THE WOOD ANATOMY OF VANGUERIEAE, CINCHONEAE, CONDAMINEAE, AND RONDELETIEAE (RUBIACEAE)*

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SUMMARY

This paper deals with the *Vanguerieae, Cinchoneae, Condamineae* and *Rondeletieae,* and concludes a study on the anatomy of the secundary xylem of the *Cinchonoideae* + *Ixoroideae.* The taxonomically homogeneous *Vanguerieae* show only little variation. Taxonomically the *Cinchoneae, Condamineae,* and *Rondeletieae,* placed near each other in the *Cinchonoideae,* are rather heterogeneous. Their woods show also more anatomical differences, with a similar scala of variation within each tribe. Numerical analysis of the pattern of variation was undertaken. Cluster analysis showed a very distinct bipartition, which remained almost invaried while calculations were executed with different character weighings. This bipartition is not expressed in the existing taxonomic classifications. An attempt to distinguish the three tribes on the basis of their wood anatomy was made, but was unsuccessful.

1. INTRODUCTION

In two previous papers the wood anatomy of *Cinchoneae, Naucleeae* and *Coptosapelteae* (KOEK-NOORMAN 1970) and of *Gardenieae, Ixoreae* and *Mussaendeae* (KOEK-NOORMAN 1972) is described and discussed in relation to classification. All these tribes belong to the subfamily *Cinchonoideae* sensu VERDCOURT (1958), that corresponds with BREMEKAMP's *Ixoroideae* + *Cinchonoideae* (1966). (For a survey of the classifications of the *Rubiaceae* as given by Schumann, Verdcourt, and Bremekamp we refer to KOEK-NOORMAN 1969b.)

The tribes *Acranthereae, Sabiceae* and *Sipaneae* of this subfamily are almost entirely herbaceous, and consequently they cannot be taken into consideration in a study of the secondary xylem.

Until now the samples available of two other tribes, the *Cremasporeae* and *Chiococceae,* are so scanty that any conclusion with regards to classification or affinity would not be justified. In this paper a treatment of the *Vanguerieae, Condamineae,* and *Rondeletieae* is given in order to conclude the wood anatomical study of the *Cinchonoideae* + *Ixoroideae.* Although the *Cinchoneae* were included in the paper of 1970, they are treated here once more, because information obtained from samples received since that time has compelled Koek-Noorman to change her opinion concerning the homogeneity of this tribe.

In previously published papers conclusions and decisions based upon wood

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anatomy, regarding conformity and difference between tribes and genera did not conflict with existing taxonomic concepts. Especially in three groups now discussed this seemed more arbitrary than justifiable. Therefore numerical pattern detection methods were used in an attempt to establish a more objective basis for our conclusions.

2. MATERIAL AND METHODS

The treatment of the material has been described in KOEK-NOORMAN's paper (1969a). The anatomical terms are in accordance with the Multilingual Glossary of Terms used in Wood Anatomy (1964), except for "libriform fibre" and "fibre tracheid". For these elements, as in the paper cited above, REINDERS' (1935) definition is accepted.

The material studied is listed at the end of the paper. Of most wood samples corresponding herbarium vouchers are known. Wood anatomical data of samples which are not provided with herbarium material, are used only when more, reliably identified material of the same genus was available.

The data from *Cinchoneae*, *Cindamineae* and *Rondeletieae* are compiled in a table, which is not included in this paper because of technical difficulties, but which is obtainable on request. The data from the *Vanguerieae* are left out, for reasons explained below.

3. VANGUERIEAE

The *Vanguerieae* form a group of closely allied genera (ROBIJNS 1928, VERDCOURT 1958). This homogeneity is also found in the anatomy of their secondary wood. The specimens studied (representing the genera *Cuviera*, *Plectronia*, *Rytigynia*, *Vangueria*) not only resemble each other strongly in wood anatomical characters, but also fit within the few descriptions of the structure of *Canthium horridum* Bl. and *C. longistylum* Merr. (CHANG 1951), and in particular with JANSSONIUS' (1926) description of *Plectronia didyma* Bth. & Hook. (*Canthium didymum* Gaertn.), *Plectronia glabra* Koord. & Val. (*Canthium glabrum* Bl.), *Plectronia scandens* Koord. & Val. (*Canthium scandens* Bl.), and *Vangueria spinosa* Koord. & Val. (*Meyna spinosa* Roxb. ex Link.). In view of the latter's very detailed data, it will be sufficient to give here a short survey of the studied wood samples of this tribe:

Vessels: exclusively or predominantly solitary, sometimes a small percentage in small radial multiples; diameter mostly about 50 μ, sometimes up to 75 μ; mostly over 40 vessels per sq. mm (with exception of the specimen of *Canthium hispidum* with 8–10 vessels per sq. mm and a diameter of up to 200 μ); perforations simple; end walls transverse to slightly oblique; intervascular pitting vestured, 4–6 μ.

Fibre tissue: fibre tracheids with mostly numerous bordered pits on radial and tangential cell walls. (In *Cuviera angolensis*, *Rytigynia neglecta*, and *Vangueria infansta* there are only few pits on the tangential walls.)

Rays: heterogeneous type I (KRIBS 1937); the multiseriate parts 2–4(-5)-seriate, often very low (height 6–12 cells, 300–500 μ), width up to 50 μ; pits to vessels similar to the intervascular pits.

Parenchyma: diffuse apotracheal, often tending to form a reticulate pattern of uniseriate bands. (In the material of *Canthium confertum* longer and broader bands occur.)

SCHUMANN (1879) listed the *Vanguerieae* in the *Coffeoideae*, *Guettardinae*. The tribe was considered to be closely allied to *Gardenieae* and *Ixoreae* by VERDCOURT (1958) as well as by BREMEKAMP (1966). The material of *Guettardeae* at my disposal is not sufficient to warrant a judgement on the position of the *Vanguerieae* in relation to this group. However, the *Vanguerieae* studied are very similar to *Gardenieae* and *Ixoreae* (KOEK-NOORMAN 1972) and there is no reason to doubt the opinion of Verdcourt and Bremekamp respectively.

For a long time *Craterispermum* has been considered as a member of the *Vanguerieae*. In 1958 Verdcourt created a new tribe *Craterispermeae*, closely related to *Psychotrieae* and *Urophylleae* because of the presence of raphides, heterostyly and a bifid style. In the anatomy of the wood *Craterispermum* differs from the other *Vanguerieae* by the presence of raphides and broad and long parenchyma bands. These two characters, next to other features, show a striking resemblance with species of *Gaertnera* and *Pagamea*, genera placed by those authors who consider them to be rubiaceous, in the *Rubioideae*, where VERDCOURT also wishes to accomodate *Craterispermum*.

In view of what has been stated above on the homogeneity of the *Vanguerieae* in anatomical respects as well as the accordance between the anatomical data and modern taxonomic opinions it did not seem necessary to include the *Vanguerieae* in the computer cluster analysis.

4. CINCHONEAE, CONDAMINEAE, RONDELETIEAE

4.1. Preliminary discussion

4.1.1. Anatomy of Cinchoneae

Previously the anatomy of a number of *Cinchoneae* has been compared with data from the literature (KOEK-NOORMAN 1970). Most of the species then studied showed the same type of libriform fibres. This was in agreement with the data given by some authors. However, SOLEREDER (1885) and JANSSONIUS (1926) mention bordered pits in the fibres in species of *Cascarilla* and *Cinchona*. As since 1970 the number of available wood specimens of the *Cinchoneae* has been tripled*, more recent investigations lead to the conclusion that the wood struc-

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* The *Cinchoneae* include about 30 woody genera, 17 of which are represented by specimens of 43 species in the present study.

ture within the tribe is less homogeneous. On one hand a number of genera show libriform fibres (*plate I, fig. 6*), on the other hand *Badusa, Cascarilla, Exostema, Ladenbergia,* and *Remijia* show fibre tracheids (*plate I, fig. 2*). The fibres of the species of *Cinchona* studied have small pits with rather small borders, septa are absent or very few. More or less connected with these differences in fibre characters are differences in vessel arrangement, width of the rays, parenchyma pattern, and presence or absence of crystal sand.

CHANG (1951) in his description of *Cinchona pubescens* describes the fibres as being non-septate and with bordered pits predominantly occurring on the radial walls. He considers them as fibre tracheids. Although, as compared to the fibre pits of many other *Rubiaceae* with true libriform fibres, the fibre pits of *Cinchona* are rather clearly bordered, we consider the fibres nevertheless as a transitional form between fibre tracheids and libriform fibres. The absence of pits from the tangential walls and the occasional presence of septa are according to Janssonius' concept (REINDERS 1935) a reason to consider these elements not as fibre tracheids.

4.1.2. Anatomy of Condamineae and Rondeletieae

As well as the *Cinchoneae*, the tribes *Condamineae* and *Rondeletieae* are placed in the *Cinchonoideae* sensu Bremekamp. The structure of the representatives investigated** shows the same range of variation in characteristics as found within the *Cinchoneae.* Here, contrary to tribes considered taxonomically homogeneous (e.g. *Vanguerieae, Ixoreae, Gardenieae, Naucleeae, Mussaendeae, Psychotrieae*) fibre tracheids as well as libriform fibres occur. No strong correlation between fibre characters and other features could be indicated.

The only exceptional species is *Pinckneya pubens*, belonging to the *Condamineae.* It is differing by the semi-ringporousness, the tangential pore chains and the concentric parenchyma bands (*plate II, fig. 5, 6*). *Gleasonia duidana* and *G. uaupensis* are noticeable by their uniseriate rays (*plate III, fig. 3, 4*).

In the literature no descriptions of the wood of *Condamineae* could be found, the *Rondeletieae* are mentioned only a few times and then a good agreement with the present data is found. The descriptions of *Greenea corymbosa* (Jacq.) K. Schum., *Rhombospora commersonii* Korth., *Wendlandia glabrata* DC., and *Wendlandia glabrata* var. *laevigata* Cowan (CHANG 1951) differ only in minor

** The *Condamineae* include 10 woody genera, 8 of which are represented here by 13 species. The Rondeletieae include about 15 woody genera. Specimens of 9 genera (28 species) were available.

Plate I.
Fig. 1. *Ladenbergia latifolia* L. Wms. (Uw 18011) transv. sect. 45 ×;
Fig. 2. *Ladenbergia latifolia* L. Wms. (Uw 18011) tang. sect. 110 ×;
Fig. 3. *Remijia amazonica* K. Sch. (Uw 18449) transv. sect. 45 ×;
Fig. 4. *Remijia amazonica* K. Sch. (Uw 18449) tang. sect. 45 ×;
Fig. 5. *Macrocnemum glabrescens* (Bth.) Wedd. (Uw 7052) transv. sect. 45 ×;
Fig. 6. *Macrocnemum glabrescens* (Bth.) Wedd. (Uw 7052) tang. sect. 110 ×.

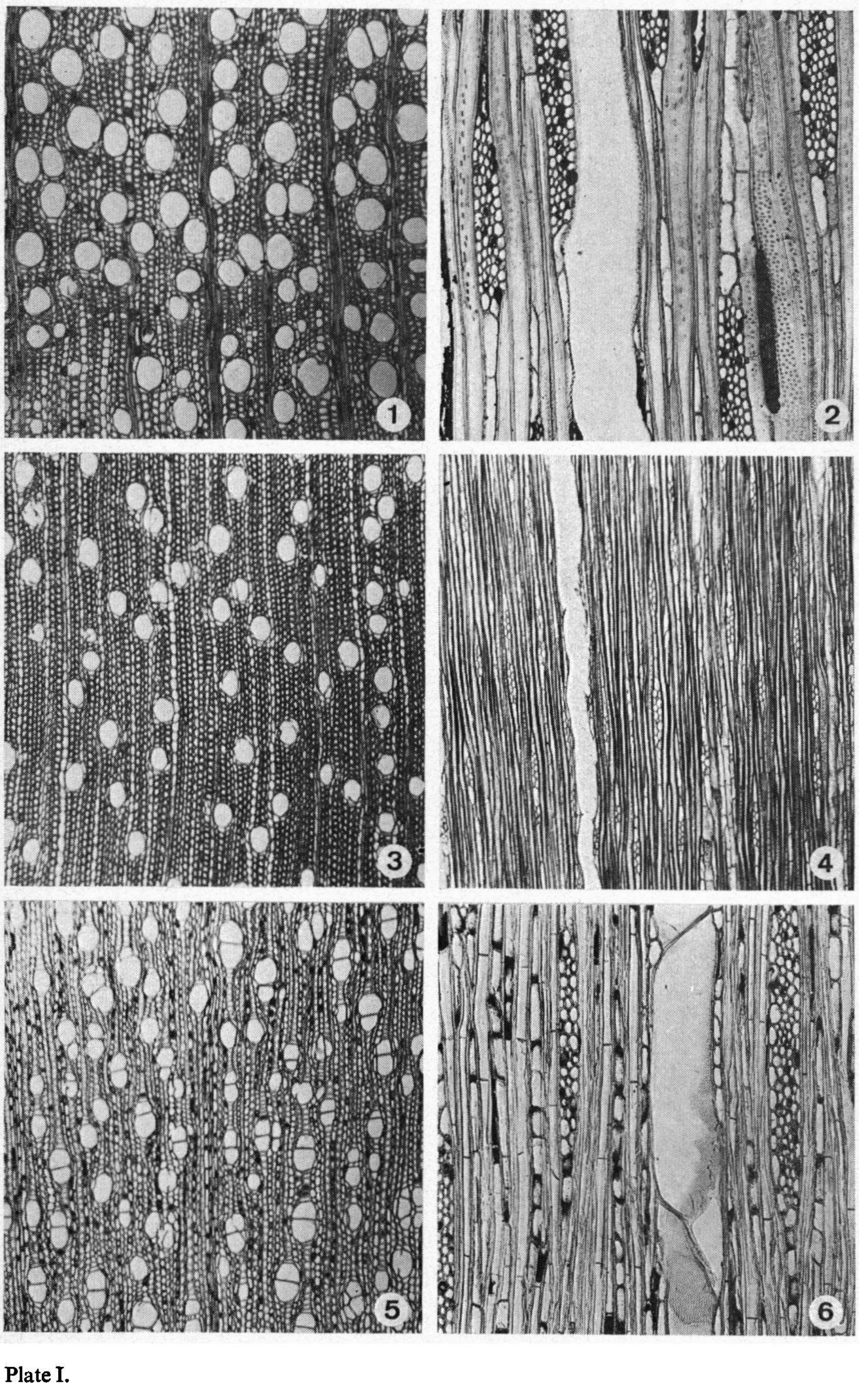

Plate I.

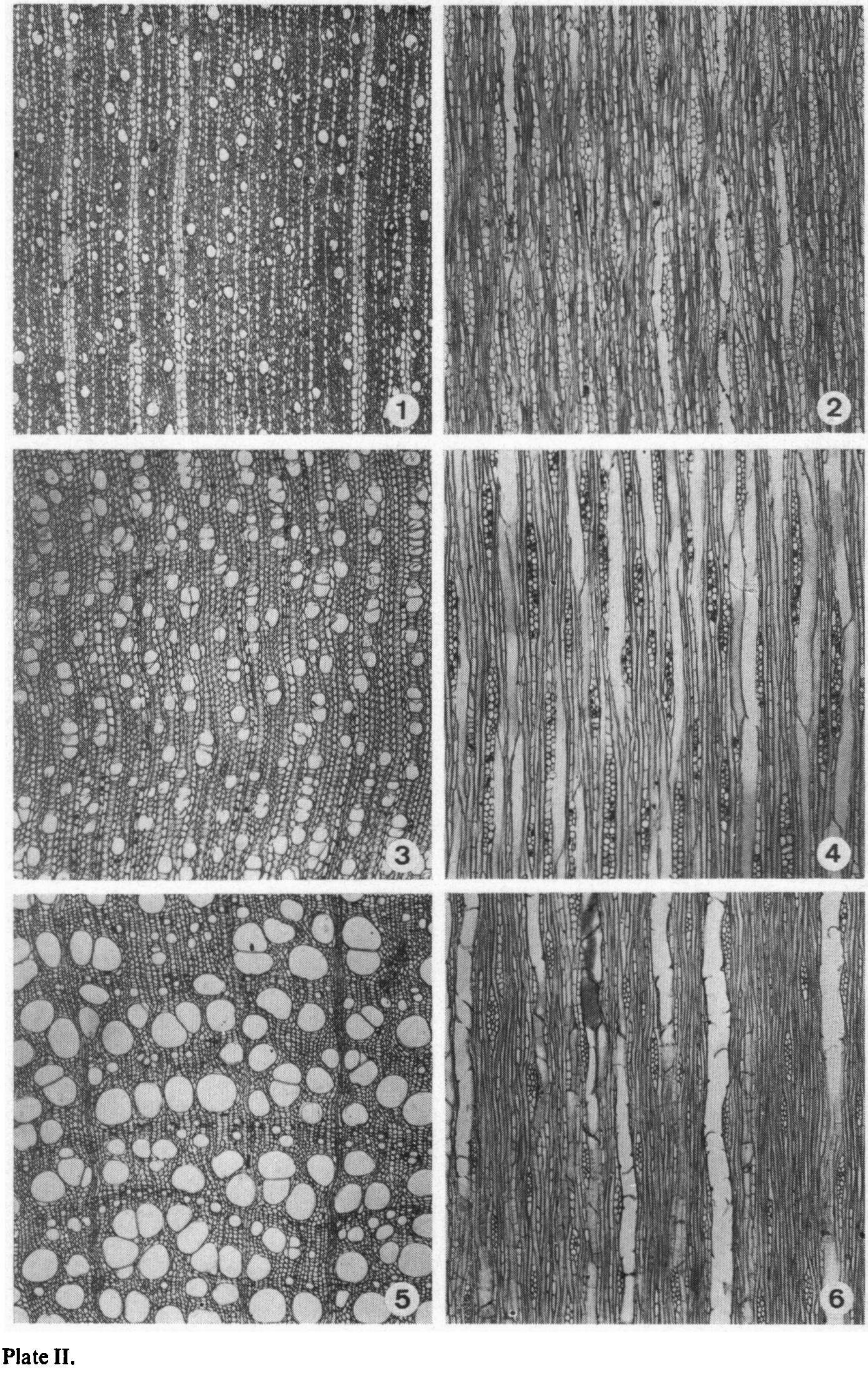

Plate II.

details. JANSSONIUS' (1926) description of some species of *Wendlandia* are in perfect accordance with our findings. In the eight species of *Simira* studied over 50% of the vessels are arranged in short radial multiples, whereas Chang mentions the vessels as being predominantly solitary. WILLIAMS (1936) describes the parenchyma in *Warzewiczia coccinea* as reticulate, in *W. cordata* as indistinct. In the specimen of *W. coccinea* available for the present study parenchyma is lacking.

4.1.3. Significance of wood anatomy for taxonomy of Cinchoneae, Condamineae, and Rondeletieae.

The *Cinchoneae*, *Condamineae*, and *Rondeletieae*, placed near to each other by all recent authors, are taxonomically not as homogeneous as other rubiaceous tribes (personal communication of Bremekamp and Ridsdale). Modern monographs of these taxa are lacking.

Wood anatomically the three tribes are also slightly more heterogeneous than the taxonomically homogeneous ones. However, it does not seem to be justified to suggest affinities or dissimilarities without further analysis of the data set, because of the non obvious correlation of the fibre characters with other features. Therefore further analysis of the pattern of variation of the wood structure was undertaken.

4.2. Pattern detection and recognition

4.2.1. Methodological preliminaries

The problem before us is to relate the wood anatomical structure of some of the species of the *Rubiaceae* to a classification of these species based on general morphological characteristics.

In any classificatory problem we should keep in mind that we are dealing with descriptions of objects (species, specimen), not with the objects themselves. These descriptions are based on sets of observations. In principle we can make an unlimited number of observations on any appointed object. The selection of a "scope of observation" is *a priori* to our further classificatory or descriptive efforts. There is no *a priori* reason whatsoever to expect that classifications based on different scopes of observations (although related to the same objects) should correspond in any way.

We can follow one of two strategies:

a. By forming a classification of the species based on wood anatomical scope of observation and compare this classification a posteriori with the given

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Plate II.
Fig. 1. *Bikkia tetrandra* (L.f.) A. Gray (Uw 16349) transv. sect. 45 ×;
Fig. 2. *Bikkia tetrandra* (L.f.) A. Gray (Uw 16349) tang. sect. 45 ×;
Fig. 3. *Rustia formosa* Klotz (Uw 16269) transv. sect. 45 ×;
Fig. 4. *Rustia formosa* Klotz. (Uw 16269) tang. sect. 45 ×;
Fig. 5. *Pinckneya pubens* Michx. (Uw 9987) transv. sect. 45 ×;
Fig. 6. *Pinckneya pubens* Michx. (Uw 9987) tang. sect. 45 ×.

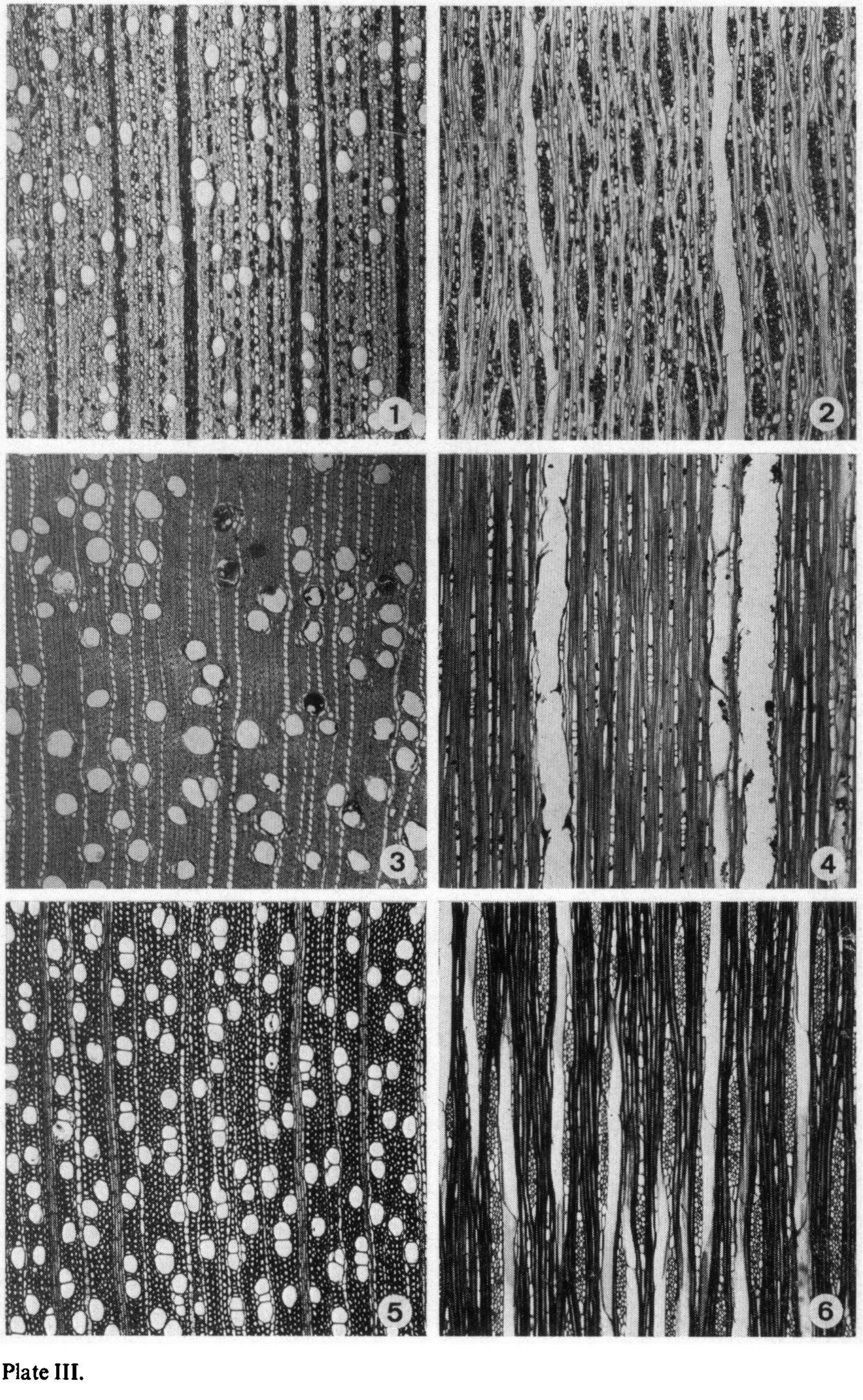

Plate III.

classification(s) based on a morphological scope of observation (Pattern-detection-approach).

b. forming a description of the wood anatomical structure of the species (based on the given scope of observation) in such a way that the descriptions for species falling in the same a priori class (here based on morphology) are more similar (homogeneous in the foregoing terminology) to each other than to species falling in other classes (Pattern-recognition-approach).

The following fundamental points should be kept in mind.

1. Given a scope of observation we may construct a description based entirely on these observations such that the similarity between all object-pairs (i.c. specimens) is equal (Theorem of the Ugly Duckling, WATANABE 1969).
2. Given a scope of observation and a priori classification we can always find a description such that we can assign the objects on the basis of this description to the proper class (corrolary of 1.). (Necessary conditions are a finite set of objects distinguishable in the scope of observation.)

In approach a. we will select a priori a description and find a classification on that basis. In approach b. we select an a priori classification and try to find a description in wood anatomical terms agreeing in this classification. The two approaches were not distinguished in previous work on other tribes of *Rubiaceae*. Intuitively the two descriptions did not seem to conflict: descriptions found to agree with the a priori classification did not differ widely from descriptions which would have been given a priori to find a classification.

In the groups at present in discussion this was not the case; some characteristics seemed to agree with the a priori classification but it seemed unreasonable to limit the description to those. Here we will investigate both approaches separately.

4.2.2. Method

Because of the above mentioned methodological arguments, pattern detection should be seen as an essentially heuristic method, to investigate the results of a priori derived descriptions. Therefore the analysis will often include several trials, with slightly different a priori descriptions. The program-system BIOPAT (HOGEWEG & HESPER 1972) is designed with this in mind. Assuming that the description of the objects is given in the form of vectors of character values (as is usual in Numerical Taxonomy and most other pattern-analysis schemes) it provides an easy means for changing descriptions as far as weighing, scaling and joining of characters is concerned.

Plate III.
Fig. 1. *Wendlandia rufescens* Miq. (Uw 16273) transv. sect. 45 ×;
Fig. 2. *Wendlandia rufescens* Miq. (Uw 16273) tang. sect. 45 ×;
Fig. 3. *Gleasonia duidana* Standl. (Uw 17790) transv. sect. 45 ×;
Fig. 4. *Gleasonia duidana* Standl. (Uw 17790) tang. sect. 45 ×;
Fig. 5. *Simira maxonii* (Standl.) Steyerm. (Uw 7134) transv. sect. 45 ×;
Fig. 6. *Simira maxonii* (Standl.) Steyerm. (Uw 7134) tang. sect. 45 ×.

Table 1. Characters and attributes.

		absent		present
Vessels				
Arrangement	1. nearly exclusively solitary	0		1
	2. short radial multiples (2–4 cells)	0	0– 10%	1
	3. long radial multiples (4 cells)	0	10– 25%	2
	4. halterlike pore clusters	0	25– 50%	3
	5. irregular pore clusters	0	50–100%	4
Distributions	6. radial pore chains	0		1
	7. tangential pore chains	0		1
	8. diagonal arrangement	0		1
perforations	9. simple	0	small	1
			as wide as vessel diameter	2
	10. reticulate	0		1
	11. scalariform	0	less than 10 bars	1
			more than 10 bars	2
Intervascular pitting	12. scalariform	0		1
	13. opposite	0		1
	14. alternate	0		1
	15. confluent	0		1
	16. ⩽ 4 μ			1
	5– 7 μ			2
	8–10 μ			3
	>10 μ			4
	17. vestured	0		1
tyloses	18.	0	thin	1
			sclerotic	2
inclusions	19. gumlike	0		1
	20. calcareous	0		1
	21. other, coloured substances	0		1
cell wall	22. thickness	thin 0	thick	1
	23. spiral thickenings	0		1
diameter of pores	24. angular	0		1
	25. round	0		1
	26. oval	0		1
	27. all vessels about the same diameter	0		
	diameter of the vessels slowly changing within each growth zone			1
	(semi) ringporous			2
diameter of the largest pore sole	28. < 50 μ			1
	50–100 μ			2
	100–200 μ			3
	200–300 μ			4
	>300 μ			5

		absent		present
Vessels				
diameter of the smallest pore, if present	29. < 50 μ	0		1
	50–100 μ			2
	100–200 μ			3
	200–300 μ			4
length of the vessel members	30. <400 μ			1
	400–800 μ			2
	800–1600 μ			3
	>1600 μ			4
number/sq. mm	31. < 5			1
	5–10			2
	10–20			3
	20–40			4
	40–80			5
	>80			6
tracheids	32. scanty	0		1
	abundant			2
Fibres				
structure	33. all septate	0		1
	34. septate fibres in bands	0		1
	35. septate fibres paratracheal	0		1
	36. septate fibres diffuse	0		1
cell wall	37. very thin, lumen 3 × cell wall thickness			1
	lumen 2–3 × cell wall thickness			2
	moderately thick			3
	very thick, lumen very narrow			4
	38. spiral thickenings	0		1
	39. gelatinous	0	partly	1
			all fibres	2
pitting	40. without or with small borders	0		1
	41. with large borders, unlike intervascular pitting	0		1
	42. with large borders, similar to intervascular pitting	0		1
presence of pits	43. on radial cell walls	0	scanty	1
	44. on tangential cell walls	0	abundant	2
length of fibres	45. < 900 μ			1
	900–1600 μ			2
	1600–2200 μ			3
	>2200 μ			4
form	46. fusiform	0		1
	47. irregularly pointed	0		1
inclusions	48. starch	0		1
	49. coloured substances	0		1
	50. crystals	0		1

		absent	present
Rays			
cell types	51. procumbent cells	0	1
	52. square and upright cells	0	1
	53. sheath cells	0	1
	54. by-pass vessel members	0	1
width	55. uniseriate	0	1
	56. 2-seriate	0	1
	57. 3-4-seriate	0	1
	58. 5-12-seriate	0	1
	59. >12-seriate	0	1
multiseriate parts	60. procumbent cells	0	1
	61. square/upright cells	0	1
marginal cells	62. 1 row of square/upright cells	0	1
	1–4 rows of square/upright cells		2
	>4 rows of square/upright cells		3
composition	63. rays vertically composed	0	1
	64. rays forming aggregate rays	0	1
ripple marks	65.	0	1
disjunctive elements	66.	0	1
number per mm	67. < 5		1
	5–10		2
	11–15		3
	>15		4
width	68. < 30 μ		1
	30– 50 μ		2
	50–100 μ		3
	100–200 μ		4
	200–300 μ		5
	>300 μ		6
height	69. < 400 μ		1
	400– 800 μ		2
	800–1500 μ		3
	1.5–3.0 mm		4
	3.0–5.0 mm		5
	5– 10 mm		6
	10– 30 mm		7
	>30 mm		8
ray-vessel pitting	70. <4 μ	0	1
	71. 5–9 μ	0	1
	72. >10 μ	0	1
	73. scalariform	0	1

		absent		present
Rays				
ray-vessel pitting	74. unilaterally composed in procumbent cells	0		1
	75. unilaterally composed in square/ upright cells	0		1
inclusions	76. crystals in margin cells	0		1
	77. crystals in other cells	0		1
	78. silica in margin cells	0		1
	79. silica in other cells	0		1
radial canals	80.	0		1
sclerotic cells	81.	0		1
oil cells	82.	0		1
Parenchyma				
apotracheal	83. diffuse	0		1
	84. reticulate	0		1
	85. short bands	0	1–2 cells wide	1
	86. concentric long bands	0	2–4 cells wide	2
			>4 cells wide	3
	87. number of bands/mm <3			1
	4– 6			2
	7–12			3
	13–18			4
	>18			5
paratracheal	88. scanty paratracheal	0		1
	89. abaxial	0		1
	90. vasicentric	0		1
	91. aliform, short wings	0		1
	92. aliform, long wings	0		1
	93. aliform-confluent	0		1
	94. aliform-confluent-banded	0		1
structure	95. strands of one cell	0		1
	96. strands of two cells	0		1
	97. strands of 3–4 cells	0		1
	98. strands of 5–8 cells	0		1
	99. strands of 9–16 cells	0		1
ripple marks	100.	0		1
disjunctive elements	101.	0		1
inclusions	102. coloured substances	0		1
	103. oil cells	0		1
	104. sclerenchymatic cells	0		1
	105. crystals	0		1
	106. silica	0		1

		absent	present
Loupe characters			
growth zones	107. vague	0	1
	distinct		2
margin of growth zone	108. radially flattened fibres	0	1
	109. marginal parenchyma	0	1
	110. zone with less vessels	0	1
	111. zone with less parenchyma	0	1
	112. ringporousness	0	1
	113. semi-ringporousness	0	1
included phloem	114. diffusely arranged islands	0	1
	115. regularly arranged islands	0	1
	116. concentric bands	0	1
	117. more than one xylem body	0	1
	118. wedges, sometimes showing a series of steps	0	1
vertical canals	119. diffusely distributed	0	1
	120. in concentric bands	0	1
crystals	121. raphides	0	1
	122. rhombic crystals	0	1
	123. elongated crystals	0	1
	124. druses	0	1
	125. crystal sand	0	1

Approach a. was realized by performing a cluster analysis on the wood samples described by a vector of 125 characters each assuming certain values. The list of characters (*table 1*) was carefully designed as to give a complete and intuitively satisfactory description of the samples. (We thank Dr. Mennega for her advice in these matters.) In many cases we decided on a binary representation of different forms of organs (e.g. intervascular pits: scalariform, opposite, alternate, confluent, are four binary characters) because no sensible ordering seemed possible. As frequently more than one of the types may occur in one sample, this gave the additional advantage that occurrences of several types could be included in the description.

Because of the mixed mode characters (i.e. binary and multistage characters intermingled) the values were normalized and a city block distance was used as dissimilarity measure.

An agglomerative, hierarchic clustering was performed using as clustering criterion minimalisation of mean square error of a new cluster to be formed (WARD 1963). Ward's averages tend to form equal sized groups, as small groups will cause less increase of mean square error. This should be kept in mind in the interpretation: if small groups are added to a large cluster while increasing the mean square error considerably, the small group is more dissimilar than readable from the dendrogram structure.

The descriptions were modified by:

1. equal weighing of all characters;
2. preferential weighing of several character groups;
3. preferential weighing on the basis of "importance of characters" as agreed upon in wood anatomical literature.

The analysis was performed on the tribes separately and combined. Optimal splitting level in the dendrogram was sought using Beale's optimality coefficient (KENDALL 1972).

Dependences between characters were sought using contingency coefficients.

To express the differences between the clusters we calculated for all characters whether, given the classification found above, the character values divert significantly from an equal distribution; for binary characters χ^2 were calculated, for multistage characters Kruskal-Wallis index (i.e. one way analysis of variance by ranks). As the result was rather clear, no attempt to use more sophisticated methods for cluster characterization have been made.

For approach b., we calculated again for which character the hypotheses of equal distribution of the characters among the tribes taxonomically distinguished was refuted: for binary characters χ^2, and for multistage characters Kruskal-Wallis index were calculated. Again it was not attempted to derive a sufficient description of the tribes on the basis of wood anatomical structure.

4.3. Results

4.3.1. Pattern-detection-approach

The most striking result of the entire analysis is the very extensive agreement between the different trials. The description with equal character weighing as well as with weighing on "evolutionary" basis gives the same, pronounced, division in two groups, differing with regard to fibre type, parenchyma distribution, and some other characters. This division arises when the tribes are taken separately as well as in the combined analyses of all tribes. This agreement of the different analyses indicates a very distinct and redundant pattern on the level of bipartition. This bipartition is not, however, expressed in the existing taxonomic classifications.

Below the different analyses are treated separately.

4.3.1.1. *Cinchoneae* – equal character weighing *(fig. 1)*

There is a partition in two groups of specimens, one of which shows libriform fibres, the other one fibre tracheids. Such a partition was already observed in the material (section 4.1.1.). One group has many vessels in (short) radial multiples, parenchyma is often lacking or scanty and then paratracheal, and crystal sand occurs often in ray cells. In the other group vessels are often solitary, parenchyma is diffuse-reticulate, and crystal sand does not occur.

The specimens of one genus are generally connected at a very high similarity level. *Hymenodictyon* is a taxonomically excentric genus of this tribe (KOEK-NOORMAN 1972). Its position in the dendrogram is rather isolated *(fig. 1)*, just

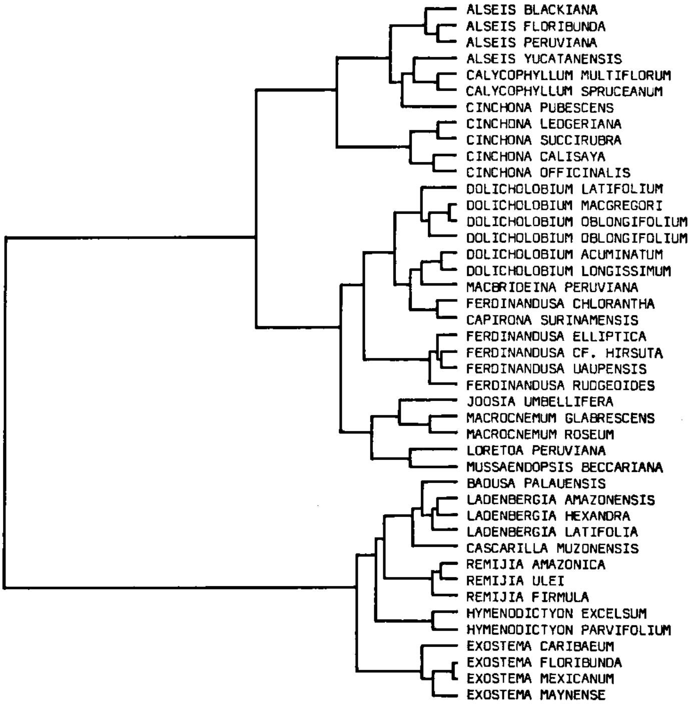

Fig. 1. *Cinchoneae* – equal character weighing.

as *Exostema*, a genus which is also deviating in some morphological respects (Bremekamp, personal communication).

Steyermark (1972, p. 230) mentions the "*Cinchona-Remijia-Ladenbergia*-complex". In our analysis *Remijia* and *Ladenbergia* are placed close together, but *Cinchona* is placed quite apart.

Standley (1930) removes *Cascarilla muzonensis* Wedd. to *Ladenbergia*. *Cascarilla muzonensis* is placed in the direct neighbourhood of *Ladenbergia* in the dendrogram.

Standley (1931) combines *Cinchona pubescens* Vahl and *C. succirubra* Klotsch; he considers also *C. officinalis* L., *C. ledgeriana* Moens ex Trimen and *C. calysaya* Wedd. to be conspecific. The dendrogram does not support these conbinations. This is especially true for *C. pubescens*, which differs from the other four species in the irregular pore clusters, the absence of oval pores, the presence of gelatinous fibres, of fusiform fibres, and the presence of some two-celled parenchyma strands.

4.3.1.2. *Condamineae* – equal character weighing *(fig. 2)*

We see again a bipartition, connected with about the same set of characters as in the *Cinchoneae*. However, the parenchyma pattern seems to be less con-

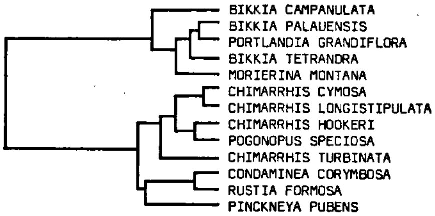

Fig. 2. *Condamineae* – equal character weighing.

nected with the fibre type, the arrangement of the vessels, and the presence of crystal sand.

Bikkia, *Morierina*, and *Portlandia* form one cluster. *Bikkia campanulata* is slightly dissimilar in the frequency of the radial vessel multiples, the relatively large intervascular pits, the uniseriate rays, the relatively large ray-vessel pitting, the presence of crystal sand, and the – vague – growth rings.

Pinckneya has been considered to be a very excentric genus (Bremekamp, personal communication). *Pinckneya pubens* Michx. is also quite dissimilar in its wood structure, as can be seen in our dendrogram *(fig. 2)*.

4.3.1.3. *Rondeletieae* – equal character weighing *(fig. 3)*

Once more a bipartition is to be seen, associated with the same characters. In this tribe the specimens of one genus are clustered, before a combination with another genus has been formed. The only exception being *Elaeagia*, *Bathysa meridionalis* and *Warzewiczia coccinea.* Their similarity was previously recognized by us.

BREMEKAMP has split up the *Rondeletieae* in *Rondeletieae* sensu stricto, *Simireae* (formed by the sole genus *Simira*) (1954) and *Gleasonioideae* (*Gleasonia*)

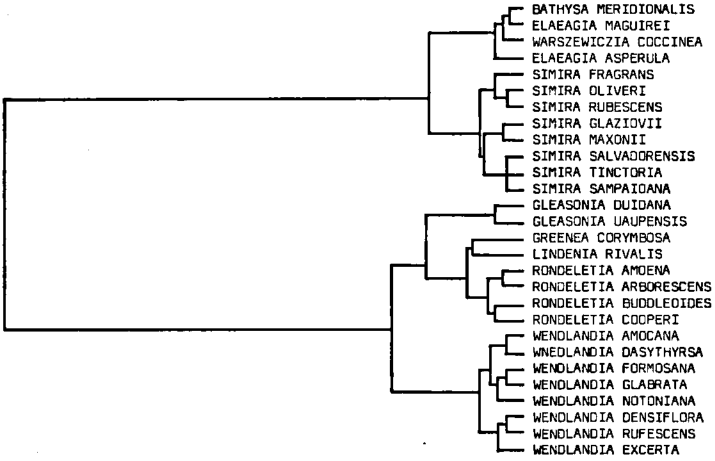

Fig. 3. *Rondeletieae* – equal character weighing.

(1956, 1966). A splitting of the tribe in this way is not supported by this analysis. *Simira* forms a rather homogeneous group with *Elaeagia*, *Bathysa*, and *Warzewiczia*. *Gleasonia* forms a cluster together with *Greenea*, *Lindenia*, and *Rondeletia*. In evaluating this latter combination we should remark that *Gleasonia* is represented by two specimens only and keep in mind that Ward's averages have the tendency to combine small groups preferentially (see section 4.2.).

4.3.1.4. Combined analysis – equal character weighing *(fig. 4)*

When we analyse the whole data set, while equally weighing all characters, we get a bipartition in the dendrogram, completely comparable to the three small dendrograms of the tribes separately. The fibre features are the only characters, which are always present and without exception specific for the two halves of the dendrogram.

In order to find which features characterize the bipartition, that means for which characters the hypothesis of equal distribution among the two halves of the dendrogram was refuted, we calculated χ^2 for binary characters, Kruskal-Wallis index for multistage characters. We found the following characters showing significant differences in distribution:
vessels solitary;
vessels in short radial multiples;
vessels in clusters;
fibres all septate;
parenchyma apotracheal diffuse;
fibre pits simple or with small borders;
fibre pits with large borders comparable to the intervascular pitting;
fibre pits present on tangential cell walls;
sheath cells present;
3–4-seriate rays present;
5–12-seriate rays present;
ray width in μ;
height of the multiseriate ray-parts;
crystal sand present;
growth rings, indicated by (slightly) radially flattened fibres.

This result agrees with previous observations on the material studied.

Optimal partitioning (Beale's coefficient) of the whole data set is in two clusters. The cluster with fibre tracheids is next partitioned in two clusters: one cossisting of species from the *Cinchoneae* and *Condamineae*, the other of species from the *Rondeletieae*. This bipartition is based upon the slightly broader rays, the more frequent presence of tracheids and the more frequent occurrence of unilaterally composed ray-vessel pitting in the *Rondeletieae*. The next optimal partitioning (having two clusters to start with) is in 4, then 7, then 10, (calculations were not proceeded any further). It is interesting to see that the partitioning in 10 clusters remains almost invaried if in the calculations the fibre characters are left out. The following features solely or combined with some others, characterize these 10 clusters:

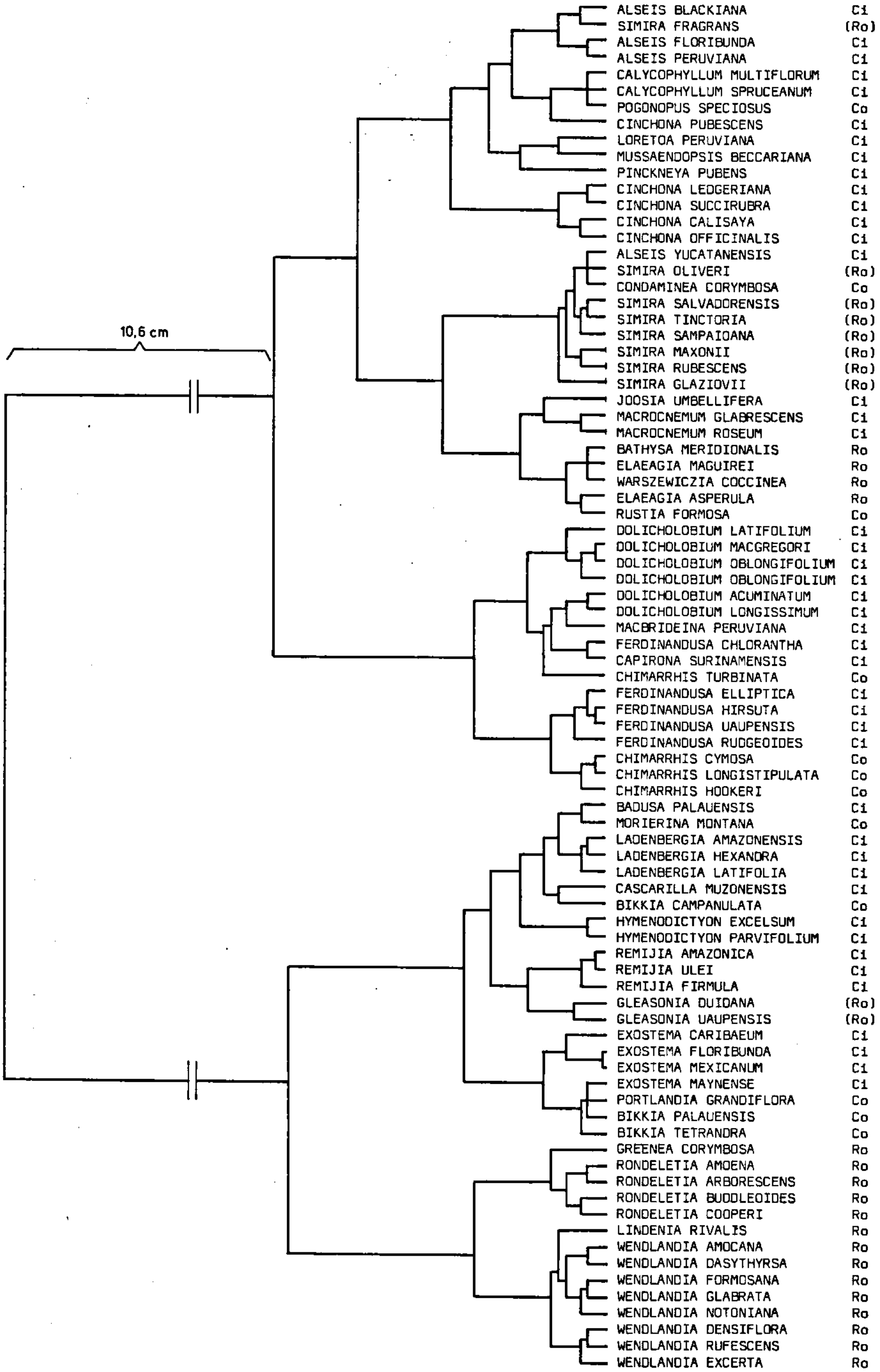

Fig. 4. Combined analysis – equal character weighing.

a. shape and arrangement of the vessels, b. vessel inclusions, c. width and height of the multiseriate ray parts, d. presence of sheath cells, e. size of ray-vessel pitting, f. parenchyma distribution, g. number of cells per parenchyma strand, and h. the presence of crystal sand.

Contingency coefficients of all pairs of characters were calculated. High contingencies were found between all pairs of the following character group:
vessels solitary;
vessels in short radial multiples;
vessels in clusters;
fibres all septate;
parenchyma apotracheal diffuse;
fibre pits simple or with small borders;
fibre pits with large borders comparable to the intervascular pits;
fibre pits present on tangential cell walls.

The high contingency of the first two characters, and of the first and third character follow from logical dependence, all others are specific for this material.

4.3.1.5. Combined analysis – exclusion of fibre characters

When we exclude the fibre characters – the only characters present in all specimens which are specific for the bipartition – from the description, the analysis results in a very similar bipartition. Moreover, the partitioning in 10 clusters remains nearly invaried. The species which are now transferred to "the other half" of the dendrogram are those of *Cinchona, Calycophyllum, Pogonopus, Mussaendopsis,* and *Rustia.* The species of *Cinchona, Calycophyllum,* and *Pogonopus* are clustered at a high level, together with *Cascarilla muzonensis. Mussaendopsis beccariana* is arranged together with *Bikkia campanulata, Remijia* and *Gleasonia, Rustia formosana* with *Rondeletia* and *Greenea.*

Cinchona shows, contrary to all other species with libriform fibres, and in accordance with the specimens with fibre tracheids, diffuse parenchyma. Remarkable is, that the fibres of *Cinchona,* by their combination of fibre characters, do not fit the definition given by Reinders (see section 4.1.1.). Previously they were considered as libriform fibres because of the absence of pits on the tangential cell walls, and the presence of (scanty) septa, but the presence of small but clear pitborders makes them transitional between the libriform fibres and fibre tracheids as occurring in other *Rubiaceae.* In *Calycophyllum, Mussaendopsis, Pogonopus* and *Rustia* fibres are, however, clearly septate, and pits on the tangential cell walls are scanty.

4.3.1.6. Combined analysis – preferential character weighing *(fig. 5)*

Many classical taxonomic studies emphasize the importance of certain characters. The concept "important character" may refer to the fact that some features often occur as characteristics for higher order partitionings (i.e. represent a group of strongly coherent characters).

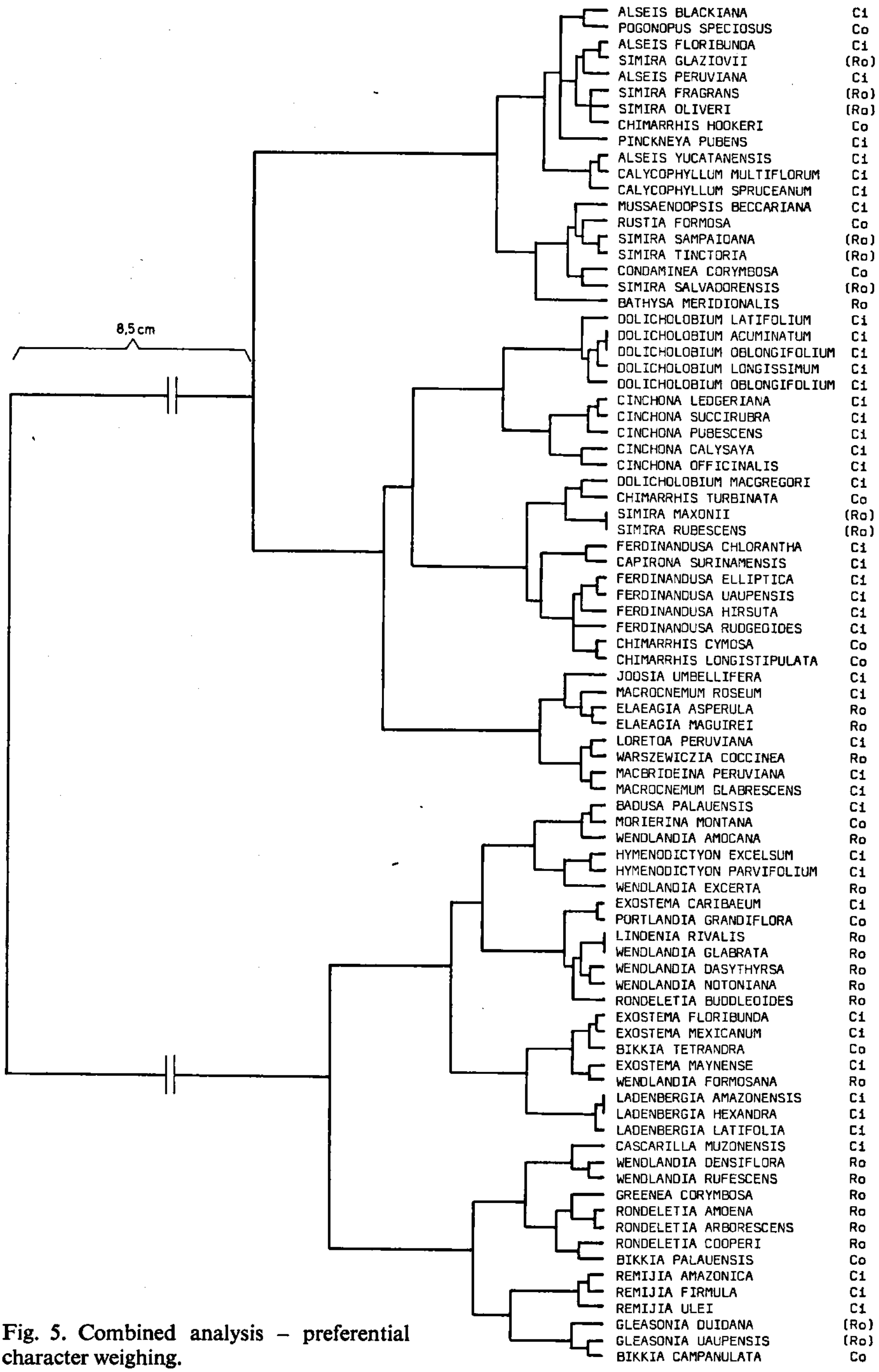

Fig. 5. Combined analysis – preferential character weighing.

On the other hand a feature is often called "important" because of supposed correlation with degree of evolutionary development. For instance, Bailey & Tupper (1918) claim to find a correlation between the length of fusiform cambium initial cells, as reflected by the length of vascular elements, and sequence of evolutionary development as hypothesized by them by studying the fossil record and extant species in a wide variety of taxonomic groups.

Bailey (1920), Barghoorn (1941), Frost (1930a, 1930b, 1931), Kribs (1935, 1937) and Tippo (1946) correlated other features of dicotyledonous wood anatomy with the length of fusiform cambium initial cells. For our study, the following characters are relevant, as they are present in the material:

a. vessel elements with scalariform vs. simple perforations;
b. long vessel elements with small diameter, angular in cross section vs. short, broad vessel elements, circular in cross-sectional outline;
c. vessel elements with long, sloping end walls vs. vessel elements with transverse end walls;
d. vessel arrangement: solitary vs. various aggregate groupings;
e. diffuse-porous wood vs. ring-porous arrangement;
f. tracheids vs. fibre tracheids and libriform fibres;
g. fibre length;
h. diffuse arrangement of parenchyma vs. various aggregate arrangements and various paratracheal types;
i. Heterogeneous ray type I and heterogeneous type IIa, IIb vs. homogeneous type I.

We will not discuss theoretical considerations about the justifiability of transporting their results between data sets, but, taking seriously the fact that the description is a priori (and does not need further justification) we used a description of our samples, weighing the characters according to the conclusions of the authors mentioned above, to compare the result of cluster analysis on this description with the results of cluster analysis on the earlier mentioned descriptions. We decided to mark the characters with different weights:

W = 6: number of marginal ray cells (62)
W = 4: size of the intervascular pits (16)
length of the vessel elements (30)
height of the multiseriate ray-parts (69)
W = 2: pores angular (24)
tracheids present (32)
position of the fibre pits (43, 44)
W = 1: vessel arrangement (2, 3, 4, 5)
perforations (9, 10, 11)
intervascular pits (12, 13, 14, 15)
diameter of the vessels (28)
thickness of fibre cell wall (37)
size of the fibre pits (40, 41, 42)
ray cell types (51, 52)
parenchyma distribution (83–86, 88–94)

W = 0: all other characters, except 56 and 57. The characters 56 and 57 are joined, as these differences in ray width are not mentioned in the literature cited above. This new character is marked with W = 1.

When comparing these values with the summary given by Tippo, we must keep in mind that all character values are normalized in the cluster analyses.

In the dendrogram *(fig. 5)* again we see a bipartition. The two halves of the dendrogram are composed of the same specimens as in the result of the cluster analysis based upon equally weighed characters. We find a difference between the two dendrograms in the position of the species belonging to one genus, with regard to representatives of other genera: in *fig. 5,* on the whole the genera are less distinguishable. We may conclude that the wood anatomical characterizations of the genera concerned are not only based upon "important characters" but also on quantitative and other "less important features".

4.3.2. Pattern-recognition-approach

To check, whether we could find single characters, distinguishing between the *Cinchoneae*, *Condamineae* and *Rondeletieae*, we tried to find characters which were not equally distributed over the three tribes (see par. 4.2.1, approach b). Only 8 characters showed significant differences in distribution between the tribes. Contrary to the results of the calculation, described in 4.3.1.4, none of these characters seem to have a reliable diagnostic value. The *Rondeletieae* are distinguished by more frequent occurrence of perforated ray cells, very small ray-vessel pits (4 μ), unilaterally composed ray-vessel pits in both procumbent and square/upright ray cells and coloured contents in parenchyma cells, while parenchyma strands of 5–8 cells occur less frequently than in the other tribes. The *Cinchoneae* show a more frequent occurrence of oval pores, less frequently fusiform fibres (i.c. *Cinchona*).

Although some of these differences in distribution were surprising, it should be emphasized, that quite some variations in anatomical structure can be found within specimens of the same species. This, combined with the fact that the above mentioned characters are not exclusive for one tribe, and constitute very few of the observed characters, persuaded us not to pursue the attempt to define the taxonomic tribes under discussion on the basis of wood anatomy.

ACKNOWLEDGEMENTS

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Part of the material was made available by the kind cooperation of the Curators of the wood collections at Amsterdam (RTIw), Kew (Kw), Madison (MADw), Oxford (FHOw), Princes Risborough (PRFw), Reinbek (RBHw), South-Melbourne (FPAw) and Washington (USw).

MATERIAL STUDIED*

Alseis blackiana Hemsl.: *Panama* – Uw 7193 (USw 776).

Alseis floribunda Schott: *Brazil* – Uw 6340 (Reitz 14444, Santa Catarina; tree, 5 m high, diam. 4.5 cm); Uw 14221 (Lindeman & de Haas 4955, Parana: Fazenda Reserva, ca. 85 km SW of Guarapuava, Alt. ± 1000 m; treelet, 2 m high, diam. 2 cm).

Alseis peruviana Standl.: *Peru* – Uw 18016 (MADw 22540, Tumbes); Uw 17999 (MADw 22255, Huanuco).

Alseis yucatensis Standl.: *Guatemala* – Uw 18023 (MADw 23130, Peten).

Badusa palauensis Val.: *Caroline Islands* – Uw 16672 (L. S. Dutton 109).

Bathysa meridionalis Smith & Downs: *Brazil* – Uw 6962 (Reitz 22543, Santa Catarina; diam. 3.5 cm).

Bikkia campanulata (Brongn.) Bth. & Hook.: *New-Caledonia* – Uw 18409 (USw 4800).

Bikkia palauensis Val.: *Caroline Islands* – Uw 16349 (FPAw NGL. 4374, Cape Vogel, Papua).

Calycophyllum multiflorum Griseb.: *Argentine* – Uw 7368 (USw W-4187).

Calycophyllum spruceanum Bth.: *Brazil* – Uw 19608 (Krukoff 7468, basin of Rio Jurua, territory of Acre); Uw 19951 (Krukoff 5416, basin of Rio Purus, territory of Acre); *Argentine* – Uw 7111 (USw 463).

Canthium confertum Korth.: *Malaysia* – Uw 17781 (G. H. Pickles 2937; Sarawak).

Canthium monstrosum (A. Rich.) Merr.: *Phillipines* – Uw 10761 (PRFw 545; Laguna).

Canthium schimperianum A. Rich.: *Ethiopia* – Uw 15264 (FIw; Eritrea).

Canthium umbellatum Korth.: *Burma* – Uw 17783 (FHOw 4521).

Canthium vulgare (K. Sch.) Bullock: *Gold Coast* – Uw 17785 (FHOw 5967 = C. Vigne 2035).

Capirona surinamensis Brem.: *Suriname* – Uw 6861 (Schulz 8583, Jodensavanne, Mapana Kreek; tree, 30 m high, diam. 45 cm).

Cascarilla muzonensis Wedd.: *Venezuela* – Uw 17748 (PRFw Y 450).

Chimarrhis cymosa Jacq.: *British Guiana* – Uw 1076 (For. Dept. 3985).

Chimarrhis hookeri K. Sch.: *Peru* – Uw 17749 (PRFw 27086).

Chimarrhis longistipulata Brem.: *Suriname* – Uw 207 (Pulle 379, Kabalebo river near Avanovero Falls).

Chimarrhis turbinata DC.: *Suriname* – Uw 261 (Stahel 261, Zanderij I).

Cinchona calisaya Wedd.: *Jamaica* – Uw 17786 (FHOw 12990 = V. J. Chapman S 255).

Cinchona ledgeriana Moens: *Tanganyika* – Uw 17787 (FHOw 5077).

Cinchona officinalis L.: *India* – Uw 17721 (J. E. Howard 1878, Madras, Ootacamund).

Cinchona pubescens Vahl: *Venezuela* – Uw 12213 (Breteler 4616; treelet, about 6 m high); Uw 17752 (PRFw 22683); *Equador* – Uw 10166 (M. Acosta-Solis 7960).

Cinchona succirubra Pav.: *Equador* – Uw 17722 (USw 4089).

Condaminea corymbosa (R. & P.) DC.: *Venezuela* – Uw 11030 (Breteler 3612, near Merida; shrub, 2 m high, diam. 2 cm).

Cuviera angolensis Welw. ex Hiern: *Cameroun* – Uw 9488 (Breteler 2318, 6 km SW of Yaoundé, trail to Eloumden Mt.; small tree, 6 m high, diam. 20 cm).

Cuviera nigrescens Wernh.: *Gold Coast* – Uw 17789 (FHOw 7155 = C. Vigne 2431).

Dolicholobium acuminatum Burk.: *Bougainville Islands* – Uw 18443 (SJRw 22832).

Dolicholobium latifolium A. Gray: *Fiji Islands* – Uw 18444 (SJRw 25649, Viti Levu).

Dolicholobium longissimum Seem.: *Fiji Islands* – Uw 18445 (SJRw 24598, Suva).

Dolicholobium macgregori Horne: *Fiji Islands* – Uw 18441 (SJRw 27771).

Dolicholobium oblongifolium A. Gray var. *degeneri* Fosb.: *Fiji Islands* – Uw 18447 (SJRw 28289).

Dolicholobium oblongifolium A. Gray var. *longissimum* (Seem.) Roxb.: *Fiji Islands* – Uw 18446 (SJRw 27795).

Elaeagia asperula Standl.: *Colombia* – Uw 12436 (Cuatrecasas 16647).

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

Elaeagia maguirei Standl.: *Suriname* – Uw 2552 (Maguire 24449, Arrowhead Basin, Tafelberg, TYPE; tree, 15 m high, diam. 30 cm).

Exostema caribaeum (Jacq.) Roem.: *Florida* – Uw 2914 (W. L. Stern 43 = Y 49402); Uw 8386 (USw 6080, Puerto Rico).

Exostema floribunda R. & P.: *Dominica* – Uw 17724 (Ind. Exhib.).

Exostema maynense Poepp. & Endl.: *Peru* – Uw 20199 (Günther Tessmann 4888).

Exostema mexicanum Gray: *Mexico* – Uw 17980 (11221, Yucatan).

Ferdinandusa chlorantha (Wedd.) Standl.: *Brazil* – Uw 16226 (Krukoff 8912, Municipality São Paulo de Olivenca: basin of creek Belem; tree, 15 m high, diam. 10 cm).

Ferdinandusa elliptica Pohl: *Brazil* – Uw 17759 (PRFw 7001 = H. B. Brown 1344).

Ferdinandusa cf. hirsuta Standl.: *Brazil* – Uw 17315 (J. M. Pires 51968, vicinity of Belem).

Ferdinandusa rudgeoides (Bth.) Wedd.: *Suriname* – Uw 1933 (Lanjouw & Lindeman 2757, Nassau Mountains; tree, diam. 15 cm); Uw 2551 (Maguire 24879 = Y 44284, Saramacca R.; tree, 20 m high, diam. 30 cm); Uw 5449 (Schulz 7990, Suriname-R., Berg en dal; tree, 8 m high, diam. 15 cm).

Ferdinandusa uaupensis Spruce: *Brazil* – Uw 17760 (PRFw 6867; Krukoff).

Gleasonia duidana Standl.: *Venezuela* – Uw 17790 (Gleason 467 = Y 16184).

Gleasonia uaupensis Ducke: *Brazil* – Uw 17791 (Ducke 223, Amazonas).

Greenea corymbosa (Jack.) K. Sch.: *Indonesia* – Uw 18405 (USw 28958, Sumatra).

Hymenodictyon excelsum Wall.: *Indonesia* – Uw 14948 (RTIw 26536); *India* – Uw 15284 (FIw 1024); Uw 15267 (PRFw 6123); *Malaya* – Uw 16268 (PRFw 7180).

Hymenodictyon parvifolium Oliver: *East-Africa* – Uw 15625 (Schlieben 531).

Joosia umbellifera Karst.: *Colombia* – Uw 18438 (Cuatrecasas 14827, Dept. del Valle, Anchicaya River basin).

Ladenbergia amazonensis Ducke: *Brazil* – Uw 17795 (Krukoff 7223, Municipality Humayta, on plateau between Rio Livramento and Rio Ipixuna; tree, 40 m high).

Ladenbergia hexandra (Pohl) Klotz.: *Brazil* – Uw 16281 (RTIw Braz. 2677).

Ladenbergia latifolia L. Wms.: *Peru* – Uw 18011 (MADw 22415 = TYPE); Uw 17767 (PRFw 27412).

Lindenia rivalis Bth.: *Panama* – Uw 18407 (USw 16038).

Loretoa peruviana Standl.: *Peru* – Uw 17768 (PRFw 27691); Uw 17797 (MADw 22194 Loreto).

Macbrideina peruviana Standl.: *Peru* – Uw 17769 (PRFw 27626); Uw 18006 (MADw 22390, Huanuco).

Macrocnemum glabrescens (Bth.) Wedd.: *Panama* – Uw 7052 (USw 92 = U.S. Nat. Herb. 716459, Canal Zone).

Macrocnemum roseum (R. & P.) Wedd.: *Peru* – Uw 17770 (PRFw 27628); *Brazil* – Uw 19827 (Krukoff 5222, basin of Rio Jurua, territory of Acre); Uw 20010 (Krukoff 5524, basin of Rio Purus, Territory of Acre).

Morierina montana Vieill.: *New-Caledonia* – Uw 18437 (SJRw 14672).

Mussaendopsis beccariana Baill.: *Indonesia* – Uw 14951 (RTIw 20827); Uw 17799 (J. A. R. Anderson S 0517, Sarawak).

Pinckneya pubens Michx.: *USA* – Uw 9987 (Barghoorn 9231); *Anapolis* – Uw 18401 (USw W-3514).

Plectronia glabra Koord. & Val.: *India* – Uw 17802 (FHOw 1456 = Gamble 6638).

Plectronia hispidum Bth.: *East-Africa* – Uw 15927 (Schlieben 290).

Plectronia odorata Bth. & Hook. f.: *Hawai* – Uw 17803 (FHOw 18674 = Y 49326).

Pogonopus speciosus (Jacq.) K. Sch.: *Venezuela* – Uw 18404 (USw 2709).

Portlandia grandiflora L.: *Jamaica* – Uw 17734 (USw 5947).

Remijia amazonica K. Sch.: *Brazil* – Uw 18449 (SRJw 22587 = Ducke 127, Amazonas).

Remijia firmula (Mart.) Wedd.: *Venezuela* – Uw 18450 (SJRw 41620 = L. Williams 14535).

Remijia ulei Krause: *Brazil* – Uw 18452 (SJRw 37161 = Krukoff 7228).

Rondeletia amoena (Planch.) Hemsl.: *Panama* – Uw 14835 (Stern, Eyde & Ayensu 2002; diam. 9 cm).

Rondeletia arborescens Griseb.: *Dominica* – Uw 14856 (Stern & Wasshausen 2567).

Rondeletia buddleoides Bth.: *Panama* – Uw 14847 (Stern, Eyde & Ayensu 2044).
Rondeletia cooperi Standl.: *Panama* – Uw 17806 (G. Cooper 600, TYPE; Buena Vista camp, Chiriqui Trail, Bocas del Toro).
Rustia formosa Klotzsch.: *Brazil* – Uw 16269 (RTIw Braz. 443).
Rytigynia neglecta W. Robijns: *East-Africa* – Uw 15920 (Schlieben 1702).
Simira fragrans (Rusby) Steyerm.: *Peru* – Uw 12438 (L. Williams 6660, Tarapoto, San Martin).
Simira glaziovii (K. Sch.) Steyerm.: *Brazil* – Uw 12345 (Ministerio da Agricultura Servico Florestal-Seçao de Technologia 3894).
Simira maxonii (Standl.) Steyerm.: *Panama* – Uw 7134 (USw 663); Uw 17808 (G. Cooper 417).
Simira oliveri (K. Sch.) Steyerm.: *Brazil* – Uw 12346 (Ministerio da Agricultura Serviço Florestal-Seçao de Technologia 664).
Simira salvadorensis (Standl.) Steyerm.: *Guatemala* – Uw 18925 (MADw 23138, Peten).
Simira sampaioana (Standl.) Steyerm.: *Brazil* – Uw 6921 (Reitz 16470, Santa Catarina).
Simira rubescens (Bth.) Brem.: *Peru* – Uw 8711 (Ellenberg 2509, El Sacramento, Andes).
Simira tinctoria Aubl.: *Suriname* – Uw 10844 (v. Donselaar 1297, Brokopondo).
Vangueria grisea Ridl.: *Burma* – Uw 17818 (FHOw 2759).
Vangueria infausta Burch.: *East-Africa* – Uw 15940 (Schlieben 1725).
Vangueria madagascariensis J. F. Gmel.: Uw 16279 (RTIw H-7-69-178).
Warzewiczia coccinea (Vahl) Klotzsch.: *Venezuela* – Uw 11841 (Breteler 4043, State of Barinas; tree, 9 m high, diam. 11 cm).
Wendlandia amocana Cowan: *East-Pakistan* – Uw 18045 (MADw 24532).
Wendlandia dasythyrsa Miq.: *Indonesia* – Uw 16270 (RTIw Ind (3) 13358).
Wendlandia densiflora DC.: Uw 16271 (RTIw H 18-68-257).
Wendlandia excerta DC.: *India* – Uw 17738 (For. Dept. 1878).
Wendlandia formosana Cowan: *Japan* – Uw 16340 (FPAw 27317; Ryukyuan Archipelago).
Wendlandia glabrata DC.: *Indonesia* – Uw 16272 (RTIw Ind (2) 4537).
Wendlandia notoniana Wall.: *Ceylon* – Uw 17739 (W. H. Wright).
Wendlandia rufescens Miq.: *Indonesia* – Uw 16273 (RTIw Ind (3) 13979).

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