WOOD ANATOMY OF THE PREDOMINANTLY AFRICAN REPRESENTATIVES OF THE TRIBE PSYCHOTRIEAE (RUBIACEAE–RUBIOIDEAE)

by

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SUMMARY

Wood samples of representatives of Chassalia, Chazaliella, Gaertnera, Hymenocoleus, Pagamea and Psychotria are examined. The generic delimitation of these predominantly African Psychotrieae, which is mainly based on fruit morphology, is compared with wood anatomical variation patterns. Part of the variation observed is related to habit, e.g. wide vessels in the tree species Psychotria dermatophylla. Other features do have systematic significance, as shown by a cluster analysis of the data obtained. The genus pair Gaertnera/Pagamea differs obviously from the other genera and is wood anatomically clearly distinguished by the presence of fibre-tracheids and parenchyma bands. Chassalia, Chazaliella, Hymenocoleus and Psychotria have rather similar wood structure, although variation in vessel diameter, vessel arrangement, ray composition and axial parenchyma occurs. Several uncommon features are recorded: the presence of few to numerous openings in one oblique perforation plate, irregular reticulate perforation plates and multiple vessel-ray perforations with marked irregularity.

Key words: African Psychotrieae, systematic wood anatomy, taxonomy, Rubiaceae.

INTRODUCTION

Although the Rubiaceae rank as the fourth largest angiosperm family and more than 80% of its genera are woody (Robbrecht 1988), the xylotomy of the family is under-explored. Wood anatomy of the family has systematically been studied by Janssonius (1926) and by Koek-Noorman from 1969 onwards. The latter author clearly demonstrated the taxonomic value of rubiaceous wood at the tribal level (Koek-Noorman 1977). However, her series of contributions show certain taxonomic gaps, and only few authors have paid attention to wood anatomy of Rubiaceae since then (e.g. Rogers 1981, 1984; Koek-Noorman & Puff 1983, 1991; Ter Welle et al. 1983).

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The Psychotrieae is one of the largest tribes of the Rubiaceae (c. 2000 species in c. 50 genera). In continental Africa, it is represented by seven genera (Robbrecht 1996): Chassalia, Chazaliella, Gaertnera, Geophila, Hymenocoleus, Peripeplus and the very large genus Psychotria (more than 200 African species). Most of the Psychotrieae, the African ones in particular, have insignificant flowers with little morphological variation. The fruits, however, are very variable and Petit (1964) pointed out that their morphological characters have a high diagnostic value. Based on these characters, he proposed new generic delimitations for Chassalia, Geophila, Gaertnera, Psychotria and Peripeplus; in addition, Verdcourt (1975, 1977) and Robbrecht (1975) have worked out unpublished ideas on species left unplaced by Petit, resulting in the recognition of two more genera, Chazaliella and Hymenocoleus, respectively. These generic concepts of the African Psychotrieae were adopted by Verdcourt (1976) in the ‘Flora of Tropical East Africa’. In a short survey of the representatives of the African tribes Psychotrieae, Triainolepideae and Morindeae, Robbrecht (1989) presented a generic identification key solely based on fruit morphology.

In contrast to the generic clarification of the African representatives, the delimitation of the Psychotrieae genera on a global scale remains very problematic. The genus Psychotria obviously served as a reservoir genus for anything problematic and consequently became inflated to more than 1000 species.

The delimitation of the Psychotrieae has been the subject of discussion, e.g. vis-à-vis the tribe Morindeae (see Robbrecht et al. 1991; Igersheim & Robbrecht 1994). Some highly derived representatives of the Psychotrieae have recently been recognised as subtribes (Hydnophytinae: Huxley & Jebb 1991; Gaertnerinae: Jansen et al. 1996b). However, the relationships inside the Psychotrieae and the tribe’s subdivision are in need of a thorough study.

The wood anatomy of the Psychotrieae has never been studied profoundly in the past. Koek-Noorman (1969b) studied 17 neotropical species of 9 different genera. She concluded that the tribe is very homogeneous in its wood structure, not only as far as the large trees and shrubs of genera like Psychotria, Mapouria, Ronabea, Rudgea and Naletonia are concerned (Koek-Noorman 1969a, b), but also when one takes into consideration representatives of Amaracarpus (small shrubs), Declieuxia (herbs and subshrubs), and the subherbaceous species of Psychotria (Koek-Noorman 1976). Although Koek-Noorman (1969b) found some variation in ray frequency, ray composition, vessel diameter, vessel arrangement and fibre length, the differences observed did not permit diagnostic conclusions. She examined two species of Pagamea but none of Gaertnera and confirmed Bremekamp’s (1966) placing of these two genera in a tribe Gaertnereae on the basis of axial parenchyma bands and the presence of fibre-tracheids.

The consolidation of the delimitation of the African genera makes the representatives from that continent an interesting test group to verify the value of wood anatomical characters for the Psychotrieae. This paper investigates the wood of the African woody genera and discusses the subdivision of Psychotrieae. Wood was available for selected species of Psychotria, Chassalia, Chazaliella and Gaertnera, but no wood samples of Peripeplus were found. The above mentioned genera Geophila and
Hymenocoleus are entirely herbaceous, except for a single subwoody species Hymenocoleus scaphus which is included in the present study. The neotropical genus Pagamea, considered very closely related to the paleotropical genus Gaertnera, was investigated as well. Also 13 neotropical Psychotria species were included to obtain a better global knowledge of the wood anatomical variation of this genus.

MATERIALS AND METHODS

Wood samples were obtained from the wood collection at Tervuren (Tw) and the herbarium of the National Botanic Garden of Belgium (BR). The material studied is listed below with reference to the habitat of the species, the collector, the diameter of the wood samples (in mm) and illustrations. One specimen of each species was observed, but for six species two specimens were examined.

Chassalia cristata (Hiern) Bremek. [liana or woody twiner 1.2–9 m], Zaire, Ille Esali, J. Louis 11694 (BR), 6 mm (Fig. 8, 17). — Chassalia subbochreata (De Wild.) Robyns [shrub or small tree 1.8–9 m], Rwanda, Gisenyi, P. Bamps 3102 (BR), 5 mm (Fig. 32). — Chassalia umbraticola vatke subsp. umbraticola [shrub or subshrub, slightly scandent, 0.9–4.5 m], Tanzania, Dar es Salaam, B. J. Harris 1623 (BR), 8 mm (Fig. 7, 37). — Chazaliella obovoidea Verdc. subsp. rhytidophloea Verdc. [shrub 0.5–3 m], Zaire, Ipamu, H. Vanderyst 10904 (BR), 7 mm (Fig. 9). — Chazaliella oddonii (De Wild.) E. Petit & Verdc. [forest shrub 1–2 m], Zaire, J. Louis 7370, Tw 38497, 10 mm (Fig. 10, 18); Zaire, J. Louis 5864, Tw 35773, 10 mm. — Chazaliella wildemanii (T. Durand) E. Petit & Verdc. [small shrub 1–2.5 m], Zaire, Kasai, A. Sapin (BR), 7 mm. — Gaertnera bieleri (De Wild.) E. Petit [shrub 1–8 m], Zaire, Maluku, H. Breyne 904 (BR), 4 mm (Fig. 35). — Gaertnera bracteata E. Petit var. glabriifolia E. Petit [shrub (or tree?)], Zaire, Maluku, H. Breyne 3081 (BR), 4 mm. — Gaertnera cooperi Hutch. & Moss [shrub 1–4 m], Liberia, Bassa, G. P. Cooper 287, Tw 26692, 40 mm; Liberia, Bassa, G. P. Cooper 202, Tw 26693, 40 mm (Fig. 33). — Gaertnera librensis E. Petit [tree 7 m], Liberia, Bassa, G. P. Cooper 277, Tw 26694, 35 mm. — Gaertnera longevaginalis (Hiern) E. Petit [shrub 1–6 m or tree up to 8 m], Zaire, R. Dechamps 8063, Tw 40362, 21 mm (Fig. 11, 19, 30). — Gaertnera paniculata Benth. [large shrub 1.5–6 m or tree 5–10 (18?) m], Zaire, J. Louis 1574, Tw 33237, 9 mm; Zaire, J. Louis 1881, Tw 33309, 10 mm. — Hymenocoleus scaphus (K. Schum.) Robbr. [monocaual dwarf], Zaire, Yangambi, J. Louis 891 (BR), 5 mm. — Pagamea coiriacea Benth. [small tree or tree 1.5–7 (12) m], Venezuela, Amazonas, B. Maguire et al. 43623, Tw 37071, > 100 mm. — Pagamea guianensis Aubl. [small tree or tree 2.5–6 (15) m], Surinam, Stahel 355, Tw 25578, > 100 mm (Fig. 20). — Pagamea thyrsiflora Spr. ex Benth. [small tree 1.5–5 m], Venezuela, Amazonas, B. Maguire et al. 43660, Tw 37026, 20 mm. — Pagamea velutina Steyerm. [tree 12 m], Venezuela, Amazonas, B. Maguire et al. 28536, Tw 36297, 55 mm (Fig. 12, 25, 31). — Psychotria antillana Howard [shrub or small tree 2–4(–10) m], The French Antilles, Guadeloupe, Rollet-CTFT 1169, Tw 47661, > 100 mm (Fig. 26). — Psychotria berteroaiana DC. [shrub or small tree 3–10 m], Cuba, Santiago de Cuba, R. Dechamps 12371, Tw 49843, 12 mm. — Psychotria brachiata Sw. [shrub or small tree 3–10 m], Cuba, Gramma, R. Dechamps 12432, Tw 49906, 20 mm (Fig. 4, 14, 38, 41). — Psychotria capitata Ruiz & Pav. [shrub or small tree 0.3–3 (6) m], Panama, M. Nee 7019, Tw 4300, 20 mm (Fig. 6). — Psychotria chalconeura (K. Schum.) E. Petit [shrub or small tree up to 8 m], Zaire, J. Louis 4168, Tw 33751, 20 mm (Fig. 1, 16). — Psychotria cyanopharynx K. Schum. [shrub or small tree 0.5–7 m], Zaire, J. Louis 1634, Tw 33258, 18 mm (Fig. 28, 29, 36); Zaire, J. Louis 6047, Tw 35832, 10 mm. — Psychotria dermatophylla (K. Schum.) E. Petit [tree up to 20 (30?) or shrub up to 7 m], Zaire, C. Donis 2421, Tw 32646, > 100 mm (Fig. 13, 22, 27, 34). — Psychotria djumaensis De Wild.
var. *djumaensis* [shrub 1.5–9 m or small tree 4–9 m], Zaire, J. Louis 1980, Tw 33348, 14 mm. — *Psychotria marginata* Sw. [shrub 1–3 m], Panama, Canal Zone, M. Nee 7082, Tw 43019, 16 mm (Fig. 42). — *Psychotria maritima* (Cham. & Schlechtend.) Fosberg [small tree], USA, Hawaii, A. Curtis, Tw 45678, > 100 mm (Fig. 15, 23). — *Psychotria micrantha* Humb. & Bonpl. [shrub or small tree 2–5 m], Panama, Colon, M. Nee 7104, Tw 43027, 33 mm (Fig. 21). — *Psychotria nervosa* Sw. [shrub 0.5–2 m], Cuba, Matanzas, R. Dechamps 12534a, Tw 50021, 6 mm (Fig. 3, 24); Cuba, Matanzas, R. Dechamps 12534b, Tw 50025, 6 mm. — *Psychotria nigropunctata* Hier [shrub or subshrub 0.3–1.5 m], Zaire, J. Louis 2813, Tw 34825, 15 mm. — *Psychotria nutans* Sw. [shrub or small tree 1–4 m], Cuba, Guantanamo, R. Dechamps 12673, Tw 51916, 13 mm. — *Psychotria pubescens* Sw. [shrub or small tree up to 4 m], Cuba, Santiago de Cuba, R. Dechamps 12282, Tw 49719, 10 mm; Cuba, Matanzas, R. Dechamps 12535, Tw 50028, 14 mm. — *Psychotria revoluta* DC. [shrub 1.5–4 m], Cuba, Santiago de Cuba, R. Dechamps 12273, Tw 49709, 16 mm. — *Psychotria shaferi* Urb. [shrub], Cuba, Guantanamo, R. Dechamps 12304, Tw 49753, 10 mm. — *Psychotria succulenta* (Hiern) E. Petit [shrub or small tree up to 10 m], Zaire, Shaba, F. Malaisse 9663, Tw 35129, 33 mm (Fig. 2, 39, 40). — *Psychotria vasiven­sis* (Müll. Arg.) Standley [shrub or small tree], Venezuela, Amazonas, B. Maguire 41621, Tw 36160, 20 mm (Fig. 5, 43); Venezuela, Amazonas, B. Maguire 43159, Tw 36695, ? mm; Venezuela, Amazonas, B. Maguire 43481, Tw 36969, ? mm.

**Microtechnique**

The wood samples were sectioned on a sliding microtome, stained with safranin and mounted in Caedax for light microscopical examination. Slides of macerated tissue were made using the method of Franklin (1937). Observations were made by LM and SEM. For SEM observations, sectioned wood blocks were coated with gold using a SPI Module Sputter coater and observed with a Jeol JSM-6400.

**Analysis**

The specimens were used as OTUs (operational taxonomic units). The characters showing significantly variable states in the study group are used for numerical analysis; they are listed in Table 1 (18 characters, 50 states) as well as the frequencies calculated for the occurrence of these states in the OTUs. The statistical programme Systat (Wilkinson 1988) was used to perform cluster analysis (options used: average linkage and Pearson correlation coefficient as distance function) on the matrix.

An attempt to convert the data matrix into a matrix for cladistics was not made because many of the characters are quantitative.

**Terminology and characters**

The wood anatomical terms are used in accordance with the ‘IAWA list of microscopic features for hardwood identification’ (IAWA Committee 1989) and observations were executed according to prescriptions in this list. The definition of the characters and their states is inspired on this list. For the terms libriform fibre and fibre-tracheid we follow the definitions given by Reinders (1935), Janssonius (1940) and Koek-Noorman (1969a). Libriform fibres show simple to minutely bordered pits on radial fibre walls and are, in the Rubiaceae, mostly septate. Fibre-tracheids however, have bordered pits on radial and tangential walls and usually no septa. This interpretation is preferable because a division between the two fibre types only based upon the
presence or absence and the size of pit borders in the fibre tissue of the Rubiaceae is difficult. In many Rubiaceae pits on imperforate tracheary elements range from distinctly bordered to minutely bordered to simple so that a complete range in imperforate tracheary elements is present (Koek-Noorman 1969a, b).

Abbreviations

The following abbreviations are used to designate the tribal position of genera other than the seven Psychotrieae mentioned in the introduction: Gar., Gardeniaceae; Hed., Hedyotidaceae; Mit., group of Mitchellia; Nau., Naucleeae; Psy., Psychotrieae; Ret., Retiniphyllaeae; Rub., Rubieae; Spe., Spermacoaceae; Van., Vanguerieae.

RESULTS

In the following sections the results of our observations are given and compared to the data found in literature. The observations on all individual specimens (OTUs) are summarized in Table 1 (pages 174–177).

Growth rings

Growth rings are often absent but can also be fairly distinct (e.g. Psychotria pubescens). They correspond to successive zones having relatively many or few vessels and showing flattened fibres.

Vessels

The wood is diffuse-porous with > 50% of the vessels arranged in radial multiples of 2–4 (Fig. 1, 2, 9) or sometimes more (as in Psychotria nervosa, Fig. 3 and P. vasi­vensis, Fig. 5). However, species of Gaertnera (Fig. 11) and Pagamea (Fig. 12), Chassalia subochreata and Chassalia umbraticola (Fig. 7) show mostly (> 50%) solitary vessels and short radial multiples of 2 (or 3) vessels (< 50%). The vessel outline is oval or rounded.

Perforation plates are nearly always simple (Fig. 26, 27, 28, 37). The wood of Chassalia subochreata, however, shows exclusively scalariform perforation plates with ± 5 to 10 forked bars (Fig. 32). There is often an unusual occurrence of two or three (rarely more) perforations in one oblique perforation plate. We observed this feature in both narrow (e.g. in Psychotria antillana, Fig. 26) and wide vessels (P. dermatophylla, Fig. 27). Similarly Koek-Noorman (1969a) observed two large openings in one perforation plate in three neotropical species: Retiniphyllum schomburgkii (Ret.), Ronabea latifolia (Psy.) and Rudgea graciliflora (Psy.). Janssonius (1926) reported two openings in a very oblique perforation plate in Psychotria robusta and several other Rubiaceae. A similar occurrence of two perforations in the same end wall was recorded in Beilschmiedia tarai (Lauraceae) by Meylan and Butterfield (1975).

The perforation plates are often slightly to very oblique with a prominent rim. Intervessel pits are absent around the perforation (Fig. 26, 27). The shape of the perforations is rounded (Fig. 26, 37), oval (Fig. 26, 27, 28), or irregular as e.g. in Psychotria vasi­vensis (Fig. 43). The irregular outline of the perforations in the latter species is
Table 1. List of the 18 characters (50 character states) used for the analysis and estimated frequencies (%) of the character states in the OTUs.

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(continuation)

9 fibres
   a with simple to minutely bordered pits
      100 100 100 100 100 100 100 0 0 0 0 0 0 0 0 0 0 100 0 0 0 0 100
   b with distinctly bordered pits
      0 0 0 0 0 0 0 0 0 100 100 100 100 100 100 100 100 100 0 0 100 100 100 100 100

10 fibre pits
   a both radial and tangent, walls
      0 0 0 0 0 0 0 0 0 100 100 100 100 100 100 100 100 100 0 0 100 100 100 100 0
   b restricted to radial walls
      100 100 100 100 100 100 100 0 0 0 0 0 0 0 0 0 0 100 0 0 0 0 100 100 100 100 100

11 fibres
   a septate
      100 100 100 100 100 100 100 0 0 0 0 0 0 0 0 0 0 100 0 0 0 0 100
   b non-septate
      0 0 0 0 0 0 0 0 0 100 100 100 100 100 100 100 100 100 0 0 100 100 100 100 0

12 fibre wall thickness
   a thin-walled
      100 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
   b thick-walled
      0 100 100 100 100 100 100 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 100

13 fibre length
   a < 700 µm
      0 5 0 0 0 0 80 30 0 10 0 20 0 0 70 0 25 5 0
   b 700–1100 µm
      100 95 20 0 60 20 70 20 70 70 70 90 30 30 35 75 90 0
   c 1100–1400 µm
      0 0 70 30 40 0 0 80 20 30 10 10 70 0 65 0 5 0
   d > 1400 µm
      0 0 10 70 0 0 0 0 0 0 0 0 0 0 0 0 0 100 0 0 0 0 0 0 0 0

14 axial parenchyma
   a absent (or extremely rare)
      100 100 100 100 100 100 100 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 100
   b scanty paratracheal
      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
   c bands 3 or 4 cells wide
      0 0 0 0 0 0 0 0 100 100 100 100 100 100 100 75 75 0 0 0 0 0 10 0
   d bands > 4 cells wide
      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

15 ray width
   a uniseriate rays
      0 0 0 0 0 0 0 0 100 0 0 0 0 0 0 0 0 0 0 0 100 0 0 0 0 0 0 0 0 0 0
   b 1 to 2 cells
      0 60 100 100 100 100 100 0 80 90 30 60 10 80 50 70 0 15 10 75 75 50
   c 3 to 4 cells
      40 0 0 0 0 0 0 0 0 20 10 70 40 60 20 50 30 0 85 20 25 25 50
   d > 4 cells
      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

16 cellular ray composition
   a all cells upright / square
      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
   b body cells procumbent + upright/square marginal cells
      100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100

17 sheath cells
   a present
      0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
   b absent
      100 100 100 100 100 100 100 0 0 0 0 0 0 0 0 0 0 0 0 50 0 0 0 0 0 25 0 0 0

18 raphides
   a present
      100 0 100 100 0 0 0 100 100 100 100 0 100 100 100 100 100 100 100 100 100 100 100 100 100 100 100
   b absent
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<td>a both radial and tangent walls</td>
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<td>a septate</td>
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<td>b non-septate</td>
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<td>a thin-walled</td>
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<td>a &lt; 700 µm</td>
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<td>b 700–1100 µm</td>
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<td>c 1100–1400 µm</td>
<td>100 0 100 60 0 0 0 30 80 30 15 20 0 20 80 10 0 80</td>
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<td>d &gt; 1400 µm</td>
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<td><strong>14 axial parenchyma</strong></td>
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<td>a absent (or extremely rare)</td>
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<td>b scanty paratracheal</td>
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<td>c bands 3 or 4 cells wide</td>
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<td>d bands &gt; 4 cells wide</td>
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<td><strong>15 ray width</strong></td>
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<td>a uniseriate rays</td>
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<td>b 1 to 2 cells</td>
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<td>c 3 to 4 cells</td>
<td>0 0 0 0 0 0 0 100 60 100 0 15 0 0 50 30 30 30 20 15 80</td>
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<td><strong>16 cellular ray composition</strong></td>
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<td>a all cells upright / square</td>
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<td>b body cells procumbent + upright/square marginal cells</td>
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<td><strong>17 sheath cells</strong></td>
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<td><strong>18 raphides</strong></td>
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clearly correlated with the occurrence of more than one small opening in a very oblique perforation plate. The unusual shape is the result of a coalescence between two small perforations very close to each other. Indeed, two small perforations were frequently observed so close to each other that they become 8-shaped or somewhat more flattened (Fig. 43). In *Damnacanthus indicus* (Mit.) and *Lasianthus japonicus* (?Psy.) Ohtani (1984) observed irregular simple perforations which he considered to be "intermediate in form between normal simple and multiple perforation plates."

In *Psychotria vasivensis* (Fig. 43), irregular perforations are very frequent: up to eight unusual openings were counted close to each other in one perforation plate. Mennega and Koek-Noorman (personal communication) considered them as 'artefacts' due to a 'soft-rot' fungal attack because their shape is irregular and they seemingly appear to be distributed at random. Therefore we studied two other specimens (B. Maguire 43159 & 43481) corroborating that the 'artefacts' are simple and very small (± 10–15 µm) perforations with an unusual outline. Indeed, all three specimens of *P. vasivensis* show many irregular openings associated with their very long and oblique perforation plates. As the presence of few openings in one oblique perforation plate is rather common in wood of Psychotrieae, *P. vasivensis* is only an extreme example of this situation.

In *Gaertnera, Pagamea* and *Psychotria* we observed a few multiple perforation plates. Sometimes it is difficult to establish whether these multiple perforation plates link up two vessel elements or are vessel-ray perforations. However, a close examination of the tangential and radial sections suggests that in *Psychotria* the multiple perforation plates (scalariform, irregular or reticulate) occur where a vessel passes through a ray (Fig. 29). *Gaertnera* (Fig. 33) and *Pagamea* (Fig. 31) rarely show multiple perforation plates between two vessel elements. The combination of simple perforations and occasional multiperforate plates in the Rubiaceae was reported by Janssonius (1926), Metcalfe and Chalk (1950), Koek-Noorman (1969a), Meylan and Butterfield (1975), Ohtani (1984), and Carlquist (1992).

Perforated ray cells are known to be of common occurrence in the wood of Rubiaceae, and this is certainly due to the abundant, long uniseriate extensions of the heterogeneous rays in representatives of the family (e.g. Chalk & Chattaway 1933; Koek-Noorman 1969a; McLean & Richardson 1973; Rudall 1982; Nagai et al. 1994). Many specimens show perforated ray cells although they are easily overlooked. The vessel-ray perforation cells, which are mostly upright cells, are somewhat wider and higher in radial section than the ray parenchyma cells adjoining them longitudinally and have perforations occurring in their tangential walls. The pits of the vessel-ray perforation cells are similar to those of vessel elements.

When the vessel-ray perforation plate is simple, the perforation rims of the perforated ray cells are usually wider than those of the corresponding vessels. It is remarkable that these differentiated rims of vessel-ray perforation plates are frequently partly or completely encircled by a ring of pits. Similar observations were reported by McLean and Richardson (1973) in *Cephalanthis*, Cep.; Meylan and Butterfield (1975) in *Melicytus ramiflorus* and *M. lanceolatus* (Violaceae); Rudall (1982) in *Canthium barbatum*, Van.; and Nagai et al. (1994) in *Adina*, Nau., and *Gardenia*, Gar.
Occasionally vessel-ray perforation plates differ in micromorphology from intervessel perforation plates. Nagai et al. (1994) suggested that these differences between vessel-ray perforations and intervessel perforation plates are probably due to lack of coordination in the ontogeny. Indeed, perforated ray cells are derived from ray initials (Chalk & Chattaway 1933, McLean & Richardson 1973) whereas vessel members are derived from fusiform initials.

Chalk and Chattaway (1933) already concluded that there is a marked tendency to irregularity when the perforations of the ray cells are scalariform, particularly in association with vessels with simple perforations as in Rubiaceae and Euphorbiaceae. Indeed, several irregular perforations were observed in Psychotria, Gaertnera and Pagoamea. Rudall (1982) mentioned that the unusual perforation plates she found in wood of Canthium barbatum (Van.) are of a type which had never been recorded in secondary xylem of dicotyledons. Now we know that many unusual types of perforation plates occur in Rubiaceae, as was also demonstrated by Ohtani (1984).

In a few scalariform perforations, we observed microfibrillar webs. These are the remnants of the former primary wall-middle lamella partitions that survived the enzymatic breakdown process during perforation plate differentiation (Fig. 30). These structures are not considered to be taxonomically significant (Meylan & Butterfield 1975).

The intervessel pits are minute (± 3 μm), alternately arranged and always vested (Fig. 36). Psychotria brachiata is the only species with clearly polygonal pits (Fig. 38). The pits can also be occasionally elongated (Fig. 39). Rubiaceae always show the presence of vested intervessel pits, which is of diagnostic value for the family because of the restricted taxonomic distribution (Bailey 1933). Observation by SEM revealed that small vestures in wood of Psychotrieae are attached to the outer pit apertures and that they are occasionally anastomosed. Small unbranched vestures are present towards the pit annulus. Sometimes the inner pit aperture shows vestures which are restricted to the pit aperture.

Vestures were not observed in fibres or parenchyma cells, neither over vessel member walls as recorded in some representatives of the Rubiaceae (e.g. Vales 1983a, b; Ohtani et al. 1983; Ohtani 1986, 1987). Reports on the presence of vestures in perforation plates are few. They have been reported in Apocynaceae, Myrtaceae, Onagraceae and Rubiaceae on simple or multiple perforation plates (Butterfield & Meylan 1974; Meylan & Butterfield 1975, 1978; Ohtani & Ishida 1976, 1978; Kučera et al. 1977; Baas 1977; Rudall 1982; Vales 1983a; Ohtani et al. 1984; Ohtani 1984; Nair & Mohan Ram 1989). In the present study, vestures have been found only on the edge of the perforation rim of the numerous irregularly shaped perforations of Psychotria vasivensis. Vestures line the borders on each side of the perforation plate. The depression between the borders in each perforation plate is, however, always free of vestures.

The vessel-ray pits are similar to the intervessel pits (cf. Fig. 39 and 40). However, in many species these pits are sometimes more oval or elongated, and arranged in short horizontal rows. In Psychotria brachiata, the vessel-ray pits have much reduced borders, are gash-like and more elongated than in the other species (Fig. 41).
Fig. 1–6. Transverse sections of wood of *Psychotria* sp. – 1: *P. chalconeura*, absence of axial parenchyma, vessels in radial multiples. – 2: *P. succulenta*. – 3: *P. nervosa*. – 4: *P. brachiata*, paratracheal axial parenchyma present. – 5: *P. vasivensis*, abundant narrow vessels in radial multiples. – 6: *P. capitata*, parenchyma cells of pith fleck present. — Scale bar = 200 μm for Fig. 1, 2, 5, 6; scale bar = 100 μm for Fig. 3, 4.
Fig. 7 & 8. Transverse sections of wood of Chassalia sp. – 7: C. umbraticola, mostly isolated, narrow vessels. – 8: C. cristata, presence of tyloses, both wide and narrow vessels, thin-walled fibres. – Fig. 9 & 10. Transverse sections of wood of Chazaliella sp. – 9: C. obovoidea, narrow vessels in radial multiples. – 10: C. oddonii, 'vesselless' appearance. – Fig. 11. Gaertnera longevaginalis, transverse section showing 3–5 cell wide axial parenchyma bands. – Fig. 12. Pagamea velutina, transverse section showing isolated vessels and 4–5 cell wide axial parenchyma bands. — Scale bar = 100 μm for Fig. 7–11; scale bar = 200 μm for Fig. 12.
Fig. 13–16. Tangential sections of wood of Psychotria sp. – 13: *P. dermatophylla*, 3-seriate rays. – 14: *P. brachiata*, 1–2–3-seriate rays rather homocellular. – 15: *P. mariniana*, multiseriate ray with few sheath cells. – 16: *P. chalconeura*, narrow vessel elements with oblique perforation plate (arrow right) and two 2-seriate ray-portions vertically fused. — Fig. 17. *Chassalia cristata*, tangential section, high rays with very long uniseriate extensions. — Fig. 18. *Chazaliella oddonii*, tangential section, 1–2-seriate rays, heterocellular. — All scale bars = 100 μm.
Fig. 19 & 20. Tangential sections. - 19: Gaertnera longevaginalis, 2-seriate rays. - 20: Pagamea guianensis, 3-seriate rays and axial parenchyma near vessel (left). — Fig. 21–25. Radial sections. — 21: Psychotria micrantha, ray cells square with upright marginal cells. — 22: P. dermatophylla, procumbent ray cells and rows of upright/square marginal ray cells. — 23: P. mariniana, procumbent cells and upright/square marginal ray cells. — 24: P. nervosa, all ray cells upright/square (right) and septate fibres (left). — 25: Pagamea velutina, procumbent ray cells with upright marginal cells and axial parenchyma band present (arrows left). — Scale bar = 100 μm for Fig. 19, 20; scale bar = 200 μm for Fig. 21–25.
Fig. 26–29. Radial sections of wood of Psychotria sp. – 26: *P. antillana*, two simple perforations in one perforation plate near the middle of the vessel element. – 27: *P. dermatophylla*, three simple perforations in one wide perforation plate at the end of the vessel element. – 28: *P. cyanopharynx*, two simple intervessel perforations, rim without pits (SEM). – 29: *P. cyanopharynx*, scalariform vessel-ray perforation (SEM). — Fig. 30 & 31. SEM photographs of perforations in radial wood sections. – 30: *Gaertnera longevaginalis*, scalariform perforation plate with remnants of the primary cell wall. – 31: *Pagamea velutina*, irregular reticulate intervessel perforation. — All scale bars = 10 μm.
Fig. 32–37. SEM photographs of radial sections. – 32: *Chassalia subochreata*, two scalariform perforation plates with few branched bars. – 33: *Gaertnera cooperi*, scalariform perforation plate with many, branched bars. – 34: *Psychotria dermatophylla*, raphides in enlarged ray parenchyma cell. – 35: *Gaertnera bieleri*, fibre pits with borders about 3 μm diameter and small prismatic crystals (arrows). – 36: *Psychotria cyanopharynx*, vestured intervessel pits viewed from the outer surface of the vessel. – 37: *Chassalia umbraticola*, ridges interconnecting vessel pits and a small simple perforation (right). — All scale bars = 10 μm.
Fig. 38–43. Tangential and radial sections of *Psychotria*. – 38: *Psychotria brachiata*, polygonal and vestured intervessel pits. – 39: *P. succulenta*, intervessel pits sometimes elongated. – 40: *P. succulenta*, vessel-ray pits with distinct borders similar to intervessel pits. – 41: *P. brachiata*, vessel-ray pitting large and gash-like with reduced borders. – 42: *P. marginata*, septate libriform fibres with minutely bordered pits. – 43: *P. vasivensis*, many simple perforations with unusual shape in one very oblique perforation plate, three 8-shaped perforations left (arrows). — All scale bars = 10 µm.
Helical thickening were not found in the vessels, but we have seen ridges which interconnect pit apertures in some vessel elements, e.g. in *Chassalia unbraticola* (Fig. 37), *C. subochreata*, *Psychotria dermatophylla* and *P. cyanopharynx*.

The tangential diameter of vessel lumina is rather narrow (average of the studied genera: 60 μm). Very small diameters are characteristic for the genus *Chazaliella* (average: 29 μm, e.g. Fig. 9, 10) and the subherbaceous *Hymenocoleus scaphus* (average: 11 μm). *Chassalia* also has narrow vessels (average: 47 μm, e.g. Fig. 7). Wider vessels are found in *Psychotria dermatophylla*. *Chassalia cristata* shows both rather wide (90 μm) and narrow (45 μm) vessels (Fig. 8). The wide vessels in this species are especially wider in radial direction (c. 100 μm).

The vessel frequency is rather high (often > 40 vessels per mm²). Abundant vessels are present in *Psychotria vasivensis* (> 400 per mm², Fig. 5), while *P. antillana* possesses only 25 vessels per mm². The mean vessel element length varies from 325 μm for *Psychotria djumaensis* and 1150 μm for *P. vasivensis*. Tyloses were found in *Chassalia cristata* (Fig. 8), *Psychotria capitata* and *P. marginata*.

**Imperforate tracheary elements**

Septate librifibres fibres with minute pit borders (Fig. 42) are found in the genera *Chassalia*, *Chazaliella*, *Psychotria* and in *Hymenocoleus scaphus*. Fibre-tracheids with pits having borders of 3 μm in diameter (Fig. 35) on the radial and tangential walls are present in *Gaertnera* and *Pagamea*. These two genera show non-septate fibres. The fibre-tracheids are rather short (around 650 μm); libriform fibres are 900 to 1600 μm long.

Lemesle (1947a, b, 1953, 1956) repeatedly reported the existence of tracheids with at least one perforation plate. Such tracheids have been mentioned in the literature also by Jayme and Azzola (1964) who observed tracheid-like cells with simple perforations in *Fagus sylvatica* L. Patel (1973a) reported fibre-tracheids with a pair of oval simple perforations opposite each other on the tangential walls in *Corokia* and *Griselinia* (Cornaceae) and (Patel 1973b) in *Hedycarya* (Monimiaceae). Lemesle (1947a, b, 1953, 1956) stated that true vessels are sometimes present in stems but absent in roots of *Cephaelis ipecacuanha* (Psy.), *Psychotria emetica* (Psy.), *Manettia ignita* (Hed.), *Uruga* (= *Psychotria*) *granatensis* (Psy.) and *Richardsonia* (= *Richardia*) *scabra* (Spe.). According to him, the vessels are replaced by tracheids with simple perforations which he termed “fibres aréolées conductrices” or “trachéides ouvertes”. He argued that the perforations at the end or sometimes near the middle of the ‘tracheid’ are superimposed, permitting these cells to play the role of true vessels. According to the same author, true tracheids were also present in the five species he studied.

Following Metcalfe and Chalk (1983), we believe that tracheids with perforations are difficult to classify, because the transition between tracheids and vessel elements is not a sharp one. However, by definition they cease to be tracheids if they are perforate. Moreover, we did not observe true tracheids. Therefore we consider Lemesle’s ‘perforate tracheids’ as narrow vessel elements; they show similar intervessel pits as wide vessel elements and often the vessels are arranged in radial multiples.
Note that the vessels in the subherbaceous genera *Chassalia, Chazaliella* (e.g. *Chazaliella oddonii*, Fig. 10) and *Hymenocoleus* are occasionally so narrow that they might be difficult to distinguish from fibres or ray parenchyma cells. At first sight, transverse wood sections sometimes may look rather ‘vesselless’. For this reason Lemesle (1956) used the term ‘pseudo-homoxylées’ to describe the wood of the ‘Ipéca-cuanhas’. Since we believe that true vessels occur, the term ‘pseudo-homoxylées’ should not be applied.

**Axial parenchyma**

Axial parenchyma is absent in the Psychotrieae or rarely scanty paratracheal (e.g. *Psychotria berteroana* and *P. brachiata*, Fig. 4). Apotracheal parenchyma bands, however, are very characteristic for the genera *Gaertnera* and *Pagamea*. There is a difference between the width of the bands and the distance between these bands for this genus pair (Jansen et al. 1996b). *Gaertnera* shows bands of about 3 cells wide (Fig. 11); wood of *Pagamea* contains bands of 5 or more cells wide (Fig. 12, 20). The distance between the parenchyma bands is mostly < 200 μm for *Gaertnera* and > 500 μm for *Pagamea*. An exception is *Pagamea thyrsiflora* with a distance between the parenchyma bands of c. 180 μm. This is also the only *Pagamea* species with a rather small vessel diameter (55 μm) and relatively many vessels/mm² (average 42).

Included phloem or interxylary phloem is not found in the species studied and should not be confused with pith flecks which only contain parenchyma cells (Fig. 6). Note that intraxylary phloem, i.e. strands of phloem between the primary xylem and the pith of the stems, is common in all families of the Gentianales except the Rubiaceae (Carlquist 1992).

**Rays**

The rays are mostly 1- to 2-seriate (Fig. 14, 16, 18, 19); sometimes 2- to 3-seriate (Fig. 13, 20). *Chazaliella wildeemania* shows only uniseriate rays. Some species are uniseriate with occasional biseriate parts which are often not wider than the uniseriate portions. Multiseriate rays of four cells wide or more are present in *Psychotria succulenta, P. antillana, P. marginata* and *P. mariniana* (Fig. 15). The latter species also shows sheath cells forming an incomplete sheath around the procumbent cells.

The rays are seemingly of two distinct sizes owing to the large number of long uniseriate margins of the multiseriate rays. We did not consider these rays as having two distinct sizes. *Chassalia cristata* (Fig. 17) shows very high uni- and multiseriate rays. The total height of the rays is therefore often more than 1 mm (Fig. 16, 17). Two or more multiseriate rays are in many species fused axially by uniseriate margins (Fig. 16).

The number of rays per mm is high, mostly 12 or more. The rays are heterocellular, mostly composed of procumbent ray cells with 4 or more rows of upright/square marginal cells (Fig. 21, 22, 23, 25). The high uniseriate margins and the occasional biseriate parts consist exclusively of upright/square cells (Fig. 24).

As already mentioned above, we observed perforated ray cells in *Psychotria, Gaertnera* and *Pagamea* but not in the species of *Chassalia, Chazaliella* and *Hymenocoleus* studied.
Crystals and other deposits

Raphides, characteristic for most tissues in the Rubioideae (Robbrecht 1988), were found in the wood of 27 out of 42 species investigated. They occur in large ray cells (Fig. 34) or axial parenchyma cells. Small crystals (cubic, navicular, spindle-shaped or star-shaped), were abundant in most species, mainly in the ray cells. Starch grains are often present in the septate fibres.

Many wood samples of the Psychotrieae react positively to the chemical spot-test for aluminium as performed by Kukachka and Miller (1980). They found that the number of positive-testing families (Melastomataceae, Proteaceae, Rubiaceae and Vochysiaceae) and genera is small and suggested there may be a systematic trend within these families. Some positive testing genera of the Psychotrieae are Cephaelis, Gillespiea, Palicourea, Psychotria and Rudgea (Kukachka & Miller 1980). Metcalfe and Chalk (1983) reported the presence of aluminium accumulation in the following Psychotrieae: Psychotria s.l. (288/507), Rudgea (113/113), Gaertnera (39/42) and Palicourea (160/166). Chenery (1948) reported an interesting high correlation between the presence of aluminium in abnormal quantities and a bright blue colour of the fruits in many Psychotrieae.

All wood samples were tested for aluminium accumulation. Only few specimens gave a positive reaction, namely Gaertnera cooperi, Psychotria brachiata, P. capitata, P. dermatophylla, P. succulenta, and P. vasivensis. For all other species, the results were negative. We doubt if this character has systematic significance on this taxonomical level, and therefore the feature was not included in the numerical analysis.

DISCUSSION

The dendrogram resulting from the cluster analysis (Fig. 44) shows two main clusters, viz. the genera Gaertnera and Pagamea (cluster B), and the rest of the study group (cluster A). The wood anatomical distinction between the genus pair Gaertnera/Pagamea (Gaertnerinae) and the other genera is obvious and based on the following characters:

- Parenchyma bands present; fibre-tracheids; vessels solitary (> 50%) Gaertnerinae
- Axial parenchyma absent or rarely present as scanty paratracheal; libriform fibres; vessels in radial multiples (> 50%) Psychotriinae

Gaertnera and Pagamea are as far as we know the only genera of the Psychotrieae without libriform fibres. Note that Koek-Noorman (1977, 1980) emphasized that the kind of fibre, namely libriform fibres as opposed to fibre-tracheids, is a very important differentiating character at the level of tribes and genera in the family. Indeed, the consistency of the fibre type at the tribal, and, to some extent, subfamilial level is remarkable (e.g. subfamily Ixoroideae with fibre-tracheids). The variation that exists in some entities (e.g. Cinchoneae and associated ‘Condamineeae’ and Rondeletieae), however, puts doubt on the hypothesis that the differentiation of the fibre types took place in a relative early phase of development of the Rubiaceae. Note that the Condamineeae (except the Portlandiinae) were recently included in the Rondeletieae s.l. (Delprete 1996).
Fig. 44. Dendrogram obtained after cluster analysis (average = linkage, distance = Pearson) of the data matrix in Table 1. Species (OTUs) of which two specimens were examined are followed by the last digit of the Tw number.
There is also a rather good distinction between the wood of *Gaertnera* and *Pagamea* (see respectively cluster B1 and B2 in Fig. 44). They differ in the following quantitative characters: diameter of vessels, width of parenchyma bands and distance between these bands. The only exception is a specimen of *Gaertnera cooperi* which clusters in the *Pagamea* group (B2). The distinction between these genera on the basis of some quantitative characters, however, is weak. Remark that in this study most *Gaertnera* species investigated are shrubs or small trees, while the *Pagameas* examined are small-sized or normal trees (except *P. thyrsiflora*; see list of material). A larger sampling of wood of the two genera is needed to verify the wood anatomical differences observed here.

Parenchyma bands are rare in the Rubiaceae—Rubioideae. Koek-Noorman (1969b) reported them also from *Morinda citrifolia*, and a recent macromolecular investigation (Bremer 1996) suggested that *Gaertnera* should be closely related to *Morinda* and not to *Psychotria*.

The distinction between the genus pair *Gaertnera/Pagamea* and the other Psychotrieae is correlated with some other features, e.g. morphological (Igersheim et al. 1994) and palynological (Jansen et al. 1996a). We have discussed this in detail in the latter contribution, where we proposed to classify the two genera in the Psychotrieae as a separate subtribe Gaertnerininae. Bremekamp (1966), however, placed *Gaertnera* and *Pagamea* in a separate tribe Gaertneriniae, which was supported wood anatomically by Koek-Noorman (1969b).

The two genera share many features with the Psychotrieae, however, e.g. the solitary ovules, the valvate aestivation of the corolla lobes and fruit morphological characters. We believe that an exclusion from the Psychotrieae on the basis of some advanced wood and pollen features is premature in the light of the bad understanding of the large Psychotrieae alliance (more than 50 genera). In depth research on Psychotrieae and other woody uniovulate tribes of the Rubioideae (e.g. Morindeae and Prismatomeriadeae) may result in new tribal concepts and elucidate which genera are truly related to the genus pair *Gaertnera/Pagamea*. Two facts are important in this context: (i) the possible relationship between *Morinda* and *Gaertnera/Pagamea* on the basis of macromolecular evidence (Bremer 1996) and (ii) our ongoing wood anatomical research indicates that three other genera of the Psychotrieae alliance, *Pagameopsis*, *Lasianthus* and *Colletoeccema* also show profound wood anatomical differences with the core genera *Psychotria*, *Chassalia* and *Chazaliella*.

The main cluster A (Fig. 44) includes *Chassalia*, *Chazaliella*, *Hymenocoleus saphus* and *Psychotria*. The generic distinction between these taxa is not congruent with the subclusters A1–A6. However, a few positions are remarkable and some wood anatomical characters need comments.

Concerning the genus *Chassalia*, the presence of exclusively scalariform perforations found in *Chassalia subochreata* is certainly no juvenile character although the wood sample examined was only 5 mm thick. Nevertheless, the two other *Chassalia* species were a few mm thicker and show only simple perforations.

*Chassalia cristata* stands rather isolated in subcluster A5 (Fig. 44). This species is a scandent shrub. Carlquist (1985) has reported that many scandent plants show vessel
dimorphism and relatively high rays. This seems to be true for *Chassalia cristata* which also shows rather thin fibre walls (Fig. 8).

The species of *Chazaliella* fall within subcluster A3 and A4 but widely apart.

The wood of *Hymenocoleus scaphus* is, as can be expected from the single subwoody species of an otherwise entirely herbaceous genus, characterized by very narrow vessels (average 11 mm), short non-septate fibres with small pits and 1-seriate rays which are poorly differentiated. It is clear that juvenile characters are present like those described by Koek-Noorman (1976) for *Rubia fruticosa* (Rub.), also a subwoody member of a mainly herbaceous genus. *Hymenocoleus scaphus* nevertheless resembles the Psychotriinae in the absence of parenchyma, and the radial arrangement of the vessels (c. 40%).

The species of *Psychotria* investigated are dispersed over all subclusters of cluster A (Fig. 44). *Psychotria brachiata* is placed in an isolated position (A6, Fig. 44). This position can be easily explained because the species appeared very deviant from other Psychotrieae; its wood is unique in the study group because the vessel-ray pits have much reduced borders and are more elongated than in all the other species (Fig. 41); it has also scanty paratracheal axial parenchyma (Fig. 4). This prompted us to ask Dr. C.M. Taylor (MO), a specialist in neotropical Psychotrieae, to confirm the determination of the voucher material. In her reply she remarked that the specimen is correctly identified. More specimens should be studied to verify its unusual wood anatomy.

*Psychotria mariniana*, placed in cluster A2, is sometimes segregated, together with other Hawaiian species, from *Psychotria* as *Straussia*. We had the occasion to examine *Straussia psychotrioides* Heller (collected by W.L. Stern at Hawaii, Uw 10431 and USw 25992), which revealed that the two species are very similar and share the multiseriate rays of 4 cells wide or more, and the sheath cells which incompletely surround the procumbent cells of the rays (Fig. 15, 23). Further wood anatomical examinations together with morphological and palynological studies should reveal if *Straussia* must be segregated as a genus from *Psychotria*.

*Psychotria dermatophylla*, the other species placed in A2 (Fig. 44), is the only studied species which is a large tree (Table 1), a habit presumably correlated with the rather wide vessel diameter (± 140 μm) and a low vessel frequency (± 15 vessels/mm²). Similarly Carlquist (1966) and Wallace (1986) found that the diameter of vessel lumina (and also the vessel element length) is greater in trees, intermediate in shrubs and smaller in subshrubs.

*Psychotria vasivensis*, placed in A1 (Fig. 44), is remarkable in the very high presence of small vessel elements having many irregular and ventured perforations in their long oblique perforation plates.

It is hardly possible to correlate the distribution of the other *Psychotria* species examined in the clusters with existing infrageneric classifications. Although one cannot exclude that wood anatomy has a weak taxonomic value within *Psychotria*, this result could also be due to the absence of a worldwide infrageneric taxonomic framework for the genus. The case of ‘*Straussia*’ discussed above makes clear that it could also be connected with our scanty sampling (2% of the species only!). All existing modern classifications of *Psychotria* are geographically restricted. The existing
infrageneric classifications relevant for our species sampling (Petit 1964, 1966; Africa; Steyermark 1974: northern South America; Burger & Taylor 1993: Costa Rica) show no correlation at all with the obtained dendrogram. The species *Psychotria brachiata*, *P. berteroana*, *P. capitata* and *P. pubescens* belong to Burger and Taylor’s (op. cit.) group 3, which they accept to be “largely monophyletic”. However, these Central American species (the Isthmus plus the West Indies) form no distinct group within subcluster A3 or A4 (Fig. 44). The more isolated position of *P. berteroana* in cluster A3 is probably due to the presence of scanty paratracheal parenchyma.

CONCLUSION

Wood anatomy has only restricted taxonomic value inside the Psychotrieae, although the tribe is clearly not as homogeneous as supposed by Koek-Noorman. A further wood-anatomical study of the tribe seems to be worthwhile and could throw more light on the delimitation of the problem genus *Psychotria* and allied genera. However, as the wood structure within genera varies rather little, we expect more promising results at a higher taxonomic level, i.e. also considering the related Morindeae, Triainolepideae, Coussareeae and Prisamatomerideae and some ‘isolated genera’ of difficult position such as *Colletoeecema*, *Damnacanthus* or *Lathraeocarpa*. As the above mentioned possible relationship *Gaertnera/Morinda* indicates, more wood anatomical data could prove to be of interest for a better phylogenetic understanding of the woody Rubioideae, of which the Psychotrieae are the largest and core group.

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