WOOD ANATOMY OF THE TRIBE SWARTZIEAE
WITH COMMENTS ON RELATED PAPILIONOID AND
CAESALPINIOID LEGUMINOSAE

by

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SUMMARY

The tribe Swartzieae, like the Sophoreae is a basal member of the Papilionoid legumes, lying at the boundary between this subfamily and the Caesalpinioideae (Polhill & Raven 1981). Recent surveys have investigated the wood anatomy of 42 out of the 48 genera in the Sophoreae (Fujii & Baas 1992; Fujii et al. 1994; Gasson 1994; Den Outer & Van Veenendaal 1992). Similar work is needed on the Swartzieae (11 genera), and in the Caesalpinioideae on Caesalpinieae (47 genera), Amherstieae (25 genera) and Detarieae (55 genera). The wood anatomy of Swartzieae is described here, the genus Baphiopsis apparently for the first time, and comparison is made especially with Sophoreae. There is no clear delimitation between the two tribes, which is confirmed by cladistic analysis on 12 wood characters of Swartzieae alone, then combined Swartzieae and Sophoreae. Baphiopsis (Swartzieae) and Baphia (Sophoreae) are so similar anatomically that they should perhaps be in the same tribe, and Bocoa is not uniform anatomically, and may not be a coherent genus. The data presented here will assist in reaching conclusions on the correct delimitation of some genera and tribes in the Papilionoid legumes.

Key words: Swartzieae, Baphiopsis, generic wood descriptions.

INTRODUCTION

The tribe Swartzieae is placed in the Legume subfamily Papilionoideae by Polhill and Raven (1981), and according to Cowan (1981) consists of 11 genera (see Table 1). With the tribe Sophoreae, which contains 48 genera (Polhill 1981a), it lies at the boundary of the Papilionoideae with the Caesalpinioideae. The phylogenetic relationships of the Swartzieae have been explored by Herendeen (1995), including 19 Sophoreae and three genera of Caesalpinieae using flower, fruit, pollen and leaf, but not wood characters. He found that Swartzieae was polyphyletic and could not support the view that the tribe is basal to the Papilionoids. This paper describes the wood anatomy of at least one species from ten out of the eleven genera recognized as Swartzieae by Cowan (1981). A similar style and format, and identical character states are used as in Gasson.
Table 1. Genera in the tribe Swartzieae.

A list of the genera in the Swartzieae following Polhill (1981), giving coding of characters suitable for cladistic analysis, and for each genus, the number of species, the number examined in this study and whether or not there is any published information on wood anatomy. The characters are the same as those coded for the Sophoreae (Gasson 1994).

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Table 1 continued: Wood anatomical characters of Sophoreae and Swartzieae.

1. **Porosity and Growth rings:**
   - Diffuse-porous without growth rings 0
   - Diffuse-porous with growth rings 1
   - Ring-porous 2

2. Vessels of one diameter class 0
   - Vessels of two distinct diameters 1

3. Vessels not in dendritic arrangement 0
   - Vessels in dendritic arrangement 1

4. Vessels without spiral thickenings 0
   - Vessels with spiral thickenings 1

5. Vascular tracheids absent 0
   - Vascular tracheids present 1

6. Fibres non-septate 0
   - Fibres septate 1

7. **Axial parenchyma:**
   - Scanty paratracheal and/or vasicentric 0
   - Aliform / confluent / unilateral paratracheal / banded 1

8. Rays not of two distinct sizes 0
   - Rays of two distinct sizes 1

9. Rays homocellular 0
   - Rays heterocellular 1

10. Axial parenchyma not storied 0
    - Axial parenchyma storied 1
    - Axial parenchyma irregularly storied 0/1

11. Rays not storied 0
    - Rays storied 1
    - Rays irregularly storied 0/1

12. Crystals not seen in ray cells 0
    - Crystals present in ray cells 1

13. Number of species in genus

14. Number of species examined in this study

15. Published information on wood anatomy exists Y
    - No published information on wood anatomy found N
(1994) on Sophoreae, although in this paper each genus is treated individually, whereas in the Sophoreae paper the groups of genera recognized by Polhill (1981a) were used as the basis for descriptions.

There is published information on the wood anatomy of nine of the eleven genera. Only Baphiopsis and Exostyles are not covered in the literature. This paper describes the wood of the former for the first time, but no material of the latter could be obtained from the most likely Brazilian sources. The wood anatomy of South American Swartzieae is almost comprehensively covered by Détienne and Ter Welle (1989) in the Caesalpinioideae issue of Flora of the Guianas, which includes the genera Aldina, Bocoa, Candolleodendron, Lecointea, Swartzia and Zollernia. The Brazilian tree Harleyodendron from the Atlantic rain forest is described by Bedell in Cowan (1979).

Other relevant publications are given with each genus account.

GENERAL WOOD DESCRIPTION

Wood diffuse-porous. Vessels solitary, in pairs, some short radial multiples and clusters, but in no predominant pattern. Vessel elements relatively short, with alternate, usually fine, vested intervacular pits and simple perforation plates. Vessel-ray pitting similar to intervacular pitting in size and shape, half-bordered. Fibres non-septate with slit-like, apparently simple pits. Axial parenchyma scanty paratracheal to vasicentric, aliform and confluent, and sometimes with bands of varying width, usually storied. Rays generally no wider than 5 cells, mainly homocellular, consisting mostly of procumbent cells, non-storied, irregularly-storied or storied depending on genus and species. Prismatic crystals in chambered axial parenchyma cells present in most species, also present in ray cells in a few species.

GENERIC WOOD DESCRIPTIONS AND PREVIOUS LITERATURE

Aldina — Fig. 1–4

About 15 species from the neotropics. The wood has been described by Dechamps (1980, A. insignis), Détienne & Jacquet (1983, A. aff. latifolia) and Détienne & Ter Welle (1989, A. insignis & A. latifolia). The description here is based on one species, A. insignis.

Vessels often in short radial multiples, some solitary. Fibres thick-walled, with virtually no lumen. Axial parenchyma very abundant, aliform and confluent, in higher proportion than fibres. Axial parenchyma in strands of 2–4 cells, storied. Rays 1–4 cells wide and up to about 16 cells high, storied, homocellular, consisting entirely of procumbent cells.

[Détienne & Ter Welle’s description of A. insignis and A. latifolia recognises “1 marginal row of weakly procumbent or square cells” (sic) and the fibres in A. latifolia (their Fig. 1.1) are in higher proportion in transverse section when compared with Figures 1 and 2 here of A. insignis.]
**Baphiopsis parviflora** — Fig. 5–9

*Baphiopsis* is monotypic from the forests of tropical Africa. The wood appears not to have been described previously, and the voucher specimen in the Kew Herbarium, shown in Figure 5, is the holotype.

Vessels narrow and relatively sparse, solitary and in small clusters of up to 4 or 5. Fibres thick-walled with little or no lumen. Axial parenchyma aliform to confluent, in lower proportion than the fibres. Axial parenchyma strands mainly 2-celled, but some fusiform, storied. Rays 1–4 cells wide and up to at least 30 cells high, low rays storied and the same height as one axial parenchyma storey, higher rays up to two axial parenchyma storeys. Composition of rays variable, many homocellular with entirely procumbent cells.

**Bocoa** — Fig. 10–19

Seven species from the neotropics, three described here: *Bocoa alternata, B. prouacensis* and *B. viridiflora*. The most detailed account of the wood anatomy is by Détienne & Ter Welle (1989, same three species as here), with other papers by Benoist (1931), Détienne et al. (1982, *B. prouacensis*) and Détienne & Jacquet (1983, *B. prouacensis*).

The genus is not uniform in its wood anatomy. *Bocoa alternata* (Fig. 10–14) has abundant vessels in radial multiples up to at least 9, parenchyma that is scanty paratracheal, in discontinuous bands up to 3 cells wide and irregularly-storied, non-storied heterocellular rays that are 1 or 2 cells wide and up to about 40 cells high, and there are abundant prismatic crystals in ray cells in some samples.

In contrast, *B. prouacensis* (Fig. 17–19) and *B. viridiflora* (Fig. 15, 16) have fewer wider vessels, fewer vessels per unit area that rarely exceed 3 vessels per radial multiple, scanty paratracheal, incompletely vasicentric, aliform and confluent parenchyma in storied strands of 2–4 cells, and storied rays 1 or 2 cells wide and about 20 cells high. Some rays heterocellular, but most are homocellular. These two species are very similar anatomically to *Swartzia*.

**Candolleodendron brachystachyum** — Fig. 20–24

This is the only species, a tree from French Guiana and near the mouth of the Amazon in Brazil. The wood has been described by Détienne & Ter Welle (1989).

Vessels narrow, solitary and in some pairs and short radial multiples. Fibres thick-walled with narrow lumina rarely exceeding the width of the cell wall. Axial parenchyma scanty paratracheal to aliform and confluent, in discontinuous bands up to 4 cells wide, storied and irregularly-storied in strands of 2–4 cells. Rays irregularly-storied, 1 or 2 cells wide and up to 20 cells high, variably homocellular and heterocellular.

**Cordyla** — Fig. 25–28

Vessels mainly solitary and in pairs. Fibres thick-walled with little or no lumen. Axial parenchyma abundant, aliform and confluent, tending towards wide bands; strands 2–4-celled, irregularly-storied. Rays irregularly-storied, 1–3 cells wide and up to 20 cells high, homocellular, with a very slight tendency towards heterocellular.

**Exostyles**

This genus consists of two species from Southeast Brazil (Cowan 1981). No wood samples could be obtained, and there appear to be no wood descriptions in the literature.

**Harleyodendron unifoliolatum** — Fig. 29–33

This tree is restricted to the Atlantic rain forest of Bahia in Brazil, and was first described by Cowan (1979). The wood anatomy was described by Bedell in the same paper.

Vessels solitary and in radial multiples up to 10. Fibres thick-walled with little or no lumen. Axial parenchyma aliform to confluent, in narrow almost continuous bands up to 4 cells wide, strands of 2–4 cells, storied. Rays irregularly-storied, uniseriate, in places biseriate, many only about 10 cells high, but some exceeding 30 cells high. Rays homocellular, consisting almost entirely of procumbent cells. Some ray cells contain prismatic crystals.

**Lecointea** — Fig. 34–37


Vessels mainly solitary and in pairs. Fibres thick-walled with virtually no lumen. Axial parenchyma aliform to confluent, in places unilaterally paratracheal, with some tendency towards banding. Axial parenchyma strands storied, 2–4 celled. Rays storied, uniseriate and occasionally biseriate, up to 15 cells high. Rays homocellular, consisting entirely of procumbent cells.

**Mildbraediodendron excelsum** — Fig. 38–41

Monotypic, from tropical Africa. The wood is described by Lebacq (1957) and Normand & Paquis (1976).

Vessels mainly solitary and in pairs. Fibres thick-walled with little or no lumen. Axial parenchyma abundant, confluent, tending towards very wide undulating bands forming a high proportion of the wood. Axial parenchyma strands storied, sometimes appearing slightly irregular, 3–5 celled. Rays storied, irregularly in places, 1–3 cells wide, up to 11 cells high, homocellular.

**Swartzia** — Fig. 42–72

This is the largest genus in the tribe, with about 135 species. The vast majority are neotropical, but two species are African, both of which are illustrated here. At least 36

The publications including new world species are: Dechamps (1980) covering 14 species, Détienne & Jacquet (1983) 3 species, Détienne & Ter Welle (1989) 26 species (8 overlapping with this study), Huerta Crespo & Becerra Martinez (1976), Ilic (1991) illustrating S. leiocalyxina, Kribs (1928 & 1959) treating 2 species, Lebacq & Staner (1964), Lebacq et al. (1973) 2 species, Lindeman et al. (1963), Loureiro & Rodrigues (1975) 3 species (S. ulei, S. recurva, S. laeucarpa), Mainieri & Pereira (1958), Mainieri et al. (1983) 5 species, Ortega (1958), Pérez Olvera et al. (1979), Pfeiffer (1926), Record & Mell (1924) 1 species (S. tomentosa), Reinders-Gouwentak & Rijsdijk (1968) 4 species, Rizzini & Mattos Filho (1967), Williams (1936) 5 species. Approximately 48 neotropical species have been covered by the above and this publication. The wood anatomy of the neotropical species is currently being studied by Angyalossy-Alfonso and Miller (pers. comm. & 1995). The following description is based on both African and American species.

Vessels mainly solitary and in pairs, occasionally in short radial multiples up to 6. Fibres thick-walled to very thick-walled, usually with little or no lumen. Axial parenchyma scanty paratracheal to aliform and confluent, sometimes unilaterally paratracheal, tending towards (usually discontinuous) bands of 2–5 cells wide in some species; axial parenchyma strands nearly always storied, 2–4-celled, but occasionally fusiform and up to 6-celled. Rays strongly storied in many species which are uniseriate or biseriate and usually less than 20 cells high, but other species have irregularly storied rays which may be wider, up to 4 cells wide in places and up to 60 or more cells high. In S. cubensis (Fig. 67) the rays are almost of two distinct sizes. Rays homocellular in the two African species, often more heterocellular in American species. Otherwise the African and neotropical species are very similar.

**Zollernia** — Fig. 73–77


Vessels narrow, sparse, solitary, in pairs and small clusters. Fibres thick-walled, with very narrow lumina. Axial parenchyma scanty paratracheal to aliform and confluent, forming discontinuous bands up to 3 or 4 cells wide, strands storied, 2–4, occasionally up to 6-celled. Many rays storied, but some axially fused, 1–3 cells wide and up to 20 cells high. Prismatic crystals present in some marginal ray cells.

(text continued on page 69)
Fig. 1–4. *Aldina insignis*. 1 & 2: TS, very abundant aliform and confluent axial parenchyma and frequent vessel groups. 3: TLS, storied axial parenchyma and rays. 4: RLS, homocellular rays, prismatic crystals in chambered axial parenchyma cells (see arrows). — Scale line is 1 mm for Fig. 1 and 200 μm for Fig. 2–4.
Fig. 5. *Baphiopsis parviflora*. The type specimen (holotype) in the Kew Herbarium. Note the handwritten references to a wood specimen (above 715 bottom left) and *Baphia?* (bottom right).
Fig. 6–9. *Baphiopsis parviflora*. – 6: TS, aliform and confluent parenchyma. – 7 & 8: TLS, storied axial parenchyma and low rays, axially fused taller rays, prismatic crystals in chambered axial parenchyma. – 9: RLS, homocellular rays. — Scale line is 200 µm for Fig. 6 & 7, 100 µm for Fig. 8 & 9.
Fig. 10–14. *Bocca alterna*. – 10: TS, vessels in radial multiples. – 11: TLS, axial parenchyma storied, rays not storied. – 12: TLS, non-storied rays and vessels with fine intervacular pitting. – 13: RLS, heterocellular rays with one or more rows of upright marginal cells. – 14: RLS, ray cells containing a single prismatic crystal (top two arrows pointing right) and chambered axial parenchyma cells with prismatic crystals (bottom arrow pointing left). — Scale line is 200 μm for Fig. 10, 11 & 13, 100 μm for Fig. 12 & 14.
Fig. 15–19. *Bocoa viridiflora* (15 & 16), *Bocoa prouacensis* (17–19). – 15 & 17: TS, wide, sparsely distributed vessels, scanty paratracheal, aliform to confluent parenchyma. – 16, 18 & 19: TLS, axial parenchyma and rays storied. — Scale line is 200 μm for Fig. 15, 17 & 18, 100 μm for Fig. 16 & 19.
Fig. 20–24. *Candolleodendron brachystachyum*. – 20 & 21: TS, vessels narrow, axial parenchyma scanty paratracheal, aliform and confluent, in discontinuous narrow bands up to 3 cells wide. – 22 & 23: TLS, mainly storied axial parenchyma and irregularly storied rays, vessels with fine intervacular pitting. – 24: RLS, slightly heterocellular rays. — Scale line is 200 μm for Fig. 20, 22 & 24, 100 μm for Fig. 21 & 23.
Fig. 25–28. *Cordyla africana*. – 25: TS, Vessels solitary and in pairs, axial parenchyma abundant, aliform to confluent. – 26 & 27: TLS, axial parenchyma and rays irregularly storied, vessels with fine intervascular pitting. – 28: RLS, homocellular rays. — Scale line is 200 µm for Fig. 25, 26 & 28, 100 µm for Fig. 27.
Fig. 29–33. *Harleyodendron unifoliolatum.* — 29: TS, vessels solitary, in pairs and radial multiples, fibres very thick-walled, axial parenchyma aliform to confluent, in discontinuous narrow bands. — 30 & 31: TLS, axial parenchyma storied, strands mainly in twos in 30, in fours in 31, rays irregularly storied. — 32 & 33: RLS, rays homocellular, intervacular and vessel-ray pitting fine. — Scale line is 200 µm for Fig. 29–32, 100 µm for Fig. 33.
Fig. 34–37. *Lecointea amazonica*. – 34: TS, vessels solitary and in pairs, axial parenchyma aliform and confluent. – 35 & 36: TLS, axial parenchyma and rays storied. – 37: RLS, homocellular rays, fine intervascular pitting. — Scale line is 200 µm for Fig. 34 & 35, 100 µm for Fig. 36 & 37.
Fig. 38–41. *Mildbraediocdendron excellum*. Fig. 38 & 39: TS, vessels solitary and in pairs, axial parenchyma abundant, confluent. – 40: TLS, axial parenchyma and rays storied. 41: RLS, abundant axial parenchyma, homocellular rays with procumbent ray cells. — Scale line is 1 mm for Fig. 38, 200 μm for Fig. 39–41.
Fig. 42–46. African Swartzia: *S. fistuloides*, TS, TLS (42, 43), *S. madagascariensis*, TS, TLS, RLS (44–46). — Scale line is 200 µm for Fig. 42–44 & 46, 100 µm for Fig. 45.
Fig. 47–50. American Swartzia with storied rays. All TS. – *S. apetala* (47), *S. langsdorffii* (48), *S. leiocalycina* (49), *S. leptopetala* (50). — Scale line is 200 μm for all.
Fig. 51–54. American *Swartzia* with storied rays. — *S. macrostachya*, TS (51), *S. schomburgkii*, TS (52), *S. tomentosa*, TS (53), *S. apetala*, TLS (54). — Scale line is 200 μm for Fig. 51–53, 100 μm for Fig. 54.
Fig. 55–59. American Swartzia with storied rays. All LS. — *S. leiocalycina*, TLS (55), *S. schomburgkii*, TLS (56), *S. leptopetala*, TLS (57), *S. apetala*, RLS (58), *S. langsdorffii*, RLS (59). — Scale line is 200 μm for Fig. 55–58, 100 μm for Fig. 59.
Fig. 60–63. American Swartzia with irregularly storied rays. All TS. – *S. caribaea* (60), *S. grandiflora* (61), *S. laevicarpa* (62), *S. sprucei* (63). — Scale line is 200 μm for all.
Fig. 64–67. American *Swartzia* with irregularly storied rays. *Swartzia arborescens*, TS, TLS (64, 65), *S. cubensis*, TS, TLS (66, 67). — Scale line is 200 μm for all.
Fig. 68–72. American Swartzia with irregularly storied rays. All LS. – S. caribaea, TLS (68), S. grandiflora, TLS (69), S. sprucei, TLS (70), S. laevicarpa, RLS (71), S. sprucei, RLS (72). — Scale line is 200 μm for all.
Fig. 73–77. *Zollernia falcata*, TS, TLS, RLS (73, 75, 77), *Z. illicifolia*, TS (74), *Z. paraensis*, TLS (76). — Scale line is 200 µm for Fig. 73, 75 & 76, 100 µm for Fig. 74 & 77.
The ten genera examined here were divided into twelve taxa for the purpose of analysis using PAUP (Swofford 1993) and MacClade (Maddison & Maddison 1992). The two African *Swartzia* species were treated as one taxon, the neotropical species as another since it has variably storied rays. *Bocoa alterna* was treated separately from *B. prouacensis* and *B. viridiflora*. All the other genera were treated as single taxa.

Twelve characters were scored for a cladistic matrix (Table 1), using exactly the same state options as those used for Sophoreae (Gasson 1994). The Swartzieae is entirely tropical, and unlike Sophoreae there are no ring-porous species, lianas with vessels or rays of two sizes (although *Baphiopsis* is borderline and could be coded with this character, as could some *Swartzia* species), no vessels in dendritic arrangement or with spirals, and apparently no vascular tracheids. This means that characters 1–5 & 8 are all identical within Swartzieae, but could be usefully included when analysing the group in association with Sophoreae. Character 6 is hardly useful with either tribe, but septate fibres are found in related tribes (in Caesalpinioideae in particular), although they appear to be absent in Swartzieae and rare in Sophoreae. As discussed in Gasson (1994), the division of character 7 is arbitrary, since the states scanty paratracheal, vasicentric, aliform and confluent form a cline, and both character states of the division occur in six of the twelve taxa. The character shows too little resolution to be helpful, and this probably applies to the Leguminosae as a whole, where paratracheal parenchyma of various degrees and combinations is the norm. Characters 10 & 11, storeying of axial parenchyma and rays respectively, are more useful, although there is some variation within genera, particularly with regard to rays. Some neotropical *Swartzia* species have irregularly storied rays, and I have treated the character as variable within this large genus, rather than divided the genus into two. Character 12, some ray cells containing prismatic crystals, is probably as useful as 10 & 11. These crystals are found only in *Harleyodendron* and *Zollernia*. As expected, cladistic analysis of the Swartzieae alone, using the data matrix in Table 1, led to completely unresolved trees (not illustrated here). When run with the Sophoreae (see Gasson 1994 for the data matrix) the Swartzieae genera fell within the Sophoreae genera and were not in a distinct clade. The analyses were unsatisfactory, partly because of the difficulty in choosing objective character states for axial parenchyma distribution, and partly because there were too few characters in relation to the number of taxa. In my opinion, wood characters should not be considered in isolation, but should be included in broader analyses using a variety of data sources including flower, fruit, leaf and pollen morphology, and *rbcL* sequences where available.

**COMPARISON OF GENERA AND SPECIES**

*Baphiopsis* is very similar to *Baphia* in the Sophoreae, particularly in ray structure (see Gasson 1994), and the two genera can be confused by taxonomists as shown in the
labelling on the holotype (Fig. 5). The axial parenchyma is very regularly-storied, and a good proportion of the rays are axially fused, some extending for up to at least four parenchyma storeys.

*Bocoa* is not a uniform genus wood anatomically, because *B. alterna* is so different from its supposed congeners (*B. prouacensis* and *B. viridiflora*) and other Swartzieae. *Bocoa alterna* has abundant radial multiples of vessels and rays which are completely non-storied. Both features are uncommon in Swartzieae and Sophoreae, although some of the former are found particularly in *Candolleodendron* and *Harleyodendron*. The other two *Bocoa* species are very similar to the storied neotropical *Swartzia*. This non-uniformity of the genus *Bocoa* seems also to be reflected in pollen morphology (Ferguson & Skvarla 1988), but *B. alterna* and *B. prouacensis* which have very different wood have similar pollen. However, Herendeen (1995) separated *Bocoa alterna* from the rest of the genus because it differs by having alternate leaflets and lacks arils. Thus the pollen data for *Bocoa* are contrary to the patterns in morphology and wood anatomy.

*Aldina*, *Lecointea* and *Mildbraediodendron* are coded as identical. There are, however, some differences not shown in the data matrix, but apparent in the figures. *Lecointea* has much less axial parenchyma and mostly uniseriate rays, and *Mildbraediodendron* has shorter rays and much shorter and broader axial parenchyma cells in TLS. *Cordyla* has a similarly high proportion of axial parenchyma to *Aldina* and *Mildbraediodendron*, but has rather less regularly storied axial parenchyma and rays.

*Harleyodendron* and *Lecointea* are similar to one another, and only differ in that the former has less well storied rays, and some ray cells contain crystals. These both appear to be minor differences. *Zollernia* is the only other genus with crystals in some ray cells.

The two African *Swartzia* species are very similar to many neotropical species with storied rays, with the exception that they have homocellular rays. Although wood anatomy does not support the separation of the African *Swartzia* species from the American ones particularly well, differences in chromosome number (Cowan 1981) and pollen morphology (Ferguson & Skvarla 1991) may be used in support of this view. Kirkbride and Wiersema (pers. comm.) are in the process of describing these two species as a new genus, which they intend to call *Bobgunnia*. The neotropical species are quite variable with regard to ray storeying, which is coded as variable in the cladistic matrix. There appears to be a cline in neotropical *Swartzia* from species with very regular ray and parenchyma storeying, through species with axially fused rays extending over two or more parenchyma storeys, to some species which have very irregularly storied rays. The axial fusion of rays is similar to that in *Baphiopsis* and *Baphia*.

Many of the above comments show how difficult it is to be consistent in coding these wood characters for cladistic analysis. The larger the genus, the more difficult it is to keep it as one taxonomic entity. Also, whereas the actual appearance of the wood may be different, because of varying abundance of, for example, parenchyma, character coding cannot take into account these fine variations and may be the same.
The wood of Swartzieae is less variable anatomically than that of Sophoreae. However, the Swartzieae has only 11 genera as opposed to 48, and Sophoreae has some temperate taxa. On the basis of the twelve wood anatomical characters examined and coded for cladistic analysis, the Swartzieae is not separable from the Sophoreae. Anatomically, Baphiopsis (Swartzieae) is so similar to Baphia (Sophoreae) that the two genera should perhaps be included in the same tribe if not genus. There is also evidence from flower, fruit, pollen and leaf characters (Herendeen 1995) and pollen morphology (Ferguson & Skvarla 1988) that would support this view. Also, the wood of many Baphia and some Swartzia species is very similar anatomically. The only resolution in any cladograms generated from the data matrices of Swartzieae and Sophoreae wood characters is found in the temperate Sophoreae and the Sophoreae lianas. Although not a perfect correlation, the former group is supported by ring porosity and spiral thickenings, the latter by vessels and rays of two distinct sizes, and both groups by the presence of vascular tracheids (see Gasson 1994; Fujii et al. 1994).

Two other tribes in the Papilionoideae (Dipteryxeae and Dalbergieae) and three in the Caesalpinioideae (Caesalpinieae, Detarieae and Amherstieae) also need to be taken into consideration. The Dipteryxeae is a small tribe of three genera (Polhill 1981b), and the Dalbergieae is larger, consisting of 19 tropical genera (Polhill 1981c), including some species, mainly lianas, with included phloem (absent from all Swartzieae and Sophoreae). There does seem to be some overlap with Sophoreae in some genera (e.g. Andira), whereas other genera (e.g. Dalbergia) tend to be less like Sophoreae with regard to axial parenchyma distribution, but very similar in storeying. I am currently surveying both tribes, and preliminary observations in Dipteryxeae suggest that ray storeying is variable within this small tribe as it is in Sophoreae and Swartzieae. The Caesalpinieae has 47 genera (Polhill & Vidal 1981), Detarieae 55 genera (Cowan & Polhill 1981a) and Amherstieae 25 genera (Cowan & Polhill 1981b). These large tribes have a wider range of characters than Swartzieae. Certain characters in legumes are restricted to the Caesalpinioideae, and are found in some genera in the first two of these tribes, e.g. axial canals and silica bodies (see Gasson 1994 for a summary and further references), and septate fibres are more common than they are in Papilionoideae. Even before the completion of surveys of the wood anatomy of these tribes, it is clear that there are problems with both generic and tribal limits within Sophoreae and Swartzieae, and that these are likely to be compounded, particularly when Dipteryxeae and Dalbergieae are considered. There is no intention of using wood anatomical information in isolation to suggest taxonomic rearrangements, but the data here provide evidence that some changes may be necessary.

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REFERENCES

Kromhout, C.P. 1975. 'n Sleutel vir die mikroskopiese uitkenning van die vernaamste inheemse houtsoorte van Suid-Afrika. Bosnavorsingsinstituut, Pretoria.


