

THE WOOD ANATOMY OF GARDENIEAE, IXOREAE AND MUSSAENDEAE (RUBIACEAE)

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SUMMARY

The tribe *Gardenieae* in the restricted delimitation proposed by Bremekamp and Verdcourt is wood anatomically homogeneous. The genera of the *Ixoreae* studied by me also agree with each other in wood structure. Within the tribe *Mussaendeae* in the delimitation accepted by Schumann the wood anatomy shows much variation. The tribe becomes more homogeneous, if some of the genera included in this tribe by Schumann are removed. The systematic position of some genera, which in the literature are said to be related to *Gardenieae*, *Ixoreae* or *Mussaendeae*, is discussed in the light of similarities and differences in the wood anatomy.

1. INTRODUCTION

The classification of the *Rubiaceae* presented by SCHUMANN in ENGLER & PRANTL's "Die natürlichen Pflanzenfamilien" (1897) is not the first one, but was preceded by several other ones. A survey of the work of his predecessors was given by BREMEKAMP (1966).

Schumann divided the *Rubiaceae* into two subfamilies, the *Cinchonoideae* and the *Coffeoidae*. The tribes *Gardenieae* and *Mussaendeae* were placed, near each other, in the *Cinchonoideae*, whereas the *Ixoreae* were included in the *Coffeoidae*. VERDCOURT (1958) distinguished three subfamilies and classified the three tribes in one of them, the *Cinchonoideae*. BREMEKAMP (1966), who divided the *Cinchonoideae* sensu Verdcourt into two subfamilies, mainly based upon the presence or absence of the 'ixoroid' pollination mechanism, placed the *Ixoreae* and the *Gardenieae* in the *Ixoroideae*, the *Mussaendeae* in the *Cinchonoideae* (see KOEK-NOORMAN 1969 b, p. 378). HALLÉ (1961, 1967) did not go into the classification of the family, but considered the *Gardenieae*, *Ixoreae* and *Mussaendeae* to be closely related. STEYERMARK (1965, 1967) accepted the *Gardenieae*, *Ixoreae* and *Mussaendeae*, but did not give his ideas on the delimitation of these tribes and on the position they occupy in the family.

In a preceding paper (KOEK-NOORMAN 1970) I suggested that the wood anatomy of the tribes referred by Bremekamp to the *Cinchonoideae* should be regarded as less homogeneous than that of the tribes included by him in the *Ixoroideae*. The purpose of the present investigation is to detect whether data obtained from a study of the wood anatomy of the genera concerned can contribute to the discussion on the delimitation and on the position of these tribes in the family.

2. MATERIAL AND METHODS

The methods applied by me have been described in a preceding paper (KOEK-NOORMAN 1969a). The material studied by me is listed at the end of the present paper. The main results of the investigation are listed in *table 1*.

3. DISCUSSION

3.1. Discussion of the anatomical data obtained in the present investigation and of those found in the literature

3.1.1. *Gardenieae*

Material of the following genera, the classification of which in the *Gardenieae* is not disputed in the literature, was available: *Alibertia*, *Amajoua*, *Amaralia*, *Borojoa*, *Casasia*, *Duroia*, *Galiniara*, *Gardenia*, *Genipa*, *Ibetrulia*, *Kotchubaea*, *Leptactinia*, *Randia*, *Rosenbergiodendron*, *Rothmannia*, *Stachyarrhena*.

Besides, I have been able to study slides made from samples of *Burchellia bubalina* (L.f.) Sims., *Dictyandra arborescens* Welw., *Diplospora malaccensis* Hook. f. and *D. viridiflora* DC., *Gardenia coronaria* Ham., *G. latifolia* Schum., and *G. norae* Swynn., *Morelia senegalensis* A. Rich., *Oxyanthus formosus* Hook. f. and *O. unilocularis* Hiern., *Scyphiphora hydrophyllacea* Gaertn., *Randia densiflora* Bth., *R. exaltata* Griff., and *R. micrantha* DC., *Rothmannia lutea* (Willd.) Ken., *Stachyarrhena heterochroa* Standl., which are present in the slide collections of the Jodrell Laboratory, Kew, and in those of the Commonwealth Forest Research Institute, Oxford. Furthermore, material of the following genera, the inclusion of which in the *Gardenieae* is disputed in the literature, was available: *Aulacocalyx*, *Bertiera*, *Hamelia*, *Heinsia*, *Hillia*, *Pentagonia*, *Posoqueria*, *Retiniphyllum*, *Tarenna*, *Tricalysia*.

The data obtained during the present investigation suggest a rather high degree of homogeneity in the wood anatomy of the first mentioned group of *Gardenieae* (i.e. of those genera the inclusion of which in this tribe is generally accepted): the vessels are either exclusively solitary or partly arranged in short radial multiples, and their diameter varies from 40–100 μ . (Plate I; see also KOEK-NOORMAN 1969a, Plate I, II, IV, VI, VII and VIII). The fibre tissue consists of thick-walled fibre tracheids with bordered pits on the tangential and radial walls. The rays are uniseriate in some species, but mostly 1- to 4-seriate, with a low multiseriate central part and high uniseriate margins. The axial parenchyma is predominantly apotracheal, varying from scanty diffuse to abundant reticulate strands, and in some species tending to form long tangential bands. The differences between the samples studied by me are mostly quantitative. It seems impossible to indicate distinct limits between the genera.

JANSSONIUS (1926) described the wood anatomy of species of *Diplospora*, *Hypobathrum*, *Petunga*, *Randia*, *Scyphiphora*, and *Zuccarinia*. His data agree with those obtained from the samples studied by me in the vagueness of the growth rings characterised by a narrow zone of tangentially compressed fibres, in which the pores show a slightly smaller diameter. There are mostly more than

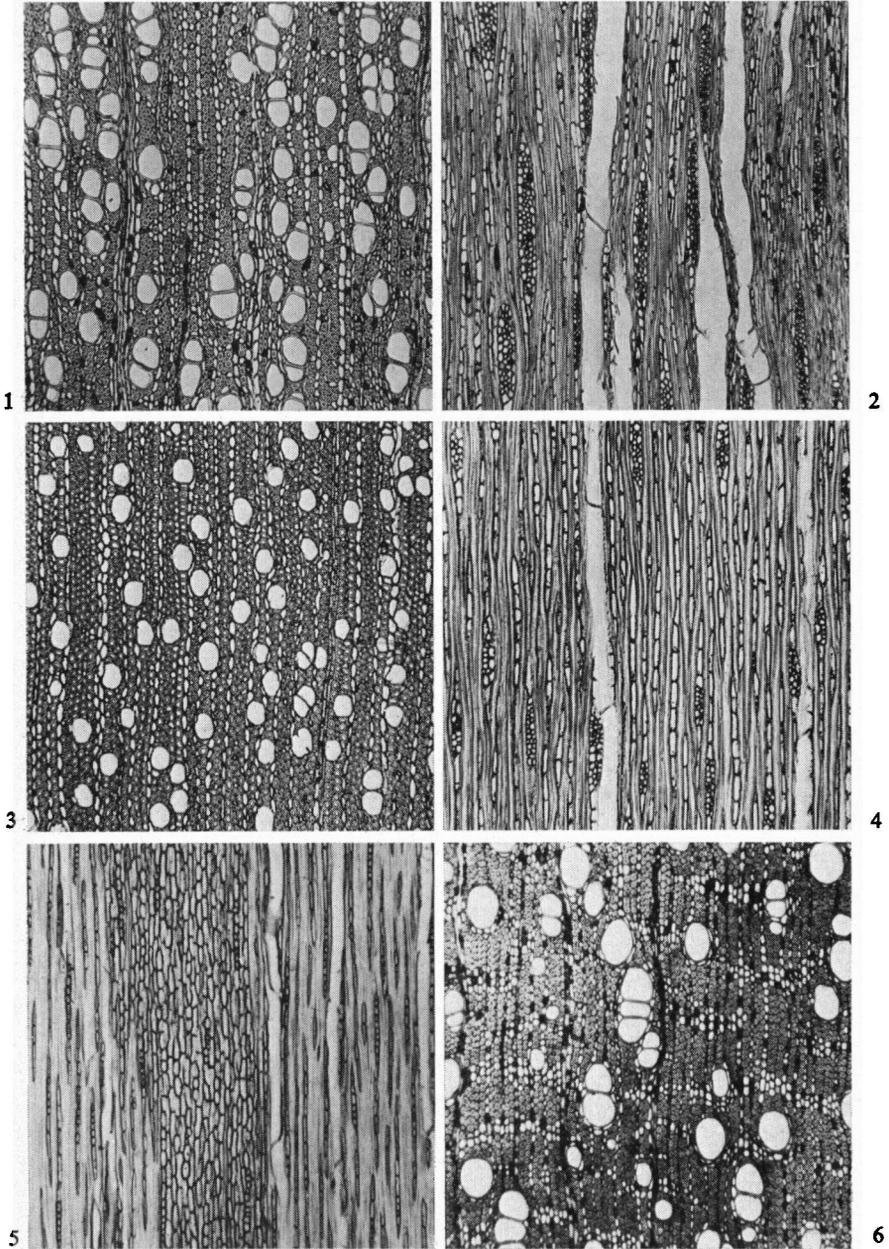


Plate I.

- fig. 1. *Amajoua corymbosa* H.B.K. (Uw 7039) transv. sect. 45 × ;
 fig. 2. *Amajoua corymbosa* H.B.K. (Uw 7039) tang. sect. 45 × ;
 fig. 3. *Gardenia remyi* H. Mann (Uw 4810) transv. sect. 45 × ;
 fig. 4. *Gardenia remyi* H. Mann (Uw 4810) tang. sect. 45 × ;
 fig. 5. *Alibertia myrciifolia* K. Schum. (Uw 8087) tang. sect. 45 × ;
 fig. 6. *Duroia eriopila* L. f. (Uw 324) transv. sect. 45 × .

20 vessels per sq. mm, partly arranged in short radial multiples. The fibre tissue consists of fibre tracheids. The narrow rays are heterogeneous and the axial parenchyma is diffuse to reticulate.

RECORD & GARRETT (1925) described the wood of *Gardenia* sp., the Siamese boxwood. In the presence of gelatinous fibre walls their data agree with those observed by me in *G. thunbergii*. They reported abundant conjugate or disjunctive elements in the upright ray cells. The data on the wood of *Gardenia imperialis* and of *Massularia acuminata* given by NORMAND (1960) are not contradictory to the above.

The information given by METCALFE & CHALK (1950), on the contrary, deviates from my results in some respects. They reported for *Kotchubaea* "wide, separated parenchyma bands that tend to be associated with the vessels", whereas in the samples studied by me short and long, 1-3 cells wide bands occur. They cited PANSIN (1932), who reported the presence of septate fibres in *Scyphiphora*, contrary to the description of Janssonius and to my own findings in the available wood sample. According to Metcalfe & Chalk bordered pits are lacking in the non-septate fibres of *Casasia*. The sample of *Casasia longipes* studied in the present investigation has non-septate fibres which show bordered pits on the tangential and radial walls. *Bothriospora* and *Fernelia* are said to show septate fibres (METCALFE & CHALK 1950). (The material of *Bothriospora* present in Oxford consists of one slide of *B. corymbosa* Hook.f., Y 34074, which deviates in some other respects too from the wood anatomy of other *Gardenieae*, i.a. in the composition of the rays.)

CHANG (1951) described the wood anatomy of *Gardenia*, *Petunga*, *Randia*, and *Tarenna* based upon the study of several species. In *Petunga* he reported rays which are up to 12 cells wide contrary to JANSSONIUS (1926), who reported 2- to 4-seriate rays. In the samples of *Randia* investigated by Chang some large tyloides occur. The height of the rays is said to be less than 1 mm. In other respects his descriptions agree with those of the samples studied in the present investigation.

As for the genera the position of which in the *Gardenieae* is disputed, *Hamelia* Jacq., a genus which because of the presence of raphides was placed by BREMEKAMP (1966) in a separate tribe in the *Rubioideae*, shows some characteristics in which it resembles other genera of *Rubioideae*: the presence of septate libriform fibres, the absence of axial parenchyma, and in *H. patens* the 1- to 6-seriate rays which, moreover, are provided with some sheath cells.

Hillia Jacq., too, possesses raphides in the xylem. Moreover the sample studied by me differs from those of the true *Gardenieae* by the presence of septate libriform fibres with thick gelatinous cell walls, the multiseriate rays which are nearly all without uniseriate margins, and broad bands of axial parenchyma tending to include the vessels.

Between the three species of *Posoqueria* Aubl. there are only quantitative differences of minor importance. In the wood anatomy they agree in the presence of non-septate libriform fibres, more paratracheal parenchyma strands than are found in the other *Gardenieae*, and some vague tangential vessel rows

(METCALFE & CHALK (1950), moreover, reported semi-ringporousness in the genus). In these characters *Posoqueria* differs from the *Gardenieae*.

Aulacocalyx Hook.f. is represented by *A. jasminiflora* and, if PETIT's opinion (1962) that *Aulacocalyx* and *Heinsenia* K. Schum. are synonyms is correct, also by *H. sylvestris*. The samples studied by me are very similar in the anatomy of the wood and agree very well with the *Gardenieae* in the presence of numerous solitary vessels, fibre tracheids, 1- to 3-seriate rays with high uniseriate margins, and diffuse axial parenchyma tending to be reticulate.

Pentagonia Bth. (Plate III) differs from the *Gardenieae* in the septate libriform fibres, in the high and rather broad multiseriate rays mainly composed of square and upright cells, and in the absence of parenchyma.

Retiniphyllum H. & B. is represented in the wood collection by four species. The genus consists of small shrubs, and the diameter of the samples varies from 1.5-4 cm. So quantitative differences are of no value. In most respects, however, the samples studied by me are very similar and agree with those of the *Gardenieae*: the vessels are predominantly solitary, sometimes partly surrounded by parenchyma strands; the fibre tissue consists of fibre tracheids; the 2- to 4-seriate rays have high margins and many diffuse axial parenchyma strands occur.

The wood anatomy of *Bertiera* Aubl. and *Heinsia* DC. is discussed in 3.1.2., that of *Tarenna* Gaertn. and *Tricalysia* A. Rich. in 3.1.3.

3.1.2. *Mussaendeae*

Material was available of *Gonzalagunia* R. & P., *Gouldia* A. Gray, *Isertia* Schreb., and *Mussaenda* L., genera, which are included in the *Mussaendeae* in all the literature studied by me, and of *Acranthera* Arn., *Bertiera* Aubl., *Heinsia* DC., *Hippotis* R. & P., *Mycetia* Reinw., *Pentagonia* Bth., *Schradera* Vahl, *Sommeria* Schlecht., and *Urophyllum* Wall. (including *Leucolophus* Brem., *Pleiocarpidia* K. Schum., and *Maschalocorymbus* Brem.). The inclusion of this last mentioned group of genera in the *Mussaendeae* has been disputed in the literature.

The samples of *Isertia* Schreb. studied by me were rather similar. Most species show vessels which are nearly exclusively solitary, fibre tracheids, rays which are composed of a low, mostly biseriate central part consisting of procumbent cells and high uniseriate margins which are composed of upright cells (Plate II), and scanty diffuse strands of axial parenchyma which sometimes form short bands between two rays. The rays in *Isertia hypoleuca* show only rarely uniseriate margins, whereas the procumbent cells form a 2- to 4-seriate part which is sometimes more than 1 mm high.

Beside by fibre tracheids and by a rather scanty diffuse and slightly reticulate axial parenchyma, *Mussaenda sphaerocarpa*, *M. zenkeri* and *M. spec.* (U 9258) are characterised by the arrangement of the vessels: contrary to the samples of *Isertia* studied by me in the samples of *Mussaenda* more than 50% of the vessels are arranged in radial multiples, partly 4-7 cells long (Plate II). This is in agreement with the description of *M. frondosa* given by JANSSONIUS (1926). CHANG (1951) mentioned for the three species studied by him that the radial multiples

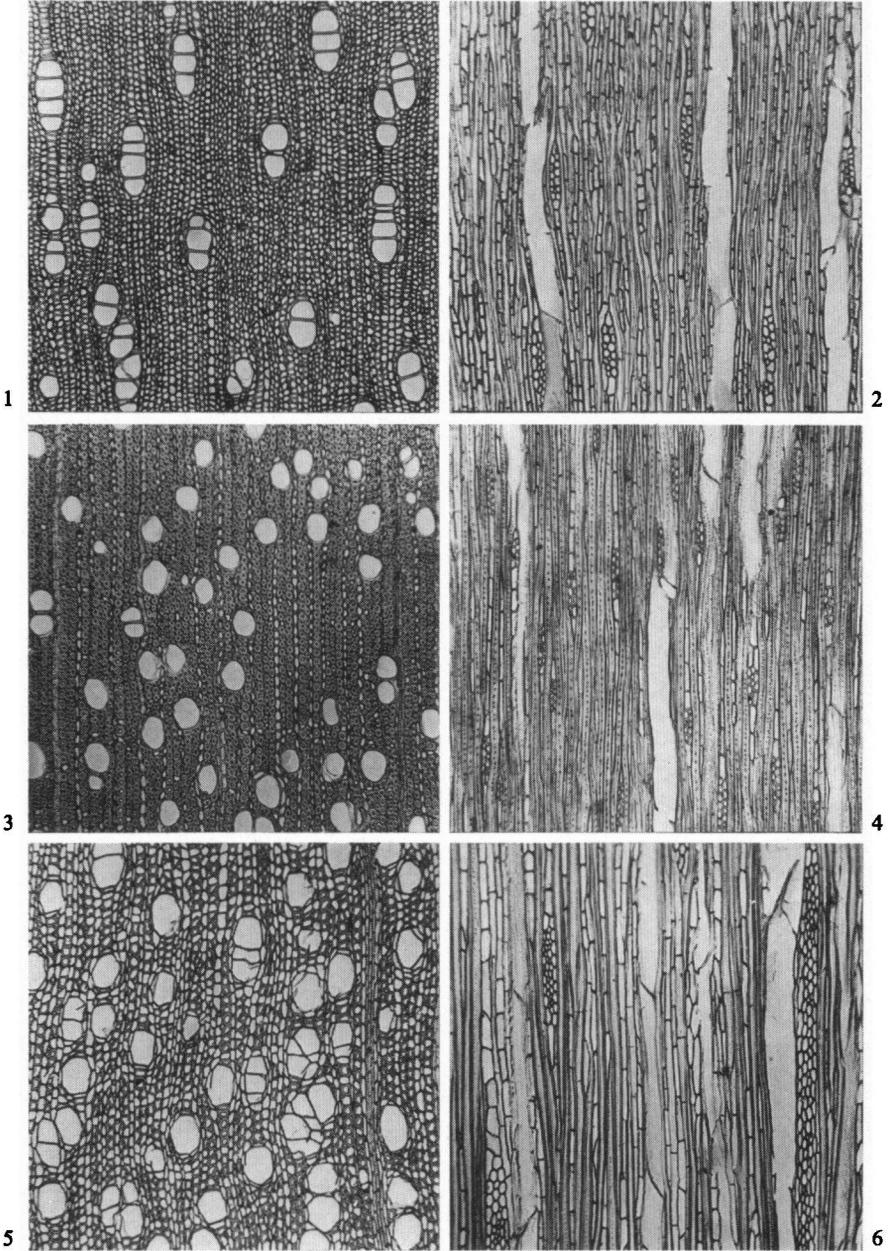


Plate II.
 fig. 1. *Mussaenda sphaerocarpa* Mildbr. (Uw 14950) transv. sect. 45 × ;
 fig. 2. *Mussaenda sphaerocarpa* Mildbr. (Uw 14950) tang. sect. 45 × ;
 fig. 3. *Isertia longifolia* K. Schum. (Uw 9042) transv. sect. 45 × ;
 fig. 4. *Isertia longifolia* K. Schum. (Uw 9042) tang. sect. 45 × ;
 fig. 5. *Urophyllum glabrum* Jack (Uw 16626) transv. sect. 45 × ;
 fig. 6. *Urophyllum glabrum* Jack (Uw 16626) tang. sect. 45 × .

or chains of vessels are usually formed by 2-5 large vessels, followed by 5 or more smaller ones in tail-like arrangement, the diameter varying from about 150 μ to less than 50 μ . He described 1- to 6-seriate rays composed mainly of square cells occasionally with sheathing upright cells, and occasionally with procumbent cells which are not much radially flattened. This agrees with the composition of the rays of *M. zenkeri* represented by a sample which is 1.5 cm in diameter.

Gonzalagunia R. & P. was represented by a sample of *G. spicata*. The wood anatomy deviates from the samples of *Mussaenda* and *Isertia* studied by me in the short 2- to 3-seriate parts of the rays, which are composed of square and upright cells. Contrary to METCALFE & CHALK (1950) I did not observe the presence of septate fibres.

Gouldia axillaris and *G. terminalis* have vessels which are partly arranged in short radial multiples. The fibre tissue consists of fibre tracheids. The rays are 1- to 4-seriate, nearly exclusively composed of square and upright cells. The axial parenchyma is scanty, vasicentric and diffuse.

Acranthera longipes Merr., "herba robusta sed altitudine ignota" (BREMEL-KAMP 1947), was represented by a stem 1 cm in diameter. The vessels are partly arranged in radial multiples, sometimes forming a radial chain; the diameter is 40-50 μ . The rays are 1- to 5-seriate and composed of square and upright cells; sheath cells are abundant. The fibres are septate, thin-walled with spiral thickenings; the pits are scanty and without distinct borders. I did not observe axial parenchyma. CHANG's description (1951) of the wood of this species agrees rather well with mine. However, he did not report the presence of septa in the fibres. Remarkable is the abundance of starch grains.

Bertia guianensis and *B. racemosa* show rays mainly composed of square and upright cells. In other characteristics there is a good agreement with *Isertia* (Plate II, III).

The wood anatomy of *Heinsia jasminiflora* and *H. pulchella* is qualitatively and quantitatively identical with that of the samples of *Mussaenda* studied by me.

Hippotis R. & P., *Pentagonia* Bth. (Plate III), and *Sommerera* Schlecht. are similar in the septate libriform fibres, the uni- and multiseriate rays composed of procumbent and square cells, and the absence of axial parenchyma. (CHANG 1951 reported in *P. orthoneura* Standl. "a single cell near the vessels"). METCALFE & CHALK (1950) mention *Sommerera* under the genera without axial parenchyma and with non-septate fibres.

Mycetia myrioneuron, represented by a sample of 2 cm in diameter, has predominantly solitary vessels, thin-walled and septate libriform fibres, uni- and biseriate rays composed of square and upright cells, and some paratracheal parenchyma strands.

Schradera rotundata was discussed in KOEK-NOORMAN (1969b). In that paper the presence of libriform fibres was reported. The samples, however, show fibre tracheids which deviate much from the usual type: between each two adjacent fibres abundant bordered pits occur, with a round or oval aperture slightly smaller than the 5 μ large border.

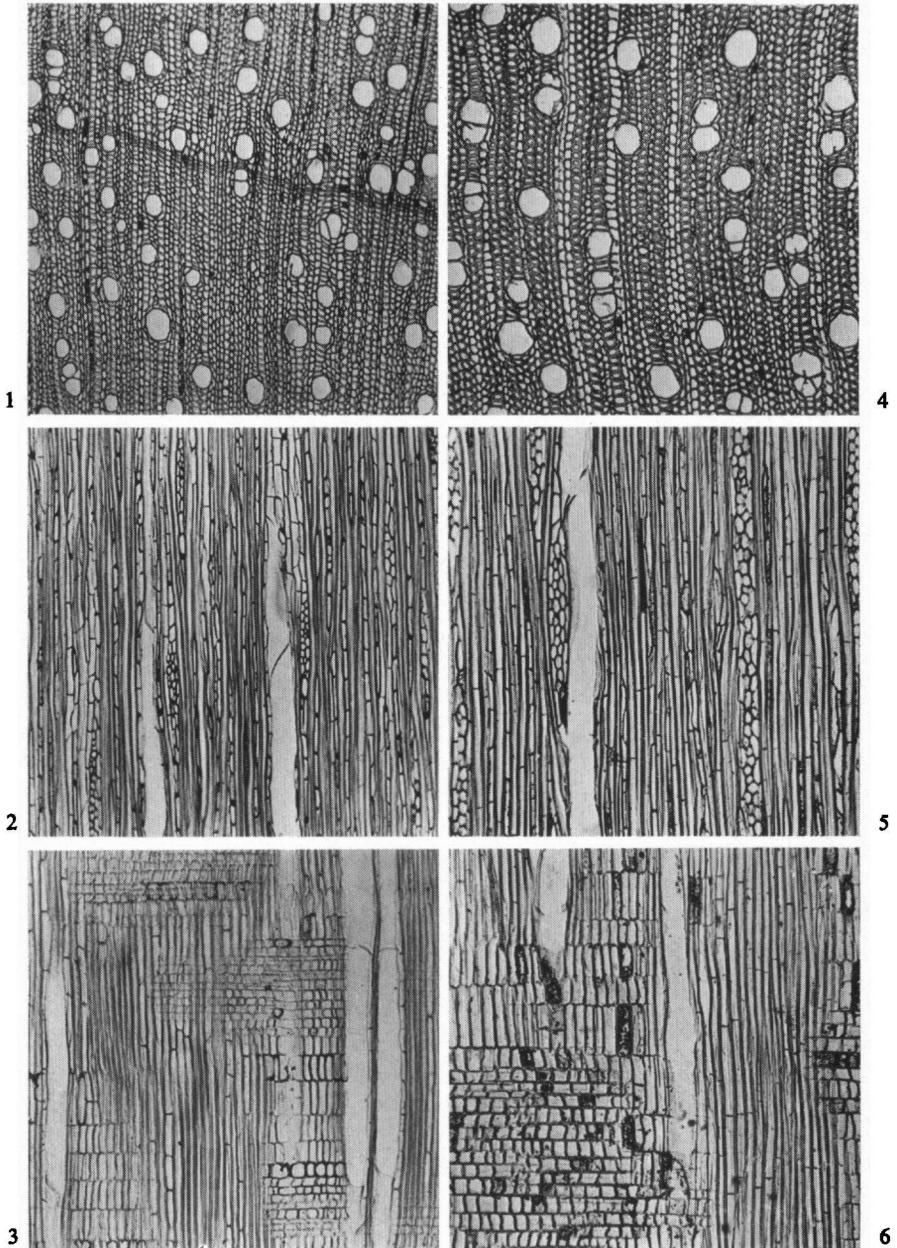


Plate III.

fig. 1. *Bertiera racemosa* K. Schum. (Uw 16622) transv. sect. 45 × ;

fig. 2. *Bertiera racemosa* K. Schum. (Uw 16622) tang. sect. 45 × ;

fig. 3. *Bertiera racemosa* K. Schum. (Uw 16622) rad. sect. 45 × ;

fig. 4. *Pentagonia macrophylla* Bth. (Uw 16625) transv. sect. 45 × ;

fig. 5. *Pentagonia macrophylla* Bth. (Uw 16625) tang. sect. 45 × ;

fig. 6. *Pentagonia macrophylla* Bth. (Uw 16625) rad. sect. 45 × .

Urophyllum Wall. was represented by two species: *U. glabrum* and *U. trifurcum*. Besides, material of some nearly related genera was available, viz. from *Leucolophus*, *Maschalocorymbus* and *Pleiocarpidia*. All samples show thin-walled, more or less angular vessels which are partly arranged in radial multiples; fibre tracheids; rays with a multiseriate part composed of predominantly square and upright cells; and scanty paratracheal and sometimes abundant, diffuse parenchyma strands (Plate II). This agrees with the description of *U. glabrum* given by JANSSONIUS (1926) and with data reported by CHANG (1951) based upon *U. grandifolium*. The spiral thickenings in the fibre tracheids of *U. rahmatii* observed by Chang agree with those found in *U. trifurcum*, in *Pleiocarpidia assahanica*, and *P. sandahanica* and in *Leucolophus tobingensis*.

3.1.3. *Ixoreae*

The wood anatomy of the available samples of *Ixora*, *Pavetta*, *Rennellia*, and *Rutidea* is very homogeneous. The vessels are exclusively or predominantly solitary, often very small and numerous. The fibre tissue consists of fibre tracheids. The rays are either exclusively uniseriate, or uni- and multiseriate, and in that case composed of a low, 2- to 4-seriate part of procumbent cells and long uniseriate margins of upright cells. The axial parenchyma is usually scanty and diffuse, but in some species for a small part paratracheal. In most samples small rhombic crystals occur in the axial parenchyma or in the procumbent upright or ray cells. The data obtained in the present investigation agree very well with the descriptions of species of *Ixora* and *Pavetta* given by JANSSONIUS (1926). The tyloides, scarcely occurring in the axial parenchyma cells of the samples of *Ixora grandifolia* and *I. macrophylla* studied by me, were reported by him for *Pavetta indica* var. *montana*. The descriptions of *Ixora* and *Pavetta* by CHANG (1951) agree completely with that given above.

The available samples of *Tarenna* and *Tricalysia*, with the exception of that of *Tarenna incerta* (see the remark made in 3.2.3. on the position of this species), agree very well with those of the genera mentioned above. (see *table 1*).

3.2. Discussion of the classifications in the light of the similarities and differences in the wood anatomy

3.2.1. Delimitation of the *Gardenieae* (see also 3.1.1.)

The *Gardenieae* sensu SCHUMANN (1897) include a number of genera which have been removed from this tribe by more recent authors. For instance, *Hamelia* Jacq. was placed by BREMEKAMP (1954, 1966) in a tribe of its own in the *Rubioideae*. This was supported by VERDCOURT (1958). The anatomy of the wood agrees with this view, because, beside other characteristics which are typical for the *Rubioideae* (KOEK-NOORMAN, 1969b), in one of the available samples raphides occur.

Posoqueria Aubl. was also removed from the *Gardenieae* by Bremekamp. Verdcourt agreed with him. Both authors suggested an isolated position within

	2	2, 10	2, 10		7	2	6
<i>Alibertia myrciifolia</i>	x x x x x x x						
<i>Alibertia acuminata</i>	x x x x x x					+	x x x x
<i>Kotchubaea semisericea</i>							
<i>Duroia saccifera</i>							
<i>Duroia sprucei</i>							
<i>Borojoa stipularis</i>							
<i>Alibertia edulis</i>							
<i>Iberialia surinamensis</i>							
<i>Amaralia streptocaulon</i>							
<i>Casasia longipes</i>							
<i>Casasia clusiiifolia</i>							
<i>Gardenia renyi</i>							
<i>Leptactinia hexamera</i>							
<i>Genipa americana</i>							
<i>Genipa caruto</i>							
<i>Randia dumetorum</i>							
<i>Randia sericantha</i>							
<i>Randia spinosa</i>							
<i>Rosenbergiodendron longifl.</i>							
<i>Rosenbergiodendron formosum</i>							
<i>Tocoyena guianensis</i>							
<i>Stachyrrhena acuminata</i>							
<i>Gardenia thunbergii</i>							
<i>Rothmannia whitfieldii</i>							
<i>Gardenia riparia</i>							
<i>Duroia fusifera</i>							
<i>Amajoua corymbosa</i>							
<i>Galiniera coffeoides</i>							
<i>Duroia hirsuta</i>							
<i>Rothmannia urcelliformis</i>							
<i>Amajoua guianensis</i>							
<i>Duroia aquatica</i>							
<i>Duroia eriopila</i>							
<i>Duroia genipoides</i>							
<i>Hamelia patens</i>							
<i>Hamelia ventricosa</i>							
<i>Posoqueria gracilis</i>							

Table 1.

- × : the feature is present
- ± : the feature is scarcely present, or exceptions occur
- 1 : starch grains abundant
- 2 : small rhombic crystals in procumbent ray cells
- 3 : small rhombic crystals in axial parenchyma cells
- 4 : crystal sand in ray cells
- 5 : many gumlike inclusions in ray cells
- 6 : raphides in upright ray cells
- 7 : gelatinous fibre walls
- 8 : styloids in axial parenchyma cells
- 9 : many gum-like inclusions in vessels
- 10 : small rhombic crystals in upright ray cells.

Schumann		<i>Bremekamp</i>	<i>Verdcourt</i>	<i>F. Hallé</i>
Alberteae	Aulacocalyx	Cremasporeae	Subtribe in <i>Ixoreae</i>	<i>Gardenieae</i>
Gardenieae	Tarenna	<i>Ixoreae</i>	<i>Retiniphyllaeae</i> <i>isolated position</i>	<i>Retiniphyllaeae</i> <i>isolated position</i>
	Tricalysia			
	Retiniphyllum			
	Posoqueria			
Cinchoneae	Hamelia	<i>Rubioideae</i> , in eccentric tribe	<i>Rubioideae</i> , in eccentric tribe	
	Bertiera	subtribe in <i>Mussaendeae</i> or	subtribe in <i>Mussaendeae</i>	<i>Gardenieae</i>
	Heinsia	<i>Urophyllloideae</i>		<i>Mussaendeae</i>
	Hillia	<i>Hillioideae</i>	<i>Rubioideae</i>	<i>Gardenieae</i> <i>Gardenieae</i>
Mussaendeae	Pentagonia	?	?	
	Hippotis			
	Sommerera			
	Acranthera			<i>Acranthereae</i>
Mussaendeae	Urophyllum	<i>Urophyllloideae</i>	<i>Rubioideae</i>	<i>Mussaendeae</i>
	Pleiocarpidia			
	Leucolophus			
	Maschalocorymbus			
	Schradera	<i>Rubioideae</i> , in eccentric tribe	<i>Rubioideae</i> , in eccentric tribe	
	Mycetia	<i>Rubioideae</i>	<i>Rubioideae</i>	

Survey of the position of some Rubiaceous genera according to Schumann, Bremekamp, Verdcourt, and Hallé.

Where the wood anatomy agrees with the opinion of one of these authors, this is indicated by printing in italics the name of the taxon to which they have been referred by him.

the family. HALLÉ (1967) and STEYERMARK (1967) classed *Posoqueria* in the *Gardenieae*, but did not give arguments for this decision. Taking into consideration the great homogeneity of the *Gardenieae* studied by me, it is noteworthy that the three available species of *Posoqueria* deviate in some important points. The fact that the libriform fibres are non-septate forms a difference with those groups of the *Rubiaceae* showing septate libriform fibres: the *Rubioideae*, *Guettardoideae*, and some species of the *Condamineae* and *Rondeletieae* studied by me. Thus the wood anatomy supports the idea that *Posoqueria* occupies an isolated position within the family.

The genus *Retiniphyllum* Humb. & Bonpl. was placed in a tribe of its own by BREMEKAMP (1934a) and VERDCOURT (1958). Verdcourt included this tribe in the *Cinchonoideae*. The wood samples support this opinion. In most characteristics the species studied by me agree with the *Gardenieae*. They differ in the presence of scanty paratracheal parenchyma strands and in the composition of the multiseriate parts of the rays, these consist of square and procumbent cells which are not much radially flattened.

Hillia Jacq., placed in the *Cinchoneae* by SCHUMANN (1897), was considered to belong to the *Gardenieae* by HALLÉ (1967). He reported the presence of raphides but considered that character not important enough to justify classification in a tribe of its own in the *Rubioideae* (VERDCOURT 1958) or in a separate subfamily *Hillioideae* (BREMEKAMP 1966). The wood anatomical characters of *Hillia illustris*, however, deviate strongly from those of the *Cinchoneae* (KOEK-NOORMAN 1970), *Gardenieae* and *Mussaendeae* studied by me and seem to justify its classification in a separate position.

Aulacocalyx Hook.f. = *Heinsenia* K. Schum., classified in the *Albertainae* by SCHUMANN (1897) (cf. *Cremasporae* sensu Bremekamp) was mentioned by HALLÉ (1967) in his treatment of the *Gardenieae*. VERDCOURT (1958) considered this genus to be so nearly related to *Ixora* that he classified it in a subtribe within the *Ixoreae*. Wood anatomically there is a good agreement with the *Gardenieae*. The same applies to *Tarenna* Gaertn. and *Tricalysia* A. Rich., genera which were removed from the *Gardenieae* into the *Ixoreae* by Bremekamp. In 3.2.3. I shall recur to these three genera.

Bertiera Aubl., *Heinsia* DC., and *Pentagonia* Bth. are dealt with in 3.2.2.

3.2.2. Delimitation of the *Mussaendeae* (see also 3.1.2.)

The *Mussaendeae* sensu BREMEKAMP (1966) and VERDCOURT (1958) include only a small number of the genera referred to the *Mussaendeae* by SCHUMANN (1897). They retain in this tribe the genera *Isertia* Schreb., *Mussaenda* L., *Cassupa* Humb. & Bonpl., "and perhaps a few other ones" (BREMEKAMP 1966).

The genera *Isertia* and *Mussaenda* differ in the percentage of vessels which are arranged in radial multiples. (In most species of *Isertia* the vessels are nearly exclusively solitary, whereas in the species of *Mussaenda* more than 50% of the vessels are arranged in radial multiples.) In the other wood characteristics they agree rather well, and in the wood anatomy therefore no reason can be found to doubt the rather close affinity between these two genera.

Gonzalagunia R. & P. is one of the small genera of the *Mussaendeae* sensu stricto. Contrary to *Isertia* and the samples of *Mussaenda* studied by me, *G. spicata* shows rays which are nearly exclusively composed of square and upright cells. As for some species of *Mussaenda* the same composition has been reported (CHANG 1951) and as, furthermore, the sample of *G. spicata* had a diameter of only 2 cm, this difference in the composition of the rays is no reason to dispute the affinity between *Gonzalagunia* and the other genera.

Gouldia A. Gray also is said to be allied to *Mussaenda*. The wood characteristics agree enough to accept this view (see table 1).

BREMEKAMP (1966) removed a number of genera from the *Mussaendeae* because of the presence of raphides, or because of a deviating structure of the testa cells. He classified them in the *Rubioideae* and *Urophyloideae*, respectively. *Schradera* Vahl and *Mycetia* Reinw., included in the first mentioned group, are represented by one sample each. The wood structure of *Mycetia myrioneuron* is quite different from that of *Isertia*, *Mussaenda*, *Gouldia*, and *Gonzalagunia*, and agrees better with the structure of the *Rubioideae* studied by me, viz. in the

presence of libriform fibres, in the composition of the rays (square and upright cells in uni- and biseriate parts), and the presence of scanty paratracheal parenchyma strands. The presence of raphides in the wood of *Schradera rotundata* fits in with Bremekamp's idea of classifying the genus in the *Rubioideae*. He remarked that the *Schradereae* are "the most deviating tribe among the *Rubioideae*". For the wood anatomy the same can be stated. With the *Mussaendeae*, however, the liana studied by me has less agreement.

Acranthera Arn. was removed from the *Mussaendeae* into a tribe of its own in the *Ixoroideae* by BREMEKAMP (1947). In a personal communication BAKHUIZEN VAN DEN BRINK suggested a position near the herbaceous *Rubioideae*. The only available sample of *A. longipes* shows some characteristics which fit in better with the *Rubioideae* studied by me than with the *Mussaendeae*.

Urophyllum Wall. and its nearest allies were classified in a separate subfamily by BREMEKAMP (1940). VERDCOURT (1958), who contrary to BREMEKAMP (1966) reported the presence of raphides in this group, included them in the *Rubioideae*. The most important difference between *Urophyllum*, *Pleiocarpidia*, *Leucolophus*, and *Maschalocorymbus* and the *Mussaendeae* seems to be the composition of the rays, which have high multiseriate parts composed of square and upright cells sometimes up to 6 cells wide. Remarkable are also the spiral thickenings of the fibre tracheids and the angular pores. The agreement with the *Rubioideae* is less close, thus Verdcourt's idea is not supported by the wood anatomy. Before the creation of the subfamily *Urophyllloideae* and its delimitation can be discussed in the light of the wood anatomy, it will be necessary to study more material of other related genera.

Heinsia DC. and *Bertiera* Aubl., placed in the *Gardenieae* by SCHUMANN (1897), were considered to form a subtribe in the *Mussaendeae* by VERDCOURT (1958). BREMEKAMP (1966) suggested that these genera may belong to his *Urophyllloideae*. HALLÉ (1961) classified *Heinsia* in the *Mussaendeae* and *Bertiera* in the *Gardenieae* (1967), be it in a marginal position. The wood of the species of *Heinsia* studied by me can not be distinguished from that of the species of *Mussaenda*, and it is improbable that these genera are not closely related. *Bertiera* agrees with *Isertia* in the predominantly solitary vessels and with *Gonzalagunia* in the composition of the rays.

Pentagonia Bth. was included in Hallé's study of the *Gardenieae* (1967). BREMEKAMP (1966) doubted whether *Pentagonia* might be regarded as related to *Hippotis* and *Sommeria*, genera which are considered to be near allies by SCHUMANN (1897). As stated in 3.1.2., the species of the three genera studied by me agree rather well. They are very similar to the *Rubioideae* studied by me (KOEK-NOORMAN 1969b). However, I observed no raphides. Further investigations are necessary to decide whether these crystals, the presence of which is required for an inclusion in the *Rubioideae* (BREMEKAMP 1966), are also absent in other parts of the plants.

3.2.3. Delimitation of the *Ixoreae* (see also 3.1.3.)

Because of the agreement in the structure of the drupe the *Ixoreae* sensu

SCHUMANN (1897) were enlarged with some genera by BREMEKAMP (1934b), i.a. with *Tarenna* Gaertn. and *Tricalysia* A. Rich. which had been included in the *Gardenieae* by Schumann. The wood structure of *Tarenna* and *Tricalysia* fits in very well with that of the other *Ixoreae* studied by me. The small variation within the *Ixoreae*, however, does not exceed that within the *Gardenieae*. It seems impossible to decide by means of the wood anatomy whether *Tarenna* and *Tricalysia* are to be referred to the *Gardenieae* or to the *Ixoreae*. *Tarenna incerta*, the only species with about 60% of the vessels arranged in radial multiples, is considered to be identical with *Randia wallichii* as stated by BAKHUIZEN VAN DEN BRINK in a personal communication. All species of *Randia* studied by me show nearly exclusively solitary vessels except *R. wallichii* which is wood anatomically rather similar with *T. incerta*. Within the *Gardenieae* however, the characteristic of radial multiples occurs in several genera.

Aulacocalyx Hook.f., classified by SCHUMANN (1897) in the *Albertheae*, was placed in a subtribe in the *Ixoreae* by VERDCOURT (1958). HALLÉ (1967) included this genus in the *Gardenieae*. PETIT (1962) combined *Heinsenia* K. Schum. and *Aulacocalyx* in one genus but did not discuss its relationship with other *Rubiaceae*. The wood samples of *H. sylvestris* and *A. jasminiflora* show only minor quantitative differences. As for *Aulacocalyx*, the same can be stated as for *Tarenna* and *Tricalysia*: the wood characteristics do not exceed those of the *Ixoreae*. Thus by means of these characteristics a decision about classification either in the *Gardenieae* or in the *Ixoreae* can not be made.

3.2.4. Relationship between *Gardenieae*, *Ixoreae*, and *Mussaendeae*

As stated in 3.2.3. the wood anatomy of the *Gardenieae* and the *Ixoreae* studied by me is very similar. The *Gardenieae* show some variation in the arrangement of the vessels, the width of the rays, and the distribution of the axial parenchyma (see table 1). The very small variation within the *Ixoreae* does not exceed that within the *Gardenieae*. This supports the classifications of VERDCOURT (1958) and BREMEKAMP (1953, 1966), in which the *Gardenieae* and *Ixoreae* are considered to be nearly related and are therefore placed in one subfamily, contrary to those of SCHUMANN (1897) and his predecessors. The wood anatomy of the *Mussaendeae* sensu Bremekamp (*Mussaenda*, *Isertia*, *Gouldia*, *Gonzalagunia*) studied here deviates in some respects from that of the *Gardenieae* and *Ixoreae* (for instance by the frequent occurrence of radial multiples of vessels in *Mussaenda*, and by the structure of the rays, which are often predominantly composed of square and upright cells). The differences, however, are not so large that they can be adduced in support of the distinction between *Ixoroideae* and *Cinchonoideae* made by Bremekamp. This question will be studied in subsequent investigations of the other tribes of these subfamilies.

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MATERIAL STUDIED*

- Acranthera longipes* Merr.: Indonesia – Uw 18412 (USw 27547, Sumatra; diam. 1 cm).
Alibertia acuminata (Bth.) Sandwith: British Guiana – Uw 1074 (For. Dept. 2403).
Amaioua corymbosa H. B. K.: Panama – Uw 7039 (USw 73, U.S. Nat. Herb. 715490).
Amaralia streptocaulon K. Schum.: Cameroun – Uw 9428 (Breteler 1867, Doumé; liana, diam. 5 cm).
Aulacocalyx jasminiflora Hook. f.: Ghana – Uw 17777 (Vigne 3149); Liberia – Uw 18442 (SJRw 13785, Cooper 142; diam. 3.5 cm).
Bertiera guianensis Aubl.: Brazil – Uw 7867 (Krukoff 6677; diam. 4 cm); Suriname – Uw 12106 (v. Donselaar 3402, Brokopondo; treelet, diam. 1.5 cm); Panama – Uw 16621 (Cooper 586).
Bertiera racemosa K. Schum.: Liberia – Uw 16622 (Cooper 258).
Borojoa stipularis (Ducke) Cuatr.: Brazil – Uw 16199 (Krukoff 8470; diam. 6 cm).
Casasia clusiifolia Urb.: Florida – Uw 17747 (F.P.R.L. 12826).
Casasia longipes Urb.: Jamaica – Uw 8333 (USw 5959; diam. 5 cm).
Duroia fusifera Hook. f. ex Schum.: Venezuela – Uw 12235 (Breteler 4843, Sipapó R.; tree, 8 m high, diam. 18 cm).
Duroia hirsuta (P. & E.) Schum.; Brazil – Uw 7734 (Krukoff 6448; large tree); Uw 16209 (Krukoff 8631; diam. 5 cm); Uw 16231 (Krukoff 8954; diam. 3.5 cm).
Duroia saccifera (Mart.) Hook. f.: Brazil – Uw 8040 (Krukoff 6911; diam. 3.5 cm).
Galiniera coffeoides Delile: East Africa – Uw 15916 (Schlieben 274; diam. 6 cm).
Gardenia remyi H. Mann: Hawaiian Islands – Uw 4810 (K. Korte, Yale 49356; large tree).
Gardenia riparia K. Schum.: East Africa – Uw 15948 (Schlieben 1734; diam. 8 cm).
Gardenia thunbergii L. f.: East Africa – Uw 15851 (Schlieben 1801; diam. 8 cm).
Genipa caruto H.B.K.: Panama – Uw 7028 (USw 54, U.S. Nat. Herb. 679845; large tree).
Gonzalagunia spicata (Lam.) Gomez: Dominica – Uw 15430 (Chambers 2670).
Gouldia axillaris Wawra: Hawaiian Islands – Uw 18440 (SJRw 26526; diam. 2 cm).
Gouldia terminalis (Hook. & Arn.) Hillebr.: Hawaii Islands – Uw 18439 (SJRw 52721; diam. 2.5 cm); Uw 18547 (Stern & Herbst 463; diam. 0.5 cm); Uw 18562 (Stern & Herbst 479; diam. 2.5 cm); Uw 18565 (Stern & Herbst 482; diam. 2 cm).
Hamelia patens Jacq.: Brazil – Uw 14186 (Lindeman & H. de Haas 4840, Paraná; treelet, diam. 2.7 cm); Florida – Uw 17765 (PRFw 12802).
Heinsenia sylvestris S. Moore: Rhodesia – Uw 17726 (Swynnerton; diam. 7 cm).
Heinsia jasminiflora DC.: Liberia – Uw 16623 (Cooper 102).
Heinsia pulchella K. Schum.: Cameroun – Uw 9490 (Breteler 2324, Yaoundé; tree, 10 m high, diam. 16 cm); Liberia – Uw 16624 (Cooper 210); Uw 18406 (USw 4531).
Hippotis brevipes Spruce: Peru – Uw 17892 (MADw 6945).
Ibetrulia surinamensis Brem.: Suriname – Uw 1706 (Lanjouw & Lindeman 2338, Nassau Mountains; diam. 2.5 cm).
Isertia hoehnei Krause: Brazil – Uw 16157 (Krukoff 8064).
Isertia longifolia K. Schum.: Brazil – Uw 9042 (Maguire c.s. 51784, Rio Araguari, Amapá; diam. 13 cm).
Ixora casei Hance: Ponape – Uw 16700 (Miller 6693).
Ixora grandiflora Z. & M.: Indonesia – Uw 17766 (Krukoff 4397, Sumatra).
Ixora macrophylla Bartl. ex DC.: – Uw 16276 (RTIw 18 – 68 – 262).
Ixora triantha Volk.: Mariana Islands – Uw 16688 (Dutton 129).

* Abbreviations are according to STERN, *Index Xylariorum* (1967).

- Ixora venulosa* Bth.: *Brazil* – Uw 13155 (Lindeman & H. de Haas 1541, Paraná; treelet, diam. 5 cm).
- Kotchubaea semisericea* Ducke: *Brazil* – Uw 16185 (Krukoff 8372; large tree).
- Leptactinia hexamera* K. Schum.: *East Africa* – Uw 15884 (Schlieben 16; diam. 6 cm).
- Leucolophus tobingsensis* (Miq.) Brem.: *Indonesia* – Uw 18402 (USw 27480, Sumatra; diam. 1.5 cm).
- Maschalocorymbus corymbosus* (Blume) Brem.: *Indonesia* – Uw 17903 (Jacobs 5290, Borneo).
- Mussaenda sphaerocarpa* Mildbr.: *East Africa* – Uw 14950 (RTIw TP 4374 – 45; diam. 7 cm); Uw 15543 (Schlieben 1605; diam. 6.5 cm).
- Mussaenda zenkeri* Wernh.: *Cameroun* – Uw 9265 (Breteler 784, Bertoua; liana, diam. 1.5 cm).
- Mussaenda* spec.: *Cameroun* – Uw 9258 (Breteler 556, Adamaoua; liana, diam. 4 cm).
- Mycetia myrioneuron* Merr.: *Indonesia* – Uw 18403 (USw 28852, Sumatra; diam. 1.2 cm).
- Pavetta crassipes* K. Schum.: *Nigeria* – Uw 17800 (Jones 6348 = FHOw 13410; diam. 3 cm).
- Pavetta megistocalyx* K. Krause: *Ghana* – Uw 17771 (Vigne 2966).
- Pentagonia macrophylla* Benth.: *Panama* – Uw 16625 (Cooper & Slater 122); Uw 17730 (USw 119; diam. 2.5 cm).
- Pentagonia velutina* Standl.: *Peru* – Uw 18460 (MADw 5280, Puerto Arturo, R. Huallaga; diam. 6 cm).
- Pleiocarpidia assahanica* Brem.: *Indonesia* – Uw 18410 (USw 28886, Sumatra; diam. 2 cm).
- Pleiocarpidia sandahanica* Brem.: *Indonesia* – Uw 17901 (Jacobs 5291, Borneo; diam. 12 cm).
- Randia dumetorum* Lam.: *East Africa* – Uw 15835 (Schlieben 1783; diam. 6 cm).
- Randia sericantha* K. Schum.: *East Africa* – Uw 15877 (Schlieben 1852; diam. 7 cm).
- Randia wallichii* Hook. f.: *Indonesia* – Uw 17906 (BW 7231, New Guinea; large tree); Uw 18289 (BW 13515, New Guinea; large tree).
- Rennellia speciosa* Hook. f.: *Malaysia* – Uw 17805 (Pickles 3720, Sarawak).
- Rennellia* spec.: *Indonesia* – Uw 17896 (Fuchs 21358, Borneo; diam. 4.5 × 6 cm).
- Retiniphyllum concolor* (Spr. ex Bth.) Muell. Arg.: *Venezuela* – Uw 18628 (Wurdack & Addersley 43234, Terr. Amazonas).
- Retiniphyllum pauciflorum* Kunth. ex Krause: *Venezuela* – Uw 18630 (Wurdack & Addersley 42752, Terr. Amazonas).
- Rothmannia urcelliformis* (Schweinfl. ex Hiern) Bullock ex Robyns: *Ethiopia* – Uw 14779 (Meyer 8819; diam. 6 cm).
- Rothmannia whitfieldii* (Lindley) Dandy: *Ivory Coast* – Uw 10885 (Leeuwenberg 4110, near Guéyo; treelet, 8 cm high, diam. 8 cm).
- Rutidea membranacea* Hiern: *Cameroun* – Uw 9322 (Breteler 1406, Ebaka; liana, diam. 2.5 cm).
- Sommeria sabiceoides* Schum.: *Peru* – Uw 17889 (MADw 1810; diam. 4 cm); Uw 17890 (MADw 2076; diam. 2.5 cm); Uw 17891 (MADw 2664; diam. 3 cm).
- Stachyarrhena acuminata* Standley: *Brazil* – Uw 9607 (Maguire c.s. 51403).
- Tarenna flavo-fusca* (K. Schum.) S. Moore: *Cameroun* – Uw 9510 (Breteler 2423, Bertoua; liana, diam. 3 cm); *Ivory Coast* – Uw 10884 (Leeuwenberg 4158, La Mé R; liana, diam. 1.5 cm).
- Tarenna fragrans* Koord. & Valet.: *Indonesia* – Uw 17810 (FHOw 8091, Malaya); Uw 18455 (SJRw 31073, Java).
- Tarenna glabra* Merr.: *Mariana Islands* – Uw 18453 (SJRw 33235; diam. 3.5 cm).
- Tarenna incerta* Koord. & Valet.: *China* – Uw 18454 (SJRw 29567, Ngai Yuen, Hainan; large tree).
- Tarenna pavettoides* (Harv.) Sim.: *Rhodesia* – Uw 17729 (Coll. Swynnerton; diam. 8 cm).
- Tarenna sambucina* Sch. & Lauterb.: *Fiji Islands* – Uw 18456 (SJRw 28264; diam. 6 cm).
- Tocoyena guianensis* K. Schum.: *Brazil* – Uw 16913 (Maguire c.s. 48072; diam. 9 cm).
- Tricalysia malaccensis* Hook. f.: *Indonesia* – Uw 17813 (For. Dept. 445 = FHOw 7625, Malaya).
- Tricalysia nyassae* Hiern: *Tanganyika* – Uw 15491 (Schlieben 1509; diam. 6 cm); Uw 18457 (SJRw 23392; diam. 4.5 cm).
- Tricalysia pallens* Hiern: *Ghana* – Uw 17814 (Vigne 2653; diam. 4.5 cm).
- Tricalysia* spec.: *Cameroun* – Uw 9255 (Breteler 538, Adamaoua; treelet, diam. 5 cm); Uw 9317

(Bretelet 1390, Bertoua; tree, 15 m high, diam. 20 cm).

Urophyllum glabrum Jack: *Malaysia* – Uw 16626 (Pickles 3670, Borneo, Sarawak; diam. 4.5 cm).

Urophyllum trifurcum Pears: *Malaysia* – Uw 16627 (Pickles 3762, Borneo, Sarawak; diam. 5 cm).

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