A SURVEY OF THE SYSTEMATIC WOOD ANATOMY OF THE RUBIACEAE

by

Steven Jansen¹, Elmar Robbrecht², Hans Beeckman³ & Erik Smets¹

SUMMARY

Recent insight in the phylogeny of the Rubiaceae, mainly based on macromolecular data, agrees better with wood anatomical diversity patterns than previous subdivisions of the family. The two main types of secondary xylem that occur in Rubiaceae show general consistency in their distribution within clades. Wood anatomical characters, especially the fibre type and axial parenchyma distribution, have indeed good taxonomic value in the family. Nevertheless, the application of wood anatomical data in Rubiaceae is more useful in confirming or negating already proposed relationships rather than postulating new affinities for problematic taxa. The wood characterised by fibre-tracheids (type I) is most common, while type II with septate libriform fibres is restricted to some tribes in all three subfamilies. Mineral inclusions in wood also provide valuable information with respect to systematic relationships.

Key words: Rubiaceae, systematic wood anatomy, classification, phylogeny, mineral inclusions

INTRODUCTION

The systematic wood anatomy of the Rubiaceae has recently been investigated by us and has already resulted in contributions on several subgroups of the family (Jansen et al. 1996, 1997a, b, 1999, 2001; Lens et al. 2000). The present contribution aims to extend the wood anatomical observations to the entire family, surveying the secondary xylem of all woody tribes on the basis of literature data and original observations. Although Koek-Noorman contributed a series of wood anatomical studies to the Rubiaceae in the 1970's, there are two principal reasons to present a new and comprehensive overview on the wood anatomical variation. At first, the work of Koek-Noorman mainly emphasised neotropical representatives, and secondly, the taxonomic framework of the family has entirely changed.

This paper starts with a historical survey of previous contributions including a comprehensive bibliography of wood anatomical literature of the family. This section does not aim at completeness but is meant to comment on the most important studies.

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- 1) Laboratory of Plant Systematics, Institute of Botany and Microbiology, K.U. Leuven, Kas-teelpark Arenberg 31, B-3001 Leuven, Belgium.
 - 2) National Botanic Garden of Belgium, Domein van Bouchout, B-1860 Meise, Belgium.
 - 3) Royal Museum for Central Africa, Leuvensesteenweg 13, B-3080 Tervuren, Belgium.

A general introduction to the subfamilial and tribal classification of the Rubiaceae is given and presently available hypotheses on the phylogeny of the family are surveyed and summarised in a hypothetical tree. This new taxonomic framework is also compared to the latest overall classification system (Robbrecht 1988, 1994). The major part of this paper focuses on the wood anatomical variation within the Rubiaceae and discusses the systematic significance of the wood types. In order to elucidate the evolution of the secondary xylem, wood anatomical characters are plotted on the hypothetical tree. The present work also illustrates the distribution and taxonomic value of mineral inclusions in wood of Rubiaceae. A short wood anatomical comparison between Rubiaceae and related families is given in a final section.

Historical survey of the systematic wood anatomy of the Rubiaceae

Upon scanning early studies from the 19th century, the work of Van Riemsdijk (1875) is, as far as we know, one of the oldest works describing wood anatomy of Rubiaceae. Figure 1 shows his drawing of a transverse section of *Coffea* wood. This Dutch anatomist paid attention to seven genera of Rubiaceae and described in detail structures such as the distribution of axial parenchyma, disjunctive ray parenchyma cell walls, crystals, pitting of parenchyma cells and growth rings. However, general wood anatomical characters of the family were not discussed. A major contribution to systematic wood anatomy of the dicotyledons from that period was made by Solereder (1885, 1893, 1899) who investigated c. 40 rubiaceous genera. Thereby, he was able to discuss general characters of the wood structure of Rubiaceae.

Fig. 1. Drawing of a transverse section of the wood of *Coffea arabica*; pa = axial parenchyma cell; kr = prismatic crystal (Van Riemsdijk 1875).

An important wood anatomical survey of the major tree and shrub species from Indonesia was published by Moll and Janssonius (1926) in volume IV of their “*Micrographie des Holzes der auf Java vorkommenden Baumarten*”. This comprehensive work includes very detailed descriptions of the secondary xylem of 26 rubiaceous genera. The application of precise terminology, accuracy and the abundant quantitative data (e.g. on the thickness of cell walls) that were compiled by Janssonius provide such a wealth of wood structural information that most of their data are even more comprehensive than most present wood anatomical descriptions. For instance, the sporadic occurrence of helical thickenings in axial parenchyma cells of a specimen of *Lasianthus purpureus* was observed for the first time (Moll & Janssonius 1926: 245). With numerous original observations and taxonomic comments, Metcalfe’s and Chalk’s (1950) “*Anatomy of the Dicotyledons*” represents the most important contribution to the vegetative anatomy of the Rubiaceae from the first half of the 20th century. These authors accumulated data from literature and new observations of all together c. 150 rubiaceous genera.

Moreover, many wood anatomical descriptions, mostly of a selected number of rubiaceous species or genera often from restricted regions, have been published. A few that may be briefly mentioned are for instance: “*Commercial timbers of India*” (Pearson & Brown 1932), “*Woods of northeastern Peru*” (Williams 1936), “*Manuel d’identification des bois commerciaux, nr. 2, Afrique guinéo-congolaise*” (Normand & Paquis 1976), and “*Atlas d’identification des bois de l’Amazonie et des régions voisines*” (Détienne & Jacquet 1983). Because detailed microscopic observations and systematic conclusions are beyond the scope of these works, there is no need to consider them in detail here.

From the late 1960’s towards the 1980’s a series of wood anatomical papers on a large number of Rubiaceae was published by Koek-Noorman. After two general papers on the wood structure of South American (mainly Surinam) Rubiaceae (Koek-Noorman 1969a, b), special attention was given to the following tribes (in the delimitation of Bremekamp 1966 followed by her): Cinchoneae, Coptosapelteae, Naucleaeae (Koek-Noorman 1970), Gardenieae, Ixoreae, Mussaendeae (Koek-Noorman 1972), Vanguerieae, Cinchoneae, Condamineae, Rondeletieae (Koek-Noorman & Hogeweg 1974), and Henriquezieae (Koek-Noorman 1980; also studied by Rogers 1981, 1984). Somewhat later, she collaborated with Puff in forwarding wood anatomical evidence for his redelimitation of the Anthospermeae and Paederieae (Koek-Noorman & Puff 1983, 1991). She distinguished two main types of secondary xylem and these types were largely found to be in accordance with the generic, tribal, and to some extent subfamilial concepts of Bremekamp (1952, 1966) and Verdcourt (1958) (Koek-Noorman 1977). Moreover, Koek-Noorman and Hogeweg (1974) applied cluster analysis using 125 wood anatomical characters in three tribes of the Rubiaceae. Irrespective of whether all varying features in their descriptions are given equal weight, or whether preferential character weighing is applied, the cluster analysis remains virtually the same with a very distinct bipartition. The success of numerical methods obtained for the Rubiaceae was further explored by Hogeweg and Koek-Noorman (1975). Apart from our own investigations, the most recent contribution to comparative wood

anatomy of Rubiaceae is from Ter Welle et al. (1983). They examined the wood structure of nearly all genera of the Guettardeae and presented suggestions for taxonomic revisions of some genera.

Ecological approaches to the wood anatomy of the Rubiaceae were made by few authors. Koek-Noorman (1976) and Carlquist (1992) found wood anatomical evidence to suggest that some representatives of the Rubieae, which predominantly is a herbaceous tribe, have radiated into more temperate climates where secondary woodiness has occurred (e.g. *Galium*, *Rubia*).

The study of fossil woods is an important aspect of systematic wood anatomy. The following fossil woods have been assigned to the Rubiaceae: *Rubioxylon naucleoides* (Hofmann 1952; Oligocene), *Rubioxylon vincenti* (Koeniguer 1975; Pliocene), and cf. *Rubioxylon vincenti* (Lemoigne 1978; Miocene), *Canthium omoensis*, *Rothmannia aethiopica* (Gros 1990; Pliocene), *Mitragynoxolon gevinii* (Gevin et al. 1971; Oligocene/Miocene; Gros 1990). A specimen of *Grangeonixylon danguense* is said to be either Rubiaceae or Apocynaceae (Sakala et al. 1999). However, some of these woods may need to be re-evaluated regarding their identification or questionable age.

In summary, most studies of the wood tissue of the Rubiaceae undertaken are limited to regional surveys, except for the series of publications by Koek-Noorman. Most authors agreed that the anatomical structure of the woods is remarkably similar, exhibiting fewer differences than is usual in much smaller natural groups than the Rubiaceae.

Bibliography of the systematic wood anatomy of the Rubiaceae

A bibliography of systematic wood anatomy of the Rubiaceae is given below. The aim of this bibliography is to provide a guide to the available literature. For a more complete list including 160 full references on Rubiaceae, the "Bibliography of Systematic Wood Anatomy of Dicotyledons" (Gregory 1994) is recommended. We also refer here to the databases of the Royal Botanic Gardens, Kew (2000a, b), which are very useful for accessing recent taxonomic literature of many taxa.

In order to keep the length of the bibliography down, only references with microscopical observations are included. The authors are listed in chronological order. Generic names are as in the papers cited.

Van Riemsdijk (1875): *Cinchona*, *Coffea*, *Greenaea*, *Guettarda*: *Nauclea*, *Psychotria*, *Uncaria*.
 Solereder (1885): *Alberta*, *Anthospermum*, *Antirhea*, *Bikkia*, *Catesbaea*, *Chiococca*, *Cinchona*, *Coffea*, *Coussarea*, *Damnacanthus*, *Discospermum*, *Faramaea*, *Gaillonia*, *Gardenia*, *Guettarda*, *Hamelia*, *Hamiltonia*, *Hedyotis*, *Ixora*, *Knoxia*, *Ladenbergia*, *Lasianthus*, *Leptodermis*, *Morinda*, *Mussaenda*, *Nauclea*, *Nenax*, *Pachystigma*, *Paederia*, *Portlandia*, *Psychotria*, *Psyllocarpus*, *Retiniphyllum*, *Rondeletia*, *Rudgea*, *Scolosanthus*, *Uncaria*, *Urophyllum*, *Vangueria*, *Wendlandia*.

Burgerstein (1912): *Calycophyllum*, *Coutarea*.

Kanehira (1921): *Chomelia*, *Diplospora*, *Gardenia*, *Morinda*, *Nauclea*, *Psychotria*, *Randia*, *Timonius*, *Wendlandia*.

Brown (1922): *Bobea*, *Canthium*, *Coprosma*, *Gardenia*, *Morinda*, *Psychotria*, *Straussia*.

Lecomte (1922): *Breonia*, *Craterispermum*, *Nauclea*, *Pyrostris*, *Schismatoclada*.

Record and Garrat (1925): *Gardenia*.

- Moll and Janssonius (1926): *Adina, Breonia, Canthium, Cinchona, Diplospora, Guettarda, Hymenodictyon, Hypobathrum, Ixora, Lasianthus, Mitragyna, Morinda, Mussaenda, Nauclea, Nostolachma, Pavetta, Prismaomeris, Psychotria, Randia, Sarcocephalus, Scyphiphora, Tarenna, Urophyllum, Vangueria, Wendlandia, Zuccarinia*.
- Kribs (1928): *Amaioua, Isertia, Palicourea, Psychotria*.
- Panshin (1932): *Scyphiphora*.
- Pearson and Brown (1932): *Adina, Breonia, Canthium, Gardenia, Hymenodictyon, Mitragyna, Morinda, Nauclea, Randia, Sarcocephalus*.
- Chalk et al. (1933): *Mitragyna*.
- Milanez (1936): *Calycophyllum*.
- Williams (1936): *Alibertia, Alseis, Anisomeris, Bertiera, Bothriospora, Calycophyllum, Capirona, Cephaelis, Chimarrhis, Cinchona, Coussarea, Coutarea, Duroia, Farama, Ferdinandusa, Genipa, Gonzalagunia, Hamelia, Hippotis, Isertia, Ixora, Ladenbergia, Machaonia, Macrocnemum, Palicourea, Pentagonia, Posoqueria, Psychotria, Randia, Remijia, Rudgea, Sickingia, Sommera, Sphinctanthus, Tocoyena, Uncaria, Warszewiczia*.
- Record and Hess (1943): General description of wood anatomical features.
- Lemesle (1947a): *Cephaelis, Psychotria*.
- Lemesle (1947b): *Cephaelis, Psychotria, Manettia, Richardsonia*.
- Metcalf and Chalk (1950): General discussion of wood anatomical characters based on c. 150 genera.
- Fouarge et al. (1953): *Mitragyna, Sarcocephalus*.
- Desch (1954): *Adina, Aidia, Anthocephalus, Canthium, Diplospora, Gardenia, Hymenodictyon, Ixora, Jackiopsis, Mitragyna, Morinda, Mussaendopsis, Nauclea, Neonauclea, Randia, Scyphiphora, Timonius, Urophyllum*.
- James (1954): *Scyphiphora*.
- De Freitas (1955): *Timonius*.
- Normand (1960): *Canthium, Corynanthe, Gardenia, Morinda, Nauclea, Mitragyna*.
- Brazier and Franklin (1961): *Adina, Calycophyllum, Gardenia, Mitragyna, Nauclea*.
- Fouarge and Gérard (1964): *Aidia, Corynanthe*.
- Lebacqz and Dechamps (1967): *Aidia, Belonophora, Canthium, Coltoecema, Crossopteryx, Cuviera, Gaertnera, Gardenia, Massularia, Mitragyna, Morinda, Pausinystalia, Psychotria, Rothmannia*.
- Kribs (1968): *Adina, Calycophyllum, Corynanthe, Genipa, Mitragyna, Neonauclea, Sarcocephalus*.
- Koek-Noorman (1969a): General description of the wood structure of the Rubiaceae.
- Koek-Noorman (1969b): *Alibertia, Amaioua, Capirona, Cephaelis, Chimarrhis, Chomelia, Coussarea, Duroia, Elaeagia, Farama, Genipa, Guettarda, Hamelia, Henriquezia, Hillia, Isertia, Ixora, Malanea, Mapouria, Morinda, Naletonia, Pagamea, Palicourea, Posoqueria, Psychotria, Randia, Retiniphyllum, Ronabea, Rosenbergiendendron, Rudgea, Schradera, Sickingia, Simira, Strepelia, Uncaria, Warszewiczia*.
- Koek-Noorman (1970): *Adina, Anthocephalus, Breonia, Calycophyllum, Capirona, Cephalanthus, Cinchona, Corynanthe, Coutarea, Crossopteryx, Exostema, Ferdinandusa, Hymenodictyon, Macrocnemum, Mitragyna, Nauclea, Neonauclea, Uncaria*.
- Koek-Noorman (1972): *Acranthera, Alibertia, Amaioua, Amaralia, Aulacocalyx, Bertiera, Borojoa, Casasia, Duroia, Galiniera, Gardenia, Genipa, Gonzalagunia, Gouldia, Hamelia, Heinsenia, Heinsia, Hippotis, Ibetralia, Isertia, Ixora, Kutchubaea, Leptactina, Leucolophus, Maschalocorymbus, Mussaenda, Mycetia, Pavetta, Pentagonia, Pleiocarpidia, Randia, Rennellia, Retiniphyllum, Rothmannia, Rutidea, Sommera, Stachyarrhena, Tarenna, Tocoyena, Tricalysia, Urophyllum*.
- Ridsdale et al. (1972): *Maschalodesme, Versteegia*.
- Mennega and Koek-Noorman (1973): *Gaertnera, Pagamea*.

- Ayensu and Bantum (1974): *Mitragyna, Nauclea*.
- Koek-Noorman and Hogeweg (1974): *Alseis, Badusa, Bathysa, Bikkia, Calycophyllum, Canthium, Capirona, Cascarilla, Chimarrhis, Cinchona, Condaminea, Cuviera, Dolicholobium, Elaeagia, Exostema, Ferdinandusa, Gleasonia, Greenea, Hymenodictyon, Joosia, Ladenbergia, Lindenia, Loretoa, Macbrideina, Macrocnemum, Morierina, Mussaendopsis, Pinckneya, Plectronia, Pogonopus, Portlandia, Remijia, Rondeletia, Rustia, Rytigynia, Simira, Vangueria, Warszewiczia, Wendlandia*.
- Leroy (1975): *Hallea, Mitragyna*.
- Lomibao (1975): *Adina, Canthium, Greeniopsis, Guettarda, Neonauclea*.
- Koek-Noorman (1976): *Amaracarpus, Coprosma, Crucianella, Declieuxia, Diodia, Galium, Hemidiodia, Othiophora, Plocma, Pomax, Psychotria, Relbunium, Rubia, Spermacoce*.
- Normand and Paquis (1976): *Brenania, Canthium, Craterispermum, Gaertnera, Morinda, Nauclea, Hallea, Hymenodictyon, Pausinystalia*.
- Fundter and Wisse (1977): *Adina, Mastixiodendron, Nauclea*.
- Koek-Noorman (1977): Survey of wood types of Rubiaceae.
- Vales and Babos (1977): *Ceratopyxis*.
- Meylan and Butterfield (1978): *Coprosma*.
- Miles (1978): *Adina, Calycophyllum, Gardenia, Mitragyna, Nauclea*.
- Aiello (1979): *Nernstia, Portlandia*.
- Bridson et al. (1980): *Phellocalyx*.
- Koek-Noorman (1980): *Gleasonia, Henriquezia, Platycarpum*.
- Rogers (1981): *Gleasonia, Henriquezia, Platycarpum*.
- Détienne et al. (1982): *Amaioua, Capirona, Chimarrhis, Coussarea, Duroia, Genipa, Isertia, Palicourea, Posoqueria*.
- Fernandez and Peters (1982): *Coffea*.
- Purkayastha (1982): *Adina, Breonia, Canthium, Catunaregam, Gardenia, Hymenodictyon, Ixora, Mitragyna, Morinda, Nauclea, Neonauclea, Randia, Tricalysia, Wendlandia*.
- Rudall (1982): *Canthium*.
- Détienne and Jacquet (1983): *Alibertia, Alseis, Amaioua, Anisomeris, Bothriospora, Calycophyllum, Capirona, Chimarrhis, Chomelia, Cinchona, Coussarea, Coutarea, Duroia, Ferdinandusa, Genipa, Guettarda, Henriquezia, Isertia, Ladenbergia, Loretoa, Macbrideina, Macrocnemum, Morinda, Palicourea, Posoqueria, Psychotria, Randia, Remijia, Sickingia, Stachyarrhena, Straussia, Tocoyena, Warszewiczia*.
- Koek-Noorman and Puff (1983): *Aitchisonia, Anthospermum, Carpacoce, Coprosma, Crocylis, Leptodermis, Nenax, Opercularia, Paederia, Phyllis, Pomax, Neogaillonia, Normandia, Spermadictyon*.
- Vales (1983a, b): *Acunaeanthus, Ariadne, Ceratopyxis, Mazaea, Phyllomelia*.
- Ter Welle et al. (1983): *Antirhea, Bobea, Chomelia, Dichilanthe, Guettarda, Machaonia, Malanea, Timonius*.
- Gill and Onuja (1984): *Canthium, Nauclea*.
- Gomes and Marchiori (1984): *Calycophyllum*.
- Ohtani (1984): *Damnacanthus, Lasianthus*.
- Rogers (1984): *Gleasonia, Henriquezia, Platycarpum*.
- Dechamps (1985): *Alseis, Amaioua, Calycophyllum, Capirona, Chimarrhis, Chomelia, Cinchona, Coffea, Coussarea, Duroia, Faramaea, Genipa, Gonzalagunia, Guettarda, Isertia, Ixora, Ladenbergia, Macbrideina, Macrocnemum, Pagamea, Palicourea, Posoqueria, Psychotria, Remijia, Rudgea*.
- Vales and Süß (1985a): *Ceratopyxis, Phyllomelia*.
- Vales and Süß (1985b): *Acunaeanthus, Ariadne, Neomazaea*.
- Ohtani (1986): *Lasianthus*.
- Ohtani (1987): *Damnacanthus*.

- Richter and Schmitt (1987): *Cosmocalyx*.
Coulaud (1988, 1989): *Gaertnera*, *Genipa*.
Barajas-Morales and Gomez (1989): *Exostema*, *Guettarda*, *Hintonia*.
Schweingruber (1990): *Asperula*, *Crucianella*, *Galium*, *Putoria*, *Rubia*.
International Tropical Timber Organisation and Research Institute of Wood Industry (1991):
Adina, *Anthocephalus*, *Hymenodictyon*, *Mitragyna*, *Mussaendopsis*, *Nauclea*.
Koek-Noorman and Puff (1991): *Paederia*.
Carlquist (1992): *Coprosma*, *Galium*.
Oteng-Amoako (1992): *Anthocephalus*, *Mastixiodendron*, *Nauclea*, *Neonauclea*.
Acevedo and Kikita (1994): *Alseis*, *Calycophyllum*, *Chimarrhis*, *Genipa*, *Simira*.
Carreras and Dechamps (1995): *Acrosynanthus*, *Calycophyllum*, *Genipa*, *Guettarda*.
Vrydaghs et al. (1995): *Adina*, *Breonadia*, *Haldina*, *Hallea*, *Metadina*, *Mitragyna*, *Nauclea*,
Neonauclea, *Ochreinauclea*, *Pertusadina*, *Sarcocephalus*.
Jansen et al. (1996): *Gaertnera*, *Pagamea*.
Purkayastha (1996): *Breonia*, *Canthium*, *Catunaregam*, *Deccania*, *Gardenia*, *Guettarda*, *Haldina*,
Hymenodictyon, *Ixora*, *Mitragyna*, *Morinda*, *Neonauclea*, *Ochreinauclea*, *Tricalysia*,
Wendlandia.
Barros and Callado (1997): *Coussarea*, *Psychotria*.
Jansen et al. (1997a): *Chassalia*, *Chazaliella*, *Gaertnera*, *Hymenocoleus*, *Pagamea*, *Psychotria*.
Jansen et al. (1997b): *Argocoffeopsis*, *Calycosiphonia*, *Coffea*, *Psilanthus*.
Ogata and Kalat (1997): *Gynopachis*, *Rothmannia*, *Tarenna*, *Timonius*.
Gasson et al. (1998): *Fernelia*.
Sosef et al. (1998): *Adinauclea*, *Canthium*, *Gardenia*, *Guettarda*, *Haldina*, *Hymenodictyon*,
Ixora, *Jackiopsis*, *Ludekia*, *Metadina*, *Mussaendopsis*, *Nauclea*, *Neonauclea*, *Ochreinauclea*,
Pertusadina, *Porterandia*, *Scyphiphora*, *Timonius*, *Urophyllum*.
Jansen et al. (1999): *Captaincookia*, *Cladoceras*, *Dictyandra*, *Doricera*, *Duperrea*, *Homollea*,
Ixora, *Leptactina*, *Myonima*, *Nichallea*, *Pachystylus*, *Pavetta*, *Rutidea*, *Tarenna*, *Tennantia*,
Versteegia.
Ceccantini and Angyalossy-Alfonso (2000): *Bathysa*.
Lens et al. (2000): *Canthium*, *Cuviera*, *Fadogia*, *Fadogiella*, *Keetia*, *Lagynias*, *Meyna*, *Pachystigma*,
Psydrax, *Pygmaeothamnus*, *Pyrostria*, *Rytigynia*, *Tapiphyllum*, *Vangueria*, *Vangueriopsis*.
Dessein et al. (2001b): *Virectaria*.
Jansen et al. (2001): *Commitheca*, *Coussarea*, *Craterispermum*, *Dammacanthus*, *Declieuxia*,
Faramaea, *Gynochtodes*, *Hindsia*, *Lasianthus*, *Leucolophus*, *Maschalocorymbus*, *Morinda*,
Pleiocarpidia, *Poecilocalyx*, *Praravinia*, *Prismatomeris*, *Rennellia*, *Saldinia*, *Stelechantha*,
Triainolepis, *Trichostachys*, *Urophyllum*.
Piesschaert et al. (In press): *Pagameopsis*.

The intrafamilial classification of the Rubiaceae

At the beginning of our wood anatomical project, we followed the then latest overall classification system of the Rubiaceae (Robbrecht 1988, 1994), which was based on character analysis of a number of features including wood anatomy (Fig. 2). It was our initial intention to sample wood from all woody tribes in Robbrecht's four sub-families.

Already in the 1990's, Bremer and Jansen (1991) and Bremer (1992) used comparative restriction site mapping of cpDNA to test relationships. The most remarkable new hypothesis forwarded then no doubt was a close relationship between the uniovulate Chiocceaceae and multiovulate genera at that time placed in Cinchoneae or

Fig. 2. Robbrecht's (1988: fig. 8) analysis of the distribution of the two wood types in Rubiaceae, plotted on his Venn diagram of the tribes of the family. The occurrence of fibre-tracheids in some anomalous members of the Guettardeae is not indicated.

Condamineae–Portlandiinae. During recent years, much progress in the phylogenetic understanding of the Rubiaceae was made by the analysis of macromolecular data (entire family: Bremer 1996; Bremer et al. 1995, 1999; Manen & Natali 1996; Bremer & Thulin 1998; Rubioideae: Natali et al. 1996; Andersson & Rova 1999; Bremer & Manen 2000; Piesschaert et al. 2000b; Ixoroideae: Andreasen & Bremer 1996, 2000; Andreasen et al. 1999; Rova 1999; Cinchonoideae: Bremer & Thulin 1998; Rova 1999). The congruence between the results of all these authors using five different DNA sequences is remarkable, and three subfamilies obviously emanate: Rubioideae, Cinchonoideae s.str. and Ixoroideae s.l. These three subfamilies are also corroborated by phytochemical findings (Young et al. 1996). They are characterised by respectively anthraquinones, indole alkaloids and iridoids. We have manually constructed a hypothetical tree that summarises the relationships in all the above papers (Fig. 3) without conducting a new phylogenetic analysis. The intrafamilial classification according to Robbrecht (1988, 1994) is indicated in the same figure.

The subfamily Ixoroideae has been enlarged during recent years. This is partly due to the collapse of the former subfamily Antirheoideae. Vanguerieae, Retiniphyllaeae and Albertae that were previously included in that subfamily are now grouped in the core Ixoroideae. Molecular evidence is unanimous in placing Craterispermeae and Knoxieae in the Rubioideae; these two former Antirheoideae tribes morphologically deviated by heterostyly and raphides. The last three tribes of the Antirheoideae should be included in Cinchonoideae: the Guettardeae are close to the Rondeletiae, for the

Fig. 3. Subdivision of the Rubiaceae followed in this study; hypothetical tree mainly based on Bremer & Thulin (*rbcL*; 1998), Andersson & Rova (*rps16*-intron; 1999), Andreassen et al. (ITS, *rbcL*; 1999), Bremer et al. (*rbcL*, *ndhF*; 1999), Andreassen & Bremer (ITS, *rbcL*; 2000), Piesschaert et al. (*rps16*-intron; 2000a), Bremer & Manen (*rbcL*, *atpB-rbcL*, *rps16*-intron; 2000), and Dessein et al. (*rps16*-intron, *rbcL*; 2001a). The classification of Robbrecht (1994*) is indicated by the following abbreviations: ANT = Antirhoeidae, CIN = Cinchonoideae, IXO = Ixoroideae, RUB = Rubioideae, I.C. = Incertae sedis. *Largely corresponding to Robbrecht (1988) as depicted in Figure 2.

Table 1. Delimitation of the Rondeletieae and the former Condamineeae following Delprete (1999) and circumscription of the Rondeletieae according to Rova (1999); ¹⁾Simireae according to many authors; ²⁾Sipaneeae according to many authors; ³⁾Con.-Cal.-Hip.-Sim. = Condamineeae–Calycophylleae–Hippotideae–Simireae-complex; ? = wood type unknown. Tribal abbreviations follow Robbrecht (1994).

Rondeletieae sensu latissimo (Delprete 1999, with his informal groups)		Rova (1999)	Wood type
<i>Bathysa</i> group	<i>Bathysa</i> <i>Phitopsis</i>	Con.-Cal.-Hip.-Sim. ³⁾ Con.-Cal.-Hip.-Sim.	II ?
<i>Rondeletia</i> complex	<i>Rondeletia</i> and segregates	Ron. s.s.	I
<i>Mazaea</i> group	<i>Mazaea</i> (syn. <i>Ariadne</i> , <i>Neomazaea</i>), <i>Phyllomelia</i>	Ron. s.s.	I
<i>Augusta</i> group	<i>Augusta</i>	close to Gar./Pav.	I–II
<i>Simira</i> group ¹⁾	<i>Simira</i>	Sim.	II
<i>Sipanea</i> group ²⁾	<i>Limnosipanea</i> , <i>Sipanea</i> , <i>Steyrmarkia</i>	Sip.	(herbaceous)
Paleotropical genera	<i>Aleisanthia</i> , <i>Greenea</i>	close to Ixoreae	I (<i>Greenea</i>)
	<i>Glionnetia</i> , <i>Spathichlamys</i>	Ron.	?
	<i>Wendlandia</i>	close to Gar./Pav.	I
Former Condamineeae	<i>Molopanthera</i>	close to Hen.	?
	<i>Rustia</i> , <i>Tresanthera</i> , <i>Condaminea</i> , <i>Picardaea</i> , <i>Pogonopus</i> , <i>Chimarrhis</i> , <i>Dioicodendron</i> , <i>Dolichodelphys</i> , <i>Parachimarrhis</i>	Con.-Cal.-Hip.-Sim.	II (<i>Rustia</i> , <i>Condaminea</i> , <i>Picardaea</i> , <i>Pogonopus</i> , <i>Chimarrhis</i>)

Cephalanthae it was proved that they should return to their original position near the Naucleae, and the Chiococceae are a relative of the Catesbaeeae. The last hypothesis is in the line of what Bremer (1992) already postulated, because Delprete (1996) proved that the former Portlandiinae should be merged with Catesbaeeae.

The circumscription of the subfamily Cinchonoideae, on the other hand, is narrowed when compared to its delimitation by Robbrecht (1988, 1994). The tribes Sipaneeae, Calycophylleae, and Condamineeae are now transferred to the Ixoroideae s.l., but Cephalanthae and Chiococceae are included in Cinchonoideae. Note that all available evidence places the genus *Coptosapelta* in a basal position to the rest of the family. It is unfortunate that Bremekamp's monogeneric tribe Coptosapelteae has been emended to be used for one of the largest tribes of the Cinchonoideae s.str. (Andersson & Persson 1991). We exclude *Coptosapelta* and use the provisional designation "*Corynanthe* group" for Andersson's alliance.

In 1987, Rogers still complained about the unsettled state of the intrafamilial classification of the Rubiaceae. The recent work surveyed above now provides a comprehensive and phylogenetically strong framework. Nevertheless, there are still a few areas with major tribal delimitation problems, the major one no doubt the Rondeletieae

and former Condamineae. For these, conflicting, modern opinions exist (Table 1; Delprete 1999 versus Rova 1999), while the latter author also made provisional suggestions, such as a monophyletic Calycophylleae–Condamineae–Hippotideae–Simireae-complex. On our hypothetical tree (Fig. 3) we have kept these four tribes as a polytomy.

MATERIALS AND METHODS

The data in this paper are based on literature and original observations. The following taxa were not included in this study because they are entirely herbaceous: Cruckshanksiae, Knoxieae, *Mitchella*, Sipaneeae and Theligoneae.

The samples studied were from the wood collection of Tervuren (Belgium, Tw xyarium) or from the herbaria of BR, K, L, U, and MO. The diameter (in cm) of each wood sample is included for branch wood; the diameter of mature wood samples is unknown and not reported. Wood blocks were sectioned and macerated according to standard methods (Jansen et al. 1998). The specimens were studied with a light microscope (LM; Leica DMLB) and a scanning electron microscope (SEM; Jeol JSM-6400). Terminology follows the IAWA list (IAWA Committee 1989).

The species and specimens studied in our earlier contributions (Jansen et al. 1996, 1997a, b, 1999, 2001) are not repeated in this paper.

Alphabetical list of material studied:

- Aidia cochinchinensis* Lour., China Guandong, *Forest Research Institue 1648* (Tw 42125) – *A. micrantha* (K.Schum.) Bullock ex F. White, Congo (-Kinshasa), *C. Donis 2302* (Tw 32559)
Alberta humblotii Drake, Madagascar, Nonokambo à Varaissa, *M.G. Cours 2369* (BR) – *A. minor* Baill., Madagascar, Tananarive, Antiaratro, Manjakatampo, *G.E. Schatz et al. 1297* (BR)
Alibertia hadrantha Standl., Brazil, Amazonas, *B.A. Krukoff 5735* (Tw 34502) – *A. myrciifolia* K.Schum., Bolivia, Santa Cruz, *Nee 36968* (Tw 51275), 2.3 cm
Alseis smithii Standl., British Guyana, *A.C. Smith 3236* (Tw 27346)
Amaioua intermedia Mart. ex Schult. & Schult.f., Brazil, Matto-Grosso, *B.A. Krukoff 1431* (Tw 34674)
Aoranthie castaneofulva (S.Moore) Somers, Congo, *Wagemans 1748* (Tw 41262), 1.8 cm
Atractogyne gabonii Pierre, Congo (-Kinshasa), *J. Louis 5725* (Tw 35734), 1 cm
Aulacocalyx lujae De Wild., Congo, Kouilou, *R. Dechamps 13237* (Tw 49303), 1.7 cm – *A. pallens* subsp. *letestui* (Pellegr.) E.Figueiredo, Congo, Kouilou, *R. Dechamps 13225* (Tw 49293), 2 cm – *A. talbotii* (Wernham) Keay, Congo, Kouilou, *R. Dechamps 13216* (Tw 49335), 1.5 cm
Belonophora coriacea Hoyle, Congo, *J. Louis 5916* (Tw 35790), 1.5 cm – *B. coriacea* Hoyle, Congo, Bumba, Dundus, *Mortehan 760* (BR), 1 cm – *B. lepidopoda* (K.Schum.) Hutch. & Dalziel, Congo, Kasai, *R. Dechamps 617* (Tw 8528)
Bertia aethiopica Hiern, Congo, Kouilou, *R. Dechamps 13158* (Tw 49218), 1.5 cm – *B. racemosa* K.Schum. var. *elephantina* N.Hallé, Congo, Kouilou, *R. Dechamps 13104* (Tw 49136), 2.2 cm
Blepharidium mexicanum Standl., Mexico, *Curtis 495* (Tw 49393)
Bobea cf. *brevipes* A.Gray, Hawaii, *W. Stern 2975* (Tw 24144)
Bothriospora corymbosa (Benth.) Hook. f., Peru, *L. Lebacqz 1163* (Tw 16163)
Brenania brieyi (De Wild.) E.M.A.Petit, Cameroon, *C.T.F.T. 1620* (Tw 30897)
Calochone acuminata Keay, Congo, Kouilou, *R. Dechamps 13138* (Tw 49183), 0.5 cm
Calycophyllum candidum DC., Cuba, Topes de Colantes, Prov. Cienfuegos, *R. Dechamps & R. Carreras s.n.* (Tw 12188) – *C. multiflorum* Griseb., Argentina, Salta, *Adm. Mac. De Bosq. s.n.* (Tw 17817)
Calycosiphonia spathicalyx (K.Schum.) Robbr., Congo (-Kinshasa), forêt de Bululu, M'Vuazi, *J. Dubois 1* (BR)

- Canephora madagascariensis* J.F.Gmel., Madagascar, Majunga, L.J. Dorr et al. 3542 (Tw 46774)
- Capirona decorticans* Spruce, Venezuela, Amazonas, B. Maguire et al. 28613 (Tw 36294) – *C. decorticans* Spruce, Peru, Loreto, *Servicia Forestal* 1114 (Tw 25258)
- Carphalea kironadron* Baill., Madagascar, Nogent 8906 (Uw 15473)
- Casasia calophylla* A.Rich., Cuba, Pitardero, near Cayuco, R. Dechamps 12121 (Tw 48637), 2.2 cm
- Catunaregam spinosa* (Thunb.) Tirveng., India, Birla Institut Madhaya Pradesh s.n. (Tw 45205) – *C. spinosa* (Thunb.) Tirveng., Congo (-Kinshasa), Katanga, F. Malaisse 6970 (Tw 24242), 1 cm
- Chassalia bojeri* Bremek. var. *longifolia* Bremek., Madagascar, Province Majunga, Station forestière d'Ampijoroa, c. 3 km from d'Andranofasika, L.J. Dorr et al. 2984A (Tw 4471)
- Chimarrhis brevipes* Steyerl., Venezuela, Amazonas, B. Maguire et al. 27971 (Tw 36277) – *C. turbinata* DC., Surinam, Stahel 261 (Tw 25849)
- Chiococca alba* (L.) Hitchc., Cuba, Guisa, Prov. Gramma, R. Dechamps 12268 (Tw 48732), 1 cm
- Chione cubensis* A.Rich., Cuba, INDAF 61 (Tw 20761)
- Colleteocema dewevrei* (De Wild.) E.M.A.Petit, Congo (-Kinshasa), R. Dechamps 7 (Tw 8040)
- Coprosma lucida* J.R.Forst. & G.Forst., New Zealand, Lewalle s.n. (Tw 46635) – *C. montana* Hillebr., U.S.A., New Mexico, Santa Fé, S.H. Lamb s.n. (Tw 32040) – *C. ochracea* W.R.B.Oliv. var. *rockiana* W.R.B.Oliv., U.S.A., Hawaii, S.H. Lamb 21 (Tw 35950) – *C. pubens* A.Gray, U.S.A., Hawaii, W. Stern 2977 (Tw 24145), 2 cm – *C. rhynchocarpa* A.Gray, Hawaii, Curtis s.n. (Tw 43920)
- Coptosapelta olaciformis* (Merr.) Elmer, Philippines, Sungao, C.A. Wenzel 2719 (BR), 6 mm
- Corynanthe pachyeras* K.Schum., Ivory Coast, P. Détienne 18 (Tw 29860)
- Cosmibuena grandiflora* (Ruiz & Pav.) Rusby, Colombia, J. Cuatrecasas 15287 (Tw 39418)
- Crossopteryx febrifuga* (Afzel. ex G.Don) Benth., Congo (-Kinshasa), Ghesquiere s.n. (Tw 666)
- Crucianella maritima* L., Portugal, Algarve, Aguiar, R. Dechamps 7240 (Tw 43547), 0.5 cm
- Danais cernua* Baker, Madagascar, Toliara, B. Randriamampionona 15 (MO), 6 mm – *D. pubescens* Baker, Madagascar, Antannanarivo, L.J. Dorr et al. 3618 (Tw 46785), 0.7 cm – *D. xanthorrhoea* (K.Schum.) Bremek., Scheffer 195 (BR)
- Dendrospanea revoluta* Steyerl., Venezuela, Amazonas, B. Maguire et al. 41665 (Tw 36217), 0.8 cm
- Dialypetalanthus fuscescens* Kuhlm., Brazil, São Lourenço, 14 km Rio Madeira, above Matuparaná, Amazonas, G. Prance 8967 (Uw 23666); Bolivia, Beni, W.R. Anderson 11865 (Uw 26787), 2.5 cm
- Didymosalpinx lanciloba* (S.Moore) Keay, Congo (-Kinshasa), Haut-Congo, J. Louis 3926 (Tw 35549)
- Diodia scandens* Sw., Congo (-Kinshasa), Cuvette, J. Louis 1916 (Tw 33319), 0.6 cm
- Drosera trilocularis* (Balf. f.) Verdc., Rodrigues, Solitude, Tirvengadam 908 (K), 0.5 cm
- Duroia aquatica* (Aubl.) Bremek., French Guyana, Bus. For. Guya. 290 (Tw 22174) – *D. petiolaris* Spruce ex K.Schum., Brazil, Amazonas, B.A. Krukoff 6699 (Tw 38639)
- Elaeagia utilis* (Goudot) Wedd., Colombia, J. Cuatrecasas 21651 (Tw 39791)
- Erithalis odorifera* Jacq., Antilles Françaises, Guadeloupe, Rollet, CTFT 1149 (Tw 47650)
- Euclinia longiflora* Salisb., Congo (-Kinshasa), J. Louis 6452 (Tw 38297), 0.8 cm
- Exostema mexicanum* A.Gray, Mexico, Campeche, INIF 165 (Tw 19185)
- Ferdinandusa chlorantha* (Wedd.) Standl., Peru, L. Lebacqz 295 (Tw 16295) – *F. hirsuta* Standl., Brazil, Amapa, B. Maguire et al. 51968 (Tw 37554)
- Feretia aeruginescens* Stapf, Congo (-Kinshasa), Kasapa, F. Malaisse 7996 (BR), 1 cm – *F. apodanthera* Delile, Senegal, Sasamance, J. De Wolf 5 (Tw 52597)
- Gardenia erubescens* Stapf & Hutch., Senegal Kolda, J. De Wolf s.n. (Tw 51568), 2 cm – *G. lucida* Roxb., India Madhya Pradesh, Brila Institute Scientific Research s.n. (Tw 45503) – *G. ternifolia* Schumach. & Thonn. subsp. *goetzei* (Stapf & Hutch.) Verdc., Senegal Thies, A. Mariaux 1282 (Tw 41467) – *G. ternifolia* Schumach. & Thonn. subsp. *jovis-tonantis* (Welw.) Verdc., Angola, R. Dechamps 1030 (Tw 28646) – *G. tubifera* Wall. ex Roxb., Congo (-Kinshasa), L. Meijer 59123 (Tw 18688)
- Genipa americana* L., Surinam, Stahel 379 (Tw 25580)
- Gleasonia duidana* Standl. var. *duidana*, Venezuela, Amazonas, B. Maguire et al. 27564 (Tw 36493)
- Gonzalagunia rosea* Standl., Panama, Calón, M. Nee 7088 (Tw 43021), 1.6 cm
- Gouldia terminalis* (Hook. & Arn.) Hillebr., Hawaii, A.B. Curtis H. 26 (Tw 26785)
- Guettarda scabra* (L.) Lam., Antilles Françaises, Guadeloupe, Beraud 1 (Tw 42429)
- Gyrostipula foveolata* (Capuron) J.-F.Leroy, Grande Comore, C.T.F.T. France Essai 386 (Tw 30834)

- Hamelia axillaris* Sw., Cuba, between Baracoa and Maisi, *R. Dechamps* 12065 (Tw 48189), 0.9 cm – *H. axillaris* Sw., Cuba, Santiago de Cuba, Gran Piedra, *R. Dechamps et al.* 12359b (Tw 49828), 1.6 cm – *H. patens* Jacq., Brazil, Amazonas, *B.A. Krukoff* 5119 (Tw 34221); Florida, *Forest Products Research Laboratory* 12802 (Uw 17765) – *H. ventricosa* Sw., Jamaica, *U.S. National Herb. Smithson. Inst.* 6017 (Uw 8356)
- Heinsia crinita* (Afzel.) G.Taylor, Congo(-Kinshasa), *J. Louis* 515 (Tw 32872), 2.4 cm; Congo(-Kinshasa), Milambo, *J. Claessens* 238 (BR), 0.6 cm
- Hillia parasitica* Jacq., Cuba, Granna, *R. Dechamps* 12414 (Tw 49892), 1 cm
- Holtonia myriantha* (Standl.) Standl., Colombia, *J. Cuatrecasas* 21625 (Tw 21625)
- Hymenodictyon floribundum* (Hochst. & Steud.) Rob., Congo(-Kinshasa), Katanga, *Malaisse* 6916b (Tw 23980) – *H. orixense* (Roxb.) Mabb., Thailand, *Royal For. Depart. s.n.* (Tw 18549)
- Hypobathrum* sp., Indonesia, *Van Balgooy & Van Setten* 5466 (Uw 31825), 2.8 cm
- Isertia hypoleuca* Benth., British Guyana, *A.C. Smith* 2517 (Tw 27353)
- Kutchubaea neblinensis* Steyerl., Venezuela, Amazonas, *B. Maguire et al.* 42084 (Tw 36604) – *K. sericantha* Standl., Venezuela, Amazonas, *B. Maguire et al.* 27882 (Tw 36283)
- Ladenbergia lambertiana* (A.Br. ex Mart.) Klotzsch, Venezuela, Amazonas, *B. Maguire et al.* 43668 (Tw 37044) – *L. spec.*, Peru, Huanuco, *TM* 74 (Tw 20135)
- Lamprothamnus zanguebaricus* Hiern, Tanzania, Dar es Salaam to Morogoro, *Welch* 387 (BR), 0.6 cm
- Lindenia rivalis* Benth., Mexico, *Hansen & Nee* 1544 (Tw 29425), 1.8 cm
- Macbrideina peruviana* Standl., Peru, Huanuco, *Servicio Forestal TM-49* (Tw 25260)
- Macrocnemum roseum* (Ruiz & Pav.) Wedd., Panama, Canal Zone, *M. Nee* 9417 (Tw 43118)
- Malanea gabrielensis* Müll.Arg., Venezuela, Amazonas, *B. Maguire et al.* 42888 (Tw 36935), 1 cm
- Massularia acuminata* (G.Don) Bullock ex Hoyle, Congo(-Kinshasa), Kasai, *R. Dechamps* 32 (Tw 8294)
- Mastixiodendron pachyclados* (K.Schum.) Melch., New Guinea, *Gov. For. Exp. St.* 11586 (Tw 31087) – *M. stoddardii* Merr. & L.M.Perry, Papua, Garo Garo, *Department of Forest s.n.* (Tw 22916)
- Mitragyna inermis* (Willd.) Kuntze, Cameroon, Fort-Lamy (Njamena), *J. Jangoux* 10020 (BR)
- Morelia* sp., Congo(-Kinshasa), *C. Donis* 2091 (Tw 32432)
- Mussaenda arcuata* Poir., Angola, Benguela, *R. Dechamps* 1065 (Tw 28290) – *M. elegans* Schumacher & Thonn., Congo(-Kinshasa), *Wagemans* 2388 (Tw 41358), 2.5 cm
- Oldenlandia filifolia* K.Krause, country unknown, Bos van Tabora, *V. Trotha* 61 (Uw 25954)
- Oxyanthus speciosus* DC. subsp. *speciosus*, Congo(-Kinshasa), Luzina, *J. Lebrun* 5410 (Tw 2512) – *O. unilocularis* Hiern, Ivory Coast, *P. Bamps* 2334 (Tw 22972)
- Pagameopsis maguirei* Steyerl. subsp. *neblinensis* var. *angustifolius* Steyerl., Venezuela, T.F. Amazonas, Cerro de la Neblina, *Maguire et al.* 42129 (Tw 36619)
- Palicourea alpina* (Sw.) DC., Cuba, Granna, Pico Turquino, *R. Dechamps* 12424 (Tw 49893), 2.2 cm – *P. crocea* (Sw.) Schult., Venezuela, Amazonas, *collector unknown* (Tw 38180)
- Pauridiantha dewevrei* (De Wild. & T.Durand) Bremek., Congo(-Kinshasa), Haut-Congo, *J. Louis* 2333 (Tw 33436)
- Pausinystalia lane-poolei* (Hutch.) Hutch. ex Lane-Poole, Liberia, Bassa, *L. Cooper* 278 (Tw 10397) – *P. talbotii* Wernham, Congo(-Kinshasa), *J. Louis* 2929 (Tw 34901), 1.8 cm
- Pentagonia macrophylla* Benth., Panama, Canal Zone, 6 km west of Gamboa, *M. Nee* 7206 (Tw 43043)
- Pentanopsis fragrans* Rendle, origin unknown, *C. Puff C.* 821227-1/4 (Uw 30887)
- Pentas lanceolata* (Forssk.) Defflers, origin unknown, *J. Lebrun* 8151 (BR), 0.4 cm – *P. nobilis* S.Moore, Tanzania, Chunya, Mbagala, *S. Bidgood et al.* 2275 (BR) – *P. schimperiana* (A.Rich.) Vatke, Congo(-Kinshasa), *J. Louis* 4877 (Tw 35658), 1.3 cm; Kivu, Goma-Sake, *D. Van der Ben* 97 (BR); Ethiopia, Menagesha State Forest, *C. Puff* 810920-1/2 (Uw 27081)
- Placopoda virgata* Balf. f., Socotra, *Schweinfurth* 43 (Uw 25955)
- Platycarpum orinocense* Humb. & Bonpl. var. *orinocense*, Venezuela, Amazonas, *B. Maguire et al.* 41463 (Tw 36710)
- Polysphaeria pedunculata* K.Schum. ex De Wild., Congo(-Kinshasa), Katanga, *F. Malaisse* 9605 (Tw 35156)
- Porterandia cladantha* Keay, Congo(-Kinshasa), *J. Louis* 2840 (Tw 34842), 2.1 cm

- Posoqueria latifolia* (Rudge) Schult., Venezuela, Amazonas, *B. Maguire et al.* 28958 (Tw 36271) – *P. longiflora* (Rudge) Schult., Venezuela, Amazonas, *Maguire et al.* 43611 (Tw 36965)
- Psychotria* sp., Brazil, Matto-Grosso, *B.A. Krukoff* 1512 (Tw 33914) – *P. brachiata* Sw., Cuba, Gramma, *R. Dechamps* 12432 (Tw 49906), 20 mm – *P. cotejensis* (Standl.) J.H.Kirkbr., Columbia, Prov. Choco, *Cuatrecasas* 17208 (Uw 25330) – *P. greenwelliae* Fosberg, Hawaii, *W.L. Stern s.n.* (Uw 10431) – *P. nuda* (Cham. & Schldt.) Wawra, Brazil, *Clausen* 64 (Uw 25972) – *P. peduncularis* (Salisb.) Steyerl., Yaunde, *Zenker* 788 (Uw 25973)
- Randia* sp., Brazil, Parana, *Lindeman & De Haas* 1082 (Tw 35235)
- Remijia papapoensis* Steyerl., Venezuela, Amazonas, *B. Maguire et al.* 28013 (Tw 36346)
- Retiniphyllum laxiflorum* (Benth.) M.E.Br., Venezuela, Amazonas, *B. Maguire et al.* 42229 (Tw 36424) – *R. pauciflorum* Kunth ex K.Krause, Venezuela, Amazonas, *B. Maguire et al.* 41892 (Tw 36476), 2 cm
- Rondeletia parviflora* Poir., French Antilles, Guadeloupe, *Rollet, C.T.F.T.* 1164 (Tw 47657)
- Rothmannia liebrechtsiana* (De Wild. & T.Durand) Keay, Congo (-Kinshasa), *C. Donis* 2300 (Tw 32557) – *R. longiflora* Salisb., Congo (-Kinshasa), *C. Donis* 2075 (Tw 32410), 2.8 cm
- Rubia fruticosa* Aiton, Canary Islands, Lanzarote, *Lindeman* 7117 (Uw 30436), 2 cm
- Rudgea cornigera* Bremek., Surinam, *Lindeman* 4582 (Uw 3177), 3 cm – *R. hostmanniana* Benth. subsp. *hostmanniana*, *Maas et al.* *M* 5884 (Uw 27401), 1.5 cm – *R. lanceolata* (Cham.) Benth., *Lindeman & De Haas* 2036 (Uw 13472), 0.9 cm; origin & collector unknown (Uw 13605)
- Sabicea calycina* Benth., Congo (-Kinshasa), Kouilou, *R. Dechamps* 13043 (Tw 49031) – *S. villosa* Roem. & Schult., Panama, Navy Reservation, North of Gamboa, *A. Robyns* 65-49 (BR)
- Saprosma foetens* (Wight) K.Schum. subsp. *ceylanicum* (Gardner) M.G.Gangop. & Chakrab., India, Cardamom Hills, *C.E. Ridsdale* 175 (L)
- Schradera brevipes* Steyerl., Venezuela, Amazonas, *Maguire et al.* 27895 (holotype) (Tw 36563) – *S. hillifolia* Steyerl., Venezuela, Amazonas, *Maguire et al.* 43316 (Tw 36978), 1.3 cm
- Schumanniphyton hirsutum* (Hiern) Good, Congo (-Kinshasa), *C. Donis* 2116 (Tw 32450) – *S. magnificum* (K.Schum.) Harms, Congo (-Kinshasa), *R. Dechamps* 8047 (Tw 40372)
- Sericanthe leonardii* (N.Hallé) Robbr. subsp. *venosa* Robbr., Rwanda, *P. Auquier* 3531 (Tw 28730)
- Sherbournia bignoniifolia* (Welw.) Hua, Congo (-Kinshasa), *Schikawa et al.* 281 (Tw 45434), 0.5 cm
- Simira rubescens* (Benth.) Bremek. ex Steyerl., Brazil, *B.A. Krukoff* 5436 (Tw 34358) – *S. tinctoria* Aubl., Peru, Loreto, Lower Huallaga, *L. Williams* 4132 (Tw 46699)
- Spermacece* ["*Borreria macrocephala* Standl. & Steyerl."], Venezuela, Amazonas, *B. Maguire et al.* 41668 (Tw 36238), 0.7 cm – *S. suaveolens* (G.Mey.) Kuntze, Venezuela, Amazonas, *B. Maguire et al.* 42698 (Tw 36671), 2 cm – *S. verticillata* L., Morro do Chapen-Bonito, km 12, *Cavalcanti et al.* 358 (Uw 33690)
- Spermadictyon suaveolens* Roxb., India, Mussoorie, *Van Steenis* 21125 (Uw 20406)
- Stachyarrhena acuminata* Standl., Brazil, Amapa, collector unknown (Tw 37873)
- Stenostomum bifurcatum* Griseb., Jamaica, *R.B. Miller s.n.* (Tw 29241)
- Tarenna laurentii* (De Wild.) J.G.Garcia, Congo (-Kinshasa), *J. Louis* 1546 (Tw 33224), 1.5 cm
- Timonius* sp., Indonesia, Service Forest. 12465 (Tw 23795)
- Tocoyena foetida* Poepp. & Endl., Bolivia, Santa Cruz, *Nee* 37033 (Tw 51279), 2.5 cm; Peru, *L. Lebacqz* 1302 (Tw 16302) – *T. pittieri* (Standl.) Standl., Colombia, *J. Cuatrecasas* 17264 (Tw 39617) – *T. williamsii* Standl., Peru, *L. Lebacqz s.n.* (Tw 16034)
- Tricalysia coriacea* (Benth.) Hiern, East Africa, *Schlieben & Reinbek* 1509 (Uw 15491) – *T. crepiniana* De Wild. & T.Durand, Congo (-Kinshasa), Cuvette Centrale, *J. Louis* 2092 (Tw 33384) – *T. elliotii* (K.Schum.) Hutch. & Dalziel, Congo (-Kinshasa), *C. Donis* 2019 (Tw 32381) – *T. pallens* Hiern, Congo (-Kinshasa), *J. Louis* 1420 (Tw 33157), 2.7 cm; Congo (-Kinshasa), Katanga, *F. Malaisse* 9662 (Tw 35130)
- Uncaria africana* G.Don. var. *xerophila* E.M.A.Petit, Congo (-Kinshasa), *J. Louis* 6105 (Tw 35857), 1 cm – *U. donisii* E.M.A.Petit, Congo (-Kinshasa), *C. Donis* 1968 (Tw 32399), 2.3 cm
- Warszewiczia coccinea* (Vahl) Klotzsch, Venezuela, Amazonas, *B. Maguire et al.* 28072 (Tw 36306)
- Wendlandia amocana* Cowan, Pakistan, *Majumdar & Islam* 107 (Tw 25264)
- Wiegmannia* sp., Hawaii, Kauai, Maryland, *Stern & Herbst* 524 (Uw 18607), 1 cm

General description of the wood anatomy of the Rubiaceae

This section summarises briefly all wood anatomical features of the family.

Growth rings

Growth rings are usually present, but often indistinct. An examination of the Tw wood sections showed distinct growth rings in circa 25% of the samples investigated (Beeckman & Jansen 1995). They are formed by changes in fibre walls as well as by differences in the vessel density, vessel diameter and/or marginal parenchyma (Fig. 5, 34).

Vessels

Porosity – The wood is nearly always diffuse-porous, only occasionally (semi-) ring-porous.

Vessel arrangement – Vessels are usually arranged in a weak radial pattern. Vessels are often in irregular tangential chains or broken concentric bands in representatives of the tribe Henriquezieae (especially *Platycarpum*), and in tangential or diagonal chains in *Genipa*, *Ladenbergia*, *Placopoda* (Fig. 34), *Rubia*, and *Triainolepis*.

Vessel groupings – Vessels are most frequently solitary with radial multiples of 2–3 vessels. In some genera they are exclusively solitary or nearly so (Fig. 16–21, 30, 31). In other genera the vessels are mainly in short radial multiples of 2–4 or with multiples in more than 4 cells (Fig. 11, 22–24, 35).

Solitary vessel outline – Vessel outline is circular or oval (e.g. Fig. 17), but also angular in numerous taxa (e.g. Fig. 23).

Perforation plates – Simple perforation plates are the most common type (Fig. 45, 46); reticular, scalariform or malformed plates are occasionally present in most groups of the family. Scalariform perforation plates are common in few representatives of *Chazaliella*, *Coprosma* (Fig. 37), *Crucianella* (Fig. 40), and *Trichostachys*. In some genera more than one perforation is found in a single perforation plate.

Intervessel pits – They are generally alternate, sometimes polygonal (e.g. *Cous-sarea*), minute ($\leq 4\ \mu\text{m}$) or small (4–7 μm), and only rarely more than 7 μm (Fig. 41).

Vestured pits – Vestures are constantly present, but sometimes difficult to determine by LM (Fig. 41, 42, 44). In few species, vestured pits are restricted to pits of small tracheary elements or fibre pits, so that non-vestured pits can be found in wider vessels (e.g. Fig. 43).

Vessel-ray pitting – They most frequently show distinct pit borders and are similar to intervessel pits in size and shape throughout the ray cell. Genera in which vessel-ray pitting shows reduced pit borders to simple pits are found in *Belonophora*, *Calycophyllum*, *Ferdinandusa*, *Galiniera*, *Hamiltonia*, *Joosia*, *Platycarpum*, *Psychotria*, *Rutidea*, *Schradera*, and *Spermadictyon*.

Helical thickenings – Helical thickenings in tracheary elements are reported in only few genera: *Anthospermum*, *Coprosma*, *Emmenopterys*, *Genipa*, and *Rubia*.

Tangential diameter of vessel lumina – Vessels are typically narrow (50–100 μm) or very narrow ($< 50\ \mu\text{m}$; Fig. 15, 30), but medium-sized (100–200 μm) in some genera (especially large trees and vines), and rarely very wide ($> 200\ \mu\text{m}$ in Henriquezieae and *Paederia*).

Fig. 4–10. Transverse (4–9) and tangential (10) wood sections of Cinchonoideae s.l. – 4: Vessels mainly solitary and axial parenchyma diffuse in *Wendlandia amocana*. – 5: Semi-ring-porous wood and indistinct growth rings in *Chiococca alba*. – 6: *Stenostomum bifurcatum*. – 7: Solitary vessels and axial parenchyma bands in *Malanea gabrielensis*. – 8: Wood type II in *Stenostomum bifurcatum*. – 9: *Hamelia axillaris* (Tw 48189) with wood type II. – 10: Low, uniseriate rays in *Platycarpum orinocense*. — Scale bar = 200 μm in Fig. 4–7; 100 μm in Fig. 8–10.

Fig. 11–15. Transverse (11, 12, 15), tangential (14) and radial (13) wood sections of Ixoroideae s.l. with wood type II. – 11: Vessels in short radial multiples and absence of axial parenchyma in *Simira rubescens*. – 12: Axial parenchyma rarely paratracheal (arrow) in *Mastixiodendron pachyclados*. – 13: Septate (arrows) libriform fibres in *Chimarrhis brevipes*. – 14: High, multiseriate rays with sheath cells in *Elaeagia utilis*. – 15: *Heinsia crinita* with thin-walled fibres. — Scale bar = 200 μm in Fig. 11, 15; 100 μm in Fig. 12–14.

Vessels per square millimetre – The vessel density varies from numerous (40–100 vessels/mm) to very numerous (> 100 vessels/mm). Occasionally less than 40 vessels/mm are found.

Mean vessel element length – Vessel elements are usually of medium length (350–800 μm), but sometimes very long (> 800 μm).

Tyloses and deposits in vessels – Tyloses are generally wanting, but they are found in several genera. Gum deposits are common to abundant.

(text continued on page 23)

Fig. 16–22. Transverse wood sections of core Ixoroideae (16–21) and *Posoqueria* (22). – 16: Axial parenchyma bands and solitary vessels in *Retiniphyllum pauciflorum*. – 17: Solitary, wide vessels in *Aoranthé castaneofulva*. – 18: Wood type I in *Alberta humblotii*. – 19: Wood type I in *Massularia acuminata*. – 20: Wood type I in *Aidia cochinchinensis*. – 21: *Duroia aquatica* with axial parenchyma in narrow lines or bands up to 3 cells wide. – 22: Vessels mainly in short radial multiples in *Posoqueria longiflora*. — Scale bar = 100 μm in Fig. 16, 18, 22; 200 μm in Fig. 17, 19–21.

Fig. 23–29. Transverse (23, 24, 27–29) and tangential (25, 26) wood sections of Rubioideae. – 23: Wood type II in *Psychotria cotejensis*. – 24: Wood type II in *Psychotria chionantha*. – 25: Septate (arrows) fibres and 1–2-seriate rays in *Rudgea lanceolata*. – 26: Uniseriate and multiseriate rays in *Psychotria green-welliae*. – 27: Scanty paratracheal parenchyma in *Schradera brevipes*. – 28: Axial parenchyma bands and solitary vessels in *Collettoecema dewevrei*. – 29: Solitary vessels and scanty paratracheal parenchyma in *Pagameopsis maguirei*. — Scale bar = 100 μ m in Fig. 23, 25, 27–29; 200 μ m in Fig. 24, 26.

Fig. 30–34. Transverse (30, 31, 33, 34) and tangential (32) wood sections of Rubioideae. – 30: *Spermacoce verticillata*. – 31: *Pentas schimperiana*. – 32. Fibre-tracheids with bordered pits at left, vessel elements and fibriform vessel elements or tracheids at right in *Spermacoce verticillata*. – 33: Diffuse axial parenchyma in *Oldenlandia filifolia*. – 34: Growth rings and radial/tangential vessel arrangement in *Placopoda virgata*. — Scale bar = 100 μ m in Fig. 30, 31, 33; 50 μ m in Fig. 32; 200 μ m in Fig. 34.

Fig. 35–40. Transverse (35, 36, 39) and longitudinal (37, 38, 40) wood sections of Anthospermeae and Rubieae (Rubioidae). – 35: *Coprosma rhynchocarpa*. – 36: Vessels in clusters or radial multiples in *Coprosma ochracea*. – 37: Scalariform perforation plates in *Coprosma ochracea*. – 38: Detail of septate libriform fibres in *Coprosma ochracea*. – 39: Radial/tangential vessel arrangement and paratracheal parenchyma in *Rubia fruticosa*. – 40: Scalariform perforation plate in *Crucianella maritima*. — Scale bar = 200 µm in Fig. 35; 100 µm in Fig. 36, 37, 39; 10 µm in Fig. 38, 40.

Tracheids and fibres

Vascular/vasicentric tracheids – Tracheids are present in numerous genera.

Ground tissue fibres – Fibres show simple, minutely ($< 3 \mu\text{m}$) to distinctly ($\geq 3 \mu\text{m}$) bordered pits (e.g. Fig. 32).

Septate fibres – They are present in about 25% of the genera (Fig. 13, 25, 38) and mainly restricted to the following tribes: Argostemmatae, Calycophylleae, Condamineae, Coussareae, Hamelieae, Hillieae, Hippotideae, Mussaendeae, Paederieae, Psychotrieae, and Simireae. The feature is also present in *Damnacanthus* and a few genera of the Anthospermeae and Guettardeae.

Fibre wall thickness – Fibres are generally thin- to thick-walled. Very thick-walled fibres (fibre lumina almost completely closed) occur in *Bothriospora*, *Mitragyna*, *Henriquezieae*, and *Pertusadina*.

Mean fibre lengths – Fibres are usually of medium length (900–1600 μm), but sometimes much shorter ($< 900 \mu\text{m}$) or longer ($> 1600 \mu\text{m}$).

Axial parenchyma

Axial parenchyma absent or extremely rare – Absence of axial parenchyma is characteristic of species with septate fibres, although there are few exceptions (Fig. 6, 8, 9, 23, 24).

Apotracheal axial parenchyma – The apotracheal parenchyma is usually present as diffuse or diffuse-in-aggregates, with tendencies to form short uniseriate lines (Fig. 4, 20, 33).

Paratracheal axial parenchyma – Scanty paratracheal parenchyma is present in few genera with either septate or non-septate fibres (Fig. 12, 27, 29, 36, 39). Aliform and confluent parenchyma is reported in *Henriquezieae*, and only occasionally in *Jackiopsis*, *Retiniphyllum*, and *Timonius*.

Banded parenchyma – This parenchyma type is uncommon in Rubiaceae but present in *Colletocema* (Fig. 28), *Craterispermeae*, *Gaertnereae*, *Ixoreae*, *Retiniphyllae* (Fig. 16), *Schradera*, several representatives of the *Morindeae*, the *Alibertia* group (*Gardenieae*, Fig. 21), and few *Guettardeae* (*Bobea*, *Malanea*; Fig. 7, *Timonius*).

Axial parenchyma cell type/strand length – Axial parenchyma strands are most commonly composed of 8 cells or more, sometimes of 4 cells. Short parenchyma strands are reported in *Paederieae* and *Anthospermeae*.

Rays

Ray width – Generally narrow, up to 2–3-seriate and with long uniseriate margins. Exclusively uniseriate or with only occasional biseriate parts in several genera (Fig. 10) and up to 8–10 cells wide in *Capirona*, *Chimarrhis*, *Coprosma*, *Coussarea*, *Elaea-*

Fig. 41–47. SEM-photographs (41–45, 47) and LM-photograph (46) of Rubiaceae. – 41: Vestured outer pit apertures of vessel element in *Macbrideina peruviana*. – 42: Vestured inner pit apertures of vessel element in *Gardenia tubifera*. – 43: Non-vestured outer pit apertures of vessel element in *Psychotria brachiata*. – 44: Vestures near outer pit aperture of vessel element in *Aulacocalyx tal-botii*. – 45: Simple perforation plates in *Psychotria spec.* – 46: Two simple vessel perforations in *Psychotria nuda*. – 47: Perforated ray cell (star) and two vessel elements (indicated by round stars) in *Chassalia bojeri*. — Scale bar = 3 μm in Fig. 41, 42, 43; 10 μm in Fig. 44; 100 μm in Fig. 45, 47; 50 μm in Fig. 46.

gia (Fig. 14), *Faramaea*, *Paederia*, *Saprosma*, and *Schradera*. Vertically fused rays are very common.

Aggregate rays – Aggregate rays are only reported in *Paederia*.

Ray height – Rays are usually very high, more than 1 mm and often joined vertically. Rays much lower than 1 mm occur in *Henriquezieae*, *Rubieae*, and representatives of *Anthospermeae* and *Paederieae*.

Rays of two distinct sizes – Rays are frequently of 2 distinct sizes (uniseriate and multiseriate) or appearing so due to the numerous uniseriate rays or long uniseriate margins of the multiseriate rays (Fig. 26).

Cellular composition of rays – Heterogeneous rays are most common, with high ray margins of upright/square cells. Rays entirely composed of upright/square cells or rays with only 1 or 2 marginal rows of upright/square cells are also widespread. They correspond with Kribs' heterogeneous ray types I, II and III. Rays that are 4 or more cells wide are usually less markedly heterogeneous: the greater part of the ray is composed of procumbent cells and generally with less than 4 marginal rows of square to upright cells.

Sheath cells – These cells are common in rays that are ≥ 4 cells wide. Upright ray cells form a complete to incomplete sheath around the procumbent cells of the multiseriate rays (Fig. 14).

Tile cells – Tile cells are lacking.

Perforated ray cells – Vessel-ray perforations are widespread in the family (Fig. 47). The perforations are simple, scalariform, reticulate or irregular, and sometimes vested.

Disjunctive ray parenchyma cell walls – Disjunctive elements are common in several tribes of the family, especially in the tribes *Gardenieae*, *Coffeeae* and *Pavetteae*.

Rays per millimetre – In about 70% of the genera there are more than 12 rays per mm. They frequently make up a very appreciable volume of the wood. Sometimes 20 or more rays per mm occur.

Storied structure

Storied structure is only reported in *Galium* (Rubieae) in which secondary woodiness is most likely.

Secretory elements and cambial variants

Secretory elements are lacking in the family. Cambial variants, in particular axes with furrowed or lobed xylem, are only reported in *Atractogyne* and *Chiococca*.

Fig. 48–56. Mineral inclusions in Rubiaceae. – 48: Crystal sand in ray cell in *Malanea gabrielensis*. – 49: Crystal sand in ray cell in *Simira rubescens*. – 50: Prismatic crystals in ray cells in *Aulacocalyx lujae*. – 51: Druse in pith parenchyma cell in *Doricera trilocularis*. – 52: Detail of twin raphides with dovetailed ends in *Cosmibuena grandiflora*. – 53: Raphides in pith parenchyma in *Pauridiantha dewevrei*. – 54: Elongate crystals in ray cells in *Rondeletia parviflora*. – 55: Silica bodies in ray cells in *Platycarpum orinocense*. – 56: Small mineral inclusions in ray cells (possibly silica bodies) in *Posoqueria latifolia*. — Scale bar = 10 μm in Fig. 48, 49, 52; 20 μm in Fig. 50, 51, 53; 30 μm in Fig. 56; 50 μm in Fig. 54; 100 μm in Fig. 55.

Mineral inclusions

Raphides – Bundles of needle-shaped crystals are frequently found in representatives of the Rubioideae (Fig. 53), but also in the Hillieae and Hamelieae (Cinchonoideae, Fig. 52). They occur in axial parenchyma or ray parenchyma, sometimes in elongated sacs.

Prismatic crystals – Solitary and prismatic crystals having an octahedral or rhombic shape are abundantly present in ray cells of the Coffeeae, Gardenieae (Fig. 50) and Octotropideae. They are most frequently found in upright/square ray cells. Prismatic crystals also occur in chambered axial parenchyma cells of *Homollea*, *Nichallea*, *Oldenlandia*, *Rondeletia* (Fig. 54), *Tarenna*, and *Timonius*.

Druses – Druses are not found in secondary xylem, but they are abundantly present in pith parenchyma, secondary phloem or leaf tissues of several taxa (Fig. 51).

Styloids – This crystal type is rare in the Rubiaceae. Styloids are observed in *Captaincookia*, *Cosmocalyx*, *Ixora*, *Versteegia* and a single species of *Morinda*.

Crystal sand – Crystal sand is common in parenchyma cells (mostly ray cells) of numerous Ixoroideae s.l. (Hippotideae, Calycophylleae, Simireae: Fig. 49, Condamineae, Mussaendeae) and to a lesser extent in wood of the Cinchonoideae (Cinchoneae, Chiococceae, Guettardeae: Fig. 48, Naucleaeae).

Silica – Silica bodies are only reported in the genera *Hallea*, *Henriquezia*, *Mitragyna*, and *Platycarpum* (Fig. 55). The inclusions in *Posoqueria latifolia* (Fig. 56) are suggested to be small silica bodies, but verification is needed.

Wood types

Based on a series of wood anatomical studies in the 1970s, Koek-Noorman (1977) concluded that there are two main types of secondary xylem in the Rubiaceae. Earlier findings of Koek-Noorman and Hogeweg (1974) and Hogeweg and Koek-Noorman (1975) not only stressed the taxonomic significance of fibre type differences (definitions following Reinders 1935), but also, on the basis of numerical analyses, pointed to a strong correlation between fibre type and other wood anatomical features within the Rubiaceae. The character complexes she distinguished were categorised in type I showing fibre-tracheids, while libriform fibres characterise type II. The distinction between the two types is given in Table 2.

Table 2. Rubiaceaceous wood types. See text for further explanation.

Type I	Type II
Fibre-tracheids	Septate libriform fibres
Axial parenchyma apotracheal: diffuse, diffuse-in-aggregates or banded	Axial parenchyma absent or scanty paratracheal
Vessels mainly solitary	Vessels in short radial multiples (2–4 or more) and solitary
Narrow rays with long uniseriate margins	Rays wider, with few rows of upright/ square ray cells

We support the taxonomic significance of these two wood types because the distribution is largely in accordance with recent phylogenetic hypotheses of the family. However, exceptions to the general homogeneity at the generic and tribal level occur, for instance in the tribe Guettardeae in Robbrecht's (1988, 1994) delimitation. *Coprosma* is also very heterogeneous with respect to its wood anatomy. Carlquist (1992) even suggested that the diversity within this single genus contradicts the frequently cited homogeneity of the rubiaceous wood structure. We suggest that the wood anatomical variation in *Coprosma* can be explained by pedomorphic features and environmental influences (see below). The combination of the two wood types in one genus or tribe indeed puts doubt on the taxonomic delimitation of the group or raises the question whether the material studied is correctly identified. However, environmental considerations and geographical distribution should also be taken into account when interpreting the anatomical variation of the wood. Hence, variation in quantitative features or the distribution of axial parenchyma can in some instances be explained by environmental influences or habit (e.g. lianescent habit in *Schradera*, *Morinda*, *Paederia*).

Wood anatomy and the classification of the Rubiaceae

This section summarises the taxonomic distribution of wood features in the Rubiaceae (Tables 3–6; Fig. 57–65) and discusses the wood anatomical variation with reference to systematic coherence and affinities of tribes and genera.

SUBFAMILY CINCHONOIDEAE s.str. (Fig. 57–59; Table 3)

Wood type I characterises most tribes of this subfamily, namely Chiococceae, the *Portlandia* group of the Catesbaeeae, Isertieae, *Corynanthe* group, Naucleaeae, Cephalanthaeae, Henriquezieae, and Rondeletieae (Fig. 57). On the other hand, wood type II is found at least in three clades: 1) Hamelieae, Hillieae, 2) several Guettardeae, and 3) Cinchoneae.

The morphological delimitation of the tribe Rondeletieae according to Delprete (1999) is summarised in Table 1 and compared to the molecular results of Rova (1999). Based on *trnL-F* and *rps16* data the latter author suggested that the circumscription of the Rondeletieae must be significantly narrowed. He therefore proposed to restrict the tribe to nine genera and included some other genera tentatively. While the two wood types are present in circumscriptions of the Rondeletieae according to Robbrecht (1988, 1994) and Delprete (1999), it is most interesting to find a much greater homogeneity in the wood structure when we follow the delimitation based on molecular sequence data. The secondary xylem of the Rondeletieae sensu Rova (1999) appears to be characterised by wood type I and the following genera that show wood type II need to be excluded from the Rondeletieae: *Bathysa*, *Elaeagia*, *Macbrideina*, *Simira*, and *Warszewiczia*. These are all included in the large complex of Calycophylleae, Condamineae, Simireae and Hippotidae (Ixoroideae). Hence, the wood anatomy shows major differences between the Rondeletieae sensu Rova (Cinchonoideae) on the one hand, and the Condamineae–Calycophylleae–Hippotidae–Simireae–complex (Ixoroideae: see also further) and several other genera that are excluded, on the other hand.

Table 3. Wood anatomy of the Cinchonoidae s. str. based on data from literature and original observations; + = present, - = absent, ? = unknown, () = rarely or indistinctly present; tribal abbreviations in the first column follow Robbrecht (1994). - **1** = wood type - **2** = solitary vessels; **3** = radial vessel multiples (number of vessels); **4** = vessel clusters - **5** = septate fibres; **6** = fibre pits simple or minutely bordered; **7** = fibres with distinctly bordered pits on radial and tangential walls - **8** = axial parenchyma diffuse; **9** = axial parenchyma diffuse-in-aggregates; **10** = axial parenchyma paratracheal; **11** = axial parenchyma banded; **12** = axial parenchyma aliform or confluent - **13** = ray width in number of ray cells; **14** = sheath cells; **15** = disjunctive cell walls; **16** = rays < 1 mm - **17** = raphides; **18** = crystal sand; **19** = prismatic crystals; **20** = silica bodies; **21** = styloids - **22** = anomalous features: ¹heartwood colour red; ²thin fibre walls; ³very thick-walled fibres; ⁴ring-porous. - For Rondeletieae see also Table 1.

Tribes and genera	Wood type	Vessels				Fibres				Axial parenchyma				Rays				Mineral inclusions					Anom. feat.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Guettardeae																							
<i>Antirhea</i>	I-II	(+)	2-8	-	-	+	-	+	(+)	-	-	-	1-3	-	-	-	-	-	-	-	-	-	
<i>Bobea</i>	I-II	+	4-8	-	-	+	-	+	+	(+)	-	-	1-4	-	-	-	-	(+)	-	-	-	-	
<i>Chomelia</i>	I	+	(+)	-	-	-	+	+	-	-	-	-	1, 2-3	-	-	-	-	-	-	-	-	-	
<i>Dichilanthe</i>	I	+	-	-	-	-	+	+	(+)	-	-	-	1-2	-	-	-	-	-	-	-	-	-	
<i>Guettarda</i>	II	(+)	2-7	(+)	+	+	-	(+)	(+)	-	-	-	2-3-(5)	-	-	-	-	+	+	-	-	-	
<i>Guettarda acraenea</i> ; <i>G. foliaceae</i>	I-II	(+)	2-5	-	-	+	-	+	-	+	-	-	2-3-(4)	-	-	-	-	-	+	-	-	-	
<i>Machaonia brasiliensis</i>	I	+	(+)	-	-	-	+	+	-	-	-	-	1, 3-6	-	-	-	-	+	-	-	-	-	
<i>Machaonia spinosa</i>	II	+	2-7	-	+	+	-	-	+	-	-	-	1, 3-6	-	-	-	-	+	-	-	-	-	
<i>Malanea</i>	I-II	+	+	-	-	-	+	(+)	(+)	-	-	-	1, 2-6	+	-	-	-	+	-	-	-	-	
<i>Stenostomum</i>	II	(+)	2-4	-	+	+	-	-	+	-	-	-	1-3	-	-	-	-	+	-	-	-	-	
<i>Timonius</i>	I-II	(+)	2-5	-	-	+	-	+	+	+	+	(+)	1-5	-	-	-	-	+	+	-	-	-	
Rondeletiaeae																							
<i>Acunacanthus</i> , <i>Blepharidium</i> , <i>Dendrosipanea</i> , <i>Mazaea</i> , <i>Rondeletia</i>	I	+	(2-4)	(+)	-	-	+	+	(+)	-	-	-	1-4-(5)	+	-	-	-	-	-	-	-	-	
Excluded: <i>Greenaea</i> (close to <i>Ixoreae</i>)	I	+	(+)	-	-	-	+	-	+	+	+	-	2-4	+	-	-	-	-	-	-	-	-	
Excluded: <i>Augusta</i> (close to <i>Gar.</i> / <i>Pav.</i>)	I-II	+	2-4	-	+	+	-	+	-	-	-	-	2-4	-	-	-	-	-	-	-	-	-	

(Table 3 continued)

Tribes and genera		Wood type	Vessel groupings				Fibres			Axial parenchyma						Rays					Mineral inclusions					Anom. feat.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22			
Catesbaeaceae <i>Catesbaea</i> group (no wood anatomical information available)																										
Catesbaeaceae <i>Portlandia</i> group																										
<i>Bikkia</i> , <i>Coutarea</i> , <i>Hintonia</i> , <i>Nernstia</i> , <i>Portlandia</i>		I	+	(2-4)	-	-	(+)	+	+	+	-	-	-	1-2-(4)	-	-	-	-	(+)	-	-	-	-			
Chiococceae																										
<i>Ceratopyxis</i> , <i>Chiococca</i> , <i>Chione</i> , <i>Erithalis</i>		I	+	-	-	-	-	+	+	-	(+)	-	-	1-3	-	-	-	-	(+)	-	-	-	-			
Excluded: <i>Mastixiaden-dron</i> (transferred to Con./Cal./Hip./Sim.)		II	(+)	2-3	-	+	+	-	(+)	-	+	-	-	1-3-(4)	+	-	-	-	+	-	-	-	-			
Exostema group																										
<i>Badusa</i> , <i>Exostema</i> , <i>Morierina</i>		I	+	(+)	-	-	-	+	+	(+)	-	-	-	2-3	-	-	-	-	-	-	-	-	-			
Cinchoneae																										
<i>Cinchona</i> , <i>Dolicholobium</i> , <i>Joosia</i>		II	+	2-5	(+)	+	+	-	(+)	-	(+)	-	-	1, 2-4-(5)	+	-	-	-	(+)	-	-	-	-			
<i>Ladenbergia</i>		I-II	+	(2-3)	-	-	+	-	+	-	+	-	-	1, 2-5-(6)	+	-	-	-	-	-	-	-	-			
<i>Remijia</i>		I-II	+	(2-3)	-	-	+	-	-	-	(+)	-	-	1-2	-	-	-	-	-	-	-	-	-			
Isertieae																										
<i>Isertia</i>		I	+	2	-	-	-	+	+	(+)	-	-	-	1-3-(4)	-	-	-	-	-	-	-	-	-

Fig. 57. Wood types plotted on the Cinchonoideae s.str. (part of the hypothetical tree in Fig. 3).

The placement of *Greenaea* within or near the Ixoreae as found by Rova (1999) can be supported by the presence of parenchyma bands (2 to 4 cells wide), but the presence of axial parenchyma bands could also have been developed by its lianescent habit. As far as we know, styloids do not occur in *Greenaea* and this crystal type is characteristic of most Ixoreae (Jansen et al. 1999). Moreover, the suggested transfer of *Lindenia* (synonymised with *Augusta*; Kirkbride 1997) to the Gardenieae or Pavetteae (Rova 1999) cannot be supported by the presence of septate libriform fibres (characteristic of type II), but the parenchyma type and vessel arrangement suggests wood type I, which is characteristic of the core Ixoroideae.

Fig. 58. Axial parenchyma types plotted on the Cinchonoideae s.str. (part of the hypothetical tree in Fig. 3).

Wood anatomy of the Guettardeae has been studied in detail by Ter Welle et al. (1983), who concluded that the tribe is heterogeneous. In fact, the large wood anatomical variation in this tribe is striking compared to the general homogeneity of other, even much larger tribes such as the Gardenieae and Psychotrieae. Wood type I is most common in the Guettardeae, but type II is observed in *Stenostomum*, most species of *Guettarda*, and *Machaonia spinosa*. Crystal sand is present in ray cells of several genera, but the occurrence of (small) prismatic crystals, sometimes in combination with crystal sand, in *Guettarda* and *Timonius* is remarkable and not observed in other Cinchonoideae (Fig. 57–59).

Fig. 59. Mineral inclusions plotted on the Cinchonoideae s. str. (part of the hypothetical tree in Fig. 3).

According to the molecular analysis of Rova (1999), the Hawaiian genus *Bobea* takes a basalmost position in a clade including several Guettardeae. Wood type I of *Bobea* shows indistinct to distinctly bordered pits, confined to radial fibre walls, and axial parenchyma which is diffuse to diffuse-in-aggregates. Darwin (1979) proposed for *Bobea* a position close to *Timonius*, *Antirhea* and *Guettarda*. While there is no wood anatomical difference between *Antirhea*, a location of *Bobea* near *Timonius* and most species of *Guettarda* appears strange from a wood anatomical point of view. Further evidence is needed to understand the isolated position of *Bobea* since this can be caused by the narrow sampling of taxa in the molecular analysis of Rova (1999).

Considerable differences in wood structure occur between *Machaonia brasiliensis* and *M. spinosa*. This may indicate that the species studied by Ter Welle et al. (1983) need verification regarding their identification, or that the genus is not monophyletic. Moreover, the results of Rova (1999) suggest that the tribe Guettardeae as described by Robbrecht (1988, 1994) is most likely polyphyletic, with two major clades: one consisting of *Machaonia* (and *Allenanthus*), and one including *Guettarda*, *Antirhea*, *Chomelia*, *Malanea* and *Timonius*. It is clear that the delimitation of the Guettardeae needs further research if we want to understand the wood anatomical heterogeneity of this tribe.

In addition to a similar wood type, the close relationship between Hillieae and Hamelieae is supported by the presence of raphides, which are also found in the secondary xylem. Initially, the tribe Hamelieae has been included in the Rubioideae because of the presence of raphides (Verdcourt 1958; Bremekamp 1966; Robbrecht 1994), but it was excluded from the Rubioideae on the basis of *rbcL* data (e.g. Bremer et al. 1995). Hamelieae also lack the large deletion containing one of the *atpB* promoters which is characteristic of the Rubioideae (Manen & Natali 1996).

Based on morphological characters, Delprete (1998) strongly advocated the inclusion of the genus *Cosmocalyx* in the Hamelieae. The heartwood of this genus turns intensely pinkish red to almost purplish when freshly exposed to air (Richter & Schmitt 1987). This rare phenomenon is shared with species of the genus *Simira* (Simireae, Ixoroideae s.l.), *Deppea* and *Hamelia* (Hamelieae), and *Syringantha* (Lorence & Dwyer 1988; Delprete & Nee 1997). McDowell (1996) recently included the monospecific *Syringantha* in the Hamelieae, which had previously been transferred from the Cinchoneae to the Condamineeae by Andersson and Persson (1991). Moreover, Richter and Schmitt (1987) reported that remarkably large styloids occur in idioblasts of *Cosmocalyx* (Fig. 59). Styloids occur only seldomly in rubiaceous wood, and are only known, as far as we know, in the wood of Ixoreae and a single species of *Morinda* (Morindeae). The presence of raphides in other tissues of *Cosmocalyx* is in accordance with the Hamelieae and Hillieae (Delprete 1998). As observed in leaves of some Rubiaceae (e.g. several genera of Psychotrieae), styloids appear to show morphological similarities to raphides (Cody & Horner 1983), which is also suggested by the occurrence of styloids in multiple groups stacked tightly in large pocket-like idioblasts of *Cosmocalyx*. The genus *Simira* (a tribe of its own or Rondeletieae sensu latissimo) has a complicated taxonomic history (Delprete & Nee 1997). In view of the genus' reddish tinged wood, *Simira* should definitely be reconsidered in the context of the Hamelieae.

The tribe Henriquezieae is wood anatomically rather isolated from the remaining Rubiaceae (Koek-Noorman 1980). Indeed, vessel elements of large diameter, the aliform to confluent axial parenchyma, and the uniseriate, relatively low rays are unusual in Rubiaceae and suggest a derived status (Fig. 57–59). Koek-Noorman (1980) suggested that *Platycarpum* and *Henriquezia* are closely related by their aliform to confluent xylem parenchyma, while the axial parenchyma in *Gleasonia* is only scanty paratracheal. Rogers (1981), however, also encountered aliform to confluent parenchyma in *Gleasonia*, suggesting that this genus cannot be separated from *Henriquezia* and *Platycarpum*. Outside the Henriquezieae, more or less aliform to confluent pa-

renchyma is only occasionally reported in *Timonius* and unilaterally aliform parenchyma is rarely observed in *Dichilanthe* (Ter Welle et al. 1983). The presence of silica bodies in *Platycarpum* and *Henriquezia* appears to support the close relationship between both genera, although this feature is only recorded in few wood samples (Fig. 59). According to Rova (1999), *Gleasonia* should belong to the subfamily Ixoroideae s.l. on the basis of *trnL*-F sequence data. He found a strongly supported group comprising the Henriquezieae with a tentative new tribe including *Posoqueria* and *Molopanthera*. Wood anatomical data of *Molopanthera* are not available, but we have data on the wood structure of *Posoqueria*. Robbrecht and Puff (1986) accepted the classical position of *Posoqueria* in the Gardenieae, despite aberrant features; the results of Andreassen and Bremer (2000), however, demonstrated that *Posoqueria* should be a member of the basal Ixoroideae s.l. Koek-Noorman (1972) pointed out that the wood structure of *Posoqueria* deviates in some important features (especially non-septate libriform fibres) from the other Gardenieae. The genus also differs in its radial vessel multiples, small (navicular or cubic) prismatic crystals and the more paratracheal axial parenchyma distribution. Although the wood of *Posoqueria* differs in several points from that of the Henriquezieae, we observed very small mineral inclusions in the ray cells of *Posoqueria latifolia*, which resemble the silica bodies as present in *Platycarpum* and *Henriquezia*. However, the combined occurrence of small prismatic crystals and silica bodies in the same specimen puts doubt on the siliceous nature of these inclusions, because silica bodies and crystals generally are mutually exclusive (Scurfield et al. 1974). Hence, verification by EDX-analysis is required to identify the precise composition.

The *Corynanthe* group, Naucleaeae and Cephalantheae all show wood type I, which supports the coherence of these groups. Razafimandimbison and Bremer (2000) suggested to include these taxa in the Naucleaeae s.l., since the delimitation of Naucleaeae sensu Ridsdale and the Coptosapelteae sensu Andersson is no longer tenable. There is one exception regarding the wood type: *Mussaendopsis* clearly shows all characters of wood type II. Since *Mussaendopsis* was only tentatively included in the Coptosapelteae (Puff & Igersheim 1994a; Robbrecht 1994) and found to fall outside the Naucleaeae s.l. (Razafimandimbison & Bremer 2000), wood anatomy supports the exclusion of this genus. Moreover, the molecular and morphological data demonstrated that *Hallea* and *Mitragyna* form a well-supported clade with a very high bootstrap value, which is supported by the occurrence of silica bodies in ray cells. Thus, silica bodies are possibly a synapomorphy for both genera, while crystal sand is present in several genera of the Naucleaeae sensu Ridsdale (*Adina*, *Breonia*, *Nauclea*) (Fouarge et al. 1953; Brazier & Franklin 1961; Scurfield et al. 1974; Normand & Paquis 1976; Ter Welle 1976). Our observation of small silica inclusions in *Crossopteryx* is new for this genus but needs verification.

Chiococceae, Catesbaeeae (*Catesbaea* group and *Portlandia* group) and the informal *Exostema* group form a complex and there is increasing evidence to merge these taxa into a single tribe Catesbaeeae s.l. (Rova 1999). We had no material available for the *Catesbaea* group, and literature does not report on its wood. In the other members of the complex, wood type I is universally present, except for *Mastixiodendron*. This genus should be excluded from the Chiococceae–Catesbaeeae complex (Huysmans

Table 4. Wood anatomical survey of Ixoroideae s.l. based on data from literature and original observations; + = present, – = absent, ? = unknown, () = rarely or indistinctly present; tribal abbreviations in the first column follow Robbrecht (1994). — **1** = wood type — **2** = solitary vessels; **3** = radial vessel multiples (number of vessels); **4** = vessel clusters; **5** = septate fibres; **6** = fibre pits simple or minutely bordered; **7** = fibres with distinctly bordered pits on radial and tangential walls — **8** = axial parenchyma diffuse; **9** = axial parenchyma diffuse-in-aggregates; **10** = axial parenchyma paratracheal; **11** = axial parenchyma banded; **12** = axial parenchyma aliform or confluent — **13** = ray width in number of ray cells; **14** = sheath cells; **15** = disjunctive cell walls; **16** = rays < 1 mm — **17** = raphides; **18** = prismatic crystals; **19** = silica bodies; **20** = styloids — **21** = anomalous features.

Tribes and genera	Wood type	Vessels				Fibres				Axial parenchyma				Rays				Mineral inclusions				Anom. feat.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Hippotideae <i>Hippotis</i> , <i>Pentagonia</i> , <i>Sommeria</i>	II	(+)	2-9	-	+	+	-	-	-	(+)	-	-	1, 4-5	+	-	-	-	+	-	-	-	-
Calycophylleae <i>Alseis</i> , <i>Calycophyllum</i> , <i>Capirona</i> , <i>Ferdinandusa</i> , <i>Macrocnemum</i>	II	(+)	2-9	(+)	+	+	-	(+)	-	+	-	-	2-4-(7)	(+)	-	-	-	+	-	-	-	-
Simireae <i>Holtonia</i> (syn. <i>Elaeagia</i>), <i>Simira</i>	II	(+)	2-5	(+)	+	+	-	-	-	(+)	-	-	1-4-(5)	+	-	-	-	+	-	-	-	-
Condamineae <i>Chimarrhis</i> , <i>Condaminea</i> , <i>Picardaea</i> , <i>Pinckneya</i> , <i>Pogonopus</i> , <i>Rustia</i>	II	(+)	2-4	(+)	+	+	-	-	-	(+)	-	-	1, 2-5-(8)	+	-	-	-	+	-	-	-	-
Mussaendeae <i>Heinsia</i> , <i>Mussaenda</i>	II	+	3-4	-	+	+	-	-	+	-	-	-	1-3-(6)	(+)	-	-	-	+	-	-	-	-
Sabiceae <i>Acranthera</i>	II	+	+	-	+	+	-	-	-	-	-	-	4	+	-	-	-	-	-	-	-	-
<i>Sabicea</i>	II	+	-	-	+	+	-	-	-	(+)	-	-	?	-	-	-	-	-	-	-	-	-

Sipaneae (entirely herbaceous)									
Virentarieae									
<i>Virentaria</i>	II	+	+	-	(+)	+	-	-	-
Retiniphyllae									
<i>Retiniphyllum</i>	I	+	(+)	-	-	+	(+)	(+)	-
Ixoreae									
<i>Capitancocokia</i> , <i>Doricera</i> , <i>Ixora</i> , <i>Myonima</i> , <i>Versteegia</i>	I	+	(2)	-	-	+	(+)	-	-
Albertae									
<i>Alberta</i>	I	+	-	-	-	+	(+)	-	-
Vanguerieae									
<i>Canthium</i> , <i>Caviera</i> , <i>Fadogia</i> , <i>Fadogiella</i> , <i>Keetia</i> , <i>Lagynias</i> , <i>Meyna</i> , <i>Psydrax</i> , <i>Pygmaeothamnus</i> , <i>Pyrostria</i> , <i>Rytigynia</i> , <i>Tapi- phyllum</i> , <i>Vangueria</i> , <i>Vangueriopsis</i>	I	+	(2-4)	-	-	+	+	-	-
Coffeae (including former Gardenieae–Diplosporinae)									
<i>Argocoffeopsis</i> , <i>Calycosiphonia</i> , <i>Coffea</i> , <i>Diplospora</i> , <i>Psilanthus</i> , <i>Scyphiphora</i> (near <i>Ixoreae</i> ?), <i>Sericanthe</i> , <i>Tricalysia</i>	I	+	(2-4)	-	-	+	+	-	-
Octotropideae									
<i>Canephora</i> , <i>Fernelia</i> , <i>Feretia</i> , <i>Galiniera</i> , <i>Hypobathrum</i> , <i>Lamprothamnus</i> , <i>Polysphaeria</i> , <i>Zuccarinia</i>	I	+	(+)	-	-	+	(+)	+	-
(continued on the next page)									

(Table 4 continued)

Tribes and genera		Wood type	Vessel groupings				Fibres			Axial parenchyma				Rays				Mineral inclusions					Anom. feat.	
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Pavetteae <i>Cladoceras</i> , <i>Dictyandra</i> , <i>Homollea</i> , <i>Leptactina</i> , <i>Nichallea</i> , <i>Pachystylus</i> , <i>Pavetta</i> , <i>Rutidea</i> , <i>Tarenna</i> , <i>Tennantia</i>	I	+	(2)	-	-	-	-	+	+	-	-	-	-	1-3-(5)	(+)	-	-	-	-	(+)	-	-	-	
	Gardenieae (incl. <i>Aulacocalyceae</i>)																							
	<i>Bertiera</i> , <i>Calochone</i> , <i>Ibetrulia</i>	I	+	(2-4)	-	-	-	-	+	+	-	(+)	-	-	1-3	(+)	+	-	-	-	(+)	-	-	-
	<i>Aidia</i> , <i>Aoranthie</i> , <i>Atractogyne</i> , <i>Aulacocalyx</i> , <i>Belonophora</i> , <i>Brenania</i> , <i>Casasia</i> , <i>Catunaregam</i> , <i>Didymosalphix</i> , <i>Duperrea</i> , <i>Euclinia</i> , <i>Gardenia</i> , <i>Gynopachis</i> , <i>Heinsenia</i> , <i>Massularia</i> , <i>Morelia</i> , <i>Oxyanthus</i> , <i>Phellocalyx</i> , <i>Porterandia</i> , <i>Randia</i> , <i>Rothmannia</i> , <i>Schumanniophyton</i> , <i>Sherbournia</i> , <i>Stachyarrhena</i> , <i>Tarennoidea</i>	I	+	(2-4)	-	-	-	-	+	+	+	(+)	-	-	1-3-(4)	+	+	-	-	-	+	-	-	-
<i>Alibertia</i> , <i>Amaïoua</i> , <i>Borojoa</i> , <i>Duroia</i> , <i>Kutchubaea</i>	I	+	(2-4)	-	-	-	-	+	+	+	-	+	-	1-(2), 3-5	+	+	-	-	-	+	-	-	-	
Excluded: <i>Posoqueria</i> (basal position in <i>Ixoroideae</i> s.l. or near <i>Henriquezieae</i>)	I-II	(+)	2-4	-	-	-	+	-	+	(+)	+	-	-	1-3	-	-	-	-	-	+	-	-	semi- ring- porous	

et al. 1999; see also below). Although *Chione* (formerly in the complex) falls in a basal position in a clade together with representatives of the Hillieae and Hamelieae (Rova 1999), the present study shows that the wood type of *Chione* differs from that of Hillieae and Hamelieae.

The tribe Cinchoneae is relatively homogeneous in its secondary xylem. Three genera within Cinchoneae show wood type II, but the wood structure encountered in *Ladenbergia* better fits with type I. *Remijia* also shows fibre tracheids with distinctly bordered pits, but axial parenchyma is only rarely paratracheal to absent, which is more characteristic of type II. A careful examination of macerated tissue did not reveal any septate fibres in *Ladenbergia* and *Remijia*. Furthermore, crystal sand is common in ray cells of the Cinchoneae and scalariform vessel-ray pitting is reported in *Joosia*.

The former tribe Isertieae collapsed and was reduced to two genera: *Isertia* (including *Yutajea*) and *Kerianthera* (Bremer & Thulin 1998). The secondary xylem of *Isertia* shows the presence of wood type I. This is in contrast to wood type II occurring in genera that were previously included in Isertieae: *Mussaenda* and *Heinsia* (Mussaendeae), and *Mycetia* (Argostemmateae). *Gonzalagunia* which shows wood type I is suggested to be closely related to Guettardeae, in which wood type I and II are both observed. The abundant presence of small prismatic (especially navicular) crystals in parenchyma cells of *Gouldia*, which is synonymised to *Hedyotis* (Wagner et al. 1989), supports the exclusion from Isertieae. This crystal type is mainly recorded in the subfamily Rubioideae.

SUBFAMILY IXOROIDEAE s.l. (Fig. 60–62; Table 4)

One of the most significant conclusions from the present survey appertains to the distribution of the wood types in the Ixoroideae, namely exclusively type I in the core Ixoroideae, versus exclusively type II in the two other clades of the Ixoroideae (Fig. 60).

A close affinity between the Hippotideae, Calycophylleae, Simireae and Condamineae is generally supported by cladistic analyses based on molecular data, but internal resolution in this clade is poor (Bremer et al. 1999; Rova 1999). All wood samples of this group show wood type II and crystal sand is very common in ray cells. Genera that recently have been transferred to this clade include: *Bothriospora*, *Elaeagia*, *Macrocnemum*, *Mastixiodendron* and *Warszewiczia* (Andersson 1995; Rova 1999). The genus *Mastixiodendron* is probably the only genus within Rubiaceae that shows free petals, a character also present in the enigmatic genus *Dialypetalanthus* (Piesschaert et al. 1997). Plastid *rbcL* sequence data has demonstrated that *Dialypetalanthus* is a member of Rubiaceae (Fay et al. 2000), in a clade with neotropical genera of the Calycophylleae, Hippotideae and Condamineae. However, this clade received very little bootstrap support. The wood structure of *Mastixiodendron* closely resembles that of *Dialypetalanthus*, but it remains necessary to turn to other fields of evidence to elucidate the exact position of *Dialypetalanthus* and *Mastixiodendron* and corroborate a possible relationship between the two genera.

The Mussaendeae were re-established as a separate tribe of Ixoroideae s.l. by Bremer and Thulin (1998). Genera included in Mussaendeae for which we have wood data

Fig. 60. Wood types plotted on the Ixoroideae s.l. (part of the hypothetical tree in Fig. 3).

are *Heinsia* and *Mussaenda*. Both genera have thin-walled fibres with septa and minutely bordered pits that are restricted to radial walls (type II).

We have little or no wood anatomical information of the more herbaceous tribes Sabiceae and Virectariae. The related tribe Sipaneeae is entirely herbaceous. Wood of the genus *Virectaria* shows absence of axial parenchyma, solitary vessels or rarely arranged in short radial multiples, and fibres with simple or reduced pit borders on radial walls (Dessein et al. 2001b). Septate fibres were not recorded in all representatives studied, but they are clearly present in a specimen of *Virectaria major*. Accord-

Fig. 61. Axial parenchyma types plotted on the Ixoroideae s.l. (part of the hypothetical tree in Fig. 3).

ingly, these features are more typical of wood type II than of type I. The very small wood samples of *Sabicea* examined by us showed septate libriform fibres, but more material should be examined of the remaining genera (e.g. *Pseudosabicea*, *Tamridea*) before we can conclude that wood type II is consistently present in Sabiceae. Bremer and Thulin (1998) noticed that *Acranthera* may perhaps not belong to the Sabiceae. Wood type II in *Acranthera*, however, can be interpreted as additional support for a position within the Sabiceae.

Fig. 62. Mineral inclusions in wood plotted on the Ixoroideae s.l. (part of the hypothetical tree in Fig. 3).

The core Ixoroideae Retiniphyllae, Ixoreae, Albertae, Vanguerieae, Coffeae, Octotropideae, Pavetteae, and Gardenieae are all characterised by wood type I. Although disjunctive elements are found in all subfamilies of Rubiaceae, this feature appears to be most common in this clade. The Retiniphyllae appear to take a basal position as sister group of the core Ixoroideae. The presence of axial parenchyma bands is found in two basal tribes of the core Ixoroideae, namely Retiniphyllae and Ixoreae (Fig. 61). As argued by Jansen et al. (1999), axial parenchyma bands in Ixoreae distinguish this group from Pavetteae. The exclusion of *Ixora* and allies from the Pavetteae s.l.

and recognition of the tribe Ixoreae was also proposed by Andreasen and Bremer (2000) on the basis of *rbcL* data. The occurrence of long and wide parenchyma bands in *Retiniphyllum*, the only genus of the Retiniphyllae, probably indicates the primitive position of this genus. *Retiniphyllum* is also recorded to show aliform to confluent parenchyma, which is very unusual in Rubiaceae. Parenchyma bands are absent in most members of the core Ixoroideae and diffuse to diffuse-in-aggregates is the main parenchyma type. However, the formation of narrow bands or lines up to three cells wide is also found in some closely related genera of the Gardenieae, namely the *Alibertia* group as proposed by Persson (1996, 2000; *Alibertia*, *Amaioua*, *Borojoa*, *Duroia*, and *Kutchubaea*; Fig. 61). Therefore, this feature probably supports the monophyly of the *Alibertia* group.

Prismatic crystals are very common in the wood of most core Ixoroideae having wood type I. In particular, they characterise the Gardenieae, Octotropideae, Coffeeae and to a lesser extent several Pavetteae (Fig. 62). The crystals are rhombic or octahedral and frequently solitary in ray cells. Styloids or elongate crystals distinguish the Ixoreae from the other core Ixoroideae. This crystal type was recorded in the wood of *Captaincookia*, *Ixora* and *Versteegia*.

Chambered prismatic crystals are frequently found in axial parenchyma cells of *Tarenna*, *Nichallea*, *Homollea* and *Pavetta*. As suggested by Jansen et al. (1999), this crystal type probably shows taxonomic significance at the generic or infrageneric level. Accordingly, the occurrence of prismatic crystals needs further verification, especially in the genus *Tarenna* s.l., the delimitation of which is the largest taxonomic problem in the Pavetteae.

Puff and Rohrhofer (1993) suggested a taxonomic position of the mangrove genus *Scyphiphora* in Gardenieae, especially within the subtribe Diplosporineae. The genus was excluded from the Gardenieae by Andreasen and Bremer (2000) since their cladistic analysis suggested a position near the Ixoreae although support for this relationship was not very strong. Wood anatomy of *Scyphiphora* shows no tendency to form small lines or bands of axial parenchyma, which is generally characteristic of Ixoreae.

Andreasen and Bremer (2000) demonstrated that Aulacocalyceae are deeply nested in and should be sunk into Gardenieae. There are no wood anatomical differences between these groups. Furthermore, the homogeneity in the wood structure of the core Ixoroideae does not allow to comment on the taxonomic position of a few genera recently discussed, viz. *Aoranth*e (Andreasen & Bremer 2000) and *Duperrea* (De Block & Robbrecht 1997).

SUBFAMILY RUBIOIDEAE (Fig. 63 & 64; Table 5)

The Rubioideae reveal a tendency to herbaceousness, although this habit presumably has one origin outside Rubioideae, namely in the clade consisting of Sipaneeae, Viretarieae and Sabiceae (Ixoroideae s.l.; Fig. 63). The clades in which herbaceous taxa are most distinctly represented, are 1) Ophiorrhizeae, 2) Cruckshanksieae and *Coccocypselum*, 3) *Mitchella* and some Psychotrieae (e.g. *Geophila*, *Hymenocoleus*), and 4) the large Spermacoceae alliance (including Spermacoceae, Knoxieae, Hedyotideae, Theligoneae, Rubieae, Anthospermeae, Argostemmatae, and Paederieae).

Table 5. Wood anatomy of the Rubioideae s.l. based on data from literature and original observations; + = present, – = absent, ? = unknown, () = rarely or indistinctly present. — **1** = wood type — **2** = solitary vessels; **3** = radial vessel multiples (number of vessels); **4** = vessel clusters — **5** = separate fibres; **6** = fibre pits simple or minutely bordered; **7** = fibres with distinctly bordered pits on radial and tangential walls — **8** = axial parenchyma diffuse; **9** = axial parenchyma diffuse-in-aggregates; **10** = axial parenchyma paratracheal; **11** = axial parenchyma banded; **12** = axial parenchyma aliform or confluent — **13** = ray width in number of ray cells; **14** = sheath cells; **15** = disjunctive cell walls; **16** = rays < 1 mm — **17** = raphides; **18** = crystal sand; **19** = prismatic crystals; **20** = silica bodies; **21** = styloids — **22** = anomalous features.

Tribes and genera	Wood type	Vessels			Fibres			Axial parenchyma					Rays					Mineral inclusions					Anomalous features
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
Pauridiantheae <i>Commitheca</i> , <i>Pauridiantha</i> , <i>Poecilocalyx</i> , <i>Stelechantha</i>	I	+	+	–	–	–	+	+	–	–	–	–	2–3–(5)	–	–	–	–	–	–	–	–	(helical thickenings in axial parenchyma)	
Urophylleae <i>Leucolophus</i> , <i>Mascholocorymbus</i> , <i>Pleiocarpidia</i> , <i>Praravinia</i> , <i>Urophyllum</i>	I	+	(2–4)	–	–	–	+	+	+	–	–	–	1–2, 4–6	+	–	–	–	–	–	–	–	(helical thickenings in axial parenchyma)	
Ophiorrhizeae <i>Ophiorrhiza</i>	II ?	+	–	–	+	?	?	(+)	–	–	–	–	?	–	–	–	–	–	–	–	–	–	
Lasiantheae <i>Allaeophania</i> , <i>Lasianthus</i>	I	+	–	–	–	–	+	+	–	–	–	–	1–2	–	–	–	+	–	–	–	–	helical thickenings in axial parenchyma	
<i>Saldinia</i> , <i>Trichostachys</i>	I–(II)	+	(+)	–	(+)	–	+	(+)	–	–	–	–	1	–	–	–	+	–	–	–	–	helical thickenings in axial parenchyma cells	

Coussareeae <i>Coussarea</i> , <i>Fareamea</i>	II	+	2-4	-	+	+	-	-	(+)	-	-	1, 4-9	+	-	-	-	-	-	very high rays
Coccocypseleae <i>Declieuxia</i> <i>Hindsia</i>	II II	+	(+) +	- -	+	+	-	-	-	-	-	1-3-(5) 1-2	+	-	-	-	-	-	-
Craterispermeae <i>Craterispermum</i>	I	+	(2)	-	-	-	+	-	-	+	-	1-2	+	-	-	-	-	-	-
Psychotrieae <i>Amaracarpus</i> , <i>Pali- courea</i> , <i>Psychotria</i> , <i>Rudgea</i> , <i>Straussia</i>	II	(+)	2-10	(+)	+	+	-	-	(+)	-	-	2-7	+	-	-	-	-	-	-
Gaertnereae <i>Gaertnera</i> , <i>Pagamea</i>	I	+	(2-4)	-	-	-	+	-	-	+	-	1-3-(5-8)	+	-	-	-	-	-	-
Schraderae <i>Schradera</i>	I-(II)	+	2-4	(+)	(+)	(+)	+	+	+	+	-	3-5-(10)	+	-	-	-	-	-	-
Prismatomerideae <i>Prismatomeris</i> , <i>Rennellia</i>	I	+	-	-	-	-	+	+	(+)	-	-	1-3	+	-	-	-	-	-	-
Mitchella group <i>Dannacanthus</i>	II	?	?	-	+	+	-	-	-	-	-	1-(2)	-	-	-	-	-	-	-
Morindeae <i>Gynochthodes</i> , <i>Morinda</i>	I-(II)	+	+	-	-	+	+	-	-	+	-	1, 3-5	+	-	-	-	(+)	-	-
Danaideae <i>Danaus</i>	I	+	-	-	+	+	+	-	(+)	(+)	-	1-3-(4)	+	-	-	-	-	-	-

(continued on the next page)

(Table 5 continued)

Tribes and genera	Wood type	Vessels				Fibres		Axial parenchyma					Rays				Mineral inclusions					Anomalous features
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Triainolepideae <i>Triainolepis</i>	I	-	+	+	-	-	+	+	-	-	-	-	1-3	-	-	-	+	-	-	-	-	diagonal vessel arrangement
Knoxiaceae (entirely herbaceous)																						
Hedyotideae <i>Carphalea</i> , <i>Hedyotis</i> (incl. <i>Gouldia</i> , <i>Wiegmannia</i>)	I	(+)	2-6	(+)	-	-	+	+	-	-	+	-	1, 2-4	+	-	-	+	-	-	-	-	navicular crystals in <i>Gouldia</i>
<i>Oldenlandia</i>	I	(+)	2-6	-	-	-	+	-	+	-	-	-	2-3	-	-	-	-	+	-	-	-	-
<i>Pentanopsis</i>	I	+	-	-	-	-	+	-	+	-	-	-	1-2	-	-	-	-	-	-	-	-	-
<i>Pentas</i>	I	+	(+)	-	-	-	+	(+)	-	(+)	-	-	1-4	-	-	-	-	+	-	-	-	-
<i>Placopoda</i>	I	-	+	(+)	-	-	+	+	-	+	-	-	1-3	-	-	-	-	+	-	-	-	diagonal vessel arrangement
Spermacoceae <i>Diodia</i> , <i>Spermacoce</i>	I	+	(+)	-	-	-	+	(+)	-	-	-	-	1-(2), 1-4	-	-	-	-	-	-	-	-	-
Anthospermeae <i>Anthospermum</i>	I	+	(2-4)	-	-	-	+	+	-	(+)	-	-	1, 2-4	-	-	-	+	-	-	-	-	(faint rays; reticulate perforation plates)
<i>Carpacoe</i>	I	+	(+)	-	-	-	+	+	-	-	-	-	1-2	-	-	-	-	-	-	-	-	(reticulate perforations)
<i>Coprosma lucida</i> , <i>C. montana</i> , <i>C. pubens</i>	I	+	(+)	-	-	-	+	+	+	+	-	-	3-8, > 10	-	-	-	+	-	-	-	-	very high, pseudo-morphic rays

<i>Coprosma rhyn-</i> <i>chocarpa</i> , <i>C. ochracea</i>	I-II	+	+	-	+	+	-	-	+	1-6	+	-	-	-	-	-	-	scalariform perforations + vessel pitting
<i>Nenax</i>	I	+	(+)	-	-	+	+	-	+	1	+	+	-	-	-	-	-	secondary woodiness?
<i>Phyllis</i>	I	+	+	-	-	+	+	-	-	1-2	+	-	-	-	-	-	-	secondary woodiness
Argostemmateae <i>Mycetia</i>	II	?	?	?	-	+	-	-	(+)	1-2	-	-	-	-	-	-	-	-
Paederieae <i>Gaillonia</i> , <i>Putoria</i>	I	+	2-4	(+)	-	-	-	-	(+)	1-(2), (4)	-	+	-	-	-	-	-	-
<i>Leptodermis</i> , <i>Saprosma</i>	II	+	2-4	-	-	+	-	-	(+)	1-4-(7)	-	-	-	-	-	-	-	-
<i>Paederia</i>	I-II	+	+	+	(+)	-	(+)	-	+	1, 2-10	+	-	(+)	-	-	(+)	-	unligunified rays and axial parenchyma
<i>Plocama</i>	I-II	(+)	2-6	-	-	+	-	-	-	1-2-(3)	+	-	-	-	-	-	-	-
<i>Spermadictyon</i>	I-II	(+)	+	+	(+)	-	(+)	-	(+)	1-5	+	-	-	-	-	-	-	reticulate perforations
Rubiceae <i>Asperula</i> , <i>Crucianella</i> , <i>Galium</i> , <i>Rubia</i>	I	+	+	-	-	-	+	(+)	+	(nearly rayless)	+	-	-	-	-	-	-	-
Theligoneae (entirely herbaceous)

Fig. 63. Woodiness and herbaceousness plotted on a hypothetical tree of the Rubiaceae based on the hypothetical tree in Fig. 3; * = secondary woodiness is likely in some species; Sip./Vir./Sab. = Sipaneeae/Virectarieae/Sabiceae.

Entirely herbaceous taxa are found in Cruckshanksieae and Theligoneae, while the other include herbs and shrubs.

Wood type I is most common in the Rubioideae, but type II appears to have evolved in more than one group (Fig. 64). Tribes that show almost exclusively type II are: 1) Coussareeae and Coccocypseleae, 2) Psychotrieae and *Damnacanthus* (*Mitchella* group), and 3) most species of Argostemmatae and Paederieae.

Fig. 64. Wood types plotted on the Rubioideae (part of the hypothetical tree in Fig. 3).

An unusual wood anatomical feature that was reported for the first time by Ohtani (1986) occurs in some basal groups of the Rubioideae. He illustrated the presence of vestures that are associated with helical thickenings in axial parenchyma cells of *Lasianthus*. This feature appears to characterise other basal Rubioideae, especially Pauridiantheae, Urophylleae, and Lasiantheae (*Lasianthus*, *Trichostachys*) (Jansen et al. 2001). Helical thickenings in axial parenchyma cells represent a unique feature in Rubiaceae (not known from other representatives) and are rare in the dicotyledons. The taxonomic value of this character, however, should be interpreted with caution,

since helical thickenings in axial parenchyma cells are only rarely present in a single wood section and can easily be overlooked.

Many authors argued that Urophylleae and Pauridiantheae, which were separated on the basis of floral and phytogeographical features by Bremekamp (1966), should be merged again (e.g. Bremer & Manen 2000). Wood anatomy confirms this close relationship, but gives no indication for merging or splitting the two tribes.

The taxonomic position of the genus *Collettoecema* was investigated in detail by Piesschaert et al. (2000a). The wood structure of this genus corroborates that this genus should be excluded from the Psychotrieae since there are major differences in fibre type, axial parenchyma and vessel arrangement. Similarly, wood type I and differences in gynoeceal and fruit structure illustrate that the small neotropical genus *Pagameopsis* is not a member of the Psychotrieae (Piesschaert et al. in press).

The genus *Coccocypselum* is entirely herbaceous. In addition to macromolecular data, support for an extended tribe Coccocypseleae was presented by Piesschaert et al. (2000b), who added the woody genera *Hindsia* and *Declieuxia* in the tribe. The wood structure of these two genera (type II) supports the position of Coccocypseleae as sister group of the Coussareeae. The latter tribe is characterised by septate libriform fibres and very high multiseriate rays, but stands apart from the other Rubioideae by the occurrence of scanty paratracheal parenchyma (Jansen et al. 2001). Bremer and Manen (2000) merged Coccocypseleae and Coussareeae into Coussareeae sensu lato. Quantitative differences in the wood structure mainly reflect differences in the habit. While the Coussareeae comprise trees and large shrubs (from 2 up to 10–18 m high), *Declieuxia* and *Hindsia* consist of shrubs (up to 1.5 m) or perennial herbs, and *Coccocypselum* only contains creeping herbs.

Banded parenchyma is present in few taxa of the Rubioideae. This type of axial parenchyma is most frequent in the rather basal taxa of the Psychotrieae alliance: Craterispermeae, and Gaertnereae, and to a certain degree in Schradereae and Morindeae. If the Psychotrieae are considered as the most derived group in this clade, one may suggest that the axial parenchyma has developed from banded to diffuse-in-aggregates, scanty paratracheal parenchyma and total absence. The lianescent habit of some Schradereae, Morindeae (especially *Morinda* and *Gynochtodes*) presumably explains the variation in axial parenchyma: wide bands are characteristic of lianas and parenchyma that is diffuse or diffuse-in-aggregates is found in non-lianescent species (Jansen et al. 2001). The presence of parenchyma bands in *Collettoecema* (Piesschaert et al. 2000a) may indicate a relationship with the Psychotrieae alliance. Based on molecular data, it has become clear that the genera *Gaertnera* and *Pagamea* should best be placed in a separate tribe Gaertnereae instead of a subtribe Gaertnerinae in the Psychotrieae (Jansen et al. 1996, 1997a). Since one wood type is usually constant within a single tribe of the Rubiaceae, a separate tribe Gaertnereae best reflects the wood anatomical variation.

All Hedyotideae studied share most features of wood type I, but vessels are rather frequently arranged in radial multiples (e.g. *Oldenlandia*, *Carphalea*, *Hedyotis*) or even in a more or less diagonal pattern (e.g. *Placopoda*). The tendency to form diagonal patterns of vessels is most distinctly observed in *Triainolepis* and in *Placopoda*, but it is possible that these have been caused by similar, dry environmental condi-

tions. Prismatic crystals are reported in ray cells and/or axial parenchyma cells of *Oldenlandia*, *Placopoda* and *Pentas*. The distribution of crystals within the Hedyotideae as well as the small number of taxa studied does not allow meaningful systematic conclusions. We therefore do not separate the genera listed in Table 5 into two groups (*Hedyotis* group and *Pentas* group) as illustrated in our hypothetical trees. Furthermore, *Carphalea* (*Pentas* group) is suggested to be closely related to *Placopoda*, a monospecific genus endemic to Socotra. Mineral inclusions seem to distinguish both genera: large idioblasts filled with raphides occur in *Carphalea*, while prismatic crystals are observed in *Placopoda*. However, a possible close affinity between *Carphalea* and *Triainolepis* is supported by the raphides in thick-walled, elongated sacs of ray parenchyma cells (Puff 1988).

Wood type I and fibre-tracheids characterise most representatives of the Anthospermeae. The genus *Anthospermum* wood anatomically resembles *Nenax* by the presence of faint rays, which are hardly recognisable on longitudinal sections. As already mentioned above, the genus *Coprosma* is heterogeneous. The wood of *Coprosma* shows considerable variation with respect to vessel arrangement, fibre type, perforation plates, intervessel pitting, ray size and height, and axial parenchyma distribution. We suggest that at least part of this variation can be explained by the presence of paedomorphic features (see below).

According to Koek-Noorman and Puff (1983), the tribe Paederieae is characterised by wood type II. However, there are several exceptions. Wood type I is more prominent in *Gaillonia*, *Putoria*, and *Plocama*. Koek-Noorman and Puff (1983) mentioned that wood anatomy supports the close affinity between these genera. Since secondary woodiness has possibly developed in some of these taxa (especially *Putoria*), the wood anatomical similarity may also be a result of paedomorphic characters. The several “unusual” characters of *Paederia* can obviously be linked to the lianescent habit of the genus: banded parenchyma anastomosing with multiseriate rays, unlignified ray parenchyma in multiseriate rays, very wide rays up to 10 cells wide, and two sizes of vessels (widest vessels up to 400 µm). Unlignified parenchyma in the Rubiaceae is only reported in the genera *Schradera* and *Paederia* and an association with the lianescent habit is unclear (Koek-Noorman & Puff 1991). Other lianas in Rubiaceae (e.g. *Uncaria*, *Rutidea*, *Mussaenda*, *Coptosapelta*, *Aoranthé*) do not show unlignified parenchyma.

As suggested by Koek-Noorman (1976) and Carlquist (1992), secondary woodiness has developed in the tribe Rubieae, especially in the representatives of this herbaceous clade that have radiated into more moderate (frost-free) climates (e.g. *Asperula*, *Crucianella*, *Galium*, *Rubia*). Most remarkable in these species is the predominance of erect ray cells or near raylessness, which has been related with Carlquist’s theories on paedomorphosis and insular woodiness (Carlquist 1962, 1969). Koek-Noorman (1976) demonstrated that for *Rubia fruticosa* the combination of the following conditions may explain raylessness: 1) a limited cambial activity, 2) short fusiform cambial initials, so that there is no great difference between length of fusiform and ray initials, and 3) juvenilism or paedomorphosis. In fact, a length-on-age curve for axial elements of *Rubia fruticosa* has demonstrated that juvenilism is most likely. This means that there are juvenile characters in the wood of the Rubieae as a result of a shift from

the primary to the secondary xylem (paedomorphosis). Examples are the scalariform perforation plates as observed in *Crucianella*. The scalariform intervessel pitting as reported for instance in *Coprosma ochraceae*, can also result from paedomorphosis or juvenilism as demonstrated by Carlquist (1962). Carlquist (1992; see his figure 6) also noticed for the first time storied wood structure in *Galium catalinense*, which is not reported in other members of Rubiaceae.

Carlquist (1992) stressed that perennial species of *Galium* occur in frost-free climates, such as southern California, which allow them to develop a moderate amount of wood. The ultimate proof, however, would be to use DNA evidence in order to evaluate the likelihood of secondary woodiness in these groups. The molecular results of Natali et al. (1996) do not allow such final confirmation, but the wood anatomical data of the Rubiaceae do provide excellent information that evolution towards herbaceousness has occurred in the family, and that in a number of the derived clades of the Rubioideae, secondary woodiness has occurred.

Within the Anthospermeae, secondary woodiness is also likely. Indications for secondary woodiness in *Anthospermum* are: 1) absence of rays or faint rays in several species of *Anthospermum*, 2) short vessel elements (low F/V ratio), and 3) short parenchyma strands (1–3 cells high). This can be explained by elongated ray initials and short fusiform cambial initials. According to Koek-Noorman and Puff (1983), the species of *Anthospermum* that most likely show primary woodiness are closely related and share the occurrence in Afromontane vegetation. In contrast, the presumed secondarily woody species are centred in the Cape Floral Kingdom and in drier parts of Madagascar.

Genera incertae sedis

The genus *Jackiopsis* (wood type I) shows a number of unusual features unique in the Rubiaceae (e.g. intra-ovarian trichomes). Following Puff and Igersheim (1994b), the genus is probably best placed in a tribe of its own. A relationship with *Carphalea* (Hedyotideae) was previously suggested by Baillon (1878). Contrary to *Carphalea*, there are no large idioblasts filled with raphides in the wood of *Jackiopsis*. The axial parenchyma distribution, which is diffuse to diffuse-in-aggregates and scanty paratracheal, agrees with the overall type in the Hedyotideae, but this feature is also found in other clades of the Rubioideae.

The genera *Ariadne* and *Phyllomelia* were recently included in the Rondeletieae (Delprete 1999). Wood type I of the two genera agrees with other genera of the Rondeletieae sensu Rova (1999) (*Acunaeanthus*, *Dendrosipanea*, *Mazaea* and *Rondeletia*). Another similarity of *Ariadne* and *Phyllomelia* with the Rondeletieae is the absence of mineral inclusions in the wood.

Although the presence of Al hyperaccumulation and raphides in *Coptosapelta* may indicate a position within or near the Rubioideae, this genus falls outside all three rubiaceous subfamilies in most molecular analyses. The unique pollen morphological features (Huysmans 1993) as well as the occurrence of T-shaped trichomes (Robbrecht 1977) seem to indicate that *Coptosapelta* may even not belong to the Rubiaceae. A small wood sample of *Coptosapelta* examined by us showed the presence of fibre-tracheids with bordered pits on radial and tangential fibre walls, solitary vessels, uni-

Table 6. Wood anatomy of genera incertae sedis based on data from literature and original observations; + = present, – = absent, ? = unknown, () = rarely or indistinctly present; tribal abbreviations follow Robbrecht (1994). **1** = wood type — **2** = solitary vessels; **3** = radial vessel multiples (number of vessels); **4** = vessel clusters — **5** = septate fibres; **6** = fibre pits simple or minutely bordered; **7** = fibres with distinctly bordered pits on radial and tangential walls — **8** = axial parenchyma diffuse; **9** = axial parenchyma diffuse-in-aggregates; **10** = axial parenchyma paratracheal; **11** = axial parenchyma banded; **12** = axial parenchyma aliform or confluent — **13** = ray width in number of ray cells; **14** = sheath cells; **15** = disjunctive cell walls; **16** = rays < 1 mm — **17** = raphides; **18** = crystal sand; **19** = prismatic crystals; **20** = silica bodies; **21** = styloids — **22** = anomalous features.

Tribes and genera	Wood type	Vessel groupings				Fibres			Axial parenchyma				Rays				Mineral inclusions					Anom. feat.
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Jackieae <i>Jackiopsis</i> (Rubioidae)	I	+	(+)	–	–	–	+	–	+	+	+	–	1, 1–3	–	–	–	–	–	–	–	–	–
<i>Ariadne</i> (syn. <i>Mazaea</i>) <i>Bothriospora</i> (Con./Cal./Sim./Hip.)	I II	+	–	–	–	–	+	+	–	–	–	–	1–3–(4) 2–3	–	–	–	–	–	–	–	–	–
<i>Colletocena</i> (near <i>Oph.</i> ?) <i>Coptosapelta</i> (isolated position)	I I II	+	(2–4)	–	–	–	+	–	–	–	+	–	3–4 1–2	–	+	–	+	–	–	–	–	–
<i>Dialypetalanthus</i> (Con./Cal./Hip./Sim.)		(+)	2–8	–	+	+	–	–	–	(+)	–	–	1, 4–5–(6)	–	–	–	–	(+)	–	–	–	–
<i>Gonzalagunia</i> (Gue.?) <i>Luculia</i> (isolated position)	I I	+	2–4	–	–	–	+	+	–	–	–	–	1–3	+	–	–	–	–	–	–	–	–
<i>Pagameopsis</i> (Hed.?) <i>Phyllomelia</i> (Ron.)	I I	+	–	–	–	–	+	(+)	–	+	–	–	1–3	–	–	–	–	?	?	?	?	–
		+	(2–4)	–	–	–	–	+	+	–	–	–	1–3–(4)	–	+	–	–	–	–	–	–	–

or biseriate rays and a lack of mineral inclusions. Although it is difficult to classify the axial parenchyma distribution in the juvenile wood sample studied, we believe that it is banded and diffuse-in-aggregates. The presence of parenchyma bands is probably an adaptation to the lianescent habit of *Coptosapelta*. The wood anatomy gives no indication for exclusion of the genus from the Rubiaceae.

Several genera that are listed in Table 6 have been discussed above: *Bothriospora* and *Dialypetalanthus* (Ixoroideae s.l. with wood type II), *Colletocema* (basal position in Rubioideae), *Pagameopsis* (Rubioideae, Lasiantheae or Hedyotideae), and *Phyllomelia* (Rondeletieae).

Notes on mineral inclusions in wood of Rubiaceae

Based on their form, size and chemical composition, mineral inclusions are frequently considered to be valuable taxonomic markers in systematic anatomy. Although the occurrence of these structures should also be investigated outside the secondary xylem, e.g. in tissues of leaf, bark or fruit, the following discussion is mainly restricted to our observations in wood.

It is well known that the family Rubiaceae shows a wide variation of calcium oxalate crystals in all tissues, including secondary xylem (e.g. Robbrecht 1988). Two crystal types are very common in Rubiaceae and appear to be mutually exclusive, viz. raphides and crystal sand. Prismatic crystals are also present in numerous taxa, but the presence of styloids, druses or silica bodies is restricted to a smaller number of taxa. Crystals in wood occur most frequently in ray and/or axial parenchyma cells. The crystal-containing cells or idioblasts are distinguished in some species (e.g. *Triainolepis*, *Ixora*, *Versteegia*) by their larger size, and in others (e.g. *Randia exaltata*) by the enhanced thickening of their walls.

We suggest that most crystals are composed of calcium-oxalate, since this is the most common crystal type in plants. However, we did not identify crystals in Rubiaceae as oxalate on the basis of precise methods, such as SEM with an X-ray energy dispersive spectrometer (e.g. Taniguchi et al. 1982; Furuno & Côté 1983). Crystals of other Ca salts or organic compounds may occur in addition to oxalate crystals.

Raphides

Raphides are defined as bundles of needle-shaped crystals and it is well known that the distribution of this crystal type characterises all Rubioideae s.l. Bremekamp's (1966) subfamily was essentially based on the presence of this crystal type. Robbrecht (1988), however, pointed out not to attribute too great an importance to this character since the delimitation of a subfamily on the basis of a single character would seem artificial. Present insights, nevertheless, reestablish the taxonomic value of this character to a great extent. Without studying any material, Bremer and Manen (2000), on the one hand, suggested that *Raritebe* appears to be the first report of a genus without raphides in Rubioideae. Our observations of *Raritebe*, however, have clearly illustrated this crystal type in parenchyma cells around the vascular bundles in leaves. On the other hand, raphides have most likely originated twice during the evolution of the Rubiaceae, namely in the Rubioideae and in the closely related tribes Hamelieae and Hillieae (see below).

Fig. 65. The distribution of mineral inclusions in the secondary xylem plotted on the hypothetical tree given in Fig. 3. The Catesbaeae–Catesbaea group is omitted since no data are available for this group.

We have found raphides in the wood of all tribes of the Rubioideae except for several taxa (Pauridiantheae, Urophylleae, Ophiorrhizeae, *Damnacanthus*, Knoxieae, and Argostemmataeae) (Fig. 65). Raphides, however, do occur in these tribes, but in tissues outside the secondary xylem (e.g., Fig. 53). Hence, the inclusion of the tribes Pauridiantheae, Urophylleae (Cinchonoideae sensu Robbrecht 1988) and Knoxieae and Craterispermeae (Antirheoideae sensu Robbrecht 1988) in the Rubioideae s.l. fits well with the distribution of raphides. Therefore, the absence of raphides in the wood should be interpreted with caution. In general, mineral inclusions are less frequently found in wood than in parenchyma cells of the pith, leaf or bark. Nevertheless, the presence and quantity of raphides in rubiaceaceous wood can be an important character for phylogenetic purposes. Genera in which raphides are very common in the wood are for instance *Craterispermum*, *Coussarea*, *Faramaea*, *Gaertnera*, and *Pagamea*.

Outside the Rubioideae, raphides are present in the related tribes Hamelieae and Hillieae, and a few other genera. The presence of raphides in the enigmatic genus *Coptosapelta* was already observed by Solereder (1893) and confirmed by Fukuoka (1980: see his figure 19B). Raphides are also observed in *Steenisia* by Bremer (1984), a genus placed in the subfamily Rondeletieae. However, Rova (1999) excluded *Steenisia* from the Rondeletieae and proposed a position in Hamelieae. Besides the presence (although very rare in *Steenisia*) of raphides, arguments for this placement may be similarities in exotesta ornamentation and a stalked placenta which is similar to *Deppea*. Much more striking is that Robbrecht (1986) observed raphides in fruit tissues of a single specimen of *Argocoffeopsis* (Ixoroideae, Coffeaeae). Likewise, we observed small needle-like crystals in the pith parenchyma of the stem of *Argocoffeopsis eketensis*. In our opinion, it is not certain whether these mineral inclusions in *Argocoffeopsis* really concern true raphides. Since they do not appear to be a constant and characteristic feature in all specimens of *Argocoffeopsis* examined by us, one cannot exclude the possibility that these “raphides” are an accidental phenomenon of traumatic origin of some kind.

A next question might be which conditions in the cells of Rubioideae or Hamelieae and Hillieae cause deposit in the size of needles? Raphides generally are monoclinic and low pH (4.4) was concluded to favour the monoclinic form of oxalate crystals, while higher pH conditions favour the tetragonal form (Pfeiffer 1925). Indeed, raphides were identified as monoclinic crystal forms (whewellite) in *Psychotria punctata* (Franceschi & Horner 1979), and in *Morinda* and *Hamelia* (Scurfield et al. 1974). It is exceptional to find both monohydric and trihydric crystals occurring together in the same plant (Pobéguin 1943; Metcalfe & Chalk 1983). Remarkably, the occurrence of raphides in Rubiaceae is obviously related with aluminium hyperaccumulation (Jansen et al. 2000a, b). Chenery (1948) concluded that a low cell sap acidity (pH 3.6–5.2) very frequently characterises aluminium plants too. It should nevertheless be stressed that the relationship between the occurrence of raphides and aluminium hyperaccumulation needs further investigation. Many taxa that possess raphides do not hyperaccumulate aluminium, e.g. a large number of monocotyledons.

Crystal sand

Crystal sand is a term applied to accumulations of minute, variously shaped prismatic crystals resembling sand when viewed under the microscope. They are com-

mon in only few dicotyledonous families, viz. *Amaranthaceae*, *Solanaceae*, and *Rubiaceae* (Metcalfe & Chalk 1983). These crystals are generally trihydric. Within the *Rubiaceae*, crystal sand is very common in the wood of numerous taxa of the *Ixoroideae* s.l. (except the core *Ixoroideae*) and to a lesser extent in the *Cinchonoideae* s. str. The feature is not observed in any representative of the *Rubioideae*.

Prismatic crystals

Besides raphides and crystal sand, other crystals are less common in *Rubiaceae* and share a restricted distribution. Prismatic crystals are characteristic of wood of most core *Ixoroideae* s. str. (*Coffeeae*, *Gardenieae*, *Octotropideae*), but there are also reports of this crystal type in some *Rubioideae* (*Schraderea*, and three genera of the *Hedyotideae*). The distribution of prismatic crystals in the *Hedyotideae*, *Guettardeae* and the genus *Rondeletia* needs verification and further examination.

Other mineral inclusions

Druses or cluster crystals are loosely aggregated crystals in more or less spherical groups with few to many components. They are one of the most common crystal types amongst dicotyledons. Since they are much more common outside the secondary xylem, a discussion of this crystal type in *Rubiaceae* is beyond the scope of this preliminary survey. The taxonomic implications of the occurrence of styloids and silica bodies are discussed in the taxonomic section above.

Comparison of the Rubiaceae with allied families

The wood structure of the *Rubiaceae* agrees well with the other families of the *Gentianales* sensu APG (1998). Wood features common in the families include: simple perforation plates, fibre-tracheids, vestured pits and heterogeneous rays (type II A or II B). Most noteworthy is the lack of intraxylary phloem in *Rubiaceae*, since this feature occurs in all other families of the *Gentianales* (e.g. Carlquist 1992).

The order *Garryales* sensu APG, including *Aucubaceae*, *Eucommiaceae*, *Garryaceae* and *Oncothecaceae*, takes a basal position within the euasterids I (APG 1998; Soltis et al. 2000). The wood anatomy of these families is characterised by mostly solitary vessels (rarely in multiples or clusters), scalariform perforation plates (except for *Eucommia*), opposite to alternate (rarely scalariform) intervessel pitting, nonvestured pits and distinct helical thickenings throughout vessel elements in *Aucuba*, *Eucommia* and *Garrya* (Tippo 1940; Moseley & Beeks 1955; Baas 1975; Carpenter & Dickison 1976; Noshiro & Baas 1998). Moreover, axial parenchyma is scanty paratracheal (especially in *Aucuba* and *Oncotheca*) and diffuse or diffuse-in-aggregates. Fibre-tracheids with distinctly bordered pits in both radial and tangential walls occur in *Eucommia*, *Garrya* and *Oncotheca*, but minutely bordered pits in radial walls and occasionally septate fibres are found in *Aucuba*. Hence, there are major differences between the *Garryales* and most representatives of the *Gentianales* with respect to the structure of the secondary xylem.

CONCLUSIONS

Although wood anatomy of the Rubiaceae exhibits a relatively narrow range of structural variability, it constitutes an important set of taxonomical characters when attempting to reconstruct an evolutionary scenario of the Rubiaceae. The two main wood types occurring in Rubiaceae are powerful tools that should be used as important elements in any data matrix of the family. In fact, wood anatomical data especially allow to confirm or negate already existing or proposed relationships among rubiaceous tribes and genera rather than to hypothesise precise taxonomic positions. Thus, wood anatomy can be used as an independent test of systematic hypothesis; relationships that are not consistent with respect to their wood anatomical pattern should be seriously questioned.

Since wood anatomy only partly resolves some taxonomic problems in the Rubiaceae, it is not possible to propose an alternative formal taxonomic classification of the Rubiaceae, containing a significantly higher degree of monophyly of the constituting groups than the current classifications. We need a much more extensive sampling of taxa for molecular systematics to increase our understanding of the phylogeny of the Rubiaceae since many relationships are obscure and resolution in several groups is poor. Also, taxa taken for monophyletic or phylogenetically closely related may prove not to be so. More importantly, combined molecular and structural analyses are required since both can contribute meaningfully to interpreting evolutionary relationships within the Rubiaceae.

Conclusions drawn from this wood anatomical study can be summarised in the following points from subfamilial level down to generic level.

Subfamilial level conclusions

- Although there is no wood anatomical support for any of the three subfamilies Rubioideae, Ixoroideae s.l. or Cinchonoideae s.str, there is an overall agreement between the two rubiaceous wood types and recent phylogenetic hypotheses. Wood type I is most widespread and characterises for instance the core Ixoroideae. Wood type II shows many parallel origins and is demonstrated to characterise the following groups: 1) Hillieae and Hamelieae, 2) Cinchoneae, 3) Ixoroideae s.l. excluding the core Ixoroideae, 4) Coussareeae and Coccocypseleae, 5) Psychotrieae, 6) Argostemmatae, and 7) Paederieae.
- Raphides are most likely to have evolved independently in two related tribes of the Cinchonoideae (Hillieae and Hamelieae) and in the Rubioideae. The raphide-bearing, isolated genus *Coptosapelta* needs further consideration and investigation.
- The herbaceous habit has originated several times in the family, but most particularly in the derived clades of the Rubioideae. There are strong indications for cases of secondary woodiness in the Rubieae and Anthospermeae.

Tribal level conclusions

- The wood anatomical heterogeneity of the Guettardeae is exceptional compared to the general homogeneity at the tribal level. A thorough study is needed addressing the problem of the taxonomic delimitation of the Guettardeae as well as a revision of its genera.

- Henriquezieae take an isolated position within the Rubiaceae on the basis of ali-form to confluent axial parenchyma and uniseriate, low rays.
- Wood type II confirms the close relationship between the following tribes: 1) Hillieae and Hamelieae, 2) Coussareeae and Coccocypseleae, 3) Hippotideae, Simireae, Condamineae, Calycophylleae and possibly Mussaendeae. Other tribes in which wood type II is represented include Psychotrieae, Argostemmatae, Paederieae, Cinchoneae, and part of the Guettardeae.
- Delprete's (1999) very wide concept of the Rondeletieae is contradicted. While many Rondeletieae are members of the Cinchonoideae s.str., the former Condamineae appertain to Ixoroideae s.l.
- Axial parenchyma bands confirm possible affinities between 1) Craterispermeae, Gaertnereae, Schradereae and Morindeae, and 2) Retiniphyllae and Ixoreae.
- Prismatic, solitary crystals are characteristic of most core Ixoroideae: Gardenieae (incl. Aulacocalyceae), Coffeae, Octotropideae, and to a lesser extent Pavetteae.
- Crystal sand is characteristic of the Ixoroideae s.l. that show wood type II.
- Helical thickenings in axial parenchyma cells are an unusual feature of the secondary xylem that links Pauridiantheae and Urophylleae to *Lasianthus* and *Trichostachys*.
- It is better to place *Gaertnera* and *Pagamea* in a separate tribe Gaertnereae instead of a subtribe Gaertnerinae in the Psychotrieae.

Generic level conclusions

- Wood anatomy supports the inclusion of the following genera in the Ixoroideae s.l. with type II: *Bathysa*, *Dialypetalanthus*, *Elaeagia*, *Macbrideina*, *Mastixiodendron*, and *Warszewiczia*.
- Silica bodies support the strong affinity between *Platycarpum* and *Henriquezia* as well as between *Hallea* and *Mitragyna*.
- Banded parenchyma is suggested to be a synapomorphy for the *Alibertia* group (Gardenieae).
- *Posoqueria* can be distinguished from the Gardenieae by several wood anatomical features.
- Wood type I corroborates the recent exclusion of *Colletocema*, *Lasianthus*, and *Pagameopsis* from the Psychotrieae (wood type II).
- *Mussaendopsis* (wood type II) should be excluded from the *Corynanthe* group (wood type I).
- The heterogeneity in the wood structure of *Coprosma* (Anthospermeae) needs further examination with respect to juvenilism and ecological and geographical considerations.

ACKNOWLEDGEMENTS

P. Baas and J. Koek-Noorman suggested numerous improvements to the manuscript. We are grateful to Anja Vandepierre for technical assistance with slide preparations, darkroom work and the preparation of the figures. We thank E.A. Wheeler for references on fossil woods of Rubiaceae. The directors and curators of the herbaria K, L, U, MO and U are acknowledged for making their specimens available and supplying us generously with study material. Steven Jansen is a postdoctoral

fellow of the Fund for Scientific Research-Flanders (Belgium) (F.W.O.-Vlaanderen). Research at the Laboratory of Plant Systematics is supported by grants from the Research Council of the K.U. Leuven (OT/01/25) and the Fund for Scientific Research-Flanders (Belgium) (G.104.01).

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