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SYSTEMATIC WOOD ANATOMY OF THE ROSACEAE

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SUMMARY

The wood anatomy of the Rosaceae is surveyed and analysed, based on the study of 280 species (c. 500 specimens) belonging to 62 genera from different parts of the world. Eighteen wood anatomical characters have been used for a phenetic and phylogenetic classification. In the phenetic classification, 12 groups are recognised and compared with Hutchinson's tribes. Groups I–V accommodate a mixture of representatives from Spiraeoideae and Rosoideae genera (or tribes); Groups VI–VII comprise the Maloideae plus *Cercocarpus*; Groups VIII–IX are composed mainly of the tribe Quillajeae, but include *Prinsepia*, and exclude *Exochorda*; Groups X–XII represent the Prunoideae. All woody tribes recognised by Hutchinson encompass few closely similar wood anatomical groups except the Cercocarpeae. The Quillajeae, characterised by presumably primitive macromorphological characters, appear to be quite derived wood anatomically, and, according to the phylogenetic analysis, should be included in the Prunoideae or be recognised as a separate subfamily close to the Prunoideae. The wood anatomical variation patterns support a broad generic delimitation in the Maloideae, and a narrow one in the Prunoideae. The wood anatomical evidence also suggests that *Cercocarpus* be moved to the Maloideae, and that *Sorbaria* is the most derived representative in the Spiraeoideae/ Rosoideae. *Prinsepia*, although distinct in its wood anatomy from the *Prunus* alliance, still forms part of a monophyletic group together with the latter. Based on wood anatomical evidence, the subdivision of the family and the origin of the Maloideae are discussed.

Wood anatomically the Rosaceae are isolated within the order Rosales. It is hypothesised that the Rosaceae might have originated in East Asia instead of in the tropics.

Individual generic descriptions, a family description and a tentative wood anatomical key to the genera studied are also presented.

INTRODUCTION

The wood anatomy of the Rosaceae native to China was described and discussed in a previous paper (Zhang & Baas, 1992). The present paper extends the observation to a worldwide survey, and aims at a contribution to our understanding of intergeneric relations and the phylogeny of the family.

The classification of the Rosaceae has long been in some dispute. Nowadays, the Neuradeae and the Chrysobalaneae, formerly two tribes or subfamilies of the Rosaceae (cf. Hutchinson, 1964; Yu, 1984), are usually treated as separate families: the Neuradaceae and the Chrysobalanaceae (Airy Shaw, 1973; Cronquist, 1981; Schulze-Menz, 1964; Stoffers, 1982; Takhtajan, 1980; Kalkman, 1988). In the present study, the Rosaceae are delimited in the narrow sense. Four subfamilies are usually recognised in the Rosaceae sensu stricto: Spiraeoideae, Rosoideae, Maloideae, and Prunoideae. The four subfamilies are rather different in homogeneity, scope and naturalness, and are often taken as units of discussion (Kalkman, 1988). For the systematic

Table 1. Enumeration of genera of the Rosaceae.

Genus[1] (subfamily, tribe)[2]	Habit[3]	Approximate number of species	Number of species (samples) studied
Acaena (R, 14)	Herb	c. 100	
Adenostoma (R, 16)	Shrub	2	2 (4)
Agrimonia (R, 14)	Herb	15	
Alchemilla (R, 14)	Herb	250	1 (1)
Amelanchier (M, 18)	Tree-Shrub	6	3 (3)
Amygdalus (P, 6)	Tree-Shrub	c. 40	10 (21)
Aremonia (R, 14)	Herb	1	
Armeniaca (P, 6)	Tree	c. 8	6 (17)
Aronia (M, 18)	Shrub	2	
Aruncus (S, 2)	Herb	1	
Bencomia (R, 14)	Shrub	5	
Cerasus (P, 6)	Tree-Shrub	c.100	20 (45)
Cercocarpus (R?, 15)	Shrub-Tree	6	2 (4)
Chaenomeles (M, 18)	Shrub	4	4 (4)
Chamaebatia (R or N, 13)	Shrub	2	1 (1)
Chamaebatiaria (S, 4)	Shrub	2	1 (1)
Chamaemeles (M, 18)	Shrub	1	
Chamaerhodos (R, 12)	Herbs	11	
Cliffortia (R, 14)	Shrub	115	
Coleogyne (R?, 15)	Shrub	1	1 (1)
Coluria (R or N, 13)	Herb	6	
Comarella (R, 12)	Herb	2	
Cotoneaster (M, 18)	Shrub-Tree	c. 50	6 (8)
Cowania (R or N, 13)	Shrub	3–4	1 (1)
Crataegus (M, 18)	Shrub-Tree	c. 280	18 (23)
Cydonia (M, 18)	Tree	1	1 (3)
Dichotomanthes (M or N, 18)	Tree	1	1 (1)
Docynia (M, 18)	Tree	5	2 (3)
Dryas (R or N, 13)	Shrub	3–4	1 (2)
Drymocallis (R, 12)	Herb	c. 30	
Eriobotrya (M, 18)	Tree-Shrub	27	4 (10)
Eriolobus (M, 18)	Tree	1	1 (1)
Exochorda (S or P, 1)	Shrub	4	1 (1)
Fallugia (R or N, 13)	Shrub	1	1 (1)
Filipendula (R, 7)	Herb	10	
Fragaria (R, 12)	Herb	c. 12	
Geum (R or N, 13)	Herb	65[5]	
Hagenia (R, 14)	Tree	2	1 (2)
Hesperomeles (M, 18)	Shrub	15	2 (2)
Heteromeles (M, 18)	Shrub	1	1 (4)
Holodiscus (S, 9)	Shrub	8	1 (2)
Horkelia (R, 12)	Herb	17	
Horkeliella (R, 12)	Herb	3	
Ivesia (R, 12)	Herb	23	
Kageneckia (S or N, 1)	Tree	3	1 (1)
Kelseya (S, 2)	Shrub	1	
Kerria (S, R or N, 11)	Shrub	1	1 (2)
Laurocerasus (P, 6)	Tree-Shrub	c. 80	9 (28)
Leucosidea (R, 14)	Shrub	1	

(Table 1 continued)

Genus[1] (subfamily, tribe)[2]	Habit[3]	Approximate number of species	Number of species (samples) studied	
Lindleya (S or M, 1)	Tree	2	1	(1)
Luetkea (S, 2)	Shrub-Herb	1		
Lyonothamnus (S, 1)	Tree-Shrub	1	1	(1)
Maddenia (P, 6)	Tree	4		
Malacomeles (M, 18)	Shrub	2		
Malus (M, 18)	Tree-Shrub	c. 25	16	(26)
Margyricarpus (R, 14)	Shrub	1		
Mespilus (M, 18)	Tree	2	1	(2)
Micromeles (M, 18)	Tree-Shrub	c. 15	6	(17)
Neillia (S, 3)	Shrub	11		
Neviusia (S, R or N, 11)	Shrub	1		
Orthurus (R or N, 13)	Herb	2		
Osmaronia (P or N, 5)	Tree-Shrub	1-2	1	(2)
Osteomeles (M, 18)	Shrub	4-5	1	(1)
Padus (P, 6)	Tree-Shrub	c. 20	13	(31)
Peraphyllum (M, 18)	Shrub	1	1	(1)
Petrophytum (S, 2)	Shrub	5	1	(1)
Photinia (M, 18)	Shrub-Tree	40	9	(22)
Physocarpus (S, 3)	Shrub	10	1	(2)
Plagiospermum (P, 6)	Shrub	2		
Polylepis (R, 14)	Shrub-Tree	15	3	(3)
Porteranthus (S, 4)	Herb	2		
Potaninia (R, 15)	Shrub	1		
Potentilla (R, 12)	Herb-Shrub	500[5]	1	(2)
Poteridium (R, 14)	Herb	2		
Poterium (R, 14)	Herb	c. 25		
Prinsepia (P or N, 6)	Shrub	3–4	2	(2)
Prunus s. str. (P, 6)	Tree-Shrub	c. 30	9	(18)
Pseudocydonia (M, 18)	Shrub-Tree	1		
Purpusia (R, 12)	Herb	1		
Purshia (R or N, 13)	Shrub	2	2	(2)
Pygeum (P, 6)	Tree-Shrub	c. 40	16	(23)
Pyracantha (M, 18)	Shrub	c. 20	1	(1)
Pyrus (M, 18)	Tree-Shrub	c. 20	17	(33)
Quillaja (S or N, 1)	Shrub-Tree	4	1	(1)
Raphiolepis (M, 18)	Tree-Shrub	14	4	(8)
Rhodotypos (R, 10)	Shrub	1		
Rosa (R, 17)	Shrub	c. 100	15	(20)
Rubus (R, 8)	Shrub	c. 250	9	(11)
Sanguisorba (R, 14)	Herb	c. 18		
Sarcopoterium (R, 14)	Shrub	1	1	(3)
Sibbaldia (R, 12)	Herb	8	1	(1)
Sibiraea (S, 2)	Shrub	2	1	(2)
Sorbaria (S, 4)	Shrub	c. 9	4	(4)
Sorbus (M, 18)	Tree-Shrub	85	23	(34)
Spenceria (R, 14)	Herb	2		
Spiraea (S, 2)	Shrub	70	11	(15)
Spiraeanthus (S, 14)	Shrub	1		
Stephanandra (S, 3)	Shrub	4	1	(2)

(Table 1 continued)

Genus[1] (subfamily, tribe)[2]	Habit[3]	Approximate number of species	Number of species (samples) studied
Stranvaesia (M, 18)	Tree	5	1 (1)
Tetraglochin (R, 14)	Shrub	8	
Vauquelinia (S or M, 1)	Tree-Shrub	10	1 (1)
Waldsteinia (R or N, 13)	Herb	6	
Totals: 102	Over 3/4 are woody genera	Over 2750 species	280 (491)

1) The generic concepts are mainly those adopted by Kalkman (1988). However, *Prunus* s. l. (in the sense of Kalkman) is presented here as seven smaller genera (see Zhang & Baas, 1992) following Yu (1986): *Amygdalus, Armeniaca, Cerasus, Laurocerasus, Padus, Prunus* s. str., and *Pygeum.* The same applies to *Photinia* which excludes *Stranvaesia* and *Heteromeles* here.

2) Following subfamily and tribe assignments according to Kalkman (1988) and Hutchinson (1964), respectively.
   - — M: Maloideae; P: Prunoideae; R: Rosoideae; S: Spiraeoideae; N: New separate subfamily, as proposed by different authors, but not generally accepted.
   - — 1 = Quillajeae; 2 = Spiraeeae; 3 = Neillieae; 4 = Gillenieae; 5 = Osmaronieae; 6 = Pruneae; 7 = Ulmarieae; 8 = Rubeae; 9 = Holodisceae; 10 = Rhodotypeae; 11 = Kerrieae; 12 = Potentilleae; 13 = Dryadeae; 14 = Poterieae; 15 = Cercocarpeae; 16 = Adenostomeae; 17 = Roseae; 18 = Maleae (or Pomeae).

3) Plant habits are given here mainly according to Hutchinson (1964) and Yu (1986; for *Prunus* s. l. only).

4) The approximate number of species for the genera listed above is based on Mabberley (1987) and Yu (1986; only for *Prunus* s. l.).

5) *Potentilla* and *Geum* include some segregates, according to Kalkman (1988).

arrangement, delimitation of subfamilies and genera, and the nomenclature presented in this study, see Kalkman (1988). However, *Photinia* s.l. (cf. Kalkman, 1973) and *Prunus* s.l. (cf. Kalkman, 1965) are presented here as smaller alliances (see the notes to Table 1). The only purpose for such a treatment in the present survey is to see whether there is any wood anatomical evidence for smaller genera. For easy reference, the genera of the Rosaceae, their approximate total number of species, and the number of species and samples studied are presented in Table 1. In addition, it is also indicated to which tribes and families the individual genera (probably) belong. As shown in Table 1, 62 genera including a few (sub)herbaceous genera like *Alchemilla, Potentilla* and *Sibiraea,* were surveyed in the present study, covering 16 out of 18 tribes recognised by Hutchinson (1964). Only the herbaceous tribe Ulmarieae (consisting only of *Filipendula*) and the woody tribe Rhodotypeae (*Rhodotypos* only) were not included.

Early studies on the wood anatomy of Rosaceae were summarised by Solereder (1899 & 1908) and Metcalfe & Chalk (1950). For an updated literature list on wood anatomy of the family, see Zhang & Baas (1992).

MATERIALS AND METHODS

Materials

In total c. 500 specimens were studied. Material was obtained from various institutional wood collections (see Acknowledgements). Many samples included in the present survey are unvouchered. However, nomenclature was brought up to date with recent taxonomic revisions, supposing that the original identification had been correct. Synonyms are given if necessary. For the microtechnical procedures and descriptive conventions followed, see Zhang & Baas (1992). The observations on Chinese species are incorporated in various generic descriptions given here. If studies of material from outside China hardly modified our earlier generic descriptions the reader is referred to the earlier paper (Zhang & Baas, 1992).

Cladistic analysis

The computer programme HENNIG86 was used in the present study for the cladistic analysis of wood anatomical characters of the Rosaceae (Farris, 1989; Van Welzen, 1989).

HENNIG86 uses the Wagner algorithm combined with parsimony (cladogram with the minimum number of character state changes, = steps, will be selected as the best hypothesis of the phylogeny). HENNIG86 was mainly used with unordered characters by giving the command CCODE-.;. As tree calculating algorithm MHENNIG, in combination with BB; was used. MHENNIG only calculates several trees, of which the most parsimonious ones will be stored. These do not have to be the most parsimonious ones among all trees by necessity, nor the only most parsimonious trees. BB (branch and bound) uses the MHENNIG trees and usually finds, by modifying branches, all most parsimonious trees (the option IE instead of the combination MHENNIG-BB is sure to find all most parsimonious trees, but when the datamatrix is complex and contains much homoplasy the running time of option IE becomes too long, days instead of hours with MHENNIG-BB).

The Wagner algorithm needs an *a priori* designated outgroup of which the character states are regarded as plesiomorphic (primitive). For each character the outgroup always (if no question mark is placed in the datamatrix) assigns one character state as the starting point of a transformation series.

If more than one parsimonious tree was found character weighting was applied with the command: XSTEPS W; followed by the branch and bound command BB;. The character weights are automatically calculated by multiplying the consistency index with the retention index (Farris, 1989) and scaling these from 0 to 10. This procedure is repeated until one cladogram remains or until the character weights do not change anymore.

WOOD ANATOMICAL FAMILY DESCRIPTION

In a previous paper (Zhang & Baas, 1992), an elaborate survey of the wood anatomical variation in Chinese Rosaceae was given. From the study of a substantial number of additional genera and species from outside China it appeared that, except for some minor extensions of quantitative ranges, this earlier survey almost covered the entire range present in the family. As a consequence, the wood anatomical description of the entire family given below hardly differs from the one given for Chinese representatives only. Where appropriate, notes (numbers between square brackets) are given on the extended range of some characters. See also Tables 2 & 6, the individual generic descriptions, and Figures 1–16.

Growth rings more or less distinct in most genera [1], rarely faint or absent, the boundaries infrequently wavy, mostly marked by rows of radially flattened latewood fibres, sometimes by differences in vessel diameter as well as vessel frequency between latewood and subsequent earlywood, or rarely by marginal parenchyma bands (Figs. 1–8). Wood diffuse-porous, semi-ring-porous or ring-porous.

Vessels 40–300 (5–600)/sq.mm, 4–99% solitary [2], remainder in oblique, tangential and radial multiples of 2–4(–12), vessels in some taxa in an oblique, radial or dendritic pattern [3], round, oval to angular, tangential diameter mostly 20–80 (16–175) µm, radial diameter 30–100 (20–220) µm, walls 1–3(–5) µm thick (Figs. 1–8). Vessel element length 150–700 (130–930) µm, length/tangential diameter (L/D) ratio 3–30. Perforations exclusively or almost exclusively simple in oblique to almost horizontal end walls; sporadic scalariform and/or irregular perforations noted in some species. Intervessel pits nonvestured (except in *Spiraea* p.p.), usually alternate, round, oval to polygonal, 2–12(–20) µm in diameter, with slit-like, occasionally oval to coalescent apertures. Vessel-ray and vessel-parenchyma pits mostly

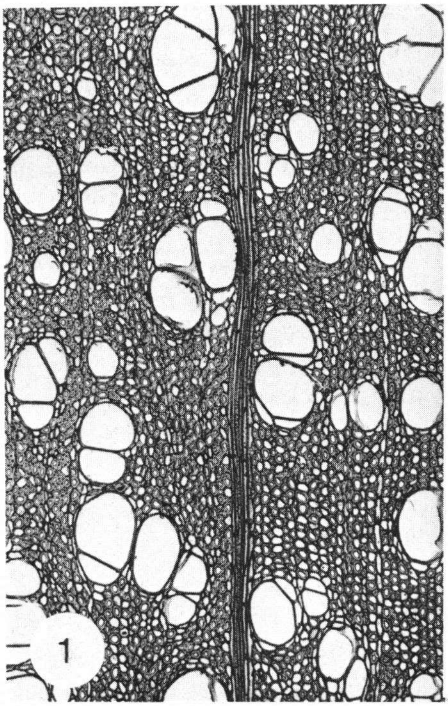
Legends to Figures 1–16:

Figs. 1–4. TS, × 43. — 1: Growth ring boundaries absent and vessels of two slightly different size classes in *Hagenia abyssinica.* — 2: Growth ring boundaries faint to absent and vessels diffuse in *Polylepis incana.* — 3: Growth ring boundaries marked by 1–3-seriate marginal parenchyma bands and traumatic gum duct present in *Laurocerasus hypotricha.* — 4: Growth ring boundaries distinct, marked by rows of radially flattened latewood fibres; vessels in a weakly oblique pattern and with a high degree of grouping in *Laurocerasus spinulosa.*

Figs. 5–7. TS, × 43. — 5: Growth ring boundaries faint, marked by marginal parenchyma band; vessels moderately large in *Pygeum topengii.* — 6: Growth ring boundaries distinct and weakly wavy, marked by rows of radially flattened latewood fibres, vessels in a weakly oblique pattern and with a high degree of grouping in *Sarcopoterium spinosum.* — 7: Wood semi-ring-porous, vessels mostly solitary and round to oval in outline, and parenchyma relatively abundant in *Cercocarpus betuloides.* — Fig. 8. TS, × 116. Wood ring-porous to semi-ring-porous, vessel outline angular in *Potentilla fruticosa.*

Fig. 9. TLS, × 116. Vascular tracheids present in *Sarcopoterium spinosum.* — Fig. 10. TLS, × 576. One to several prismatic or fragmented crystals per non-enlarged axial parenchyma chamber in *Spiraea chamaedryfolia.* — Fig. 11. RLS, × 43. Rays composed exclusively of procumbent cells in *Hagenia abyssinica.* — Fig. 12. TLS, × 116. Rays 1(–2)-seriate in *Potentilla fruticosa.*

Fig. 13. TLS, × 116. Rays 1–4-seriate, but relatively short in *Vauquelinia california.* — Fig. 14. TLS, × 116. Rays 1–3-seriate, but quite tall in *Kageneckia lanceolata.* — Fig. 15. TLS, × 43. Rays of two distinct sizes in *Hagenia abyssinica.* — Fig. 16. TLS, × 288. Juvenilistic rays in *Stephanandra chinensis.*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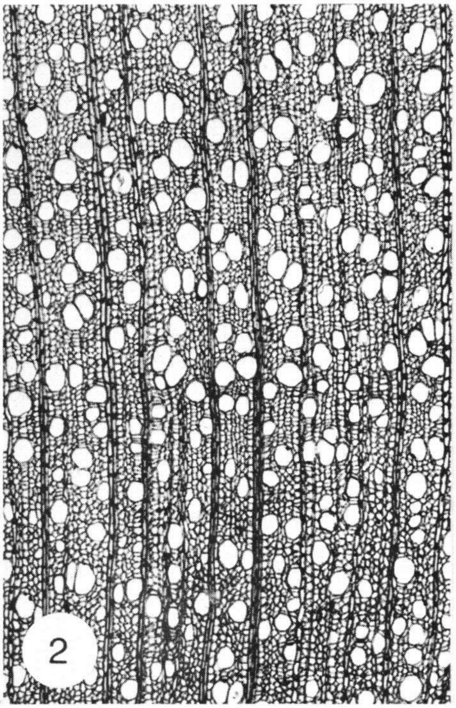
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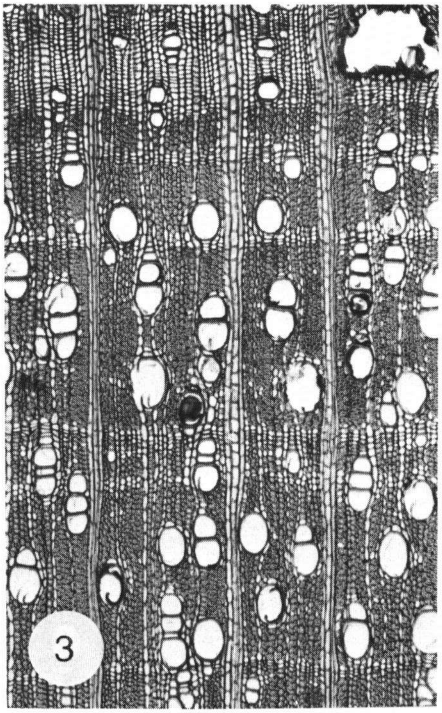
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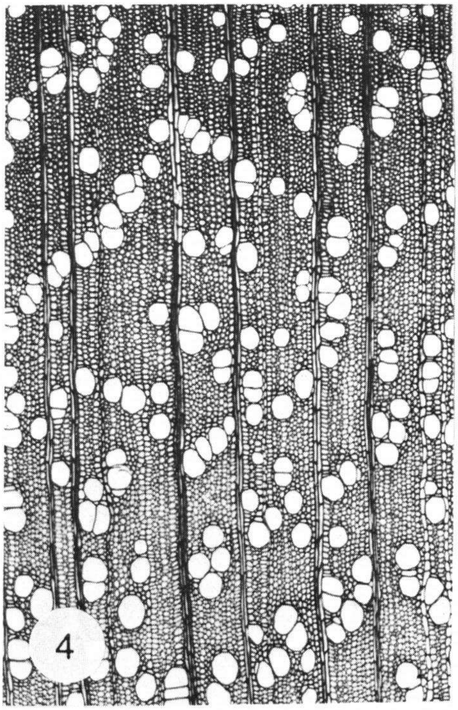
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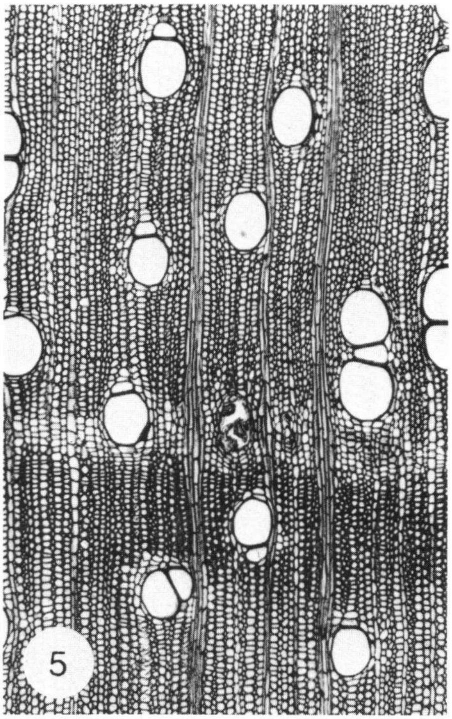
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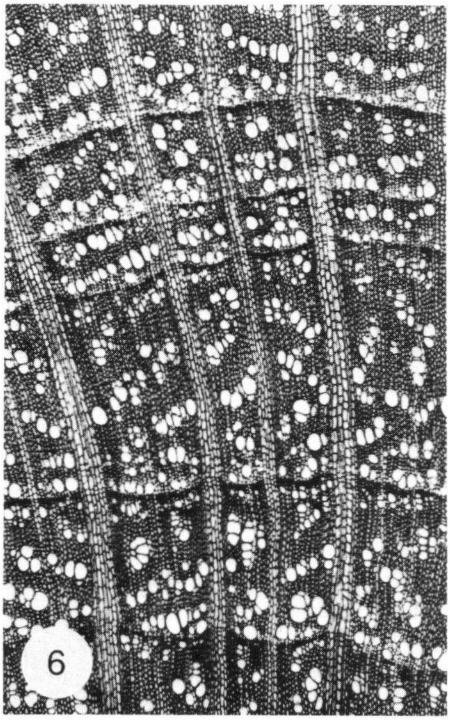
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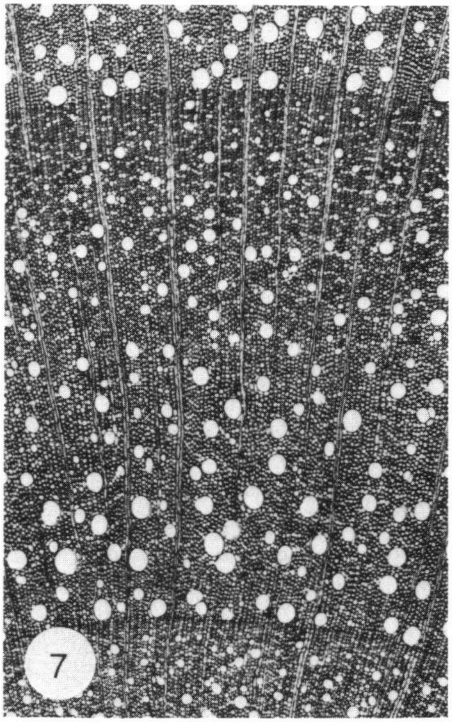
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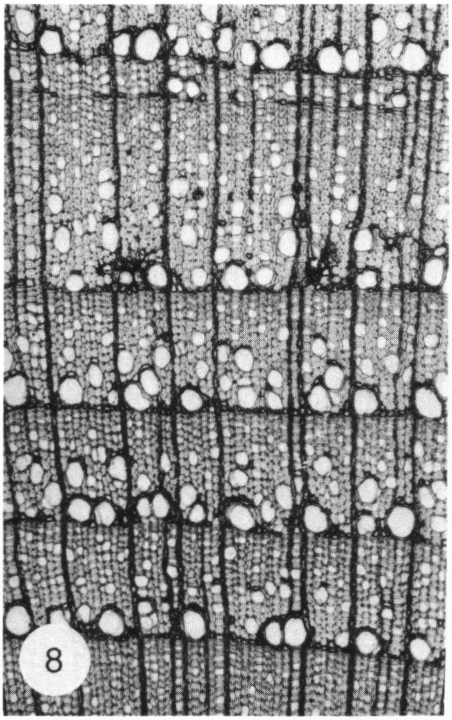
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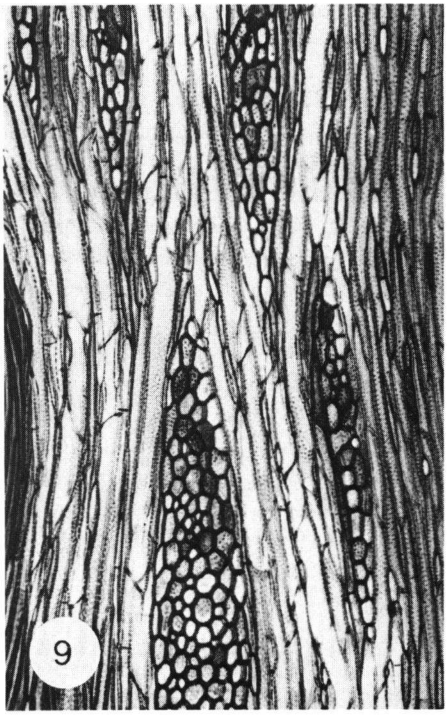
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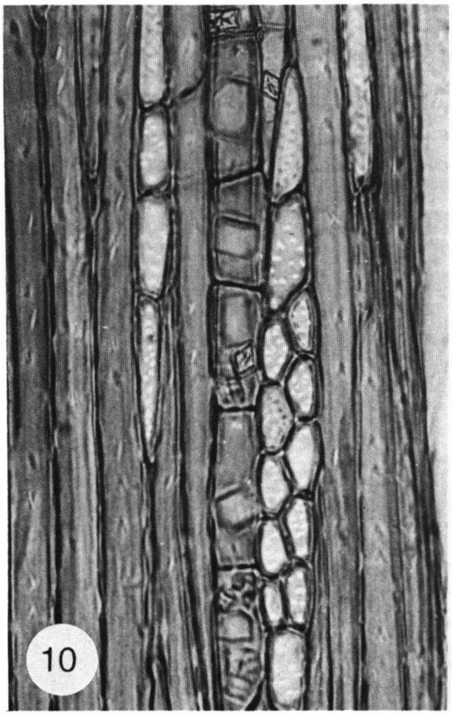
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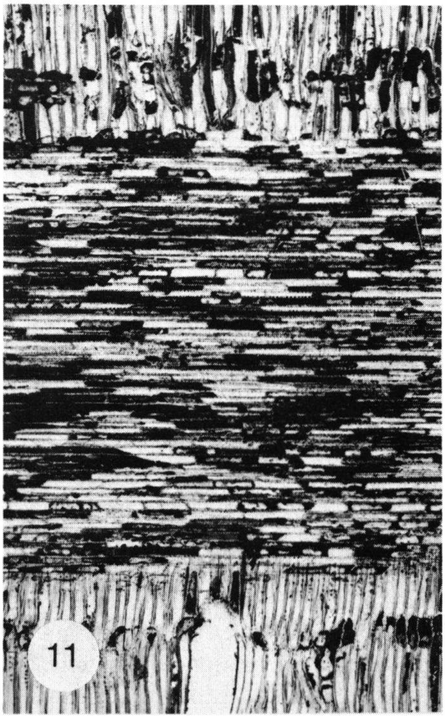
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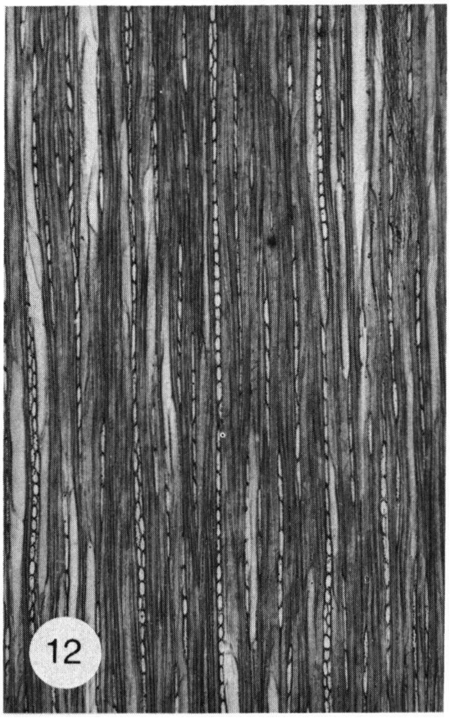
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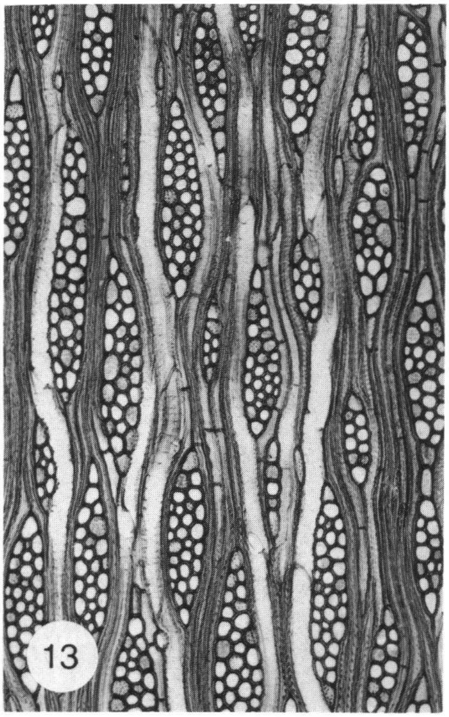
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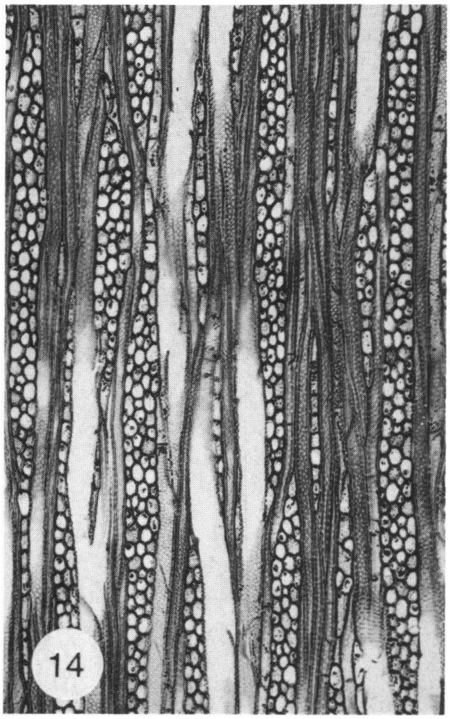
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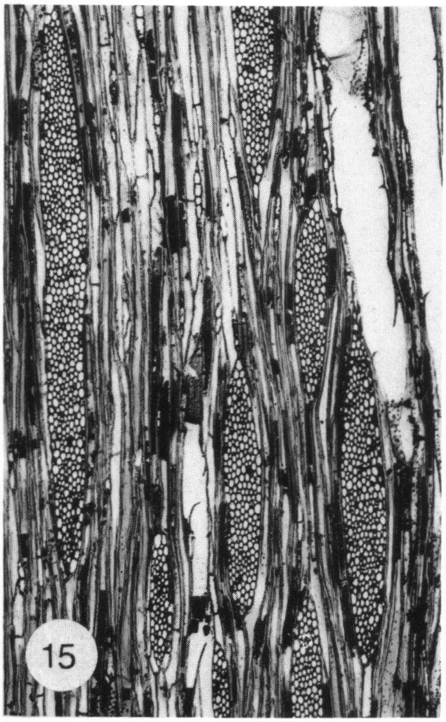
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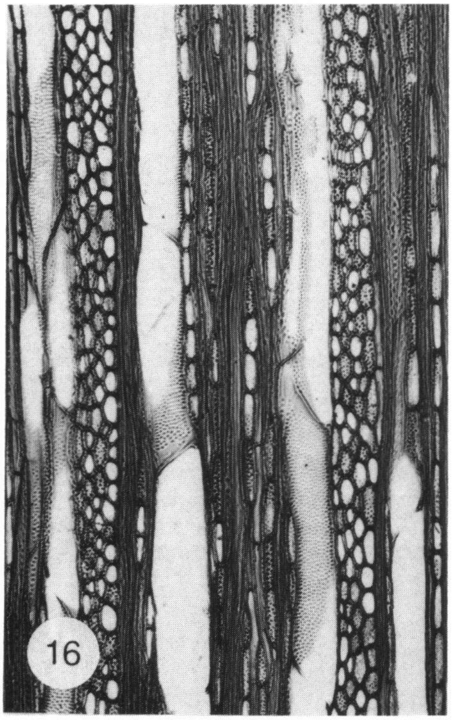
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similar to intervessel pits but usually half-bordered and slightly smaller, or clearly smaller than intervessel pits. Helical vessel wall thickenings present in many genera, closely to widely spaced, fine to coarse, throughout all vessel elements, or confined to narrow elements or to the tails only [4]. Tyloses almost always absent except in one species (*Cerasus avium*). Gummy contents sometimes present.

Vasicentric tracheids and *vascular tracheids* occur sporadically in a few genera [5] (Fig. 9).

Ground tissue fibres 300–1640 µm long, almost always non-septate [6], F/V ratio 1.3–3.9, (very thin-), medium thick- to very thick-walled, mostly with distinctly bordered pits (fibre-tracheids), but occasionally with simple to minutely bordered pits (libriform fibres), the pit chambers 1–9 µm in diameter, in both radial (densely placed in some genera) and tangential walls, or mainly confined to the radial walls [7]. Helical thickenings infrequently present, closely to widely spaced, fine to coarse. Dark contents in fibre lumina present in few genera.

Parenchyma scanty to abundant, usually apotracheally diffuse and scanty paratracheal, but diffuse-in-aggregates, marginal and/or irregular zonate parenchyma bands and vasicentric sometimes also present, in 2–11-celled strands [8].

Rays 6–15 (3–17)/mm [9] (Figs. 11–16), 1–16-seriate, of intergrading or two distinct sizes. Uniseriate rays 1–16 cells high. Multiseriate rays 0.2–5.0 (0.1–25.0) mm high, of the following three intergrading types: 1) composed of square or square to procumbent body cells and upright cells, sometimes also with weakly differentiated sheath cells (so-called juvenilistic rays), 2) composed of procumbent body cells and 1–4(–7) rows of square to upright marginal cells, 3) composed of procumbent cells only, sometimes with one row of square marginal cell [10]. Perforated ray cells almost always absent (except in *Holodiscus discolor* and *Spiraea chamaedryfolia*).

Crystals absent, sparse, or abundant, mainly prismatic, more rarely druses [11], medium-sized to large, usually present in chambered and enlarged (with exceptions as shown in Fig. 10) axial parenchyma cells (large prismatic) and/or in non-chambered and non-enlarged ray cells (medium-sized druses), one crystal per ray cell or chamber, chambered crystals in chains of 2–23. Silica grains not observed.

Pith flecks infrequently present, diffuse or in tangential bands.

Traumatic gum ducts occasionally present, mainly in tangential bands, rarely diffuse.

Notes

[1] A few tropical genera (e.g., *Hagenia, Hesperomeles, Pygeum*) are characterised by growth rings faint to absent.

[2] A few genera from the Spiraeoideae and Rosoideae (e.g., *Hagenia, Sarcopoterium, Physocarpus, Polylepis*) have a high degree of vessel grouping.

[3] Oblique, radial and dendritic vessel patterns are mainly restricted to *Laurocerasus* (both group A and B).

[4] Helical vessel wall thickenings show a large variation at different taxonomic levels (cf. Table 2 and generic descriptions). Although usually constant at the generic level, they are variable within c. 13 genera and in some instances they

are even variable at the species level (e.g. in *Heteromeles arbutifolia, Laurocerasus undulata, Pygeum africanum,* and *Pyrus communis*). Yet there is a tendency for subfamilies, wood anatomical groups or tribes to be characterised by presence or absence of helical vessel wall thickenings; however, this tendency has many exceptions.

[5] Weakly differentiated vasicentric tracheids are present in *Holodiscus* and *Rosa*. Vascular tracheids were observed in *Lindleya* and *Sarcopoterium*. They usually intergrade with narrow latewood vessels.

[6] Septate fibres are common in *Sarcopoterium*.

[7] The ground tissue in *Holodiscus, Sarcopoterium* and *Spiraea* is partly composed of libriform fibres. In *Amygdalus, Cerasus* and *Laurocerasus* B, intermediates between libriform fibres and fibre-tracheids occur.

[8] Axial parenchyma is common to abundant in the Quillajeae (*Exochorda, Lindleya, Lyonothamnus, Vauquelinia, Quillaja* and *Kageneckia*). Marginal or zonate parenchyma bands are a constant feature for *Laurocerasus* B, but variable for *Pygeum*.

[9] *Hagenia* and *Physocarpus* are exceptional for very low (3–4/mm) and very high ray frequency (15–17/mm), respectively.

[10] Ray features are very variable in the Spiraeoideae and Rosoideae. Ray width is variable: 1–3(–4)-seriate in some genera (*Alchemilla, Cercocarpus, Chamaebatia, Cowania, Dryas, Fallugia, Kageneckia, Lindleya, Physocarpus, Polylepis, Potentilla, Purshia, Sibbaldia*), or 4–16-seriate in the remaining genera. Ray height also varies greatly: some genera (*Coleogyne, Holodiscus, Kerria, Rosa, Rubus, Sarcopoterium* p.p., *Sibiraea, Spiraea, Stephanandra*) are characterised by rays higher than 1.0 mm (up to 25.0 mm), while some genera (*Alchemilla, Cercocarpus, Chamaebatia, Chamaebatiaria, Cowania, Exochorda, Fallugia, Lindleya, Lyonothamnus, Polylepis, Purshia, Quillaja, Sibbaldia, Vauquelinia*) have rays lower than 0.4 mm. Ray height in the remaining genera usually ranges from 0.4 to 1.0 mm. Ray composition in the Spiraeoideae and Rosoideae covers all types in the family: some genera (*Alchemilla, Chamaebatia, Coleogyne, Dryas, Fallugia, Holodiscus, Kerria, Lindleya, Petrophyllum, Physocarpus, Rosa* p.p., *Rubus, Sarcopoterium, Sibbaldia, Sibiraea, Spiraea, Stephanandra*) are characterised by juvenilistic rays composed of square or square to weakly procumbent body cells and rows of upright cells with or without weakly differentiated sheath cells; other genera (*Adenostoma, Cercocarpus, Hagenia, Polylepis, Purshia, Quillaja, Sorbaria*) have more homogeneous rays composed of procumbent cells only, or weakly heterogeneous rays with one row of square marginal cells. Rays in the remaining genera (*Chamaebatiaria, Cowania, Exochorda, Kageneckia, Lyonothamnus, Rosa* p.p., *Vauquelinia*) are composed of procumbent body cells and 1–5 rows of square to upright marginal cells.

[11] Druses occur in *Petrophytum* of the Spiraeoideae and in low frequency in many species of the *Prunus* alliance. Prismatic crystals, however, are of much more widespread occurrence (Table 2).

CLASSIFICATION OF THE ROSACEAE

Phenetic wood anatomical classification

Based on the survey of wood anatomical features in the family (see also Zhang & Baas, 1992), 18 wood anatomical characters were selected (Table 2). Not all 18 characters have the same diagnostic or systematic value. For instance, vessel and fibre pitting, parenchyma abundance and distribution, ray size and ray composition are all highly diagnostic at the genus level, but characters like ring-porosity, L/D ratio, F/V ratio and occurrence and distribution of crystals are more often variable than constant within individual genera. The other characters listed in Table 2 have an intermediate diagnostic value. Features with a high tendency to show associations with others and thus characteristic of suprageneric groups are helical vessel wall thickenings (5), fibre pit distribution (8–9), axial parenchyma abundance (12), ray size and composition (13–15) and presence of druses (18) (in brackets the character number of Table 2). In other words, not all characters, diagnostic at the genus level, are also characteristic of higher categories, and some characters which often show variability below the genus level (druses and to a lesser extent helical vessel wall thickenings) yet tend to characterise larger assemblages of genera.

On the basis of overall wood anatomical similarity, 12 groups can be distinguished (Table 2):

I. This group includes seven genera (*Coleogyne, Kerria, Petrophytum, Rosa, Rubus, Sibiraea* and *Stephanandra*) from both the Spiraeoideae and Rosoideae. The group is characterised by rays wider than 4-seriate, of two distinct sizes, higher than 1.0 mm and body ray cells composed of square or square to procumbent cells; scanty axial parenchyma; vessel wall thickenings usually absent; and fibre pits usually densely placed in radial walls.

II. The group, composed of *Holodiscus, Sarcopoterium,* and *Spiraea,* shares all the characters listed above with the first group, but is unique for the occurrence of libriform fibres.

III. This group comprises nine genera (*Alchemilla, Chamaebatia, Chamaebatiaria, Cowania, Dryas, Fallugia, Physocarpus, Potentilla* and *Sibbaldia*). It differs from the above two groups mainly in ray characters. Rays in this group are 1–3 (–4)-seriate, of intergrading sizes only, mostly lower than 0.4 mm.

IV. *Polylepis* and *Purshia* share the same states in most characters with Group III. But rays in this group are more homogeneous (Kribs' homogeneous to heterogeneous III) and axial parenchyma is relatively abundant.

V. The fifth group is composed of *Adenostoma, Hagenia* and *Sorbaria,* and characterised by rays wider than 4-seriate and 0.4–1.0 mm high. In ray composition and other characters this group is similar to Group IV.

VI. *Chaenomeles, Cotoneaster, Dichotomanthes, Eriobotrya, Eriolobus, Osteomeles, Photinia* A, *Pyracantha, Raphiolepis* and *Stranvaesia,* all Maloideae, constitute this group. It is quite homogeneous, characterised by 1–3(–4)-seriate rays, of intergrading sizes, usually lower than 0.4 mm; prismatic crystals frequently present in chambered and enlarged axial parenchyma cells, helical vessel wall thickenings often present.

Table 2. Wood anatomical feature datamatrix for phenetic grouping.

	1	2	3	4	5	6a	6b	7	8	9	10	11	12	13	14a	14b	15a	15b	16	17	18
Group I																					
Coleo[1]	–	–	–	–	–	+	–	–	–	+	–	–	+	–	–	+	+	–	+	–	–
Kerri	–	–	+	–	–	–	–	–	–	+	–	–	+	–	–	+	+	–	+	–	–
Petro	–	–	–	–	–	+	–	?	–	+	–	–	+	–	–	–	+	–	+	–	+
Rosa	±	–	+	–	+	?	?	±	–	±	–	–	+	–	–	+	±	–	±	–	–
Rubus	–	±	+	–	–	±	–	–	–	+	–	–	+	–	–	+	+	–	±	–	–
Sibir	±	–	+	–	–	?	?	?	–	+	–	–	+	–	–	+	+	–	–	–	–
Steph	–	–	+	–	–	–	–	–	–	+	–	–	+	–	–	+	+	–	+	–	–
Group II																					
Holod	–	–	+	–	–	±	–	–	–	–	+	–	+	–	–	+	+	–	–	–	–
Sarco	–	+	+	–	–	+	–	–	–	±	+	–	+	–	–	±	+	–	+	–	–
Spira	–	+	–	–	–	–	–	–	–	+	+	–	+	–	–	+	+	–	±	–	–
Group III																					
Alche	–	–	–	–	–	–	–	?	–	+	–	–	+	+	+	–	+	–	–	–	–
Cowan	+	–	+	–	–	?	?	–	–	+	–	–	+	+	+	–	–	–	–	–	–
C-ria	–	–	–	–	–	+	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–
C-tia	–	–	–	–	–	–	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–
Dryas	±	–	+	–	–	?	?	?	–	+	–	–	+	+	–	–	+	–	–	–	–
Fallu	±	–	+	–	–	?	?	–	–	+	–	–	+	+	+	–	+	–	–	–	–
Physo	–	±	+	–	–	+	–	–	–	+	–	–	±	+	±	–	+	–	–	–	–
Poten	±	–	–	–	–	?	?	–	–	±	–	–	+	+	±	–	+	–	–	–	–
Sibba	–	–	+	–	–	+	–	?	–	–	–	–	+	+	+	–	+	–	–	–	–
Group IV																					
Polyl	–	±	–	–	+	+	–	–	–	±	–	–	–	+	+	–	–	+	–	–	–
Pursh	±	–	–	–	–	?	?	±	–	±	–	–	–	+	+	–	–	+	–	–	–
Group V																					
Adeno	–	–	+	–	±	±	–	–	–	±	–	–	–	–	–	–	–	+	+	–	–
Hagen	–	+	–	–	–	+	–	±	–	–	–	–	–	–	–	–	–	+	–	–	–
Sorba	–	–	–	–	–	+	–	–	–	±	–	–	–	–	–	–	–	+	–	–	–
Group VI																					
Chaen	–	–	–	–	±	–	–	–	–	–	–	–	–	+	+	–	–	–	–	±	–
Coton	–	–	–	–	±	–	±	–	–	–	–	–	–	+	+	–	–	–	–	±	–
Dicho	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–
Eriob	–	–	–	–	+	–	±	–	–	–	–	–	–	+	+	–	–	–	–	+	–
Eriol	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–
Osteo	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–
PhotA	–	–	–	–	+	–	±	–	–	–	–	–	–	+	+	–	–	–	–	±	–
Pyrac	–	–	–	–	±	–	–	–	–	–	–	–	–	+	+	–	–	–	–	+	–
Raphi	–	–	–	–	+	–	+	–	–	–	–	–	–	+	±	–	–	–	–	±	–
Stran	–	–	–	–	+	–	+	–	–	–	–	–	–	+	+	–	–	–	–	+	–

[1] Explanation of the abbreviations is given after the next page.

(Table 2 continued)

	1	2	3	4	5	6a	6b	7	8	9	10	11	12	13	14a	14b	15a	15b	16	17	18
Group VII																					
Amela	–	–	–	–	+	–	±	–	–	–	–	–	–	+	+	–	–	+	–	±	–
Cerco	–	–	–	–	+	±	±	–	–	–	–	–	–	+	+	–	–	+	–	±	–
Crata	–	–	–	±	±	±	±	±	–	–	–	–	–	+	+	–	–	+	–	±	–
Cydon	–	–	–	–	±	–	±	–	–	–	–	–	–	+	+	–	–	+	–	±	–
Docyn	–	–	–	–	+	±	–	–	–	–	–	–	–	+	+	–	–	+	–	+	–
Hespe	–	–	–	–	–	–	–	±	–	–	–	–	–	+	+	–	–	+	–	–	–
Heter	–	–	–	–	±	–	–	–	–	–	–	–	–	+	+	–	–	±	–	±	–
Malus	–	±	–	±	±	–	–	–	–	–	–	–	–	+	+	–	–	+	–	±	–
Mespi	–	–	–	–	+	–	–	–	–	–	–	–	–	+	+	–	–	+	–	±	–
Micro	–	±	–	–	+	–	±	±	–	–	–	–	–	+	+	–	–	+	–	±	–
Perap	–	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	–	+	–	+	–
PhotB	–	–	–	–	±	–	–	–	–	–	–	–	–	–	±	–	–	±	–	+	–
Pyrus	–	±	–	–	±	±	±	–	–	–	–	–	–	+	+	–	–	+	–	±	–
Sorbu	–	±	–	–	+	–	±	±	–	–	–	–	–	+	+	–	–	+	–	±	–
Group VIII																					
Kagen	–	–	+	–	+	+	–	?	–	–	–	–	–	+	–	–	–	–	+	–	–
Lindl	–	–	–	–	+	–	–	–	–	+	–	–	–	+	+	–	+	–	+	–	–
Prins	–	–	+	±	+	–	–	–	–	–	–	–	±	±	±	–	±	–	±	–	–
Group IX																					
Lyono	–	–	+	–	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	±	–
Quill	–	–	–	–	+	+	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–
Vauqu	–	–	–	–	+	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–
Group X																					
Exoch	±	–	+	–	+	?	?	–	+	–	–	–	–	–	+	–	–	–	+	–	–
Osmar	–	–	+	–	+	–	–	±	+	–	–	–	–	–	–	–	–	–	–	–	–
Group XI																					
LaurB	–	+	+	–	±	+	–	+	+	–	±	+	–	–	–	–	–	–	±	±	±
Pygeu	–	+	+	–	±	+	–	±	+	–	–	±	–	±	±	–	–	–	±	–	±
Group XII																					
Amygd	+	+	+	+	+	?	?	±	±	–	±	–	+	–	–	–	–	–	±	–	±
Armen	+	+	+	+	+	?	?	±	±	–	–	–	+	–	–	–	–	–	±	±	±
Ceras	–	+	+	+	+	±	–	±	+	–	±	–	+	–	–	–	–	–	±	±	±
LaurA	–	+	+	+	+	±	–	±	+	–	–	–	+	±	±	–	–	–	–	±	–
Padus	–	+	+	+	+	±	–	±	+	–	–	–	+	–	–	–	–	+	±	±	±
Prunu	–	+	+	+	+	±	–	±	+	–	–	–	+	–	±	–	–	–	–	–	±

1: = Ring-porosity; **2:** Percentage of solitary vessels < 60%; **3:** Intervessel pits polygonal; **4:** Vessel–ray pits clearly smaller than intervessel pits; **5:** Helical vessel wall thickenings; **6a:** L/D ratio < 9; **6b:** L/D ratio > 19; **7:** F/V ratio >2.4; **8:** Fibre pits mainly in radial walls; **9:** Fibre pits densely spaced in radial walls; **10:** Libriform fibres; **11:** Marginal parenchyma; **12:** Axial parenchyma scanty; **13:** Rays 1–3(–4)-seriate; **14a:** Ray height < 0.4 mm; **14b:** Ray height > 1.0 mm; **15a:** Body ray cells square or square to procumbent; **15b:** Rays homogeneous, sometimes to Kribs' heterogeneous III; **16:** Crystals in ray cells; **17:** Prismatic crystals in enlarged and chambered axial parenchyma cells; **18:** Druses: + = present; ± = variable below the generic level; – = absent.

Explanation of the abbreviations (names of taxa) in Table 2:

Adeno = *Adenostoma*
Alche = *Alchemilla*
Amela = *Amelanchier*
Amygd = *Amygdalus*
Armen = *Armeniaca*
Ceras = *Cerasus*
Cerco = *Cercocarpus*
Chaen = *Chaenomeles*
C-tia = *Chamaebatia*
C-ria = *Chamaebatiaria*
Chama = *Chamaemeles*
Coleo = *Coleogyne*
Coton = *Cotoneaster*
Cowan = *Cowania*
Crata = *Crataegus*
Cydon = *Cydonia*
Dicho = *Dichotomanthes*
Docyn = *Docynia*
Dryas = *Dryas*
Eriob = *Eriobotrya*
Eriol = *Eriolobus*
Exoch = *Exochorda*
Fallu = *Fallugia*
Hagen = *Hagenia*
Hespe = *Hesperomeles*
Heter = *Heteromeles*
Holod = *Holodiscus*
Kagen = *Kageneckia*
Kerri = *Kerria*
LaurA = *Laurocerasus* A
LaurB = *Laurocerasus* B
Lindl = *Lindleya*
Lyono = *Lyonothamnus*
Malus = *Malus*
Mespi = *Mespilus*
Micro = *Micromeles*
Osmar = *Osmaronia*
Osteo = *Osteomeles*
Padus = *Padus*
Perap = *Peraphyllum*
Petro = *Petrophytum*
PhotA = *Photinia* A
PhotB = *Photinia* B
Physo = *Physocarpus*
Polyl = *Polylepis*
Poten = *Potentilla*
Prins = *Prinsepia*
Prunu = *Prunus* s. str.
Pursh = *Purshia*
Pygeu = *Pygeum*
Pyrac = *Pyracantha*
Pyrus = *Pyrus*
Quill = *Quillaja*
Raphi = *Raphiolepis*
Rosa = *Rosa*
Rubus = *Rubus*
Sarco = *Sarcopoterium*
Sibba = *Sibbaldia*
Sibir = *Sibiraea*
Sorba = *Sorbaria*
Sorbu = *Sorbus*
Spira = *Spiraea*
Steph = *Stephanandra*
Stran = *Stranvaesia*
Vauqu = *Vauquelinia*

VII. The remaining genera of the Maloideae, together with *Cercocarpus*, are arranged in this group, which differs from Group VI in ray composition only (more homogeneous in this group).

VIII. This group includes *Kageneckia, Lindleya* and *Prinsepia*. It is characterised by prismatic crystals usually present in ray cells, helical vessel wall thickenings, fibre pits in both radial and tangential walls, relatively abundant axial parenchyma, and rays usually 1–3(–4)-seriate.

IX. *Lyonothamnus, Quillaja* and *Vauquelinia*, as a group, differ from Group VIII in ray width and crystals.

X. Fibre pits in this group (*Exochorda* and *Osmaronia*), unlike all the genera listed above, are mainly confined to the radial walls, and intervessel pits are mainly polygonal. The group still shares a few characters (e.g. percentage of solitary vessels, helical vessel wall thickenings, axial parenchyma, ray width and composition) with Group IX.

XI. *Laurocerasus* B and *Pygeum* have wood with a high degree of vessel grouping, vessel–ray pits similar to intervessel pits, L/D ratio smaller than 9, marginal parenchyma often present, relatively abundant axial parenchyma, and rays Kribs' heterogeneous III & II.

XII. This group (*Amygdalus, Armeniaca, Cerasus, Laurocerasus* A, *Padus* and *Prunus* s. str.) has vessel–ray pits clearly smaller than intervessel pits, well developed and widely-spaced vessel wall thickenings, F/V ratio usually larger than 2.4, axial parenchyma usually scanty, rays mostly not narrower than 4-seriate and 0.4–1.0 mm high, druses sometimes present.

Each group mentioned above differs from the others in at least one character, showing its own identity. On the other hand, there are also transitions between the groups (Table 2). Group I is similar to Group II in most major characters except one (libriform fibres). These two groups also share three characters with Group III: vessel wall thickenings usually absent, axial parenchyma scanty and F/V ratio usually smaller than 2.4. Ray height links Group III to Group IV, and Group IV is connected with Group V via similar ray composition and axial parenchyma amount. In general, these five groups share the following characters: vessel–ray pits in size similar to intervessel pits, vessel wall thickenings mostly absent, L/D ratio smaller than 19, F/V ratio smaller than 2.4, fibre pits in both radial and tangential walls, fibre pits mostly densely spaced in radial walls, crystals absent or confined to ray cells. These five groups have fewer connections with Group VI and Group VII, both of which are quite similar in many characters (except in ray composition). Group VIII and Group IX are both characterised by over 60% of the vessels solitary, vessel–ray pits similar to intervessel pits, F/V ratio smaller than 2.4, fibre pits in both radial and tangential walls, and axial parenchyma common to abundant. Like Groups VI and VII, these two groups also have helical vessel wall thickenings, fibre pits in radial and tangential walls, and rays mostly lower than 0.4 mm. Groups X, XI and XII have in common that fibre pits are mainly confined to radial walls, vessel wall thickenings are usually present, rays are mostly not narrower than 4-seriate and lower than 1.0 mm, intervessel pits are mainly polygonal, and druses tend to be present (except in Group X).

A comparison of the wood anatomical groups with the current classification of the family into tribes by Hutchinson (1964) is given in Table 3. Despite obvious differences between the two classifications, it is striking that with few exceptions all woody tribes, if not characterised by a single wood type, encompass few closely adjacent wood anatomical groups. The only exceptions are the Cercocarpeae, of which the two genera studied are in the widely separate Groups I (*Coleogyne*) and VII (*Cercocarpus*), and the Neillieae and Gillenieae which have smaller wood anatomical gaps between their constituent genera. The wood anatomical Groups I–V often harbour a mixture of representatives from Spiraeoideae p.p. and Rosoideae tribes, but each of Groups VI–XII usually comprise members of a single tribe or subfamily, with the exception of Groups VII and VIII which also contain the problematic isolated genera *Cercocarpus* and *Prinsepia*, respectively. The affinities of these genera will be discussed in greater detail in the section on phylogenetic relationships.

In Table 3 the wood anatomical groups have further been clustered according to the transitions discussed above. The four resulting clusters show some, but not a complete agreement with subfamily delimitation within the Rosaceae. The remarkable similarity in wood structure of Spiraeoideae and Rosoideae has already been emphasised before (Zhang & Baas, 1992) when discussing wood anatomical diversity of the Chinese representatives.

In the present study this similarity is confirmed, but one tribe of the Spiraeoideae, the Quillajeae – not represented in China – appears to have close wood anatomical links with the Prunoideae. The position of the Quillajeae will be further discussed below.

Table 3. Hutchinson's classification (1964) compared with wood anatomical grouping.

Tribe	Wood anatomical groups
Quillajeae	VIII, IX, X
Spiraeeae	I, II
Neillieae	I, III
Gillenieae	III, V
Osmaronieae	X
Pruneae	VIII, XI, XII
Rubeae	I
Holodisceae	II
Kerrieae	I
Potentilleae	III
Dryadeae	III, IV
Poterieae	II, III, IV, V
Cercocarpeae	I, VII
Adenostomateae	V
Roseae	I
Maleae	VI, VII

Wood anatomical group	Tribes	Subfamilies
I	Cercocarpeae, Kerrieae, Neillieae, Roseae, Rubeae, Spiraeeae	Spiraeoideae p.p. + Rosoideae
II	Holodisceae, Poterieae, Spiraeeae	
III	Dryadeae, Gillenieae, Neillieae, Poterieae, Potentilleae	
IV	Dryadeae, Poterieae	
V	Gillenieae, Poterieae, Adenostomateae	
VI	Maleae	Maloideae (+Rosoideae p.p.)
VII	Maleae, Cercocarpeae	
VIII	Quillajeae, Pruneae	Prunoideae + Spiraeoideae p.p.
IX	Quillajeae	
X	Osmaronieae, Quillajeae	
XI	Pruneae	
XII	Pruneae	

Phylogenetic classification

For the cladistic analysis the same 18 wood anatomical characters were used as in the phenetic comparison with two additional characters: fruit types and chromosome numbers. For 15 binary characters (viz., characters 2–5, 7–13, 16–18, and 20, see Table 4), constant character states in individual genera were coded as 0 (for plesiomorphic state) or 2 (for apomorphic state), variable below generic level as 1; for the four 3-state characters (viz., porosity, L/D ratio, ray height and ray composition), constant character states in individual genera were coded as 0 (for plesiomorphic state), 2 (for intermediate state) and 4 (for apomorphic state) respectively, variable below generic level as 1 (variable between plesiomorphic state and intermediate state) or 3 (variable between intermediate state and apomorphic state); and the 7-state character of chromosome numbers, 7, 8, 9, 14, 15, 17, and 27 were coded as 0, 1, 2, 3, 4, 5, and 6 respectively.

The designation of an outgroup was impossible, as the sister group of the Rosaceae is not known. Only vague ideas about relations exist, see also the discussion in Kalkman (1988). For this reason an artificial outgroup, a kind of archetype, was constructed based on the Baileyan transformation series for wood anatomy (Bailey & Tupper, 1918; Baas, 1986; Carlquist, 1988; Wheeler & Baas, 1991). Character states present in the Rosaceae and thought to be most primitive (plesiomorphic) within the

Baileyan series, are coded as the character states for the outgroup: diffuse-porosity, over 60% of the vessels solitary, helical vessel wall thickenings absent, L/D ratio over 19, F/V ratio less than 2.4, fibres with distinctly bordered pits in both radial and tangential walls, libriform fibres and marginal parenchyma absent, axial parenchyma scanty, rays of two distinct sizes comprising wide and tall ones. The Baileyan transformation series were used for this purpose, because recently the general applicability of the series was supported by evidence that reversibility of wood anatomical trends is probably quite limited (Baas et al., 1988; Carlquist, 1988; Wheeler & Baas, 1991). However, parallel development of trends occur widespread throughout the angiosperms. The Baileyan trends do not apply to several characters; these are represented by question marks in the datamatrix (except crystals): intervessel pit shape, relative vessel–ray pit size, density of fibre pits in radial fibre walls, and ray composition. Although evolutionary trends in crystals are not unequivocal, here absence was coded as primitive in order to limit the number of question marks. Of the two additional characters, the primitive character state for the chromosome number is unknown, that for the type of fruit is thought to be the dehiscent type.

A first analysis of the datamatrix in Table 4 resulted in an overflow of more than 100 equally parsimonious cladograms. One of these is depicted in Figure 17. The consistency index of this cladogram is very low (0.29). The grouping in the cladograms was more or less close to traditional classifications, but too unsatisfactory to accept as the end-result.

In order to arrive at more satisfactory cladograms the method developed by Van Welzen (1989) was applied in a slightly adapted version. In order to reduce homoplasy and to raise the consistency index the cladogram in Figure 17 was cut into three parts of which the genera were analysed separately, and afterwards the parts were connected again. The cuts are shown in the cladogram, the resulting three groups of taxa are the same in all observed 100 cladograms. Two of these groups are paraphyletic, the basal group, which mainly includes the Spiraeoideae p.p. (except Quillajeae) and Rosoideae, and the middle group, which includes the Maloideae and *Cercocarpus*. The upper part is monophyletic and contains the Prunoideae and the tribe Quillajeae (*Exochorda, Kageneckia, Lindleya, Lyonothamnus, Quillaja,* and *Vauquellinia*) assigned to the Spiraeoideae by Hutchinson (1964).

These three parts were analysed separately. To all parts outgroups were assigned (see below). The middle and the upper parts were assigned the sistergroup from the lower and middle parts respectively. The two paraphyletic groups received a representative of a higher group. This representative should contain the character states of the lowest node from the group just above the group under analysis. As the lower node characters are not always unequivocal, for this reason a genus, the first to split off the higher group, was added as the representative taxon. So the lower group received a representative of the middle group and the middle group a representative of the upper group. The sistergroups which are added as outgroups in the various analyses should be the groups ending as sistergroup next to the representative taxon. So in the lower part the sistergroup ending next to the representative taxon of the middle group will be the outgroup in the analysis of the middle group. The outgroups and representative taxa can only be found by reciprocal illumination: analysis of the upper

Table 4. Datamatrix used for the cladistic analysis.
(1–18 = wood anatomical features; 19 = chromosome number; 20 = fruit type)

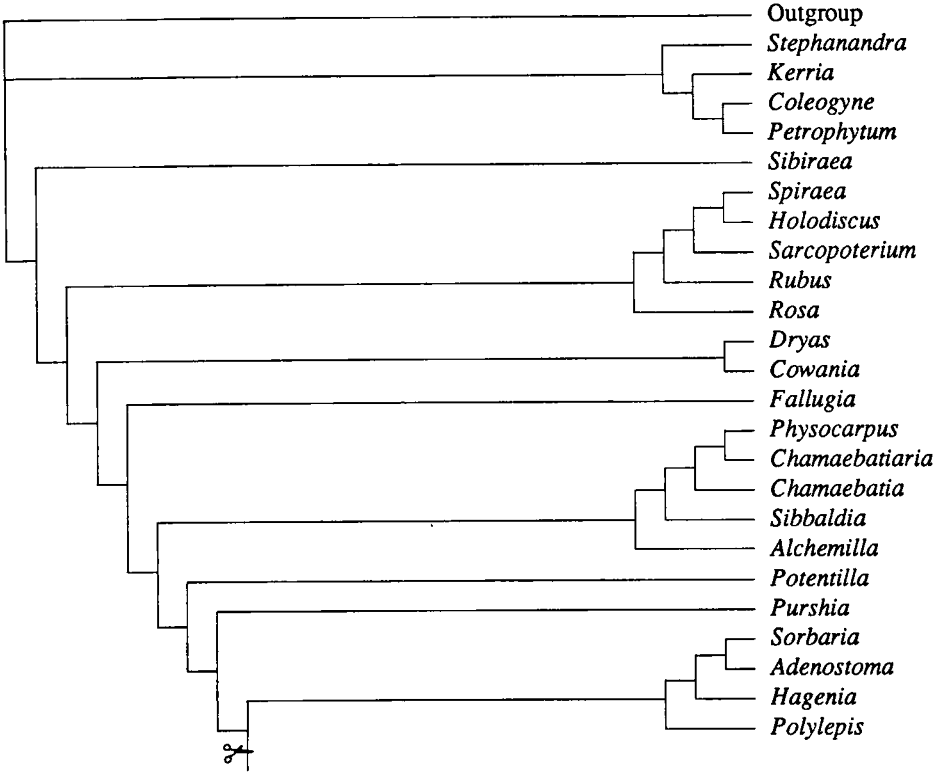
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Adenostoma	1	0	0	0	1	3	0	0	1	0	0	2	0	2	4	2	0	0	2	2
Alchemilla	2	0	2	0	0	2	?	0	0	0	0	0	2	4	0	0	0	0	1	2
Amelanchier	0	0	2	0	2	1	0	0	2	0	0	2	2	4	4	0	1	0	5	2
Amygdalus	3	2	0	2	2	?	1	1	2	1	0	0	0	2	2	1	0	1	1	2
Armeniaca	3	2	0	2	2	?	1	1	2	0	0	0	0	2	2	1	1	1	1	2
Cerasus	1	2	0	2	2	3	1	2	2	1	0	0	0	2	2	1	1	1	1	2
Cercocarpus	2	0	2	0	2	2	0	0	2	0	0	2	2	4	4	0	1	0	2	2
Chaenomeles	0	0	2	0	1	2	0	0	2	0	0	2	2	4	2	0	1	0	5	2
Chamaebatia	2	0	2	0	0	2	0	0	2	0	0	0	2	4	0	0	0	0	2	2
Chamaebatiaria	2	0	2	0	0	4	0	0	2	0	0	0	2	4	2	0	0	0	2	0
Coleogyne	2	0	2	0	0	4	0	0	0	0	0	0	0	0	0	2	0	0	2	2
Cotoneaster	1	0	2	0	1	1	0	0	2	0	0	2	2	4	2	0	1	0	5	2
Cowania	4	0	0	0	0	?	0	0	0	0	0	0	2	4	2	0	0	0	2	2
Crataegus	0	0	2	1	1	2	1	0	2	0	0	2	2	4	4	0	1	0	5	2
Cydonia	0	0	2	0	1	1	0	0	2	0	0	2	2	4	4	0	1	0	5	2
Dichotomanthes	0	0	2	0	2	2	0	0	2	0	0	2	2	4	2	0	2	0	5	2
Docynia	0	0	2	0	2	3	0	0	2	0	0	2	2	4	4	0	2	0	5	2
Dryas	3	0	0	0	0	?	?	0	0	0	0	0	2	2	0	0	0	0	2	2
Eriobotrya	0	0	2	0	2	1	0	0	2	0	0	2	2	4	2	0	2	0	5	2
Eriolobus	1	0	2	0	2	2	0	0	2	0	0	2	2	4	2	0	2	0	5	2
Exochorda	3	0	0	0	2	?	0	2	2	0	0	2	0	4	2	2	0	0	1	0
Fallugia	3	0	0	0	0	?	0	0	0	0	0	0	2	4	0	0	0	0	0	2
Hagenia	0	2	2	0	0	4	2	0	2	0	0	2	0	2	4	0	0	0	0	2
Hesperomeles	0	0	2	0	0	2	1	0	2	0	0	2	2	4	4	0	0	0	5	2
Heteromeles	0	0	2	0	1	2	0	0	2	0	0	2	2	4	3	0	1	0	5	2
Holodiscus	1	0	0	0	0	3	0	0	2	2	0	0	0	0	0	0	0	0	?	2
Kageneckia	0	0	0	0	2	4	?	0	2	0	0	2	2	2	2	2	0	0	5	0
Kerria	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	2	2
Laurocerasus A	0	2	0	2	2	3	1	2	2	0	0	0	1	3	2	0	1	0	1	2
Laurocerasus B	0	2	0	0	1	4	2	2	2	1	2	2	0	2	2	1	1	1	1	2
Lindleya	1	0	2	0	2	2	0	0	0	0	0	2	2	4	0	2	0	0	5	0
Lyonothamnus	0	0	0	0	2	2	0	0	2	0	0	2	0	4	2	0	1	0	6	0
Malus	0	1	2	1	1	2	0	0	2	0	0	2	2	4	4	0	1	0	5	2
Mespilus	0	0	2	0	2	2	0	0	2	0	0	2	2	4	4	0	1	0	5	2
Micromeles	1	1	2	0	2	1	1	0	2	0	0	2	2	4	4	0	1	0	5	2
Osmaronia	0	0	0	0	2	2	1	2	2	0	0	2	0	2	2	0	0	0	1	2
Osteomeles	0	0	2	0	2	2	0	0	2	0	0	2	2	4	2	0	2	0	5	2
Padus	1	2	0	2	2	3	1	2	2	0	0	0	1	3	4	1	1	1	1	2
Peraphyllum	2	0	2	0	0	2	0	0	2	0	0	2	2	4	4	0	2	0	5	2
Petrophytum	0	0	2	0	0	4	?	0	0	0	0	0	0	2	0	2	0	2	2	0
Photinia A	0	0	2	0	2	1	0	0	2	0	0	2	2	4	2	0	1	0	5	2
Photinia B	0	0	2	0	1	2	0	0	2	0	0	2	0	3	3	0	2	0	5	2
Physocarpus	1	1	0	0	0	4	0	0	2	0	0	1	2	3	0	0	0	0	2	0
Polylepis	0	1	2	0	2	4	0	0	1	0	0	2	2	4	4	0	0	0	0	2

(Table 4 continued)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Potentilla	3	0	2	0	0	?	0	0	1	0	0	0	2	3	0	0	0	0	0	2
Prinsepia	1	0	0	1	2	2	0	0	2	0	0	1	1	3	1	1	0	0	1	2
Prunus s. str.	1	2	0	2	2	3	1	2	2	0	0	0	0	3	2	0	0	1	1	2
Purshia	3	0	2	0	0	?	1	0	1	0	0	2	2	4	4	0	0	0	0	2
Pygeum	0	2	0	0	1	4	1	2	2	0	1	2	1	3	2	1	0	1	1	2
Pyracantha	0	0	2	0	1	2	0	0	2	0	0	2	2	4	2	0	2	0	5	2
Pyrus	1	1	2	0	1	2	0	0	2	0	0	2	2	4	4	0	1	0	5	2
Quillaja	2	0	2	0	2	4	0	0	2	0	0	2	0	4	4	0	0	0	3	0
Raphiolepis	0	0	2	0	2	0	0	0	2	0	0	2	2	3	2	0	1	0	5	2
Rosa	3	0	0	0	2	?	1	0	1	0	0	0	0	0	1	1	0	0	0	2
Rubus	1	1	0	0	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	2
Sarcopoterium	1	2	0	0	0	4	0	0	1	2	0	0	0	1	0	2	0	0	0	2
Sibbaldia	2	0	0	0	0	4	?	0	2	0	0	0	2	4	0	0	0	0	0	2
Sibiraea	3	0	0	0	0	?	?	0	0	0	0	0	0	0	0	0	0	0	2	0
Sorbaria	1	0	2	0	0	4	0	0	1	0	0	2	0	2	4	0	0	0	2	0
Sorbus	1	1	2	0	2	1	1	0	2	0	0	2	2	4	4	0	1	0	5	2
Spiraea	1	0	0	0	0	3	0	0	0	2	0	0	0	0	0	1	0	0	2	0
Stephanandra	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	0	0	2	0
Stranvaesia	0	0	2	0	2	0	0	0	2	0	0	2	2	4	2	0	2	0	5	2
Vauquelinia	2	0	2	0	2	2	0	0	2	0	0	2	0	4	2	0	0	0	4	0
Outgroup	0	0	?	?	0	0	0	0	?	0	0	0	0	0	?	0	0	0	?	0

The characters, character states and codes (in brackets):

1 = porosity: diffuse-porous (0); semi-ring-porous (2); ring-porous (4).
2 = percentage of solitary vessels: ≥ 60% (0); < 60% (2).
3 = intervessel pit shapes: at least partly polygonal (0); round to oval (2).
4 = vessel–ray pits versus intervessel pits: similar (0); clearly smaller (2).
5 = helical vessel wall thickenings: absent (0); present (2).
6 = L/D ratio: > 19 (0); 9–19 (2); < 9 (4).
7 = F/V ratio: ≤ 2.4 (0); > 2.4 (2).
8 = fibre pits: in radial and tangential walls (0); mainly in radial walls (2).
9 = fibre pits: densely spaced in radial walls (0); sparse to medium spaced in radial walls (2).
10 = libriform fibres: absent (0); present (2).
11 = marginal parenchyma: absent (0); present (2).
12 = parenchyma amount: scanty (0); common to abundant (2).
13 = ray width: the widest rays 4–15-seriate (0); 1–3(–4)-seriate (2).
14 = ray height: > 1.0 mm (0); 1.0–0.4 mm (2); < 0.4 mm (4).
15 = ray composition: ray body cells composed of square or square to procumbent cells (0); Kribs' heterogeneous III to I (2); Kribs' homogeneous to heterogeneous III (4).
16 = crystals in ray cells: absent (0); present (2).
17 = prismatic crystals in enlarged and chambered axial parechyma cells: absent (0); present (2).
18 = druses: absent (0); present (2).
19 = chromosome number: 7 (0); 8 (1); 9 (2); 14 (3); 15 (4); 17 (5); 27 (6).
20 = fruits: dehiscent (0); indehiscent (2).



(continued on the next page)

group with an outgroup from the middle group results in a cladogram. From this cladogram a representative taxon for the analysis of the middle part can be obtained. The latter analysis will perhaps confirm the choice of the outgroup for the analysis of the upper part; if not, the sistergroup to the representative of the upper part should be used as outgroup in the new analysis of the upper group. This may perhaps reveal a new representative taxon, etc. This process is continued till no changes occur anymore. The same applied to the analysis of the middle and lower groups. Unfortunately, due to lack of time, the different re-analyses had to be omitted and the entire cladistic analysis should be considered as a very tentative one, accordingly.

In the following partial cladistic analyses, an extant genus of the Rosaceae is selected as outgroup for each part. This means that character polarisation in these analyses was not primarily dictated by the Baileyan trends, but by the attributes of these selected genera.

(continued from the preceding page)

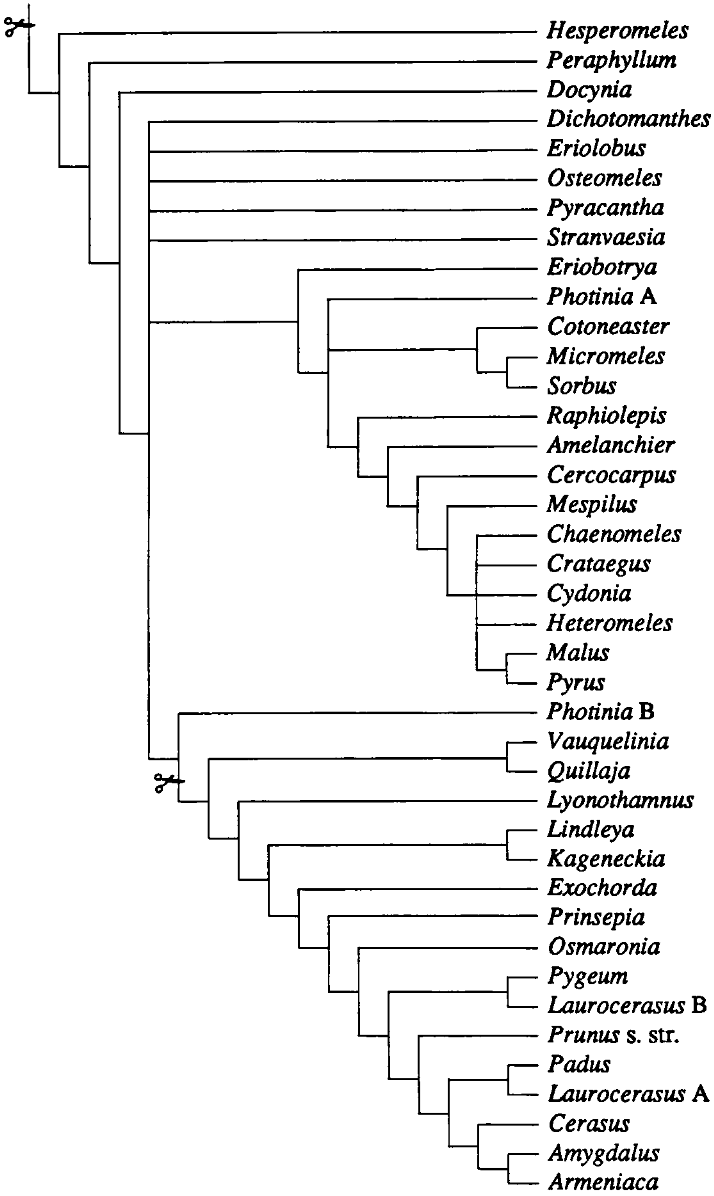


Fig. 17. Selected cladogram of the complete data matrix (Table 4). Upper, middle and lower groups indicated by ✂.

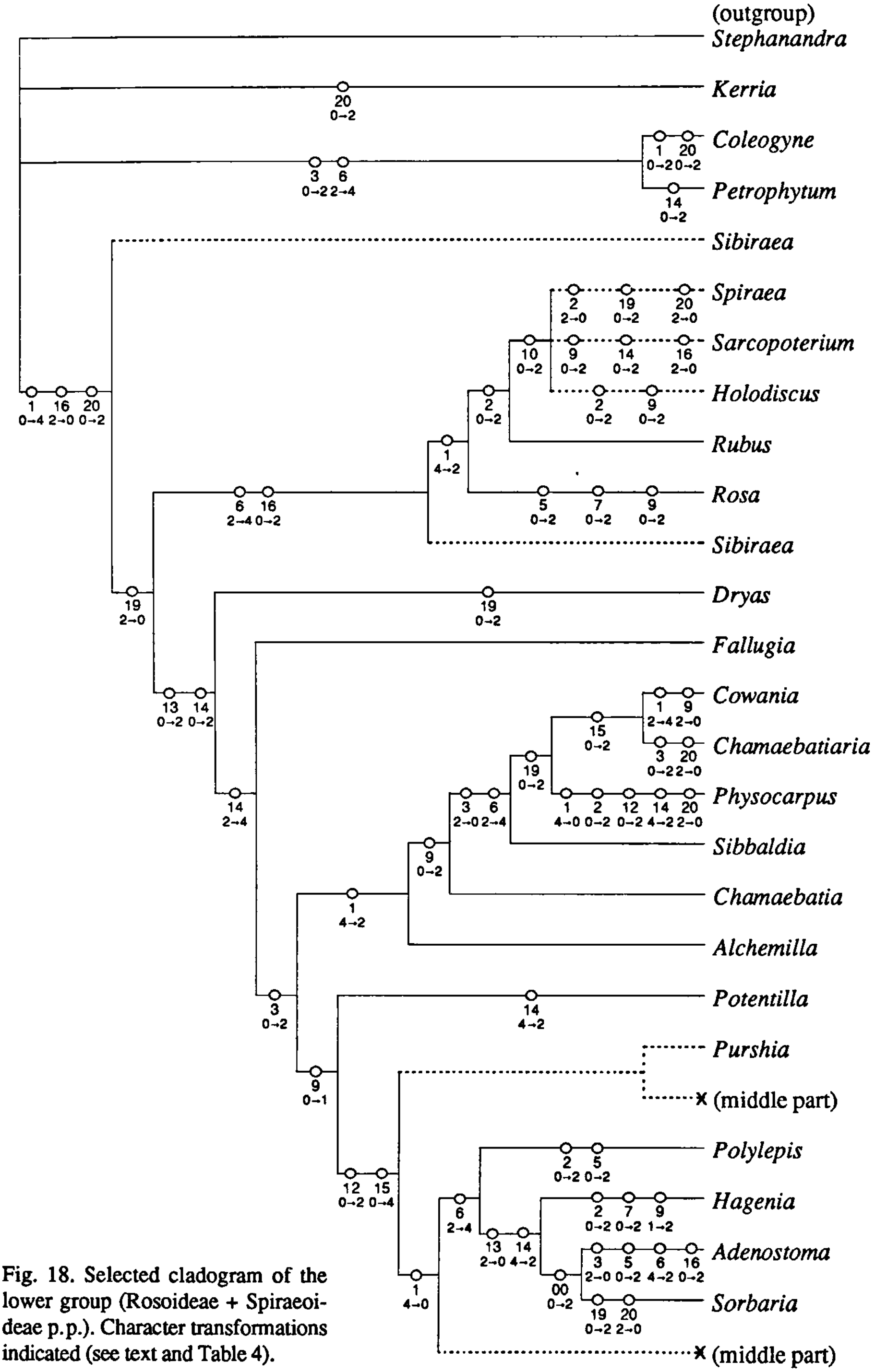


Fig. 18. Selected cladogram of the lower group (Rosoideae + Spiraeoideae p.p.). Character transformations indicated (see text and Table 4).

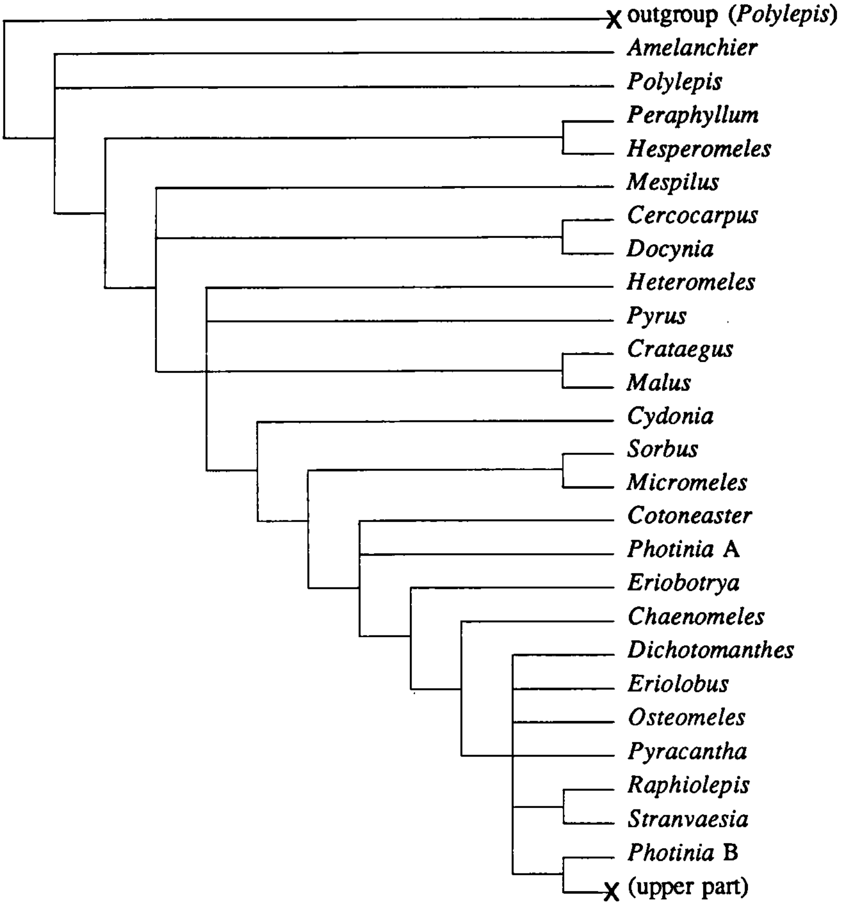


Fig. 19. Selected cladogram of the middle group (Maloideae + *Cercocarpus*).

Lower group (Spiraeoideae p.p. & Rosoideae)

This group includes 24 genera which are usually placed either in Spiraeoideae or in Rosoideae. For this group, *Stephanandra* was used as outgroup, and *Hesperomeles* was chosen as a representative of the other groups. Finally, 24 cladograms were produced after two character weightings. The consistency index is 0.64. Comparing these cladograms, there are three variable places, as shown by dotted lines in Figure 18. *Sibiraea* can be placed in two different positions; relations between *Holodiscus, Sarcopoterium* and *Spiraea* are also variable with four possibilities which have been simplified to one (Fig. 18); and *Hesperomeles* (the representative of the remaining part) and *Purshia* either form a separate monophyletic group between *Polylepis* and *Potentilla,* or form two successive groups between *Polylepis* and *Potentilla.*

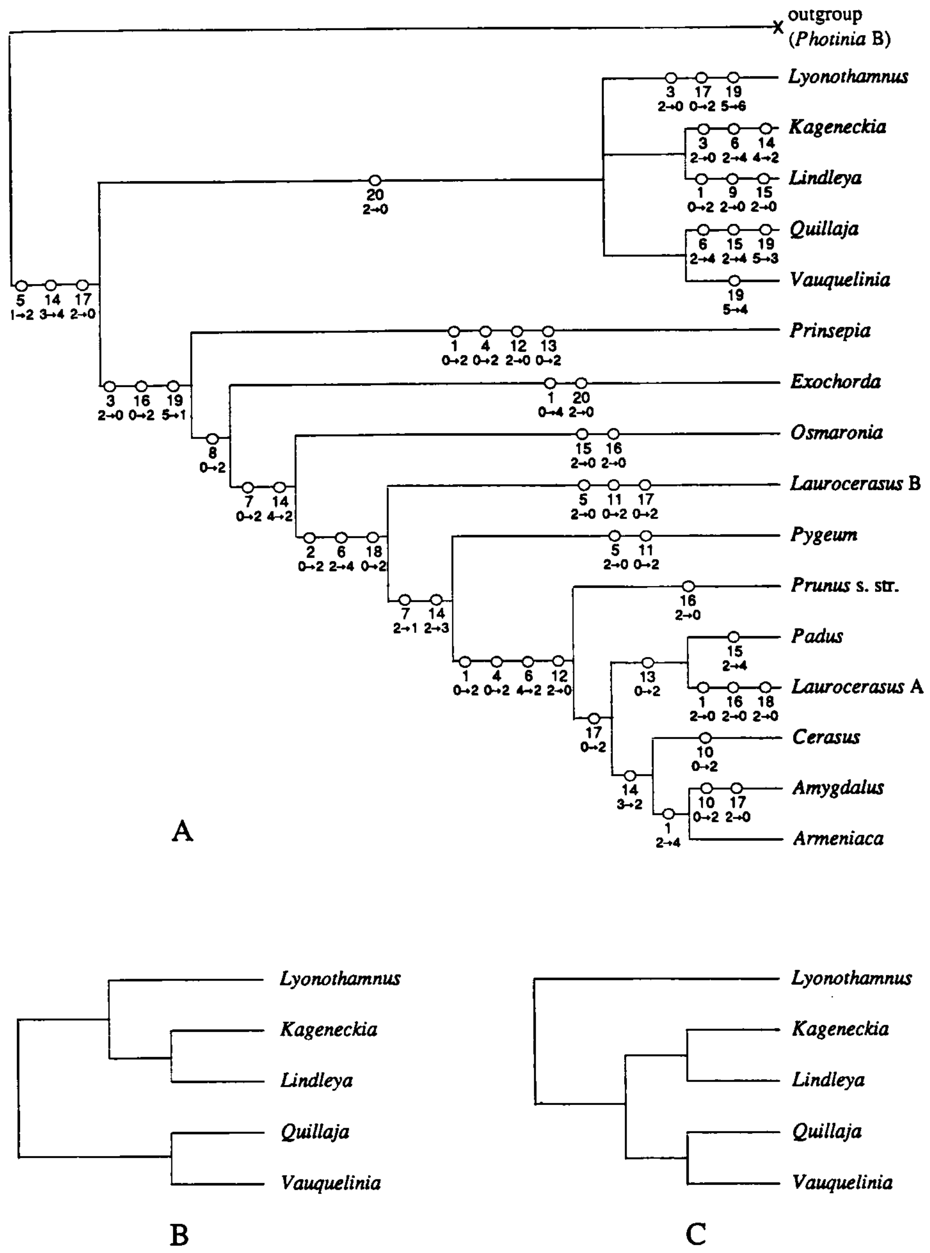


Fig. 20. Cladograms of the upper group (Prunoideae + Spiraeoideae p.p.). Character transformations indicated (see Table 4). — A: consensus tree; B & C: equally parsimonious variants for the Quillajeae (Spiraeoideae).

Middle group (Maloideae)

This group includes all 23 genera of the Maloideae plus *Cercocarpus* traditionally placed in the Rosoideae. For this group, *Polylepis* from the first group was used as outgroup and *Vauquelinia* from the next group was chosen as the representative of the remaining part. This group yields over 100 equally parsimonious cladograms with a consistency index of 0.53. Character weighting, applied several times, improves the consistency index to 0.84, but does not reduce the number of the cladograms or improve their poor resolution. One of the cladograms produced is shown in Figure 19. Some individual genera originate together with other genera from the same node. This is hardly surprising in view of the great similarity of most genera of the Maloideae (Tables 2 and 4) in both wood structure and the two selected non-wood characters (viz. fruit type and chromosome number).

Upper group (Prunoideae and Quillajeae)

This group includes all Prunoideae studied (viz. *Amygdalus, Armeniaca, Cerasus, Laurocerasus* A & B, *Padus, Prunus* s. str., and *Pygeum*) and all six genera belonging to the tribe Quillajeae (*Exochorda, Kageneckia, Lindleya, Lyonothamnus, Vauquelinia,* and *Quillaja*). *Photinia* B from the second group was used as outgroup for this part. Three equally parsimonious cladograms were produced after four times character weighting. These cladograms are pictured in Figures 20A, B and C. The cladograms have a consistency index of 0.84. The only difference between these three cladograms is the variable position of *Lyonothamnus* in the monophyletic group of *Kageneckia, Lindleya, Lyonothamnus, Quillaja* and *Vauquelinia.* None of the three cladograms can be preferred, because every node in the cladograms has at least one apomorphy. The cladogram shown in Figure 20A shows the consensus tree, with a trichotomy in the above mentioned monophyletic group.

The above partial cladograms can be connected with each other (figure omitted), and serve as a basis for discussion. It is fully realised that on the basis of wood anatomical evidence only tentative suggestions can be given. Wood anatomical similarities in derived character associations suggest close phylogenetic affinity, but can still be the result of parallel development which must have been rampant in xylem evolution (Wheeler & Baas, 1991). The cladograms presented in Figures 18, 19 and 20A may therefore still contain many artefacts resulting from the parsimony principle which is inherent in the cladistic analysis used. For instance, if the Spiraeoideae and Rosoideae cannot be separated wood anatomically, this does not imply that inflorescence, floral and fruit characters cannot provide sufficient evidence to overrule the hypothetical phylogenetic relationships presented in the cladogram of Figure 18.

Subdivision into subfamilies and their relationships

Traditionally four subfamilies (Spiraeoideae, Rosoideae, Maloideae and Prunoideae) are distinguished in the Rosaceae (Takhtajan, 1980; Cronquist, 1981). The present phylogenetic analysis of wood anatomical characters does not support this classification. The traditional Prunoideae constitute a monophyletic group and can thus be supported as a single subfamily. This also holds true for the Prunoideae in combination with the Quillajeae. The cladogram of Figure 20A offers two options:

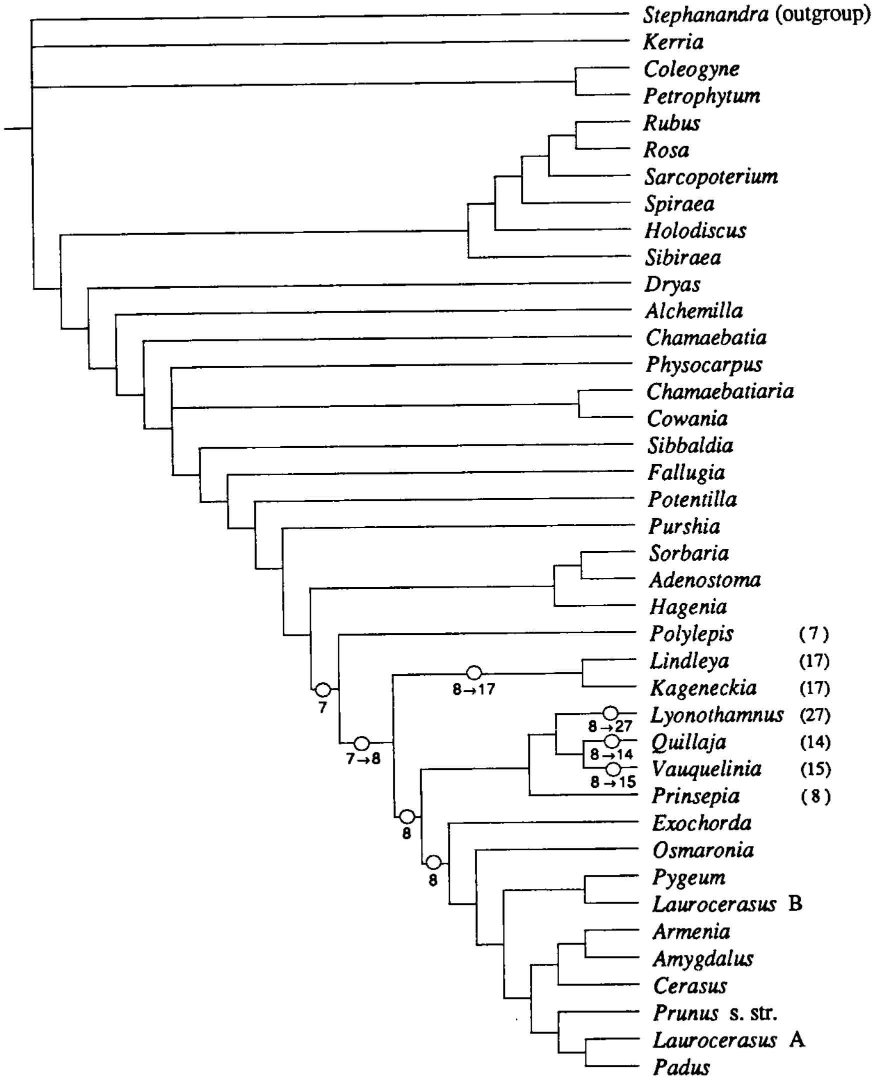


Fig. 21. Selected cladogram of the Rosaceae, excluding the Maloideae. Chromosome changes (number) indicated for the Quillajeae.

two separate suprageneric taxa (subfamilies or tribes), the Quillajeae and the Prunoideae, or a single one including both groups. The Maloideae, despite being wood anatomically a very homogeneous group, appear to be paraphyletic. The Spiraeoideae p.p. are mixed with Rosoideae (except *Cercocarpus*); together they also form a paraphyletic group. Assigning formal taxonomic ranks to paraphyletic groups is a matter of practical utility only. The wood anatomical evidence would in this case to a large extent support subfamily level for the traditional Maloideae, but would favour the combination of the Spiraeoideae p.p. and Rosoideae in one subfamily. This follows from both the phenetic and cladistic analysis of the wood anatomical diversity.

The recognition of tribes as delimited by Hutchinson (1964) finds but little support in the cladograms of Figures 18, 19 and 20A. Most tribes would be para- or polyphyletic according to the position of their genera in these cladograms.

A phylogenetic analysis of the Rosaceae presented by Kalkman (1988), based on 14 macromorphological characters, is quite different from the present one. The tribe Quillajeae, split into three operational units in Kalkman's study, is one of the most primitive taxa in his cladogram, whereas Adenostomeae, Cercocarpeae and Kerrieae, together with Maleae and Pruneae, are among the most derived taxa. In addition, the subdivision into subfamilies cannot be supported by his cladistic analysis at all.

The basal position of the Spiraeoideae p.p. and Rosoideae in the cladogram and the most derived position for the Prunoideae is a direct consequence of the *a priori* polarisation of the wood anatomical characters used. In a similar analysis of the Oleaceae (Baas et al., 1988), the polarisation was strongly supported by independent evidence on flavonoid chemistry and karyology. However, in the Rosaceae only limited support is provided by fruit type and chromosome number. As imposed by the cladogram, the derivation of the Prunoideae from the Maloideae requires an abrupt decrease from the high chromosome numbers to a much lower number ($x = 8$), which biologically seems most unlikely. As shown above, the Maloideae heavily influence the total and partial cladograms. Therefore, a cladistic analysis without the Maloideae was performed as well. Such an exercise is valid if the Maloideae as a whole are considered a terminal allopolyploid lineage. Extant *Stephanandra* was selected as outgroup. Over 100 equally parsimonious cladograms were produced. Three times character weighting did not reduce the number of cladograms, but improved the consistency index from 0.34 to 0.55. One of these cladograms is chosen and pictured in Figure 21.

This cladogram still bears much resemblance with the combined partial cladograms of the lower and upper groups (Figs. 18 and 20), but has the biological 'advantage' that it does not require the derivation of the diploid Prunoideae from polyploid Maloideae, or that the dry dehiscent fruits of the Quillajeae would have to be derived from maloid pomes. The high chromosome numbers in the Quillajeae arise independently a number of times in this cladogram.

It cannot be stressed sufficiently that the precise position of most individual genera in the cladograms of Figures 17–21, especially those of the lower and middle groups, have little phylogenetic meaning. These positions are a consequence of very minor wood anatomical differences, sometimes in features of limited diagnostic value. In a broader sample, the coding in Table 4 would probably undergo several changes, resulting in considerable shifts in position. Moreover it should be stressed that only the cladogram of the upper group (Fig. 20) should be considered as a serious phylogenetic hypothesis.

The position of some genera

Exochorda

Traditionally this genus has been placed in the Spiraeoideae (Challice, 1981; Kalkman, 1988). However, as early as 1918 Juel moved the genus to the Prunoideae and

Stebbins (1958) had this genus in mind as a possible living relic of the most primitive prunoid ancestor. Hutchinson (1964) placed it in his most primitive tribe Quillajeae. Recently Goldblatt (1976) suggested to move *Exochorda* to the Prunoideae again. As shown in Table 2 and Figure 20C, both phenetic and phylogenetic classifications support the treatment of this genus as a member of the Prunoideae, not of the Quillajeae. Like in many Prunoideae, rays in the genus are of two sizes and composed of procumbent body cells and 1–4 rows of square to upright marginal cells, fibre pits are mainly confined to radial walls, and helical thickenings are present in vessel elements.

Kageneckia, Lindleya, Lyonothamnus, Quillaja and *Vauquelinia*

The genera *Kageneckia, Lindleya, Quillaja, Lyonothamnus* and *Vauquelinia*, together with *Exochorda*, were placed in one tribe Quillajeae by Hutchinson (1964), who regarded the tribe as the most primitive in the family. Traditionally these genera are placed in the subfamily Spiraeoideae. However, Goldblatt (1976) and Li (1989) contended that it is not a natural alliance. Goldblatt (1976) and Thorne (1983) moved *Vauquelinia* to the Maloideae and advocated a separate subfamily for *Quillaja* and *Kageneckia*, and Challice (1981) also wanted these genera removed from the Spiraeoideae. Both Challice (1981) and Goldblatt (1976) proposed transferring *Lindleya* from Spiraeoideae to the Maloideae. But Robertson et al. (1991) argued that both *Lindleya* and *Vauquelinia* should be excluded from Maloideae. *Lyonothamnus* was placed in Sorbarieae by Schulze-Menz (1964) and Wallaart (1980).

Clearly, the inclusion of these genera either in the Spiraeoideae or in the Maloideae is not supported by the cladistic analysis. Figure 20A indicates that these five genera are in a monophyletic group in spite of the fact that they are not a very homogeneous group wood anatomically. Moreover, this monophyletic group is much more derived than the Spiraeoideae and should be in the position close to the Maloideae and Prunoideae. *Exochorda* does not belong in this monophyletic group. Together with the Prunoideae and *Exochorda*, the Quillajeae also constitute a monophyletic group. Therefore they should either be included in the Prunoideae or be recognised as a separate group (or subfamily) between the Maloideae and Prunoideae. The latter, however, is not in accordance with evidence from outside wood anatomy (Kalkman, personal communication).

Cercocarpus

Traditionally, *Cercocarpus* with *Coleogyne* and *Potaninia* are grouped together in the tribe Cercocarpeae, which has always been placed in the Rosoideae. The present analysis indicates that *Cercocarpus* is characterised by typical Maloideae attributes: rays 1–3-seriate, lower than 0.3 mm, homogeneous or heterogeneous III, prismatic crystals in chambered axial parenchyma cells, axial parenchyma moderately abundant, helical thickenings present in both vessel elements and fibre-tracheids. Wood anatomically *Cercoparpus* differs strongly from *Coleogyne*; the latter fits well into the Rosoideae according to its wood anatomy. A distinct relationship between *Cercocarpus* and *Coleogyne* has been doubted before by Schulze-Menz (1964) and Wallaart (1980), but a place in the Maloideae for *Cercocarpus* has not been suggested yet.

Sorbaria

This genus has always been placed in the Spiraeoideae (Kalkman, 1988). The present and earlier studies (Zhang & Baas, 1992), however, indicate that its wood anatomical characters are more derived than in the other Spiraeoideae, and that it emerges as part of a monophyletic group with three genera (e.g., *Adenostoma, Hagenia* and *Polylepis*) which are usually placed in Rosoideae.

Prinsepia

Lindley (1836) and Royle (1839) assigned *Prinsepia* to the Chrysobalanoideae. However, Bentham & Hooker (1867) placed *Prinsepia* in the Prunoideae without further explanation and the genus has been left in the subfamily since then. Hutchinson (1964) included the genus in the tribe Pruneae, together with *Prunus, Padus, Laurocerasus* and *Pygeum*, etc. However, Sterling (1963) suggested that *Prinsepia* is neither a member of the Prunoideae, nor of the Chrysobalanoideae, and proposed a new subfamily to accommodate the genus. Wood anatomically it differs to some extent from the *Prunus* alliance, but still forms part of a monophyletic group together with the latter.

Prunus s.l.

The classification of *Prunus* in the sense of Bentham & Hooker (1865) has been disputed repeatedly for over a century (Yu, 1986). McVaugh (1951), Kalkman (1965), and Yu (1986) reviewed the history of *Prunus* classification. The genus has in the past been split into several smaller genera, varying in number from 2 up to 10. Since 1865, a large genus *Prunus*, defined by Bentham & Hooker, has been widely accepted. However, more recently Komarov (1941) split it into 7 smaller genera, Hutchinson (1964) recognised 3 genera and Yu (1986) divided this large genus into 6 genera. On the other hand, Kalkman (1965) extended the genus *Prunus* further to include *Pygeum*, based on the fact that the delimitation of *Pygeum* against *Prunus* subg. *Laurocerasus* appeared to be extremely difficult. The present study indicates that *Laurocerasus* is quite diverse. Some species (Group A) are closer to *Prunus* in the sense of Bentham & Hooker, but others (Group B) are closer to *Pygeum*. Although *Prunus* s.l. (in the sense of Kalkman) is a monophyletic alliance as shown in Figure 20A, wood anatomy is not in conflict with a narrower generic delimitation, especially when the large diversity recognised in *Prunus* s.l. is compared with the wood anatomical homogeneity in the subfamily Maloideae. In addition, phylogenetic analysis indicates that *Armeniaca* and *Amygdalus* are the most derived, followed by *Cerasus, Padus, Laurocerasus* A and *Prunus* s. str., and that *Pygeum* and *Laurocerasus* B is the least advanced in *Prunus* alliance.

The origin of and generic concept in the Maloideae

The evolutionary origins of the Maloideae have often been discussed (Nebel, 1929; Darlington & Moffett, 1930; Sax, 1931, 1932, 1933; Stebbins, 1950, 1958; Bate-Smith, 1961; Sterling, 1969; Gladkova, 1972; Challice, 1973, 1974, 1981; Durrieu, 1987; Yu, 1984; Dickinson & Campbell, 1991; Phipps et al., 1991) and a number of conflicting hypotheses have been advanced.

There are two main theories about the origin of the Maloideae. The first, with variants, is that the Maloideae are of allopolyploid origin; the second theory does not require a hybridisation event (Phipps et al., 1991). Sax (1932) first suggested that the Maloideae may have originated from one or perhaps two subfamilies (x = 7, 8 and 9) by hybridisation between different primitive forms. Stebbins (1950, 1958) specified that a Spiraeoid ancestor (x = 9) and a Prunoid ancestor (x = 8) were involved in the allopolyploid origin of the Maloideae. The hypothesis of the hybrid origin has gained wide acceptance since then (Challice, 1974, 1981; Phipps et al., 1991). Gladkova (1972) and Durrieu (1987), however, did not support it, and several taxonomists consider that the Maloideae could have arisen directly from primitive Spiraeoideae without the involvement of primitive Prunoideae (Challice, 1981). It is fully realised that the present wood anatomical study can offer little to the arguments on the possible origin of the Maloideae. If the Maloideae have evolved by hybridisation, however, wood anatomy appears to suggest that the involvement of a prunoid ancestor is not necessary. One of the reasons is that only few prunoid wood anatomical characters can be found in the Maloideae. Instead, the Maloideae have most characters (except fibre pit density in radial walls and crystals) shared by at least some genera of the Spiraeoideae p.p. and Rosoideae alliance (cf. Table 2). Moreover, both putatively ancestral chromosome numbers (x = 8 and 9) are available in Spiraeoideae and Rosoideae.

Generic delimitation in the Maloideae is rather subjective and fluid (Kovanda, 1965; Robertson et al., 1991). Recently, Robertson et al. (1991) reviewed the history of this problem: the number of genera recognised by different authors ranges from 4 to 28. Sax (1931) stated that "according to the genetic system of classification perhaps all of the Maloideae could be classed as one single genus." Kovanda (1965), Kalkman (1973), and Robertson et al. (1991) all ascribed most controversies to the generic delimitation of *Pyrus*, *Crataegus* and particularly of *Sorbus*. Although Burgerstein (1895) stated that wood anatomy confirms the system of small genera in the subfamily suggested by Roemer (1847), Decaisne (1874) and Koehne (1890), the present study cannot support this statement at all. Wood anatomically the Maloideae constitute a very homogeneous alliance. As shown in Table 2, only two phenetic groups in Maloideae differing in one character only can be recognised. The phylogenetic analysis shows many polytomies. Wood anatomy, therefore, can support a broad generic delimitation in this subfamily.

The relative position of all Maloideae taxa in the chosen cladogram (Fig. 19) are phylogenetically quite meaningless. They result from very minor wood anatomical differences (Table 2) which even might have been different if some other samples or species had been included in the research material. The distance between *Photinia* A and B is associated with the evergreen versus deciduous habit of these species groups. Lu et al. (1991) also found leaf anatomical differences between these two groups.

Dichotomanthes has been considered by different authors as belonging to the subfamilies Maloideae, Prunoideae or Spiraeoideae (Challice, 1981). Gladkova (1969) even suggested a separate subfamily to accommodate the genus. Challice (1974), Yu (1974), and Robertson et al. (1991) put the genus in the Maloideae. As shown in Table 2 and Figure 19, both phenetic and phylogenetic classification indicates that from the wood anatomical point of view *Dichotomanthes* fits well into the Maloideae.

Parallel development and reversals of wood anatomical characters

As indicated before, the cladograms of Figures 18, 19, 20A and 21 represent only possible hypotheses for phylogenetic reconstruction. A cladistic analysis based on a more comprehensive set of anatomical, cytological, morphological, phytochemical and molecular attributes would generate quite different cladograms. However, the present partial cladograms based on wood anatomical characters give an idea of the *minimum* amount of homoplasy (parallel development and reversals) in the wood anatomical make-up of the family. According to the cladogram of Figure 18, the following changes may have occurred in the Rosoideae and Spiraeoideae p.p.:

1) Ring-porosity (or semi-ring-porosity) has three parallel origins but not less than four reversals: twice from ring-porous to semi-ring-porous, once from ring-porous to diffuse-porous, and once from semi-ring-porous to diffuse-porous.
2) A high degree of vessel grouping has three parallel origins and two parallel reversals.
3) Round to oval intervessel pits originate three times and have two parallel reversals to polygonal pits.
4 Vessel-ray pits and marginal parenchyma remain constant.
5) Vessel wall thickenings have three parallel origins.
6) A low L/D ratio has four parallel origins and one reversal.
7) A high F/V ratio has two parallel origins.
8) Dense spacing of pits in the radial fibre walls originates 4–5 times, and shows one reversal.
9) Libriform fibres originate only once.
10) Relatively abundant parenchyma has two parallel origins.
11) Ray width changes from rays more than 4-seriate to 1–3(–4)-seriate once, but later reverses again.
12) Ray height has four reductions, of which three are parallel, but it also has three parallel increases.
13) Ray composition changes twice according to the Baileyan trends with an increase in the proportion of procumbent cells.
14) Crystals in rays change four times in the Spiraeoideae p.p. & Rosoideae, but three belong to parallel reversals. Druses arise once in this group.

For the cladogram of the Quillajeae and Prunoideae (Fig. 20A), the following changes can be noted:

1) There are four parallel developments from diffuse-porous to semi-ring-porous, and one reversal. In addition, porosity also changes twice, from semi-ring-porous to ring-porous, and the another time from diffuse-porous to ring-porous.
2) A high degree of vessel grouping has only one origin at the base of the *Prunus* alliance.
3) Polygonal intervessel pits have three parallel origins.
4) 'Vessel–ray pits clearly smaller than intervessel pits' has two parallel origins.
5) Helical vessel wall thickenings show two parallel losses, one in *Laurocerasus* B and another in *Pygeum*.
6) L/D ratio has three parallel reductions, and one reversal.

7) F/V ratio has one increase and one reversal.
8) Fibre pits mainly confined to radial walls have only one origin.
9) The feature fibre pits densely placed in radial walls only arises once in *Lindleya*.
10) Presence of libriform fibres has two parallel origins.
11) Marginal parenchyma has two parallel origins.
12) Scanty axial parenchyma has two parallel origins.
13) Reduction of ray width to 1–3(–4)-seriate has three parallel origins.
14) Crystals in ray cells arise in parallel development two times, and are also lost three times.
15) Crystals in chambered axial parenchyma cells have three parallel origins, and are lost twice.
16) Druses originate once at the base of *Prunus* s.l., but are lost in *Laurocerasus* A, and in all segregates for which their occurrence is not constant (cf. Tables 2 and 4).

Even if one does not accept some of the details of the above analysis, it is clear that wood anatomical evolution must have involved numerous parallel developments and reversals in the Rosaceae. The total number of homoplasies (e.g. parallel development and/or reversals) for the combined cladogram was not counted due to the meaningless partial cladogram for the Maloideae shown in Figure 19. However, obviously some characters like fibre pitting, libriform fibres, marginal parenchyma, vessel grouping and ray composition show a low incidence of homoplasy, while others like L/D ratio, F/V ratio, and ring-porosity show a high degree of parallelism and reversals. The latter largely coincide with the features of limited diagnostic value at the genus level discussed under phenetic classification. In addition, the very limited number of reversals in relatively important characters such as vessel-ray pitting, fibre pitting, and parenchyma distribution add support to the general Baileyan trends.

THE WIDER AFFINITIES OF THE ROSACEAE

The family Rosaceae in a wider sense included two additional subfamilies: the Neuradoideae and the Chrysobalanoideae. Nowadays these two subfamilies are often recognised as two separate families: the Neuradaceae and the Chrysobalanaceae (Airy Shaw, 1973; Cronquist, 1981; Schulze-Menz, 1964; Stoffers, 1982; Takhtajan, 1980; Kalkman, 1988). However, Thorne (1983) included the Neuradeae in the Rosaceae and Hutchinson (1964) put both groups in the family.

When the data available on the wood anatomy of the Chrysobalanaceae (Moll & Janssonius, 1914; Metcalfe & Chalk, 1950; Desch, 1954; Ter Welle, 1975, 1976; Ter Welle & Détienne, 1986; Prance & White, 1988) are compared with our present results on the Rosaceae, several important wood anatomical differences emerged. In the Chrysobalanaceae, silica grains are always present in ray cells, rays are 1(–2)-seriate only, vessel frequency is very low (always less than 20/sq.mm), vessels are very wide (tangential diameter 200–300 µm), and typically in two size classes, helical vessel wall thickenings are absent, vessel-ray pits are large and in various shapes, tyloses are frequently present, axial parenchyma is usually arranged in numerous fine continuous bands, and helical thickenings are present in axial parenchyma cells of many species. Most of these characters are absent or atypical in the Rosaceae. Thus the wood anatomical differences between the Rosaceae and the Chrysobalanaceae are large enough to support the separation of Chrysobalanaceae as an independent family. Some authors (Record & Mell, 1924) combined the Chrysobalanoideae and the Prunoideae to form the family Amygdalaceae. Although the former is closer to Prunoideae (only to *Pygeum*) than to other subfamilies, the differences in certain important characters (e.g., silica grains, ray size, tyloses, vessel-ray pits, helical thickenings in axial parenchyma) between *Pygeum* and the Chrysobalanaceae are still appreciable. Therefore wood anatomy does not support this unification.

There seems to be no published information available on the wood anatomy of the Neuradaceae, a family of less than 10 species confined to African and Asian deserts, for a comparison with the Rosaceae.

The Rosaceae have been placed in slightly different positions in recently proposed systems of flowering plants (Takhtajan, 1980; Cronquist, 1981; Dahlgren et al., 1981; Rouleau, 1981; Thorne, 1981; Young, 1982). In three systems (Takhtajan, Rouleau and Young), the Rosaceae together with the Chrysobalanaceae and the Neuradaceae are placed in the order Rosales near Saxifragales. More or less the same was done by Cronquist and Thorne. Their only difference from the above three systems is that the order Rosales also includes many other families like Saxifragaceae, Cunoniaceae, Crossosomataceae, Crassulaceae, Cephalotaceae, etc. apart from the Rosaceae. Dahlgren et al. (1981) inserted an order Gunnerales (Gunneraceae only) between Saxifragales and Rosales.

Hutchinson (1964) believed that the Rosaceae were derived from the same stock as the Dilleniaceae (a woody family almost confined to the tropics) and argued that the most primitive tribe may be found also in the tropics. Therefore he regarded the Quillajeae, a tribe mainly distributed in the neotropics, as the most primitive, linking the Dilleniaceae with the Rosaceae. Recently, Kalkman (1988) hypothesised that the family originated in West Gondwana. The present phylogenetic analysis, however, revealed that all members of Quillajeae are quite derived wood anatomically, while the most primitive genera (e.g. *Kerria* and *Stephanadra*) are from East Asia. Therefore, from a wood anatomical point of view it is more likely that the Rosaceae originated in Laurasia instead of in Gondwana.

Although for the cladistic analysis 'Proto-Rosaceae' (or outgroup, see Table 4) were hypothesised, the 'Proto-Rosaceae' have a very generalised wood structure which probably was ancestral to many other partly unrelated dicotyledonous families. The hypothesised ancestral wood anatomy of the Rosaceae is identical to that found in extant *Kerria* and *Stephanandra* and is characterised by diffuse-porous wood, solitary vessels, simple perforations with sporadic scalariform ones, fibre-tracheids with distinctly bordered pits, axial parenchyma scanty, and heterogeneous rays of two sizes. These character states were entered as an unknown taxon in a computer-aided wood identification programme (Wheeler et al., 1986) to search for a family which is closest to the extant primitive Rosaceae. Representatives of thirteen families, each with one mismatching character, came out: Bonnetiaceae (*Marila*), Celastraceae (*Goupia*), Dilleniaceae (*Curatella, Dillenia, Doliocarpus*), Epacridaceae (*Leu-*

Table 5. Selected wood anatomical characters[1] of Cunoniaceae, Dilleniaceae, and *Kerria & Stephanandra.*

	Cunoniaceae	Dilleniaceae	*Kerria & Stephanandra*
Habit	trees & shrubs	trees, shrubs, climbers & herbs	shrubs
Distribution	mainly Australasia	tropical & subtropical regions	temperate to subtropical East Asia
Vessels	solitary, moderately small (50–100 µm), 8–130/sq.mm	solitary, medium-sized (100–200 µm) or large, usually 1–8/sq.mm	solitary, moderately small, 100–150/sq.mm
Perforations	scalariform only; simple with a few scalariform, rarely simple only	typically scalariform, or mostly simple with some scalariform	simple with sporadic scalariform
Intervessel pits	scalariform to opposite rarely alternate	opposite to scalariform	intervessel alternate occasionally scalariform to opposite
Vessel–ray pits	typically large and horizontally elongated simple or with reduced borders	half-bordered	half-bordered
Fibres	with distinctly bordered pits	with distinctly bordered pits	with distinctly bordered pits
Rays	of two sizes in some genera, up to 2–4(–5) cells wide, markedly heterogeneous	usually of two distinct sizes, the larger up to 8–10 cells wide or more, heterogeneous	of two distinct sizes, 3–7 cells wide, heterogeneous
Crystals	prismatic crystals present in some genera	absent or present as raphides	prismatic crystals present

[1] The wood anatomical data for Cunoniaceae and Dilleniaceae were mainly taken from Metcalfe & Chalk (1950).

copogon), Ericaceae (*Vaccinium*), Euphorbiaceae (*Hieronyma, Longetia*), Fagaceae (*Fagus*), Humiriaceae (*Humiria*), Icacinaceae (*Dendrobangia, Emmotum, Gonocaryum, Poraqueiba*), Myricaceae (*Myrica*), Ochnaceae (*Ochna*), Quiinaceae (*Touroulia*), and Theaceae (*Ternstroemia*). However, only Dilleniaceae is among the families placed close to the Rosaceae in the six systems mentioned above. The other 12 families are very remote from the Rosaceae on the basis of appreciable macromorphological differences and each of them differs in an important wood anatomical character (either perforation type or ray characters) from the extant primitive Rosaceae (*Kerria* and *Stephanandra*). In another approach, all families placed close to the Rosaceae in the six systems were checked with the plesiomorphic characters listed above. Many families have then to be discarded as possible candidates for different reasons (vessel perforation types, ray characters, etc.). It appears that only Cunoniaceae, in addition to Dilleniaceae, is wood anatomically relatively close to *Kerria* and *Stephanandra*. Kalkman (1988) also considered this family to be the most plausible choice as the sistergroup of the Rosaceae. The main wood anatomical characters for Cunoniaceae and Dilleniaceae are listed in Table 5. Compared with *Kerria* and *Stephanandra*, these two families are still different in certain characters. Dilleniaceae differ in perforation types, crystals, and vessel size; Cunoniaceae in vessel-ray pits and ray width. Therefore, from a wood anatomical point of view the Rosaceae constitute an isolated family within its (super)order.

GENERIC WOOD ANATOMICAL DESCRIPTIONS

1. **Adenostoma** Hook. & Arn.

Material studied: *A. fasciculatum* Hook. & Arn.: USA, California, TW 45889, diam. 18 mm, alt. 800 m. — *A. sparsifolium* Torr.: USA, California, Tw 22802.

Evergreen shrubs native in California.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood diffuse-porous to semi-ring-porous. Vessels 64–208/sq.mm, 72–94% solitary, remainder in oblique and radial multiples of 2–3, oval or weakly angular, tangential diameter 23–43 (19–70) µm, radial diameter 37–62 (22–95) µm, walls 1–3 µm thick. Vessel element length 230–270 (150–350) µm. L/D ratio 6–10. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, oval to polygonal, 4–8 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent in *A. fasciculatum*, but closely spaced, irregular thickenings noted in some vessel elements of *A. sparsifolium*. Gummy contents absent. *Fibre-tracheids* 550–580 (450–650) µm long, F/V ratio 2.2–2.4, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial (sometimes densely spaced) and tangential walls. Helical thickenings absent. *Parenchyma* moderately abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–5-celled strands. *Rays* 8–16 (7–17)/mm, of two sizes: 1(–2)-seriate and 3–5(–6)-seriate. Uniseriate rays 2–6 (1–11) cells high, composed of square and upright cells; multiseriate rays 420–540 (150–1150) µm high, composed of procumbent cells only, or occasionally with one row of square marginal cells in *A. sparsifolium* (mainly homogeneous and rarely heterogeneous III), but in the juvenile sample of *A. fasciculatum* multiseriate rays composed of procumbent (occasionally to square) body cells and 1–5 rows of square to upright marginal cells. *Crystals* very sparse, prismatic, medium-sized, in non-enlarged ray cells, one crystal per cell. *Pith flecks* occasionally present, diffuse. Traumatic gum ducts absent.

2. **Alchemilla** L.

Material studied: *A. alpina* L.: Switzerland, Schweingruber s.n., diam. 2 mm.

Perennial herbs in America, Africa, Europe and Asia.

Growth rings distinct to faint, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 700/sq.mm, 70% solitary, remainder in oblique and tangential pairs, round to oval, tangential diameter 16 (10–29) µm, radial diameter 20 (12–35) µm, walls 1–2 µm thick. Vessel element length 150 (90–250) µm. L/D ratio 9. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round and oval, 4–6 µm in diameter, with slit-like apertures. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* very scanty, apotracheally diffuse, in 1–3-celled strands. *Rays* very sparse, uniseriate only, 1–2 cells high, composed of upright and square cells. Crystals, pith flecks and traumatic gum ducts absent.

Note – Rays in this genus are exceptional. Only uniseriate rays, 1–2 cells high, were noted.

3. **Amelanchier** Medic.

Material studied: *A. alnifolia* Nutt.: locality unknown, FHOw 11224. — *A. ovalis* Medic.: Switzerland, Schweingruber s.n. — *A. sinica* (Schneid.) Chun: see Zhang & Baas (1992).

Deciduous shrubs or trees in north temperate regions, often cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 192–320/sq.mm, 70–82% solitary, remainder mainly in oblique multiples of 2–3, round, oval to angular, tangential diameter 25–42 (13–50) µm, radial diameter 30–55 (18–68) µm, walls 1–2 µm thick. Vessel element length 410–630 (250–780) µm. L/D ratio 16–23. Perforations almost exclusively simple in oblique end walls, but sporadic irregular multiple perforations also noted in all species. Intervessel pits nonvestured, alternate, round to oval, 3–5 µm in diameter, with slit-like, occasionally coalescent apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings fine and irregularly spaced, throughout body of vessel elements, sometimes associated with pit apertures. Gummy contents absent. *Fibre-tracheids* 860 (600–1220) µm long, F/V ratio 1.4, medium thick- to very thick-walled, with distinctly bordered pits of 4–6 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* moderately abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 3–5 (2–10)-celled strands. *Rays* 8–13 (7–15)/mm, 1–2-seriate. Uniseriate rays 3–6 (1–11) cells high, composed of procumbent cells, occasionally with one row of square marginal cells; biseriate rays 180–220 (50–540) µm high, composed of procumbent cells only, or with one row of square marginal cells (homogeneous and heterogeneous III). *Crystals* absent in *A. alnifolia* and *A. sinica*, or sparse in *A. ovalis*, prismatic, medium-sized to large, present in chambered and enlarged axial parenchyma cells, one crystal in each enlarged chamber; chains of 3–5 chambers. Pith flecks and traumatic gum ducts absent.

4. **Amygdalus** L. – See *Prunus* s.l.

5. **Armeniaca** Mill. – See *Prunus* s.l.

6. **Cerasus** Mill. – See *Prunus* s.l.

7. **Cercocarpus** Kunth (Fig. 7)

Material studied: *C. betuloides* Nutt.: USA, CAFw 2907, diam. 13 mm; locality unknown, FHOw 11328; USA, California, Tw 45872, diam. 20 mm, alt. 790 m. — *C. ledifolius* Nutt.: locality unknown, FHOw 11082.

Evergreen or semi-deciduous small trees or shrubs in southwestern North America, some cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 65–115/sq.mm, 90–91% solitary, remainder mainly in oblique pairs, round to oval or weakly angular, tangential diameter 34–40 (14–90) µm, radial diameter 42–53 (19–120) µm, walls 1–3 µm thick. Vessel element length 260–670 (200–870) µm. L/D ratio 8–20. Perforations almost exclusively simple in oblique to almost horizontal end walls, but sporadic irregular multiple perforations also noted in *C. betuloides* (CAFw 2907) and *C. ledifolius*. Intervessel pits nonvestured, alternate, round to oval, 4–8 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings fine, closely spaced, present in most vessel elements. Gummy contents present in a few vessels of *C. ledifolius*. *Fibre-tracheids* 630–1110 (433–1361) µm long, F/V ratio 1.7–1.9, medium thick- to very thick-walled, with distinctly bordered pits of 5–6 µm in diameter, in radial and tangential walls. Helical thickenings present in most fibre-tracheids. *Parenchyma* moderately abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 3–4 (2–6)-celled strands. *Rays* 10–13 (6–15)/mm, 1-3-seriate. Uniseriate rays 3–5 (1–12) cells high, composed of procumbent and square cells; multiseriate rays 150–280 (60–630) µm high, composed of procumbent cells only, or with one row of square marginal cells (mainly homogeneous, rarely heterogeneous III). *Crystals* sparse in *C. betuloides* (FHOw 11328), prismatic, medium-sized to large, present in chambered axial parenchyma cells, usually one crystal in each weakly enlarged and sclerified chamber; chains of up to 4 chambers. Crystals not observed in *C. betuloides* (CAFw 2907, Tw 45872) and *C. ledifolius*. *Pith flecks* occasionally present in *C. ledifolius*. Traumatic ducts absent.

8. **Chaenomeles** Lindl.

Deciduous or semi-evergreen shrubs or small trees in East Asia, widely cultivated as ornamentals. See Zhang & Baas (1992).

9. **Chamaebatia** Benth.

Material studied: *C. australis* (Bdg.) Abrams: USA, California, Rancho Santa Ana Botanic Garden, s.n., diam. 9 mm.

Evergreen shrubs native in California, also cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 328/sq.mm, 82% solitary, remainder in oblique pairs, round to oval or weakly angular, tangential diameter 23 (10–30) µm, radial diameter 30 (12–42) µm, walls 1–3 µm thick. Vessel element length 270 (160–320) µm. L/D ratio 12. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round to oval, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 410 (300–450) µm long, F/V 1.5, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 15 (14–17)/mm, 1–2(–3)-seriate. Uniseriate rays 4 (1–11) cells high, composed of square and upright cells; multiseriate rays 210 (140–400) µm high, composed of square and upright cells. Crystals, pith flecks and traumatic gum ducts absent.

10. **Chamaebatiaria** (Porter) Maxim.

Material studied: *C. millefolium* (Torr.) Maxim.: USA, southern California, RSAw 8134, diam 10 mm.

Deciduous shrubs in northwestern America, cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 525/sq.mm, 71% solitary, remainder in oblique and tangential pairs, round to oval, tangential diameter 26 (12–38) µm, radial diameter 35 (14–50) µm, walls 1–3 µm thick. Vessel element length 210 (60–290) µm. L/D ratio 8. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round to oval, 3–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 410 (150–470) µm long, F/V 2.0, medium thick- to very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 12 (10–15)/mm, 1–2-seriate. Uniseriate rays 4 (1–11) cells high, composed of procumbent and square cells; multiseriate rays 320 (120–480) µm high, composed of procumbent body cells and one row of square marginal cells (heterogeneous III). Crystals, pith flecks and traumatic gum ducts absent.

11. **Coleogyne** Torr.

Material studied: *C. ramosissimum* Torr.: USA, southern California, RSAw 10758, diam. 8 mm.

Deciduous shrubs in southern USA.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 288/sq.mm, 80% solitary, remainder in oblique, radial and tangential multiples of 2–3, angular, tangential diameter 25 (12–35) µm, radial diameter 37 (15–50) µm, walls 1–3 µm thick. Vessel element length 130 (70–240) µm. L/D ratio 5. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round to oval, 3–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 310 (220–450) µm long, F/V 2.4, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* very scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 8 (6–9)/mm, of two sizes: 1(–2)-seriate, and 3-6-(–11)-seriate. Uniseriate rays 3–4 (2–6) cells high, composed of square and upright cells; multiseriate rays 1040 (150–1500) µm high, composed of weakly procumbent to square cells. *Crystals* abundant, prismatic, medium-sized, in non-enlarged ray cells, one crystal per cell. Pith flecks and traumatic gum ducts absent.

12. **Cotoneaster** B. Ehrhart

Material studied: *C. granatensis* Boiss.: Spain, Sierra Nevada, Schweingruber s.n., diam. 15 mm. — *C. integerrimus* Medic.: locality unknown, Schweingruber s.n. — *C. microphyllus* Wall. ex Lindl.: one specimen, see Zhang & Baas (1992); locality unknown, FHOw 12692. — *C. multiflorus* Bunge: see Zhang & Baas (1992). — *C. nebrodensis* (Guss.) C. Koch: locality unknown, Schweingruber s.n. — *C. nummularia* Fisch. et Mey: Israel, Hebrew University s.n., diam. 10 mm; Cyprus, Schweingruber s.n., diam. 12 mm.

Deciduous, evergreen or semi-evergreen shrubs to small trees in north temperate regions and Mexico.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Wood diffuse-porous in *C. integerrimus*, *C. microphyllus* and *C. nebrodensis* to semi-ring-porous in *C. granatensis*, *C. multiflorus* and *C. nummularia*. Vessels 220–350 (–680)/sq.mm, 60–86% solitary, remainder mainly in oblique and tangential multiples of 2–3, oval, round or angular, tangential diameter 20–30 (13–45) µm, radial diameter 28–33 (15–53) µm, walls 1–2 µm thick. Vessel element length 280–470 (150–650) µm. L/D ratio 12–24. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round, 3–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but slightly smaller and half-bordered or with slightly reduced borders. Helical thickenings usually well developed and closely spaced, throughout body of vessel elements, but helical thickenings not observed in *C. integerrimus* and *C. nebrodensis*. Gummy contents present in a few vessels of *C. microphyllus*. *Fibre-tracheids* 580–820 (410–1000) µm long, F/V ratio 1.5–1.9, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial and tangential walls. Helical thickenings present in most samples except in *C. integerrimus* and *C. nebrodensis*. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 3–5 (1–24)-celled strands. *Rays* 11–15 (8–17)/mm, 1–2(–4)-seriate. Uniseriate rays 2–7 (1–24) cells high, composed of square (to weakly procumbent) cells and upright cells; 2–3-seriate rays 150–240 (50–480) µm high, composed of procumbent body cells and 1–3 rows of square (to upright) marginal cells (mainly heterogeneous III, rarely heterogeneous II). *Crystals* absent in *C. granatensis*, *C. integerrimus*, *C. microphyllus*, *C. nebrodensis* and *C. nummularia* (Schweingruber s.n.), or sparse in *C. multiflora* and *C. nummularia* (Hebrew University s.n.), prismatic, medium-sized to large, in chambered axial parenchyma cells, one crystal in each enlarged and sclerified chamber; chains of up to 11 chambers. *Pith flecks* absent in *C. integerrimus*, *C. multiflorus*, *C. nebrodensis* and *C. nummularia* (Hebrew University s.n.), or common in *C. microphyllus* and *C. nummularia* (Schweingruber s.n.). Traumatic gum ducts absent.

13. Cowania D. Don ex Tilloch & Taylor

Material studied: *D. stansburiana* Torr.: USA, southern California, RSAw 15829, diam. 25 mm.

Evergreen shrubs in southwestern North America.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood ring-porous. Latewood vessels 328/sq.mm, 82% solitary, remainder in oblique and tangential pairs, round to oval, tangential diameter of latewood vessels 35 (15–45) µm, radial diameter 42 (20–62) µm, tangential diameter of earlywood vessels 60 (30–80) µm, radial diameter 75 (35–105) µm, walls 1–3 µm thick. Vessel element length 210 (130–320) µm. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, oval to polygonal, 5–8 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 400 (300–470) µm long, F/V 1.9, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, densely placed in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 8 (7–11)/mm, 1–3-seriate. Uniseriate rays 2–3 (1–6) cells high, composed of square and upright cells; multiseriate rays 170 (100–220) µm high, composed of procumbent body cells and one row of square marginal cells (heterogeneous III). Crystals, pith flecks and traumatic gum ducts absent.

14. Crataegus L. – See Zhang & Baas (1992)

Additional material studied: *C. aronia* (L.) Bosc.: Israel, Hebrew University s.n., diam. 10 mm. — *C. azarolus* L.: locality unknown, FHOw 3199; Israel, Hebrew University s.n. — *C. calycina* Peterm.: Switzerland, Schweingruber s.n. — *C. douglasii* Lindl.: locality unknown, FHOw 11088. — *C. laciniata* Ucria: Yugoslavia, Bitola, Schweingruber s.n. — *C. monogyna* Jack.: Switzerland, Gesau, Schweingruber s.n.; locality unknown, FHOw 2796; Israel, Hebrew University s.n., diam. 4 mm; locality unknown, FHOw 4371. — *C. oxyacantha* L.: Switzerland, Schaffhausen, Schweingruber s.n.; locality unknown, FHOw 2814. — *C. pycnoloba* Boiss. & Heldr.: locality unknown, Schweingruber s.n. — *C. sinaicus* Boiss.: Israel, Hebrew University s.n.

Deciduous, rarely semi-evergreen shrubs or small trees in north temperate regions.

The generic description based on the Chinese material (Zhang & Baas, 1992) entirely covers the wood anatomical ranges encountered in the specimens from outside China.

15. **Cydonia** Mill.

Material studied: *C. oblonga* Mill.: China, one specimen, see Zhang & Baas (1992); locality unknown, FHOw 5100; Israel, Hebrew University s.n.

Monotypic genus of deciduous shrubs or small trees in Persia to Turkestan, much cultivated and naturalised.

For the generic description, see Zhang & Baas (1992). Some quantitative characters (e.g. vessel size and frequency) may show slightly wider ranges in the material outside China.

16. **Dichotomanthes** Kurz

Monotypic genus of evergreen shrubs to small trees, native in Southwest China. See Zhang & Baas (1992).

17. **Docynia** Decne.

Material studied: *D. indica* (Wall.) Decne.: China, one specimen, see Zhang & Baas (1992); locality unknown, FHOw 6570. — *D. hookeriana* Decne.: India, Tw 45546.

Evergreen or semi-deciduous trees in the Himalayas, Burma and western China, some species cultivated as fruit trees or ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 90–116/sq.mm, 87–93% solitary, remainder in oblique and tangential multiples of 2–3, round to oval or weakly angular, tangential diameter 38–39 (18–57) µm, radial diameter 55–57 (25–84) µm, walls 1–2 µm thick. Vessel element length 270–425 (170–550) µm. L/D ratio 7–11. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round to oval, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and slightly smaller. Helical thickenings fine and usually closely spaced, confined to a few narrow vessel elements. Gummy contents absent. *Fibre-tracheids* 620 (330–830) µm long, F/V ratio 2.3, medium thick- to very thick-walled, with distinctly bordered pits of 5–6 µm in diameter, in radial and tangential walls. Helical thickenings fine, present in one sample of *D. indica* (FHOw 6570), but absent in the remaining samples. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 3–4 (2–6)-celled strands. *Rays* 10–11 (8–13)/mm, 1–2(–3) cells wide. Uniseriate rays 3–5 (1–15) cells high, composed of procumbent cells; 2–3-seriate rays 260–290 (80–640) µm high, composed of procumbent cells only, or with one row of square marginal cells (homogeneous and heterogeneous III). *Crystals* abundant, prismatic, large, in chambered axial parenchyma cells, one crystal in each enlarged, sclerified chamber; chains of up to 10 chambers. *Pith flecks* occasionally present. Traumatic gum ducts absent.

18. Dryas L.

Material studied: *D. octopetala* L.: Switzerland, Schweingruber s.n., diam. 25 mm.; Switzerland, Schweingruber s.n., diam. 8 mm.

Evergreen dwarf shrubs in Europe and arctic America.

Growth rings distinct to faint, marked by rows of radially flattened latewood fibre and differences in vessel diameter between latewood and subsequent earlywood. Wood ring-porous to semi-ring-porous. Vessels 272–280/sq.mm, 63–74% solitary, remainder in tangential and oblique multiples of 2(–3), tangential diameter 36–38 (18–48) µm, radial diameter 45–50 (20–82) µm, walls 1–2 µm thick. Vessel element length 150–160 (80–250) µm. Perforations almost exclusively simple in oblique end walls, but sporadic scalariform perforations also noted. Intervessel pits nonvestured, alternate, oval to polygonal, 4–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* very thin-walled, with distinctly bordered pits of 3–5 µm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–4-celled strands. *Rays* 15–16 (14–19)/mm, 1–3(–4)-seriate. Uniseriate rays 4–5 (2–10) cells high, composed of square to upright cells; multiseriate rays 500–600 (320–930) µm high, composed of square to upright cells. Crystals, pith flecks and traumatic gum ducts absent.

19. Eriobotrya Lindl.

Evergreen trees or shrubs mainly from Himalayas to East Asia and western Malesia, widely cultivated as fruit trees and ornamentals. See Zhang & Baas (1992).

20. Eriolobus (DC.) M. Roemer

Material studied: *E. trilobatus* (Poir.) M. Roemer: Israel, Upper Galilee, Mt Meiron, Hebrew University s.n., diam. 18 mm.

Deciduous medium-sized trees in southeastern Europe and the Middle East.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood diffuse-porous to semi-ring-porous. Vessels 110/sq.mm, 78% solitary, remainder in oblique and radial multiples of 2–3, angular, tangential diameter 35 (18–47) µm, radial diameter 45 (22–56), walls 2 µm thick. Vessel element length 640 (240–970) µm. L/D ratio 18. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round, 5–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings fine, present in some vessel elements. Gummy contents absent. *Fibre-tracheids* 1140 (470–1500) µm long, F/V ratio 1.8, medium thick- to very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* moderately abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–7-celled strands. *Rays* 8 (7–10)/mm, (1–)2(–3)-seriate. Uniseriate rays 1–7 cells high, composed of square and upright cells; multiseriate rays 290 (140–650) µm high, composed of procumbent body cells and 1–3 rows of square to upright marginal cells (mostly heterogeneous III, occasionally II). *Crystals* sparse, prismatic, large, in chambered parenchyma cells, one crystal in each enlarged chamber; chains of up to 6 chambers. Pith flecks and traumatic gum ducts absent.

21. **Exochorda** Lindl.

Deciduous shrubs in Central Asia and China, often cultivated as ornamentals. See Zhang & Baas (1992).

22. **Fallugia** Endl.

Material studied: *F. paradoxa* (D. Don) Endl.: USA, New Mexico, Tw 32069, diam. 15 mm, alt. 1550 m.

Deciduous shrubs in South, Central and North America, cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood ring-porous to semi-ring-porous. Latewood vessels 320/sq.mm, 80% solitary, remainder in oblique and tangential multiples of 2–3, oval to angular, tangential diameter of latewood vessels 15 (10–28) µm, radial diameter 20 (15–32) µm; tangential diameter of earlywood vessels 37 (25–50) µm, radial diameter 52 (28–70) µm, walls 1–2 µm thick. Vessel element length 170 (100–220) µm. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, polygonal, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents present in a few vessels. *Fibre-tracheids* 310 (220–360) µm long, F/V ratio 1.8, medium thick- to very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 8 (7–10)/mm, 1–3-seriate. Uniseriate rays 1–10 cells high, composed of square and upright cells; multiseriate rays 320 (145–500) µm high, composed of procumbent to square body cells and upright cells. *Crystals* absent. *Pith flecks* occasionally present. Traumatic gum ducts absent.

23. **Hagenia** J. Gmelin (Figs. 1, 11, 15)

Material studied: *H. abyssinica* (Bruce) J. Gmelin: Kenya, Tw 19975; locality unknown, FHOw 9528.

Evergreen trees in tropical East Africa.

Growth rings absent. Vessels diffuse, of two slightly different size classes, 11–22/sq.mm, 25–45% solitary, remainder in radial, tangential and oblique multiples of 2–3, occasionally in clusters, round to oval, tangential diameter 115–140 (60–220) µm, radial diameter 145–175 (70–260) µm, walls 2–5 µm thick. Vessel element length 650 (375–1500) µm. L/D ratio 6. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, 6–11 µm in diameter, with slit-like, occasionally coalescent apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 1640 (625–1825) µm long, F/V ratio 2.5, medium thick- to very thick-walled, with distinctly bordered pits of 4–6 µm in diameter, in radial and tangential walls. Helical thickenings absent. Gummy contents present in lumina of some fibre-tracheids in one sample (Tw 19975). *Parenchyma* common, apotracheally diffuse and diffuse-in-aggregates, in 2–4-celled strands. *Rays* 3–4 (2–6)/mm, of two distinct sizes: 1(–2)-seriate and (3–)6–9-seriate. Uniseriate rays 1–7 cells high, composed of square and procumbent cells; multiseriate rays 700–960 (320–2000) µm high, composed of procumbent cells only, or with one row of square marginal cells (homogeneous and heterogeneous III). Crystals, pith flecks and traumatic gum ducts absent.

24. **Hesperomeles** Lindl.

Material studied: *H. heterophylla* R. et P. Hook: Colombia, Tw 38668. — *H. lanuginosa* R et P. Hook: Colombia, Tw 39727.

Evergreen shrubs in Central and South America.

Growth rings absent. Vessels diffuse, 60–88/sq.mm, 76–95% solitary, remainder mainly in oblique pairs, oval, tangential diameter 40–52 (20–60) µm, radial diameter 60–65 (25–95) µm, walls 1–3 µm thick. Vessel element length 425–450 (200–620) µm. L/D ratio 9–11. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, oval to round, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents usually absent. *Fibre-tracheids* 580–1130 (500–1500) µm long, F/V ratio 1.4–2.5, medium thick-walled, with distinctly bordered pits of 4–5 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–5-celled strands. *Rays* 11–12 (9–14)/mm, 1–2(–3)-seriate. Uniseriate rays 1–11 cells high, composed of procumbent and square cells; multiseriate rays 190–230 (130–500) µm high, composed exclusively of procumbent cells (homogeneous). Crystals, pith flecks and traumatic gum ducts absent.

25. **Heteromeles** M. Roemer

Material studied: *H. arbutifolia* (Aiton) M. Roemer: USA, California, Tw 45854, diam. 18 mm, alt. 500 m; USA, California, FHOw 11058; USA, California, FHOw 11234; USA, California, Rancho Santa Ana Botanic Garden, RSAw 6142, diam. 20 mm.

Evergreen shrubs native in California.

Growth rings distinct or indistinct (RSAw 6142), marked by rows of radially flattened latewood fibres. Vessels diffuse, 120–193/sq.mm., 75–92% solitary, remainder in oblique, radial and tangential multiples of 2–3, oval or weakly angular, tangential diameter 26–42 (15–50) µm, radial diameter 35–58 (18–72) µm, walls 2–3 µm thick. Vessel element length 440–470 (350–520) µm. L/D ratio 10–18. Perforations almost exclusively simple in oblique end walls, but sporadic multiple perforations also noted in one sample (FHOw 11058). Intervessel pits nonvestured, alternate, round, 4–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent (Tw 45854, FHOw 11058) or poorly developed (FHOw 11234, RSAw 6142). Gummy contents absent. *Fibre-tracheids* 580–740 (350–950) µm long, F/V ratio 1.3–1.7, medium thick- to very thick-walled, with distinctly bordered pits of 3–7 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–5 (2–8)-celled strands. *Rays* 11–13 (9–14)/mm, 1–2(–3)-seriate. Uniseriate rays 2–5 (1–10) cells high, composed of upright and square cells; multiseriate rays 240–310 (120–420) µm high, composed of procumbent body cells and 1–4 rows of square to upright marginal cells (mainly heterogeneous III, rarely II, but homogeneous also noted in FHOw 11058). *Crystals* abundant, prismatic, medium-sized to large, in chambered parenchyma cells, one crystal in each enlarged chamber; chains of 2–7 chambers, crystals not noted in one sample (Tw 45854). *Pith flecks* noted in one sample (FHOw 11234), in tangential bands. Traumatic gum ducts absent.

26. Holodiscus (K. Koch) Maxim.

Material studied: *H. discolor* (Pursh) Maxim.: USA, Oregon, Tw 45970, diam. 25 mm, alt. 500 m; USA, California, Rancho Santa Ana Botanic Garden, Carlquist s.n., diam. 25 mm.

Deciduous shrubs in northwestern America to Colombia, cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Wood diffuse-porous to semi-ring-porous. Vessels 53–65/sq.mm, 78–85% solitary, remainder in oblique and tangential pairs, round to oval, tangential diameter 35–60 (14–67) µm, radial diameter 50–75 (20–100) µm, walls 2–3 µm thick. Vessel element length 310–320 (250–450) µm. L/D ratio 5–9. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, oval to polygonal, 4–5 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered pits. Helical thickenings absent. Gummy contents absent. *Vasicentric tracheids* present but *vascular tracheids* absent. Ground tissue composed of libriform fibres with simple to minutely bordered pits of 1–2 µm in diameter, and fibre-tracheids with distinctly bordered pits of 3–5 µm in diameter, fibre pits in radial and tangential walls; fibres 500–550 (300–680) µm long, F/V ratio 1.6, medium thick- to very thick-walled. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–4-celled strands. *Rays* 8–10 (7–12)/mm, of two distinct sizes: 1(–2)-seriate and (3–)4–6-seriate. Uniseriate rays 2–5 (1–7) cells high, composed of upright and square cells; multiseriate rays 1200–3300 (410–5300) µm high, composed of square to procumbent cells, upright cells and weakly differentiated sheath cells. Perforated ray cells noted in one sample (Carlquist s.n.). Crystals, pith flecks and traumatic gum ducts absent.

27. **Kageneckia** Ruiz & Pav. (Fig. 14)

Material studied: *K. lanceolata* Ruiz & Pav.: locality unknown, FHOw 9871.

Evergreen trees in Bolivia, Peru and Chile.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 164/sq.mm, 70% solitary, remainder in oblique and radial multiples of 2(–3), oval or weakly angular, tangential diameter 40 (15–50) µm, radial diameter 55 (22–72) µm, walls 1–3 µm thick. Vessel element length 280 (200–410) µm. L/D ratio 7. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, oval to polygonal, 5–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits. Closely spaced thickenings present in most vessel elements. Gummy contents absent. *Fibre-tracheids* medium thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–7-celled strands. *Rays* 14 (12–15)/mm, 1–3-seriate. Uniseriate rays 5 (1–15) cells high, composed of square and upright cells; multiseriate rays 840 (180–1550) µm high, composed of procumbent (occasionally to square) body cells and 1–5 rows of square to upright marginal cells. *Crystals* sparse, prismatic, medium-sized, present in non-enlarged ray cells, one crystal per cell. Pith flecks and traumatic gum ducts absent.

28. **Kerria** DC.

Monotypic genus of deciduous shrubs in East Asia, widely cultivated as ornamentals. See Zhang & Baas (1992).

29. **Laurocerasus** Tourn. ex Duh. – See *Prunus* s.l.

30. **Lindleya** H. B. & K.

Material studied: *L. mespelioides* H. B. & K.: Mexico, Tw 44760, diam. 15 mm.

Evergreen trees in Mexico.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood diffuse-porous to semi-ring-porous. Vessels 496/sq.mm, 83% solitary, remainder in oblique, tangential and radial pairs, weakly angular, tangential diameter 23 (15–

33) μm, radial diameter 32 (18–38) μm, walls 1–2 μm thick. Vessel element length 425 (300–600) μm. L/D ratio 18. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round, 4–5 μm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Fine irregular thickenings, closely-spaced, present in some vessel elements. Gummy contents present in a few vessels. *Vasicentric tracheids* absent. *Vascular tracheids* intergrading with narrow latewood vessel elements, with distinctly bordered pits and fine thickenings. *Fibre-tracheids* 500 (380–650) μm long, F/V ratio 1.2, very thick-walled, with distinctly bordered pits of 3–4 μm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* common, apotracheally diffuse and diffuse-in-aggregates, in 5 (2–10)-celled strands. *Rays* 13 (11–16)/mm, 1–3-seriate. Uniseriate rays 1–6 cells high, composed of upright cells; multiseriate rays 320 (100–540) μm high, composed of procumbent to square body cells and rows of upright cells. *Crystals* present, prismatic, medium-sized, in non-enlarged ray cells, one crystal per cell; or fragmented crystals present in non-chambered and non-enlarged axial parenchyma, 1–3 fragments per cell. *Pith flecks* common, in tangential bands or diffuse. Traumatic gum ducts absent.

31. Lyonothamnus A. Gray

Material studied: *L. floribundus* A. Gray: USA, California, Tw 48291; USA, California, FHOw 11239.

Trees or shrubs restricted to Santa Catalina, Santa Cruz, and San Clemente Islands (off the coast of California).

Growth rings faint, marked by rows of radially flattened latewood fibres. Vessels diffuse, 62–115/sq.mm, 78–89% solitary, remainder mainly in oblique and tangential pairs, round to oval, tangential diameter 38–40 (17–50) μm, radial diameter 42–57 (20–74) μm, walls 1–3 μm thick. Vessel element length 345 (300–410) μm. L/D ratio 9. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, polygonal, 5–7 μm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings well developed, closely spaced, throughout body of vessel elements. Gummy contents present in most vessels in one sample (Tw 48291). *Fibre-tracheids* 740 (600–900) μm long, F/V ratio 2.1, medium thick- to very thick-walled, with distinctly bordered pits of 4–6 μm in diameter, in radial and tangential walls. Helical thickenings fine to coarse, in most fibre-tracheids. Gummy contents present in lumina of some fibre-tracheids in one sample (Tw 48291). *Parenchyma* moderatery abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–5-celled strands. *Rays* 10–12 (9–14)/mm, 1–4-seriate. Uniseriate rays 4–7 (1–14) cells high, composed of square and procumbent cells; multiseriate rays 310–350 (110–620) μm high, composed of procumbent body cells and 1–3 rows of square marginal cells (mainly heterogeneous III, rarely heterogeneous II). *Crystals* common in one sample (FHOw 11239), prismatic, large, present in chambered parenchyma cells, one crystal in each more or less enlarged chamber; chains of 1–4 chambers. Pith flecks and traumatic gum ducts absent.

32. **Malus** Mill. – See Zhang & Baas (1992)

Additional material studied: *M. domestica* Borckh.: Switzerland, Schweingruber s.n. — *M. rivularis* M. Roemer: locality unknown, FHOw 11235. — *M. sylvestris* Mill.: Australia, New South Wales, SFCw 87; locality unknown, 4380.

Deciduous, rarely semi-evergreen trees or shrubs in north temperate regions, widely cultivated as fruit trees and ornamentals.

The generic description based on the Chinese material (Zhang & Baas, 1992) entirely covers the wood anatomical range encountered in the specimens from outside China.

33. **Mespilus** L.

Material studied: *M. germanica* L.: Switzerland, Tw 40867; locality unknown, FHOw 5719.

Deciduous trees in southeastern Europe to Central Asia.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 256–272/sq.mm, 74–86% solitary, remainder mainly in oblique and tangential pairs, round to oval or weakly angular, tangential diameter 32–35 (20–42) µm, radial diameter 40–45 (27–58) µm, walls 1–3 µm thick. Vessel element length 410 (380–480) µm. L/D ratio 13. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round, 5–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings present in most vessel elements. Gummy contents absent. *Fibre-tracheids* 780 (500–900) µm long, F/V ratio 1.9, medium thick- to very thick-walled, with distinctly bordered pits of 4–6 µm in diameter, in radial and tangential walls. Helical thickenings present in most fibre-tracheids of one sample (Tw 40867). *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–5-celled strands. *Rays* 7–9 (6–12)/mm, 1–3-seriate. Uniseriate rays 36 (1–12) cells high, composed of square and upright cells; multiseriate rays 290 (120–400) µm high, composed of procumbent cells only, or with one row of square marginal cells (homogeneous and heterogeneous III). *Crystals* sparse, prismatic, large, present in chambered parenchyma cells, one crystal in each enlarged chamber; chains of up to 2 chambers, crystals not observed in another sample (FHOw 5719). Pith flecks and traumatic gum ducts absent.

34. **Micromeles** Decne.

Material studied: *M. alnifolia* = *Sorbus alnifolia* (S. et Z.) Koehne: China, Shanxi, Zhongtiaoshan, HEFw 138; China, Shandong, HEFw 1360; Northeast-China, CAFw 13729; China, Guangxi, CAFw 5588; China, Hobai, Dongling, CAFw 5315; China, Honan, CAFw 5499. — *M. alnifolia* var. *lobulata* = *S. alnifolia* (S. & Z.) Koehne var. *lobulata* Rehd.: China, Shanxi, Zhongtiaoshan, HEFw 140; locality unknown, FHOw 4548. — *M. caloneura* = *S. caloneura* (Stapf) Rehd.: China, Guizhou, Guizhou Forest Institute s.n. — *M. dunnii* = *S. dunnii* Rehd.: China, Guizhou, Guizhou Forest Institute s.n. — *M. folgneri* = *S. folgneri* (Schneid.) Rehd.: China, Hunan, HEFw 2657; China, Yunnan, Yinian, Yunnan Academy of Forestry 127, alt. 2000 m; China, Sichuan, CAFw 10963; China, Guangxi, Guangxi Forestry College s.n. — *M. hemsleyi* = *S. hemsleyi* (Schneid.) Rehd.: China, Sichuan, HEFw 874; China, Yunnan, Lijiang, Yunnan Academy of Forestry 393, alt. 3000 m; China, Guangdong, FRIGw 1249.

Deciduous trees or shrubs of the northern hemisphere, some species cultivated as ornamentals or fruit trees.

Growth rings distinct, marked by rows of radially flattened latewood fibres, and sometimes also by differences in vessel frequency between latewood and subsequent earlywood. Wood diffuse-porous, rarely ranging to semi-ring-porous. Vessels 106–400/sq.mm, the frequency often decreases from earlywood to latewood in some species, 54–98% solitary (mostly 63–90%), remainder mainly in oblique, rarely tangential and radial multiples of 2–4, oval, round to angular, tangential diameter 24–45 (13–64) µm, radial diameter 35–60 (15–100) µm, walls 1–3 µm thick. Vessel element length 340–770 (190–1150) µm. L/D ratio 9–22. Perforations almost exclusively simple in oblique end walls, but sporadic scalariform and/or irregular multiple perforations with 2–5 bars occur in most species, only in *S. alnifolia* (FHOw 4548), *S. alnifolia* var. *lobulata*, *S. folgneri* (HEFw 2657, Yunnan Academy of Forestry 127, CAFw 10963) and *S. hemsleyi* (Yunnan Academy of Forestry 393, FRIGw 1249) perforations are exclusively simple. Intervessel pits nonvestured, alternate, round to oval, 4–8 µm in diameter, with slit-like apertures, apertures occasionally coalescent in a few species. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and slightly smaller. Helical thickenings well developed and closely spaced throughout body of vessel elements. Gummy contents present in a few species. *Fibre-tracheids* 730–1440 (460–1920) µm long, F/V ratio 1.4–2.5, medium thick- to very thick-walled, with distinctly bordered pits of 4–7 µm in diameter, in radial and tangential walls. Helical thickenings fine to conspicuous, present in *S. alnifolia* (HEFw 138, CAFw 13729), *S. caloneura*, *S. dunnii*, *S. folgneri* (HEFw 2657) and *S. hemsleyi* (HEFw 874, FRIGw 1249), but helical thickenings not observed in the remaining species or samples. *Parenchyma* moderately common to abundant, mainly apotracheally diffuse, but diffuse-in-aggregates and scanty paratracheal also present in most species, in 3–5 (2–10)-celled strands. *Rays* 6–16 (3–20)/mm, 1–2(–3)-seriate. Uniseriate rays 3–6 cells high, composed of procumbent cells only, or with one row of square marginal cells; 2(–3)-seriate rays 150–270 (50–640) µm high, composed of procumbent cells only, or with one row of square marginal cells (mostly homogeneous, rarely heterogeneous III). *Crystals* sparse to abundant in *S. alnifolia* (HEFw 138, CAFw 5315), *S. dunnii*, *S. folgneri* (HEFw 2657) and *S. hemsleyi*, prismatic, sometimes elongated in a few species, large, present in chambered axial parenchyma cells, one crystal in each enlarged, sclerified chamber; chains of up to 20 chambers, crystals not noted in the remaining species or samples. *Pith flecks* rare to common in some samples. Traumatic gum ducts absent.

Note – According to Kalkman (1988), *Micromeles* is treated as an independent genus. Our earlier study (Zhang & Baas, 1992) indicated that there are no appreciable differences in wood anatomical features between *Sorbus* and *Micromeles*. Recently, Robertson et al. (1991) reduced *Micromeles* to *Aria*, which they suppose to be more closely related to *Pyrus* and *Malus* than to *Sorbus*. All these genera are wood anatomically more or less identical (cf. Table 2).

35. Osmaronia E. Greene

Material studied: *O. cerasiformis* (Torr. & Gray) E. Greene: USA, Oregon, Tw 32037; USA, Oregon, Tw 46422, diam. 18 mm, alt. 250 m.

Deciduous small trees or shrubs in northwestern North America, cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 72–188/sq.mm, 60–82% solitary, remainder mainly in oblique and tangential multiples of 2–3, oval, tangential diameter 30–41 (15–50) µm, radial diameter 42–57 (18–105) µm, walls 1–3 µm thick. Vessel element length 270–350 (200–450) µm. L/D ratio 9. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, polygonal, 4–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings well developed, medium-spaced, throughout body of vessel elements. Gummy contents absent. *Fibre-tracheids* 680–810 (450–1100) µm long, F/V ratio 1.9–3.0, very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, mainly in radial walls, much less in tangential walls. Helical thickenings absent. *Parenchyma* common to abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–6-celled strands. *Rays* 10–12 (9–13)/mm, more or less of two sizes: 1(–2)-seriate and 3–4(–5)-seriate. Uniseriate rays 1–15 cells high, composed of upright and square cells; multiseriate rays 490–930 (220–3930) µm high, composed of procumbent body cells and 1–3 rows of square to upright cells (mainly heterogeneous III, rarely II). Crystals, pith flecks and traumatic gum ducts absent.

36. Osteomeles Lindl.

Material studied: *O. anthyllidifolia* Lindl.: USA, Hawaii, Tw 35936, diam. 18 mm.

Deciduous or evergreen shrubs in Burma, China to Hawaii and New Zealand, some cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 192/sq.mm, 92% solitary, remainder in oblique pairs, round to oval, tangential diameter 32 (15–45) µm, radial diameter 47 (24–65) µm, walls 1–3 µm thick. Vessel element length 320 (280–580) µm. L/D ratio 10. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, round, 3–5 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings closely spaced, throughout body of narrow vessel elements. Gummy contents absent. *Fibre-tracheids* 760 (450–1000) µm long, F/V ratio 2.4, medium-thick to very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, in radial and tangential walls. Helical thickenings coarse, present in most fibre-tracheids. *Parenchyma* moderately abundant, apotracheally diffuse and diffuse-in-aggregates, in 2–8-celled strands. *Rays* 11 (10–13)/mm, 1–2-seriate. Uniseriate rays 1–8 cells high, composed of upright and square cells; multiseriate rays 200 (120–280) µm high, composed of procumbent body cells and 1–3 rows of square to upright marginal cells (mainly heterogeneous III, rarely II). *Crystals* abundant, prismatic, large, in chambered axial parenchyma cells, one crystal in each enlarged chamber; chains of up to 8 chambers. Pith flecks and traumatic gum ducts absent.

37. **Padus** Mill. – See *Prunus* s.l.

38. **Peraphyllum** Nutt. ex Torr. & Gray

Material studied: *P. ramosissimum* Nutt.: USA, southern California, RSAw 10758, diam. 8 mm.

Deciduous shrubs, in western USA.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 460/sq.mm, 65% solitary, remainder in oblique, radial and tangential pairs, mostly angular, tangential diameter 20 (10–28) µm, radial diameter 24 (14–30) µm, walls 1–3 µm thick. Vessel element length 290 (180–400) µm. L/D ratio 15. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, oval, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 430 (350–450) µm long, F/V 1.6, medium-thick to very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–4-celled strands. *Rays* 15 (12–19)/mm, uniseriate only, 8 (2–23) cells high, composed of procumbent cells only or with one row of square marginal cells (homogeneous and heterogeneous III). *Crystals* common, prismatic, medium-sized to large, present in chambered axial parenchyma cells, one crystal per enlarged chamber, chains of 2–8 chambers. Pith flecks and traumatic gum ducts absent.

39. **Petrophytum** Rydb.

Material studied: *P. caespitosum* (Nutt.) Rydb.: USA, southern California, Carlquist s.n., diam. 10 mm.

Shrubs in western and North America.

Growth rings faint to absent. Vessels diffuse, 134/sq.mm, 95% solitary, remainder in oblique pairs, round to oval, tangential diameter 20 (8–25) µm, radial diameter 26 (12–37) µm, walls 1–3 µm thick. Vessel element length 130 (65–170) µm. L/D ratio 7. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, oval, 4–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents present in some vessels. *Fibre-tracheids* very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 7 (5–10)/mm, of two distinct sizes: 1-seriate and 4–15-seriate. Uniseriate rays 1–4 cells high, composed of upright and square cells; multiseriate rays 600 (300–900) µm high, composed of procumbent and square cells. *Crystals* abundant, medium-sized, druses in non-chambered ray cells, one crystal per cell. Pith flecks and traumatic gum ducts absent.

Note –This genus is the only one in the subfamily Spiraeoideae where druses were found.

40. **Photinia** Lindl. – See Zhang & Baas (1992)

Additional material studied: *P. serratifolia* (Desf.) Kalkman = *P. serrulata* Lindl.: China, 241. — *P. villosa* (Thunb.) DC.: locality unknown, FHOw 11295.

Evergreen or deciduous trees and shrubs from Himalayas to Japan and Southeast Asia. The additional specimens studied are within the wood anatomical ranges given separately for the evergreen (Group A) and deciduous (Group B) species described by Zhang & Baas (1992).

41. **Physocarpus** Maxim.

Material studied: *P. capitatus* (Pursh) Kuntze: USA, Oregon, Tw 45953, diam. 24 mm; USA southern California, RSAw 144, diam. 12 mm.

Deciduous shrubs in North America, Mexico, and East Asia, cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres. Wood diffuse-porous, tending to semi-ring-porous. Vessels 148–184/sq.mm, 45–80% solitary, remainder in radial, tangential and oblique multiples of 2–4, round to oval, tangential diameter 35–41 (10–60) µm, radial diameter 45–57 (18–84) µm, walls 2–3 µm thick. Vessel element length 250–330 (220–400) µm. L/D ratio 7–8. Perforations almost exclusively simple in oblique end walls, but sporadic irregular multiple perforations also noted in one sample (Tw 45953). Intervessel pits nonvestured, alternate, round, oval to polygonal, 4–8 µm in diameter, with slit-like, occasionally coalescent apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents present in few vessels. *Fibre-tracheids* 600–660 (350–780) µm long, F/V ratio 2.0–2.4, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty to common, apotracheally diffuse and diffuse-in-aggregates, in 2–5-celled strands. *Rays* 15–17 (13–20)/mm, 1–2(–3)-seriate. Uniseriate rays 4–8 (1–21) cells high, composed of upright cells; multiseriate rays 340–410 (120–1100) µm high, composed of square (occasionally to procumbent) cells and upright cells. Crystals, pith flecks and traumatic gum ducts absent.

42. **Polylepis** Ruiz & Pav. (Fig. 2)

Material studied: *P. australis* Bitter: locality unknown, FHOw 9866. — *P. incana* Bitter: locality unknown, Tw 31362, diam. 40 mm. — *P. pallidistigma* Bitter: Peru, Schweingruber s.n.

Evergreen small trees or shrubs, in tropical South America.

Growth rings faint to distinct, marked by rows of radially flattened latewood fibres. Vessels diffuse, 93–159/sq.mm, 53–77% solitary, remainder mainly in oblique and tangential multiples of 2–3, round, oval to angular, tangential diameter 25–60 (14–80) µm, radial diameter 36–75 (20–90) µm, walls 2–3 µm thick. Vessel element length 350 (250–550) µm. L/D ratio 6. Perforations exclusively simple in oblique to almost horizontal end walls, but sporadic scalariform perforations also noted in *P. pallidistigma*. Intervessel pits nonvestured, alternate, round to oval, 4–8 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings fine, closely spaced, present in some vessel elements. Gummy contents present in few vessels. *Fibre-tracheids* 730 (550–880) µm long, F/V ratio 2.1, very thin- to medium thick-walled, with distinctly bordered pits of 4–6 µm in diameter, in radial (sometimes densely spaced) and tangential walls. Helical thickenings noted in some fibre-tracheids of *P. pallidistigma*. *Parenchyma* moderately abundant, apotracheally diffuse and diffuse-in-aggregates, in 2–4-celled strands. *Rays* 8–11 (7–13)/mm, 1–3(–4)-seriate. Uniseriate rays 3–4 (1–7) cells high, composed of upright and square cells; multiseriate rays 200–290 (105–470) µm high, composed of procumbent cells only, or with one row of square marginal cells (homogeneous and heterogeneous III). Crystals, pith flecks and traumatic gum ducts absent.

43. **Potentilla** L. (Figs. 8, 12)

Material studied: *P. fruticosa* L.: USA, New Mexico, Tw 42599, diam. 10 mm, alt. 2700 m; Switzerland, Schweingruber s.n., diam. 10 mm.

Herbs or deciduous dwarf shrubs, most species in north temperate and arctic regions, a few in south temperate zones, some cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood ring-porous to semi-ring-porous. Latewood vessels 148/sq.mm, 80–85% solitary, remainder in oblique, tangential and radial multiples of 2–3, round, oval to angular, tangential diameter of latewood vessels 12–14 (8–22) µm, radial diameter 17–18 (12–30) µm; tangential diameter of earlywood vessels 25–27 (15–34) µm, radial diameter 34–35 (22–42) µm, walls 1–3 µm thick. Vessel element length 210 (180–280) µm. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, 4–6 µm, with slit-like apertures. Vessel-parenchyma and vessel-ray pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents present in a few vessels. *Fibre-tracheids* 300 (200–420) µm long, F/V ratio 1.5, very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, sometimes densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* very scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 10–16 (8–18)/mm, 1(–2)-seriate. Uniseriate rays 4–10 (1–23) cells high, composed of upright cells; multiseriate rays 340–410 (200–700) µm high, composed of square to upright cells. Crystals absent. *Pith flecks* rarely present in one of the samples (Tw 42599), in tangential bands or diffuse. Traumatic gum ducts absent.

44. **Prinsepia** Royle

Deciduous erect or climbing shrubs from Himalayas to North China and Taiwan. See Zhang & Baas (1992).

45. **Prunus** L. s.str. – See *Prunus* s.l.

Prunus s.l. – Cf. Kalkman (1965)

(4) **Amygdalus** L.

Material studied: *A. communis* L. = *Prunus amygdalus* Batsch.: Israel, Hebrew University s.n., diam. 10 mm; locality unknown, Lw 4342; Switzerland, Schweingruber s.n.; Spain, Mallorca, Schweingruber s.n. — *A. davidiana* (Carr.) C. de Vos ex Henry: see Zhang & Baas (1992). — *A. dulcis* (DC.) Koehne: locality unknown, Schweingruber s.n. — *A. kansuensis* (Rehd.) Skeel: see Zhang & Baas (1992). — *A. korshinskyi* Hand.-Mazz.: Israel, Hebrew University s.n. — *A. mira* (Koehne) Yu et Lu: see Zhang & Baas (1992). — *A. nana* (L.) Stokes = *Prunus tenella* Batsch.: Switzerland, Schweingruber s.n., diam. 6 mm. — *A. persica* L.: see Zhang & Baas (1992); Spain, Schweingruber s.n. — *A. triloba* (Lindl.) Ricker: see Zhang & Baas (1992); Japan, CAFw 4173. — *A. webbii* (Spach) Vierh.: locality unknown, Schweingruber s.n.

Deciduous trees or shrubs from Central Asia to the Mediterranean region, but cultivated forms widely distributed in cold temperate, and warm temperate to subtropical regions as fruit trees.

Growth rings distinct, marked by differences in vessel diameter between latewood and subsequent earlywood and rows of radially flattened latewood fibres. Wood ring-porous, rarely ranging from ring-porous to semi-ring-porous in a few juvenile samples including *A. nana*, *A. communis* (Hebrew University s.n.), *A. triloba* (CAFw 13721, Qian Hong s.n.), with 1–2(–4) rows of large earlywood vessels. Latewood vessels 52–344(–410)/sq.mm (mostly between 100–300/sq.mm), 25–68(–80)% solitary (all below 54% except in *A. kansuensis* and *A. korshinskiy*), remainder in radial, oblique and tangential multiples of 2–7, oval to round, tangential diameter of earlywood vessels 37–109 (15–150) µm, radial diameter 45–120 (26–190) µm; tangential diameter of latewood vessels 20–48 (10–70) µm, radial diameter 30–53 (18–97) µm, walls 1–3 µm thick. Vessel element length 210–390 (90–970) µm. Perforations exclusively simple in oblique (latewood) to almost horizontal (earlywood) end walls, but sporadic scalariform and multiple perforations with 3–5 bars noted in *A. persica* (CAFw 16900, Huang Chenglin s.n.). Intervessel pits nonvestured, alternate, polygonal, round to oval, (3–)4–9 µm in diameter, with slit-like apertures, apertures rarely coalescent in *A. davidiana*, *A. kansuensis* and *A. persica* (HEFw 345). Vessel-ray and vessel-parenchyma pits clearly smaller than intervessel pits and half-bordered with reduced borders, 2–5 µm in diameter. Helical thickenings well developed, usually widely spaced, throughout body of vessel elements. Gummy contents present in some vessels of all species. *Vasicentric tracheids* present in some samples, sparse, mainly in earlywood, with distinctly bordered pits in both radial and tangential walls and irregular in shape. *Vascular tracheids* absent. *Fibres* 690–1140 (400–1400) µm long, F/V ratio (2.2–)

2.7–3.6, very thin- to very thick-walled, with (minutely to) distinctly bordered pits of (2–)3–5 µm in diameter in *A. kansuensis*, *A. mira* and *A. triloba*, largely restricted to the radial walls in most samples, but in *A. davidiana* and some samples of *A. persica*, fibres with simple to minutely bordered pits of 1–3 µm in diameter also noted. Helical thickenings absent. *Parenchyma* usually scanty, apotracheally diffuse and scanty paratracheal, in 2–5 (2–9)-celled strands. *Rays* 8–14 (6–18)/mm, of two sizes: narrow and low rays 1(–2)-seriate, and wide and tall rays (2–)4–10-seriate [the widest rays 4(–5)-seriate in *A. kansuensis* to 10-seriate in *A. dulcis*, but in a few juvenile samples, rays 1–3(–4)-seriate]. Uniseriate rays 3–12 (1–36) cells high, composed of square and upright cells, multiseriate rays 430–980 (30–2500) µm high, composed of procumbent (to square in juvenile samples) body cells and 1–4(–7) rows of square to upright marginal cells (heterogeneous III & II). *Crystals* absent in some samples, but sporadic crystals noted in *A. communis* (Hebrew University s.n.; Lw 4342; Schweingruber s.n., Costa Brava), *A. davidiana*, *A. kansuensis*, *A. korshinskyi*, *A. mira* and *A. triloba* (CAFw 13721), druses, medium-sized, one crystal per non-enlarged ray cell. *Pith flecks* mostly absent, but infrequent in *A. korshinskyi* and some specimens of *A. persica*. *Traumatic gum ducts* present in *A. persica* (HEFw 345, 3803, and Huang Chenglin s.n.) and *A. triloba* (Qian Hong s.n.), usually in short to long tangential bands.

(5) **Armeniaca** Mill. – See Zhang & Baas (1992)

Additional material studied: *A. vulgaris* Lam. = *Prunus armeniaca* L.: locality unknown, FHOw 5099; Switzerland, Schweingruber s.n., diam. 20 mm; Germany: 599.

Deciduous trees, rarely shrubs mainly distributed in Asia, widely cultivated as fruit trees and ornamentals.

The wood anatomical range of the above mentioned specimens entirely fits the generic description by Zhang & Baas (1992).

(6) **Cerasus** Mill.

Material studied: *C. avium* (L.) Moench: locality unknown, FHOw 2797; locality unknown, FHOw 11158; Switzerland, Schweingruber s.n.(1); Austria, 53; Switzerland, Schweingruber s.n. (2). — *C. avium* var. *decumana* Mordant: see Zhang & Baas (1992) — *C. campanulata* (Maxim.) Yu et Li: see Zhang & Baas (1992); locality unknown, FHOw 8230. — *C. cerasoides* (D. Don) Sok.: see Zhang & Baas (1992). — *C. clarofolia* (Schneid.) Yu et Li: see Zhang & Baas (1992). — *C. conradinae* (Koehne) Yu et Li: see Zhang & Baas (1992). — *C. dielsiana* (Schneid.) Yu et Li: see Zhang & Baas (1992). — *C. fruticosa* (Palls) Woronow: Switzerland, Schweingruber s.n. — *C. mahaleb* (L.) Mill.: Switzerland, Schweingruber s.n. — *C. maximowiczii* (Rupr.) Kom.: see Zhang & Baas (1992); locality unknown, FHOw 2166, diam. 30 mm. — *C. prostrata* Labill.: Switzerland, Schweingruber s.n., diam. 8 mm; locality unknown, Schweingruber s.n., diam. 6 mm. — *C. pseudocerasus* (Lindl.) G. Don: see Zhang & Baas (1992). — *C. serrula* (Franch.) Yu et Li: see Zhang & Baas (1992). — *C. serrulata* (Lindl.) G. Don ex Loud.: see Zhang & Baas (1992); locality unknown, FHOw 2083; Japan, CAFw 4865. — *C. serrulata* var. *sachalinensis* Fr. Schmidt.: Japan, CAFw 4199. — *C. setulosa* (Batal.) Yu et Li: see Zhang & Baas (1992). — *C. szechuanica* Yu et Li.: see Zhang & Baas (1992). — *C. tomentosa* (Thunb.) Wall.: see Zhang & Baas (1992). — *C. vulgaris* Mill. = *Prunus cerasus* L.: locality unknown, FHOw 2793; locality unknown, FHOw 2798. — *C. yedoensis* (Matsum.) Yu et Li: see Zhang & Baas (1992).

Deciduous trees or shrubs in warm regions of the northern hemisphere, mainly distributed in China, Japan, and South Korea, widely cultivated as ornamentals and fruit trees.

Growth rings distinct, marked by rows of radially flattened latewood fibres, in some species by weak differences in vessel diameter between latewood and subsequent earlywood as well. Wood diffuse-porous to semi-ring-porous. Vessels in a weakly oblique pattern in *C. campanulata* (CAFw 13055 and Northeast Forestry University s.n.) and *C. clarofolia* (HEFw 126), 53–440/sq.mm (mostly 80–220/sq.mm), 11–60(–80)% solitary (all lower than 60% except in *A. prostrata*), remainder in radial and oblique multiples of 2–5(–7), occasionally in clusters in *C. campanulata* (South China Agricultural University 2333) and *C. conradinae* (Yunnan Academy of Forestry 205), round, oval or angular, tangential diameter 22–65 (10–110) µm, radial diameter 25–82 (15–120) µm, walls 1–3 µm thick. Vessel element length 230–500 (100–680) µm. L/D ratio 6–13. Perforations exclusively simple in oblique to almost horizontal end walls, but sporadic multiple perforations also noted in *C. serrulata* (CAFw 4865). Intervessel pits nonvestured, alternate, predominantly polygonal, rarely round to oval, 4–11 µm in diameter, with slit-like apertures, apertures occasionally coalescent in *C. clarofolia* (HEFw 126), *C. pseudocerasus* (FRIGw 463), *C. serrulata* (HEFw 3160), *C. serrulata* var. *sachalinensis* and *C. setulosa* (HEFw 133). Vessel-ray and vessel-parenchyma pits clearly smaller than intervessel pits and half-bordered with slightly reduced borders, 2–5 µm in diameter. Helical thickenings well developed, usually coarse and widely spaced, throughout body of vessel elements. Tyloses noted in *C. avium* (53). Gummy contents present in some vessels of most species. *Fibres* 560–1400 (350–1620) µm long, F/V ratio 1.9–3.4, medium thick-walled, with (minutely to) distinctly bordered pits of 2–5 µm in diameter, mainly confined to radial walls, but simple to minutely bordered pits also present in thinner earlywood fibres in *C. maximowiczii* and *C. yedoensis*. Helical thickenings mostly absent, but fine helical thickenings present in some latewood fibres of *C. pseudocerasus* (Guizhou Forestry Institute s.n.) and some fibres of *C. tomentosa*. *Parenchyma* usually scanty, occasionally fairly common, apotracheally diffuse and scanty paratracheal, in 2–5 (2–8)-celled strands. *Rays* 5–14/mm, of two sizes (except in a few branch samples where rays are 1–3-seriate): narrow and low rays 1(–2)-seriate, and wide and tall rays (3–)4–6(–7)-seriate. Uniseriate rays 4–15 (1–30) cells high, composed of square and upright cells, or including some procumbent central cells; multiseriate rays 300–1490 (80–3100) µm high (all higher than 0.4 mm except in a few branch samples, but lower than 1.0 mm except in *C. clarofolia* (368)), composed of procumbent body cells and 1–4(–5) rows of square to upright marginal cells (heterogeneous III & II), but in a few shrub samples, multiseriate rays usually composed of square to procumbent body cells and one to several rows of upright cells, the proportion of square to upright cells higher. Inflated secretory (possibly oil or mucilage?) cells associated with ray parenchyma were noted in *C. campanulata* (Northeast Forestry University s.n.). *Crystals* present in most species, sparse to abundant, prismatic and/or druses, medium-sized (druses) to large (prismatic crystals), in chambered axial parenchyma and/or ray cells, one crystal in each more or less enlarged and sclerified chamber or ray cell; chains of up to 15 chambers. Crystals not observed in *C. avium* (FHOw 11153 and 53), *C. campa-*

nulata, C. conradinae, C. maximowiczii (FHOw 2166), *C. prostrata, C. serrulata* (FHOw 2083, CAFw 4865), *C. tomentosa* and *C. vulgaris* (FHOw 2793, Kw s.n.). *Pith flecks* mostly absent, but rare to common in *C. campanulata* (HEFw 5040), *C. maximowiczii, C. serrulata* (CAFw 4865, FHOw 2083) and *C. setulosa* (CAFw 564). *Traumatic gum ducts* usually absent, but present in *C. cerasoides* (FRIGw 1208), *C. vulgaris* (FHOw 2793) and *C. yedoensis*, large, in long tangential bands.

(29) **Laurocerasus** Tourn. ex Duh. (Figs. 3, 4)

Evergreen trees or shrubs, very rarely deciduous, mainly distributed in the tropics, from Africa, South Asia, Southeast Asia, New Guinea to Central and South America, rarely in subtropical to temperate regions.

Within *Laurocerasus* there are large differences in wood structure. The following two groups can be recognised.

Group A

Material studied: *L. lusitanica* L.: Switzerland, Schweingruber s.n.; locality unknown, FHOw 3127; England, KJw s.n. — *L. lyoni* Sudworth: locality unknown, FHOw 11250 — *L. officinalis* M. Roemer = *Prunus laurocerasus* L.: locality unknown, FHOw 9540; Switzerland, Schweingruber s.n. — *L. phaeosticta* (Hance) Schneid.: see Zhang & Baas (1992). — *L. spinulosa* (Sieb. et Zucc.) Schneid.: see Zhang & Baas (1992); locality unknown, FHOw 2105; Japan, CAFw 4866.

Growth rings usually distinct, marked by 1–3 rows of radially flattened latewood fibres. Vessels diffuse, in a weakly to distinctly oblique pattern in *L. phaeosticta* (FRIGw 460 and Guizhou Forestry Institute s.n.) and *L. spinulosa* (CAFw 12662, 15847, 19173, and Guangxi Forestry College s.n.), in a weakly dendritic pattern in *L. lusitanica* (FHOw 3127, Schweingruber s.n.), or in a weakly radial pattern in *L. officinalis* (FHOw 9540, KJw s.n.), 73–199/sq.mm, 5–45% solitary, remainder in radial, oblique and tangential multiples of 2–6(–11), multiples of over 4 common in a few samples, clusters occasionally present in some samples. Vessels oval to round or weakly angular, tangential diameter 36–60 (20–87) µm, radial diameter 53–79 (23–111) µm, walls 1–3 µm thick. Vessel element length 230–670 (130–810) µm. L/D ratio usually 5–12. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, mostly polygonal, rarely round to oval, 5–10 µm in diameter, with slit-like apertures, apertures rarely coalescent in a few samples. Vessel-ray and vessel-parenchyma pits half-bordered, clearly smaller than intervessel pits, 2–4 µm in diameter. Helical thickenings well developed, usually coarse and widely spaced, throughout body of vessel elements. Gummy contents present in a few samples. *Fibres* 910–1330 (500–1680) µm long, F/V ratio (1.6–)1.9–2.9(–3.9), medium thick- to very thick-walled, with (minutely to) distinctly bordered pits of (2–)3–4 µm in diameter, mainly confined to radial walls. Helical thickenings absent. *Parenchyma* scanty (in *L. phaeosticta* and *L. spinulosa*) to moderately abundant (in *L. lusitanica* and *L. officinalis*), mainly apotracheally diffuse, but diffuse-in-aggregates and scanty paratracheal also present in some samples, in 2–5 (2–8)-celled strands. *Rays* 6–11 (5–14)/mm, 1–5(–8)-seriate, of two sizes in some samples (see Table 19). Uniseriate rays 2–8 (1–24) cells high, composed of square and upright cells; multiseriate rays 290–860 (115–2800) µm high, composed of procumbent body cells and 1–3(–5) rows of square to upright marginal cells (heterogeneous III & II). *Crystals* absent in most samples, but sparse prismatic crystals noted in *L. lusitanica* (FHOw 3127) and *L. officinalis* (FHOw 9540), medium-sized to large, present in chambered and enlarged axial parenchyma cells (in *L. lusitanica*) or non-enlarged ray cells (in *L. officinalis*), one prismatic crystal per chamber or cell; chains of 4 chambers. *Pith flecks* present in *L. officinalis* (FHOw 9540). Traumatic gum ducts absent.

Group B

Material studied: *L. fordiana* (Dunn) Yu et Lu: see Zhang & Baas (1992). — *L. hypotricha* (Rehd.) Yu et Lu: see Zhang & Baas (1992). — *L. undulata* (D. Don) M. Roemer: see Zhang & Baas (1992). — *L. zippeliana* (Miq.) Yu et Lu: see Zhang & Baas (1992).

Growth rings distinct to faint in *L. fordiana, L. hypotricha* and *L. zippeliana* or faint to indistinct in *L. undulata,* mainly marked by 1–2(–4) rows of marginal zonate parenchyma bands, occasionally by weakly radially flattened latewood fibres as well. Vessels diffuse, in a radial pattern in most samples (but in an oblique pattern in *L. fordiana*), 27–62/sq.mm, 5–24% solitary, remainder mainly in radial and oblique multiples of 2–8, multiples of over 4 common in *L. zippeliana,* clusters occasionally present. Vessels oval to round, tangential diameter 61–79 (27–105) µm, radial diameter 78–108 (30–137) µm, walls 2–4 µm thick. Vessel element length 360–620 (270–880) µm. L/D ratio 5–7(–10). Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, mainly polygonal, 2–4(–5) µm in diameter, with slit-like apertures, apertures rarely coalescent in *L. fordiana.* Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings well developed, usually coarse and closely spaced, throughout vessel elements, but in *L. undulata,* fine thickenings present only in narrow vessel elements in one sample or absent in another. Gummy contents usually present. *Fibres* 810–1520 (650–1750) µm, F/V ratio (1.8–)2.7–2.9, very thick-walled, with (minutely) to distinctly bordered pits of (2–)3–5 µm in diameter, but simple to minutely bordered pits also present in *L. undulata,* mainly confined to radial walls. Helical thickenings absent. Gummy contents present in lumina of most fibres in *L. zippeliana. Parenchyma* moderately abundant, apotracheally diffuse, diffuse-in-aggregates, scanty paratracheal and in 1–3-seriate marginal or irregular zonate bands, in 3–5 (2–10)-celled strands. *Rays* 10–12 (9–13)/mm, mostly of two sizes: narrow and low 1(–2)-seriate, and wide and tall rays 3–5(–12)-seriate. Uniseriate rays 5–6 (1–15) cells high, composed of square and upright cells; multiseriate rays 500–940 (150–1600) µm high, composed of procumbent body cells and 1–5 rows of upright to square marginal cells (heterogeneous III & II). *Crystals* sparse in *L. fordiana* to abundant in *L. undulata,* prismatic (*L. undulata*) or druses (*L. fordiana*), medium-sized to large, in chambered axial parenchyma cells in *L. fordiana* or both in ray and chambered or non-chambered axial parenchyma cells in *L. undulata,* one crystal in each more or less enlarged chamber in *L. fordiana* and *L. undulata* or 1–10 prismatic crystals in each non-enlarged ray cell or axial parenchyma cell in *L. undulata*; chains of up to 17 chambers, crystals not observed in *L. hypotricha* and *L. zippeliana. Pith* *flecks* observed in *L. undulata* only. *Traumatic gum ducts* noted in *L. hypotricha* and *L. undulata*, in tangential bands.

Note – Although the present study surveys only a few species of *Laurocerasus*, this genus shows the largest diversity in *Prunus* s.l. Even within the two wood anatomical groups recognised in the genus, some variation exists. Therefore further study, based on vouchered specimens of more species is necessary.

(37) **Padus** Mill.

Material studied: *P. brachypoda* (Batal.) Schneid.: see Zhang & Baas (1992). — *P. buergeriana* (Miq.) Yu et Ku: see Zhang & Baas (1992). — *P. demissa* (Nutti) Roemer: locality unknown, FHOw 11087. — *P. grayana* (Maxim.) Schneid.: see Zhang & Baas (1992); locality unknown, FHOw 2136; Japan, CAFw 4101. — *P. maackii* (Rupr.) Kom.: see Zhang & Baas (1992); locality unknown, FHOw 2167. — *P. obtusata* (Koehne) Yu et Ku: see Zhang & Baas (1992). — *P. perulata* (Koehne) Yu et Ku: see Zhang & Baas (1992). — *P. racemosa* (Lam.) Gilib.: see Zhang & Baas (1992); locality unknown, 4364; locality unknown, FHOw 2165; Switzerland, Schweingruber s.n. — *P. racemosa* var. *pubescens* (Regel & Tiling) Schneid.: Chili, CAFw 5447. — *P. serotina* (Ehrh.) Borckh.: locality unknown, FHOw 129; locality unknown, FHOw 130. — *P. ssiori* Schneid.: Japan, CAFw 4200. — *P. virginiana* Borckh.: Belgium, CAFw 18461; Belgium, FHOw 19481; locality unknown, FHOw 11087. — *P. wilsonii* Schneid.: see Zhang & Baas (1992).

Deciduous trees or shrubs mainly distributed in the northern hemisphere, some species cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres, in some samples by differences in vessel diameter between latewood and subsequent earlywood as well. Wood diffuse-porous, sometimes ranging to semi-ring-porous. Vessels in a weakly oblique pattern in *P. brachypoda, P. grayana* (CAFw 17647), *P. maackii* (Qian Hong s.n.) and *P. obtusata* (HEFw 814, 1434, and CAFw 43), 40–250/sq.mm, 5–54(–68)% solitary (all lower than 54% except in *P. racemosa* (FHOw 2165), remainder in radial, oblique and tangential multiples of 2–7(–8), multiples of over 4 vessels frequent in *P. perulata.* Vessels oval to round or angular, tangential diameter 30–75 (15–100) µm, radial diameter 39–85 (20–160) µm, walls 1–3 µm thick. Vessel element length 260–570 (140–730) µm. L/D ratio 5–11. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, predominantly polygonal, occasionally round to oval, 4–12 µm in diameter, with slit-like apertures, apertures rarely coalescent in *P. brachypoda, P. buergeriana* (HEFw 135), *P. grayana* (Sichuan Forestry Institute s.n.), *P. maackii* (Qian Hong s.n.), *P. perulata* and *P. ssiori.* Vessel-ray and vessel-parenchyma pits clearly smaller than intervessel pits and half-bordered with reduced borders, 2–5 µm in diameter. Helical thickenings well developed, usually coarse and widely spaced, throughout body of vessel elements. Gummy contents present in most species. *Fibres* 740–1380 (390–1770) µm long, F/V ratio 1.8–3.0, very thin- to very thick-walled, mostly with minutely to distinctly bordered pits of 2–5 µm in diameter, mainly confined to radial walls. Helical thickenings absent. *Parenchyma* usually scanty, apotracheally diffuse and scanty paratracheal, rarely diffuse-in-aggregates, in 3–5 (2–10)-celled strands. *Rays* 4–15 (3–17)/mm, of two sizes [except in *P. maackii* where rays are 1–2(–3)-seriate]: narrow and low rays 1(–2)-seriate, and wide and tall rays (2–)4–8(–12)-seriate. Uniseriate rays 3–10 (1–25) cells high, composed of procumbent cells only, or with one row of square to upright marginal cells; multiseriate rays 210–970 (70–2900) µm high, composed of procumbent cells only, or occasionally with one row of square marginal cells (mainly homogeneous, occasionally heterogeneous III also present). *Crystals* sparse to common in *P. brachypoda, P. buergeriana* (HEFw 135), *P. grayana* (Sichuan Forestry Institute s.n.), *P. obtusata* (HEFw 814, CAFw 43, 812) and *P. perulata*, druses and prismatic crystals, usually medium-sized, in chambered axial parenchyma, ray cells or both, one crystal in each weakly enlarged chamber or ray cell, chains of up to 14 chambers, crystals not observed in the remaining species or samples. *Pith flecks* rare to common *P. brachypoda, P. grayana* (CAFw 4101, 17647), *P. maackii* (Qian Hong s.n., FHOw 2167) and *P. obtusata* (CAFw 43). *Traumatic gum ducts* rare to common in *P. grayana* (CAFw 4101, 17647), *P. obtusata* (CAFw 43), *P. perulata* and *P. serotina* (FHOw 129), small to large, in long or short tangential bands or diffuse.

(45) **Prunus** L. s.str.

Material studied: *P. cerasifera* Ehrh.: locality unknown, FHOw 2792. — *P. domestica* L.: locality unknown, FHOw 3079; Switzerland, Schweingruber s.n. — *P. insititia* (L.) Schneid.: locality unknown, FHOw 2827. — *P. pissardii* Carr.: locality unknown: FHOw 11248. — *P. ramburii* Boiss.: Switzerland, Schweingruber s.n. — *P. salicina* Lindl.: see Zhang & Baas (1992). — *P. spinosa* L.: locality unknown, FHOw 1971, 2815, 2822; France, Schweingruber s.n. — *P. ursina* Kotschy: Israel, Hebrew University s.n. — *P. ussuriensis* Kov. et Kost.: see Zhang & Baas (1992).

Deciduous small trees or shrubs mainly distributed in temperate regions of the northern hemisphere, widely cultivated as important fruit trees and ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres, in a few samples by differences in vessel diameter between latewood and subsequent earlywood as well. Wood usually diffuse-porous, rarely ranging to semi-ring-porous in *P. cerasifera, P. salicina* (HEFw 132) and *P. ursina*. Vessels (55–)110–288/sq.mm, 9–56(–67)% solitary [all smaller than 56% except in *P. salicina* (CAFw 15874)], remainder in radial, oblique and tangential multiples of 2–6(–8), oval to round or weakly angular, tangential diameter 30–47 (20–60) µm, radial diameter 35–62 (22–80) µm, walls 1–3 µm thick. Vessel element length 250–560 (120–760) µm. L/D ratio 6–10. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate , polygonal or round to oval, 4–11 µm in diameter, with slit-like apertures, apertures occasionally coalescent in *P. domestica* and *P. salicina* (CAFw 1241). Vessel-ray and vessel-parenchyma pits clearly smaller than intervessel pits and half-bordered with reduced borders, 2–5 µm in diameter. Helical thickenings well developed and widely spaced, throughout body of vessel elements. Gummy contents usually present. *Fibres* 580–1280 (290–1550) µm long, F/V ratio 1.9–3.1, medium thick- to very thick-walled, with (minutely to) distinctly bordered pits, (2–) 3–5 µm in diameter, mainly confined to radial walls. Helical thickenings in fibres only noted in *P. domestica* (Schweingruber s.n.). *Parenchyma* scanty, apotracheally diffuse and scanty paratracheal, in 3–5 (2–8)-celled strands. *Rays* 6–13 (5–16)/ mm, of two sizes: narrow and low rays 1(–2)-seriate, and wide and tall rays 3–8 (–9)-seriate. Uniseriate rays 3–10 (1–25) cells high, composed of square to weakly procumbent cells and one to several rows of upright cells; multiseriate rays 306–840

(130–1440) µm high, composed of procumbent body cells and 1–5 rows of square to upright marginal cells (heterogeneous III & II), but in one branch sample of *P. salicina* (He Yunhe s.n.), multiseriate rays composed of square to procumbent body ray cells and rows of upright marginal cells. Proportion of square and upright ray cells higher in juvenile wood than in mature wood. *Crystals* usually absent, but druses noted in *P. ursina,* medium-sized, present in chambered, non-enlarged axial parenchyma cells, one druse per chamber; chains of up to 5 chambers. *Pith flecks* common in *P. salicina* (HEFw 3121, Guizhou Forest Institute s.n.). Traumatic gum ducts absent.

(47) **Pygeum** Gaertn. (Fig. 5, Table 6)

Material studied: *P. annularis* (Koehne) Kovalev: locality unknown, FHOw 3640. — *P. africanum* Hook. f. = *Prunus africana* (Hook. f.) Kalkman: locality unknown, FHOw 39, 2060, 2464, 2465; Burundi, Lewalle 21598. — *P. arboreum* Blume = *Prunus arborea* (Blume) Kalkman: New Guinea, BW 9680, alt. 35 m. — *P. griseum* Blume = *Prunus grisea* (Blume) Kalkman: Malaysia, KEPw 7845. — *P. javanicum* Blume = *Prunus javanica* (Teijsm. & Binnend.) Miq.: New Guinea, BW 9217, alt. 100 m. — *P. latifolium* Miq. = *Prunus grisea* (Blume) Kalkman var. *grisea*: New Guinea, Kalkman 5173, alt. 2780 m. — *P. martabanicum* Schneid.: locality unknown, FHOw 2442. — *P.* spec. = *Prunus myrtifolia* Urb.: Surinam, Stahel 229. — *P. parviflorum* Teijsm. & Binnend. = *Prunus arborea* (Blume) Kalkman: Indonesia, Java, Tw 11004. — *P. polystachyum* Hook. f. = *Prunus polystachya* (Hook. f.) Kalkman: Malaysia, KEPw 2245, 6719. — *P. pullei* Koehne = *Prunus pullei* (Koehne) Kalkman: New Guinea, van Balgooy 327, alt. 3600 m. — *P. schlechteri* Koehne = *Prunus schlechteri* (Koehne) Kalkman: New Guinea BW 1918, alt. 50 m. — *P. topengii* Merr.: see Zhang & Baas (1992). — *P. vulgare* (Koehne) Merr. = *Prunus grisea* (Blume) Kalkman: Philippines, CAFw 4663. - *P. zeylanicum* Gaertn. = *Prunus zeylanica* (Wright) Miq.: East Pakistan, MADw 24491.

Evergreen trees or shrubs mainly distributed in the tropics, from tropical Africa, South and Southeast Asia to New Guinea and the northern regions of Oceania.

Growth rings mostly absent, infrequently faint, marked by zonate parenchyma bands in *P. africanum* (FHOw 2060, 2465), *P. annularis, P. griseum, P. javanicum, P. topengii, P. vulgare,* or by rows of weakly radially flattened fibres. Vessels diffuse, in a radial pattern in *P. africanum* and *P.* spec. 5–30/sq.mm, 4–55(–66)% solitary, remainder mainly in radial multiples of 2–8, oval to round, tangential diameter (75–)100–175 (46–250) µm, radial diameter (100–)120–220 (60–290) µm, walls 2–5 µm thick. Vessel element length 380–710 (140–1030) µm. L/D ratio 3–5. Perforations exclusively simple in oblique to horizontal end walls. Intervessel pits nonvestured, alternate, crowded, mainly polygonal, rarely round to oval, 2–5 µm in diameter, with slit-like to coalescent apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered, occasionally unilaterally compound or elongated. Helical thickenings usually absent but fine and closely spaced, confined to narrow vessel elements or to tails in *P. annularis, P. africanum* (FHOw 39, 2060, 2465), *P. latifolium* and *P. topengii.* Gummy contents noted in *P. africanum* and *P.* spec. *Fibres* 1060–1310 (720–2010) µm long, F/V ratio 2.0–2.5, very thin-walled in most species to medium thick-walled in *P. africanum, P. javanicum* and *P.* spec., usually with minutely to distinctly bordered pits of 2–4 µm in diameter, mainly confined to radial walls. Helical thickenings absent. Dark contents noted

Table 6. Variation in selected wood anatomical features of *Pygeum*.

	1	2	3	4	5	6	7	8	9	10	11	12	13
P. annularis	–	14	46	100	380	+			5(–6)	0.6	+	+	–
P. africanum													
21958	R	23	6	105	480	–			4(–5)	0.7	+	–	–
FHOw 2060	R	30	14	105	450	+			4(–5)	0.7	–	+	–
FHOw 2465	R	25	4	123	500	+			4(–5)	0.6	–	+	–
FHOw 39	R	19	5	134	440	+			4(–5)	0.5	–	–	–
P. arboreum	–	10	55	175	710	–			3(–4)	0.4	–	–	–
P. griseum	–	12	28	125	550	–			5(–6)	0.7	–	+	–
P. javanicum	–	9	26	125	580	–			4	0.5	–	+	–
P. latifolium	–	13	20	115	530	+			3(–4)	0.4	–	–	–
P. martabanicum	–	17	30	125	420	–			4(–5)	0.5	–	–	–
P. parviflorum	–	15	45	130	?	–			5	0.5	–	–	–
P. polystachyum													
KEPw 7619	–	5	66	175	570	–			4(–5)	0.6	–	–	–
KEPw 2245	–	6	33	175	450	–			4	0.6	–	–	–
P. pullei	–	17	35	75	400	–			4	0.4	–	–	–
P. schlechteri	–	10	27	160	710	–			4(–5)	0.5	–	–	–
P. spec.	R	20	13	115	460	–			5	0.6	–	–	–
P. topengii													
FRIGw 22	–	11	34	125	530	+	1180	2.3	4(–5)	0.5	–	+	+
CAFw 14370	–	8	55	100	530	+	1310	2.5	4(–5)	0.5	–	+	–
CAFw 6571	–	8	20	110	530	+	1060	2.0	4(–5)	0.4	–	+	–
P. vulgare	–	14	47	105	490	–	1050	2.1	4(–5)	0.4	–	+	+
P. zeylanicum	–	15	43	150	580	–			5(–6)	0.5	–	+	–

1 = Vessels in a radial pattern (R) or not (–); **2** = Vessel frequency (/sq.mm); **3** = Percentage of solitary vessels (%); **4** = Average tangential vessel diameter (µm); **5** = Average vessel element length (µm); **6** = Helical vessel wall thickenings present (+) or absent (–); **7** = Average fibre length (µm); **8** = F/V ratio; **9** = Width of the widest rays (number of cells); **10** = Average multiseriate ray height (mm); **11** = Crystals present (+) or absent (–); **12** = Marginal or zonate parenchyma present (+) or absent (–); **13** = Traumatic gum ducts present (+) or absent (–).

in some fibre lumina of *P. africanum*. *Parenchyma* common to moderately abundant, apotracheally diffuse and scanty paratracheal to vasicentric, narrow irregular zonate (sometimes marginal) bands also noted in some samples, in 3–6 (2–11)-celled strands. *Rays* 4–14 (2–14)/mm, usually 1–4(–6)-seriate, mostly of two sizes, uniseriate rays, and (2–)3–4(–6)-seriate. Uniseriate rays 5–10 (1–17) cells high, composed of square to upright cells; multiseriate rays 380–740 (170–980) µm high, composed of procumbent body ray cells and 1–3(–5) rows of square to upright marginal cells (mainly heterogeneous III, rarely II). *Crystals* mostly absent, but sparse druses noted in *P. annularis* and *P. africanum* (IFw 21958), medium-sized, one crystal per non-enlarged ray cell. *Pith flecks* noted only in *P. annularis*. *Traumatic gum ducts* present in *P. topengii* (FRIGw 22) and *P. vulgare*, in long tangential bands.

46. **Purshia** DC.

Material studied: *P. glandulosa* Curran: USA, California, Tw 48467, alt. 800 m. — *P. tridentata* (Pursh) DC.: USA, California, Tw 46207, diam. 15 mm, alt. 1600 m.

Deciduous shrubs in North America, cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood ring-porous to semi-ring-porous. Latewood vessels 208–288/sq.mm, 86–95 solitary, remainder in tangential and oblique pairs, round to oval or weakly angular, tangential diameter of latewood vessels 23–32 (10–45) µm, radial diameter 32–37 (15–60) µm; tangential diameter of earlywood vessels 40–52 (32–70) µm, radial diameter 52–62 (40–90) µm, walls 2–4 µm thick. Vessel element length 150–200 (100–280) µm. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, round, 4–7 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 400–420 (300–470) µm long, F/V ratio 2.1–2.8, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial (sometimes densely spaced) and tangential walls. Helical thickenings absent. *Parenchyma* common to abundant, apotracheally diffuse and diffuse-in-aggregates, in 2–4-celled strands. *Rays* 11–13 (10–15)/mm, 1–2(–3)-seriate. Uniseriate rays 3–5 (1–8) cells high, composed of square and procumbent cells; multiseriate rays 130–190 (70–320) µm high, composed of procumbent cells only, or with one row of square marginal cells (heterogeneous III and homogeneous). Crystals absent. *Pith flecks* present in *P. tridentata*. Traumatic gum ducts absent.

47. **Pygeum** Gaertn. – See *Prunus* s.l.

48. **Pyracantha** M. Roemer

Evergreen shrubs or small trees in Asia and Europe, often cultivated as ornamentals. See Zhang & Baas (1992).

49. **Pyrus** L.

Material studied: *P. amygdaliformis* Vill.: Switzerland, Schweingruber s.n. — *P. aria* M. Roemer: locality unknown, CAFw 50001; locality unknown, FHOw 2475. — *P. aucuparia* Gaertn.: locality unknown, Princes Risborough Laboratory s.n. — *P. betulaefolia* Bunge: see Zhang & Baas (1992). — *P. calleryana* Decne.: see Zhang & Baas (1992). — *P. communis* L.: locality unknown, FHOw 4578; locality unknown, 4357; Switzerland, Schweingruber s.n. — *P. malus* L.: locality unknown, FHOw 2825; locality unknown, FHOw 4581; locality unknown, FHOw 2794; Switzerland, Schweingruber s.n. — *P. pashia* Buch.-Ham. ex D. Don: see Zhang & Baas (1992). — *P. pyraster* Burgsd.: Switzerland, Schweingruber s.n. — *P. pyrifolia* (Burm. f.) Nakai: see Zhang & Baas (1992). — *P. serrulata* Rehd.: see Zhang & Baas (1992). — *P. sinensis* Decne.: locality unknown, FHOw 2089; locality unknown, FHOw 2090. — *P. syriaca* Boiss.: Israel, Hebrew University s.n. — *P. ussuriensis* Maxim.: see Zhang & Baas (1992). — *P. xerophila* Yu: see Zhang & Baas (1992).

Deciduous trees or shrubs, rarely semi-deciduous trees, in Eurasia and the Mediterranean region, widely cultivated as fruit trees and ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres, and in some species by differences in vessel frequency between latewood and subsequent earlywood as well. Wood usually diffuse-porous, but rarely ranging to semi-ring-porous. Vessels 120–340/sq.mm, 32–94% (mostly above 50%) solitary, remainder mainly in oblique, rarely tangential and radial multiples of 2–6, round, oval to angular, tangential diameter 23–47 (18–70) µm, radial diameter 30–70 (15–103) µm, walls 1–3 µm thick. Vessel element length 350–590 (180–830) µm. L/D ratio 8–22. Perforations mostly exclusively simple in oblique end walls, but sporadic scalariform and/or irregular multiple perforations with 1–4 bars also occur in *P. aucuparia, P. calleryana* (HEFw 1661), *P. malus* (FHOw 2794), *P. serrulata* (HEFw 329, FRIGw 1793) and *P. ussuriensis* (HEFw 418, CAFw 18077). Intervessel pits nonvestured, alternate, round to oval, 4–11 µm in diameter, with slit-like apertures, apertures occasionally coalescent in some species. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller, 3–6 µm in diameter. Helical thickenings well developed and closely to moderately widely spaced, throughout body of vessel elements in *P. aucuparia, P. calleryana* (HEFw 1661, 3710), *P. pyrifolia, P. serrulata* (CAFw 1793, HEFw 329), *P. sinensis* and *P. ussuriensis* (CAFw 5928), or fine helical thickenings present in narrow vessel elements and tails of large vessel elements in *P. betulaefolia, P. communis* (FHOw 4357), *P. pashia, P. serrulata* (HEFw 785), *P. ussuriensis* (Northeast Forestry University s.n.) and *P. xerophila*. Helical thickenings not observed in *P. amygdaliformis, P. communis* (Schweingruber s.n., FHOw 4578), *P. malus, P. pyraster* and *P. syriaca*. Gummy contents usually absent. *Fibre-tracheids* 780–1210 (520–1650) µm long, F/V ratio 1.5–2.4, very thin- to very thick-walled, with distinctly bordered pits of 3–8 µm in diameter, in radial and tangential walls. Helical thickenings fine to conspicuous, present in some species. *Parenchyma* fairly common to abundant, mainly apotracheally diffuse, but diffuse-in-aggregates and scanty paratracheal also present in most species, in 2–6 (1–9)-celled strands. *Rays* 7–14 (5–16)/mm, 1–2(–3) cells wide. Uniseriate rays 2–10 (1–22) cells high, composed of procumbent cells only, or occasionally with one row of square marginal cells; 2–3-seriate rays 160–320 (40–610) µm high, composed of procumbent cells only, or occasionally with one row of square marginal cells (predominantly homogeneous, heterogeneous III occasionally present in some species). *Crystals* sparse to common in *P. malus, P. pashia, P. pyrifolia* p.p., *P. serrulata, P. sinensis, P. syriaca* and *P. ussuriensis*, prismatic, occasionally elongated, large, in chambered axial parenchyma cells, one crystal in each enlarged, sclerified chamber; chains of up to 15 chambers, crystals not noted in other species or specimens. *Pith flecks* usually absent, but occasionally present in *P. pyrifolia* (Yunnan Academy of Forestry 367). Traumatic gum ducts absent.

50. **Quillaja** Molina

Material studied: *Q. brasiliensis* (St. Hil.) Mart.: Uruguay, Tw 20487.

Evergreen shrubs or trees in South America.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 40/sq.mm, 95% solitary, remainder mainly in oblique and tangential pairs, round to oval, tangential diameter 62 (26–90) µm, radial diameter 83 (31–125) µm, walls 1–3 µm thick. Vessel element length 290 (200–430) µm. L/D ratio 5. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits nonvestured, alternate, oval, 4–5 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings well developed, closely spaced, throughout body of vessel elements. Gummy contents absent. *Fibre-tracheids* 540 (470–600) µm long, F/V ratio 1.8, medium thick-walled, with minutely to distinctly bordered pits of 3–4 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 2–4-celled strands. *Rays* 5 (4–6)/mm, of two distinct sizes: 1(–2)-seriate and 3–5-seriate. Uniseriate rays 1–3 cells high, composed of square and procumbent cells; multiseriate rays 220 (100–350) µm high, composed of procumbent cells only, or with one row of square marginal cells (mainly homogeneous, occasionally heterogeneous III). Crystals, pith flecks and traumatic gum ducts absent.

51. Raphiolepsis Lindl.

Evergreen shrubs or small trees in East Asia, sometimes cultivated as ornamentals. See Zhang & Baas (1992).

52. Rosa L.

Material studied: *R. arabica* Crep.: Israel, Hebrew University s.n., diam. 6 mm. — *R. arvensis* Hudson: Switzerland, Schweingruber s.n. — *R. canina* L.: locality unknown, FHOw 2813; locality unknown, 4390, diam. 18 mm; Israel, Hebrew University s.n., diam. 6 mm. — *R. cymosa* Tratt.: see Zhang & Baas (1992). — *R. glutinosa* Sibth. & Sm.: Israel, Hebrew University s.n., diam. 6 mm. — *R. henryi* Bouleng.: see Zhang & Baas (1992). — *R. laevigata* Michx.: see Zhang & Baas (1992). — *R. macrophylla* Lindl.: see Zhang & Baas (1992). — *R. multiflora* Thunb.: see Zhang & Baas (1992). — *R. phoenicea* Boiss.: Israel, Hebrew University s.n., diam. 15 mm. — *R. pulverulenta* Bieb.: Israel, Hebrew University s.n. — *R. roxburghii* Tratt.: see Zhang & Baas (1992). — *R. sempervirens* L.: Switzerland, Schweingruber s.n., diamter 10 mm. — *R. sertata* Rolfe: see Zhang & Baas (1992). — *R. xanthina* Lindl.: see Zhang & Baas (1992).

Deciduous erect, scrambling or climbing shrubs in north temperate regions to tropical mountains, widely cultivated as ornamentals.

Growth rings distinct, mostly with more or less wavy boundaries, marked by differences in vessel diameter between latewood and subsequent earlywood, rows of radially flattened latewood fibres, and usually also by locally inflated broad rays. Wood ring-porous to semi-ring-porous, usually with 1–2 rows of large earlywood vessels. Latewood vessels 70–400 (mostly 114–192)/sq.mm, 40–96% solitary (all above 60% except in *R. macrophylla*), remainder in oblique and tangential multiples of 2–5, round to oval or angular, tangential diameter of earlywood vessels 35–155 (30–240) µm, radial diameter 45–210 (40–250) µm; tangential diameter of latewood vessels 19–52 (15–130) μm, radial diameter 23–65 (18–145) μm, walls 1–3 μm thick. Vessels of two sizes also noted in *R. sempervirens*. Vessel element length 280–400 (210–930) μm. Perforations exclusively simple in oblique to almost horizontal end walls. Intervessel pits alternate, round, oval to polygonal, 3–10 μm in diameter, with slit-like apertures, apertures occasionally coalescent in some species. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and slightly smaller, sometimes with slightly reduced borders, 2–7 μm in diameter. Helical thickenings fine, discontinuous and irregularly spaced, mainly present in body of narrow vessel elements. Gummy contents absent. *Vasicentric tracheids* present in a few samples, but only weakly differentiated from ground tissue, mainly confined to earlywood, generally shorter than ground tissue fibres but larger in diameter, with distinctly bordered pits of 4–8 μm in diameter and irregular in shape. Vascular tracheids absent. *Fibre-tracheids* 510–970 (350–1200) μm long, F/V ratio 1.7–2.8, medium thick- to very thick-walled, with distinctly bordered pits of 3–7 μm in diameter, in radial (sometimes densely spaced) and tangential walls. Helical thickenings very fine, occasionally present in a few samples. *Parenchyma* usually scanty, apotracheally diffuse and scanty paratracheal, in 2–4 (1–8)-celled strands. *Rays* 6–15 (4–20)/mm, of two distinct sizes: narrow and low rays 1(–2)-seriate, and wide and tall rays (3–)4–16-seriate (the widest rays 5-seriate in *R. roxburghii* and *R. xanthina* to 16-seriate in *R. henryi, R. macrophylla* and *R. sempervirens*). Uniseriate rays 4–12 (1–39) cells high, composed exclusively of upright cells; multiseriate rays 1.0–14.3 (0.2–22.5) mm high, mostly composed of square to procumbent body cells, upright marginal cells and weakly differentiated sheath cells, but in *R. arvensis, R. canina* (FHOw 2813), *R. macrophylla* and *R. sempervirens* multiseriate rays composed of procumbent (occasionally to square) body cells and 1(–3) rows of square to upright marginal cells. *Crystals* sparse to common, prismatic, occasionally elongated, medium-sized, present in non-enlarged ray cells. Crystals not observed in *R. arvensis, R. canina, R. macrophylla, R. sertata* and *R. xanthina*. *Pith flecks* usually absent, but infrequently in *R. cymosa*. Traumatic gum ducts absent.

53. Rubus L.

Material studied: *R. biflorus* Buch.-Ham. ex Smith: see Zhang & Baas (1992). — *R. chamaemorus* L.: locality unknown, Schweingruber s.n., diam. 4 mm. — *R. chingii* Hu: see Zhang & Baas (1992). — *R. coreanus* Miq.: see Zhang & Baas (1992). — *R. corchorifolius* L. f.: see Zhang & Baas (1992). — *R. fruticosus* L.: Switzerland, Schweingruber s.n., diam. 3 mm; Switzerland, Schweingruber s.n., diam. 12 mm; English, CAFw 5012. — *R. idaeus* L. Switzerland, Schweingruber s.n. — *R. swinhoei* Hance: see Zhang & Baas (1992). — *R. trianthus* Focke: see Zhang & Baas (1992).

Deciduous, rarely evergreen shrubs, scrambling shrubs or herbs distributed widely, many species cultivated as fruit plants or ornamentals.

Growths rings absent to faint, marked by rows of weakly radially flattened latewood fibres. Wood semi-ring-porous to diffuse-porous. Vessel diameter usually decreases gradually from pith outward, 72–150/sq.mm, 38–58% solitary, remainder predominantly in tangential, rarely oblique and radial multiples of 2–5, oval to round or weakly angular, tangential diameter 28–55 (15–110) μm, radial diameter

40–69 (18–155) µm, walls 1–3 µm thick. Vessels of two distinct sizes in *R. biflorus, R. fruticosus* (Schweingruber s.n., CAFw 5012) and *R. trianthus,* small vessels randomly scattered in *R. biflorus* and *R. fruticosus,* tangential diameter of small vessels 25–40 (15–48) µm, radial diameter 30–52 (20–60) µm; tangential diameter of large vessels 58–95 (42–115) µm, radial diameter 75–132 (50–155) µm; but small vessels in *R. trianthus* occurring between two wide rays from pith outward, tangential diameter of small vessels 40 (18–50) µm, radial diameter 47 (20–68) µm; tangential diameter of large vessels 84 (45–113) µm, radial diameter 104 (55–133) µm. Vessel element length 250–670 (110–1220) µm. L/D ratio 6–12(–19). Perforations usually exclusively simple in oblique to almost horizontal end walls, but sporadic irregular perforations also noted in *R. chingii* and *R. idaeus.* Intervessel pits nonvestured, alternate, polygonal, oval to round, 4–10(–14) µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and slightly smaller, or with somewhat reduced borders. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* 710–890 (430–1340) µm long, F/V ratio 1.3–2.4, medium thick- to very thick-walled, with distinctly bordered pits of 3–4 µm in diameter, in radial (densely spaced) and tangential walls. Helical thickenings absent. *Parenchyma* sparse, apotracheally diffuse and scanty paratracheal, in 3–4 (2–7)-celled strands. *Rays* 7–13 (3–17)/mm, of two distinct sizes (except in *R. chamaemorus* where only uniseriate rays were noted): narrow and low rays 1(–2)-seriate, wide and tall rays 3–15-seriate [the widest rays 5-seriate in *R. fruticosus* (Schweingruber s.n.) and *R. idaeus* to 15-seriate in *R. fruticosus* (CAFw 5012)]. Uniseriate rays 5–16 (2–61) cells high, composed exclusively of upright cells; multiseriate rays (0.7–)3.6–17.0 (0.5–45.0) mm high, composed of upright and square cells and weakly differentiated sheath cells. *Crystals* mostly absent, but infrequent in *R. trianthus,* prismatic, small to medium-sized, usually one crystal (occasionally two) per non-enlarged ray cell. Pith flecks and traumatic gum ducts absent.

54. **Sarcopoterium** Spach (Figs. 6, 9)

Material studied: *S. spinosum* (L.) Spach: Israel, Hebrew University s.n., diam. 14 mm; Greece, Kythira, Baas 19, diam. 18 mm; Cyprus, Schweingruber s.n., diam. 20 mm.

Deciduous dwarf shrubs in the Mediterranean region.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood diffuse-porous to semi-ring-porous. Vessels 166–310/sq.mm, 12–30% solitary, remainder in oblique, tangential and radial multiples of 2–6, sometimes in clusters, round, oval to angular, tangential diameter 32–41 (16–60) µm, radial diameter 40–50 (22–75) µm, walls 1–3 µm thick. Vessel element length 250 (140–360) µm. L/D ratio 6. Perforations almost exclusively simple in oblique end walls, but sporadic irregular perforations also noted in one sample (Hebrew University s.n.). Intervessel pits nonvestured, alternate, round to polygonal, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents not noted. *Vasicentric tracheids* absent. *Vascular tracheids* intergrading with narrow vessel elements, with distinctly bordered pits, present in the latewood. Ground tissue mainly *libriform fibres,* often septate, 340 (240–440) µm long, F/V ratio 1.4, medium thick-walled, with simple to minutely bordered pits of 1–2 µm in diameter, rarely of fibre-tracheids with distinctly bordered pits of 3–4 µm, fibre pits in radial (sometimes densely spaced) and tangential walls. Helical thickenings absent. *Parenchyma* very scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 7–11 (5–14)/mm, of two distinct sizes: 1(–2)-seriate and (2–)4–12-seriate. Uniseriate rays 1–5 cells high, composed of upright cells; multiseriate rays 600–1100 (150–2300) µm high, composed of square (rarely to weakly procumbent), upright cells and weakly differentiated sheath cells. *Crystals* common, prismatic, medium-sized, in non-enlarged ray cells, one crystal per cell. Pith flecks and traumatic gum ducts absent.

55. Sibbaldia L.

Material studied: *S. procumbens* L.: locality unknown, Schweingruber s.n., diam. 4 mm.

Perennial herbs in north temperate and alpine regions.

Growth rings distinct to faint, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 450/sq.mm, 65% solitary, remainder in tangential and oblique multiples of 2(–3), tangential diameter 20 (12–30) µm, radial diameter 25 (15–40) µm, walls 1–3 µm thick. Vessel element length 140 (70–230) µm. L/D ratio 7. Perforations exclusively simple in oblique end walls. Intervessel pits non-vestured, alternate, mostly polygonal, 4–10 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings absent. Gummy contents absent. *Fibre-tracheids* medium thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 18 (15–21)/mm, almost exclusively uniseriate, 1–11 cells high, composed of upright cells. Crystals, pith flecks and traumatic gum ducts absent.

56. Sibiraea Maxim.

Material studied: *S. laevigata* (L.) Maxim.: Switzerland, Schweingruber s.n., diam. 10 mm; Austria, Schweingruber s.n., diam. 8 mm.

Deciduous shrubs in southeastern Europe and Central & East Asia, often cultivated as ornamentals.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood ring-porous to semi-ring-porous. Latewood vessels 123–235/sq.mm, 89–97% solitary, remainder in tangential and oblique multiples of 2(–3), round to oval, tangential diameter of latewood vessels 20–22 (10–27) µm, radial diameter 30–32 (14–34) µm; tangential diameter of earlywood vessels 30–34 (15–50) µm, radial diameter 40–46 (24–60) µm, walls 1–3 µm thick. Vessel element length 170–180 (100–290) µm. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, oval to polygonal, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered. Helical thickenings absent. Gummy contents present in some vessels. *Fibre-tracheids* medium-thick-walled, with distinctly bordered pits of 3–5 µm in diameter, densely spaced in radial and tangential walls. Helical thickenings absent. *Parenchyma* scanty, apotracheally diffuse, in 2–3-celled strands. *Rays* 15–16 (13–17)/mm, more or less of two sizes, 1–4-seriate. Uniseriate rays 4–7 (1–17) cells high, composed of upright cells; multiseriate rays 1100–1200 (300–2300) µm high, composed of square and upright cells. Crystals, pith flecks and traumatic gum ducts absent.

57. **Sorbaria** (Ser.) A. Br. ex Aschers. – See Zhang & Baas (1992)

Additional material studied: *S. stellipila* Maxim.: locality unknown, FHOw 11298.

Deciduous shrubs in Afghanistan to East Asia, often cultivated as ornamentals. *Sorbaria stellipila* is entirely within the wood anatomical range given for the Chinese species (Zhang & Baas, 1992).

58. **Sorbus** L.

Material studied: *S. amabilis* Cheng ex Yu: see Zhang & Baas (1992). — *S. aria* (L.) Crantz: locality unknown, 4348; Switzerland, Gesau, Schweingruber s.n.; see Zhang & Baas (1992). — *S. aucuparia* L.: locality unknown, 4327; locality unknown, 67; Switzerland, Schweingruber s.n.; Japan, CAFw 4202. — *S. coronata* (Card.) Yu & Tsai: see Zhang & Baas (1992). — *S. chamaemespilus* (L.) Crantz: Switzerland, Schweingruber s.n. — *S. discolor* (Maxim.) Maxim.: see Zhang & Baas (1992). — *S. domestica* L.: Switzerland, Schweingruber s.n. — *S. japonica* (Decne.) Hedl.: Japan, CAFw 4108. — *S. koehneana* Schneid.: see Zhang & Baas (1992). — *S. microcarpa* Pursh: see Zhang & Baas (1992). — *S. oligodonta* (Card.) Hand.-Mazz.: see Zhang & Baas (1992). — *S. pohuashanensis* (Hance) Hedl.: see Zhang & Baas (1992); locality unknown, FHOw 11046. — *S. prattii* Koehne: see Zhang & Baas (1992). — *S. prattii* var. *tatsiensis*: see Zhang & Baas (1992). — *S. pteridophylla* Hand.-Mazz.: see Zhang & Baas (1992). — *S. reducta* Diels: see Zhang & Baas (1992). — *S. sargentiana* Koehne: see Zhang & Baas (1992). — *S. scalaris* Koehne: see Zhang & Baas (1992). — *S. tianschanica* Rupr.: see Zhang & Baas (1992). — *S. vilmorinii* Schneid.: see Zhang & Baas (1992). — *S. wallichii* (Hook. f.) Yu: see Zhang & Baas (1992). — *S. wilsoniana* Schneid.: see Zhang & Baas (1992).

Deciduous trees or shrubs in the northern hemisphere, some species cultivated as ornamentals or fruit trees.

Growth rings distinct, marked by rows of radially flattened latewood fibres, and also by differences in vessel frequency between latewood and subsequent earlywood in some species. Wood diffuse-porous, rarely ranging to semi-ring-porous in a few species. Vessels 127–477/sq.mm, the frequency often decreases from earlywood to latewood, 57–92% solitary, remainder mainly in oblique, rarely tangential and radial multiples of 2–4, oval, round to angular, tangential diameter 24–46 (13–65) µm, radial diameter 35–60 (15–105) µm, walls 1–3 µm thick. Vessel element length 350–670 (200–1020) µm. L/D ratio (9–)13–25. Perforations almost exclusively simple in oblique end walls, but sporadic scalariform and/or irregular multiple perforations with 2–5 bars noted in most species, only in *S. aria*, *S. amabilis*, *S. dis-*

color (HEFw 139), *S. pohuashanensis* (FHOw 11046), *S. prattii* var. *tatsiensis* and *S. wallichii*, perforations are exclusively simple. Intervessel pits nonvestured, alternate, round to oval, 4–8(–10) µm in diameter, with slit-like apertures, apertures occasionally coalescent in a few species. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and slightly smaller. Helical thickenings well developed and closely spaced, throughout body of vessel elements. Gummy contents present in a few species. *Fibre-tracheids* 720–1150 (440–1550) µm long, F/V ratio 1.7–2.0(–3.3), medium thick- to very thick-walled, with distinctly bordered pits of 4–7 µm in diameter, in radial and tangential walls. Helical thickenings fine to conspicuous, present in *S. discolor*, *S. koehneana* and *S. pteridophylla*, but helical thickenings not observed in the remaining species or samples. *Parenchyma* moderately common to abundant, mainly apotracheally diffuse, but diffuse-in-aggregates and scanty paratracheal also present in most species, in 3–6 (2–11)-celled strands. *Rays* 7–16 (4–20)/mm, 1–3(–4)-seriate [mostly 1–2(–3)-seriate]. Uniseriate rays 2–8 cells high, composed of procumbent cells only, or with one row of square marginal cells; 2–3(–4)-seriate rays 130–350 (50–820) µm high, composed of procumbent cells only, or with 1(–2) row(s) of square marginal cells (mostly homogeneous, rarely heterogeneous III). *Crystals* sparse to abundant in a few species, prismatic, sometimes elongated in a few species, large, present in chambered axial parenchyma cells, one crystal in each enlarged, sclerified chamber; chains of up to 20 chambers, crystals not observed in *S. aria*, *S. aucuparia*, *S. chamaemespilus*, *S. coronata* (HEFw 1187), *S. discolor* (HEFw 139), *S. domestica*, *S. koehneana* (CAFw 509), *S. pohuashanensis*, *S. prattii*, *S. prattii* var. *tatsiensis*, *S. reducta*, *S. tianschanica*, *S. vilmorichii*, *S. wallichiia*, *S. wilsoniana*. *Pith flecks* rare to common in some species. Traumatic gum ducts absent.

59. **Spiraea** L. – See Zhang & Baas (1992) (Fig. 10)

Additional material studied: *S. alpina* Pall.: locality unknown, FHOw 12693 — *S. salicifolia* L.: see Zhang & Baas (1992); locality unknown, FHOw 12694, diam. 14 mm; Switzerland, Schweingruber s.n., diam. 10 mm.

Deciduous shrubs from north temperate regions, usually cultivated as ornamentals.

The wood anatomy of the above specimens is entirely within the range given for the Chinese material (Zhang & Baas, 1992).

60. **Stephanandra** Sieb. & Zucc. (Fig. 16)

Deciduous shrubs in East Asia, sometimes cultivated as ornamentals. See Zhang & Baas (1992).

61. **Stranvaesia** Lindl.

Evergreen trees or shrubs from Himalayas to China, often cultivated as ornamentals. See Zhang & Baas (1992).

62. Vauquelinia Correa ex Humb. (Fig. 13)

Material studied: *V. california* (Torr.) Sarg.: USA, Arizona, Tw 25945.

Trees or shrubs in Arizona and Mexico.

Growth rings distinct, marked by rows of radially flattened latewood fibres and differences in vessel diameter between latewood and subsequent earlywood. Wood semi-ring-porous. Vessels 200/sq.mm, 74% solitary, remainder in oblique and tangential pairs, angular, tangential diameter 32 (12–60) µm, radial diameter 42 (15–78) µm, walls 1–3 µm thick. Vessel element length 425 (380–460) µm. L/D ratio 13. Perforations exclusively simple in oblique end walls. Intervessel pits nonvestured, alternate, oval, 4–6 µm in diameter, with slit-like apertures. Vessel-ray and vessel-parenchyma pits similar to intervessel pits but half-bordered and smaller. Helical thickenings closely spaced, throughout body of most vessel elements. Gummy contents present in a few vessels. *Fibre-tracheids* 640 (500–700) µm long, F/V ratio 1.5, medium thick- to very thick-walled, with distinctly bordered pits of 3–5 µm in diameter, in radial and tangential walls. Helical thickenings absent. *Parenchyma* moderately abundant, apotracheally diffuse, diffuse-in-aggregates and scanty paratracheal, in 3–7-celled strands. *Rays* 12 (7–14)/mm, of two sizes: 1(–2)-seriate and 3–4-seriate. Uniseriate rays 1–4 cells high, composed of upright and square cells; multiseriate rays 220 (110–400) µm high, composed of procumbent body cells and 1–3 rows of square to upright marginal cells (mainly heterogeneous III, rarely II). Crystals, pith flecks and traumatic gum ducts absent.

TENTATIVE WOOD ANATOMICAL KEY TO THE GENERA OF THE ROSACEAE

1a. Multiseriate rays on average higher than 1.0 mm 2
b. Multiseriate rays on average lower than 1.0 mm 12
2a. Libriform fibres present 3
b. Libriform fibres absent 6
3a. Over 75% of the vessels solitary 4
b. Less than 30% of the vessels solitary 5
4a. Vessel frequency mostly higher than 65/sq.mm, fibre pits densely spaced in radial walls, crystals often present .... *Spiraea*
b. Vessel frequency lower than 65/sq.mm, fibre pits medium to sparsely spaced in radial walls, crystals absent .... *Holodiscus*
5a. Fibre pits mainly confined to radial walls .... *Cerasus (C. clarofolia)*
b. Fibre pits in radial and tangential walls .... *Sarcopoterium* p.p.
6a. Vessel wall thickenings present .... *Rosa*
b. Vessel wall thickenings absent 7
7a. Crystals absent 8
b. Crystals present 9
8a. Growth rings distinct, wood ring-porous to semi-ring-porous, multiseriate rays on average lower 2.0 mm .... *Sibiraea*
b. Growth ring faint to absent, wood semi-ring-porous to diffuse-porous, multiseriate rays on average usually higher than 3.0 mm .... *Rubus* p.p.

9a. Multiseriate rays on average lower than 1.5 mm, semi-ring-porous . *Coleogyne*
b. Multiseriate rays on average higher than 2.5 mm, diffuse-porous 10
10a. Multiseriate rays on average lower than 5.0. . . . . *Stephanandra*
b. Multiseriate rays on average higher than 7.0 mm 11
11a. Over 60% of vessels solitary, growth rings distinct to faint, intervessel pits alternate and occasionally also scalariform to opposite . . . . *Kerria*
b. Less than 50% of vessels solitary, growth rings faint to absent, intervessel pits alternate . . . . *Rubus (R. trianthus)*
12a. Rays 1–3(–4)-seriate or narrower 13
b. The widest rays not narrower than 4-seriate. 29
13a. Fibre pits in radial and tangential walls 14
b. Fibre pits mainly confined to radial walls 27
14a. Body cells of multiseriate rays square or square to procumbent. 15
b. Body cells of multiseriate rays procumbent only. 21
15a. Vessel wall thickenings present. 16
b. Vessel wall thickenings absent 17
16a. Thickenings in fibres absent, fibre pits densely spaced in radial walls . *Lindleya*
b. Thickenings in fibres present, fibre pits medium to sparsely spaced in radial walls . . . . *Prinsepia (P. sinensis)*
17a. Rays uniseriate or almost exclusively uniseriate 18
b. Rays 1–3(–4)-seriate 19
18a. Fibre pits densely spaced in radial and tangential walls . . . . *Alchemilla*
b. Fibre pits medium to sparsely spaced in radial and tangential walls . . *Sibbaldia*
19a. Multiseriate rays on average not lower than 0.5 mm . . . . *Dryas*
b. Multiseriate rays on average not higher than 0.4 mm 20
20a. Average fibre length not shorter than 600 µm, wood diffuse-porous (to semi-ring-porous) . . . . *Physocarpus*
b. Average fibre length shorter than 350 µm, wood ring-porous to semi-ring-porous . . . . *Chamaebatia, Fallugia, Potentilla*
21a. Either vessel wall thickenings present or crystals present, or both 22
b. Both vessel wall thickenings and crystals absent 24
22a. Multiseriate rays composed of procumbent cells only, or sometimes with one row of square marginal cells. . . . . *Amelanchier, Cercocarpus, Crataegus, Cydonia* p.p., *Docynia, Malus* p.p., *Mespilus, Peraphyllum, Polylepis, Pyrus* p.p., *Sorbus*
b. Multiseriate rays composed of procumbent body and 1–4(–6) rows of square to upright marginal cells 23
23a. Crystals present in ray cells . . . . *Kageneckia*
b. Crystals present in chambered axial parenchyma cells or absent *Chaenomeles, Cotoneaster* p.p., *Dichotomanthes, Eriobotrya, Eriolobus, Heteromeles* p.p., *Osteomeles, Photinia* A, *Pyracantha, Raphiolepis, Stranvaesia*
24a. Multiseriate rays composed of procumbent cells only, or sometimes with one row of square marginal cells. 25
b. Multiseriate rays composed of procumbent body cells and 1–4 rows of square to marginal cells 26

25a. Wood ring-porous to semi-ring-porous .... *Purshia*
b. Wood usually diffuse-porous
Cydonia p.p., *Hesperomeles, Malus* p.p., *Pyrus* p.p.
26a. Wood ring-porous .... *Cowania*
b. Wood diffuse-porous (sometimes to semi-ring-porous)
Chamaebatiaria, Cotoneaster p.p., *Heteromeles* p.p.
27a. Vessel wall thickenings absent, or confined to narrow element or to tails only, tangential vessel diameter on average not smaller than 100 µm .. *Pygeum* p.p.
b. Vessel wall thickenings usually well developed, tangential vessel diameter on average smaller than 80 µm 28
28a. Multiseriate rays composed of procumbent cells only, or rarely with one row of square marginal cells .... *Padus* p.p.
b. Multiseriate rays composed of procumbent body cells and with 1-4 rows of square to upright marginal cells .... *Cerasus* p.p., *Laurocerasus* p.p.
29a. Fibre pits in radial and tangential walls 30
b. Fibre pits mainly confined to radial walls 42
30a. Vessel wall thickenings absent 31
b. Vessel wall thickenings present 35
31a. Over 70% of the vessels solitary 32
b. Less than 50% of the vessels solitary 34
32a. Prismatic crystals present in chambered axial parenchyma cells
Photinia B (*P. benthamiana*)
b. Druses present in ray cells or crystals absent 33
33a. Druses present .... *Petrophytum*
b. Druses absent .... *Sorbaria*
34a. Crystals present .... *Sarcopoterium* p.p.
b. Crystals absent .... *Hagenia*
35a. Multiseriate rays composed of procumbent cells only, or sometimes with one row of square marginal cells 36
b. Multiseriate rays composed of procumbent body cells and 1–4(–7) rows of square to upright cells 38
36a. Crystals absent .... *Quillaja*
b. Crystals present 37
37a. Crystals present in chambered and enlarged axial parenchyma cells
Photinia B p.p.
b. Crystals present in non-enlarged ray cells .... *Adenostoma*
38a. Wood ring-porous, less than 60% of the vessels solitary
Amygdalus p.p., *Armeniaca* p.p.
b. Wood diffuse-porous (to semi-ring-porous), over 65% of the vessels solitary 39
39a. Crystals absent 40
b. Crystals present 41
40a. Wood semi-ring-porous .... *Vauquelinia*
b. Wood diffuse-porous .... *Lyonothamnus* p.p.
41a. Crystals present in chambered axial parenchyma cells
Lyonothamnus p.p., *Photinia* B p.p.

b. Crystals present in ray cells .... *Prinsepia (P. utilis)*

42a. Tangential vessel diameter on average not smaller than 100 μm, vessel wall thickenings absent, or confined to narrow element or to tails only, growth rings usually indistinct .... *Pygeum* p.p.

b. Tangential vessel diameter on average smaller than 80 μm, vessel wall thickenings usually well developed, growth rings usually distinct 43

43a. Parenchyma bands present........................ *Laurocerasus* B

b. Parenchyma bands absent 44

44a. Multiseriate rays composed of procumbent body cells only, or occasionally with one row of square marginal cells .... *Padus* p.p.

b. Multiseriate rays composed of procumbent body cells and 1–4(–6) rows of square to upright marginal cells 45

45a. Over 70% of the vessels solitary 46

b. Less than 60% of the vessels solitary 47

46a. Wood diffuse-porous .... *Osmaronia*

b. Wood ring-porous to semi-ring-porous .... *Exochorda*

47a. Wood ring-porous .... *Amygdalus* p.p., *Armeniaca* p.p.

b. Wood mostly diffuse-porous, rarely ranging to semi-ring-porous
Cerasus p.p., *Laurocerasus* A p.p., *Prunus* s.str.

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