

WOOD ANATOMY AND CLASSIFICATION OF *HENRIQUEZIA* SPRUCE, *PLATYCARPUM* HUMB. ET BONPL. AND *GLEASONIA* STANDL.

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SUMMARY

Wood anatomical generic descriptions of *Henriquezia*, *Platycarpum* and *Gleasonia* are given and compared with data from Rubiaceae. An attempt is made to construct a cladogram according to Hennig's principles. The resulting arrangement of the taxa concerned is discussed and compared with earlier conclusions based on phenetic comparison.

1. INTRODUCTION

The taxonomic position of the genera *Henriquezia*, *Platycarpum* and *Gleasonia* has already been subject of several discussions (BREMEKAMP 1952, 1957; CRONQUIST 1968; STEYERMARK 1974). The affinity between *Henriquezia* and *Platycarpum* has never been doubted, but no definite solutions have been given of problems like: the relationship of *Henriquezia* and *Platycarpum* with *Gleasonia* or the family to which the three genera should be assigned. Are they rubiaceous or are they more closely related to the complex of Bignoniaceae, Acanthaceae, Pedaliaceae, Martyniaceae, Thunbergiaceae and Mendonciaceae, as suggested by BREMEKAMP (1957)?

At present the problems are tackled again by G. K. Rogers (Arnold Arboretum, Mich), dealing with a familiar treatment of these genera.

In the scope of a short paper on comparative wood anatomy in the Rubiaceae some preliminary remarks were made on the wood of *Henriquezia*, *Platycarpum*, and *Gleasonia* (KOEK-NOORMAN 1977), but wood anatomical descriptions were not given at that time. Furthermore, the conclusions were reached after "phenetic comparison", i. e. looking for similarity, without evaluating the value of the characters in a phylogenetic way. In the present paper the wood anatomy of the genera is described and cladistic methods are employed to compare it with the secondary xylem of Rubiaceae. Other families, mentioned by Bremekamp as near allies were not taken into account. METCALFE & CHALK's (1950) family descriptions do not indicate similar wood structures and scanning of the Utrecht slide collections did not reveal new facts.

2. MATERIALS AND METHODS

Wood samples were obtained from several institutional wood collections, referred to according to STERN (1978). Herbarium vouchers are listed if known. Sections, 15–25 μ m thick were stained with safranin. Macerations, obtained by

treatment with hydrogen peroxide and glacial acetic acid were stained with astrablue. Vessel member length, vessel diameter and -number, fibre length and -diameter, were averaged out of 25 measurements for each sample. In the generic descriptions lowest and highest averages are given. In measuring ray height the lowest rays were not taken into account. The given values are therefore no true averages but should be considered as indications for frequently occurring ray heights. Ray frequencies are based on 12 counts, each over 1 mm distance in tangential sections.

3. GENERIC DESCRIPTIONS

Gleasonia Standley (figs. 1–3).

Trees from N.-Brazil and Venezuela; 4 species.

Material studied: *G. duidana* Standley: Venezuela – Gleason 467 (SJRw16184).

G. uaupensis Ducke: Brazil, Amazonas – Ducke 223 (SJRw 31950).

Growth rings absent.

Vessels diffuse, solitary with only incidentally two pores connected tangentially or radially, round, diameter up to 100–110 μm , 13.6–29.8 per sq.mm, walls 2–4 μm thick. Vessel member length 1050–1303 μm , perforations simple in oblique end walls, intervessel pits alternate, oval, vested, 5–7 μm ; vessel-parenchyma and vessel-ray pits similar to intervessel pits, but half-bordered.

Fibres non-septate, lumen diameter 8–12 μm , walls 8–14 μm thick, with frequent, large bordered pits on tangential and radial walls. Length 1205–1609 μm .

Rays uniseriate, heterogeneous, the upright cells and procumbent cells differ clearly, and square cells are lacking, up to 8 rows of upright cells alternating with 1–4 rows of procumbent cells, and this repeated several times, up to 28 cells and 2250 μm in height, width up to 25 μm ; 8–12 per mm.

Parenchyma very scanty paratracheal and diffuse, strands of 2–4 cells.

Note: in *G. duidana* many vessels are filled with coloured, amorphous contents and small tyloses.

Henriquezia Spruce (figs. 4–7).

Trees from tropical S.-America, 9 species.

Material studied: *H. jenmani* K. Schum.: Br. Guyana – For. Dept. 3583.

H. macrophylla Ducke: Brazil, Rio Curicuriary – Ducke 293.

H. verticillata Bth.: Brazil – Ducke 36; Jard. Bot. R. de Janeiro – Ducke s.n.

Growth rings absent.

Vessels diffuse, solitary with only incidentally two pores connected tangentially, round to oval diameter up to 110–225 μm , walls 3–5 μm thick, 4.8–10.6 per sq.mm. Vessel member length 944–1217 μm ; perforations simple in more or less transverse end walls, intervessel pits alternate, round to oval, vested, 6–8 μm ; vessel – parenchyma and vessel-ray pits similar to the intervessel pits, but half-bordered; sclerotic tyloses filling the vessel lumens.

Fibres non-septate, lumen 8–12 μm , walls 8–15 μm thick, with frequent, large

bordered pits on tangential and radial walls. Length 1365–1632 μm .

Rays uniseriate, heterogeneous consisting of upright, square and procumbent cells, 2–6 rows of upright or square cells alternating with 1–10 rows of procumbent cells, some parts of procumbent cells over a very short distance biseriate. Up to 45 cells, 2250 μm in height, width up to 40 μm ; 8–10 per mm. Many procumbent and upright cells are sclerotic.

Parenchyma scanty diffuse and in short, 2–3 cells wide bands; paratracheal as narrow vasicentric rings and aliform with short wings, sometimes the wings longer and confluent; many cells sclerotic. Strands of 2–5 cells.

Note: The conspicuous sclerotic ray and parenchyma cells, and sclerotic tyloses as seen in *H. macrophylla* and *H. verticillata*, are lacking in *H. jenmani* and in *H. verticillata*, Ducke s.n.

Both specimens of *H. verticillata* show some rays with biseriate parts of procumbent cells over 2–6 cells in height.

Platycarpum Humb. & Bonpl. (fig. 8–9).

Trees from the Northern part of S. America; 12 species.

Material studied: *P. orinocense* Humb. & Bonpl.: Brazil – Ducke 237 (SJRw 31964); Venezuela – Maguire, Wurdack & Keith 42655 (MADw 21746).

P. maguirei Steyermark: Venezuela – Maguire, Wurdack & Keith 42597 (MADw 23590).

Growth rings absent.

Vessels diffuse, solitary with only incidentally two pores connected tangentially or radially, round or oval, diameter up to 150–200 μm , walls 3–4 μm thick, 3–6 per sq.mm.

Vessel member length 891–1165 μm , perforations simple in nearly transverse end walls, intervessel pits alternate, oval, vestured, 6–7.5 μm , vessel-parenchyma and vessel-ray pits similar to intervessel pits, but half-bordered.

Fibres non-septate, lumen diameter 12–16 μm , walls 6–12 μm thick, large bordered pits frequent on tangential and radial walls. Length 1453–1690 μm .

Rays uniseriate, heterogeneous, up to 20 rows of procumbent cells with 1–3 marginal rows of upright cells, up to 28 cells and 750–1000 μm in height, width 25–40 μm ; 9–9.2 per mm.

Many cells contain small coloured particles.

Parenchyma: paratracheal in narrow, sometimes incomplete, rings with one or two wings, often aliform confluent. Strands of 3–6 cells.

4. DISCUSSION

4.1. The wood anatomy of *Gleasonia*

When establishing the genus *Gleasonia*, STANDLEY (1931) placed it tentatively in the Rondeletieae. STEYERMARK (1974) agrees with this decision contrary to BREMEKAMP. In the latter's opinion, *Gleasonia* should be removed from the Rubiaceae into the Tubiflorae (1952). Later, however, he changed his first decision (1957), and accepted *Gleasonia* in the Rubiaceae, although he considered the genus deviating from all other rubiaceae groups and created a new subfamily Gleasonioideae.

In my preliminary survey of the wood anatomy of the Rubiaceae (1969a, b) *Gleasonia* was not included because at that time no material was available. In a cluster analysis of a dataset of some tribes of the subfamily Cinchonoideae (KOEK-NOORMAN & HOGEWEG 1974, HOGEWEG & KOEK-NOORMAN 1975) *Gleasonia* was included as well as representatives of 8 other genera from the Rondeletieae. As far as *Gleasonia* is concerned it appeared that, although the analysis did not suggest a definite separation of *Gleasonia* from the other Rondeletieae, the ambiguities in existing classifications were traced in the iteration: the two represented species were often placed in one cluster with Condamineae and Cinchoneae. This confirms Bremekamp's idea that *Gleasonia* does not come very close to one special group of Rubiaceae. However, all features characterising *Gleasonia* occur in other Rubiaceae, in particular within the subfamilies Ixoroideae and Cinchonoideae. For instance:

The presence of fibre tracheids* is typical for most tribes of these subfamilies, solitary vessels and uniseriate heterogeneous rays (though without the pronounced difference between upright and procumbent cells; *fig. 2, 3*) occur in several species of the Gardenieae, Ixoreae, and Cinchoneae. The very scanty diffuse and paratracheal parenchyma is not very common, but the feature occurs incidentally in some genera belonging to the two subfamilies mentioned above.

As no taxonomist (with the exception of Bremekamp, see above) ever suggested to place *Gleasonia* in another family and as I did not find arguments in the wood anatomy either, I concluded on the base of an overall similarity that the wood anatomical structure of *Gleasonia duidana* and *G. uaupensis* confirms a close relationship with rubiaceous tribes from the subfamilies Cinchonoideae and Ixoroideae, without a definite support for a position in any particular tribe.

4.2. The wood anatomy of *Henriquezia* and *Platycarpum*
 STEYERMARK (1974), contrary to BREMEKAMP (1957), considers *Henriquezia* and *Platycarpum* as true rubiaceous genera, and places them in a separate tribe in the neighbourhood of Cinchoneae, Rondeletieae and Condamineae. VERDCOURT (1958) follows Bremekamp in the exclusion of the Henriquezieae. When we compare the available wood samples of *Henriquezia* and *Platycarpum* we see a very good similarity. Conspicuous corresponding features are the solitary vessels surrounded by paratracheal, often aliform-confluent parenchyma (*figs. 4, 8*), the fibre tracheids and the presence of uniseriate heterogeneous rays (*figs. 5, 6, 9*). The only difference distinguishing between the two genera seems to be the distribution of the different types of ray cells: in *Henriquezia* we see up to 10 rows of procumbent cells alternating with 2–6 rows of upright cells, whereas the

*The fibres of *Henriquezia*, *Platycarpum*, and *Gleasonia* are typical fibre tracheids, irrespective of whether the definition according to REINDERS (1935) or as formulated in the "Multilingual glossary of terms used in wood anatomy" (1964) is used. Fibre tracheids in the sense of Reinders appeared to have taxonomic value within many groups of the Rubiaceae. Therefore his definition has been accepted in earlier papers (KOEK-NOORMAN 1969a, 1974).

samples of *Platycarpum* show procumbent cells arranged in up to 20 rows with only few rows of upright marginal cells. Furthermore, the distinct difference between upright and procumbent cells, found in *Henriquezia*, is in *Platycarpum* more or less undone by the lower upright cells and the presence of relatively more square cells. The sclerotic cells occurring in the rays and the axial parenchyma of samples of *H. marginata* and *H. verticillata* (fig. 7) have not been found in the other samples of this genus and are therefore not useful in distinguishing between the two genera.

Comparing the wood of *Henriquezia* and *Platycarpus* with the two samples of *Gleasonia*, we see a good agreement, the only conspicuous difference being found in the parenchyma pattern: in *Gleasonia* the parenchyma is very scanty in diffuse and paratracheal strands (fig. 1), in *Henriquezia* and *Platycarpum* the paratracheal parenchyma occurs in aliform-confluent arrangement. Contrary to the other features, which, as already mentioned in paragraph 4.1. occur more or less frequently within the Rubiaceae, aliform-confluent parenchyma is unknown for this family.

In an earlier paper (KOEK-NOORMAN 1977) I used a "phenetic" approach in the discussion of the position of the three genera concerned. The difference in parenchyma arrangement was my main argument to endorse Bremekamp's creation of a new family Henriqueziaceae. Besides, I mentioned some additional features. The most conspicuous one, the pronounced differentiation in procumbent and upright cells in the exclusively uniseriate rays is unusual within the Rubiaceae.

4.3. Cladistic approach

If cladistic principles (in the sense of HENNIG 1966; for an earlier application of cladistics in wood anatomy see BAAS & ZWEYPFENNING 1979) are applied on the wood anatomical data in order to elucidate the taxonomic relationship between "Henriqueziaceae" and Rubiaceae, the first assumption must be, that *Henriquezia*, *Platycarpum* and *Gleasonia* are "more related" to the Rubiaceae than to any other family (as f.i. one of the Tubiflorae; BREMEKAMP 1957). As said before, I found no striking agreement with any of the families mentioned. Therefore I feel justified to exclude the Tubiflorae from the following considerations.

Some of the features *Henriquezia*, *Platycarpum* and *Gleasonia* have in common, are considered to be "primitive" according to the "evolutionary trends" as established for wood anatomical features. These characters are the presence of fibre tracheids, the exclusively solitary, diffusely arranged vessels, the heterocellular rays (BAILEY & TUPPER 1918; FROST 1930; KRIBS 1935). Each of these characters occurs in many representatives of the Rubiaceae (KOEK-NOORMAN 1969a, b, 1970, 1972; KOEK-NOORMAN & HOGEWEG 1974). The most conspicuous deviating character found in *Henriquezia* and *Platycarpum* is the aliform-confluent parenchyma. This distribution pattern has not been found elsewhere in the Rubiaceae. The common patterns in this family are: apotracheal as diffuse or reticulate strands and paratracheal as scanty strands, or absence of parenchyma. As pointed out by BREMER & WANNTORP (1978) the fact that a

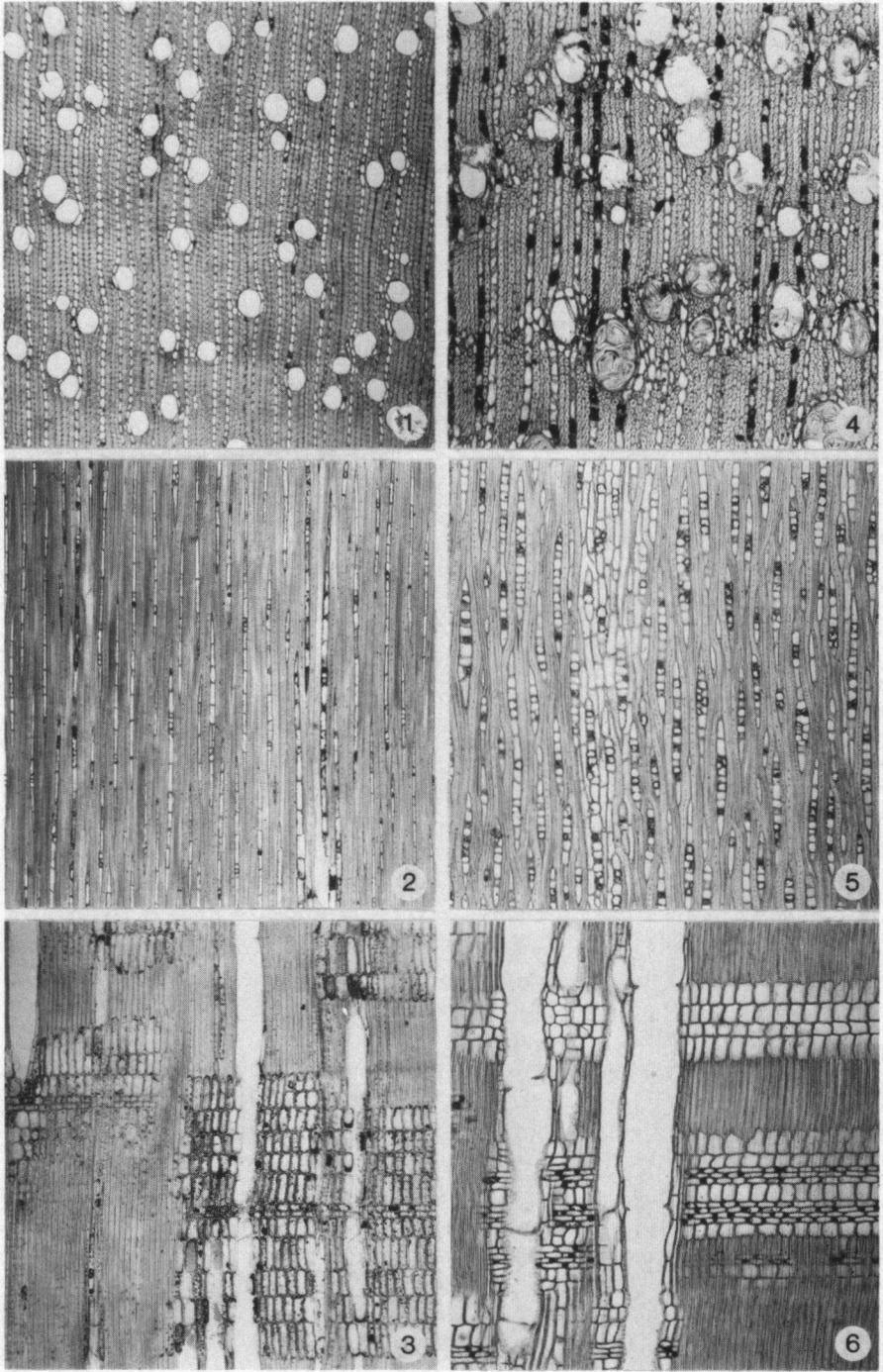


Plate I.

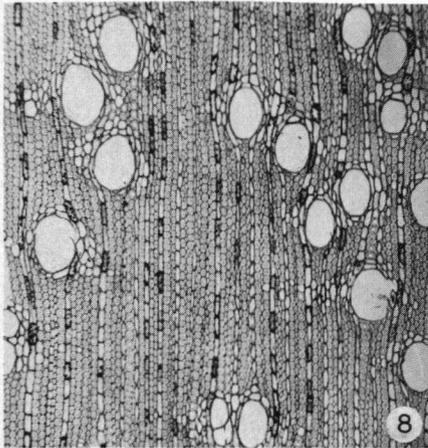
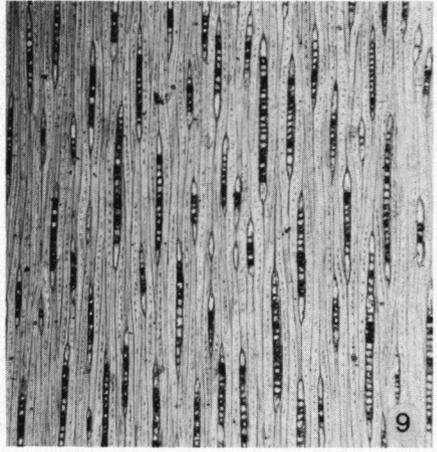
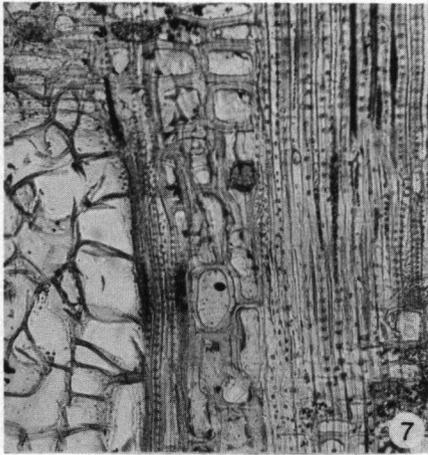


Plate II.

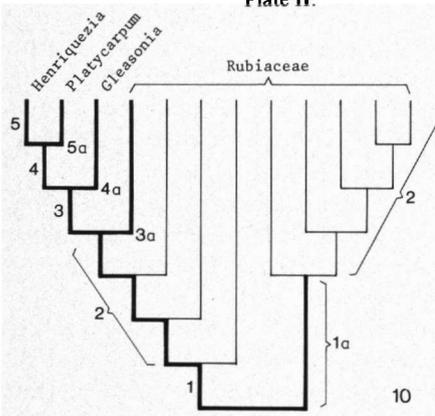


Plate I.

- Fig. 1. *Gleasonia uaupensis* Ducke (Ducke 223), transverse section, $\times 40$.
- Fig. 2. Do, tangential section, $\times 40$.
- Fig. 3. Do, radial section, $\times 40$.
- Fig. 4. *Henriquezia macrophylla* Ducke (Ducke 293), transverse section, $\times 40$.
- Fig. 5. *H. verticillata* Bth. (Ducke 36), tangential section, $\times 40$.
- Fig. 6. *H. jenmani* K. Schum. (Br. Guy. For. Dept. 3583) radial section, $\times 40$.

Plate II.

- Fig. 7. *H. verticillata* Bth. (Ducke 36), radial section, showing sclerotic cells in axial and radial parenchyma, $\times 100$.
- Fig. 8. *Platycarpum orinocense* Humb. & Bonpl. (Maguire, Wurdack & Keith 42655), transverse section, $\times 40$.
- Fig. 9. Do (Ducke 237), tangential section, $\times 40$.

Fig. 10. Cladogram representing possible phylogenetic relationships as deduced from wood anatomical features:

- 1-1a: bifurcation representing differentiation in fibre-tracheids (1) and libriform fibres (1a).
- 2: bifurcation representing successive differentiation of several wood anatomical features in Rubiaceae. Thin lines indicate that in the text no attention has been paid to the meaning of these lines.
- 3-3a: bifurcation representing uniseriate heterogeneous rays (3) and multiseriate rays (3a).
- 4-4a: bifurcation representing aliform-confluent (4) and scanty paratracheal parenchyma (4a).
- 5-5a: bifurcation representing the tendency from heterogeneous uniseriate (5) to homogeneous uniseriate rays (5a).

character occurs in one relatively small group can be strong evidence in favour of the idea, that the character is the derived, apomorphous state. The conclusion, that aliform-confluent parenchyma is an apomorphous character-state is in accordance with the literature on evolutionary trends (KRIBS 1937; CARLQUIST 1961). In a diagram representing possible phylogenetic sequences it may be used therefore, to separate *Henriquezia* and *Platycarpum* from a "sister group", to be found among the other Rubiaceae.

The number of Rubiaceae with the features mentioned for *Henriquezia* and *Platycarpum*, with the sole exception of aliform-confluent parenchyma, is restricted. Even among the tribe Gardenieae and Ixoreae for which tribes all mentioned features have been recorded, uniseriate heterogeneous rays are rare especially with a pronounced difference in procumbent and upright ray cells, as seen in *Henriquezia*. The samples of *Gleasonia*, however, have all requirements of a sister group. A satisfactory cladogram is thus obtained, if *Henriquezia* and *Platycarpum* are combined in one larger unit with *Gleasonia* (fig. 10).

To indicate the difference in ray structure in *Platycarpum* a very last bifurcation may represent the trend from heterogeneous to more homogeneous ray structure. More or less homogeneous uniseriate rays occur in species of several rubiaceous tribes which otherwise show many multiseriate heterogeneous rays. Following the cladistic method we may assume that the character of exclusively uniseriate rays has been developed more than once within the Rubiaceae, but that *Henriquezia*, *Platycarpum* and *Gleasonia* are monophyletic in this respect. Recently a comparable consideration concerning the rays of Lythraceae has been put forward by BAAS & ZWEIPFENNING (1979). It seems impossible to elaborate a further detailed phyletic diagram for the Rubiaceae. The range of variation of the other wood anatomical features is so narrow that it makes no sense to give them evolutionary or phyletic value. The only exception can perhaps be found in the fibre types. Both fibre tracheids and libriform fibres occur within the Rubiaceae. At least in some tribes of the Ixoroideae and Cinchonoideae a significant correlation with other wood anatomical features has been found (KOEK-NOORMAN & HOGEWEG 1974). Furthermore, there is a correlation between these sets of characters and existing taxonomic classifications. On account of these two facts I assume that the differentiation of the fibre types has taken place in a relative early phase of development of the Rubiaceae. This is indicated by a first bifurcation in the cladogram (fig. 10). *Henriquezia*, *Platycarpum* and *Gleasonia* should be placed high up in the branch representing the Rubiaceae with fibre tracheids. Between this basal bifurcation and the "thin twigs" at the upper side of the diagram, we must imagine a number of bifurcations, representing subsequent differentiations; often along comparable lines in the left and right half of the diagram.

Irrespective of how the intermediate part of the diagram should be worked out, the group of *Henriquezia* and *Platycarpum*, as well as *Gleasonia*, will be placed on the same hierarchic level as other parts of the family Rubiaceae as far as I can judge.

On the line of reasoning of HENNIG (1966), repeated by BREMER & WANNTORP

(1978), it is not possible to support the family rank for *Henriquezia* and *Platycarpum* (with or without *Gleasonia*) while all other Rubiaceae are maintained in one large family. The correct solution should be: either to maintain *Henriquezia* and *Platycarpum* as well as *Gleasonia* in the Rubiaceae, or to split up the Rubiaceae in a large number of small families, among them the "Henriqueziaceae" and "Gleasoniaceae". As the Rubiaceae have always been considered as a "natural", well defined family, the splitting up in small families will probably find no supporters.

I am aware of some incompleteness in the data. The number of studied samples is relatively low, and the wood anatomy of other related families should be included in the discussion, to allow a more definite answer. Furthermore a more elaborated diagram, worked out from the top to the basal side could be more convincing. Nevertheless I feel that in this phase the following conclusions are justified.

1. A comparison of the wood anatomy of *Gleasonia* with that of *Henriquezia* and *Platycarpum* and with Rubiaceae in general confirms an earlier conclusion (1977), that *Gleasonia* is more similar to Rubiaceae than are *Henriquezia* and *Platycarpum*.
2. If those taxonomists, who consider *Henriquezia*, *Platycarpum* and *Gleasonia* nearly allied to the Rubiaceae are right, the nearest relatives are to be sought among representatives of the subfamilies Ixoroideae or Cinchonoideae.
3. An analysis along cladistic lines does not endorse a division in two families Rubiaceae and Henriqueziaceae (including *Henriquezia* and *Platycarpum*, with or without *Gleasonia*). This is contrary to the conclusion based on phenetic comparison (KOEK-NOORMAN 1977).
4. If *Henriquezia* and *Platycarpum* are removed from the Rubiaceae, according to cladists the remaining family should be considered as a phenetic unity, rather than as a phyletic unity.

The two last formulated points start from the principle, that the cladistic analysis of characters not only precedes a (taxonomic) classification, but that the cladogram in itself represents the correct classification of the studied objects. As MAYR (1974) has argued, there is no reason to assume that cladistic analysis and cladistic classification should be inseparably combined. There may be several reasons to abandon the idea of equal taxonomic ranks for sister groups, or to bring together polyphyletic (in the cladistic sense) groups in a taxon of equal rank as a small 'sideline' (see also BURGER 1979). For the time being, to uncouple analysis and classification seems to be the best thing to do. Although in the cladogram the three genera are separated from a rubiaceous sister group on a high level, they are easily to distinguish from the other Rubiaceae because of the parenchyma pattern and the ray structure. Inclusion of, above all, *Henriquezia* and *Platycarpum* makes the wood structure of Rubiaceae more diverse. However, if the decision should be to keep *Henriquezia* and *Platycarpum* apart, the cladogram indicates that the wood anatomy of *Gleasonia* would justify inclusion in the "Henriqueziaceae" as much as maintenance in the Rubiaceae. It will be clear that the wood anatomy will not give the last word on this taxonomic

problem. Careful analyses of data from other plant parts are essential, before a definite solution can be given.

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