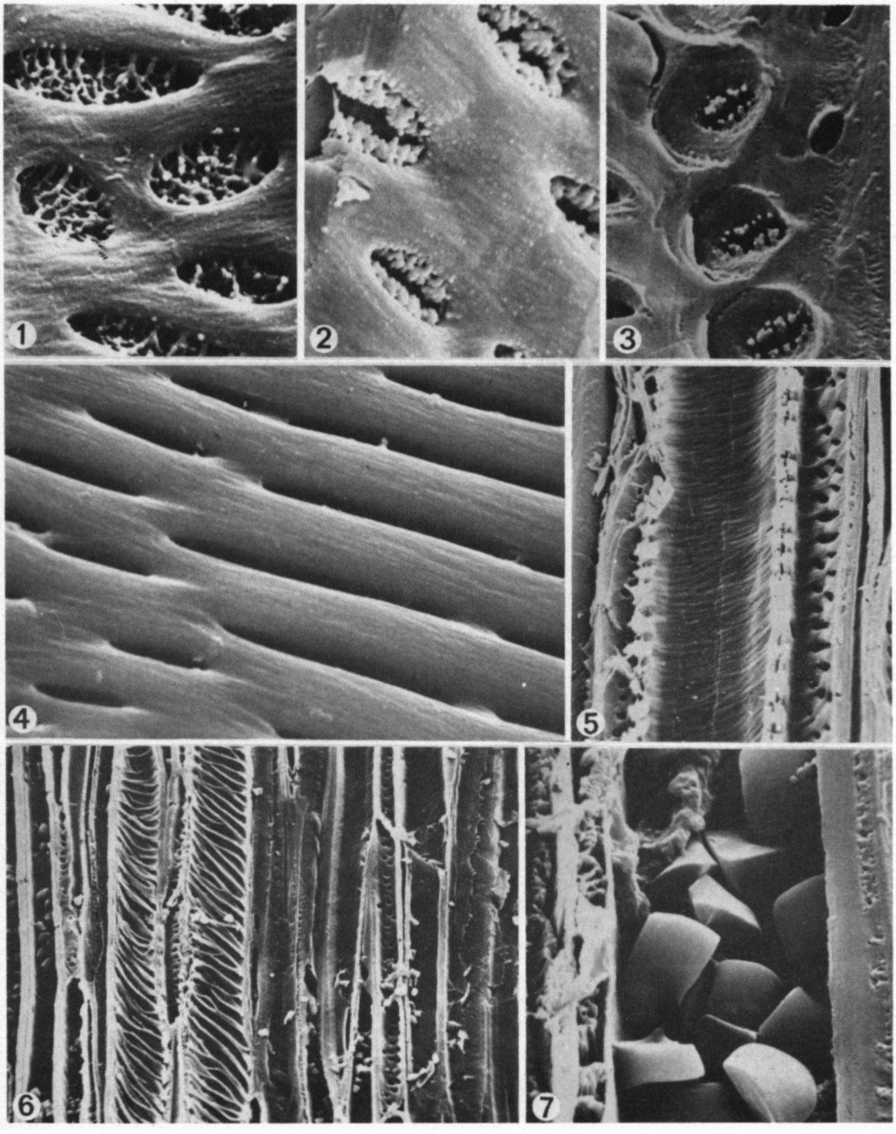

Plate VI. SEM photographs. – 1–3. Vestured pits. – 1. *Crenea surinamensis*, vestures of type B form 1, × 3900. – 2. *Cuphea carthagensis*, vestures of type B form 2, × 4200. – 3. *Heimia* spec., vestures of type B form 3, × 3800. – 4. *Lagerstroemia ovalifolia*, coalescent apertures of vessel wall pits, × 1500. – 5. *Nesaea floribunda*, faint spiral thickenings on vessel wall, × 530. – 6. *Heimia* spec., conspicuous spiral thickenings in vessels, × 380. – 7. Ibid., starch grains in fibre, × 3800.