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Sweden 1999

The Condamineae-Rondeletieae-Sipaneeae Complex (Rubiaceae)

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THE

CONDAMINEAE
RONDELETIEAE
SIPANEEAE
COMPLEX

(RUBIACEAE)



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Dissertation

**THE
RONDELETIEAE-CONDAMINEEAE-SIPANEEAE
COMPLEX
(RUBIACEAE)**

Johan H. E. Rova



Göteborg 1999

Errata

J.H.E. Rova. 1999. The Condamineae-Rondeletiae-Sipaneeae Complex (Rubiaceae). Botanical Institute, Göteborg University, Box 461, SE-405 30 Göteborg.

1. The title on the cover pages should read "The Condamineae-Rondeletiae-Sipaneeae Complex (Rubiaceae)".

2. Appendix 2 in Paper II was left out by the printing office and should read:

APPENDIX 2: Classification history

Subfamilial and tribal classifications of analyzed Rubiaceae genera as previously proposed by various authors, and compared to the results of the present *rps16* phylogeny. Only genera not listed in Rova et al. (submitted) are included. Subfamilies ("tribes" in Candolle, 1830) are given with four letters: **anti**-Antirrhoideae, **cinc**-Cinchonoideae, **coff**-Coffeoidae, **gard**-Gardeniaceae, **guet**-Guettardoideae, **hame**-Hamelieae, **hame**-Hamelieae, **hedy**-Hedyotideae, **hill**-Hillioideae, **ixor**-Ixoroidae, **oper**-Opercularieae, and **rubi**-Rubioidae. Tribes ("subtribes" in Candolle, 1830) are given with three letters: **chi**-Chiococceae, **cinc**-Cinchoneae, **con**-Condamineae, **cop**-Coptosapeltae, **gar**-Gardenieae, **gue**-Guettardeae, **ham**-Hamelieae, **hil**-Hillieae, **nau**-Nauclaeae, and **ron**-Rondeletieae. Hooker's "series" are given with one letter: a-Series A (many ovules in each locule) and c-Series C (solitary ovule in each locule). "-" means that the genus (or a synonym for it) was not considered by the author; "?" means an uncertain position according to the author. Footnotes in the table are as follows: ^a as *Laugeria*, ^b as *Anthocephalus*, ^c implicitly in that Bremekamp is supposed to follow 1) Schumann and 2) Hooker in this case, ^d as included in *Calycophyllum*.

Genus	Candolle (1830)	Hooker (1873)	Schumann (1891)	Verdcourt (1958)	Bremekamp (1966)	Robbrecht (1988)	Robbrecht (1993)	rps16
<i>Alibertia</i>	hame	a-gar	cinc-gar	-	ixor-gar	ixor-gar	ixor-gar	IXO2
<i>Amaioua</i>	gard-gar	a-gar	cinc-gar	-	-	ixor-gar	ixor-gar	IXO2
<i>Attractogyne</i>	-	-	cinc-gar	-	-	ixor-gar	ixor-gar	IXO2
<i>Bobea</i> Gaud.	-	c-gue	coff-gue	-	guet-gue ^c	anti-gue	anti-gue	CIN5
<i>Bothriospora</i>	-	a-ham	cinc-gar	-	-	?	?	IXO1
<i>Burchellia</i>	gard-gar	a-gar	cinc-gar	-	-	ixor-gar	ixor-gar	IXO2
<i>Cremaspora</i>	-	c-alb	coff-alb	cinc-ixo	-	ixor-gar	ixor-gar	IXO2
<i>Cuatrecasasiodendron</i>	-	-	-	-	-	cinc-ron	cinc-ron	CIN5a
<i>Deppea</i>	oper	a-ron	cinc-ron	rubi-?	?	rubi-ham	rubi-ham	CIN2
<i>Dolichobolium</i>	-	a-cin	cinc-cin	-	-	cinc-cin	cinc-cin	IXO1
<i>Femelia</i>	gard-gar	a-gar	cinc-gar	-	-	ixor-oct (as hyp)	ixor-oct	IXO2
<i>Hillia</i>	cinc-cin	a-cin	cinc-cin	rubi-?	hill-hil	cinc-hil	cinc-hil	CIN2
<i>Hymenodictyon</i>	cinc-cin	a-cin	cinc-cin	cinc-cin	not ixor-cop	cinc-cin	cinc-cop	CIN3
<i>Kerianthera</i>	-	-	-	-	-	cinc-con	cinc-con	CIN6
<i>Macrocneum</i> P. Br.	hedy-ron	a-cin	cinc-cin	-	-	cinc-cin	cinc-cin	IXO1
<i>Malanea</i>	guet-gue	c-gue	coff-gue	-	-	anti-gue	anti-gue	CIN5a
<i>Mastixiodendron</i>	-	-	-	-	-	?anti-chi	anti-?chi	IXO1
<i>Neolamarckia</i>	-	-	-	-	cinc-?cin ^b	cinc-nau	cinc-nau	CIN3
<i>Neolaugeria</i>	-	c-gue ^a	-	-	-	anti-gue	anti-gue	CIN5a
<i>Oxyanthus</i>	gard-gar	a-gar	cinc-gar	-	-	ixor-gar	ixor-gar	IXO2
<i>Sabicea</i>	hame-ham	a-ise	cinc-mus	cinc-mus	cinc-sab	cinc-ise	cinc-ise	IXO5
<i>Semaphyllanth</i>	-	-	-	-	-	cinc-cin ^d	cinc-cin ^d	IXO1
<i>Stilpnophyllum</i>	-	a-cin	cinc-cin	-	-	cinc-cin	cinc-?cin	CIN1
<i>Virotaria</i>	hedy-ron	a-hed	-	cinc-?	urop-oph	rubi-hed	rubi-hed	IXO5

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ABSTRACT

Rova, J. H. E. 1999. The Condamineae-Rondeletiae-Sipaneae complex (Rubiaceae). Botanical Institute, University of Göteborg, Sweden. ISBN 91-88896-16-1.

Tribal demarcations in the Condamineae-Rondeletiae-Sipaneae complex (Rubiaceae) are inferred from phylogenies based on chloroplast *trnL* intron, *trnL*-F spacer, and *rps16* DNA sequence data. Cladistic analyses of the *trnL*-F data and *rps16* data are presented in two separate papers, and a jackknife analysis of the combined data set (including 126 Rubiaceae terminals and 738 informative characters) is presented in the thesis.

It is found that the Condamineae-Rondeletiae-Sipaneae complex is not monophyletic. Condamineae in a strict sense forms a poorly resolved complex together with Calycophylleae, Hippotideae, and Simireae in subfamily Ixoroideae. Rondeletiae in a strict sense belongs in subfamily Cinchonoideae. Sipaneae is found in subfamily Ixoroideae. A number of genera should be transferred from Rondeletiae to the Condamineae complex and other parts of subfamily Ixoroideae. Other genera should be transferred from Rondeletiae to Guettardeae, which is found to be the sister tribe to Rondeletiae. Support was found for a splitting of *Rondeletia* into several smaller genera, but the generic boundaries between some of these segregates could not be finally settled. The *Portlandia*-group is closely related to Catesbaeeae and Chiococceae within Cinchonoideae. Limited support is found for a separation of Catesbaeeae from Chiococceae. Further, subfamily Antirheoideae is shown to be polyphyletic, and only three large subfamilies should be recognized in Rubiaceae: Cinchonoideae, Ixoroideae, and Rubioideae. The taxonomic history of the tribes of central importance to this study is briefly reviewed, and systematic positions are suggested for a number of hitherto unplaced genera.

KEY WORDS

Antirheoideae, Catesbaeeae, Chiococceae, Condamineae, Guettardeae, Rondeletiae, *rps16*, Rubiaceae, Sipaneae, *trnL*-F

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The Condamineae-Rondeletiae-Sipaneeae Complex (Rubiaceae)

Johan H. E. Rova

INTRODUCTION

To communicate, we need a common language. In this language, we must agree on what to call the different objects and phenomena that we find interesting enough to discuss with other people. To understand the world around us, we must also establish how these objects and phenomena are related to each other – both physically and causally. In biology, as well as in other sciences, the naming of things is the field of taxonomy, whereas the establishment of relationships is the field of systematics. Taxonomy and systematics are interconnected. In modern biology, a sound taxonomy should mirror the evolutionary relationships of a group, i.e., we should endeavor to classify groups of organisms (taxa) based on their common ancestry, not on how similar they look. Such a sound taxonomy is called natural. A natural taxonomy is the necessary basis for all studies where interest is put on more than one individual – be that character evolution, ecology, conservation biology, or the simple wish to find relatives to a medically interesting plant. The aim of this study is to provide a phylogeny for the establishment of a natural and practically useful taxonomy within the plant family Rubiaceae.

The Rubiaceae is the fourth largest family of flowering plants, comprising approximately 650 genera and 12000 species (Delprete, 1999). Most representatives are tropical shrubs or trees, but a number of predominantly herbaceous genera are found in temperate and boreal regions. The family includes several economically and medically important plants, such as *Coffea* (coffee) and *Cinchona* (source of the anti-malarial alkaloid quinine). Some Rubiaceae are also

grown for ornamental purposes (e.g., *Gardenia* and *Ixora*), or as dyes (*Rubia*) and tanning agents (*Uncaria*) (Aldén et al., 1998). A number of Rubiaceae species are Ni-hyperaccumulators attaining a dry matter Ni concentration of 1–5% (Jaffré and Schmid, 1974; Reeves et al., 1999).

A family the size of the Rubiaceae needs to be subdivided into smaller and more manageable units in order to facilitate the understanding of its diversity and evolution. Robbrecht (1988) elegantly presented a modern view of Rubiaceae interrelationships by drawing tribes and subfamilies as circles and borders in a two-dimensional landscape. The tribes Condamineae, Rondeletiae, and Sipaneeae were drawn as confluent circles within subfamily Cinchonoideae. By doing this, he stressed that tribal demarcations in this complex were in need of a more thorough investigation.

This thesis work started out as an attempt to find tribal demarcations within this predominantly neotropical Condamineae-Rondeletiae-Sipaneeae complex. As the study progressed, however, unexpected results appeared and a number of other tribes also had to be included in order to find a solution to the problem. Thus, this thesis deals not only with the tribes Condamineae, Rondeletiae, and Sipaneeae, but also with Calycophylleae, Catesbaeeae, Chiococceae, Guettardeae, and Simireae. The study is based on cladistic analyses of chloroplast DNA sequence data from three regions: the *trnL* intron and *trnL*-F intergenic spacer (Paper I) and the *rps16* intron (Paper II). A combined analysis is also performed. The results are discussed from a mainly morphologic and taxonomic-historical point of view, and the

impact of the results on current subfamilial and tribal classifications within Rubiaceae and the Condamineae-Rondeletieae-Sipaneeae complex is discussed.

BACKGROUND

Cardinal characters and early Rubiaceae macrosystematics

Early workers in Rubiaceae macrosystematics organized the family by means of a very limited number of characters. The opinion on which characters to regard as most important varied from author to author, and the resulting classifications were, although simple to follow, often highly unnatural. Candolle (1830) used mainly fruit and inflorescence characters. He put special emphasis on fruit type, number of seeds, and the occurrence of capitulate inflorescences for the characterization of infrafamilial taxa in his "Conspectus Tribuum", which contained 19 tribes and subtribes. Hooker (1873) also used number of seeds per locule, but included also characters such as type of corolla aestivation and ovule insertion; his classification comprised 25 tribes arranged in three "series". The ideas of Hooker were taken over, without major changes, by Schumann (1891), who listed 21 tribes under two subfamilies and four "supertribes". Verdcourt (1958) tried to use a phylogenetic way of thinking, and he also discussed a considerably wider spectrum of characters than previous authors. In his subfamilial/tribal conspectus he put emphasis on the presence or absence of raphides and the amount of endosperm in the seeds, but included also, e.g., seed and fruit characters, aestivation states, tendencies to be aluminum accumulators, the occurrence of secondary pollen presentation, chromosome number, and pollen characters. According to Verdcourt, three subfamilies and at least 29 tribes should be recognized in Rubiaceae. Bremekamp (1934, 1952, 1966) also used a large number of characters for his classification, stressing especially the importance of exotesta sculpturing, secondary pollen presentation, and the occurrence of raphides. His 1966 classification comprised as many as eight subfamilies (many of them very small) and 41 tribes.

Subfamilies of Rubiaceae – Robbrecht's view

The works of Robbrecht (1988, with supplement 1993a,b) are the most recent worldwide treatments of Rubiaceae macrosystematics. In his surveys, Robbrecht used Bremekamp's subfamilies and tribes as base, and emended them according to the latest achievements in the field of Rubiaceae systematics. It is worth noting that the work of Robbrecht (1988) was probably the last classification mainly based on morphological characters; the first molecular systematic papers in Rubiaceae appeared only a few years later. According to Robbrecht, the Rubiaceae should be divided into four subfamilies "based on distinct character combinations and trends": Antirheoideae, Cinchonoideae, Ixoroideae, and Rubioideae. Antirheoideae was, in general, characterized by valvate aestivation, presence of secondary pollen presentation (SPP), placentas with a single, pendulous ovule, fleshy fruits (drupes), soft and oily endosperm, very large embryos, and absence of raphides. Cinchonoideae was characterized by usually valvate or imbricate corolla aestivation, numerous ovules on each placenta, usually dry fruits (capsules), exotesta cells with thickenings on the inner tangential wall, and the absence of both raphides (except in Pauridiantheae and Urophyllaeae) and SPP. Ixoroideae was distinguished by having contorted aestivation, mostly pluriovulate placentas, fleshy fruits (berries), general absence of raphides, and general presence of SPP. Rubioideae was characterized by a mostly valvate corolla aestivation and the general presence of raphides. In total, Robbrecht (1993b) recognized 41 tribes or comparable groups of genera. The most radical action taken by Robbrecht was his creation of subfamily Antirheoideae. This subfamily was based on an emendment of Bremekamp's (1952) Guettardoideae with the inclusion of a number of former Ixoroideae tribes.

This study is initiated...

Especially in the Cinchonoideae, Robbrecht (1988) pointed out that he had problems to clearly state the distinctions between tribes. Cinchoneae,

Condamineae, and Rondeletiae were separated only by characters such as seeds “mostly” or “mostly not” winged, differences in ovule insertion, and, most consistently, by differences in corolla aestivation. Condamineae was distinguished by valvate corolla aestivation, Rondeletiae by imbricate or contorted, and Sipaneae by contorted aestivation. It was these difficulties in establishing distinct tribal delimitations that made Robbrecht (1988) present the Condamineae, Rondeletiae, and Sipaneae as a blurred complex in his graphic representation of the Rubiaceae.

Based on the assumption that Condamineae, Rondeletiae, and Sipaneae, nevertheless, formed a monophyletic group, initial taxon sampling for the present study focused on the genera listed under these tribes by Robbrecht (1988, 1993b). Other tribes, and other subfamilies than Cinchonoideae, were sampled less densely, although an effort was made to include at least one representative from each tribe in the family.

...and needs to be enlarged

After cladistic analyses of the preliminary taxon sample, it stood clear that the tribes Condamineae, Rondeletiae, and Sipaneae were far from as confluent as proposed by Robbrecht (1988). Both the entire complex and the different tribes were found to be polyphyletic, with Condamineae and Rondeletiae split between the subfamilies Cinchonoideae and Ixoroideae. While the *Portlandia*-group of Condamineae was found to have its closest relatives in the tribes Catesbaeeae and Chiococceae of Cinchonoideae, the “core Condamineae”, including *Condaminea*, were found to be affiliated with the tribes Calycophylleae and Hippotideae in Ixoroideae. *Rondeletia*, and its closest relatives, seemed to remain in Cinchonoideae, whereas a number of other Rondeletiae genera should be transferred to Ixoroideae — either to the vicinity of *Condaminea*, or to the vicinity of Vanguerieae and Gardenieae. Sipaneae was, moreover, found to belong in Ixoroideae — not at all in the vicinity

of *Rondeletia* in Cinchonoideae. Before the systematic positions of the Condamineae-Rondeletiae-Sipaneae genera finally could be settled, taxon sampling obviously had to be increased in parts of Rubiaceae previously thought to be of less interest to this study.

Furthermore, representatives of Guettardeae were shown to be closely related to *Rondeletia* (Bremer et al., 1995), and this tribe was therefore included in the study. Since all of the tribes Guettardeae, Chiococceae and Vanguerieae were listed in Robbrecht’s subfamily Antirheoideae (Robbrecht, 1988; 1993b), it was now obvious that a study on the Condamineae-Rondeletiae-Sipaneae complex had to involve representatives from at least three of the four subfamilies of Rubiaceae proposed by Robbrecht (1988, 1993b): Antirheoideae, Cinchonoideae, and Ixoroideae. Reasons for this confused situation were at least partly explained by the molecular studies that now began to be published (Bremer et al., 1995; Young et al., 1996) — studies that indicated the breakdown of Robbrecht’s (1988, 1993b) subfamily Antirheoideae and a need to re-delimitate the other Rubiaceae subfamilies.

In conclusion, the preliminary results enforced an increased taxon sampling from subfamilies Antirheoideae, Cinchonoideae, and Ixoroideae. Above all, these further sampling efforts were focused in Calycophylleae, Catesbaeeae, Chiococceae, Hippotideae, and Guettardeae, since these tribes turned out to be most closely related to the fragmented Condamineae-Rondeletiae-Sipaneae complex. Thus, circumscriptions of these tribes are also discussed in this thesis.

Relevant tribes: their circumscription and history

A concise discussion on recent and historical classifications of the entire Rubiaceae is found in Robbrecht (1988). An account on the systematic and taxonomic history of the family, with an emphasis on the Rondeletiae and related tribes (except Guettardeae), is also found in Delprete (1999). The taxonomic history of the Catesbaeeae, Chiococceae, Condamineae, and

Rondeletieae is concisely reviewed in Delprete (1996a). Nevertheless, a brief introduction to the taxonomic history of the taxa in focus of this thesis could be justified, and follows below. Here, as in other parts of this thesis, authors to genera are only included when homonymous genera exist.

Calycophylleae. The tribe Calycophylleae is the most recently described of the tribes in focus of this study. It was established by Andersson and Persson (1991) to include *Alseis*, *Calycophyllum*, *Schizocalyx*, and *Wittmackanthus*. An inclusion of *Emmenopterys* in this tribe was also discussed, but no such decision was made due to missing data. All these genera had been included in Cinchoneae subtribe Cinchoninae by Robbrecht (1988), and all of them (except *Alseis*) include species possessing calycophylls, i.e. showy, leaflike calyx lobes. The tribe was also accepted by Robbrecht (1993b), who characterized it by having, e.g., imbricate or valvate aestivation, exerted stamens, anthers without connective process, and the general presence of calycophylls.

Catesbaeae and *Hippotideae*. The *Catesbaeae* was established by Hooker (1873) to comprise *Catesbaea*, *Pentagonia*, *Phyllacanthus*, *Sommeria*, and *Tammsia*. Characteristic features for this tribe was — according to Hooker — a valvate corolla aestivation and numerous, large, and compressed seeds. García Kirkbride (1981) removed *Pentagonia* and *Sommeria* and placed them in a new tribe, *Hippotideae*, together with *Hippotis*, which had been included in *Mussaendeae* by Hooker (1873). *Tammsia* was at the same time transferred to a monogeneric tribe *Tammsieae* (sunk into *Hippotideae* by Rova and Andersson, 1995). Robbrecht (1988, 1993b) included only *Catesbaea* and *Phyllacanthus* in *Catesbaeae*; in 1988 it was listed as *tribus incertae*, but in 1993 (following the results presented by P. Delprete at the First International Rubiaceae Conference) *Catesbaeae* was noted as “apparently related to *Portlandia*-group” (see under *Chiococceae*). *Catesbaeae* was later (Delprete, 1996a) recircumscribed to include both *Catesbaea* and *Phyllacanthus*, together with *Thogsennia* and the *Portlandia*-group, i.e., *Bikkia*, *Ceuthocarpus*, *Coutaportia*, *Coutarea*,

Cubanola, *Hintonia*, *Isidorea*, *Nernstia*, *Osa*, *Portlandia*, *Schmidtotia*, and *Siemensia*.

Chiococceae. The tribe *Chiococceae* was established by Hooker (1873) to accommodate 11 genera characterized by solitary ovules, stamens inserted at the corolla base, and albuminous seeds: *Asemnantha*, *Ceratopyxis*, *Chiococca*, *Chione*, *Erithalis*, *Hodgkinsonia*, *Phialanthus*, *Placocarpa*, *Salzmannia*, *Scolosanthus*, and *Tertrea* (a synonym of *Machaonia*, now in *Guettardeae*). This view was followed by Schumann (1891), and the delimitation of this tribe remained almost unchanged until Bremer and Jansen (1991) showed a close relationship between *Chiococceae* and the genera *Exostema* and *Hintonia* (as *Coutarea latifolia*) of subfamily *Cinchonoideae*. Based on molecular and morphological data, Bremer (1992) recircumscribed *Chiococceae* to include a number of genera from Robbrecht’s (1988) *Condamineae* (subtribe *Portlandiinae*) and *Cinchoneae*, as well as some genera of uncertain systematic position. The tribe was now characterized by, e.g., slightly imbricate corolla lobes, more or less bell-shaped corollas, usually villous filaments fused into a basal ring, and linear anthers. On the other hand, Bremer excluded *Allenanthus*, *Chione*, *Hodgkinsonia*, *Phialanthus*, and tentatively also *Placocarpa*, from *Chiococceae*. Robbrecht (1993a,b) was skeptical to the idea of uniting the *Portlandia*-group with *Chiococceae*, and instead just separated it from the other *Condamineae* to an informal group at tribal level. Delprete (1996a) transferred the *Portlandia*-group from *Chiococceae* (sensu Bremer, 1992) to *Catesbaeae*, and circumscribed *Chiococceae* in a way almost identical to that of Hooker, including *Allenanthus*, *Asemnantha*, *Ceratopyxis*, *Chiococca*, *Chione*, *Erithalis*, *Phialanthus*, *Placocarpa*, *Salzmannia*, *Scolosanthus*, and *Shaferocharis*. A summary of taxa related to *Catesbaeae*, *Chiococceae*, and the *Portlandia*-group in comparison to the results presented here is found in Tab. 1.

Tab. 1. List of genera included in the Catesbaeeae according to the present study sorted by tribal position according to Robbrecht (1993b). For genera not included in the phylogenetic analyses, sources for suggested tribal placement are given. “?”-unknown position in subfamily or tribe; “-”-not treated; **anti**-Antirheoideae; **cinc**-Cinchonoideae; **rubi**-Rubioidae; **cat**-Catesbaeeae; **chi**-Chiococceae; **gue**-Guettardeae; **hed**-Hedyotideae; **por**-*Portlandia*-group.

Genus	Robbrecht (1993)	<i>trnL-F</i> (Paper I)	<i>rps16</i> (Paper II)	Combined analysis	Suggested tribal placement	Notes
<i>Coutaportia</i>	?	C4	CIN4	C4	cinc-cat	
<i>Hintonia</i>	?	C4	CIN4	C4	cinc-cat	
<i>Phialanthus</i>	?	C4	CIN4	C4	cinc-cat[chi]	
<i>Placocarpa</i>	?	-	-	-	cinc-cat[chi]	Based on Delprete (1996a)
<i>Schmidtottia</i>	?	C4	CIN4	C4	cinc-cat[chi]	
<i>Catesbaea</i>	?-cat	C4	CIN4	C4	cinc-cat	
<i>Phyllacanthus</i>	?-cat	C4	-	-	cinc-cat	To be synonymized with <i>Catesbaea</i> (Paper I)
<i>Asemnantha</i>	anti-chi	C4	CIN4	C4	cinc-cat[chi]	
<i>Ceratopyxis</i>	anti-chi	C4	CIN4	C4	cinc-cat[chi]	
<i>Chiococca</i>	anti-chi	C4	CIN4	C4	cinc-cat[chi]	
<i>Erithalis</i> P. Br.	anti-chi	C4	CIN4	C4	cinc-cat[chi]	
<i>Salzmannia</i>	anti-chi	-	-	-	cinc-cat[chi]	Based on Bremer (1992) and Delprete (1996a)
<i>Scolosanthus</i>	anti-chi	C4	CIN4	C4	cinc-cat[chi]	
<i>Shaferocaris</i>	anti-chi	-	-	-	cinc-cat[chi]	Based on Delprete (1996a)
<i>Hodgkinsonia</i>	anti-gue	-	-	-	cinc-cat[chi]	Based on Delprete (1996a)
<i>Badusa</i>	cinc-por	C4	-	-	cinc-cat[chi]	
<i>Bikkia</i>	cinc-por	C4	-	-	cinc-cat[chi]	
<i>Ceuthocarpus</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Coutarea</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Cubanola</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Exostema</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Isidorea</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Morierina</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Nernstia</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Osa</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Portlandia</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Syringantha</i>	cinc-por	-	-	-	cinc-cat	Based on Robbrecht (1993a)
<i>Thogsennia</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Siemensia</i>	rubi-?hed	C4	CIN4	C4	cinc-cat[chi]	

Condamineae. The tribe *Condamineae* (“*Condaminieae*”) was established by Hooker (1873) and was separated from *Rondeletieae* based on its mostly valvate corolla aestivation. It comprised nine genera: *Bikkia*, *Chimarrhis*, *Condaminea*, *Isidorea*, *Morierina*, *Pinckneya*, *Pogonopus*, *Portlandia*, and *Rustia*. This

delimitation was maintained with only minor changes until Robbrecht’s (1988) classification, where *Condamineae* comprised 24 included or tentatively included genera. This increase in genera was mainly caused by a splitting of *Hintonia*, *Portlandia*, and *Schmidtottia* into several smaller genera (Aiello, 1979), and the

Genus	Robb-recht (1993)	trnL-F (Paper I)	rps16 (Paper II)	Combined analysis	Suggested tribal placement	Notes
<i>Bothriospora</i>	?	-	IXO1	-	ixor-con	
<i>Emmenopterys</i>	?	I1	IXO1	I1	ixor-con	
<i>Phitopsis</i>	?	-	-	-	ixor-con	Possibly congeneric with <i>Bathysa</i> (Delprete, 1999: 13)
<i>Hippotis</i>	?-hip	I1	IXO1	I1	ixor-con[hip]	
<i>Pentagonia</i>	?-hip	I1	IXO1	I1	ixor-con[hip]	
<i>Sommeria</i>	?-hip	I1	IXO1	I1	ixor-con[hip]	
<i>Tammsia</i>	?-tam	-	-	-	ixor-con[hip]	Based on Rova & Andersson (1995)
<i>Mastixiodendron</i>	anti-?chi		IXO1		ixor-con	
<i>Alseis</i>	cinc-cal	I1	IXO1	I1	ixor-con[cal]	
<i>Calycophyllum</i>	cinc-cal	I1	IXO1	I1	ixor-con[cal]	
<i>Schizocalyx</i>	cinc-cal	-	-	-	ixor-con	Synonymized with <i>Bathysa</i> (Delprete, 1997)
<i>Wittmackanthus</i>	cinc-cal	I1	IXO1	I1	ixor-con[cal]	
<i>Capirona</i>	cinc-cin	I1	IXO1	I1	ixor-con[cal]	
<i>Ferdinandusa</i>	cinc-cin	-	-	-	ixor-con[cal]	Based on Andersson (1995)
<i>Macrocnemum</i> P. Br.	cinc-cin	-	IXO1	-	ixor-con[cal]	
<i>Semaphyllanthe</i>	cinc-cin*	-	IXO1	-	ixor-con[cal]	*As included in <i>Calycophyllum</i>
<i>Chimarrhis</i>	cinc-con	I1	IXO1	I1	ixor-con[cal]	
<i>Condaminea</i>	cinc-con	I1	IXO1	I1	ixor-con	
<i>Dioicodendron</i>	cinc-con	I1	IXO1	I1	ixor-con	
<i>Flexanthera</i>	cinc-con	-	-	-	ixor-con	Synonymized with <i>Simira</i> (Delprete, 1999 and references therein)
<i>Kajewskiella</i>	cinc-con*	-	-	-	rubi-hed	Based on Tange (1995); *tentatively included by Robbrecht (1993b)
<i>Kerianthera</i>	cinc-con	-	CIN6	-	cinc-ise	
<i>Parachimarrhis</i>	cinc-con	I1	IXO1	I1	ixor-con[cal]	
<i>Picardaea</i>	cinc-con	I1	IXO1	I1	ixor-con	
<i>Pinckneya</i>	cinc-con	I1	IXO1	I1	ixor-con[cal]	
<i>Pogonopus</i>	cinc-con	I1	IXO1	I1	ixor-con[cal]	
<i>Rustia</i>	cinc-con	I1	IXO1	I1	ixor-con	
<i>Stomandra</i>	cinc-con*	-	-	-	ixor-con	Synonymized with <i>Rustia</i> (Delprete, 1999); *as included in <i>Rustia</i>
<i>Tresanthera</i>	cinc-con	-	-	-	ixor-con	Based on Delprete (1996a)
<i>Badusa</i>	cinc-por	C4	-	-	cinc-cat[chi]	
<i>Bikkia</i>	cinc-por	C4	-	-	cinc-cat[chi]	
<i>Ceuthocarpus</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Coutarea</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Cubanola</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Exostema</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Isidorea</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Molopanthera</i>	cinc-por	I3b	IXO4	I3b	ixor-close to hen	
<i>Morierina</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Nernstia</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Osa</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Portlandia</i>	cinc-por	C4	CIN4	C4	cinc-cat	
<i>Syringantha</i>	cinc-por	-	-	-	cinc-cat	Based on Robbrecht (1993a)
<i>Thogsennia</i>	cinc-por	-	-	-	cinc-cat	Based on Delprete (1996a)
<i>Wernhamia</i>	cinc-por	-	-	-	ixor-con	Synonymized with <i>Simira</i> (Delprete and Nee, 1997)
<i>Acrobotrys</i>	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Bathysa</i>	cinc-ron	I1	IXO1	I1	ixor-con[cal]	
<i>Blandibractea</i>	cinc-ron	-	-	-	ixor-con	Synonymized with <i>Simira</i> (Delprete, 1998)
<i>Chalepophyllum</i>	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Dendrosipanea</i>	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Elaeagia</i>	cinc-ron	I1	IXO1	I1	ixor-con	
<i>Holstianthus</i>	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Macbrideina</i>	cinc-ron	I1	-	-	ixor-con	
<i>Nebelnathamnus</i>	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Warszewiczia</i>	cinc-ron	I1	IXO1	I1	ixor-con[cal]	
<i>Simira</i>	cinc-sim	I1	IXO1	I1	ixor-con[cal]	
<i>Dolichodelphys</i>	ixor-gar	I1	-	-	ixor-con	

Tab. 2. List of genera included in the Calycophylleae, Condamineae, Hippotideae, *Portlandia*-group, and Tammsieae by Robbrecht (1993b), with the addition of genera not listed by Robbrecht under those tribes but belonging in the "Calycophylleae-Condamineae-Hippotideae-Simireae complex" according to the present study. For genera not included in the phylogenetic analyses, sources for suggested tribal placement are given. "?"-unknown position in subfamily or tribe; "-"-not treated; **anti**-Antirheoideae; **cinc**-Cinchonoideae; **ixor**-Ixoroideae; **rubi**-Rubioidae; **cal**-Calycophylleae; **cat**-Catesbaeeae; **chi**-Chiococceae; **cinc**-Cinchoneae; **con**-Condamineae; **gar**-Gardenieae; **hed**-Hedyotideae; **hen**-Henriquezieae; **hip**-Hippotideae; **ise**-Isertieae; **por**-*Portlandia* group; **ron**-Rondeletieae; **sim**-Simireae; **tam**-Tammsieae.

inclusion of previously unplaced genera. This number was reduced to 12 by Robbrecht (1993b), because of the transfer of 10 genera to the *Portlandia*-group (see above under Chiococceae) and *Pseudomussaenda* to Isertieae. The only character consistently separating Condamineae from Rondeletieae was, according to Robbrecht (1988; 1993b) as well as Hooker, the difference in corolla aestivation: valvate in Condamineae vs. imbricate or contorted in Rondeletieae. A complete list of genera included in Condamineae by Robbrecht 1993b, and their positions according to *trnL-F* and *rps16* data, is found in Tab. 2.

Guettardeae. Guettardeae, as Guettardaceae subtribus Guettardeae, was established by Candolle (1830) to comprise genera characterized by drupaceous fruits with 2–10 pyrenes, only one seed in each fruit locule, terete seeds, and pedicellate flowers. With his circumscription, the tribe included about 30 genera. Hooker (1873), who instead defined Guettardeae by the character combination one-seeded locules, superior radicle, imbricate or valvate aestivation, stamens inserted in corolla throat, thickened funicle, and scanty endosperm, retained only four of Candolle's genera in Guettardeae: *Antirhea*, *Guettarda*, *Malanea*, and *Timonius*. On the other hand, five other genera were added: *Bobea* (as *Bobea*, *Obbea*, and *Rytidotus*), *Chomelia* Jacq., *Dichilanthe*, *Machaonia*, and *Neolaugeria* (as *Laugeria*). This circumscription prevailed until the works of Robbrecht (1988, 1993b), where 13 and 14 genera, respectively, were listed in Guettardeae (*Hodgkinsonia* only in the index to genera; Robbrecht, 1993b: p. 187). The increase in number was mainly due to splitting of old genera.

Rondeletieae and the Rondeletia complex. Rondeletieae was established by Candolle as

Hedyotideae subtribe Rondeletieae in his Prodrum (1830). It was characterized by many-seeded, two-locular capsules, and unwinged seeds, and it was separated from subtribe Hedyoteae by having neither sheathing, nor multisetose stipules. In total, it contained 18 genera. Of these, Hooker (1873) only retained six (*Augusta*, *Carphaela*, *Rondeletia*, *Sipanea*, and *Wendlandia*) in Rondeletieae; the other ones were transferred to Cinchoneae, Condamineae, or Hedyotideae based on, e.g., their valvate corolla aestivation. On the other hand, Hooker included a number of other genera with imbricate or contorted aestivation; most of these genera were not included in the treatment by Candolle. This circumscription of Rondeletieae as a tribe including about 15–20 genera remained relatively unchanged for over 100 years until the classification of Robbrecht, where 34 and 31 genera were listed as included or tentatively included in Rondeletieae in his 1988 and 1993b classifications, respectively. The main reasons for this increase in number were the descriptions of new, and splitting of old, genera, rather than a transfer of genera from other tribes. Robbrecht characterized Rondeletieae as "little differing from the Condamineae"; the key character for the separation being generally imbricate (sometimes contorted) corolla aestivation in Rondeletieae, vs. mostly valvate, rarely imbricate in Condamineae. The Rondeletieae genera included in the Robbrecht 1988 and 1993b classifications, and their positions according to *trnL-F* and *rps16* data, are found in Tab. 3.

The circumscription of the genus *Rondeletia* has been an issue of debate for a long time. A number of segregates have been proposed by "splitters" such as Borhidi and collaborators (e.g. Borhidi, 1982), while "lumpers" like Lorence (1991) have argued that practically no subdivisions can be made based on morphology. For a review of these

arguments, see Paper I and references therein. In addition to this, *Gonzalagunia* (Isertiace) and the Guettardeae (placed in Antirheoideae) have recently been suggested to belong in the vicinity of *Rondeletia* (Bremer et al., 1995; Andersson, 1996; Bremer and Thulin, 1998). The close affinity between Guettardeae and *Rondeletia* was rather unexpected, but a transfer of *Gonzalagunia* to Rondeletieae had been proposed already by Bremekamp based on exotesta sculpturing (1952, p. 16).

Simireae. Bremekamp (1966) argued for a separation of *Simira* (as *Sickingia*) from Rondeletieae based on differences in ovule number and seed morphology (the name was not, however, validly published until by Darwin, 1976). Robbrecht (1988) included *Simira* in Rondeletieae, but in his 1993b classification he reconsidered the arguments of Bremekamp, and placed *Simireae* separated from Rondeletieae.

Sipaneae. Bremekamp (1934) separated *Sipanea* and *Limnosipanea* from Rondeletieae, establishing the new tribe Sipaneae, because of their contorted corolla aestivation and their herbaceous habit. Robbrecht (1988) included also *Steyermarkia* in Sipaneae. Although he thus followed Bremekamp in his view to separate Sipaneae from Rondeletieae, he stated that "a revision of the Rondeletieae/Condamineae complex may well show that this is not justified". The tribe was, nevertheless, maintained in his 1993b classification, and even widened to include also *Neobertiera*.

PHYLOGENY FROM *trnL*-F AND *rps16* DATA

The phylogenetic analysis of the *trnL* intron and *trnL*-F spacer is found in Paper I, and the analysis of *rps16* data is found in Paper II. Results from these two studies can be summarized as follows.

A number of genera included in Rondeletieae should be transferred to subfamily Ixoroideae: *Aleisanthia*, *Aleisanthiopsis*, and *Greenea* to a position close to *Ixora*, and *Augusta* and *Wendlandia* as sister group to a Coffeae-Gardenieae-Octotropideae complex (in the sense

of Andreasen, 1997). The tribe Sipaneae (including at least *Limnosipanea*, *Maguireothamnus* [not included in the *rps16* study], *Neobertiera*, and *Sipanea*) was found not to be closely related to Rondeletieae as suggested by e.g. Robbrecht (1988, 1993b), but to be a well distinguished tribe in Ixoroideae. The *trnL*-F study (Paper I) showed *Gleasonia* (Henriquezieae; Robbrecht, 1993b), together with *Molopanthera* (*Portlandia*-group; Robbrecht, 1993b) and *Posoqueria* (Gardenieae; Robbrecht, 1993b), to form the sister group to this Sipaneae. *Gleasonia* was not included in the *rps16* study (Paper II). The sister group relationship between Sipaneae and *Molopanthera*-*Posoqueria* could not be confirmed from *rps16* data. The exact status of *Limnosipanea* still remains to be definitively settled (Paper II).

Representatives from Robbrecht's (1993b) tribes Calycophylleae, Condamineae, Hippotideae, and *Simireae* formed a clade in subfamily Ixoroideae, where also a number of Rondeletieae representatives (*Bathysa*, *Elaeagia*, *Macbrideina* [only *trnL*-F data available], and *Warszewiczia*) were found. *Capirona* (Cinchoneae) and *Emmenopterys* (incertae sedis) were also included in this clade. The *trnL*-F data (Paper I) showed that also *Dolichodelphys* (Gardenieae) belongs here, and *rps16* data (Paper II) demonstrated the additional inclusion of *Bothriospora* (inc. sed.), *Dolicholobium* (Cinchoneae), *Macrocnemum* (Cinchoneae), *Mastixiodendron* (Chiococceae), and *Semaphyllanth*e (Calycophylleae). Resolution in the *trnL*-F analysis (Paper I) was very poor, and no supported relationships were found within this clade. In the *rps16* analysis (Paper II), however, the Hippotideae genera were found in a monophyletic subclade. *Isertia* and *Kerianthera* formed a Cinchonoideae clade in the *rps16* study (Paper II), thus confirming the view of their close relationship proposed by Delprete (1996b) and Bremer and Thulin (1998).

The *Portlandia*-group of genera was found to be closely related to Catesbaeeae and Chiococceae, and formed a distinct clade within Cinchonoideae that also contained *Coutaportla*, *Hintonia*,

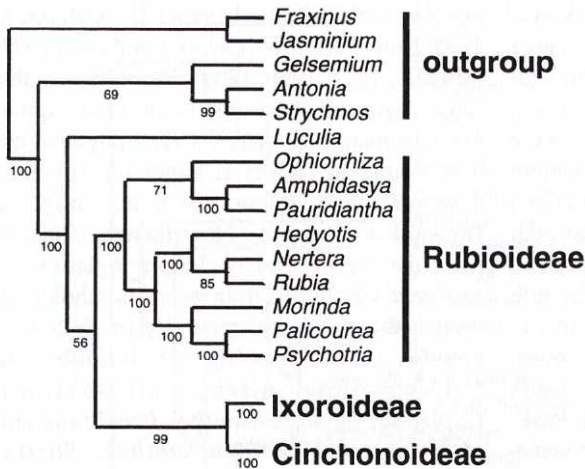


Fig. 1. Basal part of the tree produced by the analysis of the combined *trnL-F* and *rps16* data sets. Numbers below branches indicate jackknife support. The Ixoroideae and Cinchonoideae subtrees are found in Figs. 2 and 3, respectively.

Phialanthus, *Schmidtottia*, and *Siemensia*. Hence, these results corroborated the inclusion of Condamineae subtribe Portlandiinae into Chiococceae as proposed by Bremer (1992), and the close relationship between Catesbaeeae and Chiococceae suggested by Delprete (1996a). Only limited support was found for the view to keep Catesbaeeae and Chiococceae separated as suggested by Delprete (1996a). *Strumpfia* was shown to be the closest relative to this Catesbaeeae in its widest sense. *Phyllacanthus* was found within Catesbaea, and should thus be returned into that genus (Paper I). *Exostema* appeared to be polyphyletic, with *E. ixoroides* (Hook. f.) T. McDowell placed within *Coutarea* according to *rps16* sequence data (Paper II).

Both the *trnL-F* and the *rps16* phylogenies showed that *Rondeletia* and *Rondeletieae* in the broad senses of Robbrecht (1988; 1993b) are polyphyletic. A separation of *Arachnotryx*, *Javorkaea*, *Rogiera*, *Roigella*, and *Suberanthus* from *Rondeletia* was supported, but both the *trnL-F* and *rps16* results suggested that *Arachnotryx* and *Javorkaea* are congeneric. Thus, molecular data disagree with the view of, e.g., Lorence (1991) that *Arachnotryx*, *Javorkaea*, *Rogiera*, *Roigella*, and *Suberanthus* should be included in *Rondeletia*. Also *Gonzalagunia* (Paper I) and *Cuatrecasasiodendron* (Paper II) were suggested to be possibly congeneric with *Arachnotryx*. Most Guettardeae were found as sister clade to the *Arachnotryx-Gonzalagunia-Javorkaea* complex in the *trnL-F* analysis (Paper

I), but *Machaonia* and *Neoblakea* (only included in the *trnL-F* analysis) held a position separated from the rest of Guettardeae, which made Guettardeae in the sense of Robbrecht (1993b) paraphyletic. In both studies, *Allenanthus* was found to be associated with *Machaonia*. In the *rps16* study, the relationship between Guettardeae and the *Arachnotryx* complex was, however, unresolved. *Rondeletia* in a strict sense was shown to have an almost entirely Antillean distribution (Paper I), and its closest relatives are *Acrosynanthus*, *Blepharidium*, *Mazaea*, *Phyllomelia* (only included in the *trnL-F* analysis), *Rachicallis*, *Rogiera suffrutescens* (Brandeg.) Borhidi, *Roigella*, and *Suberanthus*. Hence, *Rogiera* was shown to be polyphyletic both in the *trnL-F* and the *rps16* phylogenies. The close relationship between *Gonzalagunia*, *Guettardeae*, *Rachicallis*, and the *Rondeletia* complex that had been proposed from *rbcL* data by Bremer and Thulin (1998) was consequently confirmed also from *trnL-F* and *rps16* sequence data. *Bobea* was included only in the *rps16* study (Paper II), and its position was not fully resolved.

PHYLOGENY FROM COMBINED ANALYSIS

To test if a combination of the *trnL-F* and *rps16* data would improve resolution, a jackknife run was performed where the two data matrices were combined. Taxa not occurring in both matrices were left out, which resulted in a data matrix comprising 131 terminals and 738 informative

characters. The same indel codings as in the two separate jackknife runs were used (Paper I; Paper II). A jackknife run (1000 replicates, each with 5 random addition sequence replicates) was performed with the program "Xac" (J. S. Farris, Swedish Museum of Natural History, Stockholm, pers. com.). The resulting tree is shown in Figs. 1–3. The result is practically identical to both the *trnL-F* and the *rps16* analyses, but as can be seen when compared to Papers I and II, jackknife support values are generally higher in the combined analysis than in the separate ones. Further, *Mussaenda* is found as sister to the entire Vanguerieae-Gardenieae clade, just as in Paper I. In the combined analysis, there is also some, although weak, jackknife support both for *Warszewiczia* being sister to *Chimarrhis*, and for a monophyletic Hippotideae. Perhaps most interestingly, jackknife support in the combined analysis is very high for both the C5a/CIN5a and C5b/CIN5b clades from Paper I and II; especially, support for clade C5a is considerably stronger in the combined analysis than in the individual *trnL-F* and *rps16* analyses.

IMPLICATIONS FOR RUBIACEAE SYSTEMATICS

Results from the studies presented here suggest new circumscriptions and new systematic positions of the tribes and tribal complexes Calycophylleae-Condamineae-Hippotideae-Simireae, Catesbaeae (including Chiococceae), Guettardeae, Rondeletieae, and Sipaneeae. When results are summarized tribe by tribe and compared to recent morphological investigations, preliminary circumscriptions of these groups can be suggested as follows.

The Calycophylleae-Condamineae-Hippotideae-Simireae complex

The Calycophylleae-Condamineae-Hippotideae-Simireae complex (II in Fig. 2) belongs in subfamily Ixoroideae, and is a conglomerate of genera from, mainly, the tribes Calycophylleae, Condamineae, Cinchoneae, and Rondeletieae sensu Robbrecht (1993b). A few genera should also be transferred to this complex from Chiococceae, Gardenieae, the *Portlandia*-group, and Simireae, or from "genera

incertae sedis" (Paper I; Paper II; Andersson, 1995; Delprete, 1996a; Delprete and Nee, 1997; Delprete, 1997, 1998, 1999). Resolution in this tribal complex is poor and there is no support for a distinction of neither Calycophylleae nor Condamineae (Paper I; Paper II); there is, however, some support for a monophyletic Hippotideae (Paper II). Nevertheless, if results from the *trnL-F* and *rps16* phylogenies are combined with results from recent morphological investigations, it is indicated that the following genera could possibly be included in Calycophylleae: *Alseis*, *Calycophyllum*, *Capirona*, *Semaphyllanthus*, *Ferdinandusa*, *Macrocnemum*, *Wittmackanthus*, *Simira*, *Bathysa*, *Pogonopus*, *Warszewiczia*, *Chimarrhis*, *Parachimarrhis*, and *Pinckneya* (Andersson and Persson, 1991; Andersson, 1995; Paper I). These genera are marked with the extension "[cal]" in Tab. 2. Also Hippotideae is well characterized based on morphological data (Rova and Andersson, 1995), and is probably a monophyletic group distinct from the rest of the Calycophylleae-Condamineae. The Hippotideae genera are marked with the extension "[hip]" in Tab. 2. These suggestions should, however, be regarded as hypothetical since the exact boundaries in this complex are still in need of further studies. The following list summarizes the entire tribal complex (cf. also Tab. 2):

Genera included: *Alseis*, *Bathysa*, *Blandibractea*, *Bothriospora*, *Calycophyllum*, *Capirona*, *Chimarrhis*, *Condaminea*, *Dioicodendron*, *Dolichodelphys*, *Dolicholobium*, *Elaeagia*, *Emmenopterys*, *Flexanthera*, *Hippotis*, *Macbrideina*, *Macrocnemum*, *Mastixiodendron*, *Parachimarrhis*, *Pentagonia*, *Picardaea*, *Pinckneya*, *Pogonopus*, *Rustia*, *Schizocalyx*, *Semaphyllanthus*, *Simira*, *Sommeria*, *Stomandra*, *Tammsia*, *Warszewiczia*, *Wernhamia*, and *Wittmackanthus*.

Tentatively included: *Acrobotrys*, *Chalepophyllum*, *Dendrosipanea*, *Ferdinandusa*, *Holstianthus*, *Neblinathamnus*, *Phitopsis*, and *Tresanthera*.

Excluded: *Kerianthera* (transferred to Cinchonoideae-Isertieae; Paper II) and *Kajewskiella* (transferred to Rubioideae-Hedyotideae; Tange, 1995).

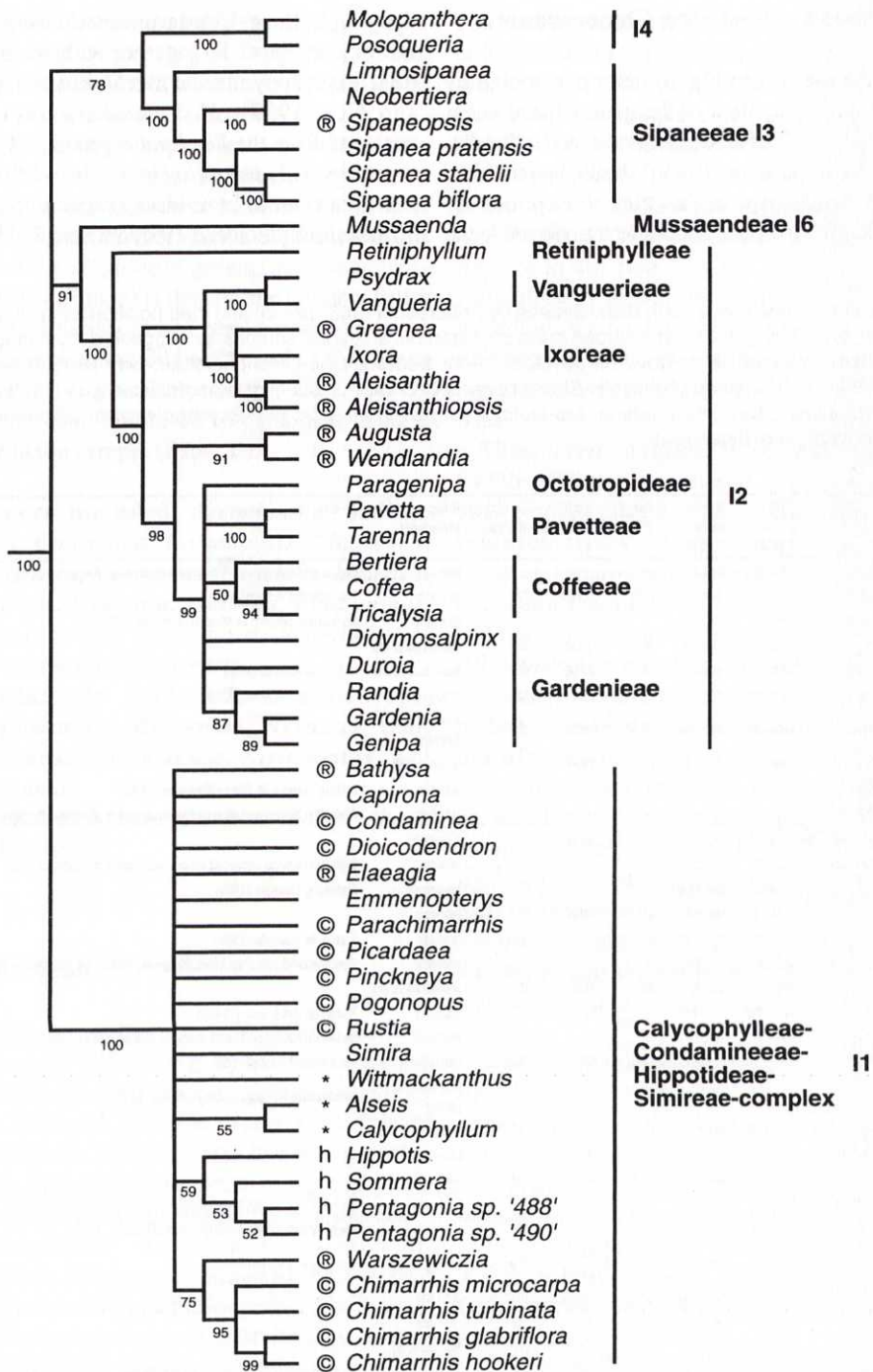


Fig. 2. The Ixoroideae subtree produced by the jackknife analysis of the combined *trnL-F* and *rps16* data sets. Numbers below branches indicate jackknife support. Symbols in front of taxon names indicate tribal position according to Robbrecht (1993b): * - Calycophylleae; © - Condamineae; h - Hippotideae; ® - Rondeletieae. Tribes are according to Robbrecht (1993b), except those in clade I2 that follow Andreasen (1997), and Mussaendeae that is according to Bremer and Thulin (1998).

Catesbaeeae (including Chiococceae)

Calycophylleae-Condamineae complex in Ixoroideae (Paper II) together with *Wernhamia* (that was synonymized under *Simira* by Delprete and Nee, 1997). *Molopanthera* should be excluded from the *Portlandia*-group and placed together with *Posoqueria* in the vicinity of Henriquezieae in Ixoroideae (Paper I; Paper II). *Siemensia* (Rubioidaeae-Hedyotideae; Robbrecht,

Catesbaeeae (C4 in Fig. 3) belong in subfamily Cinchonoideae. Most of the genera listed under Catesbaeeae, Chiococceae, and the *Portlandia*-group by Robbrecht (1993b) should be included, at least tentatively, in this tribe. Exceptions are *Mastixiodendron* that should be transferred to the

Tab. 3. List of genera treated in Rondeletieae by Robbrecht (1988; 1993b) and their position according to the present study. For genera not included in the phylogenetic analyses, sources for suggested tribal placement are given. “?”-tentative or doubtful position; “-”-not treated; **cinc**-Cinchonoideae; **ixor**-Ixoroideae; **rubi**-Rubioidaeae; **cal**-Calycophylleae; **cin**-Cinchoneae; **con**-Condamineae; **gar**-Gardenieae; **gue**-Guettardeae; **ham**-Hamelieae; **hed**-Hedyotideae; **ixo**-Ixoroideae; **pav**-Pavetteae; **psy**-Psychotriaceae; **ron**-Rondeletieae; **sim**-Simireae; **sip**-Sipaneae.

Genus	Robbrecht (1988)	Robbrecht (1993)	trnL-F (Paper I)	rps16 (Paper II)	Combined analysis	Suggested tribal placement	Notes
<i>Acrobotrys</i>	cinc-ron	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Acrosynanthus</i>	cinc-cin*	cinc-ron	C5b	CIN5b	C5b	cinc-ron	*As included in <i>Remijia</i>
<i>Acunaeanthus</i>	cinc-ron	cinc-ron	-	-	-	cinc-ron	As "closely related" to <i>Mazaea</i> (Delprete, 1999)
<i>Aleisanthia</i>	cinc-ron	cinc-ron	I2	IXO2	I2	ixor-close to ixo	
<i>Aleisanthiopsis</i>	cinc-ron*	cinc-ron*	I2	IXO2	I2	ixor-close to ixo	*As included in <i>Greenea</i>
<i>Arachnotryx</i>	cinc-ron	cinc-ron*	C5a	CIN5a	C5a	cinc-gue	*As included in <i>Rondeletia</i>
<i>Augusta</i>	cinc-ron	cinc-ron	I2	IXO2	I2	ixor-close to gar/pav	
<i>Bathysa</i>	cinc-ron	cinc-ron	I1	IXO1	I1	ixor-con[cal]	
<i>Blandibractea</i>	cinc-ron	cinc-ron	-	-	-	ixor-con	Synonymized with <i>Simira</i> (Delprete, 1996)
<i>Chalepophyllum</i>	cinc-ron	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Cuatrecasiodendron</i>	cinc-ron	cinc-ron	-	CIN5a	-	cinc-gue	
<i>Dendrosipanea</i>	cinc-ron	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Eizia</i>	cinc-ron	rubi-ham	-	-	-	cinc-ham	Following Delprete (1999)
<i>Elaeagia</i>	cinc-ron	cinc-ron	I1	IXO1	I1	ixor-con	
<i>Glionnetia</i>	cinc-ron	cinc-ron	-	-	-	cinc-ron	Based on Delprete (1999)
<i>Gloneria</i>	cinc-ron	rubi-psy*	-	-	-	rubi-psy	Synonymized with <i>Psychotria</i> (Delprete, 1999); *as included in <i>Psychotria</i>
<i>Greenea</i>	cinc-ron	cinc-ron	I2	IXO2	I2	ixor-close to ixo	
<i>Habroneuron</i>	cinc-?ron	cinc-?ron	-	-	-	cinc-ron	Based on Robbrecht (1993b)
<i>Holstianthus</i>	cinc-ron	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Javorkaea</i>	cinc-ron	cinc-ron*	C5a	CIN5a	C5a	cinc-gue	*As included in <i>Rondeletia</i>
<i>Lindenia</i>	cinc-ron	cinc-ron	-	-	-	ixor-close to gar/pav	Synonymized with <i>Augusta</i> (Kirkbride, 1997)
<i>Macbrideina</i>	cinc-ron	cinc-ron	I1	-	-	ixor-con	
<i>Maguireothamnus</i>	cinc-ron	cinc-ron	I3a	-	-	ixor-sip	
<i>Mazaea</i>	-	cinc-ron	C5b	CIN5b	C5b	cinc-ron	
<i>Neblinathamnus</i>	cinc-ron	cinc-ron	-	-	-	ixor-con	Based on having contorted corolla aestivation (Delprete, 1999)
<i>Pteridocalyx</i>	cinc-ron	cinc-ron	-	-	-	ixor-sip	Possibly congeneric to <i>Neobertiera</i> (Delprete, 1999)
<i>Rogiera</i>	cinc-ron	cinc-ron*	C5a, C5b	CIN5a, CIN5b	C5a, C5b	cinc-gue, ron	*As included in <i>Rondeletia</i>
<i>Roigella</i>	cinc-ron	cinc-ron	C5b	CIN5b	C5b	cinc-ron	
<i>Rondeletia</i>	cinc-ron	cinc-ron	C5b	CIN5b	C5b	cinc-ron	
<i>Simira</i>	cinc-ron	cinc-sim	I1	IXO1	I1	ixor-con[cal]	
<i>Sipaneopsis</i>	cinc-ron	cinc-ron	I3a	IXO3	I3a	ixor-sip	Possibly congeneric to <i>Neobertiera</i> (Paper I)
<i>Spathiclamys</i>	cinc-ron	cinc-ron	-	-	-	cinc-ron	Based on Delprete (1999)
<i>Standleya</i>	cinc-ron	cinc-ron	-	-	-	rubi-hed	Based on Delprete (1999)
<i>Steenisia</i>	cinc-ron	cinc-ron	-	-	-	cinc-ham	See discussion in text, p. 22
<i>Stevensia</i>	cinc-ron	cinc-ron	-	-	-	cinc-ron	Based on Delprete (1999)
<i>Warszewiczia</i>	cinc-ron	cinc-ron	I1	IXO1	I1	ixor-con[cal]	
<i>Wendlandia</i>	cinc-ron	cinc-ron	I2	IXO2	I2	ixor-close to gar/pav	

1993b) should be included in Catesbaeeae (Paper I; Paper II). According to Delprete (1996a), *Hodgkinsonia* should be tentatively transferred from Guettardeae to Catesbaeeae.

There is some support for a separation of a tribe Chiococceae (Fig. 3), but no support for a monophyletic Catesbaeeae including all the other genera. Until further data are presented this "Chiococceae" group of genera (marked as "cincat[chi]" in Tab. 1) is thus for the moment better treated as members of Catesbaeeae. Moreover, *Phyllacanthus* should be returned to *Catesbaea* (Paper I). The monophyly of *Exostema* is dubious, and should be re-examined using a larger taxon sample (Paper II).

Genera included: *Asemnantha*, *Badusa*, *Bikkia*, *Catesbaea*, *Ceratopyxis*, *Chiococca*, *Coutaportla*, *Coutarea*, *Cubanola*, *Erithalis*, *Exostema*, *Hintonia*, *Isidorea*, *Phialanthus*, *Phyllacanthus*, *Portlandia*, *Schmidtottia*, *Scolosanthus*, and *Siemensia*.

Tentatively included: *Ceuthocarpus*, *Hodgkinsonia*, *Morierina*, *Nernstia*, *Osa*, *Placocarpa*, *Salzmannia*, *Syringantha*, and *Thogsennia*.

Excluded: *Mastixiodendron*, *Molopanthera*, and *Wernhamia*.

Guettardeae

During its entire classification history, Guettardeae (C5a in Fig. 3) has been regarded as a fairly clear-cut group of genera, sometimes even referred to as a distinct subfamily (Bremekamp, 1952). It is thus interesting that the tribe is, in this study, shown to be a paraphyletic grade of the Rondeletieae complex in subfamily Cinchonoideae, with *Antirhea*, *Chomelia*, *Guettarda*, *Malanea*, *Neolaugeria* and *Timonius* found in one clade, and *Allenanthus*, *Machaonia*, and *Neoblakea* in another. If Rondeletieae is regarded as encompassing also *Arachnotryx* and *Rogiera*, Guettardeae must be included in the same tribe. Since Guettardeae has priority over Rondeletieae, the name of this tribe should be Guettardeae (Darwin, 1976). Two other views regarding the circumscription of Guettardeae can,

however, be proposed: to keep Guettardeae more or less as discussed in Robbrecht (1988), which means that *Rogiera*, the *Arachnotryx-Gonzalagunia* complex, and *Allenanthus* and *Machaonia* must be classified in separate tribes, or to define Guettardeae as encompassing the entire clade CIN5a, thus including also the *Arachnotryx-Gonzalagunia* complex and *Rogiera* in the tribe. The last option will allow Rondeletieae to be maintained for the tribe including *Rondeletia* with its closest relatives; this appears to be the option that best serves nomenclature stability, and it is the one advocated here.

Thus, when compared to Robbrecht (1988, 1993b), Guettardeae should include not only most genera included in his Guettardeae, but also representatives from his Rondeletieae (*Cuatrecasiodendron* and the *Rondeletia* segregates *Arachnotryx*, *Javorkaea*, and *Rogiera*) and Isertieae (*Gonzalagunia*) (Paper I; Paper II). *Allenanthus*, treated as "genus incertae" in Robbrecht (1993b) and as part of Chiococceae by Delprete (1996a), should also be included in this tribe. *Hodgkinsonia* is to be transferred to Catesbaeeae, according to Delprete (1996a), and the position of *Bobea* is not definitely settled in relation to Guettardeae and Rondeletieae (Paper II). The results presented here also suggest that parts of *Arachnotryx*, *Cuatrecasiodendron*, and *Javorkaea* might be congeneric (Paper II), and that the generic demarcation between these taxa and *Gonzalagunia* needs a special study.

Genera included: *Allenanthus*, *Antirhea*, *Arachnotryx*, *Chomelia* Jacq., *Cuatrecasiodendron*, *Gonzalagunia*, *Guettarda*, *Javorkaea*, *Machaonea*, *Malanea*, *Neoblakea*, *Neolaugeria*, *Rogiera* (except *R. suffrutescens* [Brandeg.] Borhidi), and *Timonius*.

Tentatively included: *Bobea* (Guettardeae or Rondeletieae; Paper II), *Dichilanthe*, *Guettardella*, *Ottoschmidtia*, *Pittoniotis*, and *Stenostomum*.

Excluded: *Hodgkinsonia*.

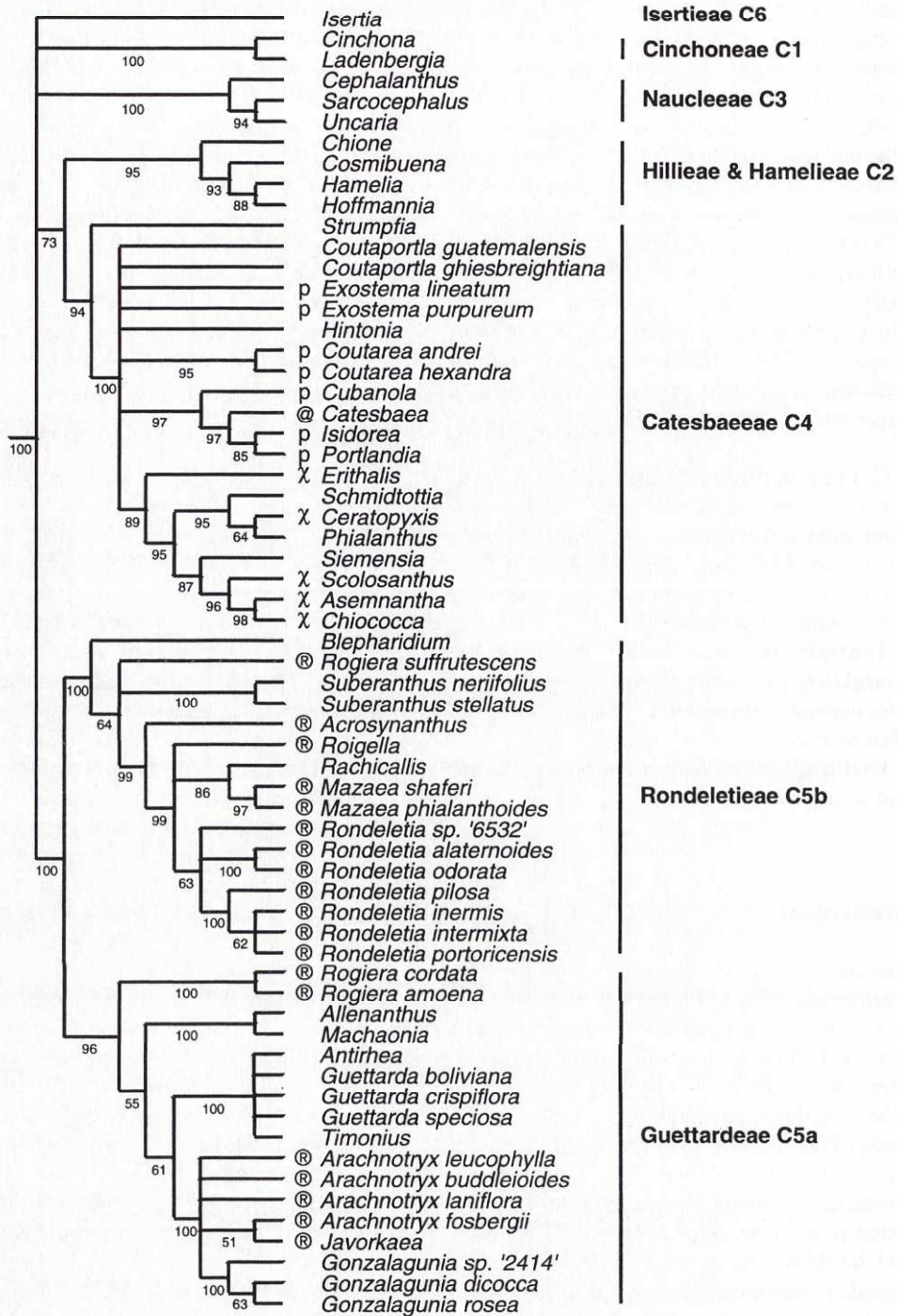


Fig. 3. The Cinchonoideae subtree produced by the jackknife analysis of the combined *trnL-F* and *rps16* data sets. Numbers below branches indicate jackknife support. Symbols in front of taxon names indicate tribal (or subtribal) position according to Robbrecht (1993b): @-Catesbaeeae; χ-Chiococceae; p-Portlandiagroup; ®-Rondeletieae.

Rondeletieae

The *trnL-F* and *rps16* data suggest that Rondeletieae (C5b in Fig. 3) must be significantly narrowed when compared to its circumscription by Robbrecht (1993b). Only *Acrosynanthus*, *Mazaea*, *Rogiera suffrutescens* (Brandeg.) Borhidi (but not the type of *Rogiera*), *Roigella*, *Rondeletia*, and tentatively *Acunaeanthus*, *Glionnetia*, *Habroneuron*, *Spathiclamys* and *Stevensia* are still to be included as suggested from recent works (Robbrecht, 1993b; Delprete, 1999; Paper I; Paper II). Four other genera are also suggested to be included (Paper I; Paper II): *Blepharidium* (Hillieae), *Phyllomelia* (unknown position), *Rachicallis* (?Hedyotideae), and *Suberanthus* (unknown position in Cinchonoideae); the positions given within parentheses are according to Robbrecht (1993b). The exclusion of *Simira* from Rondeletieae as proposed by Bremekamp (1952) and Robbrecht (1993b) is verified from *trnL-F* and *rps16* data (Paper I; Paper II). Of the 18 genera originally included in Rondeletieae by Candolle (1830), most have been transferred to other tribes. When compared to Candolle's enumeration, Robbrecht (1993b) retained only *Augusta*, *Rondeletia*, and *Wendlandia* in his Rondeletieae, and only *Rondeletia* still remains in the tribe according to the *trnL-F* and *rps16* analyses. Robbrecht (1988) apparently used plesiomorphic and homoplastic characters to distinguish the Rondeletieae (in his sense), and thus it became a polyphyletic group composed of elements from several parts of the family. After the exclusion of genera such as *Greenea*, *Aleisanthia*, and *Augusta*, the Rondeletieae can, e.g., be characterized as entirely imbricate (Paper I). Rondeletieae remains as a tribe in subfamily Cinchonoideae. New positions for excluded genera are found in Tab. 3.

Genera included: *Acrosynanthus*, *Blepharidium*, *Mazaea*, *Phyllomelia*, *Rachicallis*, *Rogiera* (only *R. suffrutescens* [Brandeg.] Borhidi), *Roigella*, *Rondeletia*, and *Suberanthus*.

Tentatively included: *Acunaeanthus*, *Bobea* (Guettardeae or Rondeletieae; Paper II), *Glionnetia*, *Habroneuron*, *Spathiclamys*, and *Stevensia*.

Excluded: *Acrobotrys*, *Aleisanthia*, *Aleisanthiopsis*, *Arachnotryx*, *Augusta*, *Bathysa*, *Blandibractea*, *Chalepophyllum*, *Cuatrecasasi-dendron*, *Dendrosipanea*, *Elaeagia*, *Greenea*, *Holstianthus*, *Javorkaea*, *Lindenia* (synonym to *Augusta*), *Macbrideina*, *Maguireothamnus*, *Neblinathamnus*, *Pteridocalyx*, *Sipaneopsis*, *Standleya*, *Steenisia*, *Warszewiczia*, and *Wendlandia*.

Sipaneae

Sipaneae (I3 in Fig 3) should be transferred from Cinchonoideae to Ixoroideae. If Sipaneae is circumscribed as suggested by the *trnL-F* and *rps16* phylogenies in combination with recent morphological works (Paper I; Paper II; Robbrecht, 1993b; Delprete, 1999), it should include both the traditional Sipaneae and a few genera hitherto referred to Rondeletieae: *Maguireothamnus*, *Sipaneopsis*, and, tentatively, *Pteridocalyx* (Robbrecht, 1993b). The potential synonymy of *Neobertiera*, *Pteridocalyx*, and *Sipaneopsis* still needs to be further investigated (Paper I; Delprete, 1999). The monophyly of *Limnosipanea* also needs to be finally tested (Paper II).

Genera included: *Limnosipanea*, *Maguireothamnus*, *Neobertiera*, *Sipanea*, *Sipaneopsis*, and *Steyermarkia*.

Tentatively included: *Pteridocalyx*.

A FEW FINAL NOTES

It should be noted that in many cases the circumscriptions proposed above still need to be further investigated. Especially morphological studies of proposed complexes are necessary, not least to investigate if the clades suggested by molecular data can be distinguished also morphologically. In several cases, molecular phylogenies can also throw new light on the interpretation of morphological characters. Paper I, for example, showed that corolla aestivation patterns still should be considered to have a significant systematic importance in Rubiaceae, just as suggested by e.g. Bremer (1987) and Robbrecht (1988), and the different modes of secondary pollen presentation described in Puff

et al. (1996) was shown in Paper II to be interpretable as synapomorphic characters when compared to the *rps16* phylogeny.

It is also obvious that a molecular phylogeny within the "Condamineae" (II in Fig. 2; clade II in paper I and clade IXO-1 in paper II) needs to be supplemented by using a locus with a higher mutation rate than the *trnL-F* region (Paper I), the *rps16* intron (Paper II), or *rbcL* (Bremer et al., 1995). Another possibility is to combine a number of different data sets in order to end up with a sufficient amount of informative data to get resolution within the clade. A data set of this size might be achieved sooner than expected, since minute signals present in the different data sets (signals too weak when data sets are analyzed separately) might get synergistic when combined with other data sets (Nixon and Carpenter, 1996). The higher jackknife support in the combined analysis compared to the individual analyses indicates that this is also the case.

Although this study focused on the Condamineae-Rondeletieae-Sipanceae complex, it has also produced some results not directly connected to these tribes. For example, according to the results presented here (Paper I, Paper II, combined analysis), as well as results from recent molecular studies (Bremer et al., 1995; Young et al., 1996; Bremer and Thulin, 1998; Andersson and Rova, 1999), there is now no doubt that Rubiaceae should consist of only three large subfamilies: Rubioideae, Cinchonoideae, and Ixoroideae. However, the genus *Luculia* holds a very isolated position at the base of the family, and, based on molecular data, *Luculia* could be placed in a fourth subfamily of its own (Fig. 1).

Also, a close relationship between *Chione* and a Hamelieae-Hillieae clade (C2 in Fig. 3) was found in both studies (Paper I, Paper II). In Paper II, *rps16* data placed this entire tribe as sister group to the *Strumpfia*-Catesbaeeae clade, but this was not confirmed from *trnL-F* data. *Steenisia* is excluded from Rondeletieae, and could possibly belong in Hamelieae because of the similarities in exotesta ornamentation (Bremer, 1984; Rova, pers. obs.), a stalked

placenta similar to *Deppea*, and the presence (although very rare) of raphides (Bremer, 1984). It should be noted that both *Steenisia* and *Strumpfia* have the anthers arranged as a cone around the style, although in *Strumpfia* the anthers are fused, while in *Steenisia* they are not (Igersheim, 1993). If *Steenisia* is placed close to Hamelieae (clade C2, Fig. 3) it would also suggest that its relation to *Strumpfia* (basal in clade C4, Fig. 3) needs to be further investigated.

Both *trnL-F* (Paper I), *rps16* (Paper II), and *rbcL* data (Bremer et al., 1995) support a "broad Naucleaeae", including, e.g., *Cephalanthus*, *Hymenodictyon*, *Neolamarckia*, *Sarcocephalus*, and *Uncaria* (C3 in Fig. 3). A closer investigation of the phylogeny of this group — including also further taxa from Coptosapeltae and Naucleaeae — and with an emphasis on the evolution of secondary pollen presentation modes, self incompatibility systems, and inflorescence architecture, would certainly be an interesting project.

The availability of DNA sequence data sets has increased dramatically over the last few years. Bremer et al. (1995) included 49 Rubiaceae terminals in their *rbcL* analysis; in 1996, Bremer presented an *rbcL* analysis that included 93 terminals from 89 genera. Andersson and Rova (1999) included 143 ingroup taxa from 112 genera, the *trnL-F* study (Paper I) included 155 Rubiaceae terminals from 119 genera, and the *rps16* study (Paper II) included 192 terminals from 124 Rubiaceae genera. If the number of Rubioideae genera included in the analysis of Andersson and Rova (1999) are added to the non-Rubioideae genera in Paper II (in both cases "Rubioideae" defined from the output of the respective studies), it is found that 190 Rubiaceae genera are now sequenced and analyzed for the *rps16* intron. This equals over 30% of the currently recognized Rubiaceae genera, and makes this intron the most thoroughly sequenced chloroplast locus in the Rubiaceae.

OM KAFFEFAMILJEN:

NÖJE, NYTTA OCH NATURLIGA GRUPPER – EN SVENSK SAMMANFATTNING

Introduktion

Denna avhandling handlar om släktskapsförhållanden inom växtfamiljen Rubiaceae, på svenska kallad kaffefamiljen eller familjen mårväxter. Trots att kaffefamiljen är en av de största blomväxtfamiljerna har den tilldragit sig förvånansvärt lite uppmärksamhet, och de evolutionära sambanden mellan olika grupper inom familjen har först på senare år kommit i centrum för mer omfattande studier. Syftet med denna avhandling är att öka förståelsen av hur släktskapsförhållandena ser ut inom vissa delar av familjen. De idéer om släktskap som läggs fram i avhandlingen grundar sig på studier av DNA-sekvenser från kloroplasten, d.v.s. den struktur i växtcellen där fotosyntesen sker.

Inte bara kaffe

Kaffeväxterna är en av världens största växtfamiljer och omfattar ungefär 12 000 arter (Delprete, 1999). Bara tre växtfamiljer är större: de korgblommiga med 21 000 arter, dit maskros och prästkrage hör, familjen orkidéer med 17 500 arter, dit brunkulla och vanilj förs, och familjen ärtväxter med ca 16 400 arter, där bl.a. rödklöver, jordnöt och bruna bönor hör hemma (Mabberley, 1993). Jämförelsevis kan nämnas att kaffefamiljen innehåller ca 2 000 fler arter än vad det finns fågelarter i världen (Monroe and Sibley, 1997). I Sverige är familjen kaffeväxter representerad av arterna gulmåra, vitmåra och ett tjugotal nära släktingar till dessa. Alla svenska kaffeväxter är örter som vissnar ner under vintern, men de flesta arterna i familjen finns i tropikerna och är buskar eller träd. Vissa trädformade kaffeväxter i Amazonas kan nå en höjd av över 50 m (Delprete, 1999).

Familjen kaffeväxter omfattar ett flertal kommersiellt intressanta arter och många har medicinska eller narkotiska egenskaper. Kaffet självt, som internationellt sett är den mest kända och ekonomiskt viktigaste representanten i

familjen, framställs ur arter i det ursprungligen afrikanska släktet *Coffea*. Världens samlade kaffeexport uppgick 1993 till ett värde av över 6 000 miljoner US\$ (UNCTAD, 1995) och Sverige hade 1990 världens näst högsta kaffe konsumtion med drygt 10 kg/person (Nationalencyklopedin, 1993). Det mot malaria verksamma ämnet kinin framställs sedan länge ur barken från det sydamerikanska (!) kinaträdet, *Cinchona* (Rehm och Espig, 1991; Aldén et al., 1998). Trots att syntetiskt producerade substanser numera används både som malariaproylax och vid behandling av malaria hör naturliga alkaloider från kinaträd fortfarande till de mest effektiva botemedlen mot resistent malaria orsakad av *Plasmodium falciparum* (Druilhe et al., 1988; Amabeoku, 1991; Barennes et al., 1995, 1998). Att framställa kinin på konstgjord väg är både komplicerat och kostsamt, och därför utnyttjas fortfarande kinaträdsplantager som råvarukälla (Amabeoku, 1991). Nuförtiden kommer annars den största efterfrågan på kinin från dryckesindustrin, där kinin används för att ge den bittra smaken åt tonic water och vermuth (Rehm och Espig, 1991).

Flera arter i det tropiska släktet *Psychotria* innehåller hallucinogena ämnen (Shephard Jr., 1998) och andra innehåller t.ex. ämnen som hindrar frigörelse av tillväxthormon (GH release inhibitory substances; Sévenet, 1991). Extrakt från *Mitracarpus villosus* (Sw.) DC. har visat sig ha negativ inverkan på tillväxten hos flera sjukdomsalstrande svampar (Irobi och Daramola, 1993), och extrakt från t.ex. morinda (*Morinda citrifolia* L.) och eldboll (*Ixora coccinea* L.) hämmar tumörtillväxt (Hirazumi et al., 1994; Latha och Panikkar, 1998). Den potenshöjande och antidepressiva alkaloiden yohimbin kommer från kaffeväxten *Pausinystalia yohimbe* Beille (Riley, 1994; Harborne et al., 1999) och polypeptiden circulin A, extraherad ur *Chassalia parvifolia* K. Schum., är verksam mot HIV (Daly et al., 1999, med däri angivna referenser). Ursprungsbefolkningen Matsigenka i Amazonas rapporteras dessutom använda kaffeväxter med narkotisk effekt för att stimulera sina jakthundars förmåga att spåra vilt (Shepard Jr., 1998).

Många kaffeväxter odlas som uppskattade prydnadsväxter (Aldén et al., 1998); hit hör t.ex.

gardenia (*Gardenia augusta* [L.] Merr.), eldboll (*Ixora coccinea* L.), flaggbuske (*Mussaenda* spp.), koralltuva (*Nertera granadensis* [L.f.] Druce) och rondeletia (*Rondeletia odorata* Jacq.). Gambir (*Uncaria gambir* [Hunter] Roxb.) används för framställning av garvämne (Aldén et al., 1998), och krapp (*Rubia tinctorum* L.) är välkänd som en av de få färgväxter som ger hållbara röda nyanser åt bl.a. textilier. Det är för övrigt just från krappsläktet som kaffeväxternas latinska namn, Rubiaceae, härstammar — också på svenska kallas kaffeväxterna ibland även för krappväxter. De tropiska släktena *Mazaea*, *Psychotria* och *Rondeletia* omfattar ett antal arter med förmåga att lagra extrema mängder nickel. Hos vissa av dem har man uppmätt nickelkoncentrationer på 1–5% av torrvikten, och dessa bedöms ha en potential som avgiftare av nickelförorenad mark eller som anrikare av nickel från annars ekonomiskt olönsamma malmkroppar (Jaffré och Schmid, 1974; Reeves et al., 1999).

Nyttan av naturlig klassificering

Det är naturligtvis svårt att hålla ordning på 12 000 arter om man inte organiserar dem på något sätt. Därför för man samman närbesläktade arter i släkten, och närbesläktade släkten i släktgrupper, tribusar. Dessutom delar man ofta in stora familjer i underfamiljer, som är en grupperingsnivå mellan familje- och tribusnivå. Inom biologin brukar arbetet med att sätta namn på arter och grupper av arter (generellt kallade "taxa") kallas för taxonomi, medan utforskandet av hur dessa taxa är besläktade med varandra kallas systematik. Systematik och taxonomi hänger givetvis ihop. I modern systematik försöker man avgränsa grupper så att alla taxa (arter, tribusar, etc.) som ingår i en grupp hör samman släktskapsmässigt, d.v.s. härstammar från gemensamma anfäder. I detta skiljer sig dagens arbetssätt från forna tiders systematik, där man oftast använde mer eller mindre godtyckliga likheter i utseende för att definiera vilka organismer som skulle höra hemma i en viss grupp. En klassificering som bygger på släktskap kallas naturlig, och en som inte avspeglar släktskap kallas onaturlig. En naturlig klassificering är en nödvändig grund för alla

studier som rör mer än en individ — oavsett om det gäller evolution, ekologi, biologisk mångfald eller en önskan att hitta släktingar till en medicinskt intressant växt. Tanken är att denna studie ska bidra till upprättandet av en naturlig klassificering av kaffeväxterna.

Systematik genom tiderna

Familjen kaffeväxter har i äldre tider delats in efter karaktärer som exempelvis hur frukten ser ut, hur många frön den innehåller, eller åt vilket håll kronbladens flikar ligger hopskruvade innan blomman slår ut (t.ex. Candolle, 1830; Hooker, 1873). Dessa indelningar gav till stor del onaturliga grupper. I mitten av 1900-talet började man att arbeta allt mer ur ett evolutionärt perspektiv, och större vikt lades därför vid ett bredare spektrum av egenskaper (Verdcourt, 1958; Bremekamp, 1934, 1952, 1966). Den senaste världsomfattande storsystematiska studien av kaffefamiljen gjordes av Robbrecht (1988, med kompletteringar 1993b). I hans klassificering delades kaffeväxterna in i fyra underfamiljer, 44 tribusar och ca 650 släkten, och det är Robbrechts klassificering som dagens forskare oftast utgår ifrån. För att förklara sambanden mellan tribusar och underfamiljer tecknade Robbrecht kaffefamiljen som en karta där han ritade ut tribusarna som cirklar och gränserna mellan underfamiljerna som tjocka streck. Men han erkände själv att allt inte var lätt att reda ut. Till exempel kunde han inte säkert ange gränserna mellan tribusarna Condamineae, Rondeletieae och Sipaneeae i underfamiljen Cinchonoideae. Därför ritade han ut cirkelarna för dessa tribusar som tre hopflytande bubblor, och poängterade att det behövdes ytterligare studier för att reda ut släktskapsförhållandena i detta komplex.

DNA, datorer och parsimoni

I slutet av 1980-talet gjorde molekylärbiologiska arbetsmetoder sitt intåg på allvar i den botaniska systematiken, och idag ingår DNA-sekvensering ofta som en del i både större och mindre studier. Parallellt gjorde allt snabbare persondatorer det möjligt att på matematisk väg räkna fram hypoteser om släktskap utifrån både

morfologiska och molekylärbiologiska data; tidigare hade man varit hänvisad till mer eller mindre kvalificerade gissningar eller "likhetsindex" av olika slag. Genom att låta datorn beräkna hur många gånger (och i vilken ordning) mutationer eller andra förändringar kan ha skett försöker man i en sådan analys hitta det släkträd som på enklaste sätt (d.v.s. med minst antal antaganden) kan förklara varför data ser ut som de gör idag. Det träd som får minst antal "straffpoäng" visar det teoretiskt sett mest troliga släktskapsförhållandet (ibland kan dock flera olika förhållanden vara lika troliga). Detta (eller dessa) träd kallas det mest parsimona, och analysmetoden kallas parsimonianalys, eller ibland lite slarvigt för "kladistisk analys", eftersom de grupper som man finner i träden kallas för "klader".

Mina studier

Med utgångspunkt från Robbrechts idé om att Condamineae, Rondeletieae och Sipaneeae skulle hänga nära samman tog jag mig an att närmare undersöka släktskapsförhållandena i och kring dessa tribusar. Eftersom studier grundade enbart på utseendet hos olika strukturer och organ hade visat sig otillräckliga för att lösa problemet tog jag hjälp av DNA-sekvensering och parsimonianalys.

Jag började således med att samla in data från så många representanter som möjligt ur detta tribuskomplex. Samtidigt försökte jag också få med åtminstone en representant ifrån alla andra tribusar i familjen för att mer exakt kunna bestämma vilka de närmaste släktingarna till hela komplexet kunde vara. Det DNA jag behövde utvann jag till en början från växter som odlades i växthus, t.ex. i Göteborgs botaniska trädgård. Men långt ifrån alla släkten som skulle ingå i studien finns odlade, och jag tvingades därför att söka material också från annat håll. Herbariematerial, d.v.s. pressade och torkade växter som botaniker har samlat in under flera århundraden, visade sig ofta gå utmärkt att använda. Allt man behöver är en välbevarad bladbit stor som en pekfinger nagel. En inbjudan till New York Botanical Garden gav mig tillgång till en av världens största herbarier (och ett mycket effektivt sekvenseringslaboratorium),

och en stor del av mitt projekt grundar sig på det material jag fick tillgång till där. När man samlar växter i tropikerna är det dock mycket lätt hänt att materialet ruttnar innan det torkar, och därför behandlar man ofta växterna med sprit eller andra konserveringsmedel innan man pressar dem. En sådan behandling gör det nästintill omöjligt att sedan utvinna för mina ändamål fungerande DNA ur materialet. Därför genomförde jag ett antal insamlingsresor till bl.a. Colombia, Kuba och Fiji för att finna färskt material som jag direkt snabbtorkade i kiselgel. På så vis konserverades DNA:t mycket skonsamt, och kunde lätt lösas ut ur bladbitarna efter hemkomsten till laboratoriet i Göteborg.

Mina preliminära analyser, tillsammans med nya data från annat håll (t.ex. Bremer et al., 1995; Delprete, 1996a; Young et al., 1996), visade dock att lösningen på problemet inte var så enkel som det först hade verkat. Dels tycktes det som om Condamineae, Rondeletieae och Sipaneeae inte alls hängde ihop i bara ett komplex, dels verkade ytterligare ett antal tribusar vara inblandade. Dessutom föreföll det som om Robbrechts underfamilj Antirheoideae inte var en naturlig grupp. Insamlingen av DNA-sekvensdata utökades därför till att omfatta också så många representanter som möjligt från tribusarna Calycophylleae, Catesbaeae, Chiococceae, Hippotideae och Guettardeae. Av den anledningen diskuterar den här avhandlingen avgränsningar och systematisk placering av också dessa tribusar.

Jag valde att jämföra sekvenser från tre områden i växternas kloroplast-DNA: *trnL*-intronet, *trnL*-F-spacern och *rps16*-intronet. "Paper I" beskriver analyserna av de två *trnL*-områdena (som ligger intill varandra och därför av praktiska skäl sekvenserades och analyserades tillsammans), och "Paper II" beskriver analysen av *rps16*-intronet. Här i avhandlingen sammanställde jag sedan de båda uppsättningarna av data för en gemensam analys.

Mina resultat

Mina resultat visar att Robbrechts (1988) karta över kaffefamiljen definitivt är i behov av en omritning. Något stöd för underfamiljen Antirheoideae står t.ex. inte att finna, och

eftersom även andra studier (t.ex. Bremer et al., 1995) visat detsamma bör Antirhoeidae därför betraktas som onaturlig. Rubiaceae skall i stället delas in i endast tre stora underfamiljer: Cinchonoideae, Ixoroideae och Rubioideae (Fig. 1).

Som de preliminära studierna antyder är både Condamineae och Rondeletieae (som de beskrivits av Robbrecht, 1988) onaturliga och sammansatta av delar som skall föras till olika ställen i både Cinchonoideae och Ixoroideae. Medan kärnan av Condamineae (klad I1 i Fig. 2) skall vara placerad i underfamiljen Ixoroideae — inte i Cinchonoideae som Robbrecht föreslagit — skall kärnan av Rondeletieae (klad C5b i Fig. 3) vara kvar i Cinchonoideae. Tribuserna Calycophylleae, Catesbaeae, Chiococceae, Hippotideae och Guettardeae hör, också i enlighet med de preliminära studierna, nära samman med vissa av de olika fragmenten från Condamineae och Rondeletieae (Fig. 2 och 3). Gränserna mellan alla dessa tribusar kan däremot inte alltid fastställas — för att göra det behövs ytterligare studier. Släktet *Rondeletia* i sig visar sig också vara onaturligt. En stundom ganska känslomässig diskussion om *Rondeletias* eventuella uppsplittring har förts under senare år (se t.ex. Borhidi, 1982; Lorence, 1991; Borhidi, 1993–94), och mina data stöder alltså en delning av släktet. Flera av utbrytarsläktena skall enligt mina resultat flyttas från Rondeletieae till Guettardeae.

Sipaneae (I3 i Fig. 2) är däremot en tämligen naturlig tribus, även om den inte alls är nära besläktad med Rondeletieae. Ett par släkten som tidigare ingått i Rondeletieae skall dock föras till Sipaneae. Sipaneae skall höra till underfamiljen Ixoroideae.

Ytterligare ett par intressanta samband har lyfts fram med hjälp av mina studier. Till exempel visar sig ett antal släkten som man tidigare fört till Rondeletieae, trots att deras kronbladsflikar är hopvikta på ett för gruppen mycket avvikande sätt, inte alls höra hemma i den tribusen utan i andra delar av familjen — där också hopvikningssättet passar bättre in (I2 i Fig. 2). Dessutom har jag kunnat pekat på nya samband mellan hur några kaffeväxter placerar sitt pollen på pistillens stift och hur de är besläktade med

varandra. Ett annat intressant resultat rör *Molopanthera* och *Posoqueria* (I4 i Fig. 2), två släkten som med hjälp av en katapultmekanism skjuter sitt pollen i en boll mot den insekt som söker nektar i blomman. Tidigare har man känt till att båda har en liknande katapultmekanism, men avfärdat alla tankar på släktskap med att växterna är alltför olika: *Molopanthera* har t.ex. blommor som bara är några millimeter långa, medan blommorna hos *Posoqueria* kan nå flera decimeter i längd. DNA-analyserna visar dock att de är mycket nära besläktade. Troligtvis har den speciella pollinationsmekanismen först uppstått hos en gemensam urmoder till de båda släktena, varefter den har anpassats till olika pollinatörer: korttungade bin hos *Molopanthera* och långtungade svärmare hos *Posoqueria*. Flera släkten som man utifrån enbart utseende tidigare varit osäker på var i kaffefamiljen de skall höra hemma, har nu också placerats med hjälp av mina DNA-sekvensanalyser.

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