WOOD ANATOMY OF THE BAPHIA GROUP (LEGUMINOSAE)

by

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Summary

The secondary xylem of 5 of the 6 genera belonging to the Baphia-group (viz. Airyantha, Baphiastrum, Leucomphalos, Dalhousiea and Baphia) and Ormosia (Leguminosae-Papilionoideae-Sophoreae) was studied, in order to aid generic delimitation in the Baphia-group.

Storied-structure features, vessel-member length, structure of rays and axial parenchyma, and presence of crystals were used to discuss generic delimitation. Based on the number of cells per axial parenchyma strand two groups are recognised: Airyantha and Baphiastrum have 2–4 cells, Leucomphalos, Dalhousiea and Baphia have fusiform parenchyma or 2-celled strands. Ormosia is very different from the other genera which closely resemble each other. A clear wood anatomical separation of the genera belonging to the Baphia-group is not possible. Especially Airyantha and Baphiastrum are almost identical wood anatomically and could be combined into a single genus. There are only minor differences between Leucomphalos, Dalhousiea and Baphia.

Key words: Airyantha, Baphia, Baphiastrum, Dalhousiea, Leucomphalos, Ormosia, systematic wood anatomy.

Introduction

The Leguminosae constitute a relatively natural taxon which can be divided into three subfamilies, viz. Caesalpinioideae, Papilionoideae and Mimosoideae. It is a matter of opinion whether these three groups should be treated as subfamilies or as separate families: Caesalpiniaceae, Papilionaceae and Mimosaceae (Hutchinson 1964).

The distribution of the three subfamilies is mainly tropical and subtropical. The Papilionoideae constitute a much larger group than the others and is the only one which is common in temperate regions. It has a worldwide range, with most of the woody representatives in the tropics and southern hemisphere. The herbaceous and shrubby members of the Papilionoideae usually are found in temperate regions, with a high concentration in Mediterranean regions (Heywood 1971). The Mimosoideae are woody; the Caesalpinioideae are primarily woody and rarely herbaceous.

The Papilionoideae consist of 10 to 11 tribes into which the genera are grouped on features of habit, leaf morphology and degree of fusion of the stamens (Chant 1979). The position of the tribe Swartzieae, if included in the Papilionoideae, and not in the Caesalpinioideae as is often done, is debatable. Also Sophoreae s.l. is a tribe of convenience between the Caesalpinioideae and the bulk of the Papilionoideae, and not sharply defined from either subfamily. The Sophoreae are mostly trees, shrubs, lianas or, rarely, herbs. The leaves are pulvinate, pinnately 1–many-foliolate or digitately 3-foliolate, sometimes stipellate; stamens free (Polhill 1981). The tribe contains nearly fifty genera, most of which are small and discrete, except for Baphia, Ormosia and Sophora. Sophoreae are divided into 8 groups, of which only the Sophora-group extends significantly outside the tropics. The Baphia-group, here considered, consists of 6 genera. Five genera (Airyantha, Baphiastrum, Bowringia, Dalhousiea and Leucomphalos) only include a few species (2, 2, 4, 3 and 1 respectively), whereas Baphia includes c. 60 species (Polhill 1981).
Several plant taxonomists feel that the number of genera in the *Baphia*-group has to be reduced. The present investigation was undertaken to find wood anatomical arguments for or against such a reduction. Samples of 5 genera of the *Baphia*-group were available; of *Bowringia* no samples could be obtained. Because *Airyantha* might belong to the *Ormosia*-group (with 3 genera, viz. *Ormosia, Pericopsis, Haplormosia*) of the Sophoreae, some *Ormosia* species were also investigated and compared with descriptions given by Reinders-Gouwentak and Rijsdijk (1968). Wood anatomical evidence is often useful in matters of generic, tribal and subfamilial delimitation. However, differences at the species level generally are less clearly expressed in the wood than in external features (Baretta-Kuipers 1981).

**Materials and Methods**

With the exception of *Ormosia* samples, this investigation is based on material from tropical Africa. The species studied are listed below, arranged alphabetically, viz. *Airyantha* with 1 species and 7 samples; *Baphia* with 20 species, 41 samples; *Baphiastrum* with 1 species, 5 samples; *Dalhousia* with 1 species, 5 samples; *Dalhousia* with 1 species, 2 samples; *Ormosia* with 5 species, 5 samples. In total 65 samples belonging to 29 species and 6 genera.

Anatomical features were studied in transverse, radial and tangential sections and in macerations. All sections were embedded in Kaiser's gelatin-glycerin. Means and ranges of the different characters are based on twenty-five or more individual measurements. Tangential vessel diameters are given and vessel member length was measured including the tails.

In the wood description quantitative data are given as a range of mean values of the different samples and/or species usually followed between brackets by extremes of all the samples together, or as a single mean value if there is no range (mean values are equal for the different samples of a species or for the different species of a genus).

Ground tissue percentages for libriform fibres and axial parenchyma together are estimated in cross sections; the remaining part is occupied by both vessels and ray tissue. The amount of axial parenchyma is given as a percentage of the ground tissue and of the total cross sectional area.

We have used the definition of libriform fibres given by Reinders (1935) and Jansonius (1940), which in this case equals the description of the IAWA Committee (1989).

Ends of axial parenchyma strands seen in tangential sections may be gable- or conical-shaped (Reinders-Gouwentak & Rijsdijk 1955). Near the top of gable-ended cells the longitudinal walls more or less abruptly bend into an oblique plane forming a roof-like top or gable (see Figs. 6, 16, 19). The angle of the gable may be obtuse but often is slightly less than 90 degrees; the angle at the abrupt bending is always obtuse. In the top part of conical ended cells the longitudinal walls gradually bend towards each other forming a cone-shaped cell top (see Fig. 24); the angle of the top is always sharp, often much less than 90 degrees. When the angle of the gable is small (about 30 degrees), the angle at the abrupt bending is large (about 165 degrees) and then the end cells of the parenchyma strands are almost conical-shaped and conical ones are then always also present in the species. The greater the angle of the gable-end, the smaller the abrupt bending angle, and the smaller the chance that also conical-ended top cells are present in the species.

Combination types of rays are according to Baretta-Kuipers (1973) based on features described by Reinders-Gouwentak and Rijsdijk (1955) and Reinders-Gouwentak (1955). Rays investigated by her and by us are nearly always homocellular, composed of procumbent cells, sometimes with one or a few rows of nearly square or upright cells at the marginal parts. Rays may be either uniseriate, or mostly uniseriate and partly multiseriate, or almost entirely multiseriate with short uniseriate marginal parts. In some species these different kinds of rays occur together, in others two of the three kinds are found. The ratio of the three kinds of rays can be used for differentiating between the species. Baretta-Kuipers (1973) distinguished four different combinations, viz.:
— combination I, in which the uniseriates dominate (more than 80%) and the partly or entirely multiseriates constitute a small part of the whole;
— combination II, in which most of the rays are uniseriate (60–80%), but quite a number are partly or wholly multiseriate;
— combination III, in which most of the rays are multiseriate (60–80%), but a considerable number are partly or entirely uniseriate;
— combination IV, in which multiseriates dominate (more than 80%) and the partly or wholly uniseriates constitute but a small part of the total number.

List of studied material
Each name is followed by an abbreviation (according to Stern 1988) of the location of wood sample and herbarium voucher, collector and number, geographical origin, habit, and stem diameter of the sample.

CTFw = Division d'anatomie des bois, Centre Technique Forestier Tropical, Nogentsur-Marne, France; Kw = Economic and Conservation Section, Herbarium, Royal Botanic Gardens, Kew, England; RBHw = Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg, Germany; Tw = Service d'anatomie des bois, Musée Royal de l'Afrique Centrale, Tervuren, Belgium; Uw = Systematic Botany, University of Utrecht, The Netherlands; WAGw = Department of Plant Taxonomy, Agricultural University, Wageningen, The Netherlands; WLw = Department of Plant Cytology & Morphology, Agricult. Univ., Wageningen, The Netherlands.

Airyantha schweinfurthii (Taub.) Brummitt [syn. Baphia schweinfurthii (Hutch. et Dalz.) Pellegr., Baphia schweinfurthii Taub., Baphia confusa Hutch. et Dalz.]: WAGw, Leeuwenberg 4232, Ivory Coast, liana, 1.5 cm; Tw, Louis 5997, Zaire, liana, 1 cm; WAGw, Breteler 1431 and 1765, Cameroun, liana, 3 and 1 cm resp.; WLw, Versteegh & Den Outer 108, 142, 551, Ivory Coast, liana, 4, 6 and 2 cm, resp.

Baphia bancoensis Aubrév.: CTFw & Tw, Détienne 204, Ivory Coast, small tree, over 10 cm. — B. bangweolensis R.E. Fries: Tw, Malaisse 9947, 11087, Zaire, liana to shrub, both 3 cm. — B. bequaertii De Wild.: Tw & Uw, Dechamps 1410, Angola, small tree, 8 cm; Tw, PHow 18235, Zambia, small tree, 5 cm. — B. cf. descampsii De Wild.: Kw, Jefford & Newbould 2071, Tanzania, shrub, 4 cm. — B. dewevrei De Wild.: Tw, Dechamps 1334, Congo, shrub, 2 cm. — B. gracilipes Harms: RBHw, Jentsch 84, Cameroun, small tree, over 10 cm. — B. laurentii De Wild.: Tw, Dechamps 222, Zaire, small tree, 4 cm. — B. laurifolia Baill.: Tw, Louis 3619, 7031, Zaire, shrub, both 1.5 cm; RBHw, Jentsch 87, Cameroun, shrub, over 1.5 cm. — B. leptobotrys Harms: Tw & CTFw, Floret 559, Cameroun, shrub, 10 cm. — B. marceliana De Wild.: Tw, Dechamps 129, Zaire, shrub, c. 10 cm. — B. massaiensis Taub.: Tw, Dechamps 1241, 1276, Angola, small tree, 5 cm; Uw, Dechamps 1326, Angola, small tree, 12 cm. — B. nitida Lodd.: Tw, Chalk, Sierra Leone, small tree, over 5 cm; Tw, Gavage, Gabon, small tree, over 5 cm; Tw, Détienne 53, Ivory Coast, small tree, over 5 cm; CTFw, Adam 5758, Guinée, small tree, 7 cm; WAGw, Bos 3390, Cameroun, small tree, 4 cm; WLw, Versteegh & Den Outer 47, Ivory Coast, small tree, 7 cm. — B. obovata Schinz: Uw, Seiner 20, Botswana, small tree, 10 cm. — B. polyantha Harms: Tw, Donis 2004, Zaire, shrub, 4 cm. — Baphia polygalacea (Hook.f.) Baker: WAGw, Breteler 1580, Cameroun, liana, 1 cm; Uw, Breteler 2991, Cameroun, liana, 2 cm. — B. pubescens Hook. f.: WLw, Versteegh & Den Outer 34, 316, Ivory Coast, small tree, 10 and 20 cm resp.; Tw, Louis 2218, 4032, Zaire, small tree, 2.5 and 1 cm resp.; Tw, Cellulco 243, Zaire, small tree, c. 6 cm. — B. spathacea Hook. f.: WLw, Versteegh & Jansen 757, Liberia, liana, 2 cm. — B. sylvatica Harms: WAGw, Meyer 15155, Cameroun, liana, 5 cm. — B. verschuerei De Wild.: Tw, Donis 2381, 2463, Zaire, shrub, 2.5 and 7 cm resp. — B. zenkeri Taub.: Uw & WLw, Breteler 2632, Cameroun, liana, 1 cm.

Baphiastrum brachycarpum Harms [syn. Baphiastrum boonei (De Wild.) Vermoesen, Baphia boonei De Wild.]: Tw, Louis 2274, 6062, Zaire, liana, both 1.5 cm; WAGw, Breteler 2457, Cameroun, liana, 3 cm; Uw, Breteler 2178, 2842, Cameroun, liana, 3 and 2 cm resp.
Dalhousiea africana S. Moore: WAGw, Breteler 6470, Gabon, liana, 2 cm; Tw, Louis 4134, Zaire, liana, 1 cm; Tw, Wagemans 1752, Zaire, liana, 2 cm; Tw, Toussaint 159, Zaire, liana, 2.5 cm; Tw, Ishikawa et al. 48, Zaire, liana, 1 cm.

Leucophalos capparidus Bentham ex Planch.: WAGw, Bos ?, Cameroon, a liana-shrub grown in the greenhouse at Wagenin- gen from seed collected by Bos, 1 cm; WAGw, Louis, Breteler & De Bruyn 1320, Gabon, liana, 1 cm.

Ormosia callavensis Azaola: WLw, formerly Dutch Colonial Forestry Service, BW 4251, West New Guinea (Irian Jaya, Indonesia), large tree, over 10 cm. — *O. coccinea* Jack.: WLw, Stahel 357, Surinam, large tree, over 12 cm. — *O. costulata* (Miq.) Klein.: WLw, Stahel 83, Surinam, large tree, over 12 cm. — *O. coutinhoi* Ducke: WLw, Welvaartsfonds WS 1025, Surinam, large tree, over 40 cm. — *O. fastigiata* Tul.: WLw, Stahel 235, Surinam, large tree, over 12 cm.

**Descriptions**

A general description of the secondary xylem of the investigated *Baphia* samples, subdivided in two habit categories, is given below; in the description of lianas differences with the erect shrubs and trees are emphasised. This is followed by short descriptions of *Dalhousiea, Leucophalos, Baphiastrum, Airy-antha* and *Ormosia*, highlighting differences with *Baphia* (see also Table 1).

**Baphia** (20 species, 41 samples, Figs. 1–10)

**Shrubs and small trees** [only *B. laurentii* (Gottwald Z25) is a large tree] (15 species, 33 samples)

Growth ring boundaries generally present (hardly visible in *B. laurifolia*), distinct (in 80% of the samples) or more or less indistinct (in 18% of the samples), marked by terminal parenchyma and/or smaller radial diameters of the latewood fibres; wood diffuse-porous.

Storied structure of both rays and axial elements (in 25% of the samples), of only axial elements (in 50% of the samples), or only a very slight tendency of storied structure of axial parenchyma to nonstoried (25% of the samples); fibres are usually not storied; storied rays of adjacent tiers often fused.

Vessels solitary and in short radial multiples, usually also present in radial multiples of more than four vessels (in 62% of the samples) and in clusters (in 83% of the samples); in *B. laurifolia* (Jentsch 87), *B. marcellana* and *B. nitida* (Détienne 53) the ves­ sels are only solitary; round to oval in cross section; number per square mm 5–42 (3–63) [5 in *B. laurifolia* (Jentsch 87) and *B. marcellana* to 42 in *B. massaiensis* (Dechamps 1241)]; tangential diameter 60–140 (15–310) μm (60 μm in *B. cf. descampsii* and *B. de­ wevei* to 140 μm in *B. bequaerti*); thickness of walls usually c. 6 μm or less, in *B. massai- ensis* 8 μm and very thick-walled (14 μm) in *B. polyantha*. Vessel member length 155–340 (85–440) μm [155 μm in *B. massaiensis* (Dechamps 1326) to 340 μm in *B. gracilipes*]; perforations exclusively simple, slightly oblique to transverse; intervessel pits bordered, very crowded, horizontal diameter 4–12 μm (4 μm in *B. gracilipes* to 12 μm in *B. bequaerti*). In addition to intervessel contact, vessels are usually in contact with axial and ray parenchyma, less frequently with libriform fibres. Vessel-ray pitting half-bordered, nearly always vested (observations with light microscopy), horizontal diameter 4–14 μm (4 μm in *B. gracilipes* to 14 μm in *B. bequaerti*); vessel–parenchyma pits half-bordered. Brown contents sometimes present in *B. polyantha*.

Ground tissue of libriform fibres together with axial parenchyma forming about 80% of the total cross sectional area; usually also some vascular tracheids present in association with clusters. Vessels and rays together occupy the remaining 20%.

Libriform fibres, thin- to thick-walled, sometimes very thick-walled, wall thickness 4–9 μm (9 μm in *B. obovata*), diameter of lumina 1–4 μm (4 μm in *B. verschuerenii*); nonseptate; with simple to minutely bordered pits with slit-like inner apertures, moderately numerous, common in both radial and tangential walls but usually more frequent in radial ones; intercellular spaces almost always absent; fibres with gelatinous layers present in 38% of the samples.

Parenchyma abundant, forming 25–45% of the ground tissue [25% in *B. gracilipes* to...
45% in *B. laurifolia* (Jentsch 87)], or 20–36% of the total cross section; diffuse and diffuse-in-aggregates in 42% of the samples; in long uni- to biseriate tangential bands (usually terminal) in 56% of the samples; in long multiseriate tangential bands 2–7 (1–12) cells wide (7 cells wide in *B. pubescens*) in all samples; vasicentric parenchyma or incomplete sheaths around the vessels always present, in *B. massaiensis* (Dechamps 1241) and *B. pubescens* paratracheal parenchyma more or less aliform. Parenchyma strands without crystals and not immediately bordering upon vessels fusiform or composed of two cells, except in *B. dewevrei*, *B. gracilipes* and *B. obovata* where 2–4 cells are present per strand; end cells of strands exhibit gable-ends in tangential section or are almost exclusively provided with gable-ends, with the exception of *B. gracilipes*, *B. laurentii* (Dechamps 222), *B. laurifolia*, *B. marceliana*, *B. obovata* and *B. polyantha* where gable-ends and conical-ends occur equally frequent; strand length 165–335 μm (165 μm in *B. obovata* to 335 μm in *B. polyantha*). Brown cell contents present in *B. bequaertii* and *B. massaiensis*.

Rays both uni- and multiseriate with short uniseriate marginal parts, but multiseriate ones dominate [71% of the samples with combination type IV of Baretta-Kuipers (1973)]. In *B. dewevrei*, *B. laurifolia*, *B. leptobotrys*, *B. pubescens* (Louis 2218) and *B. verschuerenii* most rays are multiseriate (combination type III), while in *B. nitida* (V. & O. 47) most rays are uniseriate (combination type II). Width 1.5–6 (1–12)-seriate [1.5-seriate in *B. laurifolia* (Jentsch 87) and *B. nitida* (V. & O. 47) to 6-seriate in *B. pubescens* (V. & O. 316)]; composed of predominantly procumbent cells with regularly some square and/or upright cells forming the uniseriate marginal parts of the multiseriate rays; in most samples 30–50% of the rays have marginal cells which are higher than the body cells, less than 30% in *B. dewevrei* and *B. pubescens* (V. & O. 316), 55% or more in *B. gracilipes*, *B. laurentii*, *B. laurifolia*, *B. obovata* and *B. pubescens* (V. & O. 34); height 180–1100 (35–2100) μm (180 μm in *B. leptobotrys* to 1100 μm in *B. bequaertii*; only in *B. bequaertii* the average ray height is high, in all other species it is less than 790 μm); 4–13 (3–14) per tangential mm (4 in *B. bequaertii* to 13 in *B. leptobotrys*). Rays tangentially wider when crossing tangential bands of axial parenchyma in *B. marceliana*; ray parenchyma cells with brown contents in *B. bequaertii*, *B. massaiensis* and *B. pubescens* (Louis 2218).

Crystals usually present, absent in *B. massaiensis* (Dechamps 1241) and *B. nitida* (Bos 3390); prismatic, exclusively solitary; in chambered axial parenchyma cells only (61% of the samples), in both axial and ray parenchyma cells (27% of the samples), or only in ray parenchyma cells (usually in procumbent cells, but also in marginal square or upright cells; 6% of the samples); number of compartments per crystalliferous parenchyma strand 4–18 (18 in *B. polyantha*). Pith flecks sometimes present (in 17% of the samples).

Tyloses, thick-walled, sometimes present in *B. pubescens* (Louis 2218).

**Lianas** (5 species, 8 samples)

Growth ring boundaries present (hardly visible in *B. zenkeri*).

Storied structure of axial elements (axial parenchyma and vessel elements; fibres usually not storied), but in *B. sylvatica* of rays and axial elements.

Vessels solitary, in short radial multiples, in radial multiples of more than four vessels and in clusters; in *B. bangweolensis* mainly in clusters; usually of two size classes; number per square mm 16–135 (10–150) (16 in *B. spathacea* to 135 in *B. bangweolensis*); tangential diameter 60–160 (20–240) μm (60 μm in *B. bangweolensis* and *B. sylvatica* to 160 μm in *B. spathacea*); thickness of walls in *B. zenkeri* 7 μm. Vessel member length 175–370 (140–440) μm (175 μm in *B. bangweolensis* to 370 μm in *B. spathacea*). Horizontal diameter of intervessel pits and vessel-ray pits 6–10 μm (6 μm in *B. sylvatica* to 10 μm in *B. bangweolensis* and *B. polygalacea*).

Ground tissue of libriforim fibres together with axial parenchyma, forming about 70% of the total cross sectional area.

Libriforim fibres with wall thickness of 4–6 μm, diameter of lumina 3 μm; gelatinous layers present in half of the samples, abundant in *B. bangweolensis*.
Parenchyma forming 25–50% of the ground tissue (25% in *B. bangweolensis* to 50% in *B. spathacea*), or 20–40% of the total cross section; diffuse and diffuse-in-aggregates in *B. zenkeri*; in short multiseriate tangential bands with a width of 2 (1–5) cells in *B. bangweolensis*, *B. polygalacea* and *B. zenkeri*, in long multiseriate tangential bands 3–5 (1–7) cells wide in *B. spathacea* and *B. sylvatica*; aliform parenchyma present in *B. spathacea*. Parenchyma strands without crystals and not immediately bordering upon vessels fusiform or composed of two cells; strand length 200–310 μm (200 μm in *B. bangweolensis* to 310 μm in *B. spathacea*). Rays in all samples of combination type IV of Baretta-Kuipers (1973); in *B. polygalacea* and *B. zenkeri* uniseriate rays almost absent. Width 2–6 (1–15)-seriate (2-seriate in *B. sylvatica* to 6-seriate in *B. bangweolensis* and *B. zenkeri*); square and upright cells frequently forming uniseriate marginal parts of the multiseriate rays in *B. polygalacea* and *B. zenkeri*; height 190–2100 (55 up to more than 10,000) μm (190 μm in *B. sylvatica* to 2100 μm in *B. zenkeri*; only in *B. sylvatica* the average height is low, in all other species it is over 1070 μm); 4–10 (3–12) per tangential mm (4 in *B. bangweolensis* to 10 in *B. sylvatica*); aggregate rays, often with stone cell nests, present in *B. bangweolensis*.

Crystals always present, in chambered axial parenchyma cells only (in one sample), in both axial and ray parenchyma cells (in three samples) or only in ray parenchyma cells (in four samples); number of compartments per crystalliferous parenchyma strand 4–16 (4 in *B. zenkeri* to 16 in *B. spathacea*). Pith flecks and tyloses absent.

**Dalhousia africana** (5 samples; Figs. 11, 12, 14)

Growth ring boundaries absent or indistinct. Storied structure of only axial elements (axial parenchyma and vessel elements; fibres are usually not storied) present in all samples. Vessels solitary, in radial multiples of less than four vessels, and in clusters; in two size classes; number per square mm 30–75 (25–85); tangential diameter 140–160 (15–395) μm; vessel member length 240–270 (200–320) μm. Horizontal diameter of intervessel pits 10 μm, vessel-ray pits 11 μm.

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Legend to figures 1–24. Secondary xylem of some *Baphia*-group representatives and *Ormosia*. In TS the position of the cambium is near the top side of the photograph.

Figs. 1–10. *Baphia* species. – 1: *B. marcelliana*, shrub, TS, × 20. Growth ring boundaries distinct, marked by terminal parenchyma; vessels nearly always solitary; within *Baphia* one of the two samples with the lowest number (5) of vessels per square mm; long multiseriate tangential bands of axial parenchyma abundant. – 2: *B. polyantha*, shrub, TS, × 20. Vessels very thick-walled (14 μm), frequently in radial multiples of more than four; vessel diameter 115 (25–310) μm, representing the widest range within the investigated *Baphia* species. – 3: *B. laurentii*, large tree, TS, × 20. – 4: *B. laurentii*, small tree, RLS, × 67. Multiserate ray composed of procumbent cells with square and/or upright cells forming the short uniseriate marginal parts as well as the contact areas with vessels and axial parenchyma. – 5: *B. massaiensis*, small tree, TS, × 20. Vessels frequently in radial multiples of more than four. – 6: *B. massaiensis*, small tree, TLS, × 67. Tendency to storied structure of axial parenchyma and vessel elements; parenchyma strands composed of two cells; top of end cells gable-shaped. – 7: *B. bequaertii*, small tree, TS, × 20. Rather short tangential bands of axial parenchyma, somewhat ‘festooned’ like in *Dalhousia*; axial and ray parenchyma often with dark contents. – 8: *B. sylvatica*, liana, TS, × 20. Within *Baphia* the species belongs to a group with the lowest (60 μm) average vessel diameter. – 9 & 10: *B. sylvatica*, liana, RLS and TLS respectively, both × 67. Storied structure of rays and axial elements (fibres more or less storied); parenchyma fusiform or in two celled strands; top of end cells gable-shaped; crystals in chambered axial parenchyma cells, 4 or 8 compartments per strand.
Ground tissue of libriform fibres together with axial parenchyma, forming about 50% of the total cross sectional area.

Libriform fibres with wall thickness of 6–8 μm, mean diameter of lumina 1 μm; gelatinous layers not observed.

Parenchyma forming 40–60% of the ground tissue, or 20–30% of the total cross section; in long, 3–4 (2–10) cells wide, tangential bands often ‘festooned’ (arranged in tangential arcs) and in complete or incomplete sheaths around the vessels. Parenchyma strands without crystals and not immediately bordering upon vessels fusiform or composed of two cells; strand length 240–290 μm. Brown cell contents present.

Rays in all samples of combination type IV of Baretta-Kuipers (1973). Width 5–7 (1–21)-seriate; marginal cells higher than body cells in 35–50% of the rays; height 1600–2345 (85–7500) μm; 3 (2–4) per tangential mm. Brown cell contents present. Fibres often bending horizontally in a radial direction into wider rays, between the ray parenchyma cells (see Fig. 14).

Crystals always present in rays and chambered axial parenchyma cells with 12–20 compartments per strand.

Pith flecks and tyloses absent.

**Leucophalos capparideus** (2 samples; Figs. 15–17)

Growth ring boundaries distinct.

Storied structure of only axial elements (axial parenchyma and vessel elements; fibres usually not storied) irregularly present.

Vessels solitary, in short radial multiples, in radial multiples of more than four vessels, rarely in clusters; number per square mm 32–45 (20–55); tangential diameter 50–110 (15–220) μm, vessel member length 260–270 (110–360) μm. Horizontal diameter of intervessel pits 11 μm, vessel-ray pits 6–7 μm.

Ground tissue of libriform fibres together with axial parenchyma, forming about 80% of the total cross sectional area.

Libriform fibres with wall thickness of 4 μm, diameter lumina 4 μm, gelatinous layers present.

Parenchyma forming 65% of the ground tissue, or 52% of the total cross section; in long, 3–4 (1–9) cells wide, tangential bands and in complete or incomplete sheaths around the vessels. Parenchyma strands without crystals and not immediately bordering upon vessels fusiform or composed of two cells; strand length 280–320 μm.

Rays in all samples of combination type III of Baretta-Kuipers (1973). Width 2–4 (1–8)-seriate; marginal cells higher than body cells in 60% of the rays; height 620–950 (85–4800) μm; 3–5 (2–6) per tangential mm.

Crystals always present, only in chambered axial parenchyma cells with c. 16 compartments per strand.

Pith flecks and tyloses absent.

**Baphiastrum brachycarpum** (5 samples; Figs. 13, 18, 19)

Growth ring boundaries always present, inconspicuous.
Storied structure of only axial elements (axial parenchyma and vessel elements; fibres are usually not storied) present in all samples; in Louis 6062 only with a very slight tendency towards storying.

Vessels solitary and in short radial multiples, but radial multiples of more than four vessels and clusters always rarely present; in two size classes; number per square mm 17–53 (14–65) (17 in Breteler 2842 to 53 in Louis 6062); tangential diameter 70–185 (15–270) μm (70 μm in Louis 6062 to 185 μm in Breteler 2842); vessel member length 190–320 (110–360) μm; vessel walls very thick-walled (11 μm) in Breteler 2842. Horizontal diameter of intervessel pits 10 μm, of vessel–ray pits 6–10 μm.

Ground tissue of libriform fibres together with axial parenchyma, forming about 50% of the total cross sectional area.

Libriform fibres with mean wall thickness of 4–6 μm, mean diameter of lumina 3 μm; gelatinous layers present in 80% of the samples.

Parenchyma forming 35–45% of the ground tissue (35% in Louis 6062 to 45% in Breteler 2842), or 18–23% of the total cross section; diffuse and diffuse-in-aggregates in one sample; in long uni- to biseriate tangential bands (terminal) in one sample, in short multiseriate tangential bands with an average width of 2 (1–4) cells in two samples; in long multiseriate tangential bands 2–4 (1–7) cells wide (4 cells wide in Louis 6062), and with vasicentric parenchyma or incomplete sheaths around the vessels in all samples. Parenchyma strands without crystals and not immediately bordering upon vessels, composed of 2–4 cells; strand length 210–340 μm (210 μm in Louis 6062 to 340 μm in Breteler 2457 and 2178). Axial parenchyma of Breteler 2457 and 2178 sometimes not lignified.

Rays in all samples of combination type IV of Baretta-Kuipers (1973). Width 3–7 (1–20)-seriate (3-seriate in Louis 6062 to 7-seriate in Breteler 2178 and 2842); marginal cells higher than body cells in 55–65% of the rays; height 380–9000 (40 up to over 10,000) μm (380 μm in Louis 6062 to 9000 μm in Breteler 2842); 3–8 (2–10) per tangential mm (8 in Louis 6062). Rays with stone cell nests in Breteler 2178; ray parenchyma cells with brown contents in Louis 6062.

Crystals in chambered axial parenchyma cells only (in one sample), in axial and ray parenchyma cells (in three samples), or absent (in one sample); number of compartments per crystalliferous parenchyma strand 8–12.

Pith flecks and tyloses absent.

Louis 6062 differs from other Baphiastrum-species in many aspects.

Airyantha schweinfurthii (7 samples; Figs. 20, 21, 23)

Growth ring boundaries always present, distinct (only in Breteler 1431 more or less indistinct).

Storied structure of only axial elements (axial parenchyma and vessel elements; fibres are usually not storied) present in all samples.

Vessels solitary and in radial multiples; radial multiples of more than four vessels and clusters also present in six samples; number per square mm 11–42 (8–55) (11 in V. & O. 142 to 42 in Louis 5997); tangential diameter 55–160 (15–250) μm (55 μm in Louis 5997 to 160 μm in Breteler 1431), in two size classes; vessel member length 260–290 μm; vessels very thick-walled (14 μm) in Breteler 1765. Horizontal diameter of intervessel pits 10 μm, vessel–ray pits 6–12 μm.

Ground tissue of libriform fibres together with axial parenchyma, forming about 70% of the total cross sectional area.

Libriform fibres with mean wall thickness of 4–6 μm, diameter of lumina 3 μm; fibres with gelatinous layers present in 60% of the samples.

Parenchyma forming 15–45% of the ground tissue (15% in V. & O. 142 to 45% in Breteler 1431 and 1765), or 11–32% of the total cross section; diffuse and diffuse-in-aggregates in six samples; in long uni- to biseriate tangential bands (terminal) in four samples, in short multiseriate tangential bands with an average width of 3 (1–4) only in V. & O. 142; in long multiseriate tangential bands 2–3 (1–6) cells wide in all samples (more or less so in V. & O. 142); in Leeuwenberg 4232 and V. & O. 142 vasicentric parenchyma more or less aliform. Parenchyma

strands without crystals and not immediately bordering upon vessels, composed of 2–4 cells; strand length 280–310 μm. Axial parenchyma with brown cell contents in all samples.

Rays in all samples of combination type IV of Baretta Kuipers (1973), except in Louis 5997 of combination type I. Width 1–5 (1–6)-seriate (uniseriate in Louis 5997 to 5-seriate in Breteleur 1431 and 1765), marginal cells higher than body cells in 30–40% of the rays; height 650–1400 (85–3600) μm (650 μm in Leeuwenberg 4232 to 1400 μm in Breteleur 1765); 5–9 (4–10) per tangential mm (9 in Louis 5997). Procumbent ray parenchyma cells short in Leeuwenberg 4232. Ray parenchyma cells with brown contents in all samples.

Crystals absent in five samples, or only in chambered axial parenchyma (Breteleur 1432 and 1765); number of compartments per crystalliferous parenchyma strand 6–10; prismatic or rhomboidal in shape.

Pith flecks and tyloses absent.
Ormosia (5 species, 5 samples; Figs. 22, 24)

Growth ring boundaries always present, mostly distinct; indistinct in O. coccinea and O. costulata.
Storied structure absent.
Vessels often solitary (80% of the vessels) and in short radial multiples and clusters, in O. coccinea, O. costulata and O. fastigiata also present in radial multiples of more than four vessels; number per square mm 2 (1–4); tangential diameter 140–250 (50–360) μm (140 μm in O. fastigiata to 250 μm in O. calavensis); vessel member length 330–450 (170–600) μm (330 μm in O. coccinea to 450 μm in O. calavensis). Horizontal diameter of intervessel pits 8 μm, vessel-ray pits 9 μm. Brown contents often present.

Ground tissue of libriform fibres together with axial parenchyma, forming about 90% of the total cross sectional area.
Libriboform fibres with mean wall thickness of 4–10 μm (10 μm in O. costulata); diameter of lumina 4–18 μm (4 μm in O. coccinea to 18 μm in O. calavensis); gelatinous layers not observed.
Parenchyma forming 20–40% of the ground tissue (20% in O. calavensis to 40% in O. coccinea and O. costulata), or 18–36% of the total cross section; diffuse and diffuse-in-aggregates scarcely present in three of the samples; long uni- and biseriate tangential bands (terminal) and short multiseriate tangential bands absent; in long multiserate tangential bands 4–7 (2–12) cells wide (7 cells wide in O. coutinhoi); aliform to confluent vasicentric parenchyma abundantly present. Parenchyma strands without crystals and not immediately bordering upon vessels, composed of 2–4 cells; end cells of strands exhibit conical-ends in tangential section or conical-ends are more frequently present than gable-ends; strand length 400–560 μm (400 μm in all samples except O. costulata). Brown cell contents absent.

Rays in all samples of combination type IV of Baretta-Kuiipers (1973). Width 2–3 (1–4)–seriate; upright cells almost absent in O. coutinhoi; marginal cells higher than body cells in 55–75% of the rays; height 300–450 (80–960) μm (450 μm in O. coutinhoi); 4–6 (3–7) per tangential mm.

Crystals always present in axial parenchyma; number of compartments per crystalliferous parenchyma strand 4–8 (4 in O. calavensis to 8 in the other samples).
Pith flecks sometimes present in O. costulata and O. fastigiata; tyloses absent.

Discussion
Species in this study of Dalhousiea, Leucophalos, Baphiastrum and Airyana are lianas, like 5 species of Baphia. The remaining 15 Baphia species are shrubs or small trees. Only the samples of the Ormosia-species are from large trees. In climbing species the percentage of surface area occupied by vessels, as seen in transverse section, is much higher than in non-climbing species (Ter Welle 1985). This is due either to an increase in number of vessels per square mm and/or to an increase in vessel diameter. Lianas belonging to the Connaraceae, for instance, in general have wider vessels and shorter vessel members than species of shrubs, treelets or trees of the same family (Dickison 1972). In Baphia climbing species possess more vessels per square mm than shrubs or small trees. Different vessel size classes are also more frequently represented in climbers and dwarf shrubs of dry sites than in shrubs and trees of mesic sites (Baas 1990). This is also the case in Baphia. In climbing species ray height and ray width are also larger than in non-climbing species (Ter Welle 1985). In Baphia lianoid species are mainly provided with higher rays than species of shrubs and small trees.

Senn (1943) stated that in Leguminosae the vessel arrangement varies considerably. He also assumes that a vessel arrangement in clusters or long radial multiples, usually composed of narrower vessels than the solitary ones and those in short radial multiples, is associated with a xeric habitat. Baretta-Kuiipers (1981) concluded that variation in vessel diameter and number per square mm is of interest for identification purposes and may be habitat related, but is not of much taxonomic value. Features which are considered significant in the distinction of leguminous genera according to Senn (1943), Normand (1950) and Baretta-Kuiipers (1973, 1981, 1982) are those of ray and axial parenchyma.
Table 1. Variation of selected qualitative and quantitative wood characters of the investigated genera.

<table>
<thead>
<tr>
<th>Characters \ Genera</th>
<th>Baphia (studies, small trees)</th>
<th>Baphia (intra.)</th>
<th>Dalhousia</th>
<th>Leucomphalos</th>
<th>Baphiastrum</th>
<th>Airyantia</th>
<th>Ormosia</th>
</tr>
</thead>
<tbody>
<tr>
<td>Storied structure</td>
<td>p + r, p</td>
<td>p + r, p</td>
<td>p</td>
<td>p</td>
<td>p</td>
<td>p</td>
<td>p</td>
</tr>
<tr>
<td>Vessels</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number per sq.mm</td>
<td>4–42</td>
<td>16–135</td>
<td>30–75</td>
<td>32–45</td>
<td>17–53</td>
<td>11–42</td>
<td>2</td>
</tr>
<tr>
<td>tangential diam. (µm)</td>
<td>60–140</td>
<td>60–160</td>
<td>140–160</td>
<td>50–180</td>
<td>70–185</td>
<td>55–160</td>
<td>140–250</td>
</tr>
<tr>
<td>Rays</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>seriate</td>
<td>IV, (III)</td>
<td>IV</td>
<td>IV</td>
<td>III</td>
<td>IV</td>
<td>IV</td>
<td>IV</td>
</tr>
<tr>
<td>combination type</td>
<td></td>
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</tr>
<tr>
<td>Axial parenchyma</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>no. of cells per strand with pred.</td>
<td>1–2</td>
<td>1–2</td>
<td>1–2</td>
<td>1–2</td>
<td>2–4</td>
<td>2–4</td>
<td>2–4</td>
</tr>
<tr>
<td>gable-ends</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>width of long tangential bands (cells)</td>
<td>2–7</td>
<td>3–5</td>
<td>3–4</td>
<td>3–4</td>
<td>2–4</td>
<td>2–3</td>
<td>4–7</td>
</tr>
<tr>
<td>aliform and/or confluent</td>
<td>(+)</td>
<td>(+)</td>
<td>–</td>
<td>–</td>
<td>(+)</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>arr. in tangential arcs</td>
<td>(+)</td>
<td>–</td>
<td>+</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td>Crystals</td>
<td>cp,cp+r, r</td>
<td>cp,cp+r, r</td>
<td>cp+r</td>
<td>cp</td>
<td>cp, cp+r</td>
<td>cp</td>
<td>cp*</td>
</tr>
</tbody>
</table>

Symbols and abbreviations: Quantitative data are given as a range of mean values for different species and/or samples of the genus, or as a single mean value.

+ = and; + = present; -: absent; (+) = character poorly developed; * = often only 1 or 2 cells of a strand chambered and with crystals; cp = chambered axial parenchyma cells; diam. = diameter; no. = number; p = axial parenchyma; pred. = predominant (more than 80% of the end cells of the strands); r = rays or ray parenchyma cells; sq. = square.

From the descriptions and Table 1 it is clear that there are only minor differences between the genera of the Baphia-group concerning these features. In their macroanatomy several genera in this group are also almost identical (Polhill 1981; Breteler, personal communication).

Using wood anatomy, the three leguminous subfamilies are separable according to Reinders-Gouwentak and Rijsdijk (1955) but the Swartzieae show intergrading features of the Papilionoideae and the Caesalpinioideae. The characteristics in question are storied-structure features (storied structure and units of the storied structure complex), the shape of the marginal ray cells and ray structure. Two units of the storied structure complex are especially important, viz. the shape of the end cells of the parenchyma strands in tangential section and the low number of cells in the parenchyma strands. Using the above mentioned criteria, all samples of Dalhousia, Leucomphalos, Baphiastrum and Airyantia constitute one group which has to be placed in the Papilionoideae. Most Baphia samples were also easily grouped into the Papilion-
The genera of the Baphia-group can be arranged in two groups; Airyantha and Baphiastrum with 2–4 cells per axial parenchyma strand, Leucomphalos, Dalhousiea and Baphia with fusiform parenchyma or 2-celled strands. In other aspects the genera of the Baphia-group resemble each other very much. A clear distinction of the genera based on wood anatomy, is not very well possible. Airyantha and Baphiastrum especially are almost identical. This can be used to support a merger of the two genera. There are only minor differences between the genera Leucomphalos, Dalhousiea and Baphia. The wood anatomical diversity of Baphia is relatively large, almost entirely overlapping the limited structural ranges of the other genera. However, storied structure of all elements is regularly present only in Baphia, and tangential parenchyma bands are wider. Dalhousiea is usually distinguished from Leucomphalos and Baphia by the presence of axial parenchyma arranged in tangential arcs (’festooned’); Leucomphalos is the only genus in which most of the rays are multisieriate, but a considerable number are partly or entirely uniseriate (combination type III).

Acknowledgements

We wish to express our appreciation to the curators of the following wood collections for providing valuable research materials: Royal Botanic Gardens, Kew; Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg; Musée Royal de l’Afrique Centrale, Tervuren; Systematische Plantkunde, Utrecht; Plantentaxonomie, Wageningen.

References


Joel Reinders-Gouwentak and Reinders-Gouwentak and Rijsdijk (1955) are not always appropriate for African species, since they are mainly based on material from Java (Indonesia; Moll & Janssoni

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From Table 1 it is clear that Ormosia stands apart from the other genera; storied structure is absent, end cells of parenchyma strands exhibit conical-ends or conical-ends are more frequently present than gable-ends, and Ormosia has a large percentage of high marginal ray cells. All this implies that the genus is intermediate between the two subfamilies Papilionoideae and Caesalpinioideae according to characteristics given by Reinders-Gouwentak and Rijsdijk (1955). Also the percentage of cross sectional area occupied by vessels (somewhat wider but in a small number per square mm) is much smaller than in the other genera; vessels are also more often solitary (see also Reinders-Gouwentak & Rijsdijk 1968). This, however, may be caused by the fact that Ormosia is represented by large trees, the other genera by lianas or in the case of Baphia also by shrubs and sometimes small trees. Vessel members in Ormosia are longer than in the other genera; rays are narrow and low; axial parenchyma is often aliform and/or confluent; crystals usually are only present in one or two chambered cells of an axial parenchyma strand.

The genera of the Baphia-group can be arranged in two groups; Airyantha and Baphiastrum with 2–4 cells per axial parenchyma strand, Leucomphalos, Dalhousiea and Baphia with fusiform parenchyma or 2-celled strands. In other aspects the genera of the Baphia-group resemble each other very much. A clear distinction of the genera based on wood anatomy, is not very well possible. Airyantha and Baphiastrum especially are almost identical. This can be used to support a merger of the two genera. There are only minor differences between the genera Leucomphalos, Dalhousiea and Baphia. The wood anatomical diversity of Baphia is relatively large, almost entirely overlapping the limited structural ranges of the other genera. However, storied structure of all elements is regularly present only in Baphia, and tangential parenchyma bands are wider. Dalhousiea is usually distinguished from Leucomphalos and Baphia by the presence of axial parenchyma arranged in tangential arcs ('festooned'); Leucomphalos is the only genus in which most of the rays are multisieriate, but a considerable number are partly or entirely uniseriate (combination type III).

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