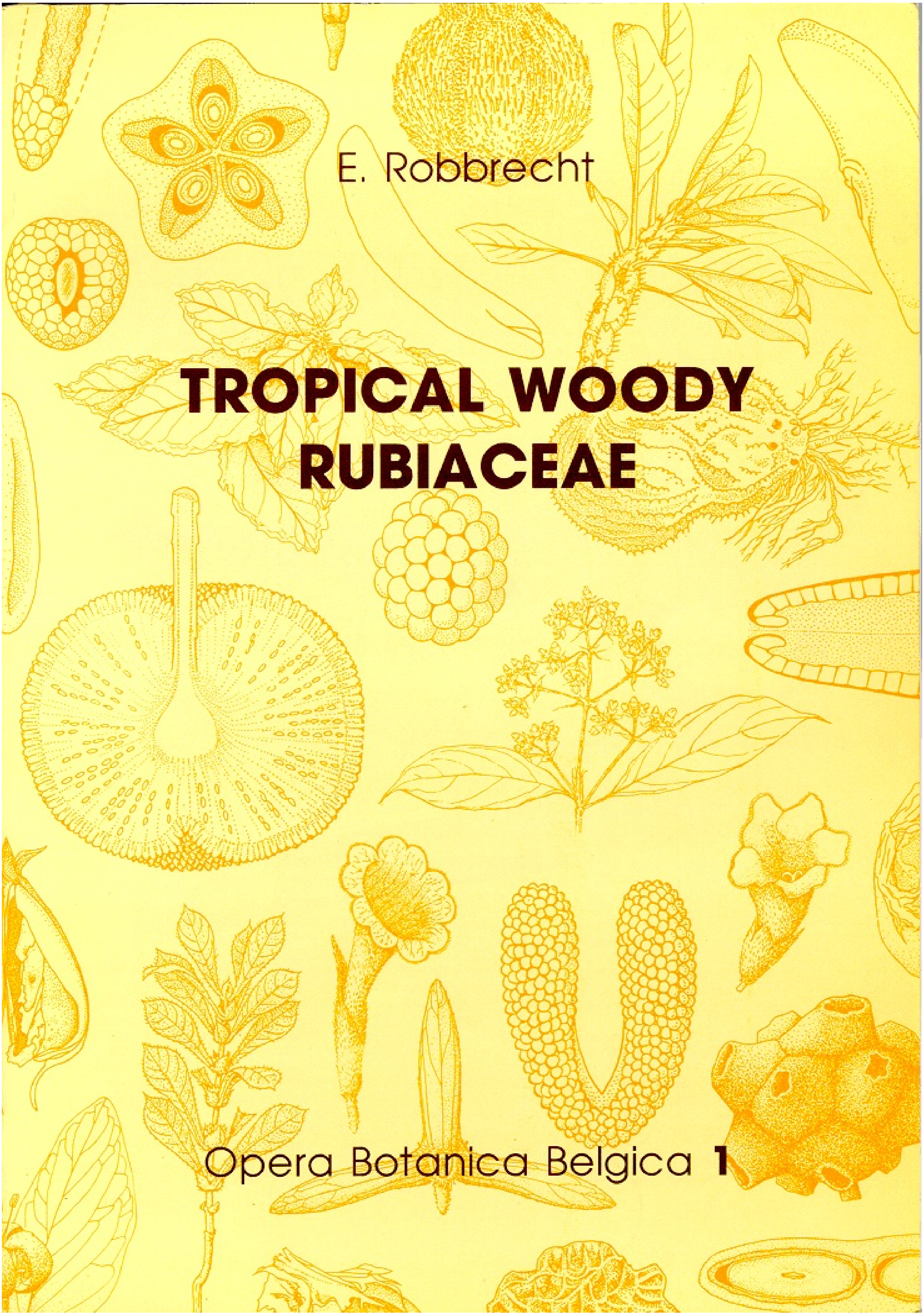
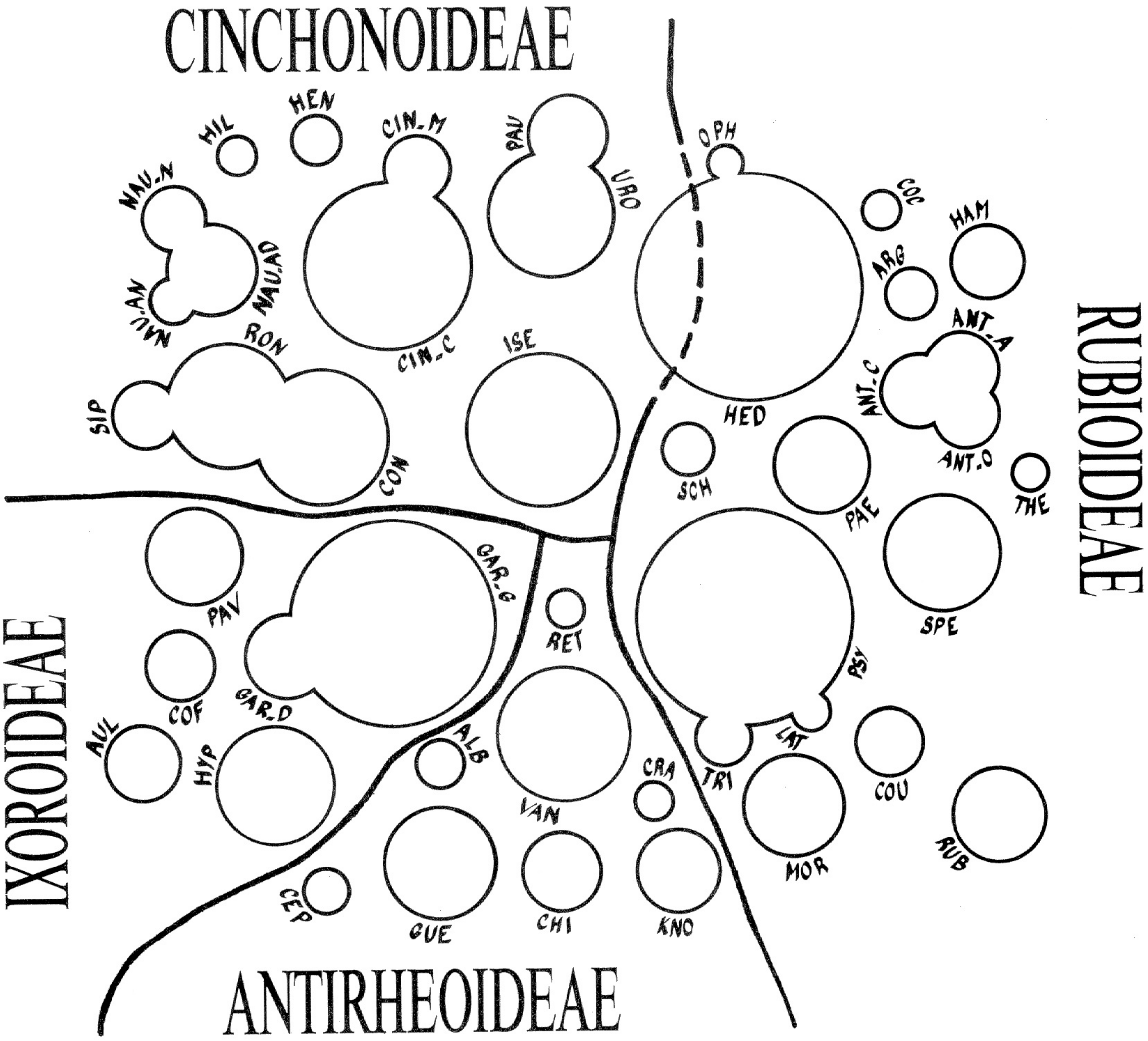


E. Robbrecht

TROPICAL WOODY RUBIACEAE

Opera Botanica Belgica **1**

Reproduced from figures 2 and 61



Mnemonic abbreviations for tribes and subtribes
(*:taxa of uncertain position not taken up in diagram)

Alb.	Alberteae	Gar.	Gardenieae	-N.	Naucleinae
Ant.	Anthospermeae	-D.	Diplosporinae	Oph.	Ophiorrhizeae
-A.	Anthosperminae	-G.	Gardenlinae	Pae.	Paederieae
-C.	Coprosminae	Gue.	Guettardeae	Pav.	Pavetteae
-0.	Operculariinac	Ham.	Hamelleae	Pau.	Pauridiantheae
Arg.	Argostemmateae	Hed.	Hedyotideae	*Per.	Perameae
Aul.	Aulacocalyceae	Hen.	Henriquezieae	Psy.	Psychotrieae
*Cat.	Catesbaeeae	Hil.	Hillieae	Ret.	Retiniphylleae
Cep.	Cephalantheae	*Hip.	Hippotleae	Ron.	Rondeletieae
Chi.	Chiococceae	Hyp.	Hypobathreae	Rub.	Rubieae
Cin.	Cinchoneae	Ise.	Isertieae	Sch.	Schradereae
-C.	Cinchoninae	*Jae.	Jackleae	Sip.	Sipaneeae
-M.	Mitragyninae	Kno.	Knoxieae	Spe.	Spermacoceae
Coc.	Coccocypseleae	Lat.	Lathraeocarpeae	*Tam.	Tammsieae
Cof.	Coffeae	Mor.	Morindeae	The.	Theligoneae
Con.	Condamineeae	Nau.	Naucleeae	Tri.	Triainolepideae
Cou.	Coussarecae	-Ad.	Adininae	Uro.	Urophylleae
Cra.	Craterispermeae	-An.	Neolamarckiinae	Van.	Vanguerleae

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Volume 1

TROPICAL WOODY RUBIACEAE

Opera Bot. Belg. 1

E. Robbrecht

Tropical woody Rubiaceae

Characteristic features and progressions
Contributions to a new subfamilial classification

with 61 illustrations and 5 tables

Meise
Nationale Plantentuin van België
1988

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Paper outcut by N.E. Nannenga-Bremekamp, commemorating her father C.E.B. Bremekamp (7 Feb. 1888 – 1 Dec. 1984), who devoted a large part of his life to the taxonomy of the Rubiaceae.

He also made significant contributions to the knowledge of the Acanthaceae; in this family, *Bremekampia* Sreemadhavan was dedicated to him.

The Dutch name "Bremekamp" signifies "Garden of brambles", and was transliterated into the Greek "*Batopedina*" by Verdcourt for a small genus of African Rubiaceae– Hedyotideae.

Aan Marleen, Katrijn, Geertrui en Veerle

PREFACE

The propagation of botanical knowledge is one of the tasks of the National Botanic Garden of Belgium. This involves primarily the publication of research results of its own scientists, but also of papers submitted by foreign botanists.

The increasing number of botanical texts submitted for publication at our institute, made it clear that there is a need for a series of publications which is particularly appropriate for larger articles. To meet this demand, it was decided to start a new series, **Opera Botanica Belgica,** which is designed especially for the publication of larger articles. The series will benefit from the fact that many authors are now able to submit camera ready texts.

The first paper in the new series deals with Rubiaceae, and so underlines the tradition of rubiaceous taxonomy at our institute. Taxonomists of our staff or other Belgian botanists have conducted a long series of studies on this large family and published their results here, namely (in chronological order) E. De Wildeman, C. Vermoesen, W. Robyns, J. Lebrun, P. Bamps, R. Germain & W. Kessler, P. Moens, E. Petit, E. Robbrecht, E. Denys, L. Pauwels, C. Somers. Many articles by these authors are referred to in the bibliography of the present work.

Foreign botanists also have used our **Bulletin du Jardin Botanique national de Belgique** (formerly **Bulletin du Jardin Botanique de l'Etat**) for the publication of important taxonomic work in the Rubiaceae, to name only some: Bremekamp (Les Lathraeocarpées, tribu nouvelle des Rubiacées, and other papers), Keay *(Randia* and *Gardenia* in West Africa) and Verdcourt. The latter's "Remarks on the classification of the Rubiaceae" became one of the most frequently cited papers on Rubiaceae; it is a synthesis of the knowledge on Rubiaceae, with an attempt on a new classification of the family.

The present work is a similarly thoroughly documented synthesis and is a fine beginning to the series. May the new **Opera Botanica Belgica** maintain the high level of this first contribution, and so fully justify its existence.

Meise, September 1988

E. Petit
Director of the
National Botanic Garden of Belgium

CONTENTS

ACKNOWLEDMENTS

The realisation of the present work would have been impossible without the willing support of my institution and its tradition in tropical taxonomy. I am much indebted to its technical staff: François Vleminckx for taking care of loans, Renée Schurmans and Antonio Fernandez for preparing most of the drawings, Marcel Verhaegen for preparing S.E.M.-graphs and Jacqueline Honoré for efficient word processing and desktop publishing.

When I joined the BR staff as a young botanist, Prof. Dr. E. Petit (after whom I named *Petitiocodon*) introduced me in the Rubiaceae. He freely gave me the full benefit of his long experience with African Rubiaceae, putting many unpublished observations and drawings at my disposal, and was always available for rubiaceous discussions and exchanges of views. The frontispiece pays tribute to Prof. Dr. C.E.B. Bremekamp, the first author who attempted to present a modern classification of the Rubiaceae. The taxonomy of the Rubiaceae owes much to his work, as well as that of other contemporary students: Dr. B. Verdcourt, Dr. J.A. Steyermark, Dr. R.C. Bakhuizen van den Brink jr., Prof. Dr. F. Hallé, Dr. N. Hallé and others. The present review incorporates many of their ideas, and it was stimulating to have personal contact with several of these workers.

Through the years, I have had many fruitful contacts or could cooperate with people engaged in Rubiaceae systematics, Univ.-Doz. Dr. C. Puff, Mrs. D.M. Bridson, Dr. J.H. Kirkbride Jr., Dr. S. P. Darwin, Dr. D. D. Tirvengadum, Dr. C.E. Ridsdale and Drs. M. Jansen in particular. I greatly appreciate the still continuing exchange of ideas we have. Dr. Kirkbride is gratefully acknowledged for his careful reading of the first draft of the text, and Doz. Dr. Puff for many critical comments on it. Mrs. Bridson very carefully checked appendix 4 against the "Kew Herbarium Generic List". I also wish to thank Dr. J. Koek-Noorman, Dr. C.R. Huxley and Dr. G. Zijlstra for their comments on the paragraphs wood-anatomy and epiphytes, and appendix 2, respectively. Dr. P. Goetghebeur's examination of the draft with the eye of a monocot taxonomist, is also much appreciated.

Dr. N. Hallé and Prof. Dr. F. Hallé have published many admirable illustrations of tropical Rubiaceae; a direct style and a subtle schematic touch make their drawings the best ones to represent many features of the Rubiaceae. I thank them for allowing me to reproduce a number of them. Drs. A. Igersheim is thanked for providing the L.M.-graphs of fig. 38.

I dedicate this book to my wife and children, in warm thanks for their daily loving support.

ABSTRACT

The Rubiaceae are an essentially tropical, woody family. More than three fourths of its tribes are predominantly woody, and only the Rubiaceae are centred in temperate regions. Details on material, methods and nomenclature are given, a Venn diagram of the tribal classification of the Rubiaceae is presented, and the concept of subfamily is discussed in Chapter 1.

A survey of (mainly morphological and anatomical, also biological and chorological) features of tropical woody Rubiaceae is provided (Chapter 2). The taxonomic occurrence of a number of features (e.g. xylem-types, presence of raphides, corolla aestivation types, floral biology) is visualized on the Venn diagram of the family.

Existing subfamilial classifications of the Rubiaceae are compared and evaluated (Chapter 3). Characters previously used to define subfamilies, viz. number of ovules per placenta, presence of raphides, reduction of endosperm, and occurrence of certain exotestal cell types, are not as important as originally thought to be. A number of character combinations and trends, mainly in placentation, flower biology, fruit and seed morphology and anatomy, allow the recognition of four subfamilies, the Cinchonoideae, Ixoroideae, Antirheoideae and Rubioideae. While these four names were used in previous classifications, their definition and delimitation is here emended.

A concluding part (Chapter 4) points to gaps in rubiaceous knowledge and formulates suggestions for future research in the family. It is argued that a concerted effort by all workers is needed to obtain a consistent taxonomic database of the Rubiaceae.

The appendices are not limited to tropical woody representatives of the Rubiaceae but encompass the entire family: a survey of the classification proposed here (Appendix 1); additions and corrections relating to Rubiaceae in "Index Nominum Genericorum" (Appendix 2); index to taxa in the present work and other important taxonomic literature (Appendix 3); and an index to the genera of the Rubiaceae and their tribal/subtribal position or synonymy (Appendix 4).

RESUME

Les Rubiacées constituent une famille essentiellement tropicale et ligneuse. Plus des trois quarts des tribus sont principalement ligneuses, et les Rubieae seules sont bien adaptées aux conditions tempérées. Le premier chapitre donne des détails sur les matériel et méthodes et la nomenclature, présente un diagramme de Venn de la classification des Rubiacées, et discute la notion de sous-famille.

Le chapitre 2 donne un aperçu des caractères (surtout morphologiques et anatomiques, mais aussi biologiques et chorologiques) des Rubiacées ligneuses tropicales. La distribution taxonomique d'un certain nombre de caractères (par exemple les types de xylème, la présence de raphides, la préfloraison de la corolle, la biologie florale) est visualisée à l'aide du diagramme de Venn. Dans le troisième chapitre, une comparaison et évaluation des sous-familles adoptées dans des classifications existantes est faite.

Plusieurs caractères autrefois employés pour la définition de sous-familles, ne sont pas entièrement significatifs, notamment le nombre d'ovules par placenta, la présence de raphides, la réduction de l'endosperme et la présence de certains types de cellules exotestales. Un certain nombre de combinaisons de caractères et de tendances évolutives (principalement dans la placentation, la biologie florale et la morphologie et l'anatomie des fruits et des graines) permettent de distinguer les Cinchonoideae, Ixoroideae, Antirheoideae et Rubioideae. Or les noms de ces quatre sous-familles ont été employés dans des classifications existantes, aussi leur définition et leur délimitation sont-elles emendées.

Dans une partie concluante (chapitre 4), les lacunes dans la connaissance des Rubiacées sont indiquées et des suggestions pour la recherche taxonomique future de cette famille sont faites. Un effort concerté de tous les chercheurs est nécessaire pour obtenir une base de données taxonomiques consistante des Rubiacées.

L'ouvrage contient des appendices non limités aux Rubiacées tropicales ligneuses mais se rapportant à toute la famille, à savoir: Appendix 1, aperçu de la classification proposée, Appendix 2, additions et corrections relatives aux Rubiacées dans "Index Nominum Genericorum", Appendix 3, index des taxons cités dans l'ouvrage et dans d'autres travaux systématiques importants, Appendix 4, index des genres de Rubiacées avec leur synonymie ou position tribale/sous-tribale.

Chapter 1

INTRODUCTION

Several dicotyledonous families have a mainly tropical distribution, consist essentially of woody members, and are represented in temperate areas by an impoverished group of advanced herbaceous taxa; this applies e.g. to the Lythraceae, Polygalaceae, Apocynaceae and Verbenaceae. The Rubiaceae are the largest angiosperm family conforming to this pattern (table 1). A rapid review shows that less than 20 % of the genera are herbaceous; 29 of the 38 currently accepted tribes are predominantly woody (fig. 3) and of the larger tribes, only two, the Hedyotideae and Spermacoceae, are primarily herbaceous. The distribution of tribes is predominantly tropical or subtropical, only the Rubiaceae being concentrated in temperate climates.

Galium and *Rubia* (tribe Rubieae), (tropical to) temperate herbs with pseudo-whorls of "leaves", are atypical members of this family comprising an array of mainly woody plants with decussate leaves and interpetiolar stipules. Within the Rubiaceae, the Rubiaceae are the tribe wherein the evolution to herbaceous habit is most extreme, only a very few representatives (*Crucianella* spp. and *Galium* spp.) being (sub)shrubby. In the other predominantly herbaceous tribes, more woody lines of evolution are also present. Conversely, the trend to herbaceousness also exists in many of the essentially woody tribes; the Psychotrieae e.g. have many large genera which are entirely woody, several woody genera containing herbaceous or semi-herbaceous species (e.g. *Psychotria* spp.), and also a few entirely herbaceous genera (e.g. *Geophila*).

It is obvious that the classification of predominantly woody families should be based on an understanding of their woody representatives and of the features, trends and progressions in these members. Most herbaceous representatives can be easily related to a classification based on the woody ones.

Table 1.- **The six largest angiosperm families**, with their number of genera and species according to Mabberley (1987). Appendix 4 (Genera Rubiacearum) contains 659 genera, and so confirms Mabberley's estimation of the number of genera, at least in Rubiaceae.
While the Asteraceae, Orchidaceae, Fabaceae and Poaceae are of worldwide importance, the Rubiaceae and Euphorbiaceae are essentially tropical and woody.

	genera	**species**
Asteraceae	**1**	**21**
Orchidaceae	**795**	**17**
Fabaceae (s.l.)	**657**	**16**
Rubiaceae	**637**	**10**
Poaceae	**737**	**7**
Euphorbiaceae	**326**	**7**

Insight into the speciation processes of plants is limited, and this applies especially to perennial plants (Brown 1985). The family overview presented in Chapter 2 has a two-fold purpose. First, it documents (mainly morphologically) the adaptations within one of the largest predominantly perennial families of the dicotyledons, and is thus a step towards later analyses of speciation processes in and phylogeny of the Rubiaceae, helpful in determining evolution of characters, and evaluating character state polarities. Secondly, an attempt is made to determine whether these features and their trends correlate with the present subfamilial concepts of the Rubiaceae.

This work was motivated by an invitation to talk on characteristic features of tropical woody Rubiaceae at a symposium, "Modes of speciation in annual vs. perennial plants", held in July 1987 during the XIVth International Botanical Congress at Berlin (Robbrecht 1987b). It was a view of a large group which is essentially perennial, in the symposium. The text is a much expanded elaboration of the lecture. Indices and check-lists relating to the entire Rubiaceae (Appendices 1-4) are included because the last worldwide survey of the family is almost a century old (Schumann 1891).

The present survey certainly emphasizes two points:

- I am especially familiar with tropical African Rubiaceae as reflected in the citation of examples and in the illustrations, although I have tried as much as possible to investigate representatives from other continents, and
- I have paid particular attention to fruit and seed characters. In the Rubiaceae, fruits and seeds exhibit a very wide range of diverse adaptations, and it is obvious that their interpretation will contribute much to our understanding of relationships within the family.

1.1 Material

The present investigation is based mainly on an intensive search through available taxonomic literature on the Rubiaceae and on the study of herbarium specimens in BR. Additional material has been received on loan, mainly from K, L, and U (herbarium abbreviations following Holmgren, Keuken & Schofield 1981).

Many illustrations are original, and others are reproduced or adapted from literature as indicated in table 2.

*Table 2.- **Alphabetical list of illustrations**, with indication of their source: original drawings from herbarium specimens (country, collection) or living material (botanical garden, cultivation number), and other illustrations reproduced ("from") or redrawn ("after").*

SPECIES	FIGURE	DRAWN FROM REDRAWN AFTER COPIED FROM
Airosperma psychotrioides Lauterb. & Schumann	53 G-J	New Guinea, Brass 32539 (K)
Airosperma trichotomum (Gillespie) A.C. Smith	53 A-F	Fiji, Smith 5935 (K)
Alberta magna E. Meyer	40 F	South Africa, Gerstner 4850 (BR)
Anthospermum aethiopicum L.	46 D, E	after Schumann 1891: fig. 41 D, E
Argocoffeopsis kivuensis Robbrecht	14 G1	Zaire, Pierlot 1834 (BR)
Aulacocalyx laxiflora E. Petit	19 A, D	Zaire, Vanderyst 23201 (BR)
Batopedina pulvinellata Robbrecht	25 G	Zaire, Duvigneaud 5154 R (BRLU)
	32 C	Zaire, Malaisse 9672 (BR)
Bertiera bicarpellata (Schumann) Hallé	7 B	from N. Hallé 1970: pl. 7/1
Bertiera bracteolata Hiern	35 A	from N. Hallé 1970: pl. 8/11, 13
Bertiera laxa Benth.	32 G	after N. Hallé 1970: pl. 9/11
Bertiera letouzeyi Hallé	9 E	from N. Hallé 1970: pl. 11/9
Boholia nematostylis Merr.	54	Indonesia, Kostermans 22135 (K)
Bouvardia triphylla Salisb.	26 H	after Baillon 1880: fig. 315
Bouvardia sp.	29 E, 35 C	Hortus BR, cult. s.n.
Calycosiphonia spathicalyx (Schumann) Robbrecht	22 A, 32 I	Zaire, Luja s.n. (BR)
Canephora madagascariensis Gmelin	21 E	Madagascar, Decary 10774 (BR)
	21 F	after Baillon 1880: fig. 303
Canthium lactescens Hiern	52 N-U	Rwanda, Becquet 424 (BR)
Carphalea angulata Baillon	26 G	after Baillon 1880: fig. 279
Carphalea glaucescens (Hiern) Verdc.	36 F	after Verdcourt 1976: fig. 26/8
Catesbaea spinosa L.	4 A	from F. Hallé 1967: pl.23/3
Cephaelis sp. ("Uragoga" phoenicea Schumann)	14 B	Costa Rica, Pittier & Durand 1867 (BR)
Cephalanthus occidentalis L.	55	U.S.A., Bayard Long 13693 (BR)
Chazaliella macrocarpa Verdc.	45 C	Zaire, Louis 1503 (BR)
Chazaliella oddonii (De Wild.) E. Petit & Verdc.	41 A-D	Zaire, Louis 5887 (BR)
Chimarrhis cymosa Jacq.	26 N	after Schumann 1891: fig. 9 B
Chiococca belizensis Lundell	52 H-F	Belize, Gentle 6796 (U)
Chiococca racemosa L.	26 L	after Baillon 1880: fig. 283

Cinchona officinalis L.	43 B, 60 A-G	Colombia, Fosberg 19275 (BR)
Corynanthe mayumbensis (Good) Hallé	26 D, 29 H	from N. Hallé 1966: pl. 9/3 & 4
Corynanthe paniculata Welw.	43 E	Zaire, J. Dubois 342 (BR)
Cosmocalyx spectabilis Standley	40 D	Mexico, Langlassé 404 (K)
Coutarea hexandra (Jacq.) Schumann	43 A	Brazil, Reitz & Klein 3738 (BR)
Craterispermum sp.	56 E-K	Zaire, Louis 9162 (BR)
Craterispermum schweinfurthii Hiern	56 A	Zaire, Troupin 3175 (BR)
	56 B-D	Zaire, Troupin 3423 (BR)
Crossopteryx febrifuga Benth.	43 C	Zaire, Malaisse 12525 (BR)
Cuviera nigrescens Wernham	31 A	Ivory Coast, Guillaumet 1224 (BR)
Dichilanthe zeylanica Thwaites	27 A	after Schumann 1891: fig. 34 K
Dictyandra arborescens Welw. ex Hook. f.	25 D	Zaire, Louis 12509 (BR)
Duroia aquatica (Aublet) Bremek.	4 C	from F. Hallé 1967: pl. 9/1
Duroia saccifera Hook. f.	9 D	from F. Hallé 1967: pl. 29/3-6
Fadogiella manikensis (De Wild.) Robyns	7 A	Zaire, Malaisse 9350 (BR)
Gaertnera longevaginalis (Hiern) E. Petit	21 B	Zaire, Louis 1881 (BR)
Gaertnera vaginans (DC.) Merr.	14 D	Sri Lanka, Thwaites 544 (BR)
Galiniera coffeoides Del.	21 C	Zaire, de Witte 1574 (BR)
Gardenia augusta (L.) Merr.	1	Hortus WU, cult. n. RR 750
Gardenia imperialis Schumann	35 F	Zaire, Evrard 2023 (BR)
Gardenia thunbergia L. f.	40 G	after Baillon 1880: fig. 300
Geophila obvallata (Schumach.) F. Didr.	23 D	after Schumann 1891: fig. 38
Geophila repens (L.) Johnston	16 D	Zaire, Breyne 2449 (BR)
Gleasonia uaupensis Ducke	45 B	Brazil, Fróes 22384 (U)
Gouldia terminalis (Hook. & Arn.) Hillebrand	26 F	after Schumann 1891: fig. 26 D
Guettarda parviflora Sw.	25 A	Martinique, Hahn 1508 (BR)
Guettarda speciosa L.	49	Tanzania, Drummond & Hemsley 3277 (BR)
Heinsenia diervilleoides Schumann	26 J	Zaire, Delvaux 550 (BR)
Heinsia crinita (Afzel.) G. Taylor	14 E1	from N. Hallé 1966: pl. 26/2
Heinsia myrmoecia (Schumann) Hallé	44 A	Cameroun, Bos 4606 (WAG)
Henriquezia verticillata Spruce	27 B	after Schumann 1891: fig. 12 A
Hillia parasitica Jacq.	58, 59	Puerto Rico, Wagner 176 (U)
Hillia tubiflora Cham.	6 B	from F. Hallé 1967: pl. 25/1
Hippotis albiflora Karsten	27 C	after Schumann 1891: fig. 26 H
Hutchinsonia barbata Robyns	26 C	after Robyns 1928: fig. 6 C
Hutchinsonia cymigera Bremek.	14 G2	Zaire, Lebrun 6103 (BR)
Hymenocoleus hirsutus (Benth.) Robbrecht	16 A	Zaire, Liben 2915 (BR)
Hymenocoleus neurodictyon (Schumann) Robbrecht	14 E2	Zaire, Louis 14889 (BR)
Hymenocoleus scaphus (Schumann) Robbrecht	7 C	after Robbrecht 1975: fig. 4 A,B
	20 A, 26 E	Zaire, Louis 12778 (BR)
Hymenodictyon floribundum (Hochst. & Steud.) Robinson	21 D	Zaire, Ghesquière 4326 (BR)
Ixora stricta Roxb.	35 B	Hortus BR, cult. n. 451
Jackiopsis ornata (Wall.) Ridsdale	40 E	Sumatra, Dumas 1559 (L)
Kerianthera praeclara Kirkbride	32 H	after Kirkbride 1985: fig. 3f
Knoxia platycarpa Arn.	46 F, G	Sri Lanka, Thwaites 1689 (BR)
Leptactina arnoldiana De Wild.	29 B	from N. Hallé 1970: pl. 16/5
Leptactina leopoldi-secundi Büttn.	14 F3	from N. Hallé 1970: pl. 17/2
Machaonia acuminata Kunth	19 F, G	Mexico, Linden 1213 (BR)
Macrosphyra longistyla Hook. f.	46 A	from F. Hallé 1967: pl. 39/4, 5
Mitchella repens L.	33 B	after Baillon 1880: fig. 294
Mitragyne ciliata Aubrév. & Pellegrin	23 B	from N. Hallé 1966: pl. 3/2
Morinda citrifolia L.	41 E-G	Malay Peninsula, King's coll. 4663 (BR)
Morinda longiflora G. Don	40 H	after Schumann 1891: fig. 44
Mussaenda nannanii Wernham	23 E, 25 H	Zaire, L. Dubois 236 (BR)
	29 L	from N. Hallé 1966: pl. 28/3

Myrmecodia sp.	45 F	Hortus BR, cult. n. 60-313
Myrmecodia sp.	45 G	Hortus BR, cult. n. 60-241
Myrmecodia tuberosa Jack.	6 A	after Beccari 1884-86: pl. 13
Nauclea vanderguchtii (De Wild.) E. Petit	5 C	from N. Hallé 1966: pl. 6/2
	14 F1	from N. Hallé 1966: pl. 6/1
Otomeria elatior (A. Rich. ex DC.) Verdc.	36 A	from N. Hallé 1966: pl. 11/7
Otomeria guineensis Benth.	14 H	from N. Hallé 1966: pl. 20/2
Otomeria volubilis (Schumann) Verdc.	29 J, 36 B, 40 C	from N. Hallé 1966: pl. 11/8 & 22/3' & 9
Paederia bojerana (A. Rich.) Drake	28 A	Mozambique, Goldsmith 13/64 (BR)
Paederia sp.	37 A	Madagascar, Puff 850804-2/3 (FPA-fixation, WU)
Pagamea guianensis Aublet	33 C, D	after Baillon 1880: fig. 270, 271
	40 B	Brazil, Campbell & al. P 21854 (BR)
Palicourea corymbifera (Müll. Arg.) Standley	45 H	Brazil, Krukoff 6792 (BR)
Palicourea lasiantha Krause	16 B	Ecuador, Asplund 9023 (BR)
Palicourea rigida Kunth	27 E	after Schumann 1891: fig. 38 B
Pauridiantha callicarpoides (Hiern) Bremek.	35 J	from N. Hallé 1966: pl. 52/6, 8
	19 C, 44 B, 57 G-K	Zaire, Kitembo 20 (BR)
Pauridiantha mayumbensis (Good) Bremek.	35 I	from N. Hallé 1966: pl. 51/5
Pauridiantha rubra (Benth.) Bremek.	57 A-F	Zaire, Louis 9352 (BR)
Pausinystalia macroceras (Schumann) Pierre ex Beille	43 D	Zaire, Corbisier-Baland 832 (BR)
Pavetta indica L.	26 I, 33 A	after Baillon 1880: fig; 257 & 258
Pentagonia tinajita Seemann	9 C	from F. Hallé 1967: pl. 27/4,5
Pentas lanceolata (Forskk.) Deflers	25 F, 29 D	Hortus BR, cult. n. 72-87
Pentas purpurea Oliver	28 B	Zaire, Malaise 11339 (BR)
Pentodon pentandrus (Schum. & Thonn.) Vat.	36 G	from N. Hallé 1966: pl. 11/6
Phitopis multiflora Hook. f.	14 A	after Hooker 1871: tab. 1093
Phyllacantha grisebachiana Hook. f.	4 B	from F. Hallé 1967: pl.24/1
Pinckneya pubens Michaux	26 B	after Baillon 1880: fig. 331
	45 A	U.S.A., Ahles 53498 (BR)
Pogonopus exsertus (Örsted) Schumann	26 A	after Schumann 1891: fig. 6 P
Preussiodora sulphurea (Schumann) Keay	17	Cameroun, Mildbraed 6801 (HBG)
Prismatomeris beccariana (Baillon) J. T. Johansson	20 F, G	after Johansson 1987a: fig. 5
Pseudomussaenda stenocarpa (Hiern) E. Petit	28 C	after F. Hallé 1960: pl. 5/3
	29 K	from N. Hallé 1966: pl. 27/3
Pseudonesohedyotis bremekampii Tennant	36 E	after Verdcourt 1976: fig. 34/8
Pseudosabicea sthenula Hallé	11 C	from F. Hallé 1961: pl. 2/5
Psilanthus lebrunianus (Germain & Kesler) J.-F. Leroy ex Bridson	9 A	Zaire, Louis 6150 (BR)
Psychotria amboniana Schumann	13 B, 25 B	from Petit 1966: fig. 5 B & C
Psychotria blakei Standley & Steyerm.	35 G	after Steyermark 1974: fig. 263e
Psychotria camerunensis E. Petit	13 D, 21 A	from Petit 1966: fig. 10 A
Psychotria gossweileri E. Petit	13 G	from Petit 1966: fig. 9 A
Psychotria hemicephaelis Wernham	35 H	after Steyermark 1974: fig. 245e
Psychotria kirkii Hiern	29 F, G, 35 D, 40 A	Hortus BR, cult. n. 53-6779
Psychotria merumensis Steyermark	14 G4	after Steyermark 1972: fig. 76f
Psychotria minuta E. Petit	19 B	Zaire, Louis 3625 (BR)
Psychotria verschuerenii De Wild.	10	Hortus BR, cult. n. 75-204
Psydrax livida (Hiern) Bridson	52 V-Z	Mozambique, Correia & Marques 2772 (BR)
Psydrax parviflora (Afz.) Bridson	16 C	Zambia, Fanshawe 4660 (BR)
	31 B	Zaire, Devred 3452 (BR)
Retiniphyllum maguirei Standley	32 E	Surinam, Maguire 24787 (U)

Retiniphyllum schomburgkii (Benth.) Müll. Arg.	52 H-M	Brazil, Prance & al. 9094 (U)
Rondeletia ochracea Urban	14 F2	Santo Domingo, von Türckheim 3530 (BR)
Rondeletia odorata Jacq.	29 C, 35 E	Hortus BR, cult. n. 39-2109
Rytigynia kigesiensis Verdc.	37 B	Zaire, Troupin 9670 (spirit, BR)
Sabicea congensis Wernham	27 D	from N. Hallé 1966: pl. 41/3
Sabicea floribunda Schumann	11 A	from F. Hallé 1961: pl. 2/1
Sabicea mildbraedii Wernham	11 B	from F. Hallé 1961: pl. 2/3
Sacosperma paniculata (Benth.) Taylor	19 I	Zaire, Vanderyst 25775 (BR)
	36 C	from N. Hallé 1966: pl. 11/11
Salzmannia nitida DC.	42	Brazil, Schol. Agr. E.A.N. 2057 (U)
Sarcocephalus pobeguinii Hua	40 I	from N. Hallé 1966: fig. 5/9 & 10
Schumanniophyton problematicum (A. Chev.) Aubrév.	9 B	from F. Hallé 1967: pl. 27/1
	20 D	after F. Hallé 1967: pl. 28/4
Sericanthe adamii (Hallé) Robbrecht	5 A	Liberia, Adam 24858 (UPS)
Sericanthe leonardii (Hallé) Robbrecht	13 A	from Robbrecht 1978a: fig. 10 B
Sericanthe pellegrinii (Hallé) Robbrecht	22 B	Gabon, Le Testu 7773 (P)
Sericanthe petitii (Hallé) Robbrecht	13 C	from Robbrecht 1978a: fig. 2 A
Sericanthe roseoides (De Wild. & T. Durand) Robbrecht	13 F	from Robbrecht 1978a: fig. 2 C
Sericanthe trilocularis (Scott Elliot) Robbrecht	13 E	from Robbrecht 1978a: fig. 2 B
	19 E	Sierra Leone, Hepper 2609 (P)
Simira sp. ("Sickingia" glaziovii Schumann)	26 K	after Schumann 1891: fig. 9 O
Sipanea biflora (L. f.) Cham. & Schlecht.	25 E	French Guyana, Billiet 1996 (BR)
Spathichlamys oblonga Parker	28 D	after Ridsdale 1982: fig. 1c
Spermacoce dibrachiata Oliver	45 E	Zaire, Schmitz 7634 (BR)
Squamellaria imberbis (A. Gray) Becc.	45 D	Fiji, Smith 1787 (US)
Stelechantha cauliflora (Good) Bremek.	36 H	from N. Hallé 1966: pl. 25/15
Stipularia africana Beauv.	13 C	from N. Hallé 1966: pl. 33/1
Strumpfia maritima Jacq.	32 A	after Baillon 1880: fig. 260
Tarenna jolinonii Hallé	25 C	from N. Hallé 1970: pl. 24/7
Tarenna zygoon Bridson	32 D	Zimbabwe, Chase 4714 (BR)
Temnopteryx sericea Hook. f.	29 I	from N. Hallé 1966: pl. 32/3
Theligonum cynocrambe L.	20 E	after Schneider in Wunderlich 1971: fig. 4b
Thieleodoxa lanceolata Cham.	26 M	after Schumann 1891: fig. 30 G
Tresanthera condamineoides Karsten	32 J	after Schumann 1891: fig. 6 K, L
Tricalysia aequatoria Robbrecht	20 H	after Robbrecht 1979: fig. 1 H
	32 F	Zaire, Louis 10913 (BR)
Tricalysia bifida De Wild.	29 A	Zaire, Germain 4674 (spirit, BR)
Tricalysia concolor Hallé	14 G3	Gabon, N. Hallé & Le Thomas 119 (P)
	20 K	after Robbrecht 1979: fig. 1 C
Tricalysia cryptocalyx Baker	46 B	Madagascar, Perrier de la Bâthie 3764 (P)
	46 C	Madagascar, Perrier de la Bâthie 3715 (P)
Tricalysia elliotii (Schumann) Hutch. & Dalz.	20 C	after Robbrecht 1983: fig. 1
Tricalysia ferorum Robbrecht	20 N	after Robbrecht 1983: fig. 1
Tricalysia glabra Schumann	20 J	after Robbrecht 1979: fig. 1 B
Tricalysia jasminiflora (Klotzsch) Benth. & Hook. f. ex Hiern	20 L	after Robbrecht 1987a: fig. 3 B
Tricalysia nogueirae Robbrecht	20 I	after Robbrecht 1979: fig. 1 F
Tricalysia reticulata (Benth.) Hiern	20 M	after Robbrecht 1987a: fig. 3 A
Uncaria africana G. Don	5 B	from N. Hallé 1966: pl. 2/1
Uncaria donisii E. Petit	23 A	Zaire, Donis 2039 (BR)
Uncaria guianensis (Aublet) Gmelin	43 F, 60 H-M	Brazil, Berg & al. P 18675 (BR)
Virectaria major (Schumann) Verdc.	20 B	Rwanda, Bouxin 383 (BR)
Virectaria multiflora (Sm.) Bremek.	36 D	from N. Hallé 1966: pl. 11/1
Wittmackanthus stanleyanus (Schomb.) Kuntze	32 B	after Steyermark & Kirkbride 1975: fig. 1b

1.2 Methods

Normal methods of herbarium taxonomy were followed. Efforts were made to increase the number of characters observed, resulting from simple, easily applied techniques. These types of characters are important, since many Herbaria have no technical facilities for anatomical research (embedding, sectioning etc.), and since taxonomic studies imply examination of much material. In the literature, description of some characters is frequently inaccurate or misleading. It is absolutely essential to study domatia, pyrenes, seed-coats, etc. following methods similar to those given here.

Domatia: these structures at the undersides of leaf-blades were mostly observed not only in surface view, but also in cross-section under low magnification. The distinction between pit- and crypt-types, e.g., can only be discerned in this manner.

Crystals: crystals can often be recognized with the naked eye as glittering bodies, in various organs, but to assess their nature (raphides, styloids, etc.) they were examined with a light microscope using polarized light. After acquiring familiarity with the Rubiaceae, raphides were easily recognizable with a binocular dissecting microscope; aggregates of crystal-sand may nevertheless have a similar appearance, and if there was the slightest doubt, L.M. verification was made. This was done in hand-sections or squashed tissues prepared in water. Permanent slides were made using Hoyer's gum.

Hoyer's gum is an interesting medium since it is water-soluble; though commonly used amongst cryptogamists, it is poorly known to angiosperm taxonomists. It slightly clears the prepared tissue; slides must be kept flat for ca. 1 month before vertical storage. Preparation: soak 30 g of arabic gum in 50 ml distilled water. Add 200 g chloral hydrate and let stand (several days) until the medium becomes clear, then add 20 g of glycerine.

Hairs and excrescences: Trichomes were mounted permanently in Kaiser's glycerol gelatin stained with methyl green; the L.M. observation (including examination of cuticular structures) was sometimes completed with S.E.M. examination. Colleters were mounted permanently in Hoyer's gum, but when they were small, Kaiser's glycerol gelatin stained with methyl green was used instead. While standard colleters visible with the naked eye were easily be prepared, reduced colleter types, often invisible under the binocular lens, had to be scraped off the inside of stipules, bracts or calyces onto a slide for microscopic examination.

Corolla: Microcharacters on the inside of the corolla-lobes were studied with the S.E.M. under magnifications of up to × 5000 from dried herbarium material or critical point dried material.

Pyrenes: Preformed germination slits in pyrenes normally become visible during germination of diaspores. Pressure from the raphal opening towards the position of the embryo radicle (first established by pyrene dissection or assumed from ovule morphology) opens the pyrenes along their preformed slits (Petit 1964a & pers. comm.).

Seed-coat, exotestal cells: Bremekamp, on various occasions (e.g. Bremekamp 1947b, summary and illustrations in Bremekamp 1952), introduced seed-coat anatomy into the taxonomy of the Rubiaceae. He studied peeled off seed-coats by transmitted light in surface view, and distinguished several testal cell types (in fact exotesta), e.g. the "pitted testa-cell", described as having strongly thickened side walls and enormous circular or oval pits confined to the equally thickened bottom wall. This cell-type is indeed so characteristic that it is easily distinguished from surface views only.

When trying to apply Bremekamp's testa criteria to my own taxonomic research in the Rubiaceae, it was apparent that in many cases the cell structure is intricate and difficult to understand; it appeared that not only the inner but also the outer tangential wall may be thickened. Also a kind of "L.O.-analysis", such as depicted by Bremekamp (1949) for Acranthera (showing a "strongly thickened bottom-wall ... in which the peripheral pit-canals converge towards the centre") or here in fig. 57 (E, J), does not clearly elucidate the three-dimensional cell structure. Therefore Verdcourt (1958: 230) rejected the pitted exotestal cell as the main criterion to define the subfamily Cinchonoideae (sensu Bremekamp 1966). Thus I observed rubiaceous seed-coats in surface view and cross-section; hand-made sections, unstained and slightly cleared in Hoyer's gum, are the easiest and most rapid way to do this. In this way, the exact anatomical nature of exotestal cells, as well as the stratification of the entire seed-coat, was observed.

S.E.M.-examinations of rubiaceous seed-coats are only valuable if they are correlated with L.M.-observations in cross-section. They provide additional information on the sculpturing of the thickenings of the radial and the inner tangential walls if these latter become exposed by (natural or artificial) withering of the outer tangential walls. Artificial removal of the outer tangential walls was effected by maceration in water (several days) followed by ultrasonic cleaning (fig. 1). A more sophisticated enzymatic treatment may replace maceration.

The following standard **cellulase-pectinase pretreatment** for Giemsa-staining is very effective (Kiehn, pers. comm.):

- soak seeds for 1-4 days in water, causing them to swell or germinate;
- fixation in Carnoy's medium (96 % ethanol/acetic acid) for a minimum of 24 h at 8-10°C (in refrigerator);
- after 1-3 days replacement of the fixative by 96% ethanol;
- transfer material to 0.01 M citrate-buffer for 15-20 min, then 1.5-2 h in the enzyme solution (1 weight-% cellulase plus 10 volume-% pectinase in 0.01 M citrate-buffer pH 4.8; stored frozen and used at 37°C);
- rinse 15 min in 0.01 M citrate-buffer, then in distilled water.

After the enzymatic treatment, execute ultrasonic cleaning, dry the seeds at room temperature, and then put them on S.E.M. specimen stubs.

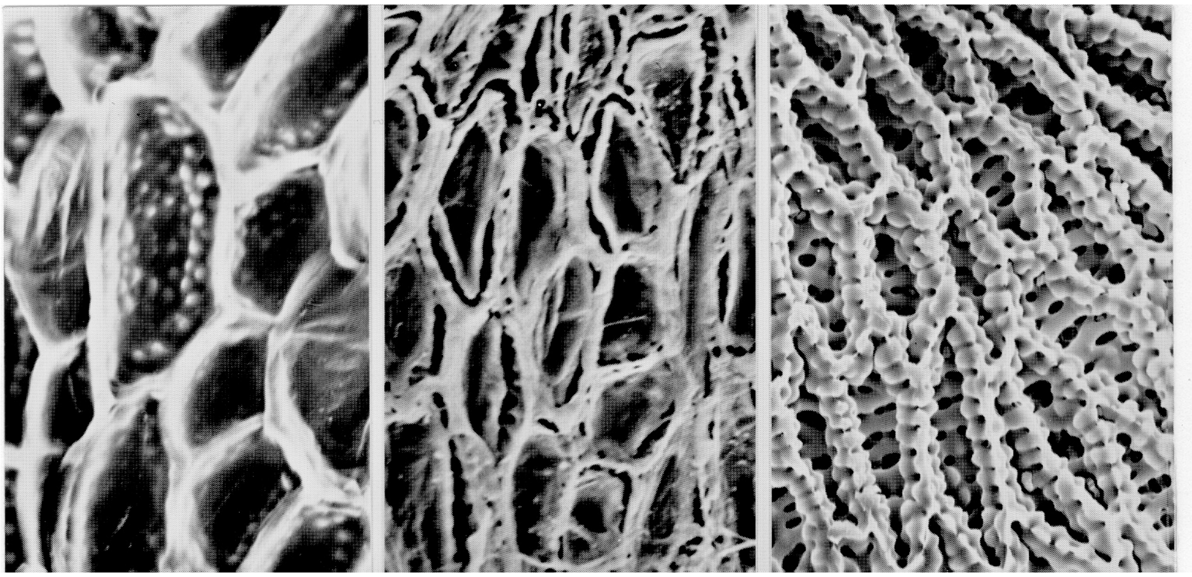

*Figure 1.- **Surface views of the exotesta, showing the effects of treatments used**: before treatment (outer tangential walls obscuring the thickenings), after cellulase-pectinase treatment (outer tangential walls loosened at their edge), and after the same enzymatic treatment followed by ultrasonic treatment (radial and inner tangential walls exposed).*
Gardenia augusta. Line = 100 µm.

Endosperm: The oily nature of the endosperm was assessed by dissecting seeds under water; a slight pressure on the endosperm caused oil droplets to escape and float to the surface of the water.

Pollen: A sound palynological investigation uses the classical technique of acetolysis. Herbarium taxonomists dissect flowers every day and each time throw away the pollen. Wodehouse's (1935) rapid and convenient method of pollen preparation (embedding untreated pollen in a drop of Kaiser's glycerol gelatin stained with methyl green) allows however, a quick examination of the major pollen characters (size; shape; nature, number and position of apertures). I have used Wodehouse's method, and, in a selected number of cases, acetolysis. For S.E.M.-observations, acetolyzed material was generally indispensable.

Mnemonic abbreviations for tribes and subtribes
(*: taxa of uncertain position not taken up in diagram)

Alb. Alberteae
Ant. Anthospermeae
-A. Anthosperminae
-C. Coprosminae
-O. Operculariinae
Arg. Argostemmateae
Aul. Aulacocalyceae
*Cat. Catesbaeeae
Cep. Cephalantheae
Chi. Chiococceae
Cin. Cinchoneae
-C. Cinchoninae
-M. Mitragyninae
Coc. Coccocypseleae
Cof. Coffeae
Con. Condamineeae
Cou. Coussareeae
Cra. Craterispermeae
Gar. Gardenieae
-D. Diplosporinae
-G. Gardeniinae
Gue. Guettardeae
Ham. Hamelieae
Hed. Hedyotideae
Hen. Henriquezieae
Hil. Hillieae
*Hip. Hippotieae
Hyp. Hypobathreae
Ise. Isertieae
*Jac. Jackieae
Kno. Knoxieae
Lat. Lathraeocarpeae
Mor. Morindeae
Nau. Naucleeae
-Ad. Adininae
-An. Neolamarckiinae
-N. Naucleinae
Oph. Ophiorrhizeae
Pae. Paederieae
Pav. Pavetteae
Pau. Pauridiantheae
*Per. Perameae
Psy. Psychotrieae
Ret. Retiniphylleae
Ron. Rondeletieae
Rub. Rubieae
Sch. Schradereae
Sip. Sipaneeae
Spe. Spermacoceae
*Tam. Tammsieae
The. Theligoneae
Tri. Triainolepideae
Uro. Urophylleae
Van. Vanguerieae

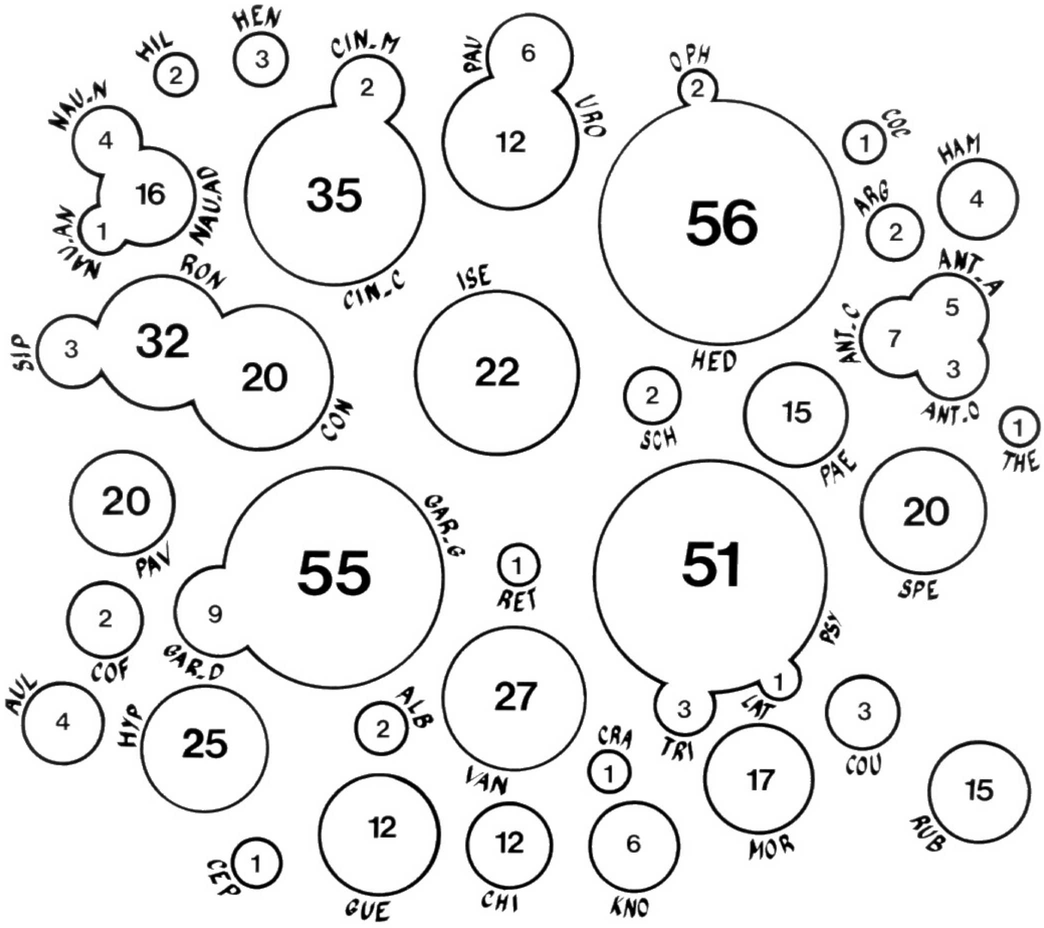

*Figure 2.- **Venn diagrammatic representation of the tribal classification** of the Rubiaceae accepted here; the area of the circles for tribes and subtribes corresponds roughly to the number of genera included in each; these (often approximative) numbers are given in each circle; for the concept of certain tribes and for some groups of uncertain position not taken up see text, 1.3. The abbreviations of the tribes are the first three letters of their names; subtribes are indicated by their first or two first letters.*
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1.3 Diagrammatic representation of the classification of the Rubiaceae

The Rubiaceae are so numerous that visual representations are indispensable in obtaining a good overview of feature distribution. I have chosen to use a Venn diagram of the tribal classification (fig. 2) inspired by Dahlgren's (1975, 1980) similar methods for the angiosperms. In contrast to the conflicting subfamilial concepts of various authors, there is a rather general consensus on the tribal classification of the Rubiaceae; nevertheless, for two major problems of tribal delimitation, viz. the Alberteae/Cremasporeae and Gardenieae/Ixoreae complexes, new concepts were recently proposed (Puff, Robbrecht & Randrianasolo 1984; Robbrecht & Puff 1986) and are followed here. My diagrammatic representation tries to present an outline of the tribal classification, but is not intended to be phylogenetic.

The following remarks concern details of the outline:

- These tribes are delimited as follows: Isertieae (incl. Acranthereae, Sabiceeae and Heinsieae; *Bertiera*, however, still of uncertain position); Cinchoneae (incl. Coptosapelteae); Rondeletieae (incl. Simireae); Hamelieae (incl. Deppeeae, Bremer 1987); Anthospermeae (incl. Durringtonieae, Puff & Robbrecht 1988); Psychotrieae (incl. Gaertnereae); and Hedyotideae (incl. Otiophora, Puff 1983 and Cruckshanksieae, Puff 1988);
- The Theligoneae [not considered by Verdcourt (1958) or Bremekamp (1966)] are included in the vicinity of the Anthospermeae (Wunderlich 1971, Robbrecht 1982b, Puff 1986a).
- *Brachytome* (Brachytomeae: Tirvengadum & Sastre 1986) provisionally remains within the Gardenieae-Gardeniinae (further study may indicate additional subdivision of the Gardeniinae; cf. Robbrecht & Puff 1986).
- The following are of uncertain position at this time pending further study: Hippotieae (3 genera), Tammsieae (1 genus), Catesbaeeae (2 genera), Perameae (1 genus) and Jackieae [1 genus; placed tentatively in subfamily Cinchoneae (sic) by Ridsdale (1979) without further indication of affinity].

To facilitate understanding for readers not familiar with tropical Rubiaceae, the same mnemonic abbreviations for tribes and subtribes as in fig. 2, indicate the position of quoted genera throughout the text.

1.4 The subfamily concept

In only a few angiosperm families, is the recognition of subfamilies remarkably constant and without controversy, for example the Fabaceae divided into Faboideae, Caesalpinioideae and Mimosoideae. In most, the subfamilial classification is less constant and the subject of extensive discussion. So, even the classification of the Asteraceae into Lactucoideae and Asteroideae has been questioned (see Cronquist 1977). In another example, the Cyperaceae, several classifications have been proposed, with the subfamilies varying from none to five with very different delimitations (for a survey see Goetghebeur 1986). Such discordant conceptions may be due to the poor definition of the rank "subfamily" as compared to family, genus and species, but also to the homogeneity of certain families. Because their members are less divergent than in others, larger entities are difficult to discern.

The Rubiaceae conform to this pattern. The recognition of subfamilies has been based on a single character or just two or three trivial characters: ovules one versus more than one in the classical systems (Hooker 1873, Schumann 1891), or raphides present versus absent and endosperm copious versus almost absent in more modern classification systems (Bremekamp 1952 & 1966, Verdcourt 1958). [Presence of raphides, however, to some extent correlated with trichome characters? See 2.6.2].

If subfamilies are so difficult to recognize, why should we try to define them? While in a number of cases the need of subfamilies is debatable, for example in the Asteraceae with less than fifteen tribes (Cronquist 1977), the reverse is no doubt true for the Rubiaceae. They consist of more than 650 genera arranged in more than fourty tribes, and insight into the classification and evolution of such a huge family (table 1) can only be gained if one has a workable main classification: if many tribes can be grouped into a few natural subfamilies, these latter can serve as important "screening areas" for detailed taxonomic research. The classification between family and genus "must provide a system within which the evolutionary problems can be clearly recognized and formulated", as Burtt (1977) stated, also emphasizing that establishment of a correct phylogeny at family level is an attainable goal, far less speculative than construction of a phylogenetic hypothesis for the whole of the angiosperms.

1.5 Nomenclature

The nomenclature of the subfamilial, tribal and subtribal names of the Rubiaceae has recently been clarified by Darwin (1976a), who showed that a limited number of well established tribal names were illegitimate at that time, viz. Mussaendeae (legitimate: Isertieae), Ixoreae (legitimate: Coffeeae) and Psychotrieae (legitimate: Psathureae). The legitimate name for the subfamily Guettardoideae is Antirheoideae. One should also bear in mind that in Schumann's (1891) system, the Hedyotideae are called Oldenlandieae. The legitimate names are always used here, except where discussions of data from the literature are clearer when using the traditional names which are then given in quotation marks.

However, Darwin's proposal to replace Psychotrieae with Psathureae can no longer be followed because of subsequent changes in the "International Code of Botanical Nomenclature". Psychotrieae A. Rich. ex Dum. was illegitimate when published because it included *Coffea*. Since the latter genus belongs elsewhere (a tribe of its own), the name Psychotrieae has priority from 1829 and Psathureae becomes synonymous (Art. 63.3). For details see Smith & Darwin (1988: 147).

The authorities of A. Richard's taxa taken over by De Candolle and first published in his prodrome, are somewhat confused; for a complete discussion see Stearn (1957). The tribes are best ascribed to De Candolle, as given by Darwin (1976a), since their definition and circumscription is the one in De Candolle's own system: Cordiereae A. Rich. ex DC., Gardenieae A. Rich. ex DC., and Isertieae A. Rich. ex DC. However, Richard's genera are simply included in De Candolle's prodrome, and I fully support Stearn's arguments that Richard is their principal author; the conjunction in should consequently be used with these genera. Farr, Leussink & Stafleu's (1979) treatment of these generic names is inconsistent (e.g. *Saldinia* A. Rich. in DC., *Tricalysia* A. Rich. ex DC.).

Throughout the text, genera are quoted without their authority. In cases of homonymy outside the Rubiaceae, I intend the generic homonym quoted in the Rubiaceae by Farr, Leussink & Stafleu (1979), Farr, Leussink & Zijlstra (1986) or the supplement to this index provided here (appendix 2), and in case of generic homonymy inside the Rubiaceae the oldest name or the nomen conservandum.

Chapter 2

CHARACTERISTIC FEATURES OF TROPICAL WOODY RUBIACEAE

In this chapter those features are reviewed which are classically or became recently important in the taxonomy of the Rubiaceae. Other characters may equally have weight, but are still too poorly known to assess their taxonomic value; these are mostly not discussed here.

For details of the life-cycle of Rubiaceae e.g., Wunderlich's (1971) survey is still practically up to date; it reviewed embryological data on anther tapetum (always uninucleate), occurrence of bi- respectively trinucleate mature pollen grains, number of female archespore cells, ovules (always tenuinucellate, unitegmic), embryo sac and its antipodes, and development of endosperm, embryo, suspensor and seed. Adronova (1988) gave references of a few additional recent embryological studies, and discussed embryological data in the light of the relationship between Rubiaceae and Gentianales. As regards the mature pollen nuclear number in Rubiaceae, a recent study examining 103 species of 32 Indian genera (Mathew & Philip Omana 1986) confirms the non-random distribution pattern of the two pollen types. Binucleate pollen characterizes the majority of the Rubiaceae, and especially the woody ones. Trinucleate mature pollen grains (the probably advanced condition) are more common in the herbaceous tribes, especially the Knoxieae, Hedyotideae and Rubieae, but are also found in a few woody groups, viz. in Cephalantheae, in some Psychotrieae and a few Cinchoneae.

For a review of chemotaxonomic studies, see p. 144.

A second limitation is that the characteristic features of tropical woody representatives are surveyed. As shown in chapter 1 (see also fig. 3), the family is essentially tropical and woody. When of particular interest, however, herbaceous representatives will be discussed for comparison.

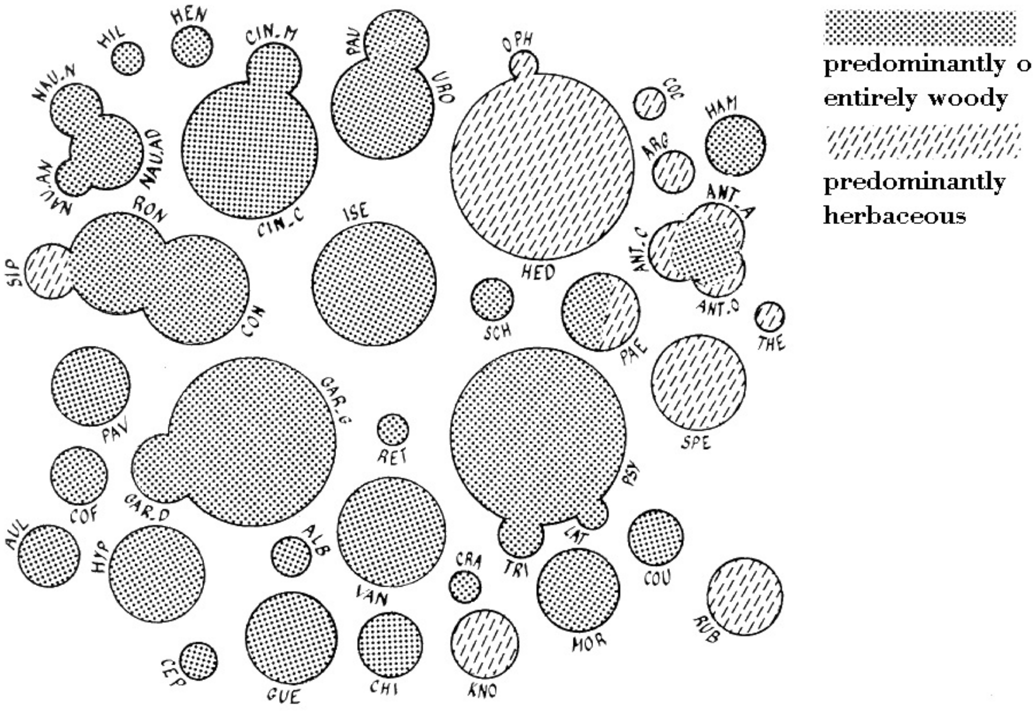


*Fig. 3.- **Occurrence of woodiness and herbaceousness** in the tribes of the Rubiaceae.*

The **adaptive significance** of a large number of features is easily understood, e.g. myrmecophilous structures, fang hooks, dispersal structures etc., and transference of function is sometimes obvious, e.g. from anthers to style (stylar pollen presentation, 2.13.3.2) or from seed-coat to endocarp (pyrenes as diaspores, 2.9) or to outer endosperm layers (seeds without seed-coat, 2.10.3). It is perilous, however, to attribute a functional explanation to every feature, especially since plant-life has probably many non-functional aspects (Van Steenis 1981). In the Rubiaceae, it seems in particular difficult to explain the enormous diversity in the seed-coat anatomy (2.10.3) from the functional viewpoint.

2.1 Habit and architecture

Large trees are common in the Cinchoneae, Condamineeae and associated tribes and in the Gardenieae. Otherwise they are very rare in the Rubiaceae. I have noted trees attaining dimensions of 20-30 m or more in the following taxa (most, but not all, the species of the genera mentioned are large trees) :

Cin.-C.: *Alseis, Cinchona, Ladenbergia, Capirona, Molopanthera, Pausinystalia*
Cin.-M.: *Mitragyna*
Nau.-N.: *Nauclea, Burttdavya*
Nau.-An.: *Anthocephalus*
Nau.-Ad.: *very common, in eleven genera*
Hen.: *Platycarpum, Henriquezia*
Ron.: *Elaeagia, Simira erythroxylon*
Con.: *Chimarrhis, Rustia, Tresanthera*
Ise.: *Isertia*
Gar.-G.: *Brenania, Duroia, Gardenia, Genipa, Posoqueria, Kutchubaea*
Gar.-D.: *Tricalysia macrophylla*
Gue.: *Guettarda*
Psy.: *Pagamea plicata*
Jac.: *Jackiopsis*

The majority of the woody Rubiaceae are small trees, treelets or shrubs; many species are recorded as either shrubby or tree-like, and are on the borderline of what is defined as a tree. Such treelets are very common in the understorey of the rain-forest.

Awareness of the taxonomic value of branching patterns in woody Rubiaceae (Fagerlind 1943; Petit 1964b) existed long before the general interest in tree architecture stimulated by the work of "the tropical troika" (Hallé & Oldeman 1970; Hallé, Oldeman & Tomlinson 1978). According to the examples given in the latter publication, fifteen different architectural models are known in the Rubiaceae; the data are too insufficient to make significant correlations between higher taxa and occurrence of architectural models. Branching patterns have nevertheless such a practical value for the recognition of genera, that they are important bases of taxonomic evidence in the Gardenieae (Petit 1964, Tirvengadum & Sastre 1979, 1986), and that their use is incorporated in recent floras (Bridson & Verdcourt 1988: fig. 75).

Monoaxial trees (Corner's model only) are rare and perhaps concentrated in the Gardenieae (*Gardenia* spp., *Pseudomantalania* spp.) and associated Pavetteae (*Captaincookia*) and Coffeeae (*Coffea* spp.); other records are in the Condamineeae (*Bikkia* spp.), Hippotieae (*Pentagonia* spp.) and in *Bertiera* spp. (inc. sed.).

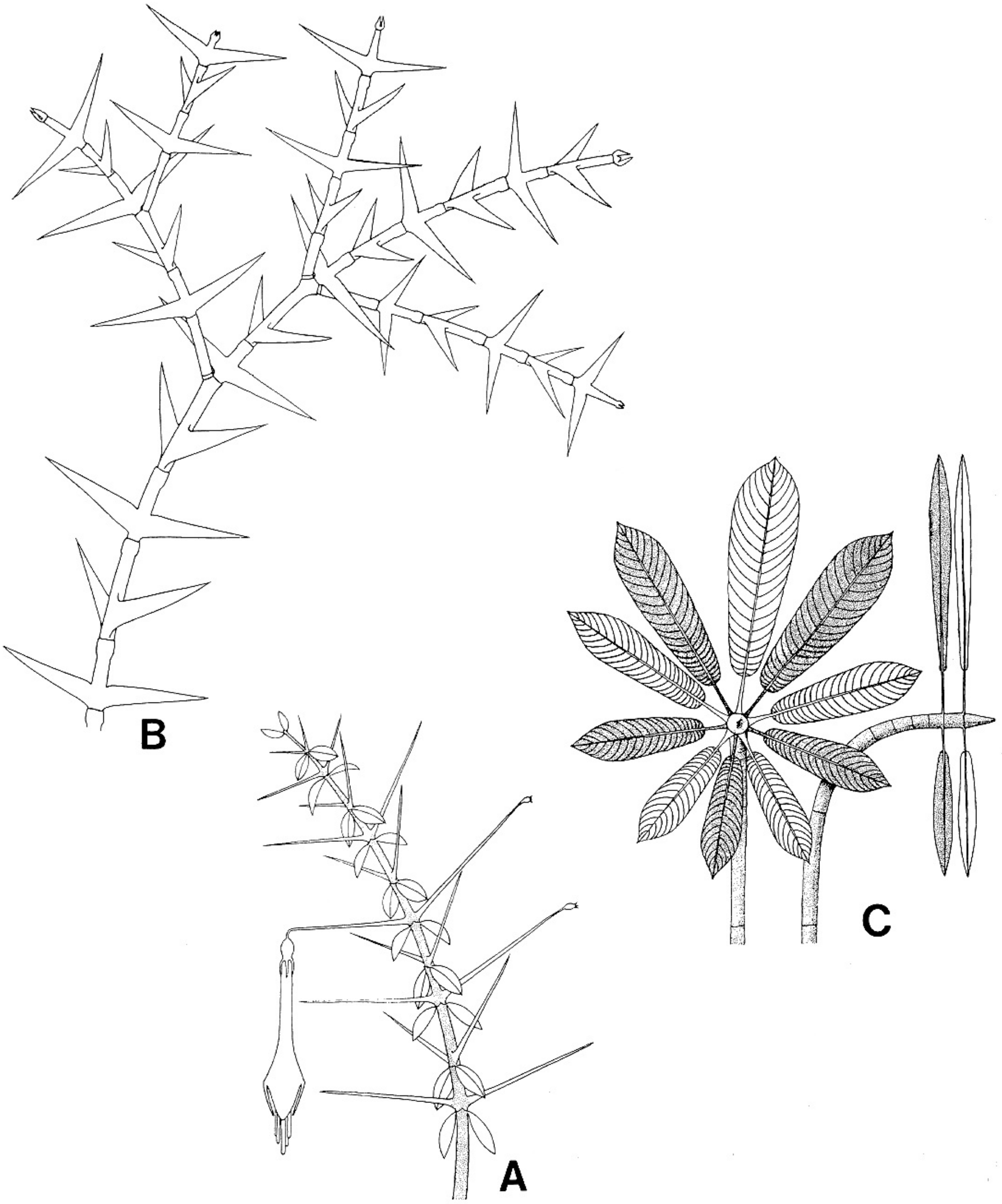


Fig. 4. - ***Thorns and phyllomorph branches****: A,* Catesbaea spinosa*, thorny twig with solitary flowers at the end of thorns; B,* Phyllacanthus grisebachianus*, flattened thorns functioning as cladodes; C,* Duroia aquatica*, apical and lateral view of a phyllomorph branch, which has two whorls of leaves (each whorl differently shaded). All from F. Hallé.*

Rubiaceous polyaxial trees mostly have orthotropic plus plagiotropic branches and belong mainly to Fagerlind's, Petit's, Roux' and Cook's model. For a complete overview of the branching modes in polyaxial rubiaceous trees see N. Hallé (1966: 7-9, fig. 1).

Despite the decussate phyllotaxis, twisting of internodes and petioles results in that the plagiotropic branches often have all the leaf-blades in one horizontal plane (e.g. *Coffea*, Cof., *Canthium*, Van., *Lasianthus*, Mor.), and thus resemble large pinnately compound leaves. Other architectural adaptations lead to twigs resembling digitately compound leaves; these result from shortening of the internodes often combined with anisophylly (4-6 leaves in a terminal pseudo-verticillate position; e.g. *Euclinia*, Robbrecht & Puff 1986: fig. 2a). Apparently true phyllomorph branches (deciduous as a whole and leaving a scar on the stem) are limited to the genera *Duroia* (fig. 4 C) and *Schumanniophyton* (Gar.-G.; see F. Hallé 1967 for a complete documentation and further illustrations).

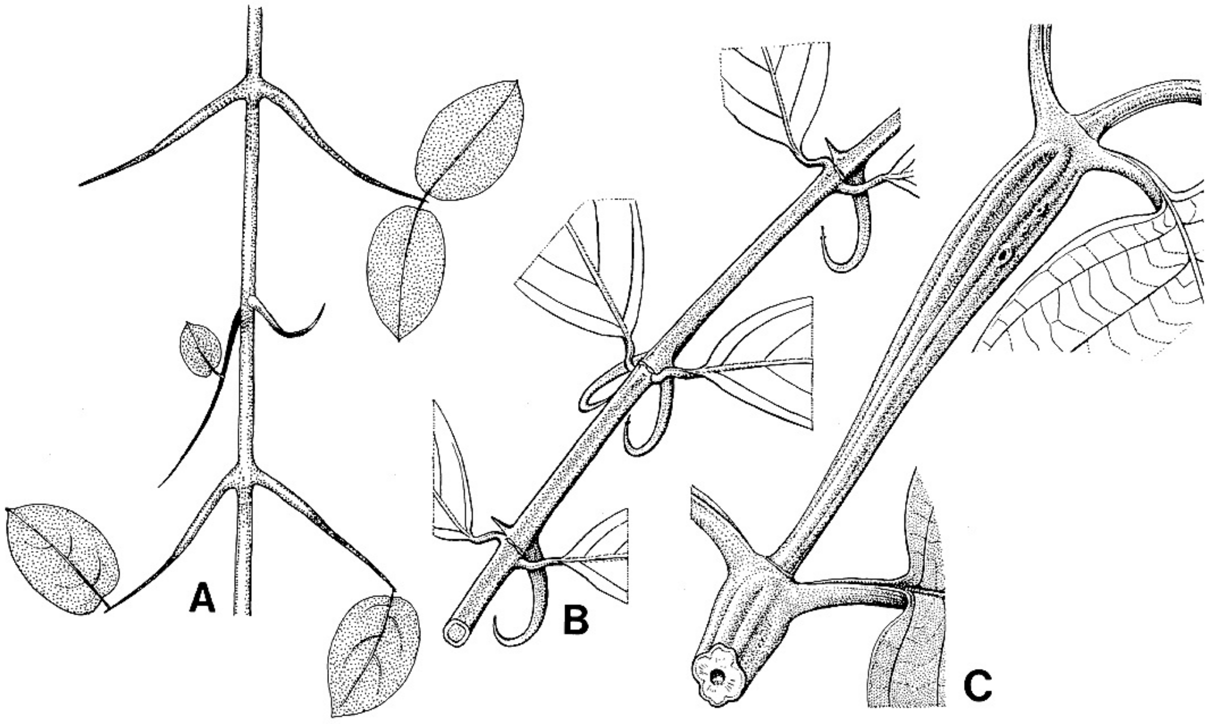


Fig. 5. - ***Modifications of the axis****: A,* Sericanthe adamii, *branch with recurved, proximally thickened and relatively short lateral shoots functioning as climbing hooks; B,* Uncaria africana, *fang hooks; C,* Nauclea vanderguchtii, *myrmecophilous internode. B, C, from N. Hallé.*

2.2 Peculiar biological groups

2.2.1 Lianas

Woody climbers are common. They occur in the following groups (genera with asterisks are entirely lianescent):

Cin.-C.: *Coptosapelta, *Ferdinandusa*
Cin.-M.: **Uncaria*
Ron.: *Greenea*
Ise.: *Mussaenda, *Pseudosabicea, Sabicea, Heinsia*
Gar.: *many genera, see Robbrecht & Puff 1986*
Pav.: **Rutidea, Leptactina, Tarenna*
Chi.: *Chiococca*
Gue.: **Malanea, Chomelia*
Van.: *Canthium s.l.*
Psy.: *Psychotria*
Hed.: *Otomeria, Sacosperma*
Sch.: *Schradera, Lucinaea*
Mor.: *Coelospermum, Morinda, Gynochthodes*
Spe.: *Emmeorrhiza (subherbaceous)*
Pae.: *Paederia*
Ant.: *Opercularia*
inc. sed. (Cin./Hed.): *Manettia, Danais*

A few climbers also evolved in herbaceous genera:

Hed.: *Lipostoma*
Spe.: *Diodia, Spermacoce*
Rub.: *Galium (climbing by means of reflexed hairs).*

The survey above shows that the large majority of climbers is confined to the two subtribes of the Gardenieae, the Pavetteae, Isertieae and the two subtribes of the Cinchoneae. In other tribes only a small number of climbing representatives have evolved (not always true vines: *Chiococca* and *Malanea* e.g. growing across other vegetation).

Climbing hooks (modified short-shoots or inflorescence peduncles; Guillaumin 1931) occur in *Uncaria* (Cin.-M., fig. 5 B) and *Oxyceros* (Gar.-G.) (Robbrecht & Puff 1986: fig. 1 c-d), but such intricate adaptations are rare. Climbing is mostly achieved by simple modes such as horizontal (e.g. *Argocoffeopsis*, Gar.-D.) or somewhat recurved positioning of lateral branches (e.g. *Atractogyne*, Gar.-G., *Sericanthe*, Gar.-D.) or twining (e.g. *Sherbournia*, Gar.-G., *Otomeria*, Hed., *Paederia*, Pae., *Emmeorrhiza*, Spe.). However, in several representatives, e.g. *Tarenna junodii, Sericanthe adamii* (fig. 5 A) and *Rutidea membranacea,* lateral branches tend to shorten, to recurve and to thicken proximally, and thus are reminiscent of fang hooks. *Psychotria serpens* (Japan) is climbing by means of sucker-like outgrowths. *Schradera* and *Lucinaea* combine epiphytism with climbing, the latter by means of adhesive rootlets on the twigs.

*Fig. 6. - **Epiphytic Rubiaceae**: A,* Myrmecodia tuberosa *(after Beccari); B,* Hillia tubiflora *(from F. Hallé).*
Lines = 10 cm.

2.2.2 Epiphytes

Approximately 250 rubiaceous species from 29 genera are epiphytic (table 3). Thus the Rubiaceae are among the ten dicotyledonous families containing the largest number of epiphytes (Madison 1977).

Apart from randomly distributed rare cases in a few tribes such as the Gardenieae, epiphytes are restricted to three circles of affinity, viz.

- the Hillieae and associated Cinchoneae (33 epiphytic species),
- the Psychotrieae (ca. 90 epiphytes), and
- the Ophiorrhizeae and Schradereae, both associated with the Hedyotideae (ca. 40 epiphytes).

The degree of epiphytism in a genus varies from complete (e.g. *Hillia, Myrmecodia*) to strong (e.g. ca. 50 % of the species in *Cosmibuena*), to weak (e.g. three out of sixty species in *Amaracarpus*), see table 3.

In most genera, the plants have no special structures for collecting water or soil (fig. 6 B) and are consequently "proto-epiphytes", the first of the four epiphytic classes distinguished by Schimper (cited in Richards 1952: 124). In the Psychotrieae, however, *Myrmecodia, Myrmephytum, Squamellaria* and *Hydnophytum* are highly advanced myrmecophytes. They are the show-pieces of extreme epiphytic adaptation in the Rubiaceae, mentioned or illustrated in many textbooks. In these bizarre plants (fig. 6 A) the hypocotyl enlarges into a swollen tuber provided with cavities, galleries and entrance holes and inhabited by ants; remarkably the tubers also develop in the absence of ants. In *Myrmecodia* the stems are highly modified and ± succulent, covered with spiny shield-like outgrowths (the spines are modified roots, see 2.3.1), but in *Hydnophytum* the stems are normal in appearance. For details see Huxley 1978; the biology of these ant-associations is discussed in 2.13.1.

A special adaptation exists in *Posoqueria* spp. (Gar.-G.); they germinate and first develop as an epiphyte, but later form roots which grow downwards along the host tree to develop a terrestrial stem, in fact a supraterranean root (de Wit 1954: 9). According to N. Hallé's (1970: 169, fig. 1) drawing, *Aidia rubens* (Gar.-G.) may facultatively show the same strangling, hemi-epiphytic behaviour.

Most rubiaceous epiphytes are woody. *Myrmecodia* and its allies are ± succulent. Herbaceous epiphytes occur only in *Ophiorrhiza, Nertera, Relbunium* and *Didymochlamys.*

The majority of tropical epiphytes have wind-dispersed dust-seeds (Madison 1977). Most rubiaceous epiphytes, however, do not have this seed-type (see table 3: only seven species in *Ophiorrhiza* and *Didymochlamys*). The majority of epiphytic species in the Rubiaceae have fleshy fruits (20

*Table 3.- **Tribes and genera with epiphytes**. For each genus, the number of epiphytic species is given followed by the total number of species in the genus separated by a slash. The type of dispersal is indicated by D (dust seeds), W (winged seeds), P (plumose seeds) or F (fleshy fruits). The area where epiphytic representatives occur, is given. Exclamation marks indicate facultative epiphytism. Most rubiaceous epiphytes are woody; the herbaceous genera are indicated with an asterisk.*
Data from Madison 1977, supplemented and adapted.
Remarks: [1] Including Myrmedoma, Huxley & Jebb in prep.
[2] The epiphytic Psychotrias probably belong to several genera.

		EPIPHYTIC/ TOTAL SPP.	DIS- PERSAL	DISTRIBUTION (OF EPIPHYTIC SSP.)
Cin.-C.	Balmea	1/1	W	Mexico
	Cosmibuena	6/12	W	neotropics
	Hymenodictyon !	1/20	W	Africa
Cin./Hed.	Neohymenopogon	3/3	W	Himalaya
	Manettia	5/130	W	neotropics
Hil.	Hillia	20/20	P	neotropics
	Ravnia	4/4	P	C. America
Ise.	Lecananthus	1/2	F	Malaysia
	Leucocodon	1/1	F	Sri Lanka
	Ophryococcus	1/1	F	C. America
Gar.-G.	Aidia !	1/2	F	Africa
	Posoqueria	some/12	F	neotropics
	Sulitia	? 1/1	F	Malaysia
Gue.	Malanea	2/27	F	neotropics
Oph.	* Ophiorrhiza	5/150	D	New Guinea
Ham.	Hoffmannia	2/125	? F	C. America
Sch.	Schradera	c.20/40	F	neotropics
	Lucinaea	15/25	F	Malaysia to New Caledonia
Psy.	Myrmecodia	26/26	F	SE. Asia to Pacific
	Myrmephytum [1]	4/4	F	New Guinea, Philippines, Celebes
	Squamellaria	2/2	F	Fiji
	Hydnophytum	45/45	F	SE. Asia to Pacific
	Psychotria [2]	? c. 10/1400	F	Africa, Malaysia, neotropics
	Procephaleium	1/1	F	Java
	Amaracarpus	3/60	F	New Guinea
Ant.-C.	Coprosma	6/90	F	Malaysia, New Zealand, Chili
	* Nertera	6/12	F	Malaysia, Pacific
Rub.	* Relbunium	2/30	F	neotropics
Inc. sed.	* Didymochlamys	2/2	D	neotropics

genera), mostly with a few, large seeds; dry fruits containing wind-dispersed winged or plumose seeds occur in only seven genera (see table 3).

Most rubiaceous epiphytes are found in tropical Asia and tropical America; they are very rare in tropical Africa (table 3); in *Psychotria*, only one African species, "*Psychotria*" *euchlora* K. Schum. (probably a *Chasallia*) is epiphytic. This geographic pattern corresponds with the well known poverty of the African epiphyte flora.

2.2.3 Geofrutices

Geofrutices or geoxylic plants, characterized by massive woody branched or unbranched underground stems and slightly ramified or unbranched supraterranean twigs occur in many of the dry areas of Africa ("the underground forests of Africa", White 1976 - where an extensive discussion of the ecological factors responsible for the evolution of geofrutices). In literature they are referred to by a diversity of terms: pyrophytic subshrub, geoxylic suffrutex, shrubby herb, subshrub or undershrub with rhizomatous rootstock. The terms suffrutex, subshrub or undershrub are vague and inappropriate and apply as well to dwarfshrubs as to halfshrubs.

In Africa, the Rubiaceae seem to be the family containing the largest number of geofrutices. They occur in several tribes :

Gar.-G.: *Catunaregam spp., Gardenia spp., Mitriostigma* sp., *Rothmannia* sp.
Gar.-D.: *Sericanthe suffruticosa, Tricalysia* spp.
Pav.: *Leptactina* spp., *Pavetta* spp.
Van.: *Fadogia, Fadogiella (fig. 7 A), Tapiphyllum, Temnocalyx, Pygmaeothamnus etc.; in many genera ± all* spp.
Kno.: *Pentanisia* spp.
Cra.: *Craterispermum* sp.
Psy.: *Psychotria* spp., *Chasallia* sp.
Mor.: *Morinda angolensis*
Hed.: *Pentas* spp.
inc. sed.: *Bertiera laurentii*

The world distribution of geofrutescent plants is very uneven and their greatest concentration is in Africa (White 1976); a search through literature on Brazilian cerrado vegetation convinced me that this statement is probably overrated. In Rubiaceae nevertheless, geofrutices seem to be concentrated in Africa. I have traced only a few cases in S. America: *Palicourea* spp., Psy. (Ferri 1973: fig. 25), "*Borreria*" *angustifolia*, Spe. (Hoehne 1939: 41, figure showing *xylopodium* !), *Declieuxia cordigera* Psy., *Relbunium hirtum* subsp. *camporum,* Rub., and probably others; in all the examples given, woodiness is mostly restricted to the underground parts, and the aerial stems are only partially woody at their bases.

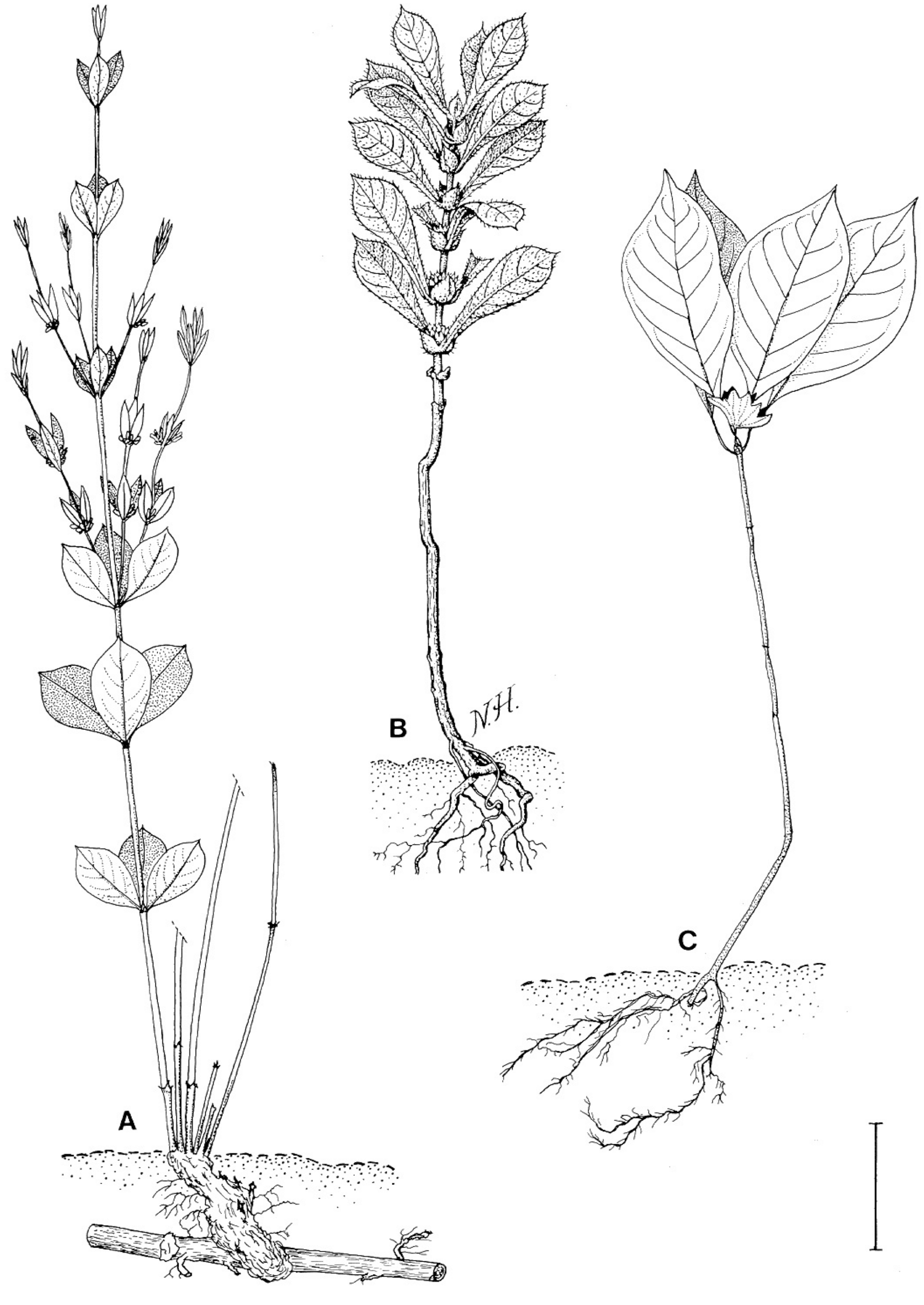


Fig. 7. - ***Geofrutex and monocaul dwarfs:*** *A,* Fadogiella manikensis, *a geofrutex; B,* Bertiera bicarpellata, *a monocaul dwarf with axillary inflorescences (from N. Hallé 1970); C,* Hymenocoleus scaphus, *a monocaul dwarf with a terminal inflorescence.*
B from N. Hallé, C after Robbrecht 1975. Line = 10 cm.

In a number of groups, the geofrutescent life-form apparently evolved long ago; this seems to be the case in Vanguerieae where several genera are entirely geofrutescent. In other cases, essentially shrubby groups may contain one or a few geofrutescent species, and so pairs of closely related species, one shrubby and one geofrutescent, are easily recognizable, in *Sericanthe* (Gar.-D.) e.g. S. *andongensis* and *S. suffruticosa*. In such cases, speciation is obviously recent and is even not always completed (White 1976). *Tricalysia* (Gar.-D.) (Robbrecht 1979, 1982a, 1983, 1987a) illustrates this; it is a large genus centred in the African rain-forest but radiating out into regions with a dry season and there evolving into inter alia geofrutices. A number of species are obligately geofrutescent (e.g. *Tricalysia cacondensis, T. nogueirae*) and closely related to a shrubby species (in the case of the examples *T. ruandensis* and *T. glabra* respectively). An interesting case is *T. repens*: the shrubby ancestor of this obligate geofrutex is apparently extinct, since no present-day shrub related to *T. repens* is known. On the contrary, other species are facultatively geofrutescent. *T. pallens* is a shrub or small tree widely spread throughout tropical Africa, and only a few Angolan populations are geofrutescent. In *T. griseiflora* one observes a gradual transition from the shrubby to the geofrutescent habit, and the latter one predominates more in one variety.

On the whole, geofrutices in Rubiaceae exhibit a rather wide range of variation :

- supraterranean: stems woody to almost entirely herbaceous, fastigiate or not, very low (a few cm) or rather tall (1 m or more), branched or not.
- subterranean (parts mostly unknown): variously branched (horizontally, vertically etc.) or massive ("xylopodium"); the latter case seems rare (only in the American *Borreria* cited above ?) and not unknown in African Rubiaceae; in general, plants with xylopodia are rare in Africa (White 1976).

2.2.4 Rheophytes

Van Steenis (1981, 1987a) lists 46 obligate rheophytic species in 23 different genera of Rubiaceae; they seem randomly distributed over the tribes. His census (in general) enumerates especially tropical Asian and Oceanic taxa. In the Rubiaceae, only three African (*Breonadia salicina*, Nau.-Ad., *Pouchetia baumanniana*, Hyp., *Virectaria angustifolia*, Hed.) and four neotropical rheophytes (*Lindenia rivalis*, ? Ron., *Exostemma polyphyllum, E. stenophyllum,* Cin.-C., "*Borreria*" *cataractarum*, Spe.) are mentioned. For Africa at least *Polysphaeria aethiopica* and other spp. (Puff, pers. comm.), *Chazaliella* spp*., Psychotria* spp. (Psy.), and for S. America at least *Psychotria lourteigiana* (Psy.) should be added.
The genus *Lindenia* (? Ron.; 3 species) appears to be entirely rheophytic, and *Myrmeconauclea* (Nau.-Ad.) contains very many rheophytes. Also *Cephalanthus* (Cep.) is very often

rheophytic. In all other genera, rheophytes occur occasionnally.

2.2.5 Monocaul dwarfs

Many rain-forest understorey Rubiaceae are low (c. 1 m), unbranched woody plants, which I tentatively call "monocaul dwarfs". The single stem often bears its mostly rather large leaves aggregated towards the tip. Flowering is either terminal (fig. 7 C), axillary (fig. 7 B) or "cauliflorous", i.e. in the leafless lower part of the stem. It seems that no life-form system (all mainly conceived for temperate plants !) has yet proposed a term to designate this peculiar group. Consequently, it is reported either under vague terms (subshrub, treelet...) or by means of intricate circumscriptions, e.g. "small pachycaul treelet" (Ridsdale, Bakhuizen van den Brink & Koek-Noorman 1972) or "unbranched understorey treelet" (Ridsdale 1975). These authors report that monocaul dwarfs are extremely common in New Guinea Rubiaceae, and suppose that they are frequently overlooked as they grow amongst the sterile saplings in the forest understorey.

Monocaul dwarfs exist in several tribes :

Ron.:	*Steyermarkia*
Ise.:	*Temnopteryx*
Pau.:	*Pentaloncha*
Gar.:	*Oxyanthus fraterculus, juvenile plants of Tricalysia amplexicaulis*
Pav.:	*Ixora* spp., *Versteegia*
Hyp.:	*Maschalodesme*
Arg.:	*Neurocalyx*
Ham.:	*Hoffmannia spp., Pinarophyllum*
Psy.:	*many cases: Aphanocarpus; Coryphothamnus; Hymenocoleus* spp., fig. 7 C*; Psychotria* spp.
Mor.:	*Trichostachys*
Hed.:	*Lerchea*
inc. sed.:	*Airosperma; Bertiera bicarpellata* (fig. 7 B)

2.2.6 Ericoid plants

Small woody plants with a broom-like branching and small ± tough leaves have evolved in several cases, e.g.

Ron.:	*Rhachicallis*
Hed.:	*Arcytophyllum, Oreopolus* (cushion-forming)
Ant.:	many: *Anthospermum* spp., *Coprosma* spp. etc.
Spe.:	*Psyllocarpus*
inc. sed:	*Strumpfia, Trailliaedoxa*

Amphiasma merenskyanum (Hed.) and *Plocama pendula* (Pae.) are dwarf-shrubs with long, narrow, linear leaves.

Comparable leaf-reductions in herbaceous Rubiaceae may result in a graminoid habit with cladode-like stems (e.g. *Manostachya*, Hed., *Spermacoce* spp., Spe., *Declieuxia oenanthioides,* Psy.).

2.2.7 Succulents

The most remarkable rubiaceous succulents are certainly the ant-inhabited epiphytic members of the Psychotrieae discussed above. Other rubiaceous epiphytes are reported to have succulent leaves (e.g. *Hillia*, F. Hallé 1967). It is obvious that more xeromorphic adaptations including succulence will be discovered upon in-depth studies of more epiphytic representatives; see 2.2.2. Although it must be stressed that (sub)succulence is difficult to recognize on herbarium material, it seems that succulents are otherwise extremely rare in the Rubiaceae. Bremer (1987) reported a certain degree of succulence (particularly in stem, peduncle and pedicels) in *Hoffmannia* spp. (Ham.) and *Argostemma* (Arg.). This was also observed in *Ophiorrhiza* sp. (Puff pers. comm.) The single species of the Madagascan subshrubby genus *Nematostylis* (Alb.) has somewhat succulent stems and leaves (Puff, Robbrecht & Randrianasolo 1984).

2.3 The vegetative axis

2.3.1 Roots

Information available on the root system of the Rubiaceae is very scanty (N. Hallé 1966). Generally there is an orthotropous main root and verticillate plagiotropous roots. Pneumatophores occur in *Mitragyna* (Cin.-M.; McCarthy 1962). The spine-like structures on the tubers of *Myrmecodia* and allied genera (Psy.) are modified adventituous roots (Huxley 1978). Adventitious roots are sometimes formed near the nodes; they take adventage of the humus collected inside the stipules. In *Schradera* and *Lucinaea* (Sch.), they are adhesive and have a climbing function (see 2.2.1).

2.3.2 Stems

The internodes are cylindrical or quadrangular, hollow or not. They only rarely show features which are worth mentioning, such as myrmecophilous adaptations (swollen internodes with perforations; fig. 5 C, 14 C; see also 2.13.1). Thickened nodes, and consequently stems constricted below the nodes in herbarium material (reminiscent of many Acanthaceae !), characterize a number of *Psychotrieae*, e.g. *Cephaelis* spp., *Palicourea* spp. and *Hymenocoleus* spp. (fig. 7 C).

Thorns (modified short-shoots, sometimes modified inflorescence-pedicels) are apparently limited to four tribes, viz. the Gardenieae (*Randia, Didymosalpinx* etc.), the Vanguerieae (*Cuviera, Canthium, Vangueria* etc.), the Guettardeae (*Machaonia, Chomelia, Scolosanthus* and many other genera) and the Catesbaeeae (*Catesbaea*). The thorns sometimes bear leaves (frequently in Vanguerieae). In lianas, these thorns may be ± reflexed and function as fang hooks; genuine climbing hooks occur only in *Oxyceros* (Gar.-G.; Robbrecht & Puff 1986 : fig. 1c) and *Uncaria* (Cin.-M.; fig. 5 B). In the monotypic Cuban genus *Phyllacanthus* (Cat.; fig. 4 B) the leaves are completely reduced; large flattened thorns (modified lateral shoots; for details see F. Hallé 1967) function as cladodes and ensure photosynthesis.

2.3.3 Nodal anatomy

An increasing amount of data concerning the nodal anatomy of the Rubiaceae has become available in recent years (Lorentz 1980, Neubauer 1981, Puff, Robbrecht & Randrianasolo 1984, Puff 1986a, Robbrecht & Puff 1986). A 3:3 pattern is probably the basic vascular pattern within the family. Two trends repeatedly occur:

- reductions of the vascularisation over 1:3 to 1:1 patterns,

and

- multiplication in the number of leaves from two opposite to several verticillate ones.

These trends even occur within genera, and their distribution seem to have no bearing on the delimitation of higher taxa.

2.3.4 Wood anatomy

From 1969 to 1980 the Rubiaceae were the subject of a series of wood anatomical investigations (Koek-Noorman 1969a, b, 1970, 1972, 1976; Koek-Noorman & Hogeweg 1974; Hogeweg & Koek-Noorman 1975; Koek-Noorman 1977, survey of previous work; Koek-Noorman 1980).

She distinguished two main types of secondary xylem in rubiaceous wood, the distribution of which is largely in accordance with the generic, tribal, and, to some extent, subfamilial concepts of Bremekamp (1966) and Verdcourt (1958). The two types are

- xylem with fibre tracheids, dominantly apotracheal parenchyma, more or less isolated vessels and narrow rays, and
- xylem with libriform fibres, without or with little paratracheal parenchyma, with vessels arranged in longer radial rows, and with broader rays.

The consistency of the occurrence of a xylem-type with the tribes is remarkable. The Cinchoneae and associated Rondeletieae and Condamineeae are the only three tribes where the two xylem types occur; Koek-Noorman found "no strong correlation between fibre characters and other features". Some pattern may well be detectable; it is e.g. remarkable that all the African representatives of the Cinchoneae investigated have fibre tracheids. On the whole these three tribes deserve careful reinvestigation in regard to their mutual delimitation. In a number of cases, however, Koek-Noorman found it difficult to include the xylem in one of these two main types. In the five *Cinchona* species examined e.g., intermediates between fibre tracheids and libriform fibres occur. [There is one other exception to the stated consistency: *Posoqueria* is the only member of the Gardenieae with libriform fibers; the genus is advanced in many other features too.]

Koek-Noorman also found that the woody representatives of the predominantly herbaceous Rubieae deviate from other predominantly herbaceous Rubiaceae because of the juvenile structure of the secondary xylem; she suggested an eccentric position for the tribe.

Since these investigations, relatively little attention has been paid to the wood anatomy of the Rubiaceae. Koek-Noorman & Puff (1983) gave detailed wood anatomical descriptions of the woody representatives of the Anthospermeae and Paederieae. Wood anatomy largely supported the newly proposed delimitation of the two tribes (Puff 1982), the Anthospermeae being characterized by fibre tracheids and the Paederieae by libriform fibres. Ter Welle & al. (1983) examined the

Guettardeae in more detail and found that this tribe too is inconsistent in regard to the two major xylem types of the Rubiaceae; while most examined taxa are characterized by libriform fibers, some anomalous ones (e.g. *Dichilanthe*) possess fibre tracheids. Their wood anatomical studies suggest that *Machaonia, Timonius* and *Dichilanthe* need to be excluded from the tribe, as well as two *Guettarda* spp. from the genus and the tribe. Rogers (1984) investigated the wood anatomy of the three genera of the Henriquezieae in great detail; his work, containing many data other than wood anatomical ones, corroborated Koek-Noorman's conclusion that is not acceptable to separate the Henriqueziaceae from the Rubiaceae.

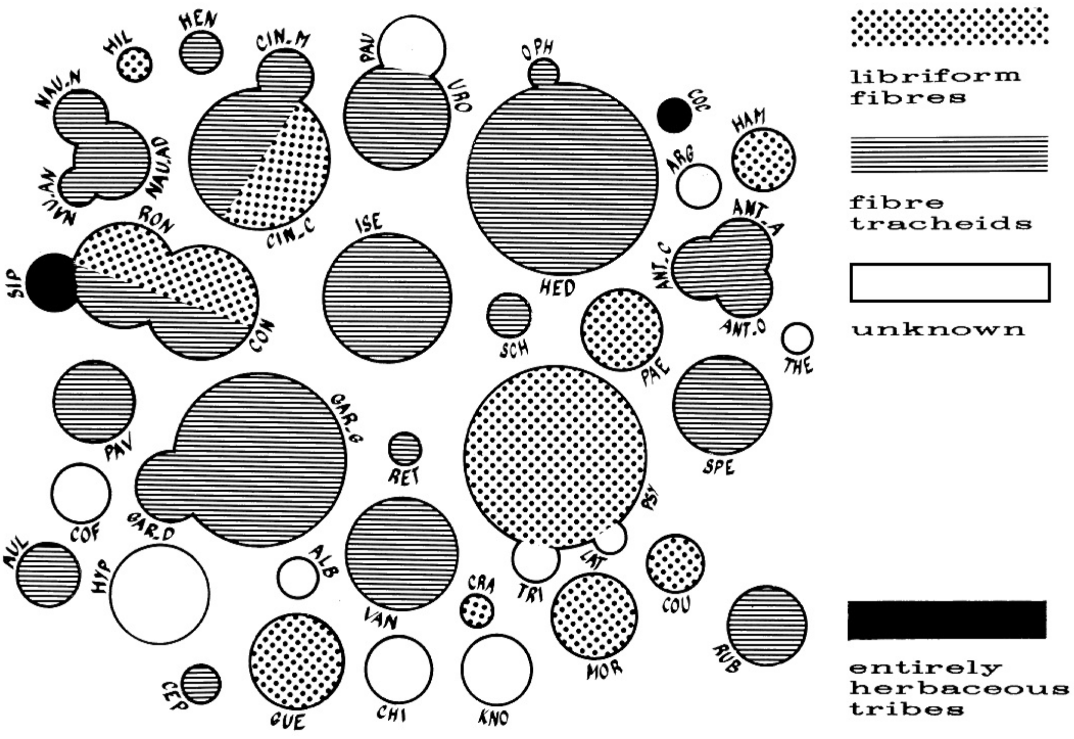


Figure 8.- ***Distribution of the two xylem-types*** *occurring in the Rubiaceae. The occurrence of fibre tracheids in some anomalous members of the Guettardeae (see text) is not indicated. The following information relative to uncertain groups is not included on the diagram: fibre tracheids occur in* Bertiera*, libriform fibers are found in the Acranthereae and Hippotieae.*

Fig. 8 gives a survey of the distribution of the two xylem types in the Rubiaceae, based on the literature cited above. A number of gaps in the knowledge of the wood anatomy of the Rubiaceae remain, first of all in the essentially woody Pauridiantheae, Coffeeae, Hypobathreae, Alberteae, Chiococceae, Triainolepideae and Lathraeocarpeae. The

Sipaneeae and Coccocypseleae are entirely herbaceous, but in the Knoxieae, Ophiorrhizeae, Argostemmateae and Theligoneae, a number of woody representatives would allow completion of our knowledge.

The fibre tracheid type of xylem is slightly more frequent, and the less common type with libriform fibres is generally thought to be more derived. This seems to a large extent corroborated by the situation in the Rubiaceae. The Hillieae, Guettardeae, Craterispermeae and Hamelieae at least can be considered as advanced groups. Based on a cladistic analysis of wood anatomical features, Koek-Noorman (1980) assumed that "the differentiation of the fibre types has taken place in a relative early phase of development of the Rubiaceae"; she presents a cladogram for the family with a main bifurcation representing the differentiation in fibre-tracheids and libriform fibres. It is sure that the two xylem types characterize very large natural entities within the Rubiaceae (e.g. Gardenieae and related tribes: fibre tracheids, Psychotrieae and related tribes: libriform fibres), but the variation existing in other groups (see above !) puts doubt on her hypothesis. As for many other features, the xylem type may have become fixed early in certain lines of evolution and have remained more plastic in other ones.

2.3.5 Sieve-element plastids

As to the type of sieve-element plastids occurring in the Rubiaceae, Behnke (1975) investigated fourteen species in eleven tribes (Gar., Pav., Cof., Cep., Ham., Ant., The., Psy., Mor., Spe. and Rub.); they all have S-type sieve-element plastids, widespread in the dicotyledons. Thus this feature seems without importance for the higher taxa of the Rubiaceae, except that it does not contradict the inclusion of *Theligonum* in the family.

2.4 Leaves

2.4.1 Leaf morphology

The easy recognition of the Rubiaceae as a family is inter alia based on very constant features of the leaves: decussate arrangement and undivided blades, with entire margins; stipules (see 2.5) are constantly present. The complete reduction of the leaves in *Phyllacanthus* (Cat.; replaced by thorny cladodes), discussed above (2.3.2), is a unique feature in the family.

Phyllotaxis: In certain taxa the number of leaves at each node increases (whorls of three or more leaves, see also 2.3.3; fig. 4 C, 7 A); this may occur occasionally (e.g. in *Cinchona, Cin.-C.*) or be ± constant at the specific (*Gardenia ternifolia, G. vogelii, Gar.-G.*) or generic level [*Fadogia,* Van.: (2-)3-5-verticillate leaves]. Alternate leaves, placed in a 1/4 spiral, occur only in a few herbaceous representatives and are obviously due to the suppression of one of the leaves of an opposite pair (discussed further under anisophylly).

Petiole: The petiole is generally well developed. Remarkable is the occurrence of glands (nectar-secretion) on the abaxial base of the petioles in *Henriquezia* and *Platycarpum* (Hen.; Rogers 1984; occurring in no other Rubiaceae?); see further 2.13.1.

Leaf-blades: Most frequently, the blades are ± elliptic, with a cuneate base and an acute tip. Rain forest taxa often have distinctly acuminate leaf-blades; the acumen may be enlarged apically into a typical spathulate drip organ (e.g. *Psilanthus lebrunianus*, fig. 9 A, Cof., *Calycosiphonia spathicalyx*, Gar.-D., *Commitheca letestuana*, Pau.). Rarely, the base of the blade is asymmetric; this seems frequently combined with anisophylly (fig. 11 B). A few species have variegate leaves, and have therefore long been in cultivation, e.g. "*Enterospermum*" *borbonicum*, Pav. [Heine & Hallé 1970; a *Tarenna* if one accepts Bridson's (1979) wide delimitation of that genus; combination not available].

Dimensions: Medium-sized leaf-blades, some 10-20 cm long and 5-8 cm wide, are predominant in Rubiaceae. Many rain-forest taxa, especially in the Gardenieae and Naucleeae, have very large leaf-blades, exceeding 30 cm in length; the probably largest dicotyledonous blades are reported in the Rubiaceae, viz. in *Pentagonia gigantifolia* (up to 180 x 50 cm) (Hip.; F. Hallé 1967: 29, 90). On the other hand, microphylly is also common in Rubiaceae (see e.g. 2.2.6).

Nerves: The secondary nerves are pinnate and mostly brochidodromous, sometimes reticulodromous. In a very limited number of taxa, the leaves show a characteristic fingerprint-like ("moiré") striation pattern (Metcalfe & Chalk 1950: "superficial vein-like network") (fig. 9 E); this occurs

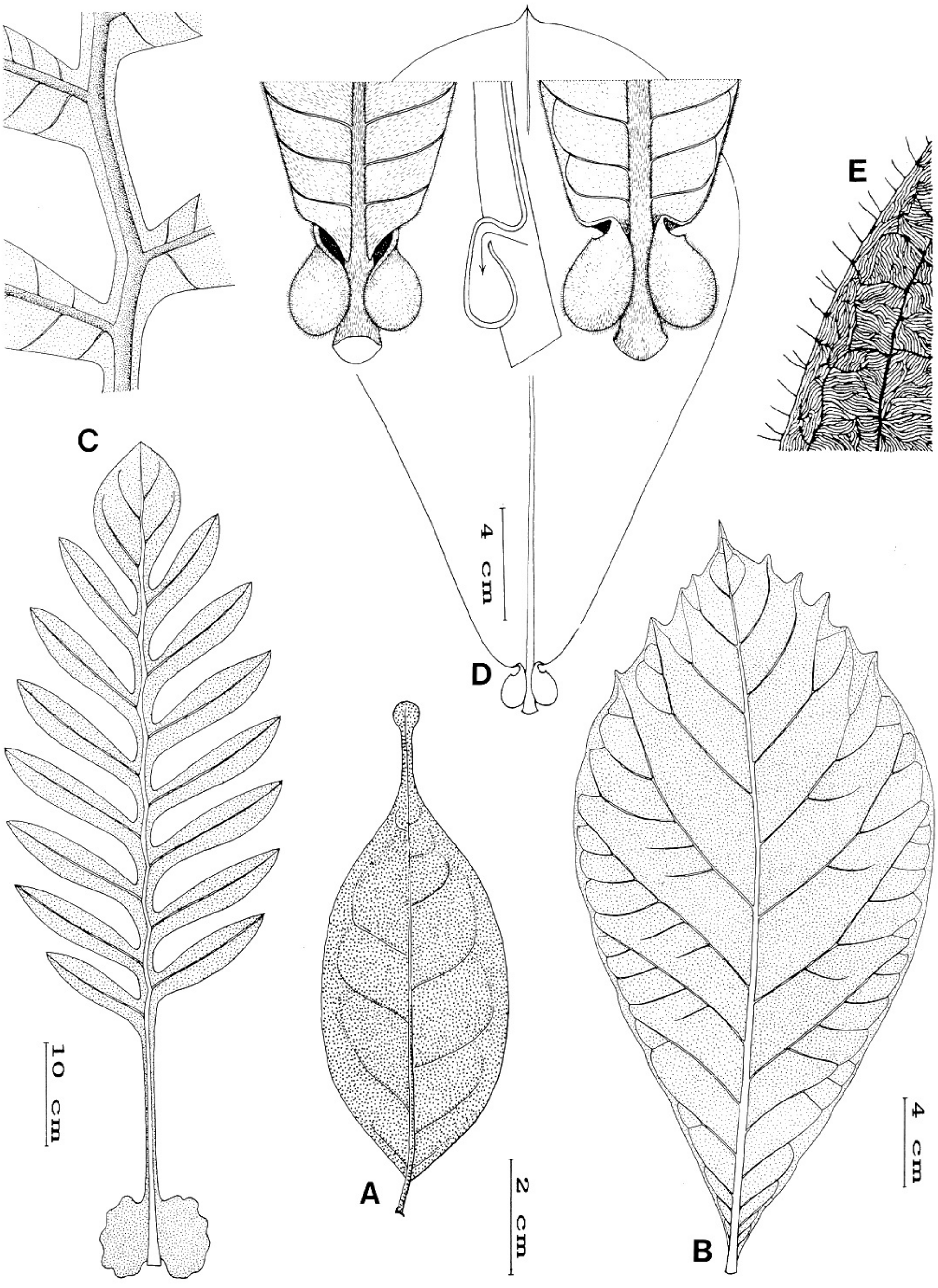


*Figure 9.- **Leaves**: A, leaf with spathulate acumen (*Psilanthus lebrunianus*); B, anomalous leaf with traces of lobation at the tip (*Schumanniophyton problematicum*); C, deeply lobed leaf with a detail (*Pentagonia tinajita*); D, leaf with two myrmecophilous vesicles at its base with details (*Duroia saccifera*); E, detail of leaf-blade with fingerprint venation pattern (*Bertiera letouzeyi*). B-D from F. Hallé, E from N. Hallé.*

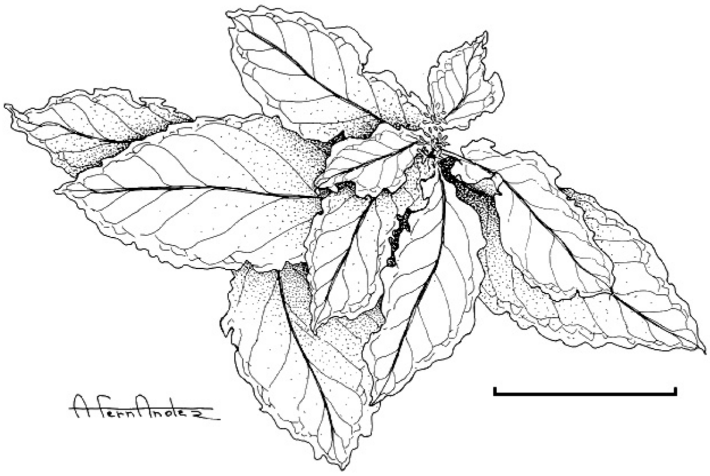


Figure 10.- ***Leaves with crispate margins****: flowering twig of* Psychotria verschuerenii. *The leaves are not only crispate but also have an apparent white margin. Line = 5 cm.*

more frequently in the Guettardeae than in any other tribe. Metcalfe & Chalk (1950) and Darwin (1980b, c) enumerate the feature in many Guettardeae (occasional but common in *Timonius*) and in a total of ten other genera (*Rutidea*, Pav., can be added; Bridson 1978), scattered throughout the family. Darwin (1980b) discovered that in *Habroneuron* (? Ron.) the pattern is caused by the swollen tertiary conducting elements; he suspected that similar venation patterns in other genera are not entirely homologous.

Leaf-margin: The margin of the leaf-blades is almost uniformly entire. A crispate margin occurs in some rubiaceous species, as far as I know (! difficult to observe on herbarium material) only in the Psychotrieae (*Psychotria* spp., fig. 10; *Myrmecodia* spp.: Beccari 1884-86: fig. 12/7). The very few true exceptions to the entireness of the leaf-margin are:

(i) Divisions of the leaf-margin, independent from the secondary venation (± crenate or dentate margins), occur (in most taxa occasionally) in *Heterophyllaea pustulata*, Cin.-C., **Sericanthe* spp. (fig. 13), Gar.-D., *Rutidea* spp., Pav., **Psychotria* spp., *Psy*., *Lasianthus* spp., Mor., and *Neurocalyx* spp., Arg. A number of these taxa (indicated with asterisks) also have bacterial leaf galls (see 2.4.4) in their leaf-blades; accepting a relation between the occurrence of galls and the crenation of the leaf-margin is speculation in need of further consideration (compare the situation in *Ardisia*, Myrsinaceae: bacterial galls marginal, situated opposite to the limb incisions; see Miller, Gardner & Scott 1983).

(ii) Divisions of the leaf-margin corresponding to the secondary venation characterize only three *Pentagonia* species (Hip.; fig. 9 C); they have deeply lobed leaves. Traces of leaf lobation occur occasionally in many other taxa, however: in part of the leaves of some individuals, the secondary nerves protrude in acumens, especially in the distal portion of the blade (fig. 9 B), or the blade-margins are waved, having sinuses between the secondary nerves. This occurs in many genera of the Gardenieae (*Gardenia, Preussiodora, Brenania,* *Tricalysia* etc.); outside of this tribe odd dentate or waved leaf-blades are very rare. I know them only in *Simira erythroxylon,* (Ron.; Steyermark 1974: 347) and *Remijia chelomaphylla* (Cin.-C.; Sullivan 1986; considered characteristic for the species which is only known from the type, however).

The myrmecophilous vesicles occurring at the base of the leaf-blade (fig. 9 D) in a number of species (see 2.13.1) are considered (F. Hallé 1967) to be another expression of leaf-lobation in Rubiaceae. In this connection Corner (1954: 149) was the first to report occasionally lobed leaves in Genipa americana (Gar.-G.); he brought them in relation with his Durio theory ("the only evidence I know in explanation of the rubiaceous simple leaf").

Anisophylly: Anisophylly, the unequal development of the two leaves of an opposite pair, is very common, especially in the Gardenieae and Isertieae (fig. 11 A, B). In a number of cases, the second leaf is completely reduced (fig. 11 C). A few interesting herbaceous Rubiaceae also exhibit this condition. In *Argostemma humilis* (Arg.), low plants with simple stems just a few internodes long, only one leaf (of the uppermost pair) is well-developed (Schumann 1891: 22, fig. 8 V). In *Theligonum* (The.) the lower leaves are opposite, the upper ones look alternate by complete reduction of one leaf from each pair (Wunderlich 1971: 364).

Anisophylly, combined with shortening of some internodes, can lead to the formation of (pseudodigitate or pseudopennate) phyllomorph branches (see 2.1).

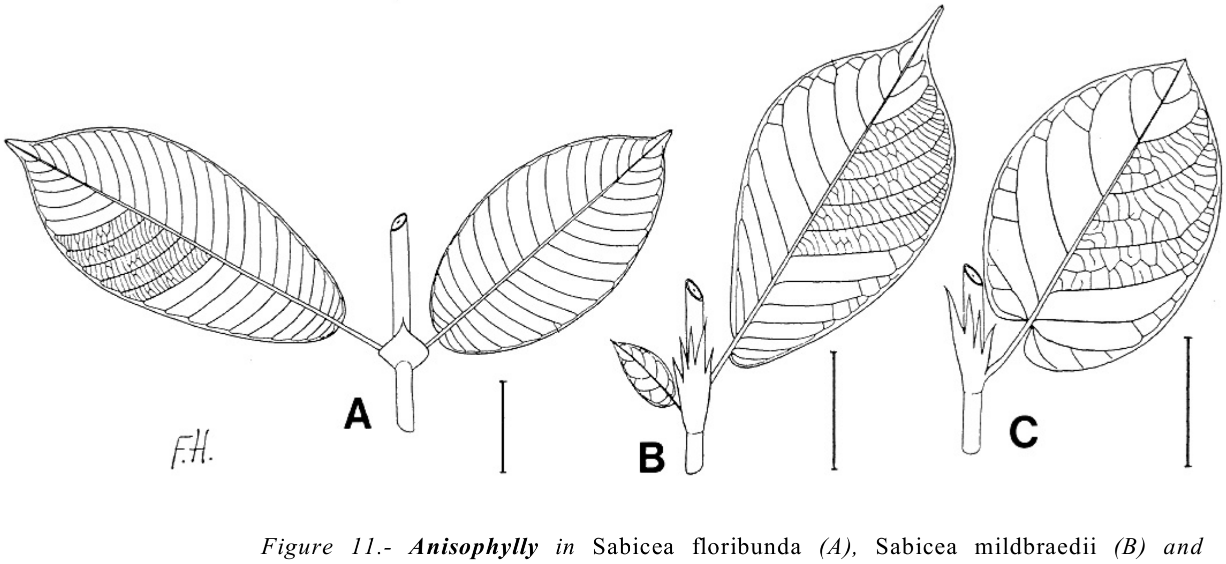


*Figure 11.- **Anisophylly** in* Sabicea floribunda *(A),* Sabicea mildbraedii *(B) and* Pseudosabicea sthenula *(C). Indumentum not drawn.*
From F. Hallé. Lines = 3 cm.

Heterophylly: Heterophylly is also a rather common feature among tropical woody Rubiaceae. The following types can be distinguished:

(i) Differences between leaf-blades from orthotropous and plagiotropous twigs, the former often much shorter and ± cordate; this kind of heterophylly is common in the Vanguerieae, the Gardenieae-Diplosporinae (Robbrecht & Puff 1986: fig. 1 e-g) and the Hypobathreae.

(ii) Leaves on juvenile twigs linear compared to leaves on adult twigs, a peculiar kind of heterophylly apparently confined to Madagascar and the Mascarene Islands. Friedmann & Cadet (1976) list the following three (? only) cases in the Rubiaceae:
Pav.: *Doricera trilocularis* (as *Pyrostria*) [Verdcourt 1983: fig. 5 A (foliage on young twigs) & B (foliage on adult twigs)]
Hyp.: *Ramosmania heterophylla* (as Randia)
Van.: *Scyphochlamys revoluta*

(iii) The occurrence of odd dentate leaf-blades on a plant with all the rest of the blades normal and entire, as discussed above.

2.4.2 Domatia

For a general discussion of this leaf feature confined to woody dicotyledons I refer to the classic papers of Schnell (1963), Jacobs (1966) and Schnell & Tchinaye (1968). Older literature (e.g. Schumann 1891) sometimes referrred these structures as scrobiculae. I accept Jacobs' restriction of the term domatia to structures in the nerve axils of the underside of the leaf-blade (thus excluding the myrmecophilous sacs at the base of the leaf-blade, fig. 9 D).

It is probable that more taxa are provided with domatia in the Rubiaceae than in all other woody dicotyledons (Jacobs 1966: 11). In an enumeration of African plants possessing domatia (De Wildeman 1938), out of 250 taxa 165 ones (or 65 %) are indeed rubiaceous.

In Rubiaceae, domatia are mostly limited to the axils of the secondary veins; they may also occur in the axils of the tertiary veins, e.g. in *Aoranthe* (? Ise.), *Pleiocoryne* and *Oligocodon* (Gar.-G.).

All known **types** of domatia (tufts of hairs, pocket-, pit-, cave- and dome-excavations; glabrous, ciliate or hairy excavations) and a number of transitional types occur in the Rubiaceae (fig. 12). Their systematic value is mostly restricted to the specific level; sometimes higher taxa (subgenera, genera) are characterized by a peculiar type of domatia. Careful evaluation during revisions is needed, since many species are known to be variable with respect to presence/absence and/or type of domatia. In *Tricalysia*

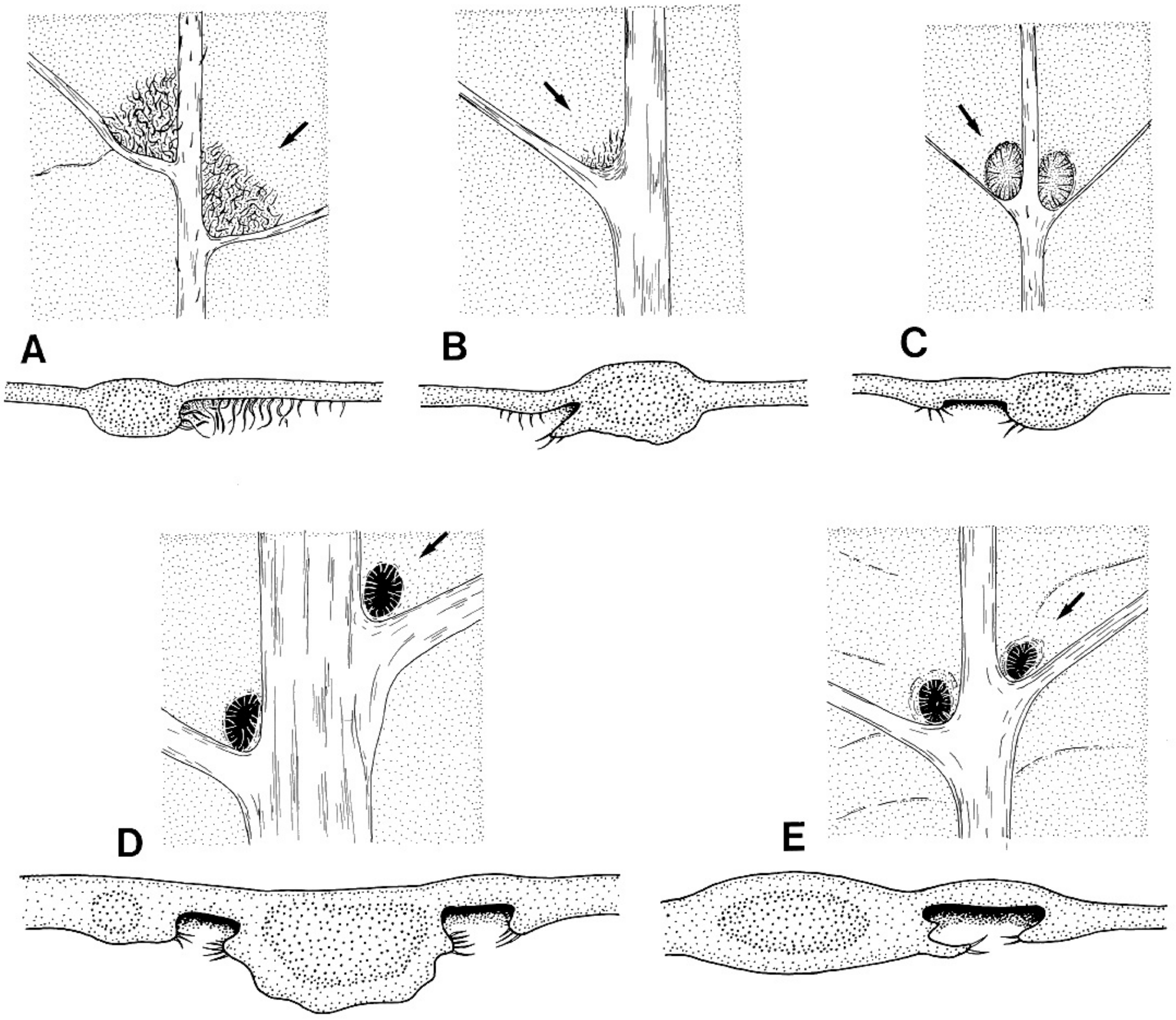


*Figure 12.- **Types of domatia** occurring in* Tricalysia. *Drawn: detail of leaf-blade beneath showing one or two domatia in the axil of secondary nerves, and a cross-section in the direction indicated by the arrow.*
*A, tuft-domatia (*T. capensis*), B, hairy pocket-domatium (*T. yangambiensis*), C, ciliate pit-domatia (*T. pallens*), D, domatia intermediate between pit- and crypt-type (*T. coriacea*), E, crypt-domatia (*T. biafrana*).*
From Robbrecht 1987.

(Gar.-D.) e.g., domatia have a limited value at subgeneric (subg. *Empogona*: almost exclusively tuft-type, subg. *Tricalysia*: all other types) and at specific level; whilst many species are strictly characterized by the absence of domatia or the presence of a well-defined type, many other species are very variable with regard to presence/absence and type of domatia (Robbrecht 1979: 248 & 1987a: 45).

2.4.3 Bacterial leaf-galls

Swellings in the leaf-blades containing symbiotic bacterial colonies are only known from the Myrsinaceae and the Rubiaceae (and possibly one species of Dioscoreaceae); a number of records in other angiosperm families are uncertain (Lersten & Horner 1976). These have previously often been referred to as "bacterial nodules" (e.g. Lersten & Horner 1976, Verdcourt 1976, Bridson & Verdcourt 1988). Because of the considerable variation in shape, I reject the term "bacterial nodule" for these structures, since it implies a more or less globose shape. Petit's (1962) or N. Hallé's (1970) use of "galles bactériennes" or "bactériocécidies" is better. Although "gall" and "cecidium" sometimes imply a teratological signification, the definition in the standard treatise of galls (Küster 1911) is wide enough to cover its use for the structures discussed here.

In the Rubiaceae, bacteriocecidia occur in certain species of three unrelated genera : *Sericanthe* (Gar.-D.), *Pavetta* (Pav.) and *Psychotria* (Psy.); altogether more than 400 species exhibit the feature.

- *Sericanthe* is an entirely African genus, and 12 of its 17 species are bacteriophilous. In Lersten & Horner's (1976) review, these are included under *Tricalysia,* see Robbrecht (1978a) for their generic segregation.
- In the large pantropical genus Psychotria [more than 1000 species if one accepts Steyermark's (1972) large delimitation], bacteriophilous species occur only in Africa (67 species, revised by Petit 1966) and Madagascar (7 species, revised by Bremekamp 1960).
- *Pavetta*, with a wide paleotropical distribution from Africa to Australia, consists of about 400 species of which about 85 % are bacteriophilous; these occur throughout its range [Lersten & Horner (1976) gave exactly 87 %, but their percentage is based on Bremekamp's (1934) monograph of Pavetta which is now out of date].

So bacteriophilous Rubiaceae predominantly occur in Africa, and are absent from the Neotropics. It is obvious that the occurrence of bacterial leaf-galls has no bearing on the higher taxa of the Rubiaceae.

Young galls have an opening, towards the upper (most *Pavetta* spp.) or the lower surface of the leaf-blade (*Pavetta urophylla, Sericanthe* and *Psychotria*). The place, shape and size of the galls shows much variation. They are situated either in the blade tissue (fig. 13 C-F) or associated with the main or lateral veins (fig. 13 B); galls situated along the base of the midvein may continue along the petiole (fig. 13 A). The shape is ± spherical, ± ramified, or linear (then galls usually along the midnerve). The size varies from one or more mm in diameter (for ± isodiametrical structures) to several cm in length (for linear galls). This broad morphological variation in the bacterial galls is found in each of the three genera; thus my depictions of their variability in

Sericanthe species (Robbrecht 1978a: fig. 1 & 2) is illustrative for *Pavetta* and *Psychotria* also. For a discussion of the bacteriophilous *Psychotria* species, see Petit (1966; many photographs of these structures).

For the biology of the bacterial galls see 2.13.2.

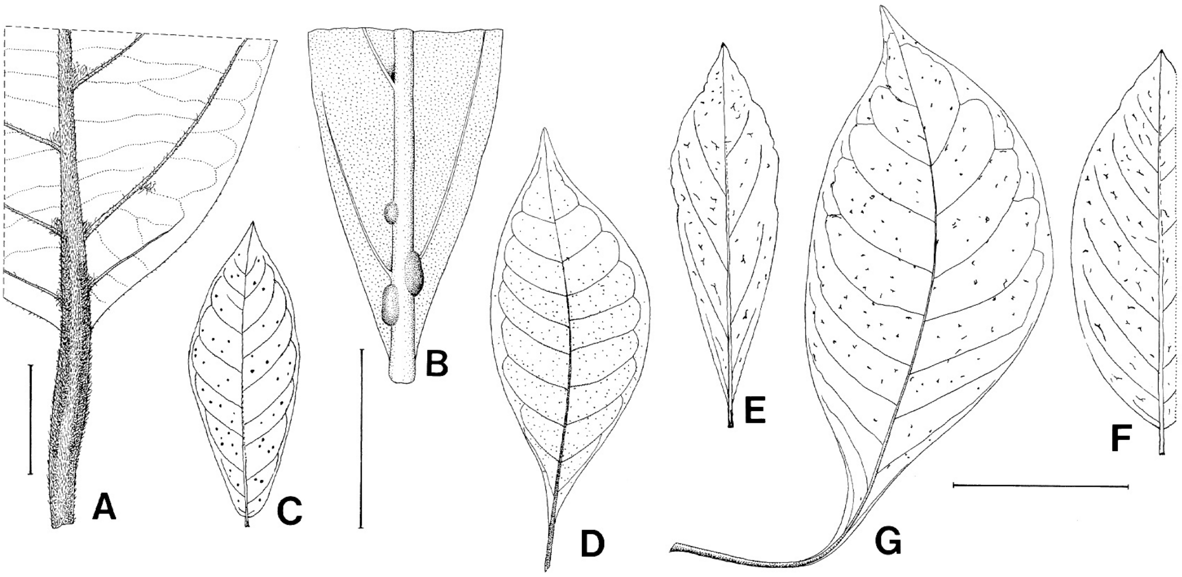


*Figure 13.- **Bacterial leaf-galls** in African Rubiaceae: A, B, galls along base of midnerve and/or petiole; C-G, galls dispersed in the leaf-blade, punctiform (C, D) or linear to branched (E-G).*
A, Sericanthe leonardii*; B,* Psychotria amboniana*; C,* Sericanthe petitii*; D,* Psychotria camerunensis*; E,* Sericanthe trilocularis*; F,* Sericanthe roseoides*; G,* Psychotria gossweileri. *From Petit and Robbrecht.*
Lines: to A and B = 0.5 cm, horizontal one to all other = 5 cm.

2.4.4 Leaf anatomy

Detailed investigations are presented in a number of recent revisions (e.g. Puff, Robbrecht & Randrianasolo 1984; Puff 1986a, 1988; Rogers 1984). In-depth leaf anatomy studies have also been carried out for a number of representatives (e.g. Pavetta, Pav., Herman, Robbertse & Grobbelaar 1986, 1987, Vanguerieae, Tilney 1986). These two types of studies have added to the general knowledge summarized in Metcalfe & Chalk (1950) and Napp-Zinn (1973-74), but on the whole, leaf anatomy data remain too scanty and isolated to assess their value in regard to the delimitation of higher rubiaceous taxa.

Translucent dots in leaf-blades are reputed practical characters allowing field identification of some angiosperm taxa. In the Rubiaceae, this feature is relatively rare, and reflects from the occurrence of either intercellular secretory cavities (Solereder 1893: *Rustia, Tresanthera*), or very large crystals in the mesophyll of the leaf-blade. These may be druses (e.g. *Preussiodora,* Gar.-G., Robbrecht 1978b) or large styloid crystals (? common in the Psychotrieae: *Palicourea* spp., *Hymenocoleus* spp.: Robbrecht 1975). In the dried state, the crystals do not render the blades translucent, but are visible as minute dots on the surface. See further 2.6.2.

Rubiaceous leaves seem to be largely hypostomatic; there are scattered records of amphistomatic leaves (e.g. *Hyptianthera*, Hyp., Robbrecht & Puff 1986). The **stomata** are always paracytic ("rubiaceous type" of Metcalfe & Chalk 1950 !) with minor variation recorded in the Gardenieae (Keddam-Malplanche 1985; comparable observations from other tribes lacking).

Mesophyll sclereids are recorded in species belonging to eight genera (Rao & Das 1979: five genera; Robbrecht & Puff 1986: three genera marked with *):

Gar.-G.:	*Burchellia*
Gar.-D.:	**Tricalysia*
? Aul.:	**Belonophora*
Cof.:	*Coffea*
Hyp.:	*Jovetia, *Gallienia*
Pav.:	*Tarenna (as Chomelia)*
? Ret.:	*Scyphiphora*

Remarkably all known taxa (except *Scyphiphora*) with sclereids belong to the Gardenieae and associated tribes. *Scyphiphora*, the exception, deviates from the other known cases (with diffuse sclereids) in that it has terminal sclereids (definition following Rao & Das op. cit.).

Also anatomically interesting is the occurrence and distribution of brown substances, probably **tannins**, in the leaf-blades (also frequently found in ovaries and fruits, fig. 38 B). Apart from Solereder's (1893) early records in scattered genera, reported observations are practically limited to the Gardenieae and relatives (Robbrecht & Puff 1986) and to the Anthospermeae (Puff 1986a), however.

2.5 Stipules

The presence of stipules is one of the most characteristic vegetative features of the Rubiaceae, distinguishing them from most other Asteridae. The stipules are mostly fused to an interpetiolar structure on either side of the stem between the opposite leaves. The stipules of the youngest internode often cover the entire growing apex, especially when they are blade-like or fused into a cone. A waxy secretion (blastocolla) produced by colleters on their inside surface (see 2.6.4) ensures further protection of the bud. Upon growth of the apex, the stipules are either early deciduous or long persistent. When cone-like or sheathing, they are often deciduous by a circumscissile split.

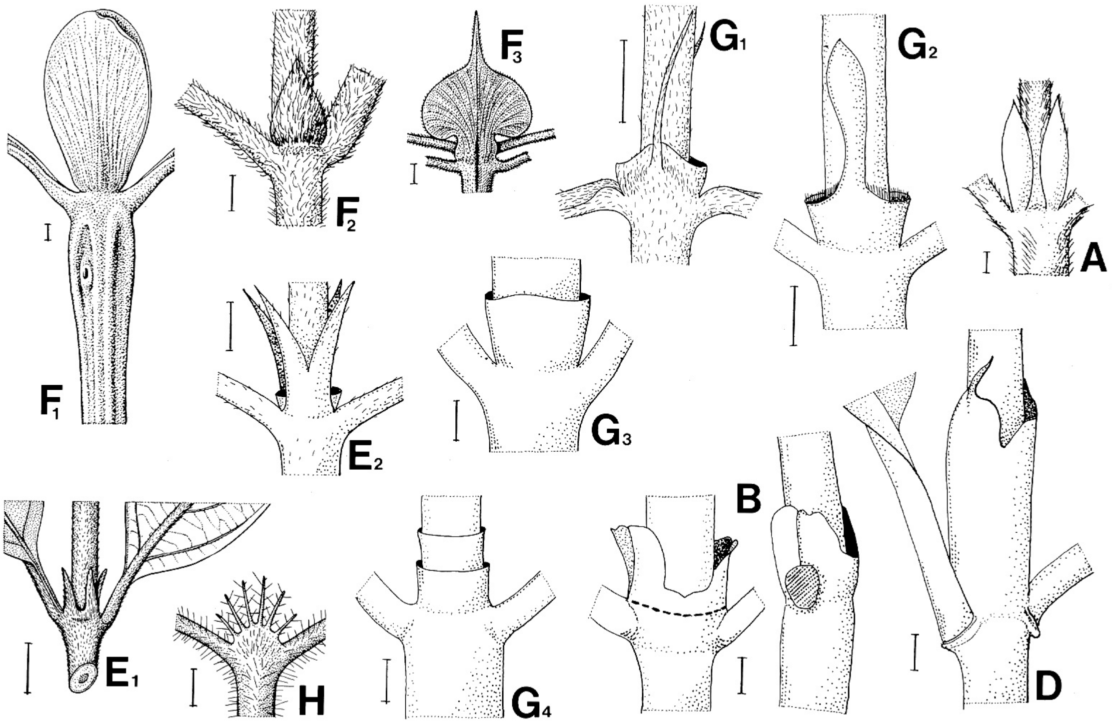


*Figure 14.- **Stipules**: A, free stipules; B, intrapetiolar; D, sheathing intrapetiolar; E, interpetiolar, bilobed; F, interpetiolar, entire and ± foliaceous; H, interpetiolar, divided; B, E_2, G_4, with inner membranous sheaths (not visible in B, the dashed line indicates the position of the upper margin of the membranous sheath).*

A, Phitopis multiflora*; B,* "Uragoga" phoenica *(with lateral view after removal of petiole); D,* Gaertnera vaginans*; E_1,* Heinsia crinita*; E_2,* Hymenocoleus neurodictyon*; F_1,* Nauclea vanderguchtii*; F_2,* Rondeletia ochracea*; F_3,* Leptactina leopoldi-secundi*; G_1,* Argocoffeopsis kivuensis*; G_2,* Hutchinsonia cymigera*; G_3,* Tricalysia concolor*; G_4,* Psychotria merumensis*; H,* Otomeria guineensis.

A after Hooker, E_1, F_1, F_3, H from N. Hallé and G_4 after Steyermark. Lines = 2 mm.

There are only a few representatives with the supposed "primitive" condition, i.e. each petiole with two stipules, one at each side (e.g. *Phitopis*, inc. sed., fig. 14 A; *Myrmecodia* spp., Psy.; *Prismatomeris* spp., Mor.). Equally rare is partially intrapetiolar, partly inserted on the stem, partly on the adaxial side of the petiole (*Henriquezia*, Hen.). Completely intrapetiolar stipular blades are also rare, but recorded in species of about ten genera [quite a number of Rondeletieae (e.g. *Elaeagia*), and associated tribes: Condamineeae (*Condaminea*), Isertieae (*Isertia*), Henriquezieae (*Gleasonia*); more isolated cases: Gardenieae (*Melanopsidium*); Psychotrieae (*Psychotria*)]. In a number of cases, the stipules are essentially intrapetiolar, but extend into the interpetiolar region. In "*Uragoga*" *phoenicea* K. Schum. (fig. 14 B), a *Psychotria* when one follows Steyermark's (1972) broad concept of that genus, there are two large intrapetiolar blades opposite to each petiole; at the base, however, the stipule forms a low sheath surrounding the stem.

Generally, however, the insertion of the stipules is entirely interpetiolar (fig. 14 E-H). Similar to intrapetiolar stipules, there is a progression by fusion [bilobed stipular blade fused at base → entire interpetiolar blade → stipular cone or sheath (i.e. complete fusion of all stipular parts at one node)]. In a number of taxa (mainly herbaceous tribes), there is a strong opposite trend towards division of the interpetiolar stipule which may become 3- to multifimbriate. Thus there is extensive morphological diversity in the interpetiolar stipules of the Rubiaceae, which may be:

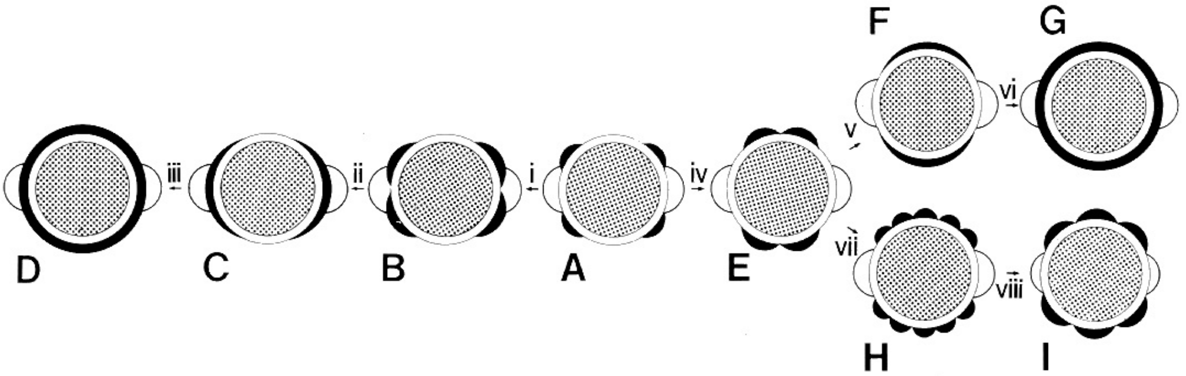


*Figure 15.- **Hypothetical scheme indicating relations between stipular types** in the Rubiaceae (shaded : stem; black : stipules; white : petioles). Progressions are probably caused by **(i)** intrapetiolar shift of the stipular insertion, **(ii)** intrapetiolar fusion of two stipules of the same leaf, **(iii)** complete fusion of the four intrapetiolar stipules at a node (sheathing stipules), **(iv)** interpetiolar shift of the stipular insertion, **(v)** interpetiolar fusion of adjacent stipules of the opposite leaf-pair, **(vi)** complete fusion of the interpetiolar stipules at a node (sheathing stipules), **(vii)** division of the interpetiolar stipule (fimbriate sheath) and **(viii)** complete division of multifid interpetiolar stipules (becoming foliaceous; being the classical interpretation of the "whorled leaves" of the Rubieae).*
A, B and C are rare, and I is restricted to the Rubieae; the other cases are common in the Rubiaceae. The lettering of the present scheme corresponds with the letters in fig. 14.

- entire (triangular, ovate, bullate, ..., becoming sometimes very large; fig. 14 F_1-F_3),
- more or less bifid (fig. 14 E_1-E_2),
- multifid (fimbriate stipules especially well repanded amongst herbaceous Rubiaceae; fig. 14 H), or
- sheathing (sheaths mostly short, becoming several cm long in e.g. Gardenia, Gar.-G.; sheats truncate, fig. 14 G_3, G_4, or frequently with a single interpetiolar short to long appendage at each side of the stem, fig. 14 G_1, G_2).

Stipular sheaths may result from fusion of interpetiolar as well as intrapetiolar stipules. Although only ontogenetic studies ascertain the distinction between the two, the nature of the sheath can be deduced when awns tip the sheaths. In *Gaertnera vaginans* (Psy.; fig. 14 D) e.g., the awns are intrapetiolar, and in *Argocoffeopsis kivuensis* (Gar.-D.; fig. 14 G_1) they are interpetiolar.

Hypothetically, all these cases may be derived from one another (fig. 15). In the case of truly whorled leaves, features similar to the ones depicted in fig. 15 (two opposite leaves) occur.

The "whorled" leaves of the (herbaceous) tribe Rubieae (not depicted on fig. 14) have classically been interpreted as true leaves plus interpetiolar leaf-like stipules (fig. 15 I). See Rutishauser (1984) for two alternative hypotheses:

- all whorled leaves are true phyllomes (sometimes with anisophylly), and
- there are also intermediates between phyllomes and stipules ("continuum" theory).

Bremekamp (1952: 13 & 1966: 29) developed arguments to support the first hypothesis. On the other hand, Puff & Robbrecht (in press) point to cases in the Knoxieae supporting the classical hypothesis.

A remarkable feature is the occurrence of thin diaphanous chlorophyll-less sheaths inside the stipules of several Psychotrieae. They were fully described and discussed in the protologue of *Hymenocoleus* (fig. 14 E_2), an African genus of monocaul woody dwarfs and perennial creeping herbs which is characterized by these sheaths (Robbrecht 1975). They also occur in a number of South American *Psychotria* species (fig. 14 B & G_4). I have two hypotheses to explain the origin of these extra stipular sheaths: it are modifications of either colleters or of hairs. In some *Hymenocoleus* spp., the extra stipular sheaths are partly replaced by colleters, providing evidence for the first hypothesis.

Colleters are always closely associated with the stipules (and the calyx). See 2.6.4.

Few ontogenetic and anatomical (vascularisation!) studies have been carried out on rubiaceous stipules. The only profound studies are the works of Majumdar & Pal (review 1958; enumerated in Pal 1959) and (mentioned above) Rutishauser

(1984: Rubieae compared with two other herbaceous genera; general discussion of available data). Whether Guédès (1972; examined only adult structures; not cited by Rutishauser) can be followed in that the rubiaceous interpetiolar stipule is at least partly ligular, is a question which remains open. Ontogenetic studies have been limited to interpetiolar rubiaceous stipules; from the theoretical viewpoint, a comparison with intrapetiolar ones would be worthwile.

2.6 Other vegetative features

2.6.1 Exsudates

The occurrence of latex is one of the most reliable field criteria to distinguish between the Apocynaceae (latex) and the Rubiaceae (no latex). However, the latter may occasionally have exsudate canals in the bark. The most famous example is of course *Cinchona* (Cin.-C.), whose exsudate (a gummy resinous substance) has long been known as a febrifuge because it contains quinine. Solereder (1893) reported secretory canals also in *Remijia* and *Ladenbergia* (Cin.-C.), and in *Isertia* (Ise.).

For histories of cinchona, see Standley (1931 a, b) and Taylor (1945).

I know of only three other records of exsudates in the Rubiaceae, viz. in *Pausinystalia macroceras* (Cin.-C.; Zaire, Nsola 721, BR: "parfois latex jaune"), in *Pleiocoryne fernandense* (Gar.-G.; Ivory Coast, Versteegh & den Outer 138, BR, WAG: "bark ... much colourless latex") and in *Macrosphyra longistyla* (Gar.-G.; yellow juice in stems and fruit wall, Puff, pers. comm.).

2.6.2 Idioblasts with Ca-oxalate crystals

The common occurrence of calciumoxalate crystals in all organs of rubiaceous plants has long been known. The first detailed study was already made in the nineteenth century. Solereder (1893: 309-317) not only determined their chemical nature, but also surveyed their occurrence throughout the family, examining some 200 genera from all the tribes in Bentham's system. Rubiaceous crystals were classified as

- raphides (bundles of ± parallel needle-shaped crystals, fig. 16 D, 38 A),
- styloids (large elongated solitary crystals, fig. 16 A, B),
- crystal sand (minute particles),
- druses (star-like to ± spherical aggregations, fig. 17) and
- solitary crystal needles (fig. 16 C).

His morphological classification of crystal types remains workable to day.

Raphides typically consist of strongly elongated bundled needles, but rarely are shorter; Solereder cited the occurrence of such ones in *Ophiorrhiza* (Oph.), I have observed them in *Argocoffeopsis* (Gar.-D., Robbrecht 1986c; fig. 6 A) and *Colletoecema* (? Mor.).

These crystals are often observable with the naked eye or under low magnifications. Druses and styloids may attain large dimensions and are then visible as translucent points in leaf-blades, and so may serve as practical field identification characters. In dried material, they are visible as minute pale dots because they do not follow the shrinking of the rest of the leaf tissue. Raphides are often just as visible with the naked eye, especially in tiny tissues such as corollas or papery leaf-blades, or, in thicker organs such as fruits, when they are situated just below the epidermis. Upon dissecting rubiaceous flowers and fruits, raphides are frequently met with since they are often concentrated, e.g. in the dissepiments of ovaries and fruits; they then appear as elongated glittering bodies. Microscopical verification using polarized light is needed, however (see 1.2).

Solereder's survey showed that the distribution of crystal sand, druses, styloids and isolated needles over the tribes and genera of the Rubiaceae is not closely related to their taxonomy. Raphides are also widespread but limited to a number of groups; he mentioned them in the Hedyotideae, Hamelieae, Knoxieae, Morindeae, Coussareeae, Psychotrieae, Paederieae, Anthospermeae, Spermacoceae and Rubieae, and equally in isolated genera whose position does no longer agree to the system followed by him, viz. *Deppea* (in Ron., now Ham.), many "Mussaendeae", now all in other tribes (viz. Sch., Coc., Uro.), and many Cinchoneae. Therefore he urged reconsideration of the delimitation of the latter tribe against the Hedyotideae. Fig. 18 gives an updated survey of the occurrence of raphides in the Rubiaceae.

Solereder's recommendation was taken up by Bremekamp (1952) who moved the raphid-possessing Cinchoneae into the Hedyotideae. Moreover, and more importantly, the limited distribution of raphides led him to a reformation of the subfamilial classification; he believed that all the tribes characterized by raphides should be brought together in one subfamily Rubioideae. That viewpoint was followed by Verdcourt (1958), who observed, however, raphides in a number of tribes in which Bremekamp did not detect them. Therefore, his Rubioideae contain a number of tribes not included by Bremekamp, viz. the Urophylleae (s.l.) and the

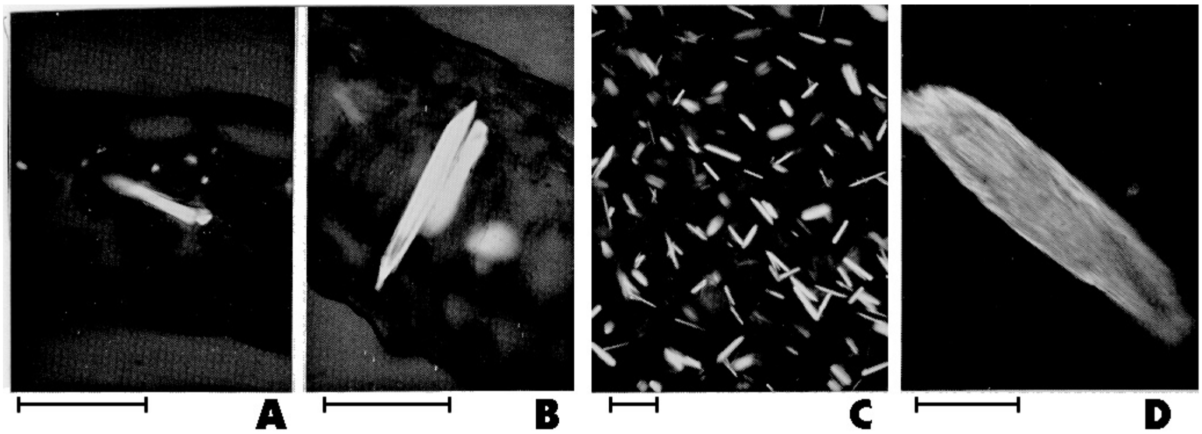


*Figure 16.- **Calciumoxalate crystals in idioblasts** from various rubiaceous tissues:*
A, styloid crystal in mesophyll and sparse crystal sand in subepidermal mesophyll of leaf-blade in Hymenocoleus hirsutus*; B, styloid crystals perpendicular to leaf-blade surface in mesophyll in* Palicourea lasiantha*; C, isolated needle-shaped crystals in endotesta in* Psydrax parviflora*; D, raphide in mesocarp in* Geophila repens.
A & B cross-sections of leaf-blades, leaf surfaces accentuated. L. micrographs in polarized light. Lines = 40 µm.

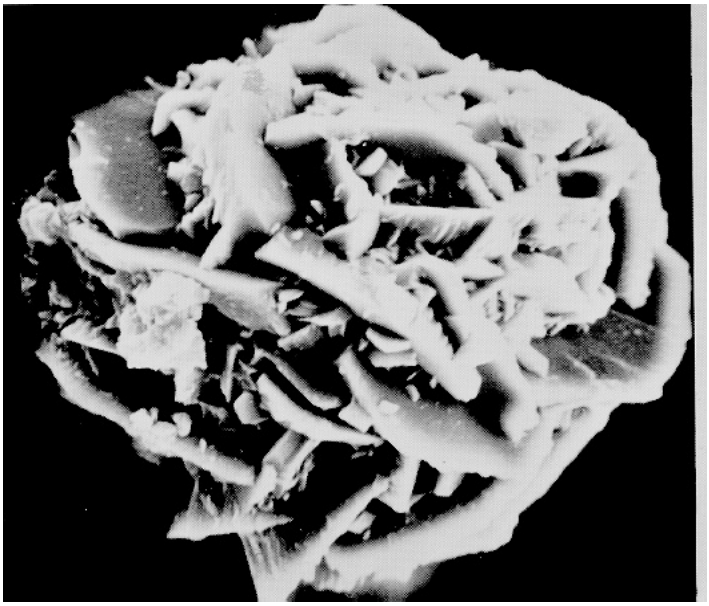


*Figure 17.- **Druse** (star-like aggregate of Ca-oxalate crystals) removed and cleaned from a petiole idioblast in* Preussiodora sulphurea.
S.E. micrograph. Line = 10 µm.

Ophiorrhizeae, see table 5. Indeed, while in tribes such as the Hedyotideae and Psychotrieae raphides are copious and abundant in almost all tissues, their presence is much more limited or even sparse in other groups. In *Colletoecema* (? Mor.) e.g., they are limited to the corolla lobes, style, anthers and endotesta (Petit, pers. comm.).

Verdcourt (1958) also suggested that the presence of raphides is often correlated with the articulate external hair-type (see 2.6.3). This is certainly not general; in *Pauridiantha* (Pau.) e.g., the occurrence of raphides is combined with cylindrical external hairs. In addition, raphides seem to occur ± anomalously in groups typically lacking them. After examining thousands of herbarium specimens of the Gardenieae for revision and identification purposes, I only once discovered raphides, notably in a fruit wall of an *Argocoffeopsis* (Robbrecht 1986c: fig. 6A). Similarly, Bremer (1984) detected raphides in the fruits of a single specimen during a revision of the genus *Steenisia* which she moved into the tribe Rondeletieae characterized by the absence of raphides.

Thus I am inclined to accept F. Hallé's (1967: 134) idea that the presence of raphides is a parallel adaptation that evolved several times in the family, and to consider the use of this crystal-type as the sole criterion for an otherwise diverse subfamily, is as artificial as the previous use of one versus more ovules on the placentas to distinguish the two major subfamilies of the Rubiaceae. The case of *Hillia* (Hil.) is illustrative in this respect. This highly advanced epiphytic genus is doubtless related to the Cinchoneae (see 3.2.5) but was excluded from that alliance because it has raphides. Neither a placement in the Rubioideae (Verdcourt 1958), nor the recognition of the monogeneric Hillioideae (Bremekamp 1966) can be followed, since the two decisions rely only on the single mentioned character.

The raphid-containing Pauridiantheae and Urophylleae provide another important piece of evidence. F. Hallé (1961) amply documented, in many morphological and biological features, their close relationship to the "Mussaendeae" (Isertieae) without raphides. A segregation of these three tribes over two different subfamilies is no doubt unnatural.

At the tribal level, nevertheless, the absence of presence or raphides is remarkably constant (fig. 18). Their presence characterizes roughly half the tribes of the Rubiaceae, including all the predominantly herbaceous ones except the Sipaneeae (compare fig. 3 with fig. 18).

The knowledge of crystals in Rubiaceae is still very limited, in spite of their widespread and conspicuous occurrence, and their bearing on taxonomy. A new thorough compilation of known records upon the type and distribution of crystals in the various organs is much needed.

As to functional considerations regarding the occurrence of calciumoxalate crystals in plants, I refer to Franceschi &

Horner's (1980) general review. Taxonomists and morpho-logists often attribute the crystals a function of protection against foraging animals, but what about the occurrence of raphides in the fleshy wall of apparently zoochorous fruits? There is inter alia evidence that crystals function in removing excess calcium ("excretory idioblasts") or as a storage form for either calcium or oxalate. An interesting relationship between the crystals and bacteria in certain Rubiaceae (bacteria utilizing the oxalic acid) is in full discussed in the same review.

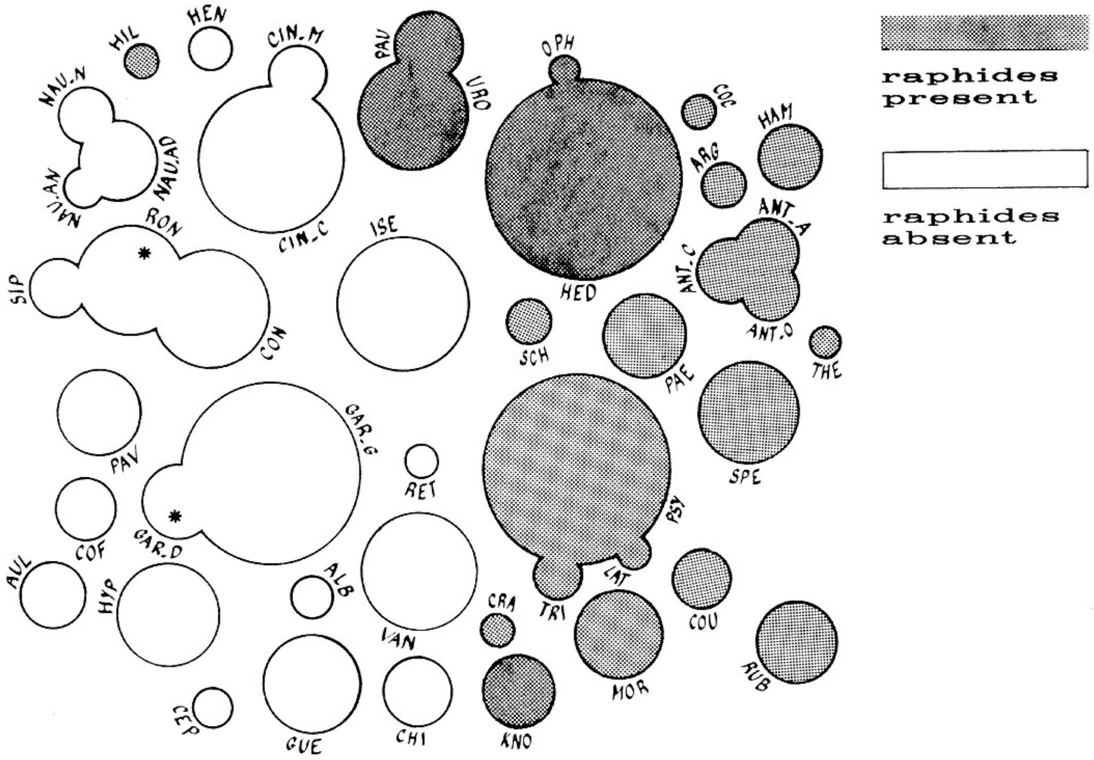


Figure 18.- ***Occurrence of idioblasts with Ca-oxalate raphides*** *in Rubiaceae tribes. Shaded = general occurrence; the asterisks indicate the rare occurrence in* Steenisia *(Ron.) and* Argocoffeopsis *(Gar.-D.).*

2.6.3 Trichomes

In contrast to many other groups of the Asteridae (e.g. the Dipsacales; Weberling 1977a), Rubiaceae trichomes have a relatively simple structure and present only minor diversity. They are unbranched, unicellular or uniseriate. The T-shaped trichomes of *Coptosapelta* seem to be the only exception to this (see further). Pares & Ruat (1953: fig. 17) reported multiseriate trichomes in inflorescences of "*Octodon*" *setosum* (a species of *Spermacoce*, Spe.). The capitate inflorescences contain numerous scales between the flowers which are not trichomes, but scaly bracts and bracteoles provided with

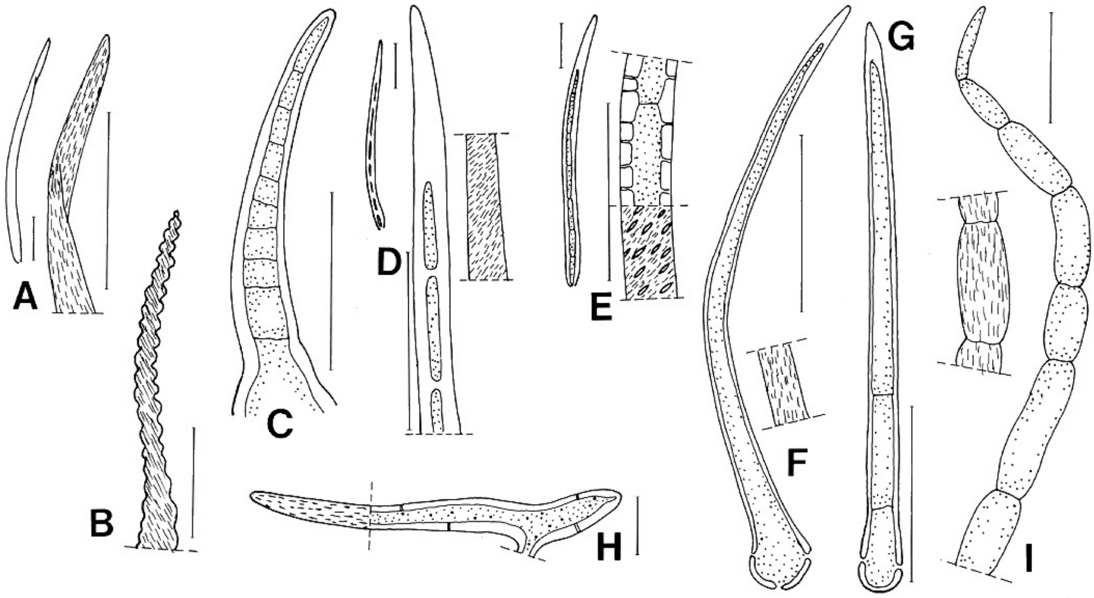


*Figure 19.- **Trichomes** [in surface view or optical section (lumina stippled)]: A, B, "internal indumentum" from corolla inside; C-I, "external indumentum" from various other organs.*
A, Aulacocalyx laxiflora, *ribbon-like unicellular thin-walled hair; B,* Psychotria minuta, *moniliform unicellular thin-walled hair; C,* Pauridiantha callicarpoides, *cylindrical type; D,* Aulacocalyx laxiflora, *cylindrical type; E,* Sericanthe trilocularis, *cylindrical type with pitted walls; F, G,* Machaonia acuminata, *non- and pauciseptate cylindrical hair; I,* Sacosperma paniculata, *articulate type.*
Lines = 100 μm.

numerous raphides and crystal sand and crowned at their tip with a small group of papillar unicellular trichomes.

Glandular hairs are entirely lacking (for non-trichomatic secreting structures called colleters see 2.6.4). Bremekamp (1958: 153) has reported glandular hairs with a pluricellular head in *Aitchisonia* (Pae.) and for that reason (also for the stamens inserted at different levels) excluded the genus from the Rubiaceae. *Aitchisonia*, however, presents many typical rubiaceous features, including the presence of raphides and the occurrence of normal rubiaceous trichomes (of the cylindrical type described below); only some of its organs are also provided with stalked, pluricellular glands which appear to be excrescences (not of colleter nature) and may well be similar to the "pustules" of *Heterophyllaea* (Cin./Hed.; cfr. Solereder 1893: 286).

Verdcourt (1958: 222-224) examined the trichomes of many Rubiaceae and distinguished two groups, called "internal indumentum" (inside the corolla, viz. on the tube inside, the stamens and the style) and "external indumentum" (on all other plant organs). He found that the **internal indumentum** always consists of unicellular thin-walled trichomes which are mostly flat- and ribbon-like (fig. 19 A) or sometimes moniliform (fig. 19 B; appearing pluricellular at first sight). Their surface frequently bears a distinct cuticular pattern, often a striation. There are only a few exceptions to this; Verdcourt reported the occurrence of pluricellular hairs on the anther filaments of *Otiophora* sp. (Hed.) and *Timonius* (Gue.).

The **external indumentum** is more variable. Verdcourt recognized three types,

(i) "septate, uniseriate, composed of separate cells",
(ii) "incompletely septate i.e. with hairs with rather thick walls and the lumen with weak or strong septae which do not cut the walls", and
(iii) "non-septate hairs".

The third type he considered to be derived from the other ones by reduction, non-septate hairs frequently being short and papillar. I do not fully agree with this, since in a number of instances unicellular hairs may be relatively long; some groups, e.g. *Pentanisia* (Kno.) or *Machaonia* (? Gue.), have hairs of equal length varying from non- to pauciseptate (fig. 19 F, G).

Verdcourt's terms for and distinction between types (i) and (ii) is somewhat confusing, since in both types the septa are similar, thin but complete, i.e. entirely separating the cells of the hairs. The following terminology and typology is less ambiguous:

Outer hair walls thin, weakly or not optically active; individual cells easily distinguished on the outline of the hair by furrows at the septa, frequently many of them collapsing after drying; septa thickness comparable to that of outer wall (fig. 19 I) **articulate type**

Outer hair walls thickened, often strongly optically active; individual cells not distinguishable on the straight outline of the cylindrical hair; septa much thinner than outer walls (fig. 19 C-H) **cylindrical type**

The cylindrical hair-type shows some further variation. The outer walls are often provided with pits (fig. 19 E, H). Their cuticle shows frequently striate or verrucate patterns; helical patterns are very rare (e.g. *Pavetta* sp.: Lersten & Curtis 1977). The number of septa varies from many to very few (or none if one includes cylindrical unicellular hairs here). In *Coptosapelta* (? Cin.; fig. 19 H) the hairs are T-shaped with a short base and one short and one long arm, and otherwise they fit the unicellular, pitted, cylindrical type.

The following scheme summarizes the typology of rubiaceous external hairs:

pluricellular:
- **articulate (fig. 19 I)**
- **cylindrical**
  - **outer wall pitted (fig. 19 E)**
  - **outer wall not pitted (fig. 19 C, D, G)**

unicellular:
- **long, cylindrical (fig. 19 F)**
- **short, papillar, thick-walled (derived from pluricellular cylindrical)**
- **short, papillar, thin-walled (derived from pluricellular articulate)**
- **T-shaped (fig. 19 H)**

Finally, **crystals** occur in the hairs of the Guettardeae, as already extensively reported by Solereder (1893). In this tribe, Ca-oxalate crystals are formed in the lumen of the young hairs; upon further growth of the hairs, the crystals become enclosed in the strongly thickened outer walls. In lateral view, the crystals are quadrangular and arranged in rows.

The external indumentum of a particular rubiaceous taxon is always remarkably uniform; all parts bear hairs of the same type, showing only minor diversity, e.g. in size. The hairs inside stipules, bracts and calyces are the only exception to this, since they are frequently thin-walled, articulate when the rest of the indumentum is composed of thick-walled, cylindrical hairs (e.g. *Tricalysia* spp.: Robbrecht 1979: fig. 3).

Verdcourt (1958) stated that the articulate type is often correlated with the occurrence of raphides (see 2.6.2), but that there are too many exceptions to regard this hair type as a reliable character to define his Rubioideae. Indeed, in the Psychotrieae e.g. as well articulate as cylindrical hairs occur.

2.6.4 Colleters

The pluricellular mucilage-secreting structures occurring inside stipules and on other organs in Rubiaceae, Loganiaceae, Apocynaceae and other families of the Asteridae have been designated by a long series of terms, such as

- "Drüsenzotten" (Solereder 1893),
- "shaggy hairs" (Solereder 1908),
- "glandular shaggy hairs" (Metcalfe & Chalk 1950),
- "harzsecernierende Drüsen" (Krause 1909),
- "cérocystes" (F. Hallé 1967),
- "squamellae" (Ramaya & Bahadur 1968) and
- "annexes glanduleuses" (Boiteau & Allorge 1978).

Hanstein (1868) used two terms, namely

(i) the purely descriptive "Zotten" (op. cit.: 700), so named "da sie nicht allein in ihrer Verrichtung, sondern auch in ihrer Gestalt einigermaassen an die sogenannten Zotten im thierischen Darmkanal erinnern", and

(ii) the more functional "Colleteren", signifying "Beleimer, Bekleber"; the secretion he accordingly terms "Blastocolla".

Hanstein's second term, with equivalents in English (colleters), French (collétères) and botanical Latin, is now generally used (Foster 1949, Uphof 1962, Esau 1965, Lersten 1974a, b, 1975, Robbrecht 1978a, 1979, Verdcourt 1976, Puff 1986a, Rogers 1987). In Latin, "colleter" should be treated as masculine and is declined as "aster" (acc. colleterem, nom. & acc. pl. colleteres).

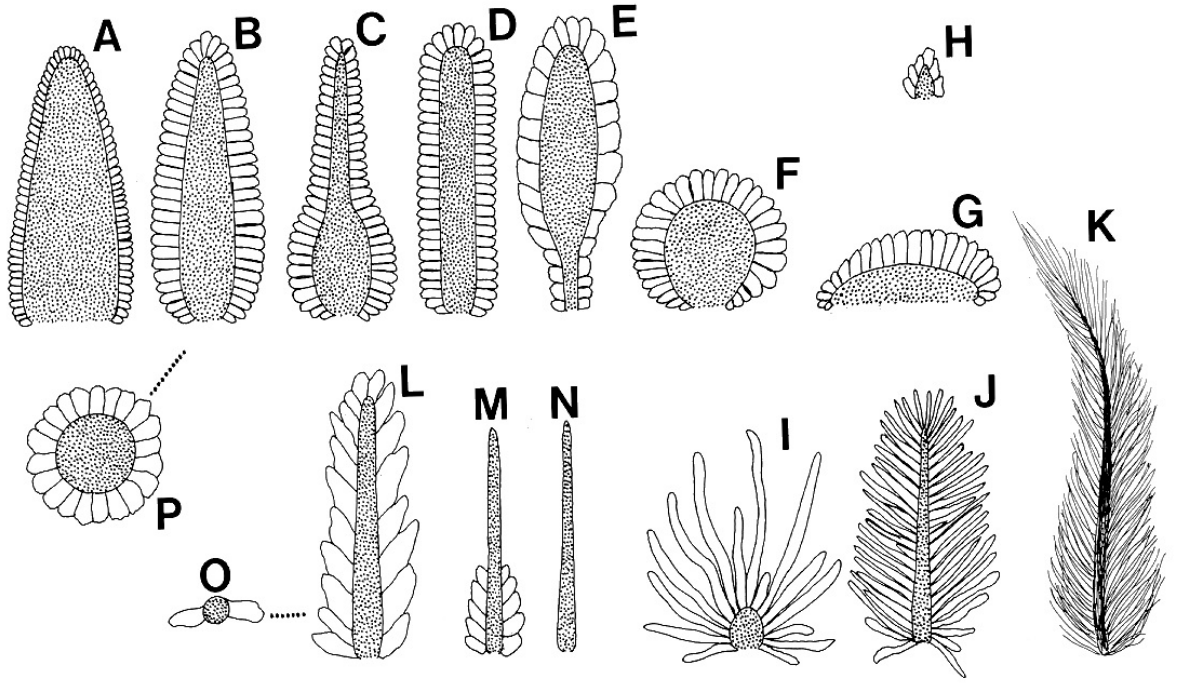


Figure 20.- ***Colleter morphology*** *(A-N, longitudinal sections of colleters; O, P, cross-sections, P corresponding to B and ± to all depicted in A-G, O corresponding to L; the shaded area represents the axis of ± elongated cells; all drawings semi-schematic): A-H, variants of the standard Rubiaceae colleter (A, B, conical, C, obpyriform, D, cylindrical, E, stalked, F, rounded, G, cushion-shaped, H, reduced); I-K, deviant types, ± restricted to the genera* Pavetta, Psychotria, Tricalysia *and* Sericanthe *(I, brush-like, J, dendroid, K, feathery, L, winged, M, reduced type with pallisade only at the base, N, filiform).*
A, Hymenocoleus scaphus*; B,* Virectaria major*; C,* Tricalysia elliotii*; D,* Schumanniophyton problematicum*; E,* Theligonum cynocrambe*; F, G,* Prismatomeris beccariana*; H,* Tricalysia aequatoria*; I,* T. nogueirae*; J,* T. glabra*; K,* T. concolor*; L,* T. jasminiflora*; M,* T. reticulata*; N,* T. ferorum.

Karsten (1859-1869) was probably the first to describe and depict (as "Zotten") in detail the occurrence of colleters, and their number and position in many genera of the Rubiaceae.

Occurrence: Krause (1909) examined representatives of 21 tribes of the Rubiaceae. Only in the Rubieae were no colleters detected; since then reduced colleters have been found in representatives of that tribe too (Rutishauser 1984). The occurrence of colleters is indeed one of the most ubiquitous rubiaceous features. The genera *Henriquezia* and *Platycarpum* (Hen.) seem to be the only exceptions, and this was one of the arguments used by Bremekamp (1957: 353) to separate them from the Rubiaceae as the Henriqueziaceae. Rogers (1984: 27) also failed to observe colleters in these genera, "despite extensive searching, including examination of living plants".

Nature: colleters are probably best considered to be "emergentia"; Ramaya & Bir Bahadur (1968) demonstrated in some Apocynaceae that they originate not only from epidermal but also from subepidermal cell layers. This ontogeny was confirmed in the rubiaceous genus *Schumanniophyton*, Gar.-G. (F. Hallé 1967: 95).

Number and position: colleters occur inside of or at the margin of stipules (including parts of bracts and bracteoles derived from them) as well as calyces, generally together with genuine trichomes.

The number of colleters and their mode of insertion is highly variable. They may be in large numbers and more or less cover the entire inside of the stipules; this occurs e.g. in many Gardenieae, and is perhaps the primitive condition. Mostly, however, the colleters are inserted in a single row on the inner edge of the stipule base. They may also be placed at the rim of the stipule, and in the case of multifid stipules often tip the fimbriae. The colleters associated with the calyx show a similar range of variation in number and position.

Morphology: In the majority of the Rubiaceae, the colleters are cylindrical to somewhat conical, consisting of an axis of elongated cells covered by a palisade-like epidermis (fig. 20 A, B). The same type of colleters occurs also in Apocynaceae, Loganiaceae, etc. When Lersten (1974a, b) discovered morphologically different types in some Rubiaceae, he called it the standard type. Deviant colleters are limited to a number of species in only a few genera: Calycophyllum (Cin.-C.), *Alibertia* (Gar.-G.), *Tricalysia* and *Sericanthe* (Gar.-D.), *Pavetta* (Pav.), *Vangueria* (Van.) and *Psychotria* (Psy.). Remarkably, the occurrence of modified colleters is concentrated in the three genera which are characterized by bacterial leaf-galls (see 2.4.3). However, not all the taxa possessing bacterial galls have deviant colleters, and vice versa. Nevertheless, Lersten & Horner (1976) suggested that there may be a relation between the symbiotic cycle of the bacteria and modified colleter morphology, particularly between the latter and the secretion of bacteria-compatible blastocolla (see 2.13.2).

Apart from the standard-type, Lersten (1974a, b, 1975) described four other colleter types. After having examined colleters in many representatives in *Tricalysia* and *Sericanthe* (Robbrecht 1978a, 1979, 1982a, 1983, 1987a), I could not fully confirm his typology, but can distinguish between five deviant types:
(i) dendroid colleters (fig. 20 I), with elongated and ± free epidermal cells on an extremely short common base (= dendroid type of Lersten);
(ii) brush-like colleters (fig. 20 J), with elongated and ± free epidermal cells on a longitudinal axis (= brush-like type of Lersten);
(iii) feathery colleters (fig. 20 K), similar to (ii) but with extremely long axis (not recognized as a type by Lersten, but vaguely described in *Pavetta* spp. as "more exaggerated dendroid colleters, ..., with a long slender axis and widely separated epidermal cells";
(iv) winged colleters (fig. 20 L), with two opposite wings on either side of an elongated axis, their general shape flattened (= Lersten's "reduced standard" and "standard with irregular, bulging epidermal cells" types); and
(v) filiform colleters (fig. 20 N), reduced to only an axis (only known from *Tricalysia ferorum*, Robbrecht 1983: fig. 1).

The standard colleters show some minor variation. Most are constricted at base and slightly conical, tapering towards the tip (fig. 20 A, B). Their diversity (fig. 20 A-H) is in size, general shape (cylindrical, obpyriform, rounded, cushion-shaped), development of the basal constriction (stalked or sessile), degree of development (sometimes strong reduction, fig. 20 H), and relative diameter of the central axis (equalling the palisade to exceeding it ca. 5 times in diameter).

Secretion: F. Hallé (1967: 97) gave a survey of the investigations carried out to determine the secretory mechanism and the chemical nature of the colleter secretion or blastocolla; he examined the substances secreted in *Gardenia imperialis*, a species with copious mucilage production (liquid drops up to 1 cm in diameter cover the tips of the branches of this tree, personal field obs., Zaire). In all examined cases the secreted substances are of a waxy nature (esters of higher fatty acids and higher alcohols); they first accumulate as oil droplets under the cuticle of the epidermal cells of the colleters, then are dispersed onto the surface of the buds by these cells rupturing.

The biological significance of the colleter secretion is obviously enhancing the meristematic tissues' protection already offered by stipules or calyces. In the genera provided with bacterial leaf galls, the blastocolla also plays an important role in the symbiotic cycle (see 2.13.2).

Taxonomic significance: While the occurrence of colleters is an important criterion to define the Gentianales (Wagenitz 1959) or to include *Theligonum* in the Rubiaceae (Wunderlich 1971), their variation inside the Rubiaceae, as described above, has no bearing on the higher taxa of the family. At the generic level, however, colleter variation is well consistent with other features. Petit (1954) redelimited Pseudomussaenda (? Con.) against *Mussaenda* (Ise.), and his views are corroborated by the colleter position on the calyx, marginal at the base of the calyx-lobes in *Pseudomussaenda,* in-between the lobes in *Mussaenda*. Standard, brush-like, dendroid, feathery and winged colleters occur in *Tricalysia* (Robbrecht 1979, 1982, 1983, 1987); their distribution confirms the subgenera and sections recognized in the genus.

2.7 Inflorescences

Position: Inflorescences are either terminal (fig. 21 A, B, C) or axillary and paired at nodes (fig. 21 D, E); occasionally, axillary inflorescences are single at nodes (Robbrecht & Puff 1986: fig. 5k). Truly axillary inflorescences could be explained as terminal inflorescences on extremely contracted short-shoots. Terminal inflorescences very often become pseudo-axillary after one of the axillary buds below the inflorescence continues its (sympodial) growth (Robbrecht & Puff 1986: fig. 5d). The axillary inflorescences of *Canephora* (Hyp.; fig. 21 E, F) deserve special attention; they are unique in that the inflorescence peduncle transforms into a flattened, assimilating axis (cladode). Cauliflorous taxa are rare in the Rubiaceae (e.g. *Ecpoma, Ise., Stelechantha,* Pau.). Accessory shoots giving rise to two or several coaxillar inflorescences are common (e.g. *Tricalysia,* Gar.-D.: Robbrecht 1987: fig. 4, 13A; Anthospermeae: Puff 1986a).

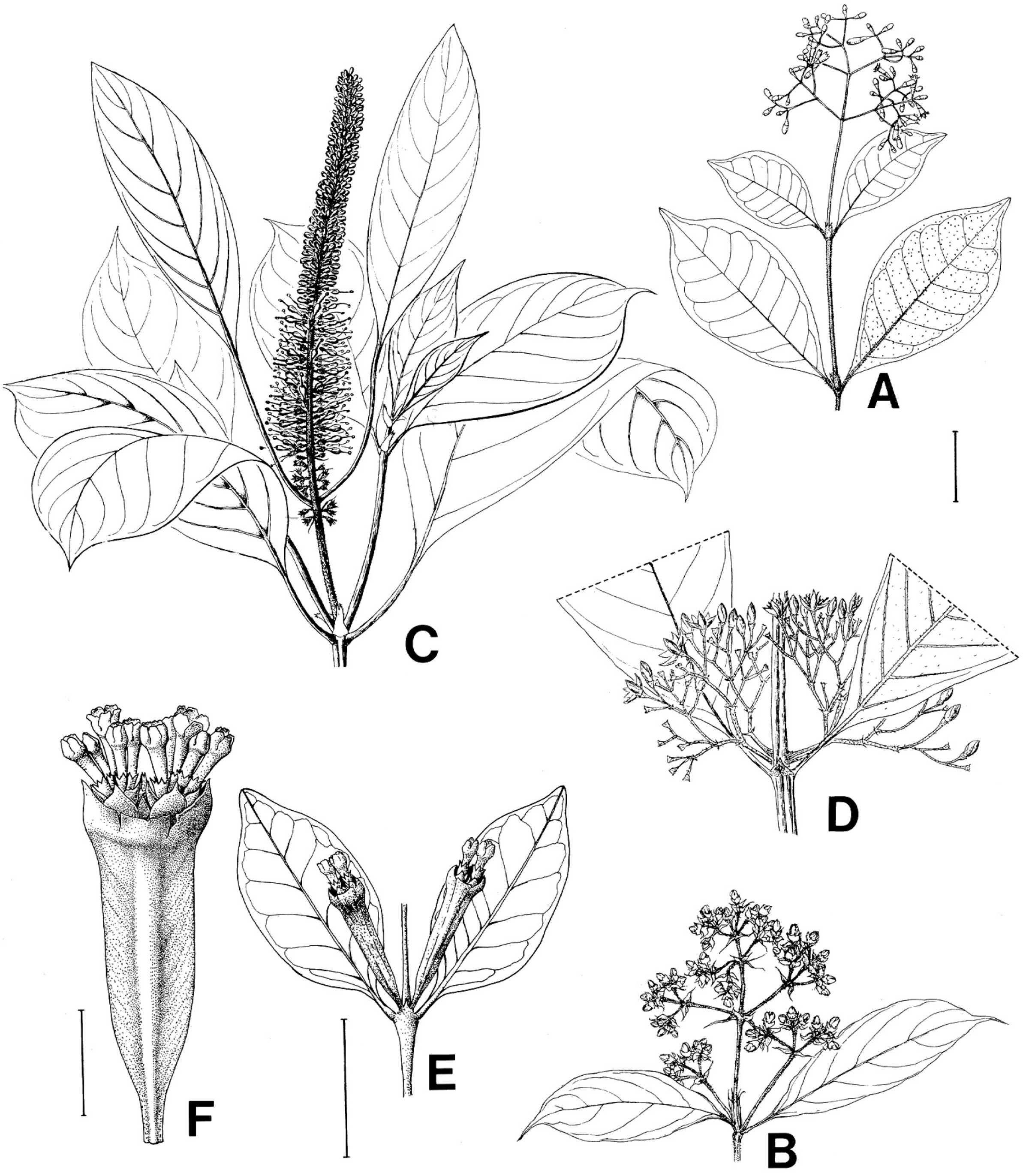


*Figure 21.- **Inflorescences**: A-C, terminal; D-E, axillary and paired at nodes; F, detail of E.*
A, Psychotria cameronensis*; B, Gaertnera longevaginalis; C,* Hymenodictyon floribundum*; D,* Galiniera coffeoides*; E, F,* Canephora madagascariensis.
F after Baillon. Lines = 2 cm, except to F = 0.5 cm.

Bracts and bracteoles: Most rubiaceous inflorescences are bracteose. Bracts and bracteoles may be fused into conspicuous structures reminiscent of the calyx, consequently often named "calyculi"; this occurs e.g. in *Calycosiphonia* (fig. 22 A), *Sericanthe* (fig. 22 B), *Tricalysia* (Gar.-D.), and *Belonophora* (Aul.). In *Blandibractea* (Ron.), the bracts are modified in petaloid blades and function as the attractive system of the inflorescence.

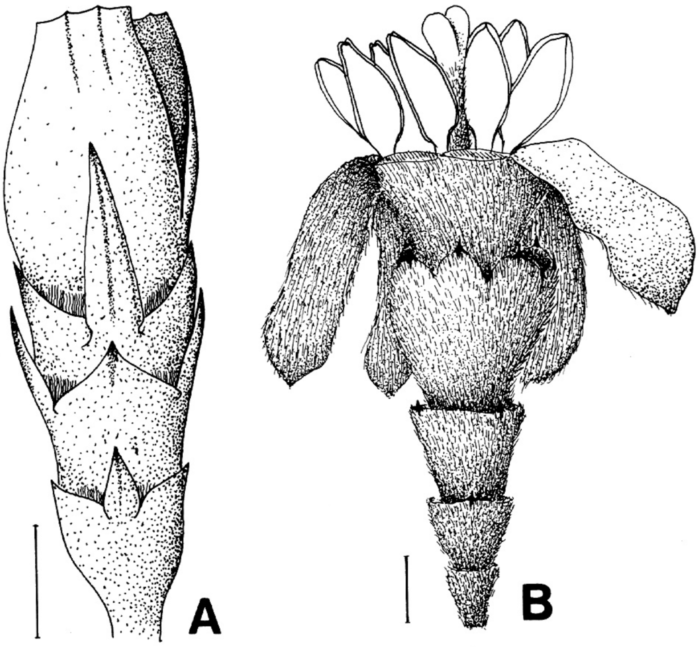


*Figure 22.- **"Calyculi", pairs of bracts and bracteoles modified in cupular calyx-like structures**: A, flower-bud of* Calycosiphonia spathicalyx *(from above: corolla-bud with contorted aestivation, calyx with deep longitudinal split, three calyculi wherein stipular and foliar appendages can clearly be discerned); B, uniflorous inflorescence of* Sericanthe pellegrinii *(from above: opened corolla, two lobes cut away, calyx, three calyculi). Lines = 2 mm.*

Morphology: Weberling (1977b) gave a good overview of inflorescence morphology in the Rubiaceae; he considered thyrsic or pleiothyrsic many-flowered inflorescences with an end flower as the "central type of rubiaceous inflorescence" (fig. 21 A, B); he mentioned three main modifications of this basic type,

- impoverishment (sometimes leading to uniflorous inflorescences, fig. 22 B; bracts, bracteoles and undeveloped primordia indicating a former multiflorous condition),
- unequal development of certain inflorescence parts (partial inflorescences or axes), and
- congestion of the entire inflorescence or parts of it (clustered flowers).

The second tendency often results in spike-like inflorescences (e.g. *Hymenodictyon*, fig. 21 C) or partial inflorescences with helicoidally arranged flower-pairs, e.g. in *Otiophora* (Hed.; Puff 1983: fig. 1) and *Declieuxia* (Psy.; Kirkbride 1976: fig. 1).

Pseudanthia: The third tendency often results in pseudanthia (fig. 23), which in certain cases may be truly capituliform, i.e. the flowers are placed on an enlarged receptacle with interfloral scales [fig. 23 A, B; see also longitudinal section of *Cephalanthus* (Cep.) infructescence, fig. 55 A].

Claßen (1984) recognized four modes of development of pseudanthia in the Rubiaceae:

(i) strong inflorescence congestion and flowers remaining undifferentiated (fig. 23 A, B),

(ii) "calycophyllous" pseudanthia, superficially similar to *Hydrangea* and *Viburnum*, but wherein the enlarged coloured calyx-lobes of the outer flowers, differentiated into a petiole and a blade (fig. 25 H), function as additional visual element (fig. 23 E),

(iii) hyperfloral differentiation, whereby bract leaves develop into an involucre surrounding the strongly congested inflorescence (involucral bracts free or connate, green, e.g. *Geophila*, Psy., fig. 23 D, or vividly coloured, red or blue, e.g. *Cephaelis* spp., Psy.), and

(iv) the case of *Sabicea* and *Stipularia* (Ise., fig. 23 C), where axillary opposite pseudanthia are strongly congested and surrounded by a large involucre resulting from either the two bracts of first-order lateral flowers or the stipules of the supporting leaf pair.

Pseudanthia of type (i) are characteristic for the Naucleeae, the Cinchoneae-Mitragyninae, the Cephalantheae and a few members of the Psychotrieae [e.g. *Hymenocoleus globulifer*, Robbrecht 1977: fig. 6: here possibly derived from type (iii) by loss of involucre]. The Morindeae have similar inflorescences which cannot be considered pseudanthia because the flowers are larger and less numerous and have no simultaneous anthesis; they are interesting since the ovaries are completely fused and develop into a syncarp (fig. 40 H). The inflorescences of certain herbaceous or semi-herbaceous genera also remind type (i), e.g. *Spermacoce* (Spe.) and *Calanda* (Kno.). In the latter genus flower pairs have their ovaries and calyces completely fused (Puff & Robbrecht in press: fig. 16).

Type (ii) pseudanthia are characteristic of the Isertieae and associated tribes (see 2.8.1 for distribution of enlarged coloured calyx-lobes). Weber (1955) gave a detailed discussion of this inflorescence type in *Mussaenda* (Ise.) and *Warszewiczia* (Ron.). It is not always as marked as in these genera. In e.g. Alberta and *Nematostylis* (Alb.) (Puff, Robbrecht & Randrianasolo 1984: fig. 6H, J), all flowers of the inflorescence have enlarged calyx-lobes.

Type (iii) is limited to the Psychotrieae. The involucres are extremely variable in their morphology (e.g. extremely zygomorphic, *Cephaelis* spp., and/or colours attractive, frequently red or purple in *Cephaelis* spp., white in *Faramea* spp.).

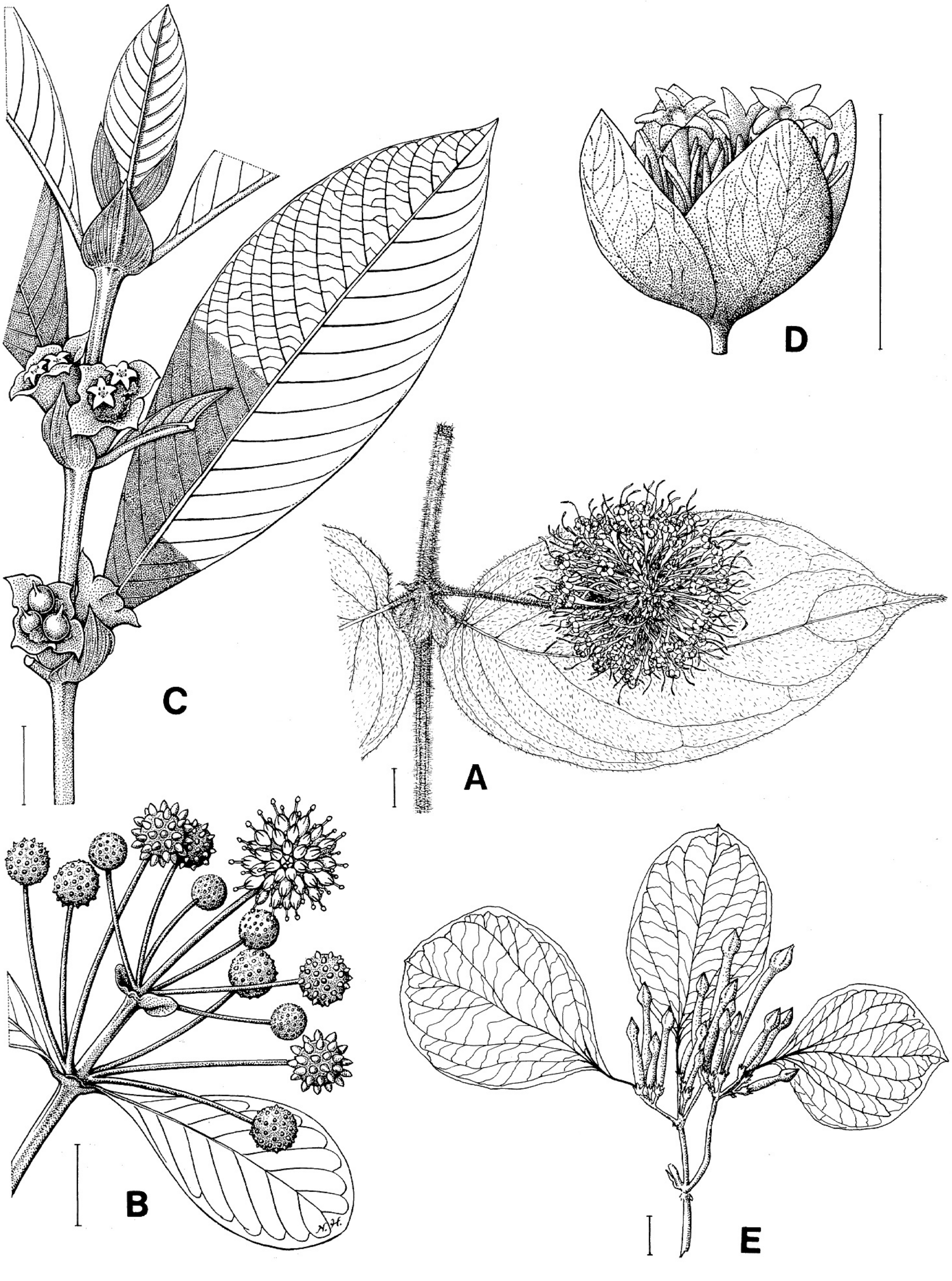


Figure 23.- ***Pseudanthia****: A, B, strong congestion of inflorescence and flowers undifferentiated (A,* Uncaria donisii*, B,* Mitragyna ciliata*); C, axillary opposite pseudanthia, strongly congested and surrounded by involucre (bracts),* Stipularia africana*; D, terminal congested pseudanthium surrounded by bract leaves,* Geophila obvallata*; E, "calycophyllous" pseudanthium, three outer flowers with an enlarged, coloured calyx-lobe (semaphyll, detail see fig. 25 H),* Mussaenda nannanii.
A-C from N. Hallé; D after Schumann. Lines = 1 cm

The importance of the inflorescence morphology lies mainly at the lower taxonomic ranks. Inflorescence position, however, may be characteristic for tribes, e.g. nearly always terminal in Pavetteae (exceptions: *Doricera*, *Versteegia*), Knoxieae and Psychotrieae (exception: *Hymenocoleus* sp.), or truly axillary in Hypobathreae and Gardenieae-Diplosporinae. On the other hand the position may be different in closely related taxa; *Pampletantha* (Pau.) with terminal inflorescences is sometimes segregated from *Pauridiantha* with truly axillary inflorescences. Also other morphological trends may be constant at tribal level; in the Knoxieae e.g., the inflorescences or partial inflorescences tend to be spike-like with spirally arranged flower-pairs (for details see Puff & Robbrecht, in press).

2.8 Flowers

The Rubiaceae have flowers characterized by a number of features common in the Asteridae viz. tetracyclic arrangment, mostly actinomorphic symmetry, epipetalous stamens equalling the number of corolla-lobes and with a filament fused with the corolla-tube, and inferior ovaries.

The flowers are mostly pentamerous. However, the trend to tetramerous flowers is present in almost every tribe. Trimerous flowers are exceptional (frequent in *Theligonum*, The., and sometimes even 2-merous; occasionally 3-merous in *Corynanthe*, Cin.-C., *Alibertia*, Gar.-G., *Pouchetia,* Hyp., *Scolosanthus,* Chi., *Paraknoxia,* Kno., *Opercularia,* Ant.-O., and *Mitchella*, inc. sed.). A tendency to increase the number of floral parts also occurs; pleiomerous flowers are found in many tribes, and are especially common in the Gardenieae and associated Coffeeae where the flowers are up to 12-merous. Fig. 24 gives a detailed survey of merousness in rubiaceous flowers.

Nozeran (1955: 194 e.s.) assumed that in the Rubiaceae pleiomery may result from two phenomena, either fusion of flowers or dédoublement. Evidence for fusion is discussed in 2.8.4.

Flower **size** is extremely diverse and varies from a few millimeters to several decimeters in length. Small and medium-sized flowers are by far the commonest. However, it is difficult to get an overview of flower size variation within the family. F. Hallé (1967: 105) calculated the medium corolla-tube length for the Rubiaceae species in the flora of the Ivory Coast; large flowers (corolla-tube 5-30 cm in length) occur only in the Gardenieae.

2.8.1 Calyx

In the Rubiaceae, the calyx is most probably restricted to the structures placed above the ovary (strictly hypanthium). The frequent position of colleters inside the base of these structures is comparable to the colleter position in leaves and their stipules, and thus adds evidence to Leinfellner's (1954) data supporting the view that the rubiaceous hypanthium consist of only gynoecial and axial tissue.

The calyx generally consists of a tube plus distinct apical lobes. Much of its variation results in the relative development of one of both; the calyx may be a well-developed tube with distinct lobes (fig. 26 E) or without lobes (truncate, fig. 25 A, 26 N), or a very short tube with foliaceous lobes (fig. 25 C-F, 26 C, D, 27 A, D). Almost complete reduction of the calyx also occurs (a short rim: *Coffea*, Cof.; minute lobes: *Spermacoce* spp., Spe.; calyx absent: *Theligonum*, The., *Neogaillonia*, Pae.; further examples of reduction or absence: Wunderlich 1971: 366). The lobes

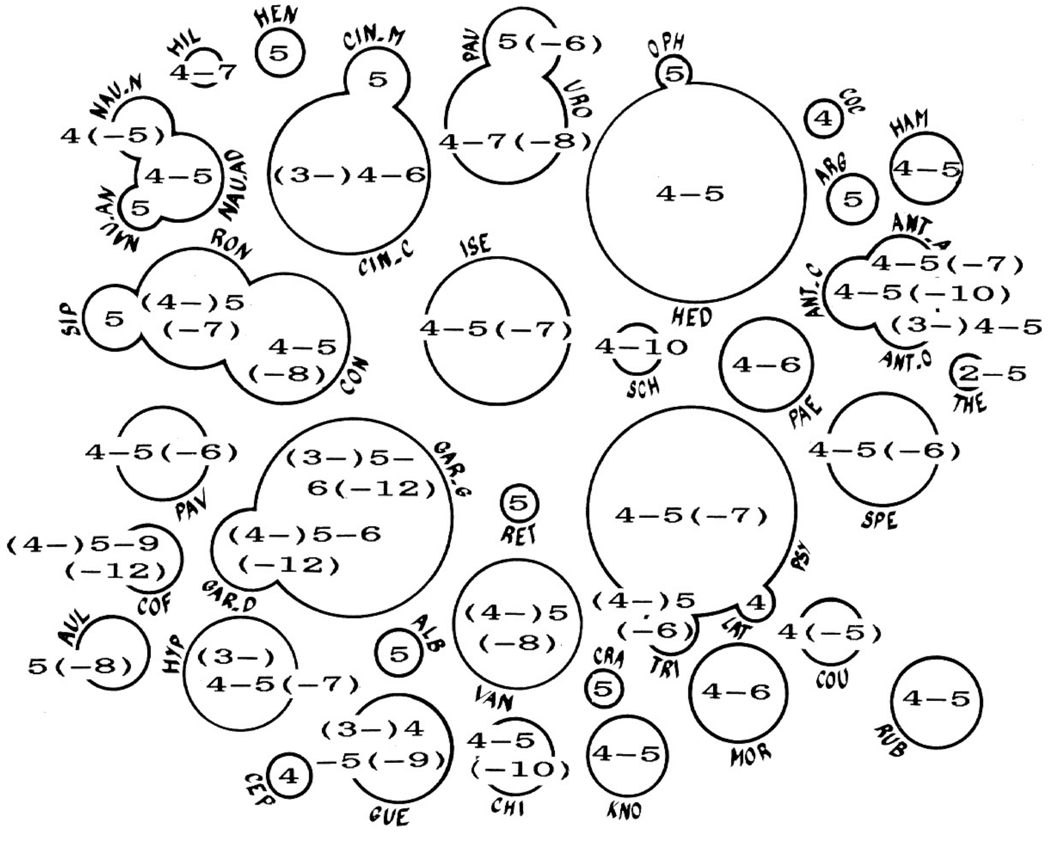


*Figure 24.- **Merousness of the flowers**: variation in the Rubiaceae tribes.*

generally do not overlap each other; when they do so (fig. 25 C, D), their relative position does not necessarily repeat the aestivation of the corolla-lobes. Small lobes interstitial between the "normal" lobes, most easily detectable when the calyx is observed from the inside, occur in a few genera, to my knowledge only in *Sherbournia* spp. (Gar. G.; Robbrecht & Puff 1986: fig. 7r) and *Strumpfia* (inc. sed.; Schumann 1891: fig. 37S). In these two genera, the calyx is actinomorphic and has large "normal" lobes plus small interstitial ones in the same number; this case can not be compared with that of zygomorphic calyces (see below), where one or a few small additional lobes are common.

In several large genera, the variability of the calyx has a high practical value in classifying and naming the species (e.g. *Sabicea*, Ise., Wernham 1914, *Tricalysia*, Gar.-D.: Robbrecht 1979, 1987a: fig. 6, *Carphalea*, Hed., Puff 1988: fig. 5).

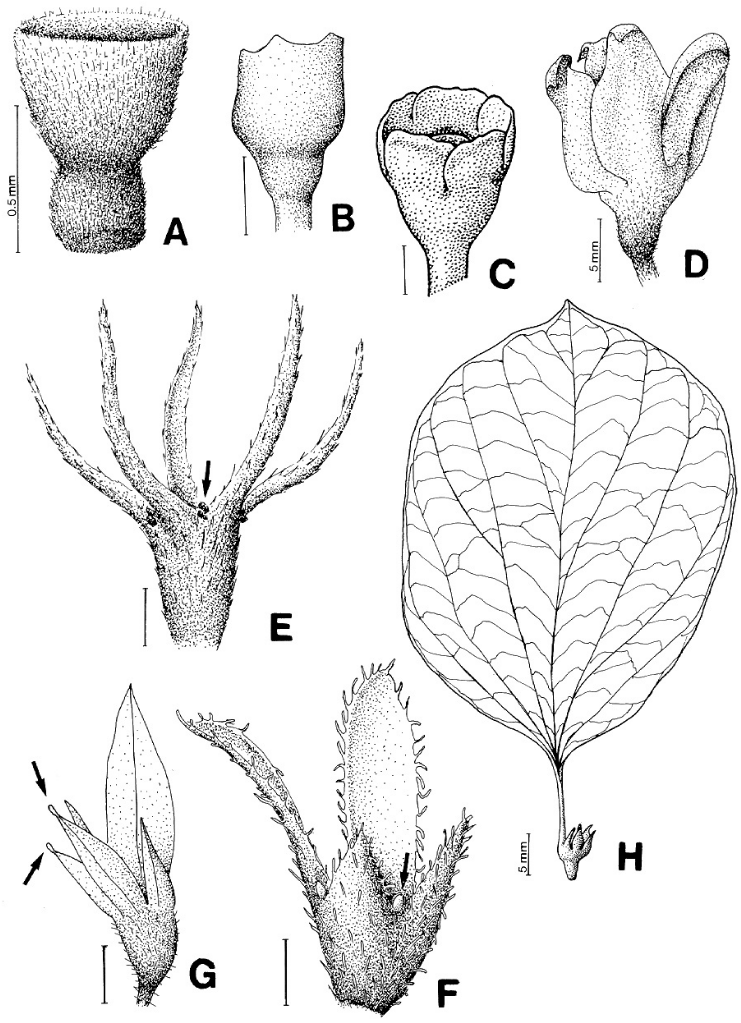


*Figure 25.- **Calyces and ovaries ("hypanthia")**: A, B, truncate calyces; C-H, calyx with short tube plus distinct lobes, lobes unequal in G-H [G, F, enlarged lobes green and foliaceous; H, enlarged lobe ("semaphyll") coloured, optically attrac-tive]. Arrows point to col-leters; see fig. 26-28 for further examples af calyx variation.*
A, Guettarda parviflora;
B, Psychotria amboniana;
C, Tarenna jolinonii;
D, Dictyandra arborescens;
E, Sipanea biflora;
F, Pentas lanceolata;
G, Batopedina pulvinellata;
H, Mussaenda nannanii.
C from N. Hallé. Lines = 1 mm, except otherwise indicated.

Colleters: The inside of the calyx is beset with colleters of the same type as those on the stipules. Colleter number and position is diverse. They may cover the entire inside or only a part of it, occur in a ring all around the inside of the calyx-base, or be limited to small groups (sometimes isolated colleters) on the inside between or at the margin of the lobes. A position on top of calyx-lobes (fig. 25 G), or a marginal position, in the sinuses between the calyx-lobes (fig. 25 E, F) or on the rim of a truncate calyx is much more rare.

Symmetry: The calyx is frequently zygomorphic as opposed to the corolla which is mostly strictly actinomorphic. This may result from a deep longitudinal division (already in bud) or split (caused by the expansion of the corolla at anthesis); thus the calyx is or becomes ± spathaceous. This type of calyx zygomorphy is frequent in the Gardenieae and associated tribes; it occurs in species of *Schumanniophyton, Rothmannia, Gardenia, Sericanthe, Tricalysia* and *Calycosiphonia*. It is also found in *Hillia* spp. (Hil.) and *Hippotis* (Hip., fig. 27 C). A two-lobed calyx occurs in a number of herbaceous representatives, e.g. *Declieuxia* sp. (Psy.) and *Perama* (Per.).

Far more frequent are zygomorphic calyces with unequal lobes. Enlargement (and foliaceousness) of one (or some) calyx-lobe(s) (fig. 25 F, G) is very common especially in the predominantly herbaceous tribes Hedyotideae, Anthospermeae and Knoxieae. Flowers with one or some petaloid, red, white or yellow enlarged calyx-lobes (fig. 25 H, 26 A, B; semaphylls sensu Leppik 1977) are almost exclusive to woody species in the groups enumerated below; rarely all lobes are petaloid and enlarged, and in a few instances are they fused to large coloured cups with hardly detectable lobes (*Carphalea* spp., Hed., fig. 26 G; *Phyllomelia*, inc. sed.).

The following survey of taxa with petaloid calyx-lobes updates the enumeration of Jansen (1979). [The report of semaphylls in the small African genus *Trichostachys* (Mor.; Leppik 1977: 165) is a misinterpretation; in species such as T. aurea, the very small flowers are aggregated into head-like inflorescences which are violet because of the coloured but not enlarged calyx-lobes].

Cin.-C.: *Manettia, Calycophyllum, Monadelphanthus, Capirona, Schizocalyx, Wittmackanthus*
Ron.: *Steenisia, Warszewiczia*
Con.: *Kerianthera, Pinckneya, Pogonopus, Pseudomussaenda*
Ise.: *Mussaenda, Schizostigma, Temnopteryx, Pentaloncha*
Alb.: *Alberta sambiranensis, Nematostylis*
Mor.: *Morinda latibractea*
Hed.: *Carphalea* (calyx very variable, see Homolle 1937, Puff 1988)
inc. sed.: *Cosmocalyx, Phyllomelia*

Such calyces also occur in a few herbaceous species (Hed.: Kadua and *Pentas* subg. *Phyllopentas*). In several genera, the semaphylls are restricted to the outer flowers of the inflorescences (e.g. in *Mussaenda, Warszewiczia*, see 2.7 "calycophyllous pseudanthia"), but a few have all flowers with semaphylls [*Neurocalyx* (Arg.); Alberta (Alb.); *Cruckshanksia* (Hed.)]. In *Alberta minor* and relatives and in *Neurocalyx*, the calyx is not zygomorphic since all its lobes are transformed into semaphylls.

Petaloid sepals may also occur occasionally in taxa normally not having this condition, such as *Mitchella* (LeC. Blaser 1954: 537).

Postfloral enlargment of one or more calyx-lobes (pterophylls) takes place in very few Rubiaceae. In *Phialanthus* (Chi.), and *Neogaillonia* (Pae.) all, in *Jackiopsis* (Jac.; fig. 40 E) three or four calyx-lobes enlarge postflorally. In the genus *Alberta* (Alb.) above cited, all species have flowers with bright red prefloral semaphylls, except *A. magna* with two (of five) calyx-lobes enlarging only in the fruiting stage; it is noteworthy that the pterophylls of this species are bright red and thus increase the optical attractiveness of the tree (flowering and fruiting at the same time) for possible pollinators (for further details see Puff, Robbrecht & Randrianasolo 1984: 330).

2.8.2 Corolla

Shape (fig. 26): Hypocrateriform corollas with a tube generally longer than the lobes are the most frequent type in the Rubiaceae; frequently the tube is widened at the level of the anthers. Many other corolla shapes occur, e.g. campanulate, infundibular or rotate. Zygomorphic corollas are discussed below, symmetry.

Noteworthy here are pairs of closely related genera distinguished by divergent corolla morphology. So *Leptactina* (Pav.) and *Oxyanthus* (Gar.) have hypocrateriform corollas with very long tubes and are closely related to respectively *Dictyandra* (see Robbrecht 1986b) and *Mitriostigma* with short tubes.
Pleiocoryne (Gar.) and *Aulacocalyx* (Aul.) have hypocrateriform corollas and are allied respectively to *Oligocodon* and *Heinsenia* (fig. 26 J) with campanulate corollas.

The corolla-lobes do not show much diversity. The tips vary from acute to rounded or emarginate. In the case of valvate aestivation, the acute lobes often have a characteristic hood-like shape, at the tip shortly recurved and with a convex outer side and two flat inner sides corresponding to the contact zones of the corolla-lobes in bud stage (fig. 27 D, 29 F, G). In addition, the outside of the lobe-tips may develop into a distinct ± linear appendage (fig. 26 C, D, 28 C), which may render the inflorescences very showy, e.g. in *Corynanthe* and *Pausinystalia* (Cin.-C.). A number of *Cinchoneae*, e.g. *Joosia*, and also *Guettarda* spp. (Gue.) and *Didymochlamys*

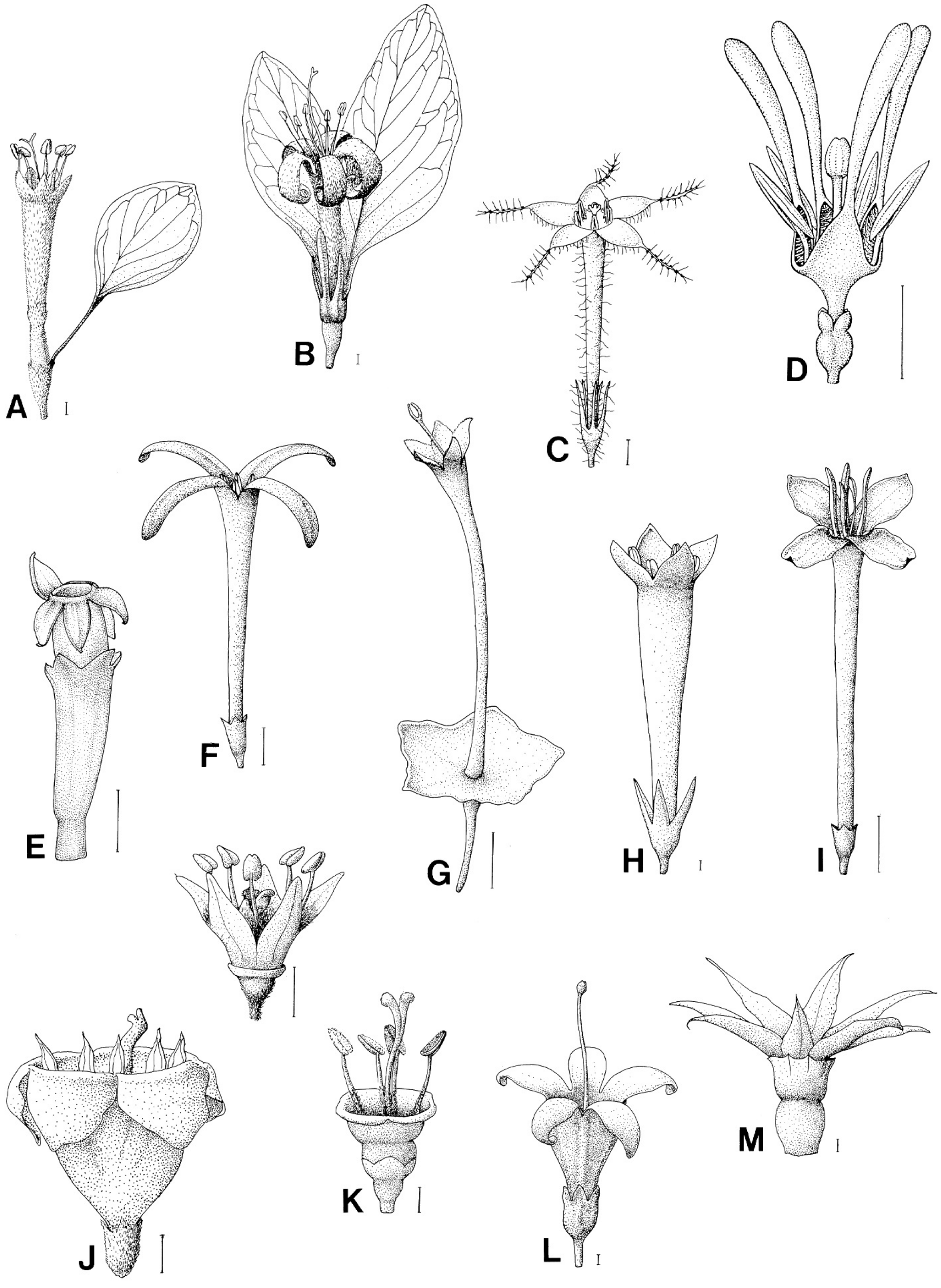


Figure 26.- ***Variation in flower morphology****: see discussion in text.*
A, Pogonopus exsertus*; B,* Pinckneya pubens*; C,* Hutchinsonia barbata*; D,* Corynanthe mayumbensis*; E,* Hymenocoleus scaphus*; F,* Gouldia terminalis*; G,* Carphalea angulata*; H,* Bouvardia triphylla*; I,* Pavetta indica*; J,* Heinsenia diervilleoides*; K,* Simira *sp. (*"Sickingia" glaziovii*); L,* Chiococca racemosa*; M,* Thieleodoxa lanceolata*; N,* Chimarrhis cymosa.
Partly from N. Hallé and after Baillon, Robyns and Schumann. Lines = 2 mm.

(inc. sed.), have the corolla-lobes strongly expanded and fringed at anthesis; such lobes often also are dichotomously branched (Schumann 1891: fig. 16 B). Vogel (1954) correlates this with the sphingophilous pollination syndrome.

Colour: White corollas are dominant in the Rubiaceae. Blue or bluish corollas have evolved in many herbaceous representatives, e.g. in all the members of the tribe Knoxieae and in many Hedyotideae, and in a few large, tropical woody genera, e.g. *Faramea* (Cou.). Yellow and yellowish colours characterize the Hamelieae and are more or less frequent in the Isertieae and the Gardenieae. The large flowers of the latter tribe often have intricately coloured flowers, frequently with purple spots. Vividly red flowers are rare and e.g. occur in *Burchellia* (Gar.-G.), *Alberta* (Alb.), *Isertia, Mussaenda, Sabicea* (Ise.) and *Warszewiczia* (Ron.).

Symmetry: The corolla is generally strictly actinomorphic, but zygomorphic corollas (fig. 27) occur in 25 woody genera of the Rubiaceae (table 4); they are absent from herbaceous Rubiaceae. In general, a curving of the corolla-tube (and style) accounts for the zygomorphy (fig. 27 D); sometimes, the base of the tube is asymmetrically bulging (e.g. in most species of *Palicourea*, Psy., fig. 27 E). In a few instances, the lobes are also unequal, and the flowers then are reminiscent of Bignoniaceae or Gesneriaceae (fig. 27 A, B). Sometimes, the corolla zygomorphy is accentuated by unequal anther-filaments.

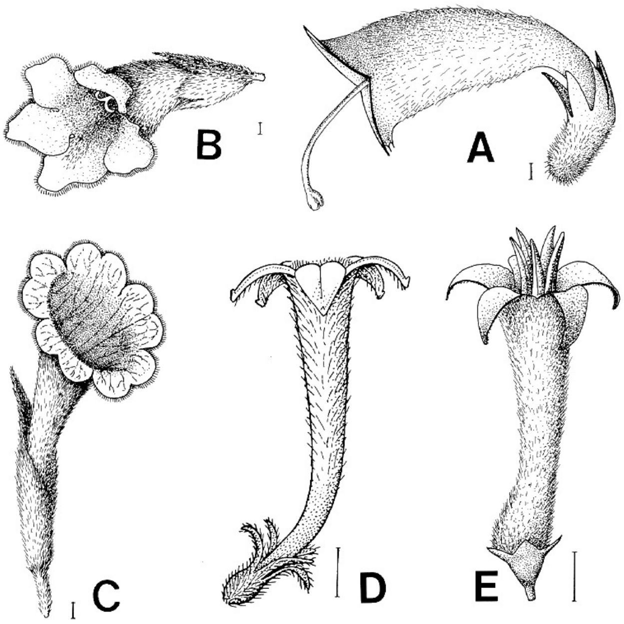


*Figure 27.- **Zygomorphic flowers**: A-D, zygomorphy mainly by curving of corolla-tube (see also text), E by asymmetrically bulging corolla-tube base.*
A, Dichilanthe zeylanica;
B, Henriquezia verticillata;
C, Hippotis albiflora;
D, Sabicea congensis;
E, Palicourea rigida.
After Schumann and (D) from N. Hallé. Lines = 2 mm.

While in most tribes zygomorphy is more or less occasional, it is standard in the Henriquezieae and Alberteae. In the first tribe all species of *Henriquezia* and *Platycarpum* and a few species of *Gleasonia* have distinctly zygomorphic corollas (tube + lobes !; Rogers 1984). In the second tribe, all species of *Alberta* and *Nematostylis* generally have ± curved corolla-tubes and styles (Puff, Robbrecht & Randrianasolo 1984: fig. 1A, 7, 8). These two tribes fall within the three affinity circles where zygomorphic flowers are encountered (i - iii in table 4):

- the Cinchoneae and associated Hillieae, Henriquezieae, Rondeletieae and Condamineae, to which taxa of ± uncertain position, Hippotieae, Tammsieae and *Acranthera*, may be added;
- the Vanguerieae, Alberteae and Guettardeae; and
- the Psychotrieae and Morindeae.

In addition, *Posoqueria* is the only representative of the Gardenieae and relatives with zygomorphic corollas.

Splits: In some Rubiaceae, the corolla shows a deep longitudinal split at anthesis, resulting in a zygomorphic appearance (fig. 28 D). Jansen (1979) mentions this in *Aulacocalyx* (Aul.), *Spathichlamys* (Ron.) and perhaps also *Molopanthus* (Cin.) and *Synaptantha* (Hed.); this occurs also in *Dictyandra congolana* (Pav.; Robbrecht 1986: fig. 4D). In *Aulacocalyx*, it is only occasional.

Other flowers of the Rubiaceae are reminiscent of the Stackhousiaceae, in that the base (fig. 28 A, B) or the middle (fig. 28 C) of the corolla-tube is fenestrated by short longitudinal splits, one in between each lobe. This feature is rare, though more common in the Isertieae and associated Condamineeae and Hedyotideae; it also occurs in species of *Heinsia, Mussaenda* (Ise.), *Pseudomussaenda* (Con.), *Sacosperma, Pentas, Pentodon* (Hed.), *Caelospermum* (Mor.) and *Paederia* (Pae.). In the Isertieae and Hedyotideae, the

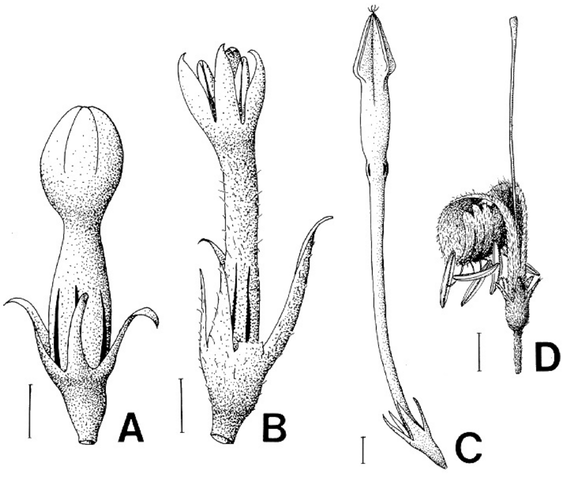


*Figure 28.- **Corolla-splits**:*
A-C: corolla-tube fenestrated between lobes, at base or in middle; D, corolla-tube with a single deep longitudinal split appearing at anthesis.
A, Paederia bojerana;
B, Pentas purpurea;
C, Pseudomussaenda stenocarpa; D, Spathichlamys oblonga.
C after F. Hallé, D after Ridsdale. Lines = 5 mm.

*Table 4.- **Tribes and genera with zygomorphic corollas** (after Jansen 1979, adapted and supplemented). Not included are the genera with corollas appearing strongly zygomorphic because of unilateral splitting of the tube at anthesis (see text).*

+ *: curved corolla-tube or unequal calyx- or corolla-lobes*

\- *: actinomorphic*

* *: zygomorphy accentuated by unequal length of anther-filaments*

The feature concentrates in the three affinity circles indicated as i - iii; the occurrence in Posoqueria *(°) is more isolated.*

			CALYX	COROLLA-TUBE	COROLLA-LOBES
(i)	Cin.-C.	Ferdinandusa*	-	+	+
		Coutarea	+	+	-
		Merumea	+	+	-
		Duidiana	+	+	-
		Macrocnemum*	-	+	-
	Hil.	Ravnia	+	+	-
	Hen.	Henriquezia	+	+	+
		Platycarpum	+	+	+
		Gleasonia spp.	+	+	+
	Ron.	Augusta	-	+	-
		Wittmackanthus	+	+	-
		Cuatrecasasiodendron	-	+	+
	Con.	Kajewskiella	+	+	+
	Ise.	Sabicea spp.	-	+	-
		Acranthera	-	+	-
	Hip.	Hippotis	-	+	-
	Tam.	Tammsia	-	+	-
(°)	Gar.-G.	Posoqueria	-	+	+
(ii)	Ret.	Retiniphyllum	-	+	+
	Van.	Ancylanthos	-	+	-
		Temnocalyx	-	+	-
	Gue.	Dichilanthe	-	+	+
		Ottoschmidtia	-	-	+
	Alb.	Alberta	+	+	-
		Nematostylis	+	+	-
(iii)	Psy.	Chasallia spp.	-	+	-
		Palicourea	-	+	-
		Psychotria spp.	-	+	-
	Mor.	Sarcopygme	-	+	+

filament part opposite the split in the corolla-tube is free (F. Hallé 1961: 281, fig. 7), while in *Paederia* the filament is almost entirely free and inserted at the very base of the corolla, i.e. well below the splits.

Aestivation: The three major types of corolla aestivation, contorted (fig. 29 A, B), imbricate (s.l.; fig 29 C), and valvate (fig. 29 D-F, H-L), occur in the Rubiaceae. Valvate corolla-lobes are the dominant type (fig. 30); they characterize entire large tribes such as the Hedyotideae, Anthospermeae and Spermacoceae. The Gardenieae and rela-ted tribes are characterized in having exclusively contorted corolla-lobes and thus reminiscent of other families of the Gentianales, such as the Apocynaceae. Contorted corolla

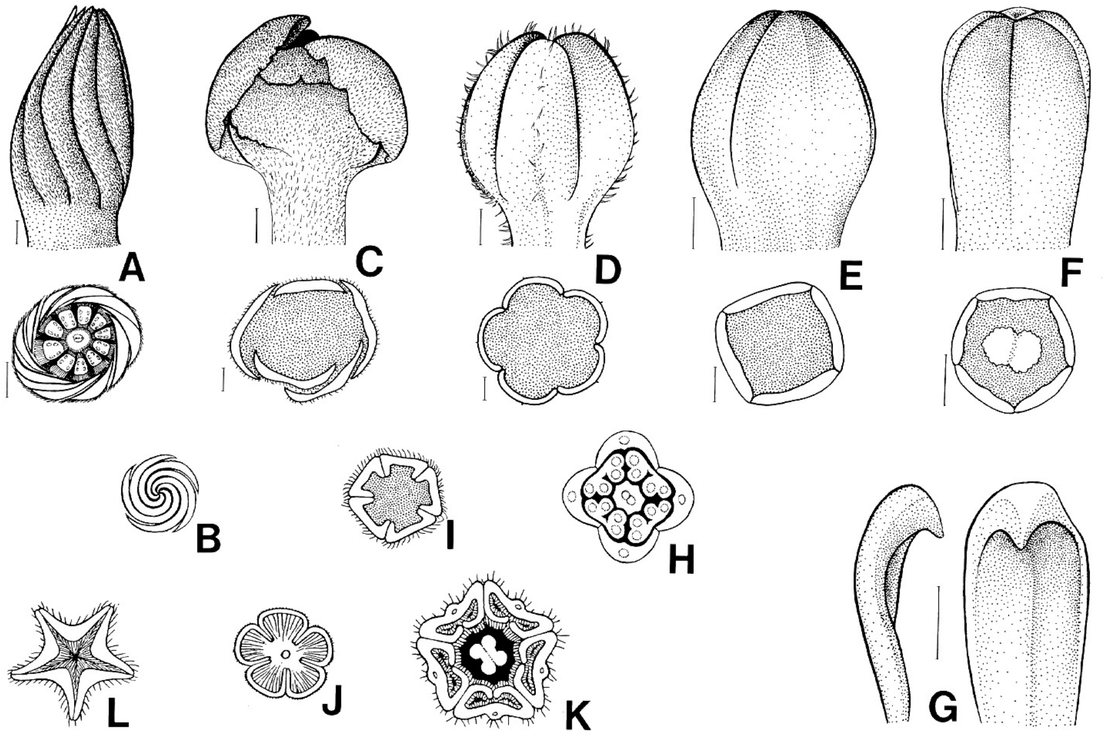


*Figure 29.- **Types of corolla aestivation**: A, B, **contorted** (A,* Tricalysia bifida *and B,* Leptactina arnoldiana*); C, **imbricate** (Rondeletia odorata); D, E, F, H, **valvate-typical** (D,* Pentas lanceolata*, E,* Bouvardia *sp., F,* Psychotria kirkii *and H,* Corynanthe mayumbensis*; G is a lateral and adaxial view of one corolla-lobe from F); I, J, K, **valvate-induplicate** (I,* Temnopteryx sericea*, J,* Otomeria volubilis *and K,* Pseudomussaenda stenocarpa*); L, **valvate-reduplicate** (*Mussaenda nannanii*).*
B, H-L from N. Hallé. Lines = 1 mm.

aestivation also characterizes the Hillieae, Retiniphylleae and Alberteae. The Cinchoneae and associated Naucleeae, Rondeletieae and Isertieae are very variable in regard to the corolla aestivation; the three types of aestivation occur in this group of tribes as well as in the Hamelieae, which are in that respect very similar to them.

In corollas with contorted aestivation, the lobes are almost always left-contorted. Corolla-lobes contorted to the right occur in *Hillia* (Hil.), *Coutarea hexandra, Coptosapelta* (Cin.), *Hyperacanthus, Phellocalyx,* some *Rothmannia* spp. (Gar.-G.), *Gardeniopsis* (? Aul.), *Airosperma* (? Alb.), and *Deppea* and *Omiltemia* (Ham.).

Aestivation thus clearly provides an important set of taxonomic evidence. The interpretation of these characters, however, is still perilous; it is probable that the cases of dextrorse-contorted aestivation quoted above are not homologous. A few in depth studies (which must be done on living or fixated material) indicate that there are numerous aestivation types in the Rubiaceae, each of which may have evolved several times. So Bremer (1987) proposed a complex

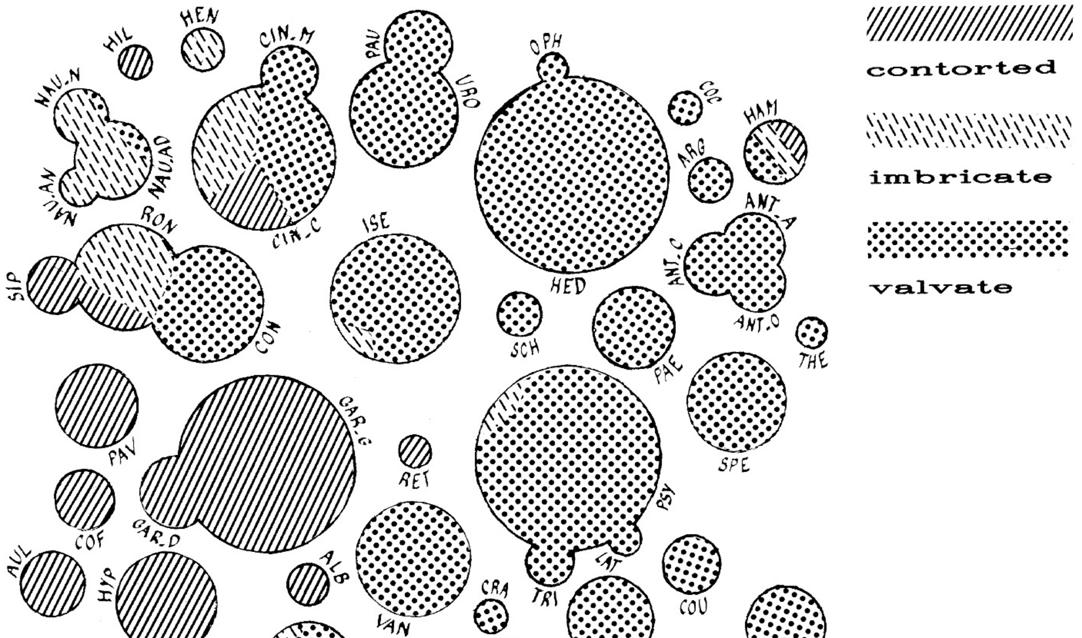


*Figure 30.- **Occurrence of contorted, imbricate or valvate corolla aestivation** in the Rubiaceae tribes. Remarks : contorted mostly to the left, very rarely to the right (see text); Psychotrieae : rarely imbricate [*Naletonia, Psychotria *spp. ("*Notopleura*")]; Isertieae : rarely imbricate (*Heinsia, Yutajea*).*

transformation series for aestivation in the Hamelieae, which is imbricate (s.l.; six different types), contorted to the right or valvate. F. Hallé (1961; see also Petit 1954) documented the aestivation of the Isertieae (and associated taxa since his definition of "Mussaendeae" is wider than the one followed here) with detailed drawings from living material. He distinguished three types of valvate aestivation in this group, viz.

- "typical" (the lobes only in contact by their margins, fig. 29 D-F)
- induplicate (margins folded inwards, outer surface in contact with those of adjacent lobes, fig. 29 I-K), and
- reduplicate (lobes folded inwards, entire inner surface of each lobe in contact with those of adjacent lobes, fig. 29 L).

Moreover he showed that on the valvate lobes of *Mussaenda* spp. the indumentum is disposed in a manner which is reminiscent of the imbricate-quincuncial aestivation of the related *Heinsia*.

A remarkable type of valvate aestivation must certainly exist in those taxa which have the corolla-lobes strongly expanding and fringing at anthesis (see above). No detailed studies have been conducted of these taxa.

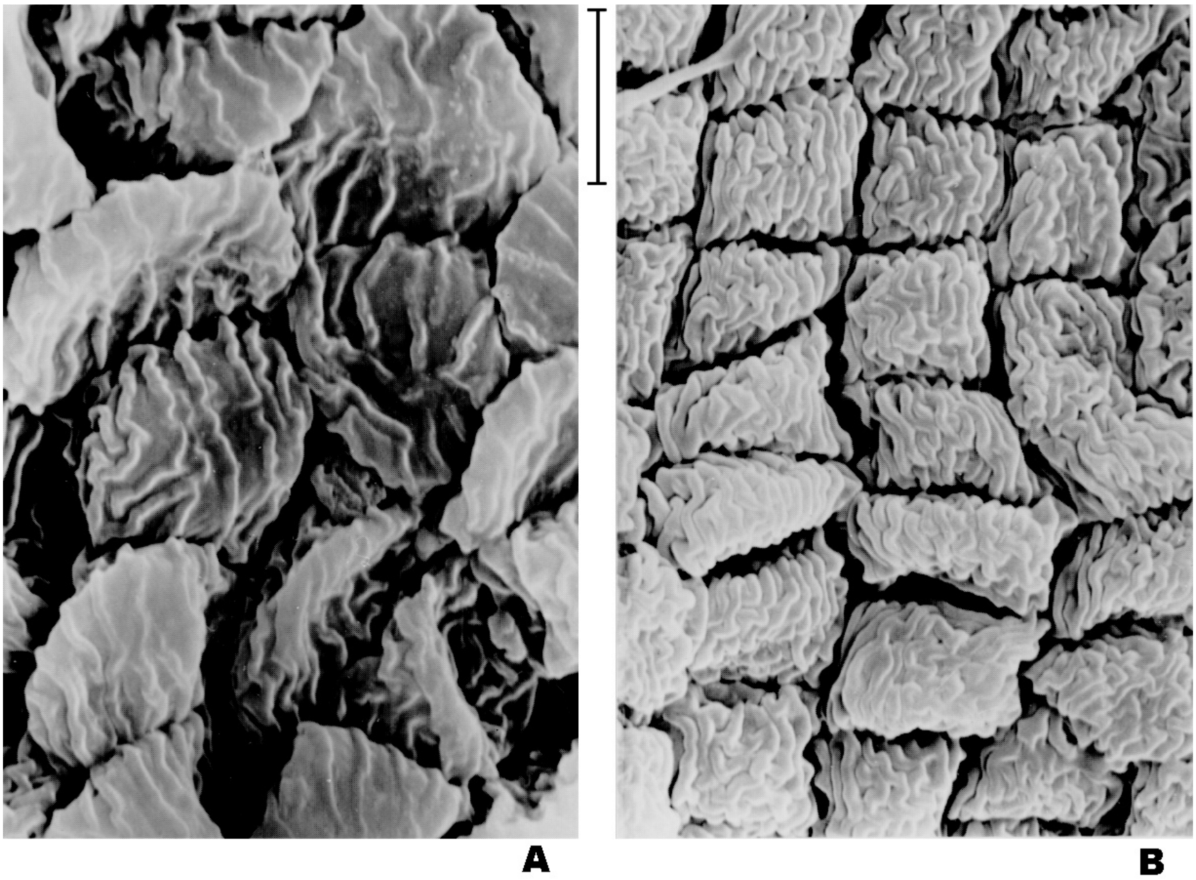
Indumentum: Corollas are frequently hairy outside and/or inside (for the differing anatomy of the outer and inner hairs see 2.6.2).

The disposition of inner hairs, sometimes difficult to observe on herbarium material, plays an important role in pollination biology; for an example of variation within a single tribe, see F. Hallé's (1961) study of the Isertieae.

Microcharacters: The occasional discovery of apparent cuticular patterns on the inside of the corolla-lobes in *Tricalysia* (Gar.-D.; Robbrecht 1987: 51), together with their systematic importance in other families of the Asteridae (BaagÝe 1977), prompted a short series of S.E.M.-observations of corollas throughout the family.

It appears that there is only slight variation. Bulging epidermal cells with striate to rugulate cuticular surface pattern (fig. 31) are predominant, and were observed in species of numerous genera, inter alia *Cinchona* (Cin.), *Simira* (? Ron.), *Feretia* (Hyp.), *Sericanthe* (Gar.-D.), *Psydrax, Vangueria* (Van.) and *Guettarda* (Gue.). Corolla-insides with papillar epidermal cells are also common, e.g. in species of *Fadogia* (Van.), *Mussaenda* (Ise.), and *Psychotria* (Psy.); the papillar cells are smooth or striate, and may be strongly elongated, almost trichomatic. Seemingly the corolla-surface is of no significant systematic importance in the Rubiaceae, except perhaps at lower ranks.

*Figure 31.- **Inside of corolla-lobes** (S.E.-micrographs in surface view, untreated herbarium material): A,* Cuviera nigrescens*; B,* Psydrax parviflora*.*
Lines = 40 µm.



2.8.3 Androecium

Number of stamens: As many other Gentianales, the Rubiaceae have a single, complete whorl of stamens separating from the corolla-tube in between the lobes. Only *Theligonum* (The.) differs from this, having a large number of stamens arranged in bundles (e.g. *T. cynocrambe*: 2-3 corolla-lobes and 6-30 stamens, *T. japonicum*: 3 corolla-lobes and 19-23 stamens; fide Wunderlich 1971). The "dédoublement" of the androecium in *Theligonum* is exceptional for the Asteridae.

Filaments: The stamens are sometimes sessile, but mostly borne on distinct filaments which separate from the tube at the throat (anthers exserted) or sometimes in the tube (anthers exserted or more or less included). The filament rarely separates from the tube near its base, viz. in the Hamelieae, Argostemmateae (Bremer 1987) and Chiococceae (Bremekamp 1966); in other than these three tribes, this feature is very scattered and confined to some genera of the Condamineeae and *Joosia, Alseis* (Cin.-C.), *Paederia* (Pae.), and *Xanthophytum* (Hed.). In *Aitchisonia* (Pae.), the stamens are inserted at different levels in the corolla-tube. In

Macrocnemum, Wittmackanthus (fig. 32 B) (Cin.-C.), *Henriquezia* (Hen.), *Elaeagia* (Ron.), and *Didymochlamys* (inc. sed.), the filaments are unequal. Sometimes, the filaments are fused at the base (monadelphic) e.g. in *Capirona* (Cin.-C.), *Bikkia* (Con.) or in most Chiococceae (combined with filament insertion near base of the corolla-tube !).

Anthers: The anthers are generally introrse and more or less (dorsi)medifixed, very rarely basifixed (e.g. in *Sericanthe*, Gar.-D.); a nearly basal, inframedifixed, attachment of the filament to the anther is rather common in the Gardenieae-Gardeniinae.

The anthers consist of four thecae generally opening by longitudinal splits. The pollen is shed through apical pores in in the woody genera *Rustia, Stomandra* and *Tresanthera* (fig. 32 J) (Con.) and in the the herbaceous, annual genus *Argostemma* (Arg.).

Hairy anthers are scattered throughout the family. In *Steenisia* (Ron.), *Argostemma* (Arg.) and *Strumpfia* (fig. 32 A; inc. sed.), the anthers are adnate into a cone. In *Acranthera* (Ise.) the sterile appendages of the anther-connectives are fused (compare Asclepiadaceae !).

The anther connective is sometimes narrow (fig. 32 C), very often somewhat enlarged abaxially (± triangular in cross-section (fig. 32 D), or more rarely conspicuously enlarged and flat (fig. 32 I). The anthers are sometimes sagittate (fig. 32 G).

Sterile appendages: The connective often extends above the thecae into a short or conspicuous, ribbon-like apical appendage (fig. 32 D, F, G). Rarely the bases of the thecae have sterile appendages. The anthers of *Retiniphyllum* (Ret.; fig. 32 E) have both basal and apical appendages.

Transverse septa (multilocellate anthers): Horizontal division of the pollen sacs is known to occur sporadically or consistently in scattered genera of the angiosperms [for a survey and phylogenetic significance of this character in the angiosperms see Lersten (1971) and Endress & Voser (1975); the Rubiaceae are not included in either study; more and more cases of septate microsporangia are turning up throughout the angiosperms]. In the Rubiaceae, two different types occur, each limited to a narrow group within the family:

(i) In the monotypic genus *Kerianthera* (Con., fig. 32 H) and in seven species of *Isertia* (Ise.) (Kirkbride 1985), the locules are divided into numerous small chambers by bands of sterile tissue running in all directions (in *Kerianthera* about 300 locelli per anther); opened anthers appear reticulate.

(ii) In the Gardenieae and related tribes and in *Airosperma* (? Alb.; Smith & Darwin 1988: fig. 86 B), a limited number of transverse septa divides the locules into horizontal chambers. This feature (ii)

- characterizes two genera [*Anomanthodia*, Gar.-G. (*Tirvengadum* 1982) and *Calycosiphonia*, Gar.-D. (fig. 32 I; Robbrecht 1981)];
- consistently occurs in some species of *Pavetta, Dictyandra, Leptactina* (Pav.), *Sherbournia* (Gar.-G.) and *Airosperma* (? Alb.);
- occasionally occurs in one species (*T. anomalura*) of the large genus *Tricalysia* (ca. 100 spp.; Gar.-D.; Robbrecht 1987).

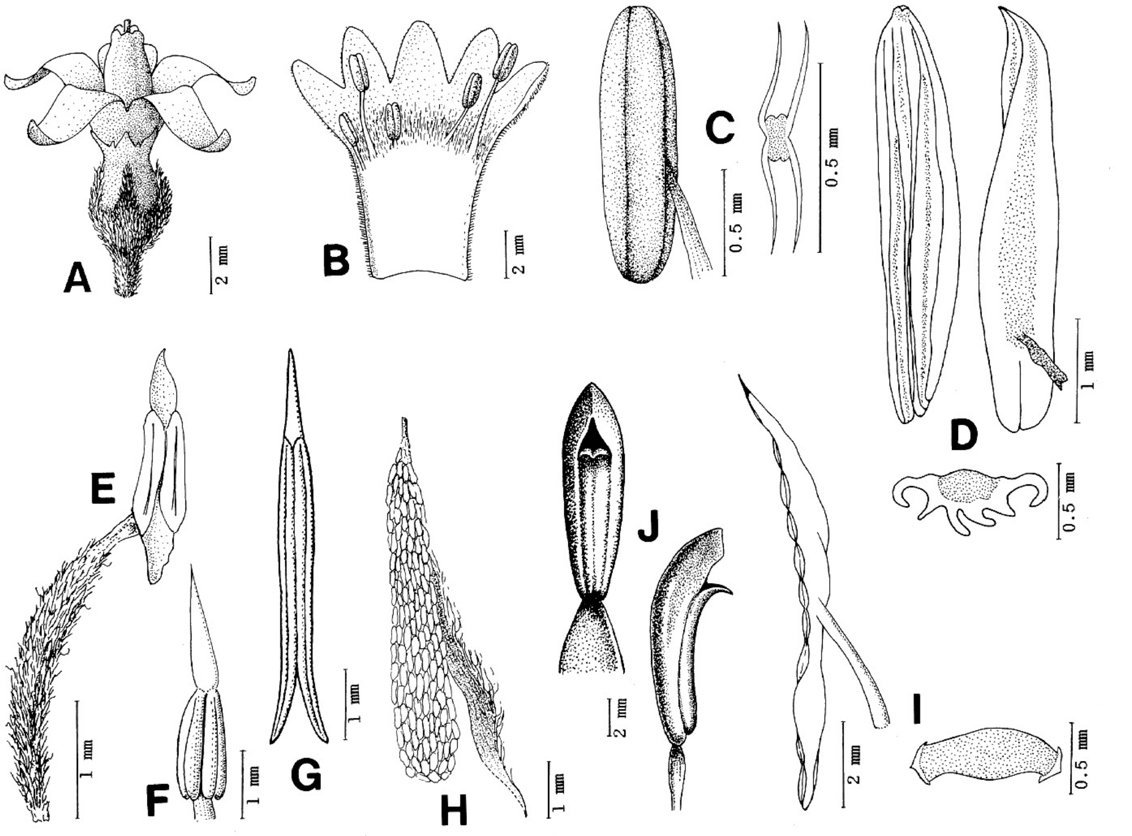


Figure 32.- ***Androecium****: A, flower showing anthers fused into a cone (*Strumpfia maritima, *after Baillon); B, opened corolla showing stamens with unequal filaments (*Wittmackanthus standleyanus, *after Steyermark & Kirkbride); C, lateral view of stamen with cross-section of anther (*Batopedina pulvinellata*); D, ad- and abaxial view of stamen with cross-section of anther (*Tarenna zygoon*); E, stamen with hairy filament and anther with apical and basal sterile appendages (*Retiniphyllum maguirei*); F, stamen with anther with apical sterile appendage (*Tricalysia aequatoria*); G, sessile, sagittate anther with apical sterile appendage (*Bertiera laxa, *from N. Hallé); H, I, stamens with septate anthers (H,* Kerianthera praeclara, *after Kirkbride, and I,* Calycosiphonia spathicalyx*); J, stamens with anthers opening through apical pores (*Tresanthera condamineoides, *after Schumann).*

2.8.4 Gynoecium

Ovary position: The inferior position of the ovary is one of the most reliable features to define the Rubiaceae and to recognize them as a family, but its importance should not be overrated (Bremekamp 1966: 6), since there are a few exceptions. Superior or semi-superior ovaries occur in several genera, of which *Gaertnera* and *Pagamea* (Psy., fig. 33 C) are most commonly cited; because of their ovary position, these genera were, in the past, very frequently associated with the Loganiaceae. However, the similarity of *Gaertnera* and *Pagamea* in all other features to the Psychotrieae is convincing, and since Schumann (1891) there has been general agreement on the inclusion of these genera in the Rubiaceae. Semi-superior or quasi-superior ovaries occur also in another member of the Psychotrieae, viz. *Coryphothamnus* (Steyermark 1974: 1018, fig. 158). Outside the Psychotrieae, semi-superior or quasi-superior ovaries characterize the following taxa:

Con.: *Tresanthera (Utzschneider 1947)*
Pav.: *Canthiopsis (Bridson & Robbrecht 1985)*
? Chi.: *Mastixiodendron (Darwin 1977)*
Hed.: *Synaptantha, Lucya, Leptomischus, Pleiocraterium, Arcytophyllum, Oldenlandia* spp. *(Utzschneider 1947); Astiella* spp., *Mitrasacmopsis (Jovet 1941)*

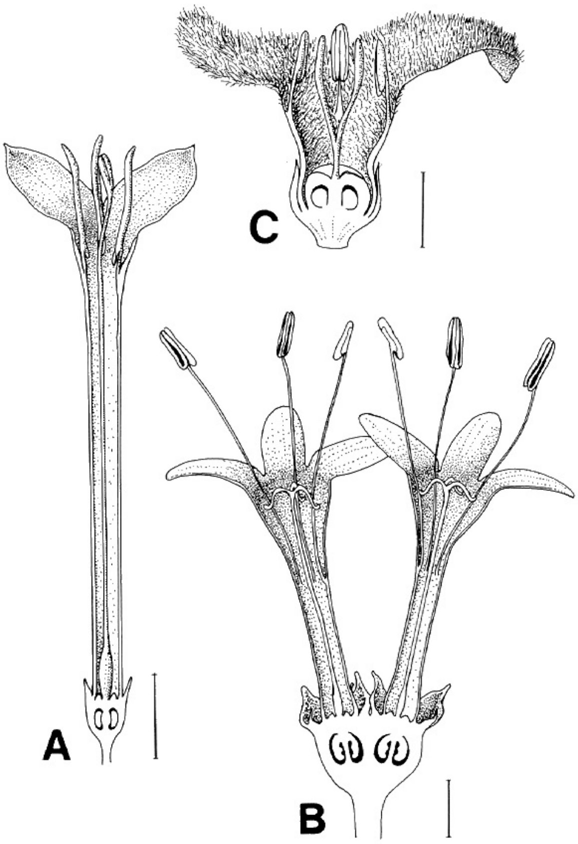


*Figure 33.- **Longitudinal section of flowers**: A,* Pavetta indica*, style with swollen base; B,* Mitchella repens*, flower pair with fused ovaries; C,* Pagamea guianensis*, superior ovary.*
After Baillon. Lines = 2 mm.

In these genera, the position of the ovary is relatively variable, in *Mastixiodendron* e.g. from nearly 3/4 superior to wholly inferior, or depends on the age of the flower, in *Astiella* e.g. fully inferior in bud but becoming semi-superior when older. As in the Psychotrieae, several of these genera have been involved in problems of familial position (*Mitrasacmopsis* e.g. originally assigned to the Loganiaceae).

Hayden (1968: 45) stated that "many species and genera of the Spermacoceae possess partly superior carpels". However, she alone presented that interpretation of their ovaries, which is probably based on the often strong development of the disk in the fruiting stage.

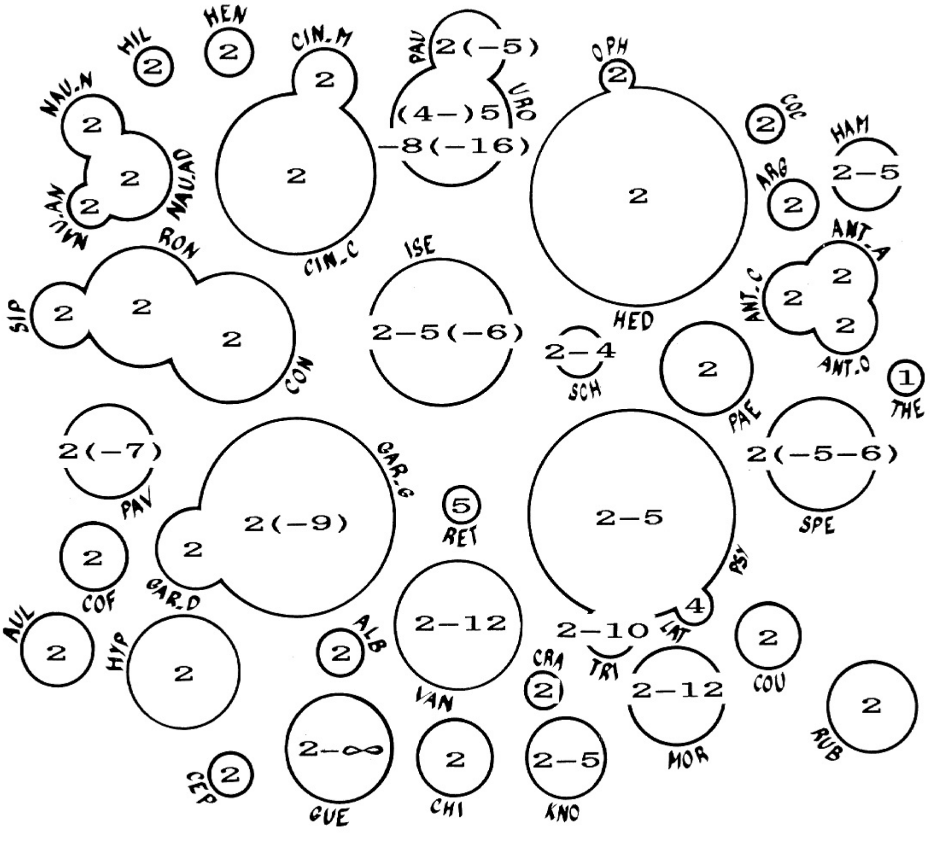


*Figure 34.- **Number of carpels** in the Rubiaceae tribes. Reductions in the fruiting stage are not represented.*

Number of carpels (fig. 34): The bicarpellate ovary by far predominates in the Rubiaceae; it characterizes a large number of tribes, such as the Naucleeae, Cinchoneae, Hypobathreae, Chiococceae, Hedyotideae, Anthospermeae
and Rubieae. A number of tribes are characterized by a tendency to have pluricarpellate ovaries consisting of more than two, frequently five, carpels; an even larger number of carpels occurs in genera of the Gardenieae, Vanguerieae, Guettardeae, Triainolepideae and Morindeae (only the large genus *Lasianthus*). Finally, the bicarpellate state is entirely absent from three tribes. In the monogeneric Lathraeocarpeae

and Retiniphylleae, the ovaries are always 4- or 5-locular, respectively. In the Urophylleae, they are (4-)5-8(-16)-locular; in some species of *Praravinia* (Uro.), the number of carpels may be double the number of other flower parts (Bremekamp 1940: 175). Up to sixteen carpels may be present, false septa apparently being absent, since there are an equal number of stigmata and each dissepiment bears a placenta on both sides. A similar increase in the number of carpels seems to occur in the Vanguerieae and Guettardeae. In *Timonius* (Gue.) e.g., the number of ovary-cells exceeds twenty; in this case it is difficult to assess whether the (uniovulate) locules correspond to carpels.

In bicarpellate ovaries, a tendency towards reduction of one carpel frequently repeats itself throughout the family. This sometimes occurs as early as in the flowering stage (unilocular ovaries with a trace of the second carpel, e.g. *Otiophora lebruniana*, Hed., Robbrecht & Puff 1981, *Calanda*, Kno., Puff & Robbrecht in press); only in *Theligonum*, The., the flowers have a unilocular ovary without a trace of a second locule. But even more frequently the same feature is expressed in the fruiting stage, development of unilocular fruits from bilocular ovaries being fairly common. In certain taxa, both uni- and bilocular fruits develop (e.g. in the Vanguerieae), but in other ones (e.g. *Nichallea, Rutidea*, Pav., *Craterispermum*, Cra., fig. 56) the fruits obligately have only one developed locule. Comparable to the reduction of one carpel in bilocular ovaries, one or more carpels of plurilocular ovaries may be reduced pre- or postflorally; the latter is e.g. common in 5-locular Vanguerieae.

Syncarpy: Many Naucleeae are characterized by the fusion of the numerous ovaries of much-congested globose inflorescences into syncarps (fig. 40 I). A smaller number of connate ovaries occurs in the genera of the Anthospermeae-Operculariinae (two-three ovaries fused) and in *Morinda* and *Rennellia* (Mor.; c. five-ten, fig. 40 H), *Mitchella* (inc. sed.; two ovaries fused, fig. 33 B) and *Calanda* (Kno.; two). In the latter two genera, ovary fusion is correlated with pairing of flowers in the inflorescences (see 2.7). In various cases cited here, not only the ovaries but also the calyces take part in the fusion. In the Morindeae, ovary fusion is characteristic of the two genera cited above, but also occurs occasionally in several other genera, such as *Caelospermum* and *Prismatomeris* (Johansson 1987a).

Septa: False septa, complete or incomplete, are sometimes present, e.g. in many Pauridiantheae and Morindeae and in a few Gardenieae (Bremekamp 1940, Utzschneider 1947). In *Faramea* (Cou.) the opposite occurs with the dissepiment between the two locules disappearing very early; its ovaries are unilocular because of septum reduction.

Style: Generally there is one style, which is much longer than the stigmatic lobes which are equal in number to the carpels. Rarely, the styles are free to base (e.g. *Coprosma*, Ant.-C.). Frequently the lobes are exserted, but in various taxa the stigmatic lobes are at the level of the throat (e.g. many Gardenieae); deeply included stigmata, below the level of the anthers, are rare (e.g. *Cladoceras*, Pav.). In heterostylous taxa, however, included stigmatic lobes are of course common in one of the floral morphs (see 2.13.3.2). The style is mostly linear, glabrous or variously hairy. Local swellings occur, frequently towards the top (associated with swollen stigmas, see below), rarely at the base (fig. 33 A).

Mostly, the stigmatic lobes are free and equal in number to the ovary-cells; rather frequently the lobes are fused (more or less, with the original number of lobes commonly distinguishable) into massive clubshaped or knobshaped stigmas. This fusion, accompanied by enlargment of the receptive surface by folds, ridges, hairs etc., plays an important role in the pollen reception function of the style in many Rubiaceae (see 2.13.3.2: "stylar pollen presentation").

Disk (fig. 35): A fleshy disk sits on top of the ovary, surrounding the base of the style, and is almost universally present. Wind-pollinated taxa (see 2.13.3.1) lack a floral disk, and, according to Hayden (1968: 17), it is also missing from

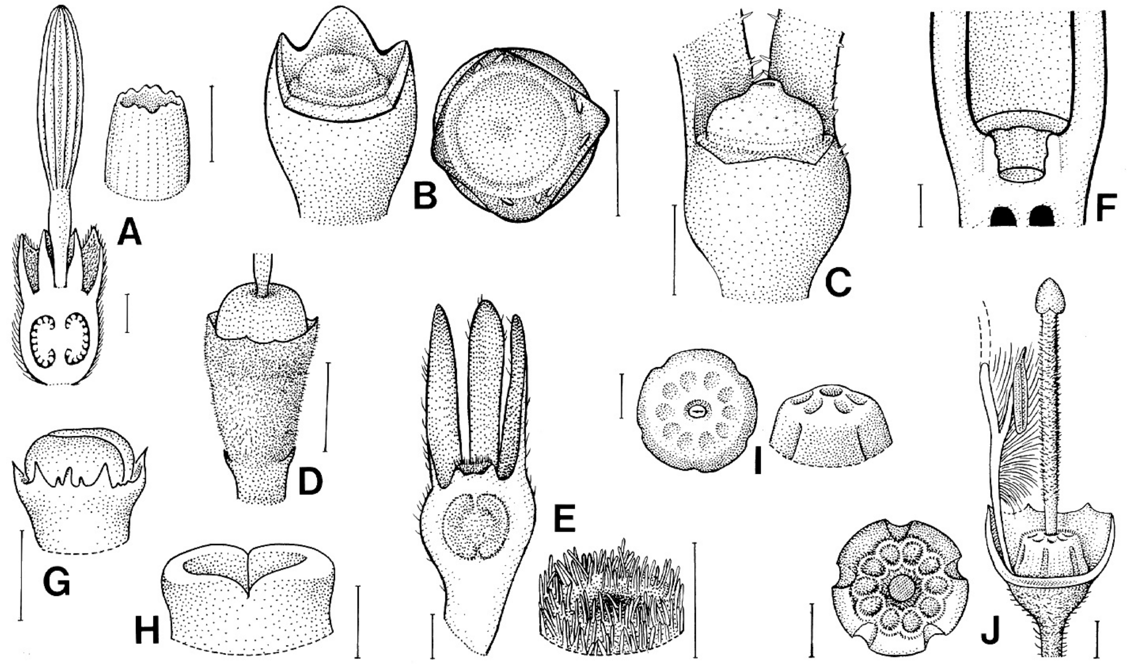


*Figure 35.- **Epigynous disks**, various views, either prepared and seen from above and/or laterally, or in dissected or sectioned flower parts: A-E: cylindrical to annular disks; F, cylindrical disk fused with the receptacle; G, H, bilobed disks; I, J, lobed disks; E, J, hairy disks.*

A, Bertiera bracteolata; B, Ixora stricta*; C,* Bouvardia *sp.; D,* Psychotria kirkii*; E,* Rondeletia odorata*; F,* Gardenia imperialis*; G,* Psychotria blakei*; H,* Psychotria hemicephaelis*; I,* Pauridiantha mayumbensis*; J,* Pauridiantha callicarpiodes.

A, I and J from N. Hallé. Lines = 1 mm (to A, I and J approximative).

the Rubieae and some Spermacoceae; her statement is probably incorrect, since the Rubieae seem characterized by the presence of a two-lobed more or less massive disk (*Galium*: Puff 1978: 216, fig. 8).

The disk produces nectar through pores (verified by me in only a few genera, e.g. *Tricalysia*, Gar.-D., Robbrecht 1987a: fig. 8 E). The disk is frequently more or less cylindrical, annular or conical (fig. 35 A-D), but may show morphological peculiarities. In the Gardenieae-Gardeniinae, the disk is frequently deeply sunken in and fused with the base of the calyx-tube (fig. 35 F). In other taxa, the disk is lobed, e.g. in many Rubieae and Psychotrieae (2-lobed, fig. 35 G, H, sometimes each lobe with a crescent-shaped pit, Petit 1964: fig. 3D), Isertieae, Urophylleae or Pauridiantheae (5-lobed, fig. 35 I-J). In the Urophylleae, Bremekamp (1940) explained lobation of the disk as resulting from impression by the decurrent anther filaments (at its periphery) and the basal part of the anthers (at its top). In these genera, consequently there are morphological differences between disks in male and female flowers, the latter lacking the conspicuous impressions.

In general, disks are glabrous, but they may be covered with papillae or hairs (fig. 35 E), e.g. in certain Isertieae, Rondeletieae, Urophylleae or Hedyotideae.

Placentation: Axile placentation (fig. 36) is characteristic of the entire Rubiaceae, except in many genera of the Gardenieae-Gardeniinae, a few Hypobathreae, and *Tammsia* (Tam.) with parietal placentas and transitions between axile and parietal placentation (for a further discussion and examples see Robbrecht & Puff 1986). Fukuoka's (1978) statement that the placentation in *Morinda* (Mor.) is parietal (each carpel with two pendulous ovules) is not supported by evidence and certainly erroneous.

The insertion of axile placentas is variable; they may be attached to the entire septum (fig. 36 A) or only to a small part of it (peltate placentas attached to top, middle or base of septum, fig. 36 D). The placentas themselves are generally more or less hemi-ellipsoidal; in many Pauridiantheae they are divided in two in their upper part (and then have an insertion area on the septum which is forked or even separated, fig. 36 H).

The Hedyotideae and associated tribes are a good example of the extreme variability of the axile multiovulate placentas. The following progression series may tentatively be proposed for them:
(i) placenta adnate over part of its length to the septum, ± fleshy and peltate, bearing up to a hundred ovules or more (fig. 36 A); this kind of placenta is also characteristic of the Cinchoneae, Isertieae (fig. 36 I) and associated tribes;
(ii) a similar peltate placenta with numerous ovules, the area ofattachment to the septum becoming constricted in the centre of the ovary-cell (fig. 36 B, C);

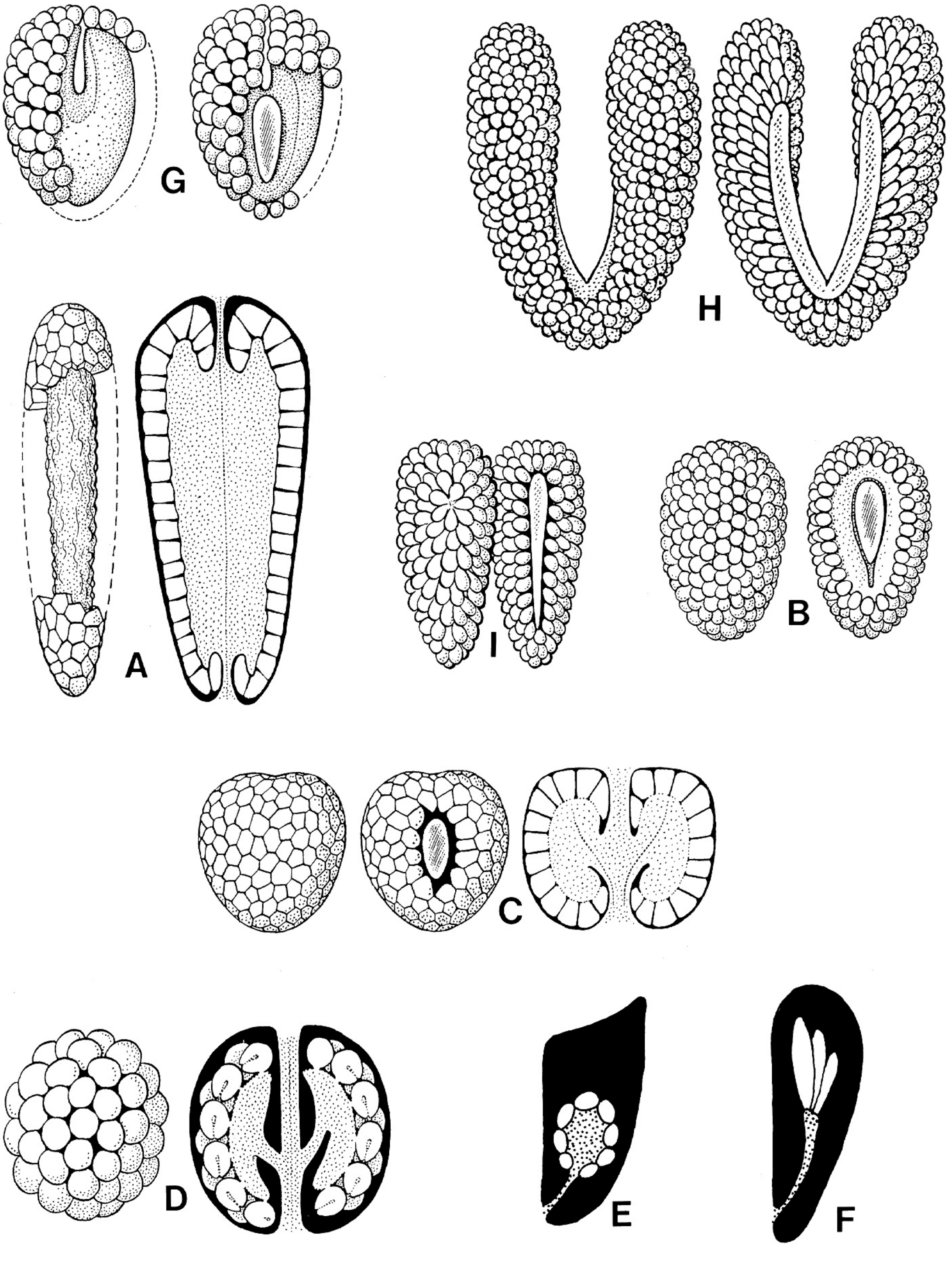


Figure 36.- ***Axile multiovulate placentas*** *of the Hedyotideae (A-G) compared to Pauridiantheae (H) and Isertieae (I). Placentas removed from dissepiment and drawn in ad- and abaxial view, some (A, G) with ovules partly removed to show placenta structure, some depicted in longitudinal section.*
A, Otomeria elatior*; B,* O. volubilis*; C,* Sacosperma paniculata*; D,* Virectaria multiflora*; E,* Pseudonesohedyotis bremekampii*; F,* Carphalea glaucescens*; G,* Pentodon pentandrus*; H,* Stelechantha cauliflora.
All from N. Hallé, except E, F, after Verdcourt.

(iii) further constriction of the attachment into a distinct stalk which is first ± horizontal and attached to the middle of the septum (fig. 36 D), and then tends to be
(iv) inserted at the base of the locule; the number of ovules is often reduced to less then ten, and the placenta itself becomes much smaller and ± spherical or elongated (fig. 36 E, F).

Hedyotideae placentas of type (i) or (ii) may be bilobed or branched (fig. 36 G) and are then reminiscent of those of the Pauridiantheae.

From the theoretical viewpoint, this series is important, because it offers a transition from a typical phyllosporous placentation (i, ii) to a type which can be characterized as stachyosporous (iii, iv).

Ovules: The number of ovules on each placenta varies from one to numerous, and has traditionally been used for as the main character for subdivision of the family (see 3.1). Many tribes indeed are strictly characterized by the occurrence of only one ovule on the placenta; the feature holds perfectly for large tribes such as the Vanguerieae, Guettardeae, Knoxieae, Psychotrieae, and Spermacoceae, while other large entities, e.g. the Naucleeae, Cinchoneae and Isertieae, are uniformly pluriovulate (see fig. 37 for further examples). Elsewhere in the Asteridae the distinction, one versus many ovules, is even useful to distinguish families, e.g. the Scrophulariaceae against the Lamiaceae, but in the Rubia-ceae, it does not entirely hold. The situation in the large African genus *Tricalysia* (Gar.-D.) e.g. is additional to historical evidence against the absolute value of the number of ovules. *Tricalysia* was often described as 2-many-ovulate, but my revision (Robbrecht 1979, 1987a) clearly documents that several species are 1-2-ovulate and that a small number is even consistently uniovulate. Similar variation patterns occur in three areas of affinity within the family, namely in the Gardenieae and related tribes, the Hedyotideae, and the Psychotrieae and related tribes (fig. 37).

The actual number of ovules in the pluriovulate genera remains on the whole rather imperfectly documented. While "many ovules" generally means ten to some hundreds ovules per placenta, the number may even reach one thousand, as e.g. documented for *Lindenia* (Ron.; Darwin 1976c).

The ovules are unitegmic and anatropous. Their orientation is frequently variable and space-dependent in the many-ovulated taxa. When the ovule number is reduced, the micropyle is either inferior (ovules erect) or superior (ovules pendulous; fig. 37: tribes indicated with heavy black outline). In the Hypobathreae, the (fairly large number of) ovules are imbricately descendent. In the few- or two-ovulated Naucleeae-Adininae and Retiniphylleae and in the uni-ovulated Guettardeae, Chiococceae and associated tribes the ovules are pendulous, and the micropyle is inside (fig. 38 B). Most uni-ovulated tribes, however, have erected ovules and micropyle outside (fig. 38 A).

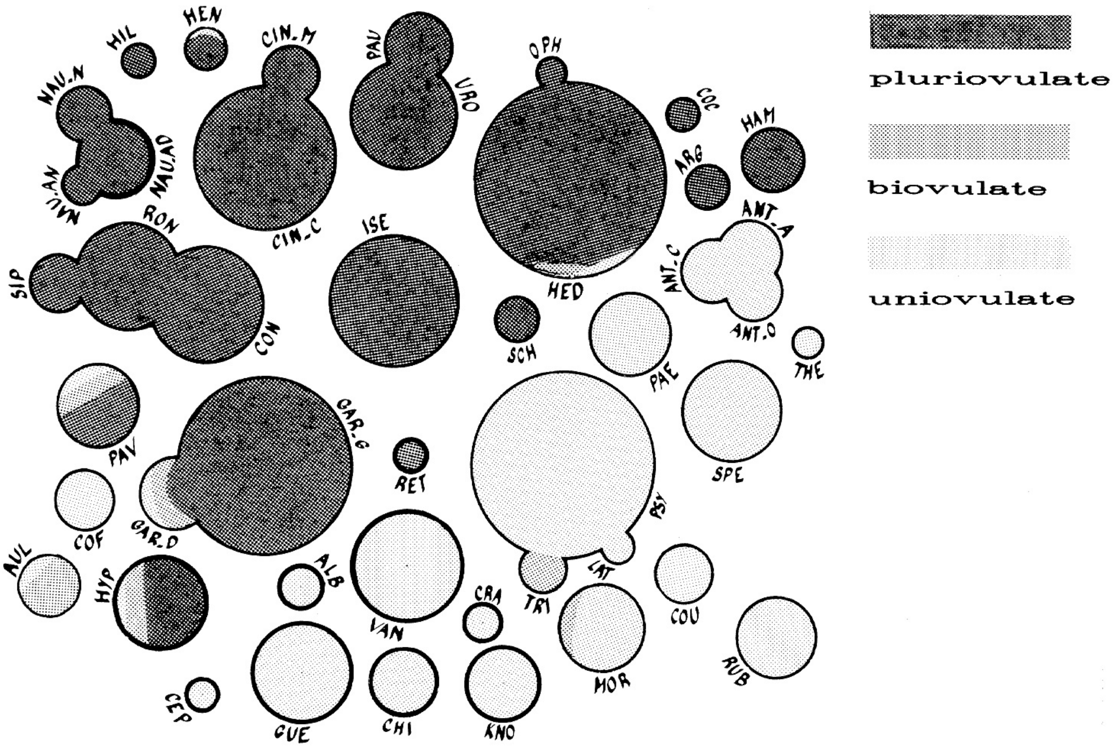


Figure 37. - ***Occurrence of placentas with respectively one, two (mostly collateral) or many ovules*** *in the Rubiaceae tribes. Remarks : Hedyotideae : rarely 1-ovulate placentas (*Otiophora*); Trianiolepideae : two or three collateral ovules. Occasional variants (e.g. two instead of one ovule in* Coffea*, Cof., or* Declieuxia*, Psy.) are not represented. In most tribes ovules erect (inferior micropyle), attached to base or middle of septum or variable in micropyle-orientation (many ovules: often space-dependent); micropyle superior and ovules pendulous (if one or few ovules: ± from top of septum) in tribes indicated with heavy black outline.*

In certain groups, the ovules are deeply to almost completely embedded in the placental tissue. The placenta is then easily mistaken for an ovule. Since major emphasis was given to the number of ovules in the past, this mistake repeatedly resulted in genera being described twice, once in the uniovulate Coffeoideae and once in the pluriovulate Cinchonoideae. So *Belonophora* (? Aul.) was incorrectly described as uniovulate, and its later synonym *Diplosporopsis* correctly as having a placenta with two deeply embedded ovules. The same applies to *Aulacocalyx* (Aul.) and its synonym *Dorothea* (Petit 1962). Inversely, *Scepseothamnus* is a uniovulate redescription of *Alibertia* (Gar.-G.).

Figure 38.- ***Uniovulate placentas*** *(longitudinal section) with A, erect and B, pendulous ovule.*

A, Paederia *sp. (arrow points to micropyle; r: idioblasts with raphides); B,* Rytigynia kigesiensis *(s: "strophiole"; many large idioblasts with brown substances (? tannins) in ovary tissue; also brown substances in ovule integument).*

L.-micrographs by A. Igersheim. Line = 500 µm.

2.9 Fruits

"Die Früchte der Rubiaceae sind ausserordentlich mannigfaltig und können zur Einteilung der ganzen Familie mit grossem Vorteile benützt werden; ..." (Schumann 1891: 8).

Size: Very large fruits, exceeding 5 cm in their largest diameter, are rare and apparently confined to the Gardenieae-Gardeniinae where the largest fruits are found in genera such as *Rothmannia* (*R. macrocarpa*, ellipsoid fruits up to 18 x 6 cm), *Atractogyne* (*A. gabonii*, cylindrical fruits up to 15 x 1.8 cm) and *Kutchubaea* (*K. sericantha*, ellipsoid fruits up to 11 x 7 cm). Although the Gardeniinae in general are characterized by large fruits, several genera, e.g. *Aidia* and *Amaioua*, have small fruits. This trend exists in both paleotropical and neotropical representatives of the subtribe as shown by a comparison (fig. 39) of fruit size variation of the Gardeniinae in Venezuela and Gabon; also in African representatives, the fruits tend to be slightly larger. On the whole, very large fruits are rare, even within the Gardeniinae; if one considers the sizes at species level, only a limited number of taxa has fruits exceeding 5 cm.

Fruits about one cm in diameter are by far predominant and characterize the huge genus *Psychotria* (Psy.) and other large genera such as *Pavetta, Tarenna* (Pav.) and *Tricalysia* (Gar.-D.).

Very small fruits, a few mm in diameter, are relatively rare and generally confined to herbaceous tribes, e.g. Hedyotideae, Spermacoceae and Rubieae.

Shape: Fruit shapes are mostly very simple, i.e. spherical, ellipsoidal, ovoidal or obovoidal; these shapes are frequently ± lobed, the lobation corresponding with the fruit-locules. The fruit wall is mostly smooth; ribbed or warty fruits are rather exceptional. In the Guettardeae, Chiococceae and other associated tribes, fruits (and seeds) tend to be elongated (fig. 53-55).

Colour: Red fruits (e.g. *Coffea*, Cof., *Psychotria, Psy.*) are fairly dominant; yellow (e.g. Oxyanthus, Gar.-G.), orange (e.g. *Sericanthe*, Gar.-D.) or blackish fruits (e.g. *Pavetta*) are equally common. In *Tricalysia* subg. *Empogona*, the fruits are first white but later turn blackish. Blue fruits are rather exceptional save in the Psychotrieae and associated tribes; they characterize genera such as *Cephaelis* (Psy.), *Trichostachys*, *Lasianthus* (Mor.) and *Coccocypselum* (Coc.). Sometimes, also the fruit-pedicel becomes fleshy and coloured, e.g. in *Chasallia*; the fruit may then contrast in colour to the pedicel (red/black or blue/white). Frequently the calyx, when it persistent, is green and also in contrast with the colour of the fruit.

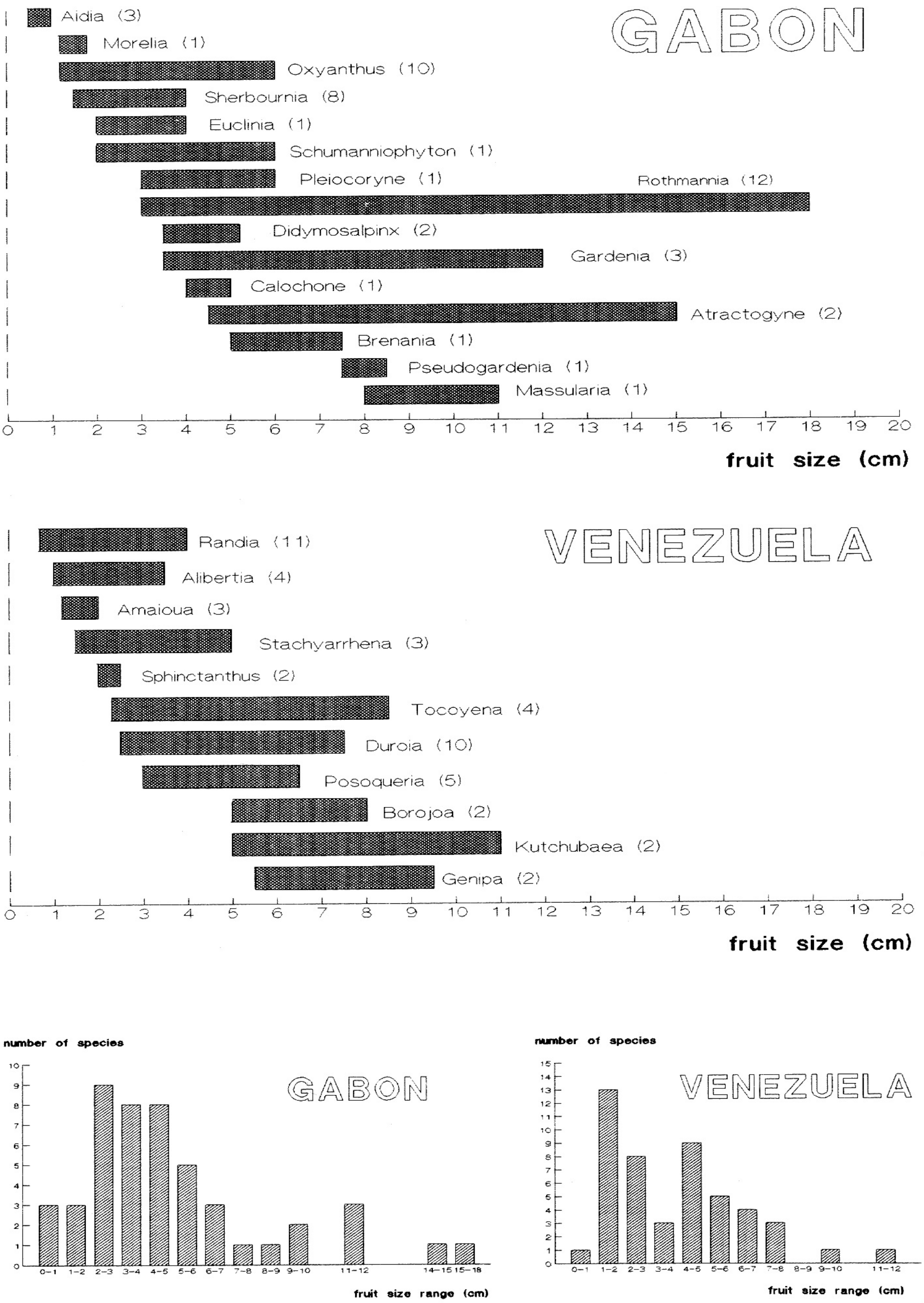


*Figure 39.- **Fruit size in the Gardenieae-Gardeniinae**: comparison of variation in a paleotropical (Gabon) and neotropical country (Venezuela), based on measurements given in resp. Flore du Gabon (N. Hallé 1970) and Flora de Venezuela (Steyermark 1974).*
Above: horizontal bars representing variation in the genera (between brackets: number of species concerned).
Beneath: variation in the species of all genera.

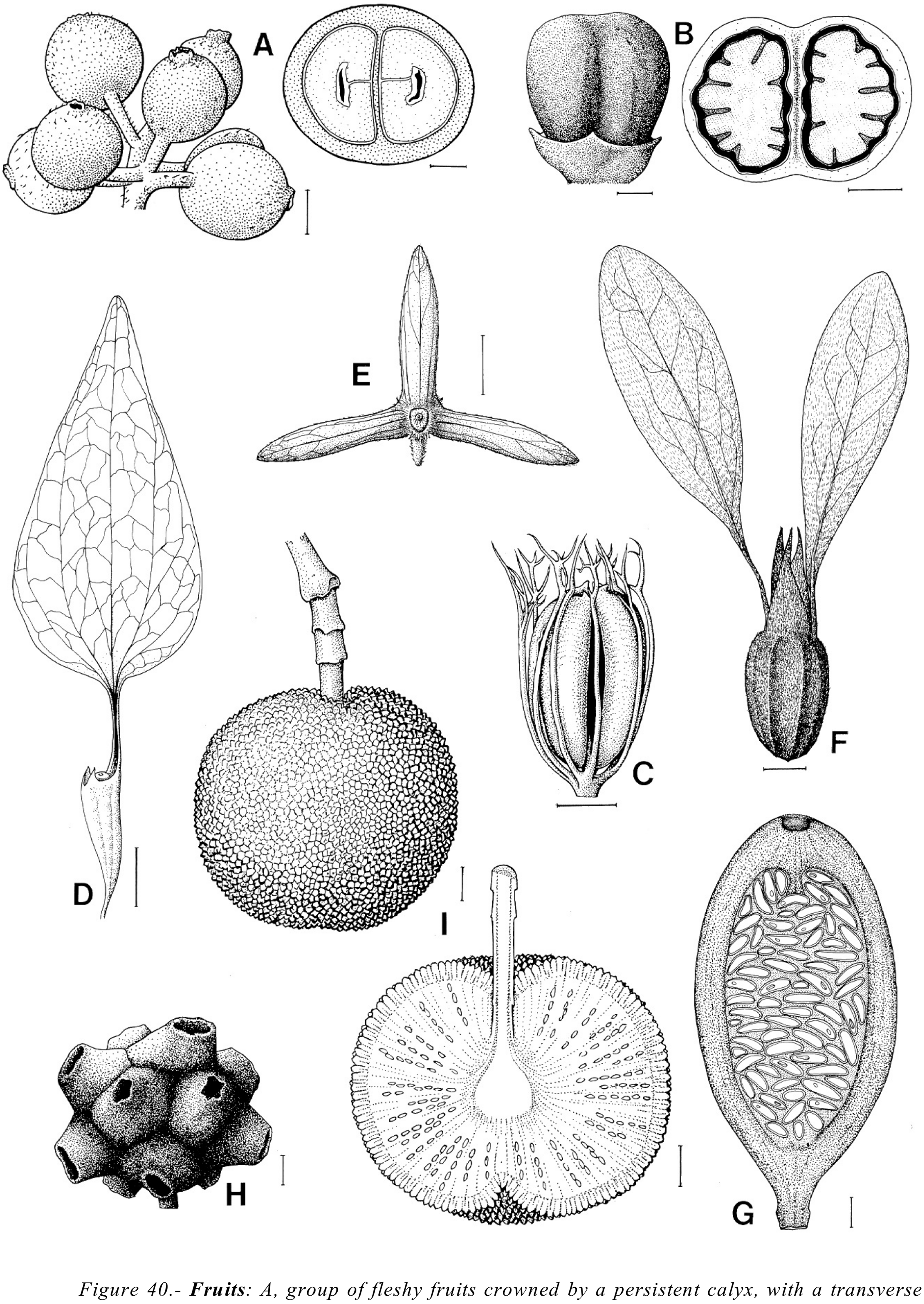


*Figure 40.- **Fruits**: A, group of fleshy fruits crowned by a persistent calyx, with a transverse section; B, fleshy fruit with inferior calyx, with a transverse section; C, aged dry fruit, the two endocarp cells held together by mesocarp ribs; D-F, dry fruits with pterophylls; G, transverse section of large unilocular fruit with numerous seeds in placental pulp; H, I, syncarps.*
A, Psychotria kirkii*; B,* Pagamea guianensis*; C,* Otomeria volubilis, *from N. Hallé; D,* Cosmocalyx spectabilis*; E,* Jackiopsis ornata*; F,* Alberta magna*; G,* Gardenia thunbergia, *after Baillon; H,* Morinda longiflora, *after Schumann; I,* Sarcocephalus pobeguinii, *from N. Hallé. Horizontal lines = 2 mm, vertical lines = 5 mm.*

Type: Fruits are fleshy (fig. 40 A, B, 52, 56, 57 A, G) or dry (fig. 40 C-E, 58 A, 60 A, H), and in a number of genera difficult to characterize in this respect; in *Alberta* (Alb.) e.g., the well developed endocarp is surrounded by a thin fleshy layer (fig. 40 F). Verdcourt (1958: 228) questioned the importance of the nature of the fruit which was central to defining tribes in the older classifications. He cited *Pentanisia* (Kno.) as an example of a natural group in which dry indehiscent fruits, dry fruits dehiscent into mericarps and fleshy drupaceous fruits occur. Nevertheless, most tribes are characterized by rather distinct trends as regards the nature of their fruits. The Vanguerieae, Pavetteae, Psychotrieae and other tribes are characterized by fleshy fruits, the Cinchoneae, Rondeletieae, Hedyotideae and other by dry ones.

Dry fruits are mostly dehiscent [septicidal, loculicidal or a combination of both; mostly opening from above (fig. 58 A, 60 H), rarely from below (fig. 60 A), or transversely] or separate into dehiscent or indehiscent mericarps. *Virectaria* (Hed.) is unique in that one mericarp is detached from the capsule while the other locule remains on the pedicel.

Carpophores are sometimes present between the mericarps; for a survey and further discussions see Puff & Robbrecht in press; they distinguish two types of carpophores in the Rubiaceae,

- "true" carpophores, mericarp holders bearing pendulous cocci, developed from vascular strands in the septum (only in *Knoxia*, Kno. and *Machaonia*, Gue.), and
- "false" carpophores, structures to support carpels, recorded from many genera in the Knoxieae, Anthospermeae, Paederieae and Psychotrieae.

In dry fruits, the vascular tissue of the ovary-walls may remain as ribs after the rest of the mesocarp is macerated away; they form a characteristic basket-like network holding the opened endocarps together (e.g. in several Hedyotideae, fig. 40 C; ? functional in seed-dispersal, cfr. 2.13.4). The large, more or less dry and indehiscent fruits of many Gardenieae-Gardeniinae (fig. 40 G), with a leathery or ± woody wall, are of a peculiar type since they are fleshy inside (cfr. 2.10.2, a pulpy outgrowth of the placenta in which the seeds are embedded).

Fleshy fruits may have a very thin, papyraceous or membranous endocarp, hence are berry-like, e.g. in *Sabicea*, Ise., or *Bertiera*, inc. sed. More commonly, they are drupaceous, sometimes with a plurilocular stone (e.g. Triainolepideae, many Guettardeae, fig. 49), mostly with individual pyrenes (fig. 52-56), e.g. in all the Vanguerieae and in many Psychotrieae and Morindeae.

Syncarps (fig. 40 H, I) occur in a number of groups and originate from prefloral fusion of ovaries (see 2.8.4).

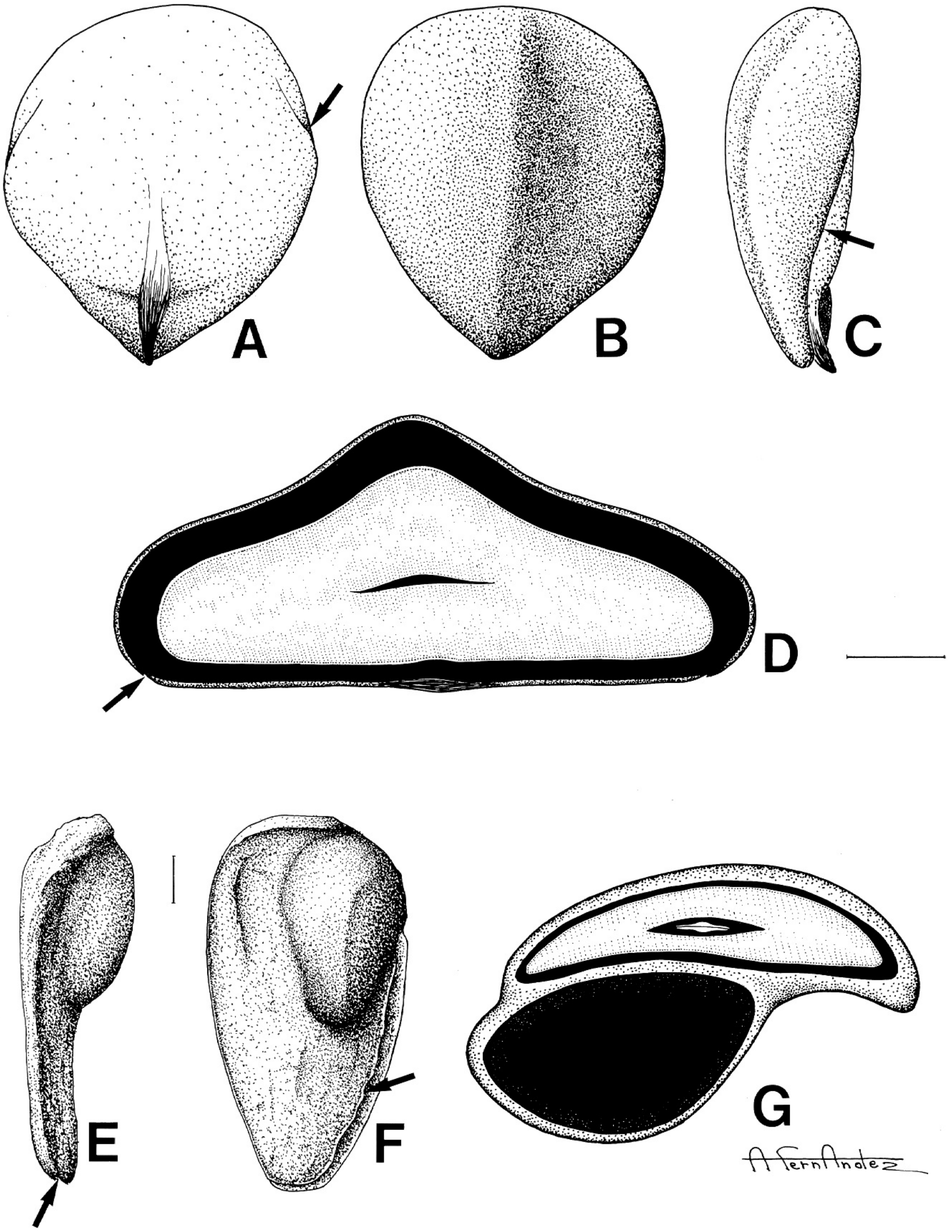


Figure 41.- ***Pyrenes with basal marginal preformed slits*** *(indicated by arrows). A, F, adaxial, B, abaxial and C, E, lateral views; D, G, cross-sections [from ouside to inside: endocarp, air-space (black), endosperm, embryonal cavity]. The large air-chamber in F, G is discussed in 2.13.4, long distance dispersal.*
A-D, Chazaliella oddonii*; E-G,* Morinda citrifolia.
Lines = 1 mm.

Pyrenes: Petit (1964a: fig. 3) was the first to draw attention to the wide variation of germination mechanisms in rubiaceous pyrenes. This is of course observed normally when studying germinating stones, but a slight pressure exercised upon a pyrene, notably in the region of the embryo radicle, easily reveals preformed germination slits (fig. 41, 52, 55); Petit (op. cit.) emphasized that, in the Psychotrieae at least, the presence or absence of such slits and their number and position have a high diagnostic value at the generic level. While African *Psychotria* spp. are characterized by relatively thin pyrenes without preformed germination slits, the allies of the genus have thicker pyrenes with distinct preformed slits (Peripeplus: 4 abaxial; *Gaertnera*: 2 marginal + 1 adaxial; *Chasallia*: 1 adaxial; *Chazaliella*: 2 marginal + sometimes 1 adaxial; *Geophila* and *Hymenocoleus*: 2 short submarginal slits).

These slits are inferior (fig. 41) or superior (fig. 52, 55 E) depending upon the inferior or superior embryo position. Thus in the Vanguerieae and Chiococceae, the pyrenes have apical slits, while in the Psychotrieae they are basal. When germination slits are short (Psychotrieae quoted above, many Vanguerieae), the pyrene wall easily breaks above the preformed slits, so that a kind of lid falls off, often leaving

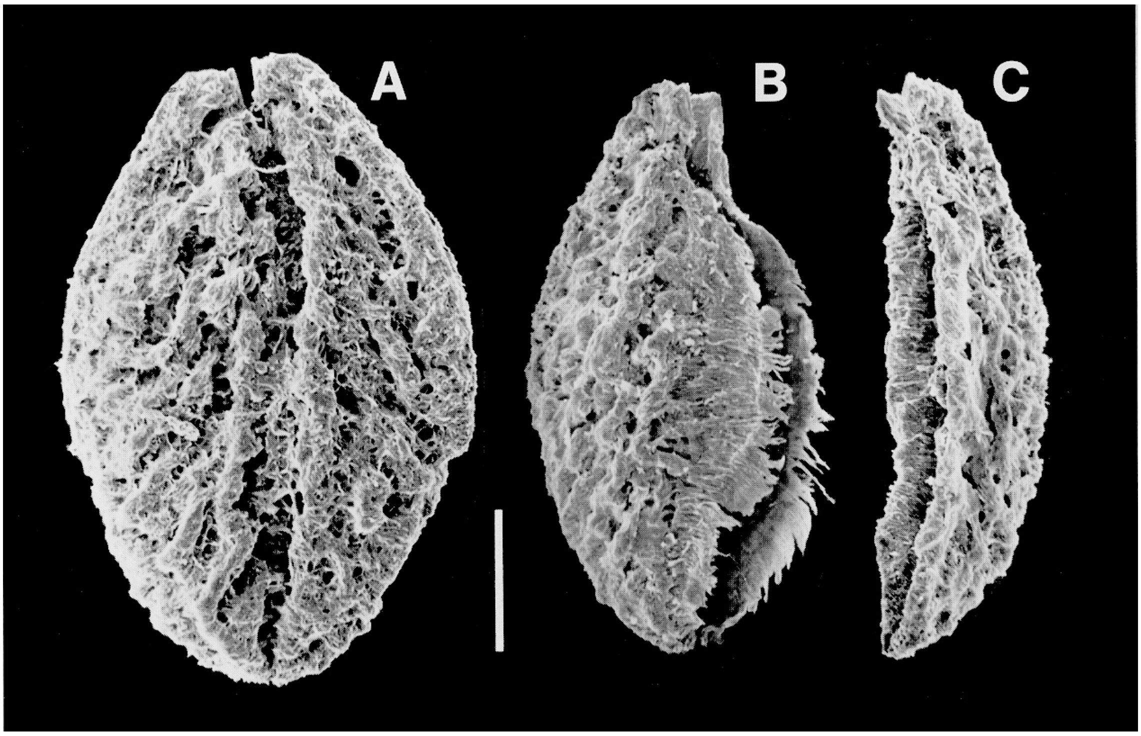


Figure 42.- ***Pyrene opening as box with lid*** *(*Salzmannia nitida*); A, entire pyrene prepared from fruit, B, "box" separated from C, lateral "lid". See apical preformed slit in B & C.*
S.E.-micrographs. Line = 1 mm.

an opening just large enough to permit the radicle to leave the diaspore. *Salzmannia* (Chi.) has highly specialized pyrenes (fig. 42). Its soft fleshy fruits contain only one flattened pyrene which opens as a box with a lateral lid; in addition, the "box" as well as the "lid" have an apical-marginal preformed slit.

For a different but functionally similar pyrene mechanism, see 2.10.2 (embryo radicle protected by stony arilloid stopper, fig. 49 "pl"). In the pyrenes of *Cephalanthus* (Cep.; fig. 55), a combination of preformed slits and stony stopper is found.

2.10 Seeds

2.10.1 Number, size and shape

Number: The number of seeds per locule varies greatly, because of the variable number of ovules per placenta and because of a tendency to abort a part of the ovules during maturation. Thus a few-seeded fruit may result from a few-ovuled as well as from a many-ovuled ovary. Remnants of aborted ovules ("ovulodes") or aborted locules (fig. 56 H, I) are often detectable in mature fruits.

Size: the largest seeds in the family are found in the Gardenieae-Gardeniinae where sizes between 10 and 20 mm are common. In many-seeded taxa, seeds are frequently only a few millimeters in diameter. There is only a limited tendency to have still smaller seeds, especially in the herbaceous representatives. A number of Hedyotideae have minute dust-seeds with a size range of about a fifth of a millimeter (e.g. *Lerchea*, Hed., Axelius 1987).

Shape: Seed shape is inter alia dependent upon available space. In *Tricalysia* (Gar.-D.) e.g., where the number of seeds per fruit varies between one and ca. 40, the seeds are spherical or ellipsoidal in one-seeded fruits, have the shape of half or quarter of a sphere or an ellipsoidal body in fruits with 1- or 2-ovuled chambers, respectively, and are angular in many-seeded fruits. Small seeds with a ± convex abaxial side and angular radial (lateral) sides, tapering towards a short adaxial side, have the most common shape type in many-seeded fruits, e.g. in the Rondeletieae and Hedyotideae. However, in the many-seeded Gardenieae-Gardeniinae whose seed development is not mutually effected because they are completely embedded in the growing placental pulp, the seeds are flat and lenticular. Solitary seeds are frequently hemi-ellipsoidal (e.g. in the Psychotrieae and Spermacoceae) or elongated (e.g. in the Cephalantheae, fig. 55 H, or Guettardeae).

The adaxial side of the seeds is often concave, e.g. in the Spermacoceae (seeds with a longitudinal groove), or provided with a deep central excavation, e.g. in many Pavetteae and in *Craterispermum* (fig. 56 J).

Wings: In a number of taxa, the seeds have flat marginal outgrowths of the seed-coat (fig. 43). However, winged seeds have a rather restricted taxonomic distribution; they char-acterize the Cinchoneae and many Naucleeae. Bremekamp (1952: 14) dismissed the value of this character and transferred a number of genera with winged seeds, e.g. *Bouvardia, Manettia* and *Danais,* from the Cinchoneae to the Hedyotideae; he argued that these genera possess other characteristic features of the Hedyotideae, viz. raphides, testa structure and stalked placentas. One can add that the trend to have a narrow testa wing around the edge of the seed also exists in other Hedyotideae, as well as in several scattered groups of the family, e.g. *Psyllocarpus* (Spe.), a number of Hypobathreae (basal wings), and *Wendlandia* (Ron.).

The morphology of seed-wings is very diverse. They may be
- regular and equal all around the edge of the seed, (i) entire (e.g. Cin.-C., *Coutarea*, fig. 43 A) or (ii) more or less deeply fringed (e.g. Cin.-C., *Coptosapelta, Crossopteryx,* fig. 43 C),
- unequal, i.e. more extended at the two poles of the seeds (e.g. Cin.-C., *Cinchona*, fig. 43 B),
- strongly bipolar or divided in an apical and a basal wing, the latter frequently split up in several parts (e.g. Cin.-C., *Joosia, Corynanthe, Pausinystalia,* Cin.-M., *Uncaria*, fig. 43 D-F), or
- unilateral (e.g. Ron., *Simira*).

Hair-like outgrowths: *Hillia* and *Ravnia* (Hil.) are characterized by seeds with an apical tuft of "hairs", thus superficially reminiscent of the diaspores of many Asteraceae. A detailed examination (see 3.2.5; fig. 58, 59) shows that these narrowly linear outgrowths may be considered homologous with the seed-wings described above.

In *Didymochlamys* (? Cin./Hed.), the seeds are provided with "nonseptate spirally twisted hairs at the edges of the seed" (Garcia Kirkbride 1979: 324, fig. 32, 33). In *Merumea* (Cin.), the seeds are pilosulose all over (Steyermark 1972: fig. 51k). These two cases of hairiness seem unique in rubiaceous seeds, and need a sound reinvestigation for a correct anatomical understanding.

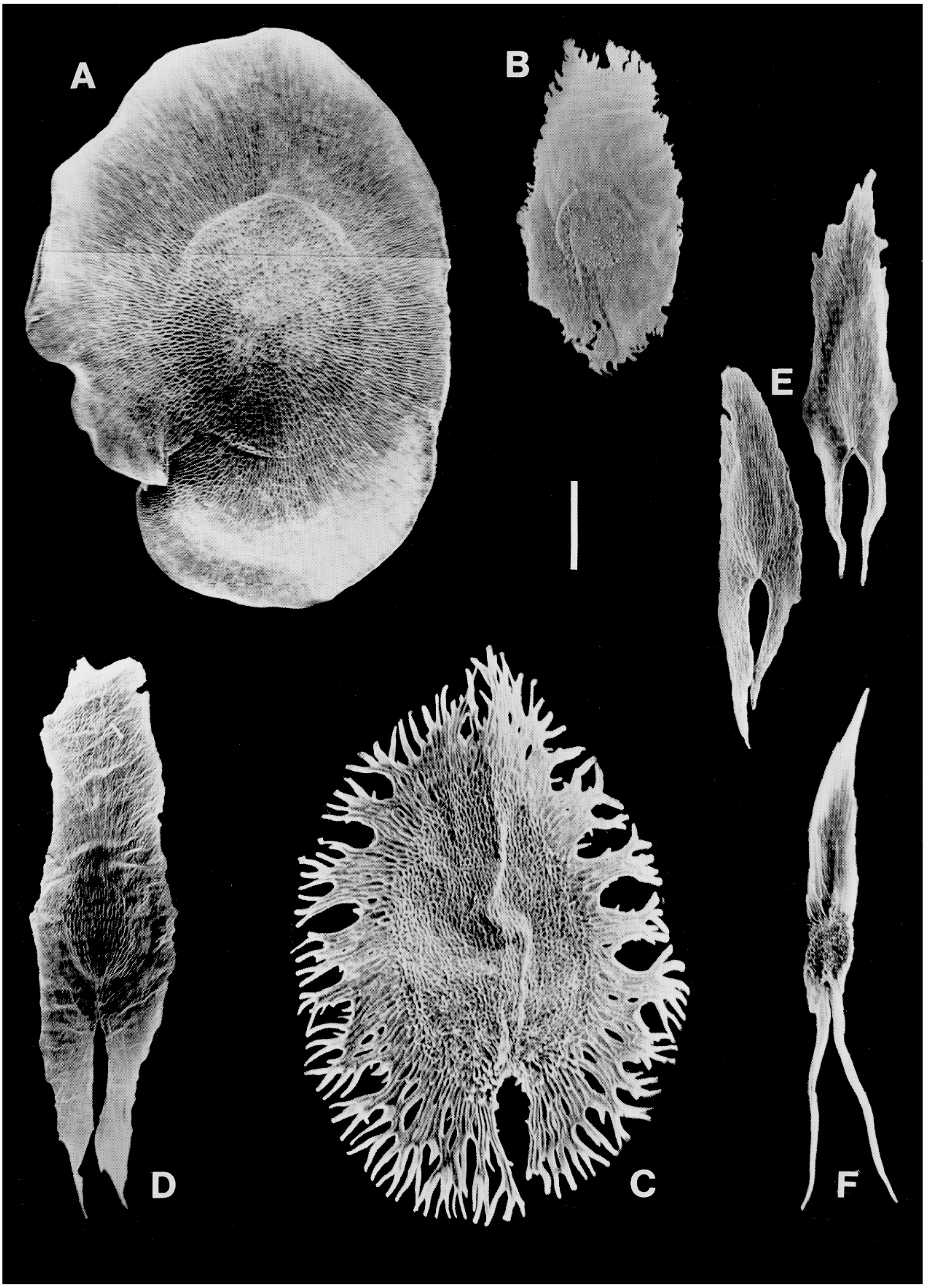


Figure 43.- ***Winged seeds****: A, seed with a ± equal wing all around seed; B-E, seeds with wing tending to be unequal and bilobed at one side, in C the wing is also fimbriate; F, seed with two basal tail-like and one apical wing.*
A, Coutarea hexandra*; B,* Cinchona officinalis*; C,* Crossopteryx febrifuga*; D,* Pausinystalia macroceras*; E,* Corynanthe paniculata*; F,* Uncaria guianensis.
S.E.-micrographs. Line = 1 mm except for C = 0.5 mm.

Hilum: The hilum varies from short, ± rounded (fig. 58 C) or comma-shaped to long and linear; in the flattened seeds of the Gardenieae-Gardeniinae, it extends almost all the way around the sharp edge of the seed. In a number of taxa with one-seeded fruit-chambers, e.g. the Spermacoceae and Psychotrieae, the adaxial side of the seed has a characteristic raphal line often provided with a vascular bundle and frequently characteristic because of its accumulation of raphide-cells causing the outside of the raphe to glitter. The raphe is usually linear, sometimes branched toward the apex.

Vascular supply: Vascular bundles are generally absent from rubiaceous seeds. However, the raphe may be vascularized, e.g. in the Guettardeae and Psychotrieae.

2.10.2 Arilloids

In a number of taxa the seeds are embedded in a pulp or provided with fleshy or ± stony appendages. Since there are very few ontogenetic studies of these structures, I use the general and anatomically neutral term arilloids for these extra-ovular outgrowths.

In the Gardenieae-Gardeniinae, the seeds are deeply or frequently completely embedded in a soft or watery pulp, obviously an outgrowth of the placenta; in Griffithia malabarica is recorded that the placental tissue becomes actively meristematic after fertilization (Periasamy 1965, as "*Randia*" *malabarica*). It is likely that arilloid (partial) coverings of individual seeds in some *Sericanthe* (Robbrecht 1978a: fig. 7) and some *Tricalysia* spp. (Robbrecht 1979: 252) (Gar.-D.) have a similar origin. Such placental proliferations are rare throughout the angiosperms; in the Asteridae, the Rubiaceae-Gardenieae-Gardeniinae share it only with the Solanaceae according to Roth (1977); they may also occur, however, in certain Apocynaceae (e.g. *Landolphia*) and Loganiaceae (e.g. *Strychnos*) having large fruits with a ± leathery pericarp and seeds embedded in a pulp. In *Landolphia*, the pulp is not interpreted as a placental proliferation, but rather as an outgrowth of the seed-coat (Schumann 1895).

Other extra-ovular outgrowths in Rubiaceae are clearly associated with individual seeds and generally mentioned as "obturators" or "strophioles". However, Fagerlind's (1937: 253) supposition that all outgrowths are placental proliferations, received support from various cases studied in depth (for a survey see Wunderlich 1971: 349).

In the Guettardeae, the placental arilloids (fig. 49 "pl") often become more or less stony; they function as stoppers in the plurilocular stone or tip of the pyrene, whose part opposite the embryo radicle is very thin compared to the rest of the endocarp.

In the Spermacoceae, the raphal area (or adaxial groove) of the seed is provided with parenchymatous, mostly fugaceous, outgrowths which may develop into basal outgrowths, e.g. in "*Borreria*" *compressa*. In the latter species, Miège & Assemien (1962) demonstrated the presence of lipid cells, so the outgrowth may be considered an elaiosome.

2.10.3 Seed-coat

The seeds of the Rubiaceae are exotestal (sensu Corner 1976), as in most other families of the Asteridae (fig 55 I, 57 F, K, 58 G, 60 G, L; "xt" exotesta, "nt" endotesta). The outer epidermis (exotesta) is the mechanical layer; it is one cell thick. The inner cell layers (endotesta) are mostly parenchyma-like and in mature seeds crushed by the development of the endosperm; the endotesta is visible in cross-section as a deep brown layer (? impregnated with tannins) of collapsed cells. Only where the pressure of the endosperm is reduced, e.g. at the edge of seeds, or at the edge of ruminations or exotesta-folds, the endotestal cells remain ± intact. In such cases, the endotestal cells may thicken in a way reminiscent of the exotesta (e.g. in *Lamprothamnus*, Hyp., Robbrecht & Puff 1986: fig. 27j). A strong folding of the exotesta with regard to the endotesta, is a peculiarity until now recorded only from the Gardenieae and related tribes (Robbrecht & Puff 1986: 102, fig. 27d); it results in extra thickness of the mechanical layer of the seed-coat.

Only two genera are known to deviate from all other Rubiaceae in that their seeds (with entire endosperm !) have a coat with a many-layered exotesta. In *Paragenipa* (Hyp., Tirvengadum & Robbrecht 1985: fig. 5), there are only one or two additional layers of thickened cells, and the seed-coat still largely conforms to the normal rubiaceous exotestal type. In *Didymosalpinx* (Gar.-G.; Robbrecht 1986a: fig. 1, 2), the strongly modified exotesta is bistratose (each stratum composed of many layers of fibres in a direction ± perpendicular to each another) and irregularly runs out in the surrounding placental pulp.

The main exception to the exotestal seed type, however, is the absence or near-absence, in certain groups, of a seed-coat from mature seeds. The outer layers of the endosperm, with relatively small and thick-walled cells, ensure the mechanical protection of the seed, the outside of which is markedly glossy. At most, a thin, membranous, rudimentary seed-coat is detectable between the pericarp and the endosperm. This feature characterizes the Aulacocalyceae, and further occurs in *Macrosphyra* (Gar.-G.), *Argocoffeopsis, Calycosiphonia* (Gar.-D.) and *Craterispermum* (Cra.; fig. 56). For a complete documentation of such a case see Robbrecht (1986c: 158, fig. 5). Ontogenetic studies of such coatless seeds (and the ovules from which they develop) are unfortunately not available.

The outline of exotestal cells in surface view is variable; I have assessed its taxonomic value below the generic level in *Tricalysia* (Gar.-D., Robbrecht 1979: fig. 2), but in general there are very little data. More or less isodiametric, polygonal cells seem to prevail, but the following variations exist:

- cells strongly elongated (e.g. in many Hypobathreae, in *Sabicea*, Ise.),
- cells almost circular, loosely arranged (e.g. *Tricalysia* spp., Gard.-D.) or
- cells with wavy walls (jig-saw pattern, common in the Hedyotideae).

Intercellular openings in the exotesta are frequent in a number of tribes, e.g. the Vanguerieae. In many Pavetteae, the exotesta is lacunar (becomes so as a result of the maturation of the seed ?), its cells being arranged in little groups scattered over the endotesta (Adams, Bridson & Robbrecht 1987: fig. 1 G, 2).

In cross-section, the exotestal cells are mostly flattened or isodiametric. They may also be radially elongated, palisade-like, often only so near the hilum. The cells may become bulging and papilla-like, e.g. in the Hillieae (fig. 58 F, G), Henriquezieae and some Spermacoceae (e.g. *Psyllocarpus* sp., Kirkbride 1979: fig. 20).

Thickenings of exotestal cells: Bremekamp (1947b, etc., summary and illustrations in Bremekamp 1952) introduced the use of seed-coat characters in the taxonomy of the Rubiaceae. He distinguished several testal cell types (in fact exotestal), e.g. the "pitted testa-cell" described as having strongly thickened side walls and enormous circular or oval pits confined to the equally thickened bottom wall (fig. 44 A). His observations were based on surface views of peeled off seed-coats examined with the optical microscope. Using this technique, cell-wall structures are sometimes difficult to interpret (see 1.2). Therefore Verdcourt (1958: 230) rejected the "pitted testa-cell" as the main criterion for the delimitation of the Cinchonoideae (sensu Bremekamp 1952), because pits or thinnings of various kinds have been found in several tribes; he stated "actually the pits are not always clearly pits but the lumen sculpture would be better described as a reticulation of anostomosing ribs", and he suggested a "much more detailed classification of the types of testa" [the types of exotestal cell thickenings]. I have done so, according to methods set out in 1.2, in the Gardenieae and related tribes (Robbrecht & Puff 1986: fig. 16-20), and less systematically in other groups of Rubiaceae.

The exotesta-cuticle varies from thin and inconspicuous to well developed. Structural cuticular patterns may well exist in the Hedyotideae; according to Bremer (1987) they characterize the related tribe Hamelieae.

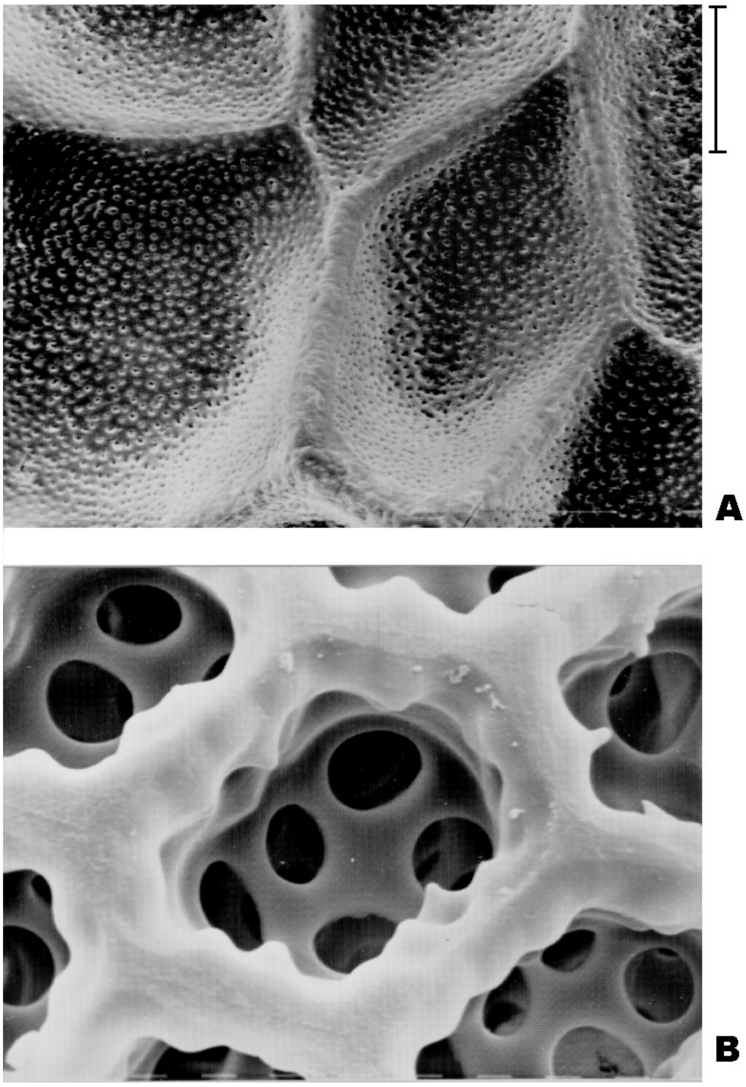


Figure 44.- ***Exotestal cells*** *(surface views after artificial removal of outer tangential walls, showing thickenings of inner walls):*
A, Heinsia myrmoecia, *radial walls with tuberculate thickenings, inner walls with large pits;*
B, Pauridiantha callicarpioides, *radial and inner tangential walls with numerous small pits (compare fig. 57 K drawn from the same).*
S.E.-micrographs.
Lines = 20 µm.

The exotestal cells are either parenchyma-like (then often filled with brown substances, ? tannins) or provided with thickenings,
(i) along the outer tangential (periclinal) wall,
(ia) as a continuous plate,
(ib) as a plate with narrow, canal-like intrusions, or
(ic) as more or less interconnected ribs,
(ii) along the base of or the entire radial (anticlinal) wall, and
(iii) along the inner tangential wall, never continuous but forming
(iiia) a perforated plate (the "pitted testa" of Bremekamp if the perforations are large) or
(iiib) a various network of more or less anostomosing ribs.

The cell-thickenings may be limited to (i), (ii) or (iii), but combinations are common. In e.g. *Aoranthe* (Ise.), a pitted plate along the inner wall continues in a circular thickening around the base of the radial wall; in addition the outer tangential wall of the exotestal cells is provided with delicate, more or less interconnected ribs (Somers 1988: fig. 8

E, exotestal cell in cross section, showing different types of thickenings in outer and inner tangential wall).

The thickenings themselves (of the inner tangential and radial walls) are smooth or variously sculptured with wart-like or spine-like projections.

Finally, the size and shape of the exotestal cells are frequently not uniform. In *Pauridiantha* spp., Pau., the cells differ since they have unequally developed radial walls (fig. 57 I, K), resulting in seeds with crests on their surface (fig. 57 H). For various other examples of "exotestal cell dimorphism" in the Gardenieae and related tribes, see Robbrecht & Puff (1986: 102, fig. 17).

2.10.4 Endosperm

In all Rubiaceae, the seed contains endosperm. The Guettardeae are sometimes characterized as exalbuminous (and because of that main criterion even regarded as a monotribal subfamily, see 3.2.2), but upon close examination, a few layers of endosperm cells are detectable in between the large embryo and the seed-coat. In fact, the Guettardeae are only an extreme in the trend to early endosperm resorption existing in other tribes with large embryos such as the Vanguerieae.

The texture of the endosperm is mostly horny, probably with starchy storage products. A number of tribes, e.g. the Morindeae, Vanguerieae and Guettardeae are characterized by a soft endosperm with copious oil. This also occurs in other tribes as isolated cases; *Doricera* is the only genus of the Pavetteae having oily endosperm. The early adepts of chemotaxonomy considered oily endosperm as a derived character, and the situation in the Rubiaceae seems to confirm this view.

Petit (1963) emphasized the occurrence of oil in the endosperm as an important taxonomic character and used it for the delimitation of the Morindeae (oily endosperm) against the Psychotrieae (horny endosperm). Since I have observed the presence of small quantities of oil in the endosperm of several Psychotria spp., a careful reinterpretation is needed.

Rumination: Shallow invaginations of the seed-coat into the endosperm are common in the family. Deeply ruminate endosperm has a restricted taxonomic distribution, however; it occurs only in a number of taxa with larger seeds, viz. (* indicates genera characterized by rumination) in the following tribes:

Pav.: **Nichallea*, **Rutidea*, *Tarenna*
Gar.-D.: *Tricalysia*, *Nostolachma*
Hyp.: **Nargedia*, **Lamprothamnus*, **Polysphaeria*, **Galiniera*
Psy.: *Psychotria*, *Gaertnera*, *Pagamea*.

In some of these, e.g. *Psychotria*, progression series (for details see below) exist from entire endosperm to endosperm with one or a few shallow adaxial invaginations to deeply ruminate endosperm. In the latter, the invaginations are always ± radially arranged around the embryo cavity. The ruminations may completely encircle the seed or be limited to either the adaxial or the abaxial side.

Seeds with a single adaxial invagination (in cross-section I-, T-or V-shaped or assymmetrical) are reminescent of ruminate seeds. The entire tribe Coffeeae (= *Coffea* and *Psilanthus*, together more than one hundred species) is characterized by "coffee-beans", seeds with a single, deep asymmetrical, sometimes bilobed, adaxial invagination (Robbrecht & Puff 1986: fig. 24g). From the developmental viewpoint, such seeds are comparable with seeds with concave adaxial sides; both may result from differential local (marginally favoured) growth of the developing seed.

In some Vanguerieae, the endosperm is pseudoruminate. Bridson (1986) depicted and described the endosperm of *Keetia* as streaked with patches of resinous granules.

The taxonomic significance of rumination is only at (genera with * in list above) and below the generic level. In the Hypobathreae, I first accepted that ruminate seeds were a good criterion supporting the definition of two subtribes (Robbrecht 1980a), but later inclusion of a few problematic genera in the tribe showed that rumination is inconsistent with the other used characters, and has led to the dismission of the subtribal distinction (Robbrecht & Puff 1986).

Petit's (1964a, 1966) studies in African Psychotrias are an example of the variation which may exist within a genus; according to the species, their endosperm

- may be entire, or have
- a single adaxial invagination, I-, T- or V-shaped in cross-section,
- abaxial ruminations combined with a T-shaped adaxial invagination, or
- ruminations all around, eventually combined with a T- or V-shaped adaxial invagination.

This progression series is in contradiction to the taxonomic value once ascribed to rumination in the Psychotrieae; *Grumilea*, defined by its ruminate seeds, can not be upheld and is synonymous with *Psychotria*.

Existing typologies of seed rumination in the angiosperms do not take into account such taxonomically useful morphological variation observed in mature seeds. Periasamy (1962) e.g. distinguished between seven types of rumination, based mainly on developmental features. He included only three rubiaceous genera (and eight species) in his investigations, all having ruminate seeds belonging to the *Spigelia* type. This is characterized by mature seeds with definite ingrowths of the seed-coat, a one-layered mature seed-coat, unitegmic ovules, rumination preformed in the tissues of the seed-coat, chalazal hypertrophy during post-fertilization development and late endosperm development.

2.10.5 Embryo

The size of the embryo is very variable, from very large and almost completely filling the seed (see endosperm reduction discussed in 2.10.4) to minute; Martin's illustrations (1946: pl. 44, 45) of selected taxa of the Rubiaceae give a good survey of the existing variation.

The position of the radicle, superior or inferior, is of course related to micropyle position and ovule orientation (see 2.8.4); it is an important tribal-constant and a very useful practical character.

The embryo shape is always very simple; generally Martin's (1946) spathulate embryo type or a reduction of it occurs (fig. 52 F, M, U, 53 E, 55 H, 56 K, 58 E, 60 D, J). The main diversity of the embryo results from differential development of the radicle or cotyledons. In the Henriquezieae, the cotyledons are large and foliaceous and the radicle small, but generally the radicle is well-developed. The latter is cylindrical with a conical or flat base, and generally straight, rarely curved, e.g. in the Vanguerieae (fig. 52 W) and some Guettardeae (fig. 49 E). The cotyledons are frequently very simple with weak venation, rarely foliaceous. Fagerlind (1937: 265, fig. 23g) reported a remarkable development of the cotyledons in *Leptodermis* (Pae.); they are very large and twisted around one another.

The position of the cotyledons is mostly transversal, i.e. with their flat sides parallel to the septum (in bilocular fruits) and their upper surfaces against one another (fig. 52 M, W). In the Chiococceae and Vanguerieae, however, the cotyledons may also be perpendicular to the septum (fig. 52 F, U). Capuron (1969) first observed this in Madagascan Vanguerieae; he applied the terms "accumbent" and "incumbent" to these two different positions of the cotyledons of the Vanguerieae, and this terms may be followed since the Vanguerieae embryo is more or less curved. Capuron used cotyledon position as an important criterion to distinguish genera (reputedly problematic in the Vanguerieae), and its taxonomic importance was later confirmed for the delimitation of the African genera (Verdcourt 1987).

2.10.6 Germination and seedlings

Very little is known about germination of seeds of tropical woody Rubiaceae, and only some general works may serve as sources of information. De la Mensbruge (1966) included thirteen rubiaceous species in his investigations of tree seedlings from the Ivory Coast, and concluded that germination is always epigeal and phanerocotylar. The cotyledons are foliaceous, and show only minor variation (from linear to ± rounded). The first leaf pair has stipules and is very similar to normal leaves. I observed (greenhouse) germination and seedlings in some fifteen other rubiaceous genera and found no exception to this pattern, except that in *Vangueria* germination is cryptocotylar; the radicle leaves the pyrene through the preformed slits, but the cotyledons remain included (Robbrecht 1980b: fig. 2.25).

De Vogel (1979) confirmed the uniform morphology of Rubiaceae seedlings. He reported a sole seedling type (*Macaranga* type, the most common one in dicotyledons) in 21 tropical woody rubiaceous genera.

It thus is obvious seedling morphology can only be significant for rubiaceous taxonomy at lower ranks.

2.11 Pollen morphology

It is far beyond the scope of the present work to make a complete survey of the palynological knowledge of the Rubiaceae. There are many older data. As early as 1922, Vermoesen stressed the taxonomic importance of pollen features in the Gardenieae and concluded that the African species of "Randia" were in need of segregation into several genera; his paper, written in Dutch, remained unknown, and as a result of his sudden death the same year, the formal and detailed elaboration of his work was never published.

Classical (light microscopical) palynological contributions to the Rubiaceae are: Erdtman's (1952, reprint 1971) short family survey, Verdcourt's (1958) very general overview (mentioning mainly the pollen types, without distinction between colpate and colporate), Lewis' (1965) palynological study of *Hedyotis*, a treatment of Madagascan Rubiaceae (Keraudren-Aymonin, Straka & Simon 1969) and two studies of a number of Brazilian representatives (Melhem, del Bianco Rossi & Silvestre 1974; Jung-Mendaçolli 1984).

The number of more modern approaches, including S.E.M., examination of broken grains and T.E.M., is limited. The most important ones are Lobreau-Callen's (1978) work on the compound aperture of Rubiaceae pollen, my own treatment of the Anthospermeae and Paederieae (Robbrecht 1982b), a study of the pollen of *Coffea* and related genera (Lobreau-Callen & Leroy 1980), Keddam-Malplanche's (1985) work on Gardenieae from Gabon, and Johansson's (1987b) treatment of the Morindeae.

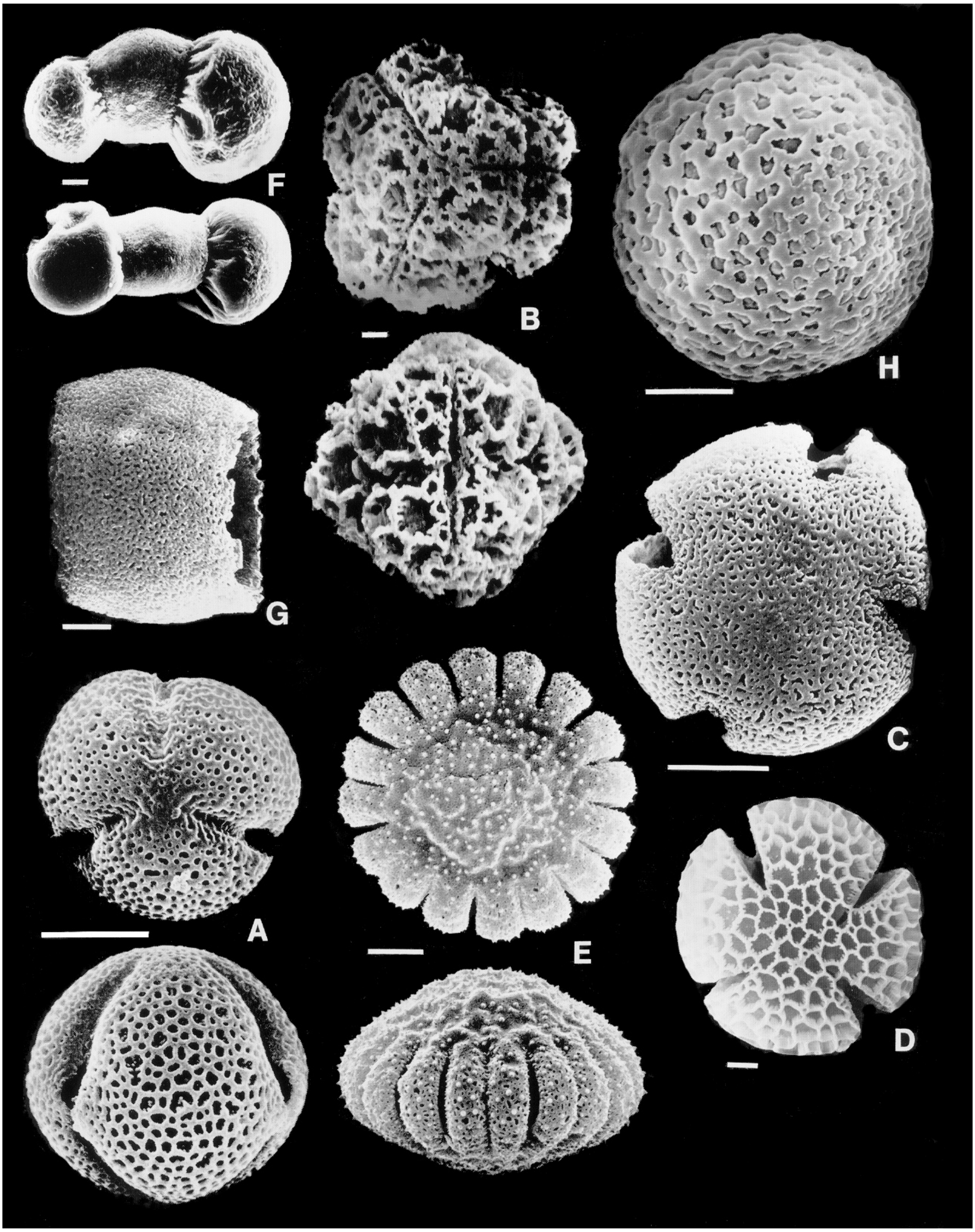
The tricolporate pollen type (fig. 45 A) by far dominates in the Rubiaceae; it characterizes a large number of tribes, such as the Pavetteae, Hypobathreae, and Anthospermeae. The Paederieae have tricolpate pollen, and the Spermacoceae and Rubieae are characterized by pluricolpate (fig. 45 E) or pluricolporate pollen. In the pollen of all representatives of the family, the apertures are situated in the equator (zonoaperturate grains). The only exception to this seems to be found in a few South American *Spermacoce* spp. (Spe.) which are pantoporate (Jung-Mendaçolli 1984 and personal observations).

A number of tribes are eurypalynous, e.g. the Psychotrieae with colpate (fig. 45 C, D), colporate, porate (fig. 45 G) and nonaperturate grains (fig. 45 H); a palynological survey of this tribe, with reputedly difficult generic delimitation, is lacking, though it might be one of the most promising research topics in the Rubiaceae.

Pollen grains united in permanent tetrads occur in thirteen, mainly African, genera of Gardenieae (Robbrecht & Puff 1986: fig. 21g, h, table 1; tetrads of porate grains) and in the distant genus *Gleasonia* (Hen.; tetrads of colporate grains, fig. 45 B). In both instances, the tetrads are tetrahedrical, homodynamosporous and calymnate, with apertures meeting two and two at six points.

The exine is generally tectate or semitectate, varying from almost closed to reticulate. Supratectal elements often are lacking, but if present (fig. 45 E) have a wide array of morphological variation. The exine is generally typically columellate, but columella reductions may lead to ± massive exines.

Figure 45.- ***Pollen types****: A, tricolporate, reticulate grain in polar and equatorial view (*Pinckneya pubens*); B, two views of permanent tetrad of tricolporate grains with wide-meshed reticulum (*Gleasonia uaupensis*); C, tetracolpate grain with perforated tectum, polar view (*Chazaliella oddonii*); D, tetracolpate, reticulate grain in polar view, colpi with distinct margo (*Squamellaria imberbis*); E, pluricolpate grain in polar and equatorial view, tectum with bordered perforations, conical supratectal elements (*Spermacoce dibrachiata*); F, living and G, acetolysed biporate grains with perforated tectum (Myrmecodia sp.); H, nonaperturate grain (*Palicourea corymbifera*).*
S.E.-micrographs of acetolysed (except F) material. Lines = 10 µm.


F
B
H
G
C
A
E
D

The compound apertures are very variable too. The endoaperture is generally lalongate, sometimes connate into a cingulum; H-shaped endoapertures and endoapertural horns occur (Robbrecht 1985). The inside of the exine is usually verrucate; it may show endocracks (Puff & Robbrecht 1988). Living pollen grains of Rubiaceae often have large protoplasmic vesicles protruding through the apertures; in *Myrmecodia* (Psy.; fig. 45 F) these are so large that the grains are presumably short-viable and thus function as pollen types with thin exines, known from rain forest taxa in other angiosperm families (Kress 1987).

For a discussion of pollen dimorphism in heterostylous taxa, see p. 124.

2.12 Chromosomal data

Only a brief survey of rubiaceous chromosomes is presented here, since recent in depth karyosystematical studies are available (Kiehn 1986, dissertation). The older data (surveyed by Verdcourt 1958 and Ehrendorfer 1977) are largely consistent with Kiehn's (1985, 1986) first reports.
The basic number x = 11 is predominant throughout the family, particularly in the woody tribes. Especially the herbaceous lines of evolution are involved in deviation from this basic number, e.g. x varying from 8 to 17 in the Hedyotideae and x = 11, 14 or 20 in the Spermacoceae.

Polyploidy is at least as common as diploidy, not only in herbaceous but also in woody groups. Only a few tribes seem consistently diploid, e.g. the Pauridiantheae, the Condamineeae, and the Hamelieae. All the larger tribes show a more or less marked degree of polyploidy (e.g. Cinchoneae: 2x - 4x, Gardenieae: 2x - 6x, Hedyotideae: 2x - 8x, and Psychotrieae: 2x - 12x). In a number of tribes, the tetraploid condition seems to have become ± fixed, e.g. in the Guettardeae, Alberteae (all records tetraploid) or Vanguerieae (rarely diploid).

2.13 Biology

2.13.1 Ant and mite associations

The extreme myrmecophilous adaptations of *Myrmecodia* (fig. 6 A) and associated genera (Psy.) have already been mentioned in 2.2.2. In these succulent epiphytes the hypocotyl grows out into a ant-inhabited tuber. Apparently these ant-epiphytes grow better in the presence of *Iridiomyrmex*, and the ants supply minerals to the plants (Huxley 1978; review of investigation of ant-plants, field study, morphological observations and experiments). For a general discussion of symbiosis between ants and vascular ant-inhabited epiphytes, see Huxley (1980). The Rubiaceae contain ca. 80 epiphytic species which are regularly associated with ants; in that number they strongly exceed all other families of ferns and flowering plants with ant-inhabited epiphytes.

The flowering branches of many trees and shrubs, belonging to diverse rubiaceous tribes, are also frequently inhabited by ants. The stems are perforated by the ants (often one opening per internode, sometimes a series of openings at the base of each internode); rarely they are just hollow (for a complete documentation of such a case in *Tricalysia crepiniana*, Gar.-D., see Robbrecht 1979: 334), and generally they are also distinctly swollen (e.g. *Nauclea sp.*, Nau.-N.: fig. 5 C, 14 F1, *Heinsia myrmoecia*, Ise., *Canthium* spp., *Cuviera* spp., Van.). For biological details on the ants inhabiting the branches of *Cuviera, Nauclea*, and other genera, see Bequaert (in Wheeler 1922).

Leaf-structures too may be by ant-associated. In a very limited number of species (Cinchoneae: *Remijia physophora*; Gardenieae: *Gardenia imperialis* and *Duroia saccifera*; Pavetteae: *Ixora hippoperifera*), the base of the leaf-blade is on either side of the midnerve transformed into vesicle-like myrmecophilous structures (fig. 9 D). For a possible morphological interpretation of the sacs see 2.4.1. Bequaert (in Wheeler 1922) reported extrafloral nectaries (visible pale brown glands, secreting sweet substances) inside the vesicles of *Gardenia imperialis* (as "*Randia physophylla*"); the observed visiting ants normally inhabit neither the leaves nor the tree.
A fourth kind of myrmecophilous adaptation exists in *Henriquezia* and *Platycarpum* (Hen.); in these genera the petiole-bases have one or more abaxial glands.

While the ant-tubers of epiphytic Psychotrieae and the leaf-base sacs are "obligate", i.e. also formed in the absence of ants, apparently the myrmecophilous stem internodes are often "facultative". In *Tricalysia crepiniana* e.g., a very common Central African rain forest species, individuals with ant-inhabited internodes are rare and occur only in a small part of the species area of distribution (Robbrecht 1979: 334, fig. 27).

The **biological significance** of the ants in tuber-bearing epiphytes is relatively well documented (see above), but relevant data on other myrmecophilous structures are sparse. Obviously flowers are protected when occurring on twigs inhabited by ants. Besides habitation, an additional advantage for the ants may be resources for feeding, see the abovementioned extrafloral nectaries in *Gardenia imperialis*; also Rogers (1984) observed that the petiolar glands of *Henriquezia* and *Platycarpum* (Hen.) are nectaries (exuding sweet liquid) and are visited by ants.

Domatia (see 2.4.2, fig. 12) are likely to be always inhabited by mites (and are therefore often termed "acaridomatia"), but after years of routine naming of many Rubiaceae and revision of several groups, I have only observed mites in domatia a few times on herbarium material. Any way, domatia often develop in the absence of mites (Jacobs 1966).

2.13.2 Associations with Bacteria and Fungi

For a review of the literature on the biological significance of bacteriocecidia (see 2.4.1) in rubiaceous leaf-blades, I refer to Lersten & Horner (1976). The first hypothesis suggested that nitrogen is fixed in these bacterial galls, what is now rejected. Evidence indicates that growth regulating substan-ces are produced in the galls. As to the symbiotic cycle between bacteria and "hosts", the bacteria not only live in the galls, but also in the blastocolla secreted by the colleters and surrounding the growth apex. From there they are able to "infect" the ovules (and consequently seeds). The nomenclature of the Bacteria in rubiaceous leaf-galls was reviewed by Horner & Lersten (1972).

F. Hallé (1967: 59-63, fig. 16) discovered an endophytic siphomycete in the colleter secretion inside vegetative buds of *Schumanniophyton* (Gar.-G.). Although the transmission of the fungus from one bud to another is similar to the transfer of bacteria living in bud-secretion of bacteriophilous Rubiaceae, the initial "infection" of young *Schumanniophyton* individuals appears to result from germination of a spore on the bud of a seedling; the seeds are thus devoid of fungus diaspores. This endophytic fungus association seems to be the only one recorded from the Rubiaceae.

2.13.3 Flower biology

N. Hallé (1966) has distinguished two variants as regards the flowering rhythm of the Rubiaceae. It may be either synchronous (all flowers of an inflorescence opening at the same time, e.g. in *Nauclea*, Nau., *Ixora*, Pav., *Coffea*, Cof.), or asynchronous (consecutive anthesis within the inflorescences, e.g. in *Psychotria*, Psy., *Sabicea*, Ise. or *Otomeria*, Hed.). Detailed observations on the flowering rhythm of the Rubiaceae are generally lacking, however. The asynchronous condition is probably confined to more advanced groups.

Wagenitz (1977) stated that in the Asteridae three major floral morphological / pollination ecological syndromes occur, viz.
(i) extremely zygomorphic flowers with anthers often reduced to two or four, and highly specialized insect-pollination,
(ii) flowers with long, narrow corolla-tubes, pollinated by animals with long mouth parts, and
(iii) numerous small flowers aggregated into a dense inflorescence.
All three are present in Rubiaceae. While (i) is certainly rare and not characteristic of the Rubiaceae as it is in Lamiaceae or Acanthaceae, (ii) and (iii) are common throughout the family (see 2.7 for discussion of condensed inflorescences and 2.8.2 for shape and symmetry of corollas).

Cleistogamy is apparently limited to annual herbaceous Rubiaceae and is not reported from woody ones. Inside the unopened cleistogamous flowers of Crusea spp. (Spe.), pollen is shed directly on the stigmatic surfaces or pollen tube grows through the anther wall to reach the stigma; cleistogamous Crusea flowers set a very high percentage of viable seeds (Anderson 1972). Mantell (1985) suspected that cleistogamous flowers occur in the annual species *Kohautia microflora* (Hed.). This species has tiny flowers of an inconspicuous green colour. The pollen in closed flowers is mature, and sometimes remnants of closed corollas remain attached to the capsules.

2.13.3.1 Pollination

The Rubiaceae, in tropical ecosystems, are one of the dominant families among the group of nectariferous plants (Opler 1983). Accordingly, most Rubiaceae are **zoophilous**. The flowers generally produce nectar from the epigynous disk at the base of the corolla-tube. Vogel (1954) reports melitto-, psycho-, phalaeno- and sphingophily in the family. Ornitophily is rare; it is recorded from red-flowered species of *Burchellia*, Gar.-G., Alberta, Alb., *Bouvardia* and *Manettia*, ? Cin./Hed. (Vogel 1954; details on the ornithophily of *Alberta magna* in Puff, Robbrecht & Randrianasolo 1984). Hummingbird pollination was also recorded in *Hamelia patens* (Opler 1983) and Henriquezieae, e.g. *Platycarpum rhododactylum* (Rogers 1984: 67, 121). Robbrecht & Puff (1986: 108) suspected that chiropterophily may occur in *Rothmannia* (Gar.-G.). As to the optical attractivity of the flowers (colour, formation of pseudanthia, semaphylls etc.), see 2.7 and 2.8.

Anemophilous flowers characterize the tribes Anthospermeae and Theligoneae. In these two tribes, the flowers are hermaphroditic and/or unisexual and exhibit a set of specialized features, inter alia striking sexual dimorphism, increased receptive surface of the stigmas and pendulous anthers (fig. 46 D, E). For a detailed discussion see Puff (1982, 1986a; in fact, he redelimited the Anthospermeae to include taxa sharing the anemophilous syndrome with a number of other morphological features).

2.13.3.2 Floral organisation

Though the Rubiaceae are almost uniformly characterized by hermaphroditic flowers, they have a number of adaptations promoting outbreeding. This may be realized by simple mechanisms such as proterandry or spatial isolation alone; according to White (1962), the latter is likely "especially in those species in which the flowers only function for a few hours (some Hedyotideae)". Proterandry may be particularly pronounced, e.g. in *Galium* species. In the South African *G. mucroniferum* and *G. subvillosum* pollen is released as soon as the flowers open, after which the empty anthers move into a ± horizontal position; the female stage is 4-6 days later, when the styles have achieved their full length and stigmas are receptive to pollen (Puff 1978). Proterogyny is a rare feature in the Rubiaceae; it is (? only) known in the Anthospermeae-Coprosminae and -Operculariinae (Puff 1982).

Stylar pollen presentation, heterodistyly, and unisexual flowers, three complex reproductive strategies common in the Rubiaceae, are discussed below. Each of these favours allogamy. In addition, self-incompatibility systems also are present. A sample of fourteen rubiaceous species from one tropical forest community had four monomorphic and nine of ten dimorphic species self-incompatible (Bawa & Beach 1983); this seriously weakens Anderson's (1973) supposition that the Rubiaceae are essentially self-compatible.

(i) Stylar pollen presentation (fig. 46 A)

In many groups, e.g. the Gardenieae and related tribes, the flowers are proterandrous and the pollen is shed early (often in the bud stage) onto the outside of the stigmas and/or the upper part of the style, which serve as a "receptaculum pollinis". Increased surface area and irregularity of the pollen receptacle, caused by swellings, hairs, grooves or ridges often ensure a more efficient pollen deposition. After elongation of the style, animals transport the pollen to flowers in the female or receptive stage with exposed stigmatic surfaces.

This mechanism, comparable to the stylar pollen presentation of the Asteraceae, was reported as early as 1884 by Burck in numerous genera, inter alia *Sarcocephalus*, Nau., *Scyphostachys*, Hyp., *Griffithia*, Gar. and *Pavetta*, Pav. Bremekamp (1934, 1952, 1966), who introduced the terminology "ixoroid pollen mechanism", considered it to be of great taxonomic importance, and accepted it as the major criterion to define his subfamily Ixoroideae. "This type of pollination mechanism [proterandrous condition combined with a particular position of style-head and anthers + stylar morphology details] is therefore a much more complex arrangement and accordingly of much greater taxonomic importance than most other pollination mechanisms" (Bremekamp 1966: 4). He stressed the fact that similar mechanisms are only recorded from the Asteraceae, Goodeniaceae and Campanulaceae, which can also be turned as an argument against his merging of all Rubiaceae with the mechanism in one subfamily. If stylar pollen presentation evolved several times in the Asteridae, it might also have evolved several times in the Rubiaceae. Bremekamp certainly over-estimated its importance, as Verdcourt clearly pointed out (1958: 227). *Cladoceras* should not be removed from Pavetteae because it lacks the mechanism (for a discussion of this case see Bridson & Robbrecht 1984), nor *Coptosapelta* and *Crossopteryx* from the Cinchoneae because they exhibit

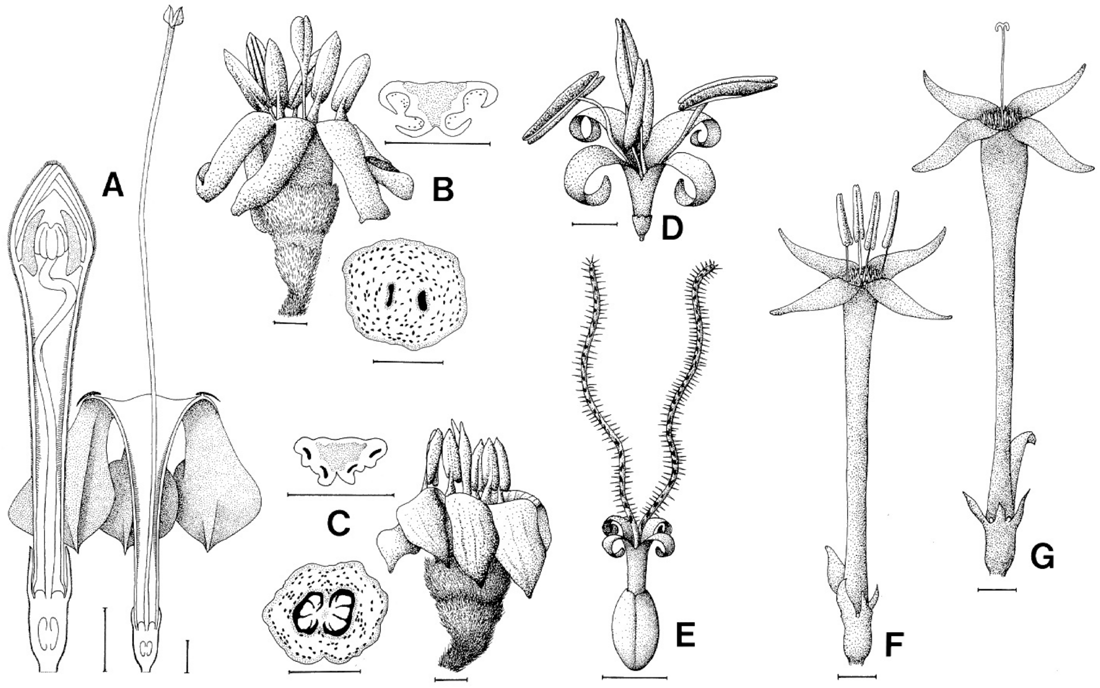


Figure 46.- ***Three complex floral biological adaptations****: A, proterandry with stylar pollen presentation in* Macrosphyra longistyla *[longitudinal sections; the pollen is shed onto the outside of the stigmatic lobes in bud; at anthesis, the style (strongly curved in bud!) elongates]; B, male and C, female flower of* Tricalysia cryptocalyx*, each with a transverse section of stamen (staminode in the former) and ovary; D, male and E, female flower of anemophilous* Anthospermum aethiopicum*; F, G, "complete" heterodistyly, F, thrum and G, pin flower of* Knoxia platycarpa.
A from F. Hallé, D, E after Schumann. Horizontal lines = 1 mm, vertical lines = 5 mm.

it. Though the mechanism is not always easy to identify on herbarium material and can even be mistaken for heterostyly if observed in plants at only one stage, it characterizes the following groups (generally present in all their representatives): Naucleeae, Cinchoneae-Mitragyninae, Gardenieae, Pavetteae, Coffeeae, Aulacocalyceae, Hypo-bathreae, Retiniphylleae, Vanguerieae, Guettardeae, Chio-cocceae, Alberteae and Cephalantheae (fig. 48). Moreover it occurs sporadically in the Cinchoneae-Cinchoninae, e.g. in the abovementioned genera *Crossopteryx* and *Coptosapelta*. Stylar pollen presentation is thus confined to a number of essentially woody tribes. Very remarkably, however, it also occcurs in the Rubieae. In this tribe, the herbaceous perennial *Phuopsis* has proterandrous flowers in which pollen is shed onto the style in bud stage; a slight pressure on the tip of the bud causes the (valvate) corolla-lobes to pop open (S. Vogel, pers. comm. to C. Puff).

A proterandrous mechanism somewhat comparable to stylar presentation is **pollen projection** in species of the South American genus *Posoqueria* (Gar.-G.), first described by Muller in 1866. The bilaterally arranged anthers of the (strongly zygomorphic) flowers adhere to one another and open introrsely, the pollen being shed as one spherical mass. When visited by Sphingidae, the anther-tube pops open and the pollen mass is projected onto the insect. One of the filaments bends back and closes the throat of the corolla. Later, the stamens loose their turgescence; thereby the opening of the corolla-tube towards the stigmatic surface becomes free. Anther adherence in the first stage is due to an intermingling of their hairs; the anther-tube of *Posoqueria* is not really fused (compare 2.8.3). A detailed description and depiction of this mechanism is given by F. Hallé (1967: 130, fig. 40). Not all *Posoqueria* species possess this mechanism (Burck 1884), but it definitely occurs in *P. fragrans* (Müller 1886), *P. latifolia* and *P. longiflora* (F. Hallé 1967). Schumann (1891: 10) reported similar pollen projection in *Molopanthera* (Cin.-C.).

(ii) Heterodistyly (fig. 46 F, G)

In his classical book on flower biology, Darwin (1877) was one of the first to declare that the Rubiaceae have more heterostylous species than any other angiosperm family; perhaps there are even more heterostylous species in the Rubiaceae than in all the other angiosperm families put together (Anderson 1973). This latter author suggested that the initiation of heterostyly in the Rubiaceae lies in a modification of their common proterandry.

In the nineteenth century literature, the heterostylous condition was often overlooked, and the two floral morphs were sometimes described as separate species. Bremekamp (1940) first suggested that heterostyly is an important feature for the delimitation of higher taxa of the Rubiaceae;

he used it as one of the main criteria to distinguish the Pauridiantheae from the Urophylleae. He finally concluded (Bremekamp 1966) that heterostyly has an only limited taxonomic weight, since it "is found in several but distantly related families, that is always restricted to part of the genera and that it is even in these genera but rarely a general feature". Verdcourt (1958) also attributed relatively limited taxonomic value to it. Nevertheless, the systematic distribution of heterostyly is limited; it occurs mainly in the tribes referred to the Rubioideae by Verdcourt and Bremekamp. Bir Bahadur (1968) reviewed the literature and found it occurs in almost 400 species; the actual number of heterostylous Rubiaceae may well be double that.

Bir Bahadur's review of heterostyly in the Rubiaceae should be interpreted critically, especially as regards the tribal positions he attributes to the taxa cited. He generally followed Verdcourt's (1958) system, but had some odd placings, e.g. *Heinsia* in the Hamelieae and *Pentanisia* in the Hedyotideae. His records of heterostyly in a few species of "Ixoreae", Chiococceae and Guettardeae are doubtful, and therefore not included in fig. 48. For example, he accepted Hiern's (1878) record of heterostyly in *Tricalysia* (Gar.-D.), even though this author mentioned it only with doubt. Heterostyly is no doubt absent from *Tricalysia*, except for a peculiar case in section *Ephedranthera*, discussed further and definitely unknown to Hiern since his 1877 treatment of the genus included no species of that section.

The tribes containing the largest number of heterostylous species are the Hedyotideae and the Psychotrieae; for the other tribes with heterostyly see fig. 48. Heterostyly would also be expected in the Condamineeae since that tribe shows many similarities to the Rondeletieae and the Cinchoneae where it is common. It definitely does not occur in the Condamineeae (Aiello 1979: 50), probably because the generally campanulate corollas of this tribe may well imply a rather different floral biology. The same applies to the Hillieae and Henriquezieae, two advanced tribes related to the Cinchoneae; their floral biology, especially in the Hillieae, is poorly known.

In the Argostemmateae and Hamelieae, related to the frequently heterostylous Hedyotideae, the flowers are monomorphic according to Bremer (1987). However, she does cite one species of *Hoffmannia* which might be heterostylous; she nevertheless believes that the floral organization is advanced and derived from an ancestor with only short-filamented forms. Similar cases are reported from the Psychotrieae (see further: homostylous *Hymenocoleus* spp.). This special type of floral mechanism, in which the monomorphic flowers have the anthers in the upper part of the corolla-tube and the stigma at a much lower level, also occurs in a number of Guettardeae, *Cladoceras* (Pav.), *Belonophora* (Aul.) and *Kohautia* (Hed.) (Bremekamp 1963b; Robbrecht & Puff 1986). It probably evolved independently as a modification of the dimorphic condition (in Hamelieae, Hymenocoleus etc.) or as a modification of stylar pollen presentation (in Guettardeae, *Cladoceras*, etc.). For a de-tailed discussion and experiments with *Kohautia*, see Mantell (1985).

The complete absence of heterostyly in the main groups with stylar pollen presentation (the Gardenieae and relatives and the Vanguerieae, Guettardeae and associated tribes) is remarkable. However, it is not a total surprise since the highly advanced pollination mechanism of these groups is based on an entirely different plan, from which it is difficult to imagine heterostyly evolving. Nevertheless, in a small section of *Tricalysia* (Gar.-D.; subg. *Tricalysia* sect. *Ephedranthera*), stylar pollen presentation is apparently combined with a simple case of heterodistyly. The dimorphism relates only to the length of the style which has its lobes either among the anthers in the throat (longistylous form) or deeply included (brevistylous); for a complete description, see Robbrecht (1982a). All other groups of *Tricalysia* have monomorphic flowers with characteristic stylar pollen presentation.

In rubiaceous heterostylous species, thrum flowers characteristically have included styles and exserted anthers, and pin flowers exserted styles and included anthers; this type (fig. 46 F, G; fig. 47, sect. *Hymenocoleus*) is sometimes designated as "complete heterostyly" (e.g. Verdcourt 1958: 277). In the other extreme case, style and anthers are located in the corolla-tube (fig. 47, sect. *Gynandrocryptus*),

- the anthers immediately below the throat and the style low in the tube in thrums,
- the style in the throat and the anthers low in the tube in pins.

These features have systematic importance at only lower taxonomic levels, e.g. specific. However, in *Hymenocoleus* (Psy.), an African rain forest genus of creeping perennial herbs and monocaul dwarfs, the type of heterostyly corresponds well with other morphological features and is used in defining sections (fig. 47); in that genus, the loss of one of the two floral morphs is a further line of evolution (sect. *Solenocalyx*, monomorphic flowers with included style and anthers).

Pollen dimorphism: in the Rubiaceae, heterostyly is often, but not always, associated with heteropalyny. Pollen dimorphism was documented in heterostylous taxa in the last century by Müller (1869; *Faramea* sp., Cou.), Burck (1884; *Cinchona* sp., Cin.-C.) and Darwin (1877; many taxa). For a further review see Baker (1956) and Bir Bahadur (1968). In the last two decades several cases have been described in detail, e.g. in *Hymenocoleus* discussed above, *Carphalea* (Hed.; Puff 1988) and the Knoxieae (Puff & Robbrecht in press).

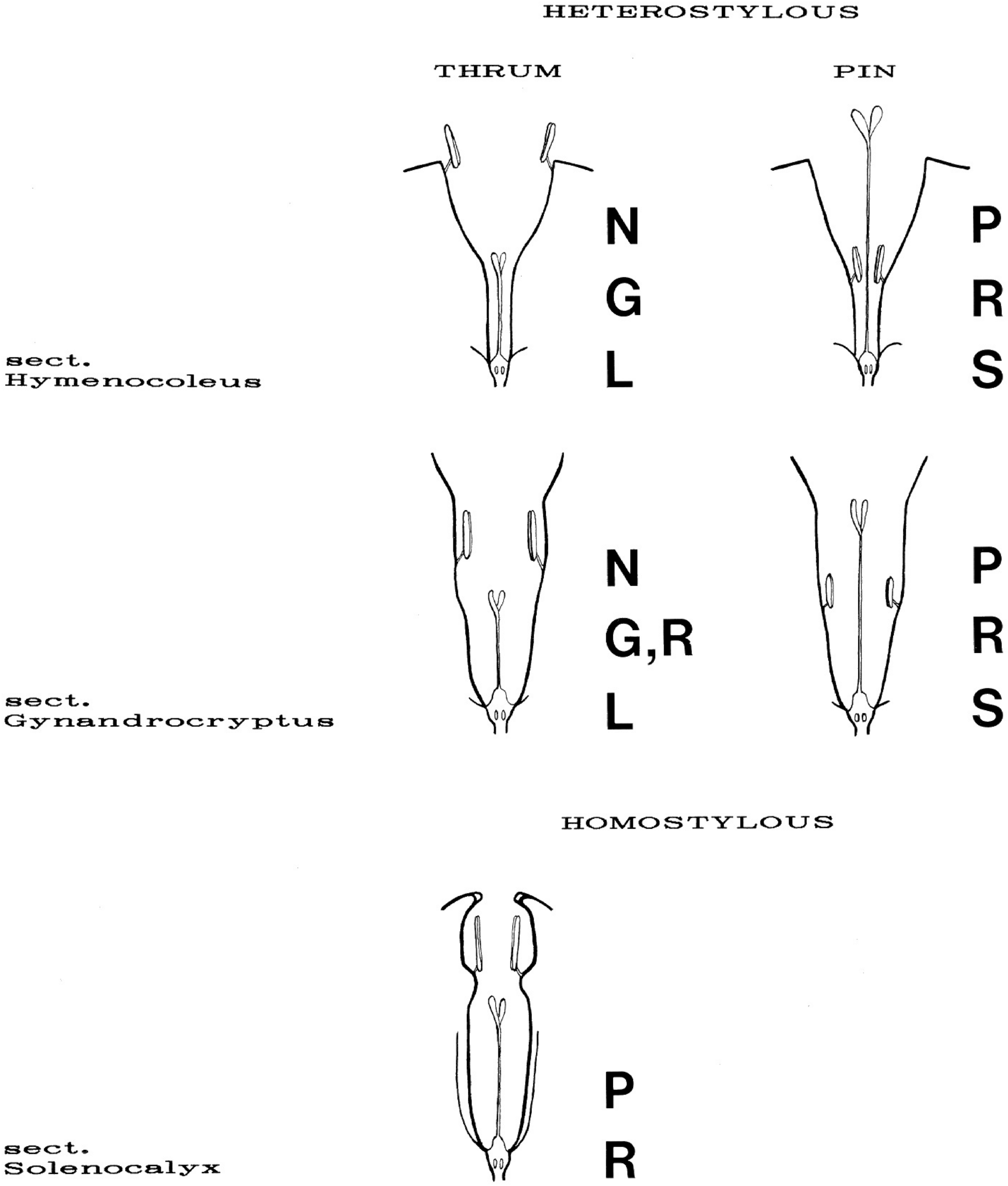


*Figure 47.- **Heterodistyly and pollen dimorphism** in the three sections of* Hymenocoleus. *The letters beside the schematics of the floral organization indicate pollen characters (N, nonaperturate; P: 2-5-porate; G, exine with large supratectal granules; R, exine reticulate; L or S: pollen diameter large or small compared to the pollen of the other floral morph).*
After Robbrecht (1975, 1977).

Homostylous individuals may occasionally occur along with the long- and short-styled ones; such cases have been documented in the Hedyotideae [*Pentas lanceolata* (Bir Bahadur 1970) and *Hedyotis coerulea* (Ornduff 1977)].

(iii) Unisexual flowers (fig. 46 B-E)

Unisexual flowers are reported in many taxa and occur perhaps in ca. 10 % of the genera. Whether these taxa are monoecious or dioecious is difficult to decide from herbarium data only, but apparently the dioecious condition prevails. Unisexuality has most probably evolved numerous times. It is obvious that heterodistyly often implies functional unisexuality, and may also lead to morphological unisexuality (Bawa 1980, 1984). The unisexuality of the Urophylleae e.g., is perhaps the ultimate consequence of heterostyly since this tribe is closely related to the heterostylous Pauridiantheae. Isolated cases of unisexuality occur in other typically heterostylous tribes, e.g. in *Dolicholobium* (Cin.-C.; Jansen & Ridsdale 1983), *Gouldia* (Ise.), *Kadua* (Hed.) and *Straussia* (Psy.) (Skottsberg 1944).

Unisexuality also occurs in other groups, e.g. in those Rubiaceae possessing the stylar pollen presentation. This was for the first and in great detail reported by Burck (1884) for *Canthium laeve*, Van., a dioecious species. In male individuals, the flowers behave exactly as in the hermaphrodites described above under (i); at anthesis the pollen is deposited on the ± spherical stigmatic organ; in females, the anthers are empty and the style has well developed receptive surfaces. This kind of unisexuality remained long undiscovered in many genera since is not easily observed on herbarium material, especially when the two flower morphs are rather similar, and differences are only revealed after careful dissections. Frequently the male flowers have a pistillode externally similar to the gynoecium of female flowers, with the ovary-cells empty, and the female ones have empty, somewhat smaller anthers (staminodes). For the rest male and female flowers are similar. This occurs in numerous Madagascan, Asiatic and American taxa of e.g. the Gardenieae and related tribes (Madagascan species of *Tricalysia*: fig. 46 B, C) and Vanguerieae; remarkably, it is almost absent from African representatives of the same groups. This kind of unisexuality becomes more obvious when the dimorphism involves other features than just the androecium and gynoecium. So in a number of dioecious genera, the female inflorescences are uni- or pauciflowered, while the male ones are many-flowered; for other cases of dimorphism and examples in the Gardenieae and relatives, see Robbrecht & Puff (1986: 106). In the past, this pronounced type of sexual dimorphism has resulted in the description of separate genera for female and male individuals, e.g. *Melanopsidium* (Gar.-G.) described from male material, redescribed *Rhyssocarpus* and *Pleurocarpus* from female material (Schumann 1891: 83).

Highly specialized unisexual flowers have evolved in a number of groups. Burck (1884: 22) described floral dimorphism in *Timonius sericeus*, Gue.: male flowers with five corolla-lobes, five anthers in the throat, a rudimentary style without lobes in the base of the corolla-tube, and a rudimentary ovary, and female flowers with ten corolla-lobes and ten staminodes, a ten-lobed exserted style and a well-developed ovary. Extreme sexual dimorphism is also found in the anemophilous flowers of the Anthospermeae (fig. 46 D, E) and the Theligoneae; generally the flowers have inconspicuous to hardly discernible remnants of the other sex. In the former tribe there is a wide array of variation in the distribution of hermaphroditic, male and female flowers, and the dimorphism of the corollas in size and shape (Puff 1982, 1986a). The monogeneric Theligoneae are generally monoecious; they have few male flowers in the upper part of the plants (viz. in the axils of alternate leaves) with only a well-developed corolla and a large number of versatile anthers. The female flowers are more numerous and occur in the basal parts of the plants, in the axils of opposite leaves; they are much smaller than the male flowers and have much-reduced corolla and a narrow gynobasic style on the originally inferior ovary (Wunderlich 1971).

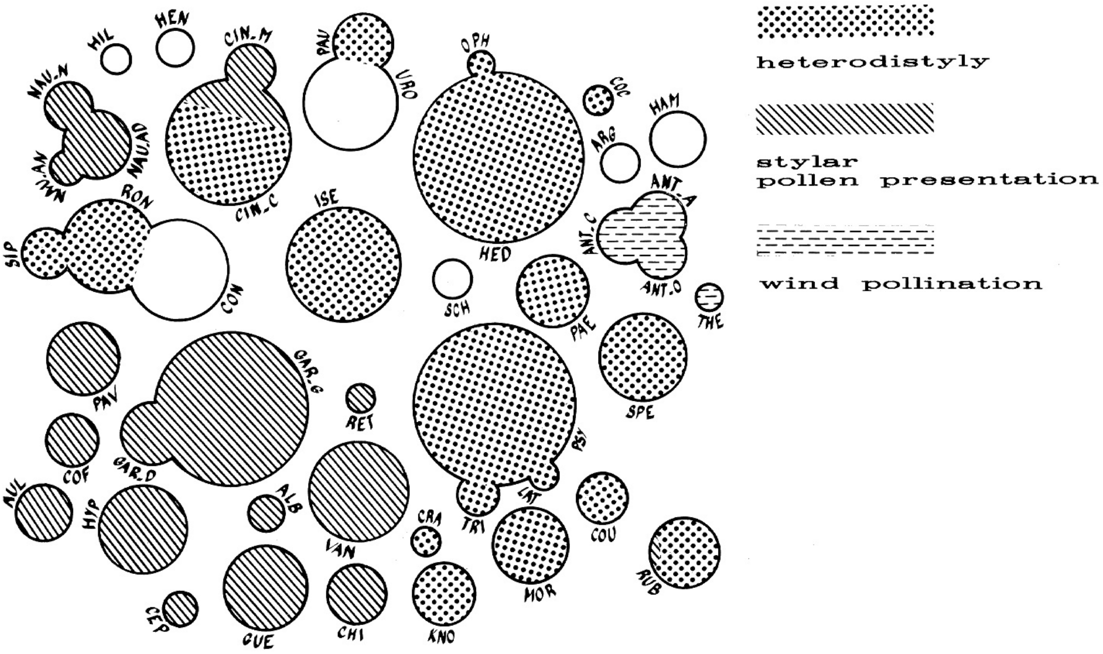


Figure 48.- ***Distribution of three complex floral mechanisms*** *in the tribes of the Rubiaceae, viz. heterodistyly, stylar pollen presentation, and wind pollination. Stylar pollen presentation and wind pollination are general in the shaded tribes; heterodistyly occurs in many species of the shaded tribes. White tribes: no peculiar floral mechanism known.*

Taxonomic significance: The distribution of the above discussed floral biological adaptations is strongly tribal-constant and even characterizes aggregates of tribes (fig. 48). Wind pollination is very restricted (Anthospermeae circle of affinity). Heterodistyly only occurs in the Isertieae and Hedyotideae aggregate, the Psychotrieae and associated tri-bes, as well as in the advanced Craterispermeae, Knoxieae, Spermacoceae and Rubieae. Apart from its occurrence in the Naucleeae and some Cinchoneae and Rubieae, stylar pollen presentation (often combined with unisexual flowers) characterizes only the tribes asociated with the Gardenieae and with the Vanguerieae, respectively. Bremekamp (1934: 11) was the first to realize that this latter mechanism characterizes "one of the main groups of the Rubiaceae" (his later subfamily Ixoroideae). Flower biology is indeed well correlated with a number of other trends, so that it has a high value for the delimitation of subfamilies (see 3.3).

2.13.4 Fruit biology

Reproduction rate: N. Hallé (1966: 17) distinguished two biological tendencies in the fruit set of the Rubiaceae. Their degree of reproduction is either low, only a small number of fruits attaining maturation in an inflorescence, or high, many of the ovaries developing into mature fruits. He gave no examples but stated that the former case is characteristic for the more primitive groups such as the Gardenieae. However, detailed observations throughout the family are needed; the results should be related with other features of the r and K strategies both of which are represented in the family. Also, flower and fruit abortion is a complex phenomenon strongly influenced by environmental factors; many important general questions concerning it remain unanswered (Stephenson 1981).

Diaspore dispersal: Entire fruits as well as syncarps, mericarps, pyrenes or seeds, may function as dispersal unit.

The fleshy-fruited taxa (e.g. Pavetteae, Hypobathreae, Psychotrieae; fig. 40 A, B) are probably all (endo)zoochorous. The larger fruits of some of the Gardenieae are probably eaten by larger mammals, including elephants (Robbrecht & Puff 1986), but smaller mammals and birds are probably the main dispersing agents of most of the rubiaceous fleshy fruits.

The diaspores of the dry-fruited taxa with one seed per locule (e.g. Knoxieae, Spermacoceae) are most frequently mericarps whose dispersal is often unspecialized (falling on the ground and moved around by chance; the mericarps frequently have thick endocarps ensuring a long viability). Wind-dispersed fruits (fig. 40 D, E) or mericarps also occur [e.g. *Alberta*, Alb.: mericarps with pterophylls, Puff, Robbrecht & Randrianasolo 1984; *Nenax*, Ant.-A. (from de-serts !): mericarps with lateral portions functioning as wings, Puff 1986a: 162].

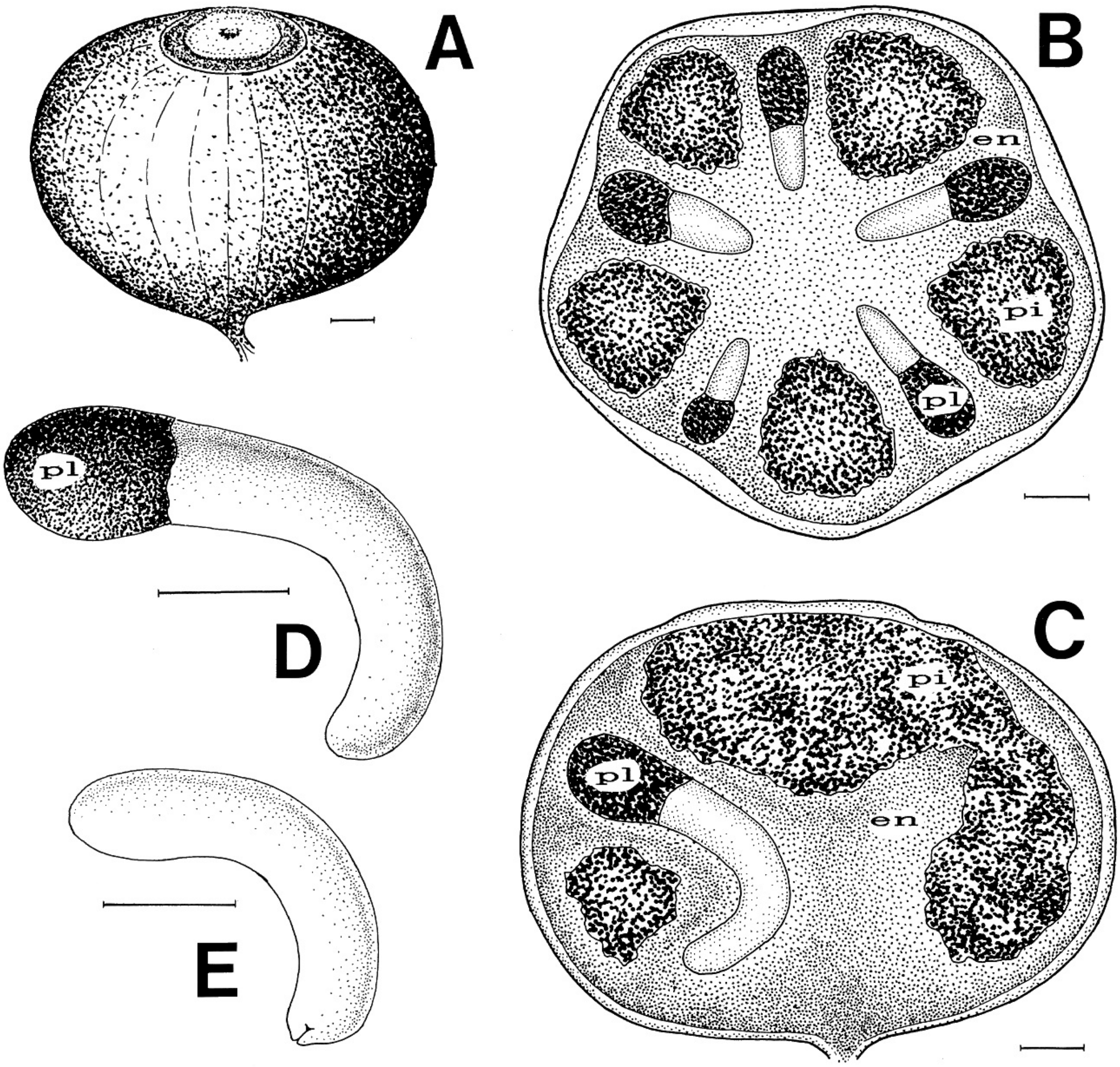


Figure 49.- ***Fruit with floating organ (long distance dispersal)*** *in* Guettarda speciosa*: A, fruit; B, C, transverse and longitudinal section of fruit; D, seed with stony arilloid tissue; E, embryo (en, endocarp; pi, cavities with pith-like, lacunar tissue in the endocarp; pl, stony outgrowth of the placenta).*
Lines = 2 mm.

In the many-seeded dry-fruited taxa (e.g. the Hedyotideae), the seeds generally function as diaspores. The dispersal is either anemochorous or hydrochorous. The dry fruits often show "pepper-box mechanisms" and open by narrow slits through which the seeds are sprinkled during a longer period; in *Otomeria* (fig. 40 C) or *Sacosperma* (Hed.) e.g. the endocarp valves are probably shaken inside the pericarp ribs where they remain enclosed. Taxa with small seeds with an apparent superficial exotesta network are probably hydrochorous (e.g. *Nauclea* sp., Nau., Abbiw 1988); it is likely that the meshes trap and hold air bubbles making the seeds float.

Of the seven types of wind-dispersed diaspores distinguished in the angiosperms (Van der Pijl 1982), three are present in the Rubiaceae.

- Dust seeds are relatively rare; they occur in a number of Hedyotideae, e.g. in *Lerchea*;
- plumed diaspores are limited to the Hillieae (see 2.10.1 for both categories); and
- winged diaspores, on the contrary, exist in many groups [winged seeds of the Naucleeae and Cinchoneae, see 2.10.1, fig. 43), fruits or mericarps with ("pterophylls") or wings, see above and 2.8.1.].

Long distance dispersal by sea-currents is very rare. In the widely distributed strand tree *Morinda citrifolia* (Mor., coasts from India and Malaysia to tropical Australia and eastern Polynesia), floating is effected by a large air-chamber, as already reported by Ulrich (1928: 143). The pyrenes have a bubble-like, excentric, air-containing outgrowth on one of their sides (fig. 41 F, G); this cavity in the inner wall of the pyrene is apparently schizolysigenous since it contains some traces of pith. The seashore tree *Guettarda speciosa* (Gue.; common on sandy beaches, rocky shores, and coral reefs, from East Africa to tropical Asia and Polynesia) has fruits which are common objects of the drift (Corner 1952: 542); they contain a plurilocular stone with a large cavity, situated between and above each of the 4-5 single-seeded cells, and filled with light pith tissue functioning as a floating organ (fig. 49). The mangrove shrub *Scyphiphora* (? Ret.; found from India to Australia) has fruits which abound in the sea-drift; they float, according to Tomlinson (1986), "because of the spongy layers of the inner fruit"; in fact the fruit contains a very hard and thick but light and fibrous pyrene, covered with a thin, fleshy mesocarp. The fleshy fruits of *Airosperma* (? Alb.) contain two pyrenes which are adapted for floating. Each pyrene (fig. 53) has - besides the cavity containing the seed - an adaxial core of lacunar tissue which widens towards the base; long-distance dispersal seems therefore the most plausible explanation for the discontinuous distribution of the genus (see Darwin 1980a). Finally Puff (1986a: 163) suggested that the diaspores of the coastal dune species *Anthospermum littoreum* (Ant.-A.) may be dispersed by sea currents; floatation results from air trapped by the long hairs of the mericarps.

Other dispersal mechanisms are absent or at least very rare in the Rubiaceae. Spermacoceae having seeds provided with an elaiosome (see 2.10.2) are probably myrmecochorous. Epizoochorous taxa seem limited to herbaceous Rubieae; the fruits of the European Cleavers (*Galium aparine*), densely covered with hooked bristly hairs, are the most common example. Schumann (1891: 8) also reported "Klettfrüchte" in a few Anthospermeae without mentioning them by name. Although Puff (1982, 1986a) deals in detail with the diaspore dispersal of the Anthospermeae, he does not mention such cases, and only tentatively suggests that the long, band-like persistent calyx lobes on the fruits of a few *Anthospermum* species may aid in epizoochorous dispersal. With regard to peculiarities of dispersal in epiphytic Rubiaceae, see 2.2.2.

2.14 Chorology

In the following, Takhtajan's (1986, English edition of 1978 Russian work) "Floristic Regions of the World", the most recent worldwide chorological division, is adopted. It has certain disadvantages, however. Generally accepted recent concepts for Africa (White 1983) e.g. are not incorporated.

2.14.1 Distribution of tribes

Many tribes, including all the larger ones, have a ± pantropical distribution, viz. the Cinchoneae, Isertieae, Gardenieae, Pavetteae, Guettardeae, Cephalantheae, Hedyotideae, Psychotrieae, Morindeae, Paederieae, Anthospermeae and Spermacoceae. The Rubieae are cosmopolitan and centred in temperate regions.

A few have a more restricted distribution. The Naucleeae, Coffeeae, Aulacocalyceae, Hypobathreae, Alberteae, Van-guerieae, Knoxieae and Argostemmateae are paleotropical; the Pauridiantheae and Craterispermeae are restricted to tropical Africa, and the Urophylleae to tropical Asia. The following tribes are neotropical: Henriquezieae, Hillieae, Retiniphylleae, Chiococceae (one genus, *Hodgkinsonia*, in Australia !), Coccocypseleae and Hamelieae.

2.14.2 Distribution of genera

2.14.2.1 Widely distributed genera

(i) Pantropical wide genera: Only a few genera of woody Rubiaceae are pantropical, e.g. *Uncaria* (Cin.-M.), *Ixora* (Pav.), *Cephalanthus* (Cep.), *Psychotria* (Psy.) and *Morinda* (Mor.). *Lasianthus* (Mor.) too is pantropical, but its distribution is very uneven. The genus is centred in tropical Asia (ca. 120 spp.) and Africa (ca. 20 spp.), and has two representatives in Central America (Robbrecht 1982c; see Gentry 1982 for a general discussion of the tropical Laurasian elements in the Isthmian area, and similar distributions in other families).

Guettarda (Gue.) is an essentially tropical American genus (ca. 100 spp.), but has two representatives in New Caledonia. In addition, the Old World coastal species *G. speciosa* is widely distributed from the eastern coast of tropical Africa eastward to the Pacific (see 2.13.4 for its dispersal by sea-currents).

(ii) Afro-Asiatic wide genera: Many genera are paleotropical, e.g. *Hymenodictyon* (Cin.-C.), *Mitragyne* (Cin.-M.), *Nauclea* (Nau.-N.), *Gardenia, Aidia, Catunaregam* (Gar.-G.), *Tarenna* and *Pavetta* (Pav.), *Psilanthus* (Cof.) and *Psydrax* (Van.). A few genera are centred in one of the two continents of the Paleotropis, but penetrate the other, e.g. *Kohautia* (Hed.; throughout tropical Africa and Madagascar, and a few spp. in Arabia, Pakistan, Iran and India; Mantell 1985), *Wendlandia* (Ron.; many species throughout tropical Asia, and one species reaching Arabia and NE Africa), and *Knoxia* (Kno., throughout tropical Asia, and two narrow endemic species disjunct in tropical Africa; Puff & Robbrecht in press).

Madagascan-Asiatic distribution patterns are of particular biogeographical interest; they are rare in Rubiaceae. The large genus *Timonius* (Gue.) occurs from the Mascarenes, Seychelles and Sri Lanka eastwards throughout Malesia to tropical Australia, Fiji and the Tuamotu Islands (Smith & Darwin 1988). The herbaceous genus *Paederia* (Pae.) is centred in SE Asia (to Japan) and Madagascar, and it also occurs on Mauritius, in eastern Africa and South America (Puff 1982).

(iii) Disjunct genera: Afro-American distributions are rare. Only two are well known, *Sabicea* (Ise.; ca. 60 spp. in tropical America, about as many in tropical Africa, and four in Madagascar) and *Bertiera* (inc. sed.; ca. 40 spp. in tropical Africa and a few species in tropical America).

Lindenia (Ron.) shows an interesting disjunction: one species limited to tropical Central America, one endemic to Fiji, and one to New Caledonia (Darwin 1976c: map 1). *Cephalanthus* (Cep.) has three species in tropical America, two from India to southeast Asia and one in southern Africa. *Mitchella* (inc. sed.) has one North American and one Japanese species.

For a discussion of the fragmented distribution of *Theligonum* (The.; one species Mediterranean + Canary Isl., another one Tibet, and a third one in Japan), see Puff (1986a: 519).

(iv) Continental wide genera

Asiatic wide: There are many Asiatic wide genera, to cite only a few examples: *Hypobathrum* (Hyp.), *Myrmecodia* and *Hydnophytum* (Psy.), *Coprosma* (Ant.-C.; centred in Neozeylandic Region !) and *Scyphiphora* (inc. sed.).

African and Afro-Madagascan wide: *Heinsia* (Ise.), *Pauridiantha* (Pau.), *Sericanthe* (Gar.-D.), *Otomeria*, *Pentodon* and *Virectaria* (Hed.) are examples of the numerous wide genera occurring throughout the tropical African continent.
The Afro-Madagascan genera are of particular interest.

- Some are widely distributed in Africa and Madagascar, e.g. *Breonadia* (Nau.-Ad.), *Tricalysia* (Gar.-D.), *Polysphaeria* (Hyp.), *Pentanisia* (Kno.), *Otiophora* (Puff 1981: map 687) and *Pentas* (Hed.).
- Others have a very limited distribution in eastern Africa, e.g. along a part of the Indian Ocean coast; examples are *Alberta* (Alb.; Puff, Robbrecht & Randrianasolo 1984), *Hyperacanthus* (Gar.-G.; Bridson & Robbrecht 1985b), *Carphalea* (Hed.; Puff 1988), *Danais* (Cin./Hed.), *Triainolepis* (Tri.) and *Phylohydrax* (Spe.; Puff 1986b: map 9).

According to Leroy (1978), the Madagascan Rubiaceae have much stronger affinities with the African flora than with the Asian one. This is certainly so for the first category above; these genera have the majority of their species throughout continental Africa. The genera quoted in the second category, however, have only one or two continental African and many Madagascan species; they are best interpreted as Madagascan elements penetrating in southern and eastern Africa.

American wide: Many genera have a wide distribution in tropical America, ranging roughly from Mexico (and S Florida) throughout Central America and the West Indies southwards through South America. A few examples are *Capirona, Remijia, Ladenbergia* (Cin.-C.), *Hillia* (Hil.), *Chimarrhis, Condaminea, Pogonopus, Rustia* (Con.), *Gonzalagunia* (Hed.), *Alibertia, Genipa, Amaioua, Tocoyena* (Gar.-G.), *Declieuxia, Palicourea* (Psy.), *Arcytophyllum* (Hed.), and *Hamelia* and *Hoffmannia* (Ham.).

2.14.2.2 Endemic genera

Most of the tropical and subtropical floristic regions of the world have endemic rubiaceous genera. The Guineo-Congolian, Madagascan, Indo-Chinese, Malesian, Neocaledonian and Amazonian Region in particular each harbour numerous endemic genera of Rubiaceae. The Region of the Guyana Highlands is the only montane area where numerous endemic rubiaceous genera have evolved, see (III 24) below. Prominent island endemism in the Rubiaceae occurs especially in Madagascar, Malesia, Fiji, New Caledonia and the West Indies, see (IIB 15), (IIC 18-19), (II D22) and (III 23) below. In Madagascar, the Rubiaceae are represented by 70-80 genera, of which more than one thirth are endemic; at the specific level, nearly all the 600 rubiaceous species are endemic (Leroy 1978).

The distribution of the endemic genera reflects the essentially tropical nature of the Rubiaceae. The temperate or subtropical Holarctis, Capensis, Australis and Holantarctis count only sixteen, two, four and three (sub)endemic rubiaceous genera respectively. The tropical kingdoms, Paleotropis and Neotropis, on the other hand each have a very large number of such genera.

The following list of endemic and subendemic (*) genera is adapted from Takhtajan (1986) and augmented; the indications in parentheses are his numbers and letters for the phytochoria. Regions not taken up lack endemic rubiaceous genera. Kirkbride (pers. comm.) completed the list for the (III 25) Amazonian, (III 26) Brazilian and (III 27) Andean Regions.

(I) HOLARCTIC KINGDOM **(I 2) Eastern Asiatic Region**	Cin.-C.: Himalaya, Yunnan: *Luculia* Cin./Hed.: *Dunnia* Van.: Taiwan + Ryukyu Isl.: *Tetraplasia* Mor.: *Damnacanthus* Pae.: *Pseudopyxis* inc. sed.: China, Yunnan: *Trailliaedoxa*
(I 3) North American Atlantic Region	Con.: *Pinckneya*
(I 5) Macaronesian Region	Pae.: *Plocama* Ant.-A.: *Phyllis*
(I 6) Mediterranean Region	Pae.: *Putoria* Rub.: **Warburgina* (Israel, Syria)
(I 7) Saharo-Arabian Region [after Léonard 1984; most genera penetrate also in (IIA 12) which is in need of redelimitation, however]	Pae.: *Choulettia, Jaubertia, Pseudogaillonia, Pterogaillonia*

(I 8) Irano-Turanian Region	Pae.: **Neogaillonia* (also Socotra!); Afghanistan: *Aitchisonia*
(II) PALEOTROPICAL KINGDOM **(IIA) AFRICAN SUBKINGDOM** **(IIA 10) Guineo-Congolian Region**: numerous genera, inter alia:	Cin.-C.: *Corynanthe, Pausinystalia* Ise.: *Ecpoma, Pseudosabicea, Temnopteryx* Pau.: *Commitheca, Stelechantha* Gar.-G.: *Preussiodora, Pleiocoryne, Oligocodon, Calochone, Macrosphyra, Atractogyne, Schumanniophyton, Pseudogardenia, Brenania, Morelia* Gar.-D.: *Sericanthe, Argocoffeopsis, Calycosiphonia, Petitiocodon* Pav.: *Leptactina, Dictyandra, Coleactina* Hyp.: *Pouchetia* Hed.: *Parapentas, Sacosperma* Psy.: *Hymenocoleus* Mor.: *Colletoecema* Cou.: *Schizocolea*
(IIA 11) Usambara-Zululand Region	Pav.: *Cladoceras* Hyp.: *Lamprothamnus* Hed.: *Chamaepentas, Dolichometra, Pseudonesohedyotis*
(IIA 12) Sudano-Zambezian Region Socotra: *Placopoda*	Nau.-N.: *Burttdavya* Kno.: *Calanda, Paraknoxia, Neopentanisia* Hed.: Somalia/Ethiopia Province: *Pentanopsis, Dibrachionostylus*;
(IIB) MADAGASCAN SUBKINGDOM **(IIB 15) Madagascan Region**: numerous endemic genera, probably *Janotia* only a few missing from the list; most of the genera *endemic* to Madagascar (frequently also Comores), a few to the *Mascarenes* (Masc.) or the Seychelles (Seych.):	Cin.-C.: *Paracorynanthe* Cin./Hed.: *Danais, Schismatoclada* Nau.-Ad.: *Breonia, Neobreonia, Gyrostipula,* Ron.: Seych.: *Glionnetia* Gar.-G.: **Hyperacanthus* (also SE Africa), *Mantalania, Pseudomantalania* Pav.: *Homollea, Homoliella, Paracephaelis, Schizenterospermum*; Masc.: *Doricera, Myonima* Hyp.: Canephora, Chapeliera, Flagenium, Gallienia, *Jovetia*; Masc.: *Fernelia, Ramosmania*;
Seych.:	*Paragenipa* Alb.: **Alberta* (also S Africa), *Nematostylis* Van.: *Peponidium*; Masc.: *Scyphochlamys* Psy.: *Psathura, Cremocarpon, Trigonopyren*;
Seych.:	*Neoschimpera* Tri.: **Triainolepis* (also E Africa), *Paratriainia, Thyridocalyx* Lat.: *Lathraeocarpa* Hed.: *Astiella* Spe.: **Phylohydrax* (also SE Africa)

(IIC) INDOMALESIAN SUBKINGDOM **(IIC 16) Indian Region**	Ise.: *Schizostigma*; Sri Lanka: *Leucocodon* Gar.-G.: *Byrsophyllum, Deccania* Hyp.: Hyptianthera, Scyphostachys; Sri Lanka: *Nargedia* Pae.: *Spermadictyon* Spe.: **Hydrophylax* (also Malay Penins.) ? Psy.: *Fergusonia*
(IIC 17) Indo-Chinese Region	Ron.: Burma: *Spathichlamys* Ise.: *Schizomussaenda* Gar.-D.: *Xantonneopsis* Aul.: *Alleizettella* ? Hyp.: *Pubistylus* Hed.: *Leptomischus, Mouretia, Paedicalyx, Xanthophytopsis*
(IIC 18) Malesian Region: numerous genera especially in the Malesian Subregion, inter alia (mostly after Van Steenis 1987b): ***(IIC 18A) Malesian Subregion*** *Didymo-* *Antherostele* *Sulitia*	Cin.-C.: Philippines: *Greeniopsis* Ron.: Malaya: *Aleisanthia*; Borneo: *Steenisia* Ise.: Borneo: *Streblosiopsis* Uro.: *Maschalocorymbus*; Borneo: *Crobylanthe, Stichianthus, Rhaphidura*; Sumatra: *pogon, Lepidostoma*; Philippines: Gar.-G.: Malaya: *Kochummenia*; Philippines: Aul.: Sumatra + Borneo: *Gardeniopsis* Hyp.: *Villaria, Zuccarinia* Van.: Malaya: *Perakanthus* Hed.: *Lerchea, Coptophyllum*; Borneo: *Siderobombyx, Phyllocrater* Psy.: Streblosa; Java: *Proscephaleium* Mor.: Sumatra: *Didymoecium* Jac.: *Jackiopsis*
(IIC 18B) Papuan Subregion	Ise.: *Siphonandrium* Pav.: **Versteegia* (also Polynesian), *Pachystylus* Hyp.: *Maschalodesme, Rhadinopus* ? Alb.: **Airosperma* (also Fijian) Psy.: *Chaetostachydium*
(IIC 19) Fijian Region *Squamellaria*	Gar.-G.: *Pelagodendron*, Sukunia Psy.: *Gillespiea, Hedstromia, Readea,* Mor.: *Sarcopygme*
(IID) POLYNESIAN SUBKINGDOM **(IID 21) Hawaian Region**	Gue: *Bobea*
(IID 22) Neocaledonian Region	Con.: *Morierina* Gar.-G.: *Atractocarpus, Neofranciella* Pav.: *Bonatia, Captaincookia* Mor.: *Imantina* Ant.-C.: *Normandia*

(III) NEOTROPICAL KINGDOM
(III 23) Carribean Region

Stylosiphonia,
Steyermarkia;

Cin.-C.: Mexico: Balmea, Syringantha; Cuba + *Hispaniola: Suberanthus*
Cin./Hed.: *Bouvardia*
Con.: Haiti: *Picardaea*
Ron.: *Rogiera, Arachnothryx*; Mexico: *Eizia, Habroneuron*; Guatemala: Honduras: *Javorkaea*; Panama: *Oregandra*; Cuba: *Acrosynanthus, Acunaeanthus, Roigella*; Cuba + Hispaniola: *Suberanthus*
Ise.: **Raritebe* (also Venezuela, Peru)
Gar.-G.: *Casasia*
Chi.: *Chione*; Cuba: *Shaferocharis*
Psy.: Panama: *Montamans*
Cat.: W. Indies: *Catesbaea*; Cuba: *Phyllacanthus*
inc. sed.: W. Indies: *Strumpfia*

(III 24) Region of the Guyana
Maguireocharis
Highlands (after Steyermark 1986)

Holstianthus,

Pagameopsis,

Cin.-C.: *Cephalodendron, Duidiana,*

Cin./Hed.: *Merumea*
Hen.: *Gleasonia*
Ron.: *Chalepophyllum, Dendrosipanea, Sipaneopsis, Neblinathamnus, Maguireothamnus*
Ise.: *Yutajea*
Psy.: *Coccochondra, Coryphothamnus, Aphanocarpus*

(III 25) Amazonian Region (all endemic to Amazonian Province, except Tammsia: Llanos Province)

Cin.-C.: *Capirona*
Hen.: *Henriquezia*
Con.: *Kerianthera*
Ret.: *Retiniphyllum*
Tam.: *Tammsia*
inc. sed.: *Bothriospora*

(III 26) Brazilian Region

Cin./Hed.: Atlantic Province: *Hindsia*
Ron.: Province of Uplands of Central Brazil: Augusta; Atlantic Province: *Standleya*
Gar.-G.: Atlantic Province: *Melanopsidium*
Chi.: *Caatinga: Salzmannia*
Hed.: *Caatinga: Leptoscela*; Atlantic Province: *Bradea*
Spe.: *Caatinga: Diacrodon*; Province of Uplands of Central Brazil: *Schwendenera*

(III 27) Andean Region

Cin.-C.: Joosia, Pimentelia, Wernhamia
Gar.-G.: *Dolichodelphys*
Hed.: *Arcytophyllum*
Ant.-C.: *Nertera*
Hip.: *Hippotis*
inc. sed.: *Phitopis*

(IV) CAPE KINGDOM
(IV 28) Cape Region

Ant.-A.: *Carpacoce*, **Nenax*

(V) AUSTRALIAN KINGDOM

(V 29) NE Australian Region	Chi.: _Hodgkinsonia_ Ant.-C.: _Durringtonia_ Ant.-O.: *_Pomax_, *_Opercularia_
(V 30) SW Australian Region	Ant.-O.: _Eleutheranthus_

(VI) HOLANTARCTIC KINGDOM

(VI 33) Chile-Patagonian Region	Cin./Hed.: *_Heterophyllaea_ (also Andean Region) Hed.: _Cruckshanksia, Oreopolus_

Chapter 3

DISCUSSION OF THE CLASSIFICATION OF THE RUBIACEAE

In this chapter, three subfamilial classifications of the Rubiaceae nowadays used are compared and evaluated against the trends and progressions of characters as surveyed in the previous chapter.

A survey of the history of the subfamilial classification of the Rubiaceae is not presented here, since a good one was given by Bremekamp (1966).

3.1 Existing subfamilial classifications

Three classifications of the Rubiaceae are now in general use. The first is the classical system of Hooker (1873), taken over with only a few modifications by Schumann (1891). This system remains the last worldwide treatment of the family at the generic level; it is still followed in certain recent floras (e.g. N. Hallé 1966, 1970, Steyermark 1974). Only two subfamilies are distinguished: the Cinchonoideae, character-ised by more than one ovule in each locule, and the Coffeo-ideae having one ovule in each locule. This distinction was criticized in the previous century because of the distant position of two obviously related tribes, the Gardenieae with many ovules in the Cinchonoideae and the "Ixoreae" with one

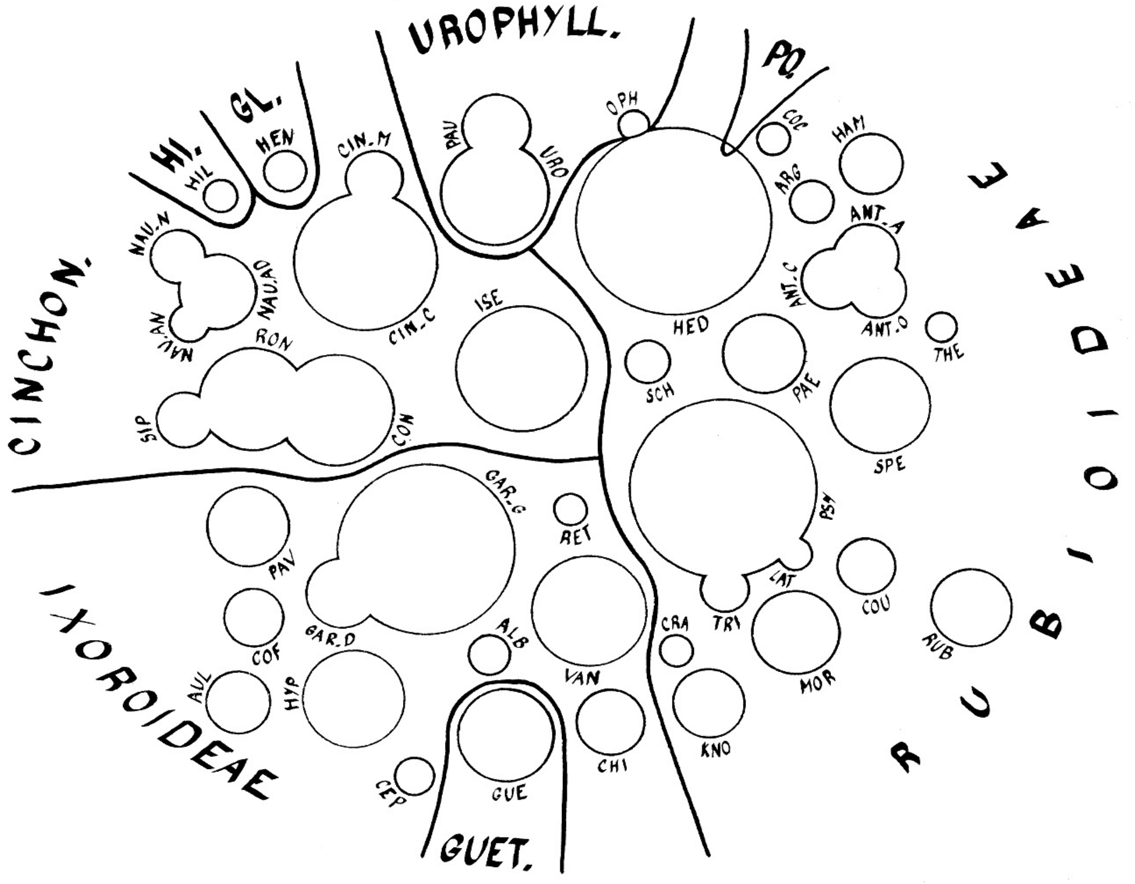


Figure 50.- Tribes and subtribes accepted here, arranged in ***Bremekamp's (1966) eight subfamilies*** *(HI., Hillioideae; GL., Gleasonioideae; GUET., "Guettardoideae"; PO., Pomazotoideae).*
*The Theligoneae (THE) and some other tribes (see table 5) were not considered by Bremekamp; the Cephalantheae (CEP) were included in Naucleeae; the Henriquezieae (HEN) in his system were split into the Rubiaceae-Gleasonioideae (*Gleasonia *only) and Henriqueziaceae (*Henriquezia *and* Platycarpum*).*

ovule in the Coffeoideae; Baillon (1878: 215) stressed that in species of *Tarenna* (then known as Webera) the number of ovules varies from one to several in each locule. Solereder (1893: 276) confirmed this after a comparative morphological study of the "Ixoreae" and Gardenieae and transferred "*Webera*" from the latter to the former tribe.

This historical evidence is confirmed by facts later discovered, and the number of ovules (2.8.4; fig. 37) no longer can be used for the main division of the family. **Bremekamp** searched for entirely different characters to define subfamilies. His classification slowly evolved throughout a life-time of taxonomic research in the family. In 1934 he indicated that a number of representatives, with the "ixoroid pollen mechanism" (stylar pollen presentation, see 2.13.3.2) in common, are "one of the main groups of the Rubiaceae". This group later became his subfamily Ixoroideae. In 1947(b), on the occasion of an evaluation of the differences between

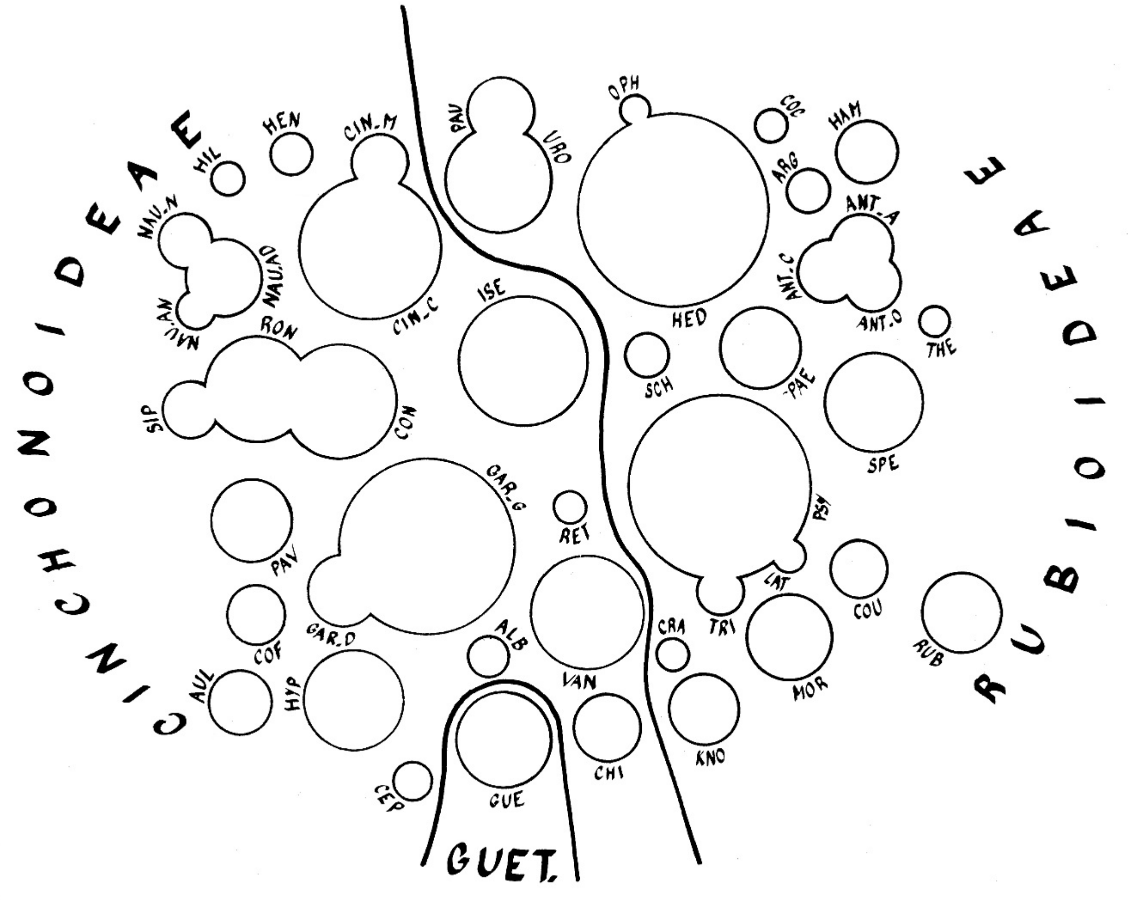


*Figure 51.- Tribes and subtribes accepted here, arranged in **Verdcourt's (1958) three subfamilies** (GUET., "Guettardoideae").*
Several tribes were not considered by Verdcourt (see table 5), and the Cephalantheae (CEP) were included in the Naucleeae.

Table 5.- **Comparison of Verdcourt's** (1958), **Bremekamp's** (1966) **and the present classification** of the Rubiaceae (dashes represent taxa not considered by Verdcourt or Bremekamp); in the middle the here proposed subfamilial placements of the tribes is indicated (CIN: Cinchonoideae; IXO: Ixoroideae; ANT: Antirheoideae; RUB: Rubioideae).
Notes: [1]: included in the Cinchoneae in this study; [2]: Bremekamp regarded the type genus of Alberteae to be of uncertain position; [3]: legitimate name Coffeeae (but present definition of that tribe much narrower than in Verdcourt's and Bremekamp's system); [4]: legitimate name Isertieae; [5]: Verdcourt only mentions inclusion of *Hillia* in the Rubioideae, without tribe indication; [6]: here included in the Hedyotideae; [7]: legitimate name Antirheoideae.
Also compare to figures 50, 51 and 61.

Schumann's tribes "Oldenlandieae" and "Mussaendeae", he introduced two other characters later crucial to defining his subfamily Cinchonoideae, characterized by a peculiar type of exotesta ("pitted testa", cfr. 2.10.3), and his subfamily Rubioideae, characterized by the presence of idioblasts with Ca-oxalate in the form of raphides (2.6.2). The main lines of his final classification are presented in 1952 (four subfamilies: Cinchonoideae, Ixoroideae, Rubioideae and Guettardoideae, and a number of tribes and genera of uncertain position). Later publications added minor alterations and principally concerned the recognition of several small, mostly monotribal subfamilies. In a survey in 1966, he recognized eight subfamilies (fig. 50; see 3.2.1-3.2.8), some of them doubtful and mainly intended provisionally; he declared that "before a fully satisfactory classification can be obtained, a con-siderable number of genera will have to be reinvestigated". In Thorne's (1983) classification of the angiosperms, the six main rubiaceous subfamilies of Bremekamp are accepted.

Verdcourt (1958) carried out a comparative study of representatives from 104 genera selected amongst all tribes accepted in the classification of Hooker (1873). He examined traditional morphological features and also the seed-coat anatomy (exotesta in surface view), trichomes, and pollen, and determined the presence or absence of raphides. He accepted Bremekamp's subfamilies Rubioideae (bringing together all representatives with raphides) and "Guettardoideae" (monotribal, characterized by a large embryo and strongly reduced endosperm), but rejected the "pitted testa" as a taxonomically unimportant character. All Rubiaceae with normally developed endosperm and without raphides were therefore united in the Cinchonoideae with much broader delimitation than Bremekamp's subfamily of the same name. Besides this, Verdcourt also accepted a smaller number of tribes, including e.g. the Sabiceeae in the "Mussaendeae", the Gaertnereae in the Psychotrieae, etc. Verdcourt's classification is the one that is now mostly followed in general treatises of the flowering plants (e.g. Heywood 1978, Mabberley 1987).

Table 5 and fig. 50 & 51 compare these two modern classifications in detail. In paragraph 3.2, Bremekamp's subfamilies are used as the units of discussion.

VERDCOURT 1958			BREMEKAMP 1966	
	--	CIN	Coptosapelteae[1]	IXOROIDEAE
	--	CIN	Acranthereae	
CINCHONOIDEAE S.L.	Alberteae	ANT	?[2]	
	Ixor. Cremasporinae	IXO	Cremasporeae	
	Ixoreae[3] Ixorinae	IXO	Ixoreae[3]	
	Gardenieae	IXO	Gardenieae	
	Chiococceae	ANT	Chiococceae	
	Vanguerieae	ANT	Vanguerieae	
	Catesbaeeae	???	--	
	Retiniphylleae	ANT	--	
	Cinchoneae	CIN	Cinchoneae	CINCHONOIDEAE S.S.
	Naucleeae	CIN	Naucleeae	
	(incl. Cephalantheae)	ANT	(incl. Cephalantheae)	
		CIN	Condamineeae	
	Rondeletieae s.l.	CIN	Rondeletieae s.s.	
	(incl. Cond., Sip.)	CIN	Sipaneeae	
	Mussaendeae[4]	CIN	Mussaendeae[4]	
	(incl. Sabiceeae)	CIN	Sabiceeae	
RUBIOIDEAE	Urophylleae s.l.	CIN	Urophylleae s.s.	UROPHYLLOIDEAE
	(incl. Pauridianth.)	CIN	Pauridiantheae	
	Ophiorrhizeae	RUB	? Ophiorrhizeae	
	Hedyotideae	RUB	Hedyotideae	RUBIOIDEAE
	Cruckshanksieae	RUB	Cruckshanksieae	
	Argostemmateae	RUB	Argostemmateae	
	Coccocypseleae	RUB	Coccocypseleae	
	Schradereae	RUB	Schradereae	
	Hamelieae	RUB	Hamelieae	
	Spermacoceae	RUB	Spermacoceae	
	Anthospermeae	RUB	Anthospermeae	
	Rubieae	RUB	Rubieae	
	--	RUB	Perameae	
	Psychotrieae	RUB	Psychotrieae	
	(incl. Gaertnereae)	RUB	Gaertnereae	
	--	RUB	Triainolepideae	
	--	RUB	Lathraeocarpeae	
	Coussareeae	RUB	Coussareeae	
	Paederieae	RUB	Paederieae	
	Morindeae	RUB	Morindeae	
	Knoxieae	ANT	Knoxieae	
	Craterispermeae	ANT	Craterispermeae	
	Hillia[5]	CIN	Hillieae	HILLIOIDEAE
	--	CIN	Gleasonieae	GLEASONIOIDEAE
	--	RUB	Pomazoteae[6]	POMAZOTOIDEAE
GUETTARDOIDEAE[7]	Guettardeae	ANT	Guettardeae	GUETTARDOIDEAE[7]

Recent studies: Despite Bremekamp's emphasis on the provisional nature of his classification, and the profound differences between his and Verdcourt's system, no attempt has been made to improve or reconcile the two classifications. Only Takhtajan (1980), in his general outline of the classification of flowering plants, proposed a system with five subfamilies (Cinchonoideae, "Guettardoideae", Ixoroideae, Rubioideae and Henriquezioideae). The scope of his work did not allow discussion of his subfamilial delimitation, and it is not clear whether he followed Bremekamp's (1952) classification or intended a system in-between the ones of Verdcourt (1958) and Bremekamp (1966). However, there have been several recent amendments to the circumscription of the family (Wunderlich 1971: inclusion of Theligonaceae as Theligoneae; Rogers 1984: inclusion of Henriqueziaceae as Henriquezieae, with the three genera *Henriquezia*, *Platycarpum* and *Gleasonia*) and discussions of the delimitation of several tribes, e.g. redelimitation of the Naucleeae s.l. (Ridsdale 1975b, 1976, 1978a, b), Paederieae and Anthospermeae (Puff 1982), Alberteae (Puff, Robbrecht & Randrianasolo 1984), Gardenieae s.l. (Robbrecht & Puff 1986), and Argostemmateae and Hamelieae (Bremer 1987). Some recent studies approached the problems of the subfamilial classification of the Rubiaceae using methods beyond those of classical taxonomy:

Chemotaxonomy: A **serological** study (Lee & Fairbrothers 1978) in the first place attempted to determine the most appropriate position of the Rubiaceae in the Asteridae, a subject not dealt with in the present paper. This research compared various taxa belonging to fourteen genera of Rubiaceae with various taxa mainly from Gentianales and Dipsacales families. As to intrafamilial relationship, they concluded the following grouping of the examined genera:

- Cof.: Coffea; Gar.: *Gardenia, Posoqueria*; Van.: *Vangueria* (and possibly Cin./Hed.: *Manettia*);
- Rub.: Asperula, *Galium* (and possibly Spe.: *Richardia*);
- Psy.: *Psychotria* and *Palicourea*; and
- Mor.: *Morinda* and Hed.: *Pentas*.

This groups correspond better with present-day (Verdcourt 1958, Bremekamp 1966 and system proposed here) than with earlier classifications (Schumann 1891) of the Rubiaceae, but of course include far too few representatives to allow further conclusions.

Kisakürek, Leewenberg & Hesse (1983) found that the main **alkaloids** occurring in the Rubiaceae are indole alkaloids, quinoline alkaloids (including quinine type), and isoquinoline alkaloids (including emetine types).

At present, the Cinchoneae-Cinchoninae are the only group from where all three types are recorded. However, the taxonomic distribution of these alkaloid types in the rubiaceous tribes is only fragmentarily known. These authors' paper is in the first place a sound chemotaxonomic investigation of the indole alkaloids of Apocynaceae, Loganiaceae and Rubiaceae. They classified these constituents in eight main skeletal types, of which only three were found in Rubiaceae, namely alkaloids of the corynanthean, vincosan and vallesiachotoman type, which have a relatively simple structure and occur in all three families. While the presence of alkaloids is known from many rubiaceous genera, the structure of the indole alkaloids is determined in only 17 rubiaceous genera (the Apocynaceae and Loganiaceae are better documented). Biochemical research of Rubiaceae has concentrated on the Cinchoneae and Naucleeae (cfr. the importance of quinine), and these 17 genera essentially belong to them. Otherwise indole alkaloids are only identified in *Isertia* (Ise.), *Pauridiantha* (Pau.), *Antirhea* and *Guettarda* (Gue.), *Cephalanthus* (Cep.) and *Palicourea* (Psy.). It is thus obvious that the present knowledge of rubiaceous indole alkaloids is insufficient for chemotaxonomic conclusions on the subfamilial classification. Kisakürek, Leeuwenberg & Hes-se evaluated their results in comparison with the "classification of Leeuwenberg" and the "classification of Ehrendorfer", two variants of Verdcourt's system. Their main conclusion is that the "Mitragyneae" (Cinchoneae-Mitragyninae) and Cephalantheae biochemically differ from the Naucleeae.

A numerical chemotaxonomical study of the Rubiaceae (Kiranmai & al. 1985) deals with only 19 species (from 11 genera) screened for 19 secondary constituents. The resulting data are to scanty to admit discussion at tribal or subfamilial level. Two other chemotaxonomic papers deal with the occurrence of **iridoid glycosides** and their biosynthetic pathway. Although they are also too limited in regard to the number of taxa investigated to allow far-reaching taxonomic conclusions, they are interesting in that Kooiman (1969) detected asperuloside and *Galium* glycosides only in members of Bremekamp's (1966) subfamily Rubioideae, and *Gardenia* glycosides only in taxa of the Gardenieae (Bremekamp's Ixoroideae), while these three types of glycosides were not found in Bremekamp's other subfamilies. He concluded that Bremekamp's system was the one best relied to this chemical findings. On the other hand, Inouye & al. (1988) compared their findings to the subfamilial classification proposed in the present paper (3.3) and concluded that the examined Ixoroideae contain various types of iridoid glycosides such as gardenoside, geniposide and ixoroside, the studied Cincho-noideae and Antirheoideae loganin, secoiridoids and/or indole alkaloids, and the examined Rubioideae asperuloside and/or deacetylasperulosidic acid.

Cladistics: The only cladistic study encompassing the entire family is Garcia Kirkbride's (1982) "preliminary phylogeny for the neotropical Rubiaceae". It is no more than an attempt to give a cladistic interpretation to Verdcourt's (1958) division into three subfamilies, based on a polarity determination of the two characters considered of primordial value in this classification, viz. the presence or absence of endosperm and the presence or absence of raphides. The above-mentioned study of Argostemmateae and Hamelieae (Bremer 1987) was conducted according cladistic principles.

3.2 An evaluation of Bremekamp's subfamilies

3.2.1 Ixoroideae

Bremekamp (1966) included here all those tribes in which the upper part of the style acts a pollen presenter, in his terminology have the "ixoroid pollen mechanism" (2.13.3.2). Other important features are the undivided interpetiolar stipules, insertion of the stamens in the corolla-throat, and absence of raphides.

Three of the tribes included here, the Cremasporeae, the Gardenieae and the "Ixoreae" were not well delimited in 1966. New delimitations for the Gardenieae and related tribes have recently been proposed. Robbrecht & Puff (1986) recognized five tribes: the Gardenieae, Pavetteae (syn. "Ixoreae"), Hypobathreae, Aulacocalyceae and Coffeeae. These tribes have many important features in common, viz.

- more or less peltate fleshy placentas attached to the middle, rarely towards the top of the septum, and ± growing out in the fruiting stage, in the Gardenieae to completely embed the seeds,
- contorted aestivation of the corolla-lobes,
- stylar pollen presentation,
- common occurrence of unisexual flowers, especially in tropical Asian or American representatives,
- fleshy nature of the fruit, and
- generally horny endosperm.

I propose to restrict the Ixoroideae to these five tribes.
Indeed, the other tribes included in the Ixoroideae by Bremekamp, are related to other groups of Rubiaceae or remain of uncertain position. The Vanguerieae and Chiococceae show remarkable similarities to one another and to the Guettardeae; accordingly, they occupied a position close to one another in Hooker's (1873) and Schumann's (1891) classification. See 3.2.2.

The Acranthereae are monogeneric. *Acranthera* is characterized by a feature reminiscent of the Asclepiadaceae and occurring in no other Rubiaceae: the sterile appendages of its anther-connectives are fused. I had no material of *Acranthera* available for examination. Bremekamp stressed the peculiar exotestal cells ("with a very densely punctate wall"), but his depiction (1947b: fig. 1) and description can only be understood after additional study of material in cross-section. From later statements (Bremekamp 1952: 16) it seems plausible to accept that the exotestal cell structure in *Acranthera* fits well with that of many members of the Pauridiantheae and Urophylleae (thickened radial and inner tangential walls provided with a large number of narrow pit-canals, fig. 44 B, 57 K). Since the situation in *Pauridiantha* shows that this exotestal cell type may be derived from the type with larger pits (cfr. 3.2.3), *Acranthera* might be referred again to its original position in the Isertieae.

The Coptosapelteae were erected by Bremekamp (1952: 17) to include two former members of the Cinchoneae, viz. *Coptosapelta* and *Crossopteryx*, both exhibiting stylar pollen presentation and contorted aestivation of the corolla-lobes. Verdcourt (1958: 252) agreed with the transfer of *Coptosapelta* to a position near the "Ixoreae", but retained *Crossopteryx* in the Cinchoneae, a viewpoint that I share since *Crossopteryx* has dry capsular fruits with winged seeds and exotestal cells characteristic of the Cinchoneae. Bremekamp certainly overemphasized the value of the single character of the stylar pollen presentation.

I am also in doubt about the inclusion of *Coptosapelta* in the Ixoroideae. Although its exotestal cells have thickenings along the radial walls only, the genus has many other features in common with the Cinchoneae, inter alia dry fruits, winged seeds, and placentation. The Cinchoneae and associated tribes are much in need of a revision of their delimitations (see e.g. Aiello 1979) and in the mean time *Coptosapelta* may best be maintained in its original position where it seems, however, rather isolated; this is confirmed by its 3-porate pollen, and peculiar T-shaped trichomes (see 2.6.3, fig. 19 H) which probably occur nowhere else in the family.

3.2.2 "Guettardoideae"

Bremekamp's (1952) main criteria to distinguish this subfamily are the thinness of its endosperm (in his 1966 version overrated as "exalbuminous seeds") and the comparatively large size of its embryo; he further mentions the uni-ovular locules, the absence of raphides, the drupaceous fruits, and the presence of Ca-oxalate crystals in the wall of the hairs. It should be noted also that the single ovule is pendulous and consequently the embryo-radicle superior.

The latter feature is relatively rare in the Rubiaceae. All the Rubiaceae having a single pendulous ovule attached to a small placenta at the top of the ovary cells, are united in Schumann's classification in a supertribe "Guettardinae" comprising the Alberteae, Knoxieae, Vanguerieae, Guettar-deae and Chiococceae (compare fig. 37). All these tribes show so striking similarities in their flowers and fruits, that Bremekamp's and Verdcourt's dispersal of the "Guettardinae" over different subfamilies resulted, no doubt, in a more artificial classification.

The Knoxieae, Guettardeae, Vanguerieae and Chiococceae have the following characteristics in common:

- placentation (see above),
- drupaceous fruits,
- relatively thin seed-coat with exotestal cells parenchymalike or with delicate thickenings along the inner tangential wall,
- occurrence of one or more vascular strands in the seed-coat, and
- oily endosperm.

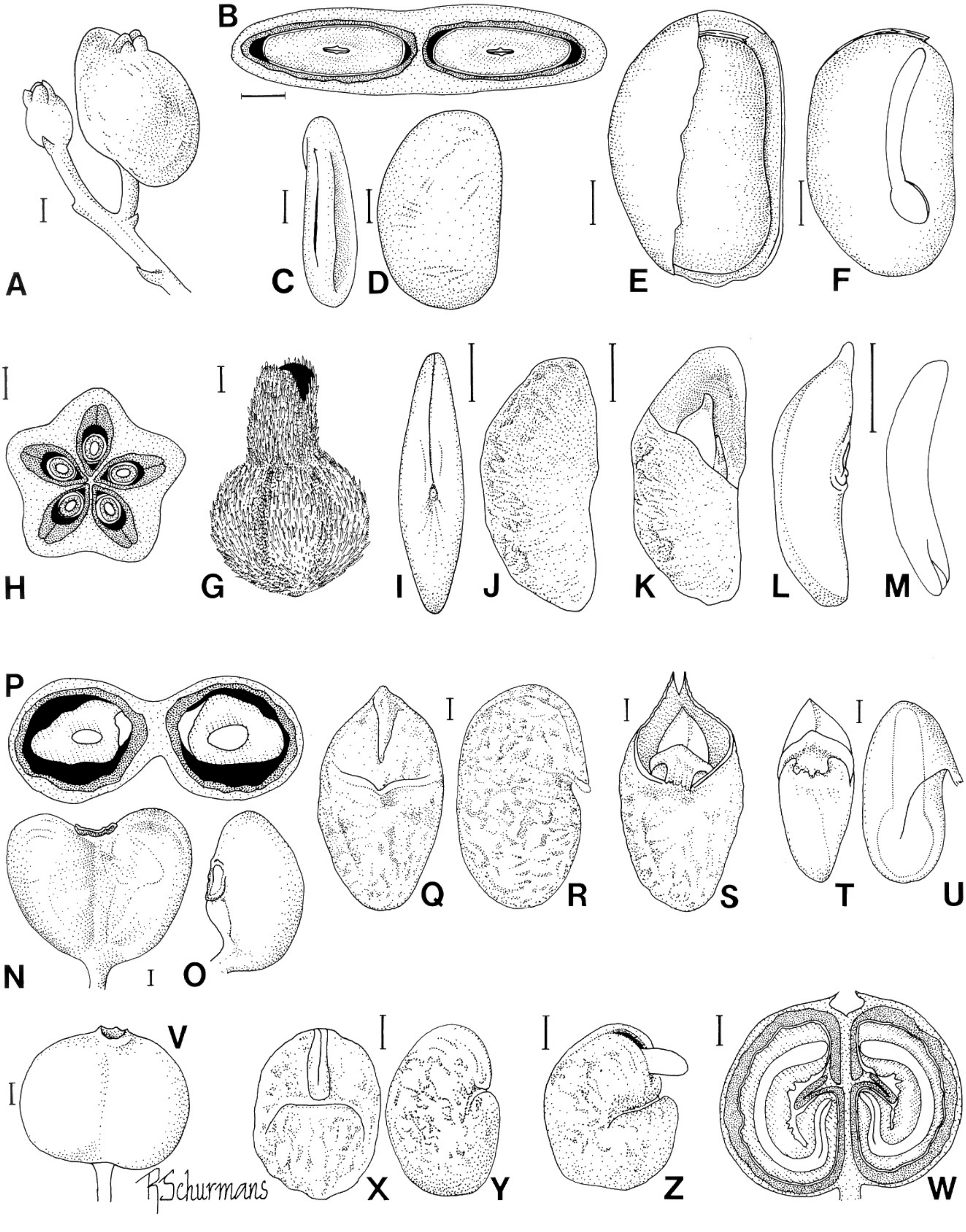
The last three tribes also share

- floral biological adaptations, viz. pollen presentation by means of swollen or capitate styles, and flowers also often unisexual, and
- entire interpetiolar stipules.

The Knoxieae are different in respect to these two last characters; they have heterostylous flowers and fimbriate stipules. Further common features are the frequent occurrence of crystals in the lumina of the often elongate, unicellular trichomes (not only in Guettardeae) and the common development of placental outgrowths in the fruiting stage.

Among the variable characteristics are aestivation of the corolla-lobes, presence of raphides (only in the Knoxieae; isolated needle-shaped crystals in some Vanguerieae !), and development of the endocarp; individual pyrenes (fig. 52) occur in Vanguerieae, Chiococceae and some Knoxieae and Guettardeae, and have apical preformed opening slits, while in some Knoxieae and most Guettardeae (fig. 49) the endocarp becomes massive and plurilocular. The amount of endosperm in the seed is also variable, and correspondingly the relative size of the embryo. In the Guettardeae, there is only a thin remnant (sometimes only a few cell layers) of endosperm around a large embryo; these may easily be overlooked (cfr. Bremekamp's 1966 over-statement on "Guettardoideae": "endosperm absent"). In fact early endosperm resorption, and consequently large embryos, exist in most other groups related to the Guettardeae; the embryos are quite large (length ± equal to length of the seed), but the endosperm is easily distinguishable.

Figure 52.- ***Fruits and seeds of Antirheoideae****: A, G, N, O & V, fruits; B, H & P, cross-section of fruits; C, I, Q & X, adaxial and D, J, R & Y, lateral view of pyrenes; E, K, S & Z, pyrenes opened artificially to show preformed slits; F, L, U, lateral view of seeds (embryo position indicated); M, embryo; T, adaxial view of a seed; W, longitudinal section of a fruit. Sections, from outside to inside: exocarp, mesocarp (stippled), endocarp (coarsely stippled), air-space (black), seed-coat, endosperm (striped) and embryo.*
A-F, Chiococca belizensis*; H-M,* Retiniphyllum schomburgkii*; N-U,* Canthium lactescens*; V-Z,* Psydrax livida.
All lines = 1 mm.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Because of the above, I propose to give Schumann's supertribe "Guettardinae" subfamilial rank. The following elements can also easily be accommodated in the thus emended Antirheoideae (the legitimate name for "Guettardoideae", see 1.5):

(i) The Alberteae (after transferring the majority of the genera to the Gardenieae and related tribes)

Puff, Robbrecht & Randrianasolo (1984) came to the conclusion that the Alberteae are to be limited to the genera *Alberta* and *Nematostylis* (and perhaps a few other poorly known genera) and that they are best placed near the Vanguerieae and Chiococceae. Features of *Alberta* and *Nematostylis* corresponding to my definition of the subfamily are the stylar pollen presentation, single pendulous ovule, well developed endocarp with apical preformed splits, tendency to zygomorphy, anatomy of the exotestal cells, development of placenta in fruiting stage, and oily endosperm. More or less anomalous on the other hand, is the contorted aestivation of the corolla-lobes and the small size of the embryo. For a complete documentation and illustrations of these features, see Puff, Robbrecht & Randrianasolo (1984).

We briefly discussed *Boholia* and *Airosperma* in the same paper, but no material was available then, so it was concluded that the two genera could only tentatively be maintained in the Alberteae. However, material of both genera was available for the present study, allowing more extensive comments.

The genus ***Airosperma*** was recently revised and documented (Darwin 1980a), including detailed S.E.-micrographs depicting the pollen of all species; the pollen is consistently 3-porate, but the exine is very variable (from tectate and semitectate to intectate); information about fruit and seeds is lacking, however. The fruits (fig. 53) of *Airosperma* are fleshy and contain two pyrenes which are adapted to floatation (see 2.13.4: long distance dispersal). As a result of the pendulous position of the ovules in the flower, the seeds are pendulous and the embryo-radicle points upwards. The exotesta consists of parenchyma-like cells; from the top of the seed, vascular bundles penetrate deeply in the seed-coat. The endosperm is very oily.

Boholia comprises a single species from the Philippines (*B. nematostylis*). The terminal inflorescences consist of alterna-te flowers disposed in raceme-like partial inflorescences. The very short corolla-lobes are contorted to the left. The sagittate anthers are subsessile in the throat and have one apical and two basal sterile appendages. The long exserted style is swollen at the tip (perhaps a receptaculum pollinis) and crowned by two very short lobes. The pollen grains are radially symmetric, isopolar, circular in polar view and

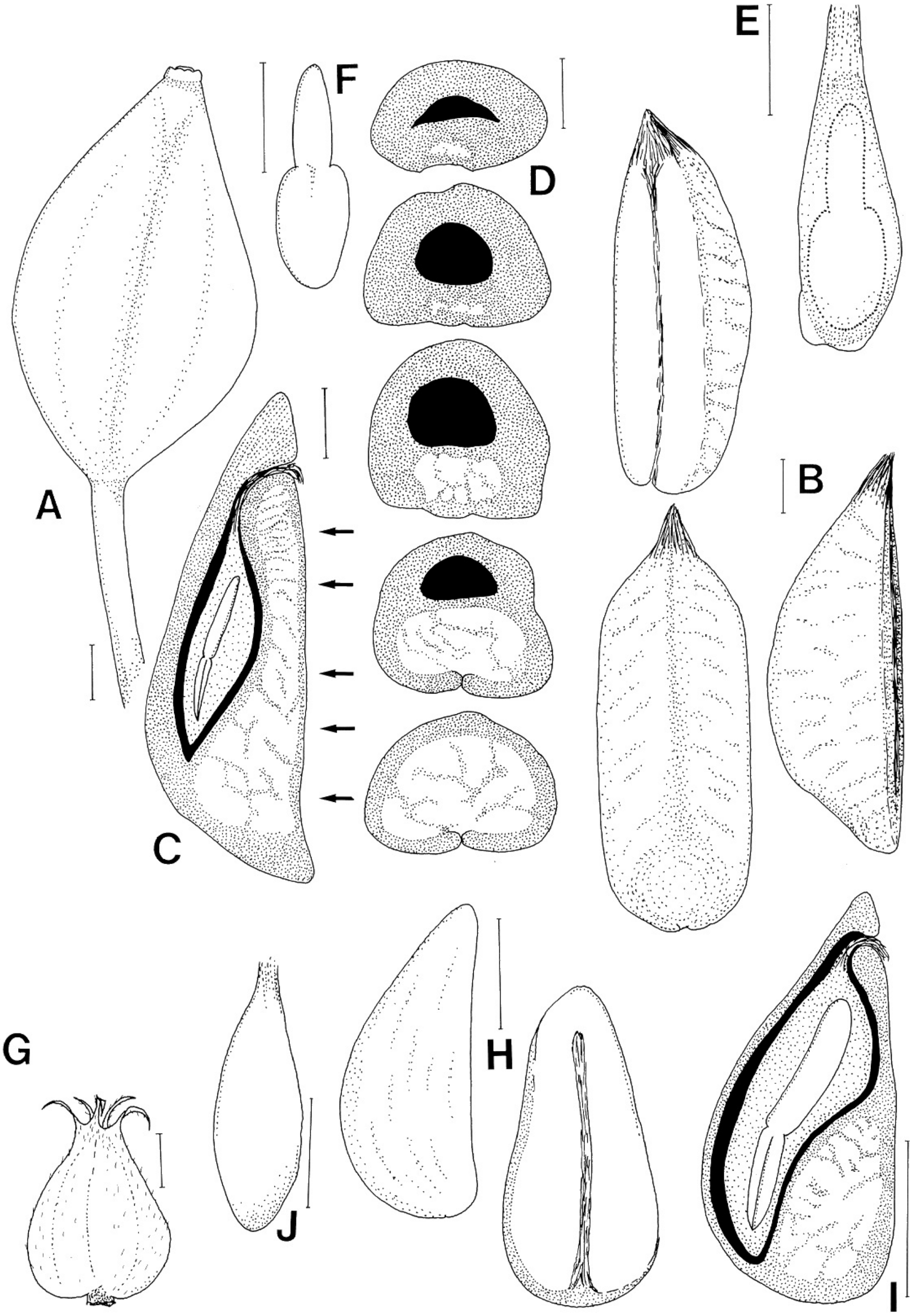


Figure 53.- ***Fruit and seed of Airosperma*** *(A-F,* A. trichotomum *and G-J,* A. psychotrioides*): A, G, fruit containing two pyrenes; B, adaxial, abaxial and lateral view of a pyrene; C, I, longitudinal section of a pyrene [from outside to inside: endocarp with lacunar tissue at adaxial side, air-space (black), endosperm and embryo]; D, series of cross-sections of a pyrene, as indicated by arrows in C [endocarp (with lacunar part) stippled, seed cavity black, seed not shown]; E, J, seed (in E embryo position indicated by dotted line); F, embryo; H, lateral and adaxial view of a pyrene.*
Lines = 2 mm.

3-zonoporate. The grains are suboblate and large (P = 64-74 µm and E = 68-80 µm). The exine is semitectate; the lumina of the reticulum are wide, ca. 3 µm in diameter. The fleshy fruits (fig. 54 A) contain two pyrenes (fig. 54 B); the mesocarp has abundant crystal sand; elongated aggregates of it remain attached to the endocarp and superficially resemble raphides. At the top of the endocarp, there are two short lateral grooves (fig. 54 C) having no obvious function; a preformed opening slit was not detected. The seeds (fig. 54 F) are pendulous and winged at the base; they contain a very short embryo with superior radicle. The exotestal cells of the seed-coat are parenchyma-like; the endotesta is crushed by the development of the endosperm; the outer layers of the latter contain abundant crystal sand.

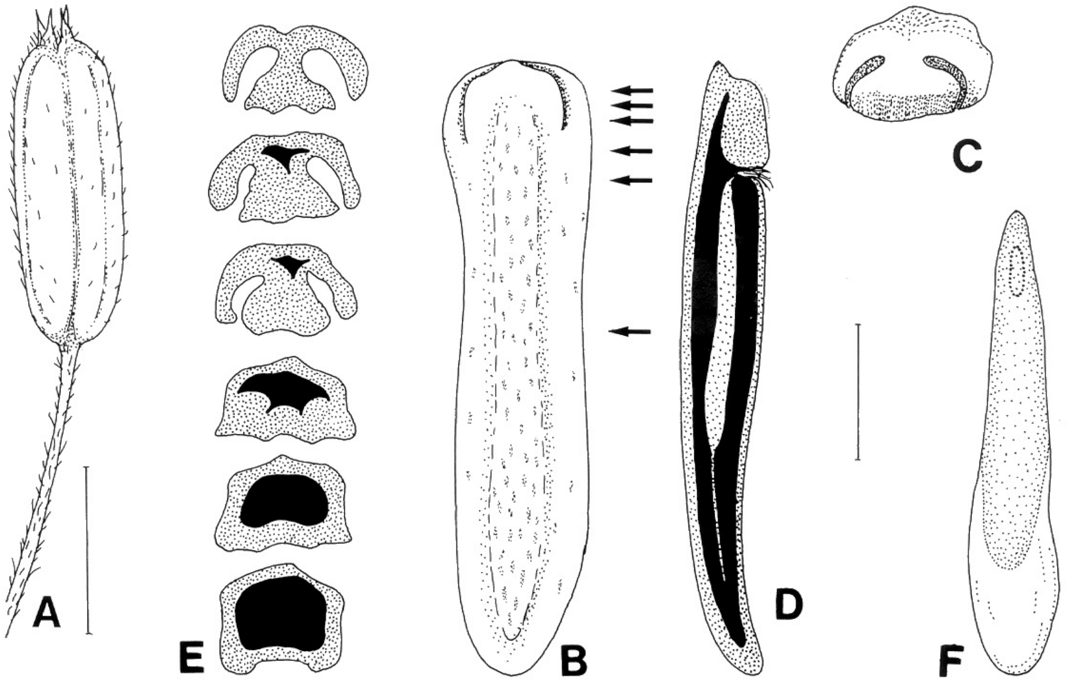


*Figure 54.- **Fruit and seed of Boholia nematostylis**: A, fruit, containing two pyrenes; B, adaxial view of a pyrene (numerous elongated aggregations of crystal sand adherent to it, especially in the central groove); C, apical view of a pyrene, showing its two lateral grooves; D, longitudinal section of the pyrene [from outside to inside: endocarp, air-space (black) & seed]; E, series of cross-sections through pyrene as indicated by arrows in B [endocarp stippled; central cavity, the seed removed, black; the apical grooves do not connect to the seed cavity] ; F, seed (embryo position indicated by dotted line).*
Line to A = 5 mm, to all other ones = 2 mm.

Thus it is obvious that these two genera belong to the Antirheoideae sensu meo; they are probably best maintained in the Alberteae. There are remarkable similarities

- between *Boholia* and *Nematostylis* in the corolla shape, the style and the anther appendages,
- between *Alberta magna* and *Airosperma* in the formation of cavities of lacunar tissue in the endocarp, *and*
- between *Airosperma, Rhopalobrachium, Boholia* and the Vanguerieae in the large 3-porate pollen.

(ii) The Retiniphylleae

Hooker (1873) united two South-American genera, *Retiniphyllum* and *Kutchubaea*, and the Asiatic genera "*Jackia* " and *Scyphiphora* in this tribe. Schumann (1891) rejected the tribe and transferred the first three genera to the Gardenieae and "*Jackia* " to the "Oldenlandieae" (= Hedyotideae). Verdcourt (1958) suggested a relationship between the Retiniphylleae and the "Ixoreae". Bremekamp (1966: 14) discussed *Retiniphyllum* (I do not agree with his statement that stylar pollen presentation is absent) but nowhere did include it in his system.

Kutchubaea is obviously a member of the Gardenieae (Robbrecht & Puff 1986). *Scyphiphora* is a difficult genus to position and is discussed below at the end of this section. "*Jackia* " (= *Jackiopsis*) was considered to represent a monogeneric tribe (Jackieae; Ridsdale 1979) which is also difficult to place.

The Retiniphylleae are thus monogeneric. *Retiniphyllum* is characterized by an often ± curved corolla-tube, contorted aestivation, stylar pollen presentation, 5-locular ovaries with two collateral ovules in each cell attached to a placenta in the middle of the septum (but clearly pendent) and 3-colporate pollen. The fruits (fig. 52 H-M) are drupes with five pyrenes, each one-seeded (so one ovule of each cell aborts). The pyrenes and seeds agree in many details with the Vanguerieae; starting from the raphal opening, the pyrene shows a preformed apical median split. The seed exhibits a large saddle-like outgrowth in the hilar area. The exotestal cells are parenchyma-like. The embryo is large with a superior radicle.

From these features, it is obvious that the Retiniphylleae are best placed in the Antirheoideae, as defined here. They share contorted aestivation with the Alberteae; two collateral ovules are the only other feature not found elsewhere in the subfamily.

(iii) The Cephalantheae

The position of *Cephalanthus*, classically placed in the Naucleeae, has long been the subject of debate. Schumann

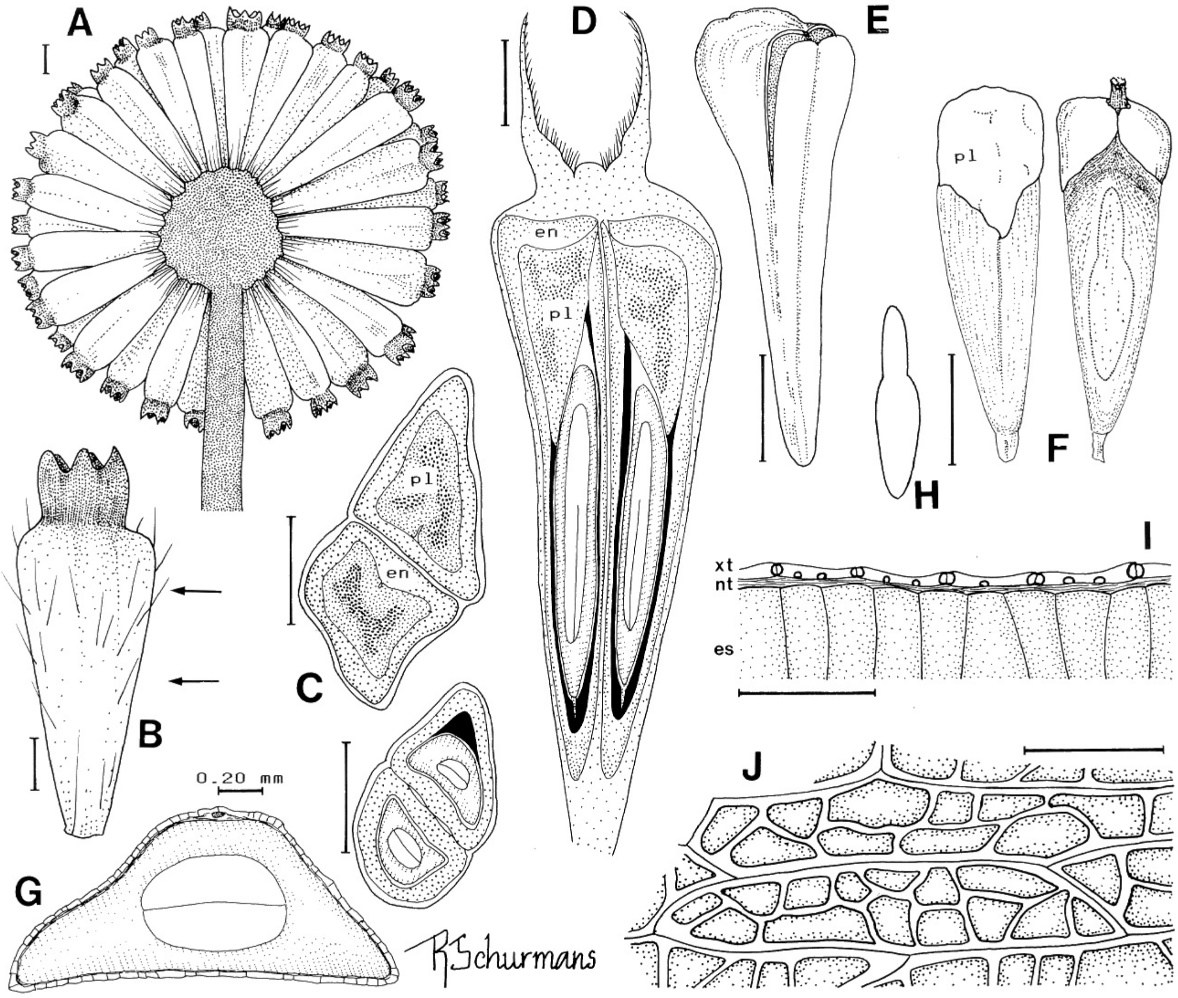


Figure 55.- ***Fruits and seeds of*** **Cephalanthus occidentalis***: A, longitudinal section of infructescence; B, fruit; C, two cross-sections of a fruit at levels indicated by arrows in B (compare D); D, longitudinal section of a fruit [from outside to inside: exo- and mesocarp, endocarp en, stony arilloid tissue pl, air-space (black), seed-coat, endosperm (striped) and embryo]; E, pyrene showing preformed opening slit; F, two views of a seed (crowned by stony arilloid tissue pl, in one view embryo position indicated); G, cross-section of a seed [from outside to inside: exotesta, endotesta with abaxial vascular bundle, endosperm (striped) and embryo]; H, embryo; I, cross-section of seed-coat (xt exotesta, nt endotesta) and adjacent endosperm cells es; J, surface view of exotesta.*
Lines to macroscopical drawings = 1 mm, except otherwise indicated; to microscopical ones = 50 µm.

(1891) e.g., albeit maintaining it in the Naucleeae, stated that the genus shows a distinct relationship to the Guettardeae, and Bremekamp (1966) considered it to be of uncertain position. Verdcourt (1958) maintained it in the Naucleeae because of "general habit, corolla shape and inflorescence structure". Ridsdale (1976) erected a monogeneric tribe to accomodate the genus, and believed that its affinity is with the Naucleeae or the Cinchoneae.

Verdcourt's and Ridsdale's opinions are certainly influenced by the very strong similarity in habit and inflorescences in *Cephalanthus* and the Naucleeae and Cinchoneae-Mitragyni-nae. This is no doubt due to convergent evolution (incidentally, globose congested inflorescences also occur in the Morindeae, Psychotrieae, Spermacoceae etc., see 2.7, pseudanthia), since the following features of *Cephalanthus* fit perfectly with the Guettardeae and tribes associated with them here:

- in each cell one pendulous ovule on an apical placenta,
- fruits fleshy (fig. 55 A, B), with two pyrenes (fig. 55 C-E) opening by apical-marginal preformed slits,
- in each pyrene an elongated seed (fig. 55 F-G) crowned by a massive outgrowth of the placenta,
- seed-coat provided with a vascular bundle (fig. 55 G),
- exotestal cells with delicate reticulate thickenings along the inner tangential wall (fig. 55 I, J),
- endosperm oily in several species and,
- embryo large with superior radicle (fig. 55 H).

All these features compare very well with e.g. *Antirhea*, *Chomelia*, and *Timonius* (Guettardeae), or *Chione* and *Hodgkinsonia* (Chiococceae).

(iv) The Craterispermeae

Craterispermum was previously always placed in the Vanguerieae because of its single pendulous ovules and axillary, opposite, congested inflorescences. Verdcourt (1958) excluded it from that tribe because of the heterostylous flowers and the presence of raphides; he recognized the monogeneric tribe Craterispermeae and placed it in his subfamily Rubioideae near the Urophylleae and Psychotrieae.

I propose a return of *Craterispermum* close to its original position, i.e. near the Vanguerieae and associated tribes. Besides the placentation mentioned above, the fleshy fruits (fig. 56 E), pyrenes with a lid-like fibrous apex (fig. 56 G-I) and superior embryo-radicle (fig. 56 F) are all characters favouring this position. As in many bilocular Vanguerieae, the second ovule aborts in *Craterispermum* (fig. 56 A-D); the fruit contains only one ± spherical pyrene with chartaceous endocarp (fig. 56 F). As the genus occupies a rather isolated position (advanced in: heterodistyly, raphides, and seed-coat absent), the Craterispermeae should be maintained as a monogeneric tribe within the Antirheoideae.

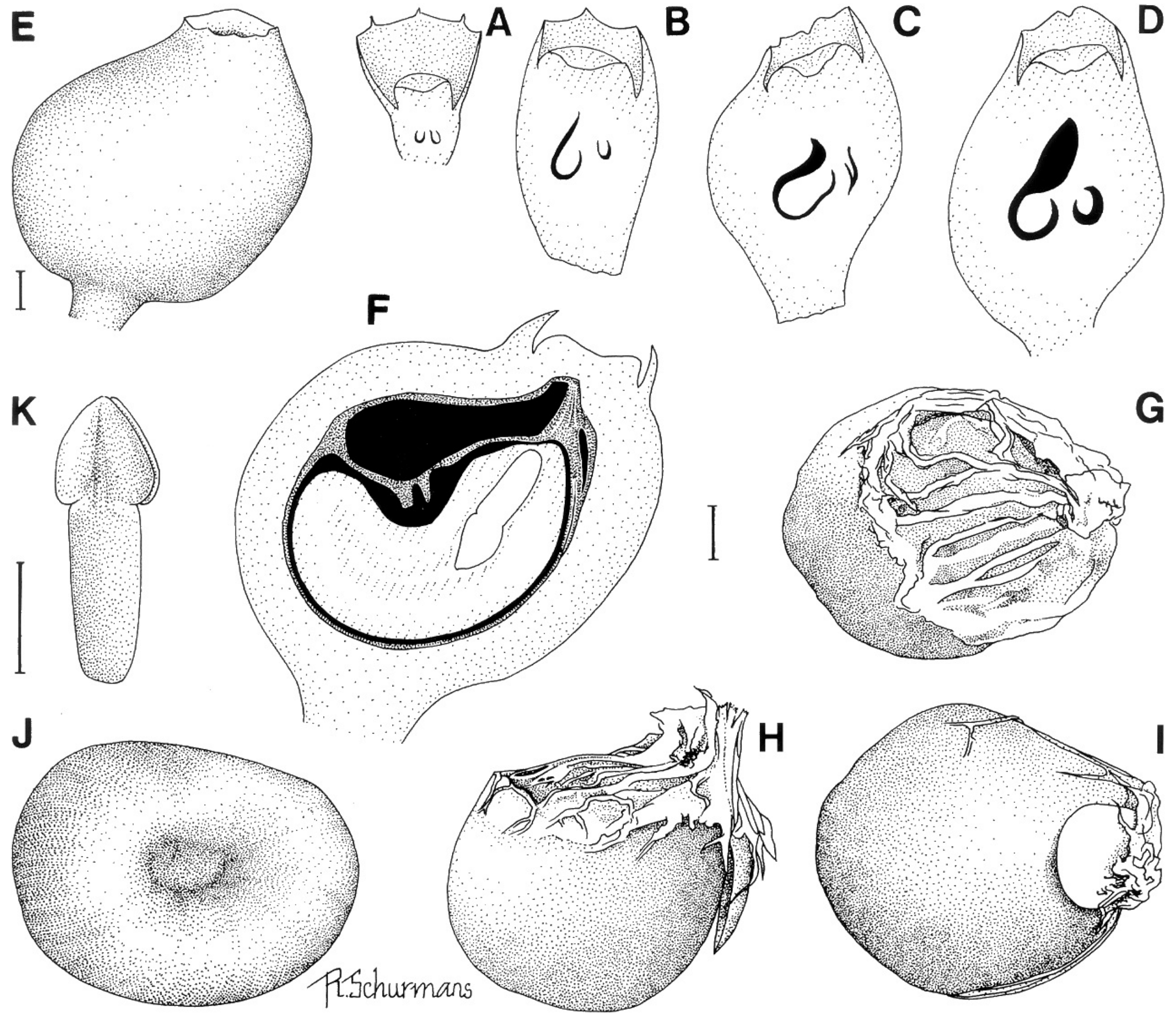


Figure 56.- ***Ovary and fruit of*** **Carterispernum** *(A-D,* Craterispernum schweinfurtii*; E-K,* Craterispernum *sp.): A, longitudinal section of ovary and calyx; B-D, longitudinal sections of developing fruits (black = air-space); E, mature fruit; F, longitudinal section of mature fruit [from outside to inside: endocarp, mesocarp (stippled), endocarp (densely stippled; in upper part closely associated with fibrous tissue = ? vascularisation of mesocarp), air-space (black), endosperm (striped; seed-coat absent!) and embryo; see the small cavity of the aborted second locule at right]; G, H, I, apical, lateral and basal view of pyrene (? endocarp and associated tissue: fibrous lid may well be vascularisation of mesocarp; see the aborted second locule as a small, flat endocarp plate at right in H and I); J, seed, apical view; K, embryo.*

Lines equal 1 mm, central one applies to all figures, except E & K.

(vi) Scyphiphora

Hooker (1873) referred *Scyphiphora* with doubt to the Retiniphylleae, and Schumann (1891) transferred it to the Gardenieae (his Eugardenieae). Darwin (1979: 13) included it in the Cremasporeae, a tribe no longer maintained (Robbrecht & Puff 1986). For an excellent and complete overall description and depiction of this monospecific genus of mangrove shrubs I refer to Tomlinson's mangrove book (1986: 36, fig. B77, 78), where its stylar pollen presentation is completely described; very few other Rubiaceae (including several Guettardeae!) are adapted to coastal habitats (see 2.13.4: long distance dispersal).

The placentation is doubtless the most striking feature of *Scyphiphora*; in each of the two elongated ovary-cells two ovules are inserted on a small placenta in the middle of the septum, one pendulous and one directed upwards. The following details may be added to the characteristics of this genus: raphides absent; 3-colporate pollen; bilocular drupes with corky endocarp, each cell with two super-posed seeds; seed-coat with delicate exotestal cells with ± warty thickenings along radial walls and pitted plate along inner tangential wall; embryo very large with inferior radicle in two upper and superior radicle in two lower seeds; endosperm a thin layer, very oily.

Scyphiphora is obviously best placed in the Antirheoideae; its peculiar placentation, occurring nowhere else in the Rubiaceae, may be derived from a condition similar to that of *Retiniphyllum* (two collateral pendulous ovules, placenta on the middle of septum), and the genus might therefore be reassociated with the Retiniphylleae.

3.2.3 Cinchonoideae

In the delimitation of Bremekamp (1966), this subfamily consists of the Cinchoneae, Naucleeae, Condamineeae, Rondeletieae, Sipaneeae, "Mussaendeae", and Sabiceeae.

The Cinchoneae and Naucleeae are characterized by winged seeds. Ridsdale (1975b, 1978b) recently redefined the Naucleeae, transferred some genera to the Cinchoneae (in a separate subtribe Mitragyninae) and separated *Cephalanthus* at tribal level (see 3.2.2: Cephalantheae; here included in the Antirheoideae).

The Condamineeae, Rondeletieae and Isertieae are certainly closely related, and the first two were united by Verdcourt (1958).

Bremekamp characterized the subfamily by the exotestal cell anatomy (radial and inner tangential walls thickened, the latter provided with conspicuous pits), elongated form of the placenta, and also (characters not confined to the subfamily) multiovular placentas and the absence of raphides. Important characters that I would add are the mostly dry fruits (fleshy in Isertieae) and the frequent occurrence of heterostyly.

The Urophylleae and Pauridiantheae match the Cinchonoideae in all characteristics (see 3.2.4) but have raphides, and so one can not maintain the absence of raphides as an absolute character of the subfamily (see also 2.6.2).

In this subfamily, the aestivation of the corolla-lobes is extremely variable: contorted, imbricate or valvate in the Cinchoneae, contorted or imbricate in the Rondeletieae, valvate or imbricate in the Isertieae, and valvate in the Naucleeae, Condamineeae, Urophylleae and Pauridiantheae. Otherwise, the subfamily as defined by Bremekamp is very homogeneous and his concept may be maintained, except for the above mentioned inclusion of two raphid-possessing tribes.

3.2.4 Urophylloideae

Bremekamp (1966) defined this "still imperfectly characterizable" subfamily by large thick-walled exotestal cells wherein wide perforations ("pits") are absent; the thickenings [of the radial and inner tangential wall] are, however, "traversed by an enormous number of very narrow pit-canals". He further characterized the subfamily by the absence of raphides. He included the Urophylleae and Pauridiantheae, two tribes that he (Bremekamp 1952) separated from the Isertieae, and that are obviously very closely related to one another (supported by cytological evidence, Kiehn 1986). The Pauridiantheae were merged into synonymy of Urophylleae by Verdcourt (1958).

Bremekamp tentatively added to the Urophylloideae a number of small groups of uncertain position: Simireae, Ophiorrhizeae, and Verdcourt's subtribe Heinsiinae from the "Mussaendeae"; he suggested, with hesitation, to raise the latter to the rank of tribe and to include *Bertiera* in it. [The position of *Heinsia* with *Bertiera* is an old concept, Schumann 1891: Gardenieae subtribe Bertierinae].

Raphides have been mentioned in *Pauridiantha* (Verdcourt 1958: 242) and *Ophiorrhiza* (Darwin 1976b); I have already pointed out that a too great importance should not be attributed to their presence.

F. Hallé (1961) very convincingly documented the similarity, in many morphological, anatomical and biological features, between the "Mussaendeae" and two genera of Bremekamp's Urophylloideae, *Pauridiantha* and *Heinsia*. Therefore, they should not be placed in a position distant from the Isertieae. To F. Hallé's evidence may be added the following:

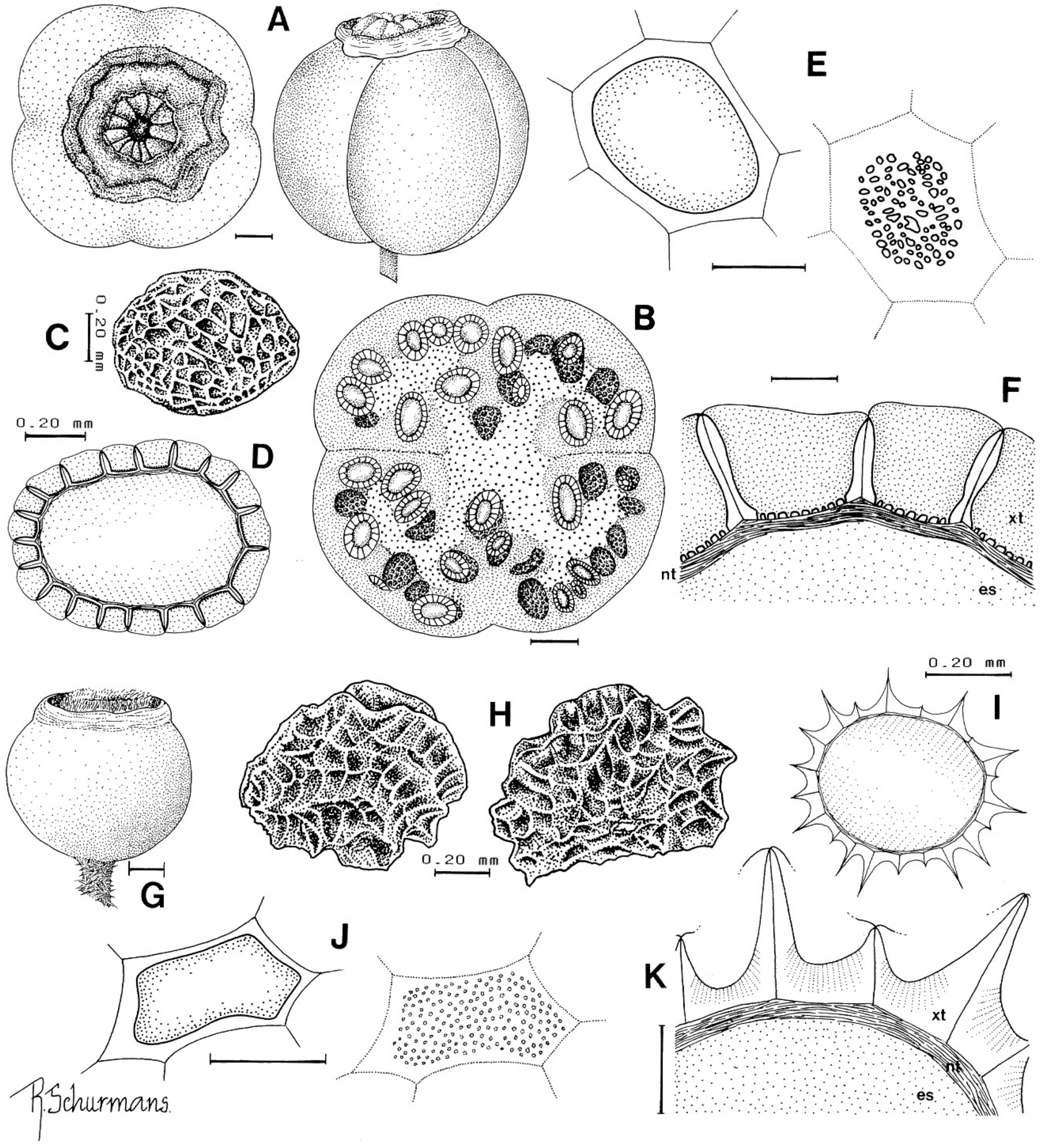


*Figure 57.- **Fruits and seeds of*** **Pauridiantha** *(A-F,* P. rubra*; G-K,* P. callicarpioides*): A, apical and lateral, and G, lateral view of fruits; B, cross-section of a fruit; C, H, seeds; D, I, section of seeds; E, J, exotestal cell in surface view, focused at two different levels; F, K, cross-section of seed-coat, showing large exotestal cells xt and crushed endotesta tissue nt (endosperm es represented by stippling).*

Lines to macroscopical drawings 1 mm unless otherwise indicated; to all microscopical drawings = 50 µm.

- *Heinsia* has an exotestal cell structure (fig. **44** A) comparable to *Mussaenda*, *Sabicea* etc., so the genus deviates from the Isertieae in a single character, imbricate aestivation of its corolla-lobes. Taking into account the great variability of this feature in the Cinchonoideae (see 2.8.2), there is nothing to restrain placement of *Heinsia* in the Isertieae.
- A number of Pauridiantha species have exotestal cells exhibiting the structure described by Bremekamp (e.g. *Pauridiantha callicarpoides*, fig. 44 B, 57 K: radial + inner tangential walls with strong continuous thickenings with many narrow perforations), but others (e.g. *P. rubra*, fig. 57 F) have seeds with exotestal cells similar to the Isertieae, i.e. with thickened radial and inner tangential walls and large pits in the inner thickenings (Bremekamp's "pitted testa"). A more general screening of seed-coat anatomy in the Urophylleae and Pauridiantheae may well show that there is a progression from the latter into the former exotestal cell type. In any event, the peculiar exotestal cells used to originally define the Urophylloideae have absolutely no value.

Obviously the Urophylloideae can not be maintained; their main element, viz. the Urophylleae and Pauridiantheae, should be placed near the Isertieae in the Cinchonoideae; *Heinsia* might be included in the Isertieae. It is more difficult to suggest placements for the groups tentatively included in the subfamily by Bremekamp.

(i) *Bertiera*, the second element of the Heinsiinae, is a large pantropical genus much in need of a general revision in order to determine its delimitation and position (cf. Garcia Kirkbride 1979). It is characterized by contorted aestivation of the corolla-lobes, presence of the stylar pollen presentation, and fleshy fruits, features that suggest an alliance with the Ixoroideae as defined in 3.2.1, but its placentation and the small angular seeds fit better in the Isertieae. Moreover, at least some species seem to have exotestal cells with large perforations in the thickenings of the inner tangential walls. Thus *Bertiera* seems to be another genus whose position is ± intermediate between the Ixoroideae and the Cinchonoideae (compare *Brachytome, Anomanthodia*: Robbrecht & Puff 1986: 113).

(ii) The Ophiorrhizeae are the only semi-woody to herbaceous group in Bremekamp's Urophylloideae, segregated by him from the Hedyotideae (Bremekamp 1952: 21). He included *Ophiorrhiza, Spiradiclis* and *Virectaria* in the tribe, because they share the absence of raphides and a peculiar exotestal cell type, described from surface views as possessing "thick walls ornamented with strongly reflecting warts". He believed the first two genera to be close to one another because of similar leaves, stipules, inflorescences and flowers; he stated, however, that *Virectaria* did not resemble the first two genera, except for the characters mentioned above.

Verdcourt (1958) accepted the Ophiorrhizeae and placed them, because he discovered raphides, in the Rubioideae. However, he excluded *Virectaria* (inter alia raphides absent) from the tribe, and suggested for the genus a tribe of its own occupying an isolated position near the Rondeletieae. Darwin (1976b), based on a revision of the Pacific species of *Ophiorrhiza*, suggested including that genus in the Hedyotideae again. I also support that *Virectaria* may be returned to the Hedyotideae, since its removal was based only on the absence of raphides; otherwise, this herbaceous to semi-woody genus fits extremely well within the Hedyotideae (N. Hallé 1966: fig. 11-14).

(iii) The Simireae are a monogeneric tribe separated by Bremekamp from the Rondeletieae (1966) because of their smaller number of ovules, inserted in two rows on the placenta, and their large seeds with the upper half developed into a wing. I haved examined no representatives of the tribe, but suggest that *Simira* should be compared again with the Rondeletieae in the light of the present discussion of features.

3.2.5 Hillioideae

Hillia is a remarkable neotropical genus of epiphytic Rubiaceae for which Bremekamp (1952, 1966) proposed a new tribe and a new subfamily defined by
(i) presence of raphides,
(ii) contorted aestivation of the corolla,
(iii) a tuft of hair-like appendages on top of the seeds, and (iv) exotesta cells reminiscent of *Gleasonia*.
The combination of (i) and (ii) he stated to be extremely rare in Rubiaceae, and (iii) was felt unique in the family. Verdcourt (1958) emphasized (i) and included *Hillia* in the Rubioideae, stating that it probably needs a special tribe. F. Hallé (1967) placed it in the Gardenieae; his concept of that tribe is extremely wide, and his opinion is based mainly on convergences in floral morphology.

In the classical systems, *Hillia* was placed in the Cinchoneae, and its fruits (fig. 58 A) fit well in that tribe: they are dry and loculicidal, with numerous seeds. Detailed comparison of the fruit and seeds of *Hillia* (fig. 58, 59) and the Cinchoneae (fig. 60), further strengthens the agreement. In many Cinchoneae and Naucleeae, the seeds are winged and often have two more or less different poles (see 2.10.1, fig. 43 B-F). *Hillia* may well be considered as the extreme case of this trend; its seeds have a small ± bilobed wing at one pole, while the large number of trichome-like excrescences at the other pole may be regarded as extremely divided parts of the testal wing. Such a division of one pole in two or more linear parts also exists in *Uncaria* (fig. 43 F). In addition, the exotestal cell structure of Hillia (fig. 58 G) is also similar to the Cinchoneae (fig. 60 G, L) and the Naucleeae [and to *Gleasonia* (Hen.) as already remarked by Bremekamp];

the cells are more or less bulging and radially elongated and provided with ± reticulate bands. The trichome-like excrescences are multiseriate, and their cell-anatomy (fig. 60 C, D) is similar to the normal exotestal cells (except for that they are more elongated).

Thus, the tuft of "hairs" on *Hillia*-seeds may be considered as homologous with one of the wings in bipolar seeds of Cinchoneae and Naucleeae, and so Bremekamp's characterist-ic (iii) of the subfamily is of minor importance. Nonetheless, *Hillia* possesses many characteristics justifying its separation as a monogeneric tribe. I include it in the Cinchonoideae (present circumscription) where its contorted corolla aes-

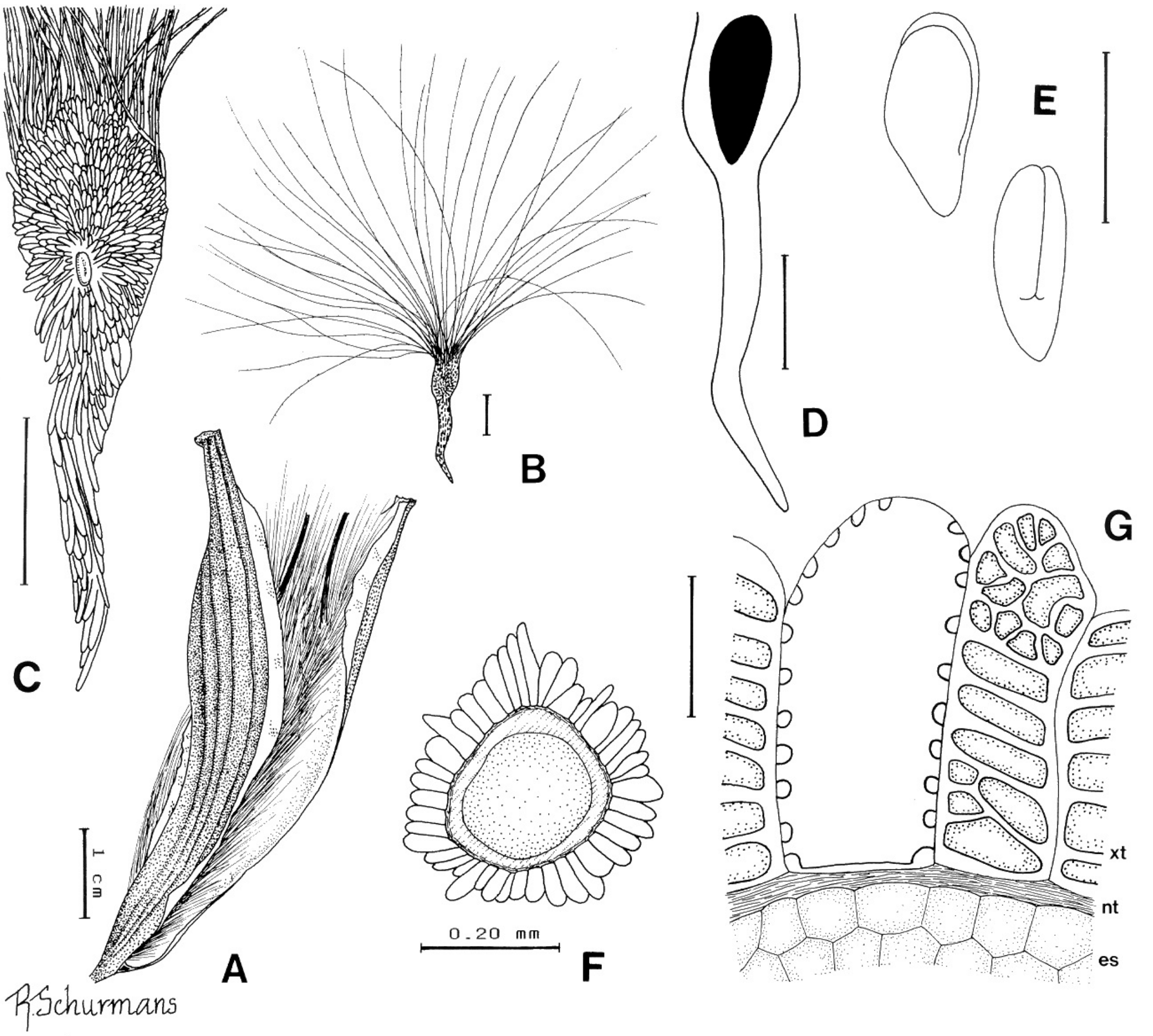


*Figure 58.- **Fruit and seeds of*** **Hillia parasitica***: A, dehisced fruit; B, seed with apical tuft of "hairs"; C, body of seed, with rounded hilum in centre; D, embryo position; E, two views of embryo; F, cross-section of seed; G, section of seed-coat (xt exotesta, nt, endotesta) and adjacent endosperm es.*
Lines to macroscopical drawings = 1 mm, except otherwise indicated; to microscopical one = 50 μm.

tivation occurs in several other tribes and its raphides compare to those of the Urophylleae and Pauridiantheae.

Ravnia, originally placed in the Cinchoneae, must be added to the Hillieae (Jansen 1979); it agrees in great detail with *Hillia* (see description and illustrations in Dwyer 1980).

Deppea was tentatively included in the Hillieae (Bremekamp 1966). Kirkbride (1984) recognized the Deppeeae, which was recently included in the Hamelieae, however (Bremer 1987). An in-depth study of the genus remains desirable.

3.2.6 Rubioideae

This subfamily of Bremekamp differs little from the subfamily of the same name in Verdcourt's system; the latter's Rubioideae only have a somewhat larger composition, since they include the Urophylleae (s.l., comprising Pauridiantheae), the Ophiorrhizeae, and the Hillieae. The Rubioideae are defined by the presence of raphides. The foregoing shows that absolute use of this single character is not justified. Several groups possessing raphides are closely related to others not having Ca-oxalate in this peculiar form; therefore, the Urophylleae, Pauridiantheae, Knoxieae, Craterispermeae and Hillieae are better considered as allied with other groups of Rubiaceae (see 3.2.2, 3.2.4 and 3.2.5).

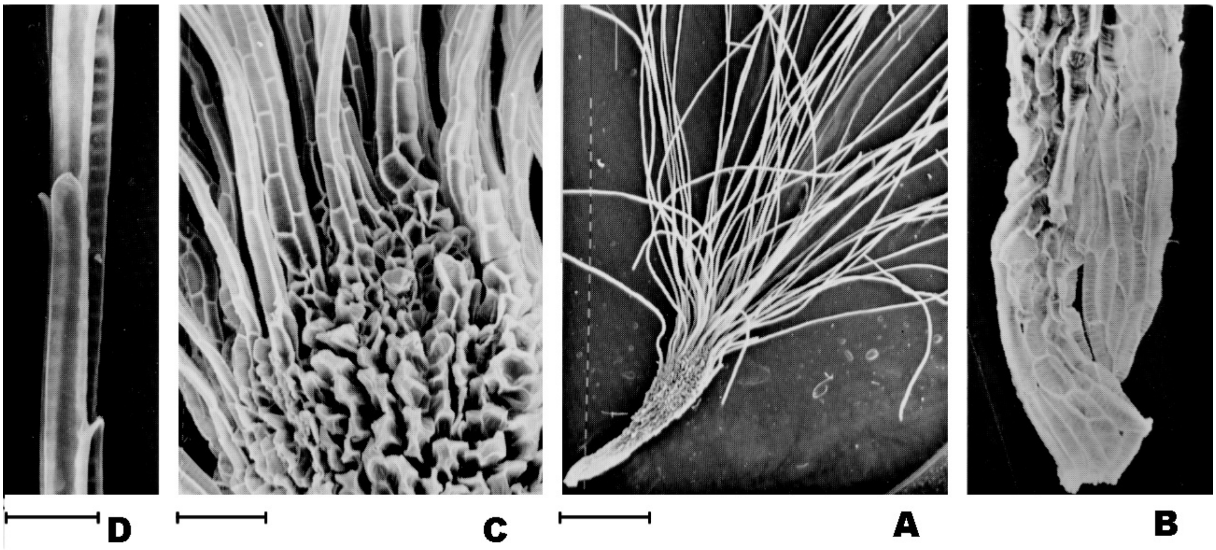
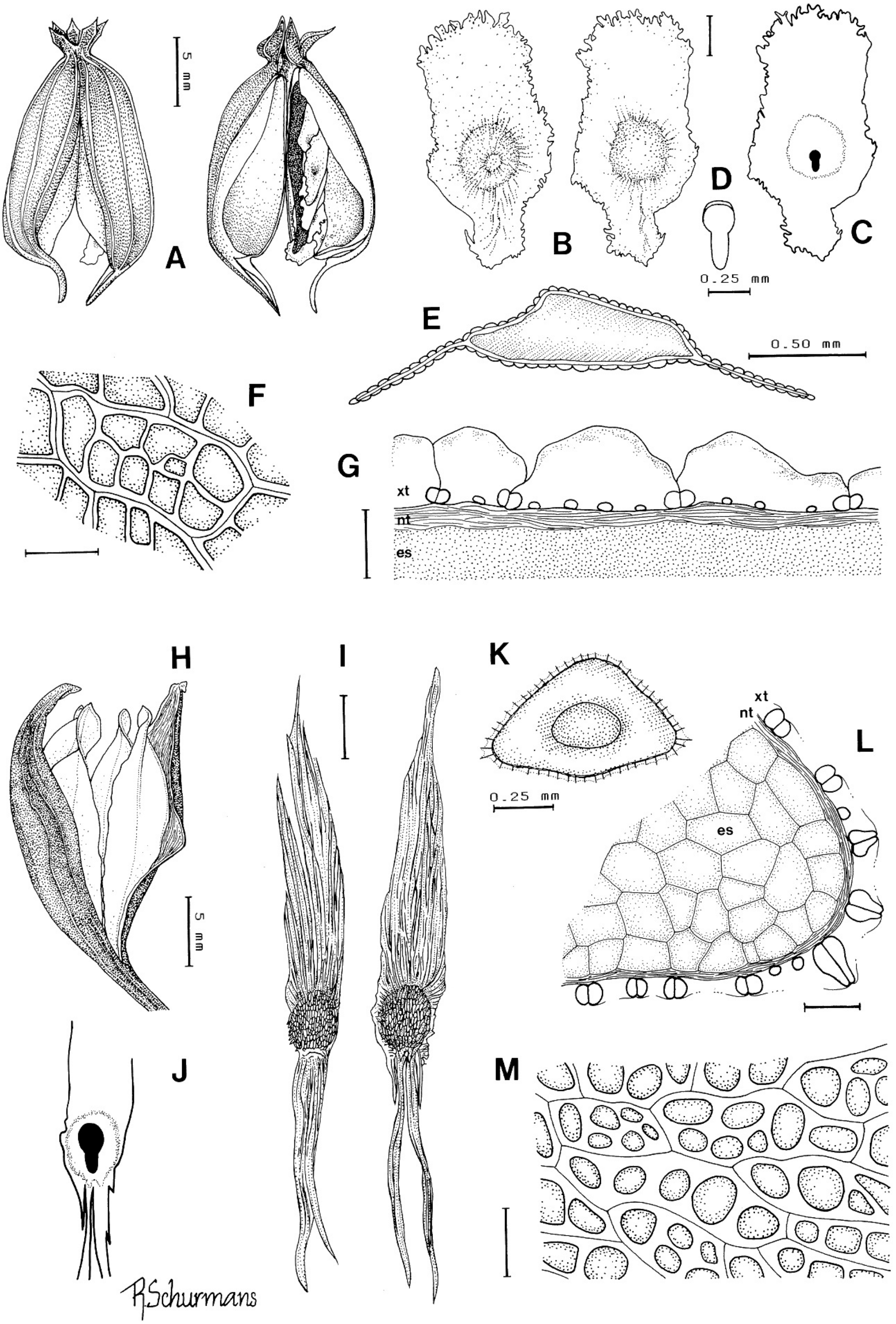


*Figure 59.- **Seed of** **Hillia parasitica**: A, seed with apical tuft of "hairs"; B, bilobed base of seed; C, bases of the trichome-like seed-coat excrescences; D, detail of trichome-like excrescence, showing individual exotestal cells.*

In B, C & D the thickenings of the inner walls appear visible through the thin outer tangential walls.

S.E.-micrographs; no treatment was executed. Lines = 1 mm (A), 100 µm (B), 14 µm (C) and 4 µm (D).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R.Schurmans

In the remaining Rubioideae, two major groups seem discernible:
(i) a number of tribes which have numerous ovules on each placenta (mainly the Hedyotideae, and associated with them: Ophiorrhizeae, Hamelieae, Argostemmateae, Coccocypseleae and Schradereae), and
(ii) tribes with solitary erect ovules (numerous tribes, inter alia Psychotrieae and associated tribes).

Group (ii) is surely a natural one. The close association between the Psychotrieae, Morindeae and Coussareeae, and the problematic delimitation of the two first tribes against one another has been emphasized by several authors (Verdcourt 1958, Petit 1963, 1964a, Darwin 1979). The three tribes are predominantly woody and characterized by fleshy fruits. Petit (1964a; followed by Verdcourt 1976) proposed new definitions for the Psychotrieae and Morindeae, based especially on seed characters and implying a transfer of *Lasianthus* and *Trichostachys* to the Morindeae; he characterized the two tribes by seeds with soft oily endosperm and large embryos (Morindeae) versus seeds with horny endosperm and small embryos (Psychotrieae). His definition, based on African representatives, seems more plausible than the previous one (Morindeae characterized by ovaries frequently connate and by more central attachment of ovules which are basal in Psychotrieae), though the value of the occurrence of oil in the endosperm needs some reconsideration (see 2.10.4).

Bremekamp segregated three genera from this circle of affinity as a tribe Triainolepideae since they have not a single but two collateral ovules, but that latter character is not as rare here as he believed. Convincing depictions and illustrations of Morindeae with two collateral ovules, from the nineteenth century, such as the protologue of *Tetralopha*, were apparently overlooked later; since Schumann (1891) the tribe was always described as uniovulate. Johansson's (1987a) revisions in the Morindeae have again drawn the attention to the existence of several genera with (always or facultatively) two ovules per ovary cell, and so the value of the distinctive character of the Triainolepideae becomes questionable.

On the whole, the Morindeae and Psychotrieae (+ its two satellite tribes Lathraeocarpeae and Triainolepideae) need further study emphasizing characters of pollen, fruits, seeds, endosperm and embryo.

*Figure 60.- **Fruits and seeds of*** **Cinchona officinalis** *(A-G) **and*** **Uncaria guianensis** *(H-M): A, H, dehisced fruits; B, I, two views of a seed; C, J, embryo position; D, embryo; E, K, cross-section of seeds; F, M, exotestas in surface view; G, L, cross-sections of seed-coat (xt exotesta, nt endotesta) and endosperm es (represented by stippling in L).*
Lines to macroscopical drawings = 1 mm except otherwise indicated; to all microscopical ones = 50 µm.

The Anthospermeae, Paederieae, Theligoneae, Spermacoceae and Rubieae are associated with them, and show an increasing trend to herbaceousness and dry fruits. The fleshy and the dry fruits of these tribes, however, are similar in structure, especially by the comparable occurence, in many taxa, of basal preformed opening slits in the pyrenes or basal dehiscence slits in capsules. In all these tribes, vascularisation of the endotesta is also common.

Returning to group (i), the multiovulate Rubioideae, a progression series exists in de Hedyotideae from peltate multiovulate placentas adnate to the septum over a large part of their length, to small stalked globoid placentas with relatively few ovules (see 2.8.4, fig. 36). The placentation of the Psychotrieae is probably a further step of this trend. Consequently, the Hedyotideae and related tribes may be associated with the uniovulate Rubioideae; since the two groups also share a number of other features (aestivation mainly valvate, raphides copiously present, and heterostyly common), the subfamilial concept Rubioideae may be maintained. In this connection one should mention that Puff (1983) transferred *Otiophora* from the (uni-ovulate) Anthospermeae to the (multi-ovulate) Hedyotideae, because he interpreted the shield-like, stalked, uni-ovulate placenta of *Otiophora* as a typical but reduced Hedyotideae placenta.

The separation between the Isertieae (Cinchonoideae) and Hedyotideae (Rubioideae) is not clear (F. Hallé 1961). Bremekamp transferred many genera from the Isertieae (and Cinchoneae) to the Hedyotideae, but this was solely based on absence or presence of raphide cells. Many genera need to be reinvestigated to establish the dividing line between these two tribes; it seems that in the Isertieae woody habit, absence of raphides, ± fleshy fruits and conspicuously thickened exotestal cells prevail, while in the Hedyotideae herbaceous habit, dry fruits, presence of raphides and more simple or parenchyma-like exotestal cells predominate.

3.2.7 Gleasonioideae

The Gleasonioideae are one of Bremekamp's smaller subfamilies and comprise only the nominating genus. He defined the subfamily by the large size of the cotyledons and the exalbuminous seeds and by (characters differential for his "Guettardoideae") absence of crystals in the hairs, pluri-ovular placentas and capsular fruit.

Henriquezia and *Platycarpum* were traditionally associated with *Gleasonia*, but were excluded from the Rubiaceae by Bremekamp (1957) as the family Henriqueziaceae, said to be related to the Bignoniaceae.

The three genera were soundly reinvestigated (wood, leaves, flowers, pollen, fruits, seeds, seed-coats, etc.) by Rogers (1984) who concluded that the resemblances to the Bignoniaceae are few and unconvincing, while the similarities between the three genera obviously show

- that they are closely related and should reside in Hooker's (1873) and Schumann's (1891) tribe Henriquezieae, and
- that the Henriquezieae definitely belong to the Rubiaceae. Rogers did not, however, indicate a position in the Rubiaceae for the tribe.

Hooker (1873) and Schumann (1891) placed the Henriquezieae near the Cinchoneae. Characters pointed out by Rogers indicate that the tribe is best maintained in that position:

- raphides lacking;
- dry loculicidal capsular fruits with several flattened seeds in each locule;
- exotestal cells in the three genera (unlike Bremekamp's statement) with pitted or reticulated thickenings on the inner tangential walls, thus agreeing with the Cinchonoideae (in the present delimitation), and in *Gleasonia* and *Platycarpum* outer tangential walls also thickened; and
- cymose, terminal inflorescences.

Rogers did not discuss the floral biology of the Henriquezieae. Based on his descriptions, the flowers seem to be homostylous, without any of the peculiar floral adaptations of the Rubiaceae discussed in 2.13.3.2. The zygomorphic flowers with reddish corollas suggest bird pollination.

The Henriquezieae are obviously strongly derived Rubiaceae, best accommodated in the Cinchonoideae (sensu meo), and showing some adaptations paralleling other groups of Rubiaceae:

- large embryos (and consequently strongly reduced endosperm) as in most Antirheoideae;
- zygomorphic flowers as in many Antirheoideae;
- pollen grains in tetrads (*Gleasonia* only; individual grains colporate, fig. 45 B) as in many Ixoroideae-Gardenieae (but here individual grains porate).

3.2.8 Pomazotoideae

Bremekamp (1952, 1966) erected the Pomazoteae, the single tribe of this subfamily, for a number of genera (*Pomazota, Klossia, Siderobombyx, Xanthophytum* and *Lerchea* plus tentatively five other imperfectly known genera) previously placed in the Hedyotideae or Isertieae.

The nomenclature of the nominating genus is somewhat puzzling. Bremekamp (1947a) documented the synonymy of *Pomazota* Ridl. (1893) and *Coptophyllum* Korthals (1850); he retained the first name because of the existence of the earlier homonym *Coptophyllum* Gardner (1842, in Pteridophyta). Nevertheless *Coptophyllum* Korthals has later been conserved against *Coptophyllum* Gardner.

The Pomazotoideae were characterized by their exotestal cells (thin-walled with finely dotted or tuberculate basal wall) and absence of raphide cells. Verdcourt (1958: 243) examined only a few representatives of this tribe, and suggested placing *Lerchea* and *Xanthophytum* in the Hedyotideae, although saying that they "form a link with the Cinchonoideae" (in his delimitation).

Axelius (1987) found that the foliar and floral tissues of *Lerchea* (and also those of *Xanthophytum* and *Pomazota*) contain raphides. The genera of the Pomazotoideae should therefore be returned to their original positions in the Hedyotideae or Isertieae (the delimitation of these two tribes needs to be reconsidered in comparison to one another: see 3.2.6). The tuberculate basal wall of the exotestal cells may well be homologous with the pitted wall of the Isertieae.

3.3 Concluding remarks on the subfamilial classification

The definition of subfamilies in the Rubiaceae hitherto was based on a few individual character states (number of ovules, presence of raphides, "absence" of endosperm, and presence of stylar pollen presentation) and (for Bremekamp's system) on a number of anatomical exotestal cell types; the latter now appear to have been imperfectly interpreted, since they were only examined in (L.M.) surface view. Problems of subfamilial delimitation in the Rubiaceae are certainly linked with the extreme naturalness of the family, hence a relatively low divergence of its members. Nevertheless, the rank of subfamily is needed for clarifying the relationships (1.4).

The present survey of features and trends in woody Rubiaceae and the subsequent discussion of one of the existing modern systems of subfamilial classification has shown that it is possible to arrive at a satisfactory delimitation of four subfamilies (fig. 61) based on distinct character combinations and trends. Bremekamp's Cinchonoideae and Rubioideae can more or less be maintained after the emendations proposed in 3.2 (inclusion of Hillioideae, Gleasonioideae, Pauridiantheae and Urophylleae in Cinchonoideae; inclusion of Pomazotoideae in Hedyotideae, and transfer of Knoxieae and Craterispermeae to Antirheoideae). His Ixoroideae comprise a core of tribes associated with the Gardenieae, for which the subfamily can be maintained. Other former Ixoroideae, however, viz. the Retiniphylleae, Vanguerieae and Chiococceae, should be associated with the "Guettardoideae". The emendation of the latter subfamily (legitimate name Antirheoideae) is the most drastic redelimitation proposed here and in some respects is a return to the nineteenth century classification of the Rubiaceae; my Antirheoideae agree well with Schumann's supertribe Guettardinae.

In the **Cinchonoideae** terminal inflorescences, dry fruits, and winged seeds are predominant. The placentas always bear numerous ovules. The exotestal cells are always provided with thickenings along their inner tangential wall in the form of a pitted plate, a pattern of anastomosing ribs or a reticulation. The aestivation of the corolla-lobes is extremely variable and valvate, imbricate or contorted.

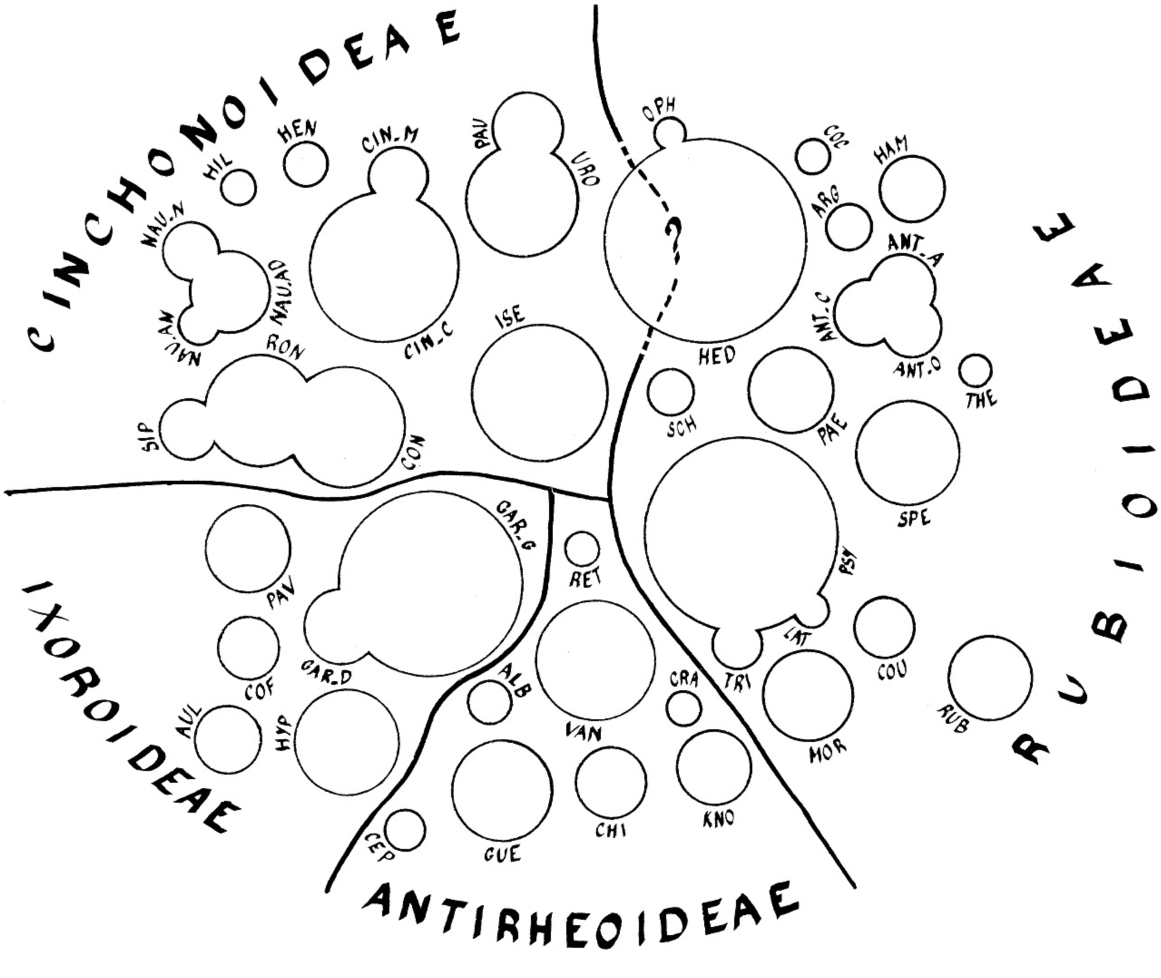

*Figure 61. - **Subfamilies, tribes and subtribes of the Rubiaceae accepted here.** The uncertain delimination of the Hedyotideae (Hed: ?) Is discussed in the text.*

Raphides occur in the Hillieae, the Pauridiantheae and the Urophylleae (also in many original Isertieae later transferred to Rubioideae-Hedyotideae; these transfers should be reconsidered). Heterostyly is the most common floral biological adaptation, but stylar pollen presentation occurs in a few representatives (Naucleeae, *Crossopteryx*, *Coptosapelta*).
The Isertieae (with fleshy fruits !) may be considered to form a link with

- the Ixoroideae [several Gardenieae (e.g. Brachytome) show progressions toward this tribe, see Robbrecht & Puff 1986] as well as
- the Rubioideae (see previous comments on the close association Isertieae-Hedyotideae, 3.2.4).

The **Ixoroideae** are probably the most primitive subfamily of the Rubiaceae. The position of their inflorescences is very variable. Their fruits are always fleshy (in the Gardenieae, however, of a peculiar type), and their corolla-lobes always contorted. The ovules are generally numerous, but a few taxa outside the Gardenieae-Gardeniinae (Coffeeae, *Tricalysia, Pavetta* ...) tend to have solitary ovules. The disposition and shape of the exotestal cell thickenings show a great variation; thickenings occur along the radial and the inner and outer tangential walls (in a number of taxa along all three). Raphides are almost universally absent (there is an anomalous record in *Argocoffeopsis*, see Robbrecht 1986c). The style acts as pollen presenter in all the taxa (with a very few exceptions, e.g. *Cladoceras*, see Robbrecht & Bridson 1984).

The **Antirheoideae** have a single ovule pendulous from an apical placenta in each ovary cell; rarely there are two collateral (Retiniphylleae) or one erect and one pendulous ovule (*Scyphiphora*). The inflorescences are mostly axillary. The fruits are drupes containing individual pyrenes or pluri-locular stones. The endosperm of the seeds is oily (a rare feature in other subfamilies), and the generally large embryos have a superior radicle. The exotestal cells are usually reduced and parenchyma-like or provided with a ± delicate reticulation along the inner tangential wall. The aestivation of the corolla-lobes is variable. Raphides are usually absent. The frequently club-shaped stylar heads generally act as pollen presenters. The Knoxieae and Craterispermeae are unusual in that they have raphides and heterostylous flowers without stylar pollen presentation.

Finally the **Rubioideae** contain, without doubt, the most advanced members of the family. It is the only subfamily in which large herbaceous groups have evolved. Raphides are abundant in many parts of the plants and occur in all the tribes (with perhaps very few genera making exception to this: see note on position of *Virectaria* in 3.2.5). The corolla aestivation is almost universally valvate, and heterostyly is very frequent. The subfamily contains two major groups, tribes with multiovulate and others with uniovulate ovary-cells; evidence from the Hedyotideae, however, indicates that a link between the two seems plausible. This same tribe also seems to link the subfamily Rubioideae with the Cinchonoideae, viz. the Isertieae.

I am well aware that increasing knowledge of the family (especially through monographs of certain tribes or genera) will result in further refinements of the proposed system. Fortunately, subfamilial names for the four entities recognized already exist, so that only circumscriptions need be emended and that the embarassing establishment of additional new names is unnecessary. The conclusions reached in the foregoing review are summarized in the survey of the subfamilies and tribes of the Rubiaceae in appendix 1.

Chapter 4

GENERAL CONCLUSIONS

For a long time, I doubted that it was possible to complete and publish this review of the tropical woody Rubiaceae. The task of a worldwide survey encompassing this large angiosperm family is hardly a one-man-job; completion of present work fully convinced me of that. Also, modern revisions and in-depth knowledge are lacking for many rubiaceous groups, and the available data are distributed unevenly across the family, both taxonomically and geogra-phically.

Schumann's system (1891), "the only clear, comprehensive one" (Rogers 1987), is now almost a century old, and consequently difficult to use. Since its publication, many rubiaceous genera new to science have been discovered, numerous adjustments to his classification have been proposed, and a number of new taxonomic criteria have been accepted and applied. Therefore, it has been a real challenge to incorporate into a single volume a discussion of taxonomically important characters, a survey of the classification, and new subfamilial concepts for the Rubiaceae.

The completion of this review has made it possible to indicate the major gaps in our knowledge of the Rubiaceae and to propose suggestions for directions of future systematic research on the group.

4.1 Gaps in our rubiaceous knowledge

(i) The morphological-anatomical basis of taxonomic evidence, as presented in chapter 2, is far from complete. Especially fruits and seeds have not been adequately described for all Rubiaceae. So, it is not possible to extend a comparative overview of the exotestal cell types discovered in the Ixoroideae (Robbrecht & Puff 1986: table 10) to the other three subfamilies of Rubiaceae. Other characters in need of critical study throughout the family include: trichome anatomy, corolla aestivation, placenta morphology, palyno-logy, and floral biology.

(ii) While a comprehensive, comparative survey of the Ixoroideae (Robbrecht & Puff 1986) has recently been completed, a series of similar studies is needed for the other three subfamilies. Each has major unresolved problems of tribal delimitations.

In Cinchonoideae, the Cinchoneae, Condamineeae, Rondeletieae, Sipaneeae and Isertieae need thorough study and comparison to establish their correct delimitations; the relationship of this tribal grouping to Hedyotideae (Rubioideae) should also be investigated. In Antirheoideae, the tribal position of numerous genera is uncertain, under scoring the need for intensive study of tribal delimitations throughout the entire subfamily. In Rubioideae, the Psychotrieae are certainly the single largest source of problems requiring resolution. There is not only the vast question of how to delimit the immense pantropical genus *Psychotria*, but also the problem of how te define the tribes in the Psychotrieae/ Morindeae/Coussareeae aggregate.

At tribal level, the questions are to numerous to enumerate here. Examples are given in 1.3 (iv) above and also include the question of what to do whit the small Hedyotideae satellites. Are Ophiorrhizeae, Coccocypseleae and Schradereae really distinct?

(iii) The geographical distribution of published research, as well as current investigations, is very unequal. In the paleotropics, the African and Pacific Rubiaceae are best known, several floras having been completed recently (N. Hallé 1966, 1970; Verdcourt 1976; Bridson & Verdcourt 1988; Smith & Darwin 1988). The preparation of rubiaceous accounts for other African floras (Flora of Ethiopia, Flore d'Afrique Centrale, Flora Zambesiaca) is progressing steadily.

Rubiaceae from the Flora Malesiana area and neighbouring Asiatic regions received in recent times only partial attention (e.g. Ridsdale 1978; Tirvengadum 1982; Wong 1984, 1988); the only more general account soon forthcoming is Wong's treatment of the family in a "Tree Flora of Malaya".

For the Madagascan region, only the relatively small group of Mascarene Rubiaceae is well understood; the family account for the "Flore des Mascareignes" was recently completed (proceeded by Verdcourt 1983). However, the infinitely richer Rubiaceae of Madagascar itself have only received partial attention in recent times (e.g. Leroy 1974, 1976; Puff, Robbrecht & Randrianasolo 1984; Puff 1986a, 1988). Bridson's studies (1979, 1985, 1987a) have clearly demonstrated that Madagascan Rubiaceae often occupy "key positions" for the resolution of higher level problems involving Afro-Asiatic groups. It is disappointing that the study of Rubiaceae from this biologically important island is practically dormant. The Australian and New Caledonian Rubiaceae are in a very similar state.

For the neotropics, detailed rubiaceous accounts have recently appeared for the Botany of the Guayana Highlands (Steyermark 1964, 1965, 1967, 1972), Flora de Venezuela (Steyermark 1974), Flora of Guatemala (Standley & Williams 1975) and Flora of Panama (Dwyer 1980). West Indian Rubiaceae have received only partial attention (Aiello 1979, Borhidi 1982 and other papers), and there are almost no adequate, modern data available for the Amazonian region or the southern areas of South America. In the Flora Neotropica, a single monograph (on the three genera of the Henriquezieae) appeared (Rogers 1984).

Thus, the broadest gaps in our rubiaceaous knowledge are for the taxa of Madagascar, tropical Asia, Australia, New Caledonia, and selected neotropical areas.

4.2 Directions of future research

Future research should not only produce consistent, comparable results within each group, but should also be comparable with studies in other rubiaceous groups, especially at the generic level. Clearly, the set of characters used within a given taxon (genus, tribe, etc.) may be more or less exhaustive and depends on the taxon, but within the family as a whole, a minimal set of comparable characters is needed for future studies such as the present review or Robbrecht & Puff's (1986) survey of the Ixoroideae. Most of the characters discussed above in chapter 2 are easily and rapidly observable by simple techniques (see 1.2), and the characters of the minimal set should be of the same type.

The present study clearly shows that the determination of the following characters is the absolute minimum for every member of the Rubiaceae: presence or absence of raphides, anatomy of external hairs, corolla aestivation, floral biology, anatomy of seed exotestal cells, and pollen type (position, number and type of apertures; exine type). A next step is thus the development of "descriptors" for taxonomic analyses of the Rubiaceae (see Jeffrey 1987).

Collection of a comparable minimal character set, such as the above, will not be an easy task for the following reasons:

- Most of the characters in the minimal set are multistate.

- Many of them are dependent. If a particular structure has character state Y rather than X, then the characters that describe X are unavailable because they are dependent on its presence in order to be expressed. In the case of endocarp papery or crustaceous, a whole suite of pyrene characters that describe the crustaceous endocarp can not be determined when the endocarp is papery.

- A given character state in a certain taxon is not necessarily homologous with the same apparent state in another taxon. In Hamelieae with all the aestivation types known to occur in the Rubiaceae, corollas "contorted to the right" are derived from corollas "imbricate to the right" (Bremer 1987). Right-contorted corollas are also present in a few Gardenieae, but they could not have evolved in the same manner as the right-contorted corollas of the Hamelieae, and therefore this aestivation type is not homologous in the two tribes.

The Rubiaceae are so vast a family that a single researcher can not hope to gather all the essential taxonomic data for an in-depth analysis of the family. A concerted effort is required by all workers to produce fully comparable descriptions with the minimal information for a comprehensive analysis. The present study is a first, minor step towards a more natural and finally phylogenetic classification of the Rubiaceae. I warmly hope that it will foster these attitudes in others, the only ones which will finally lead to a unified taxonomic database for the Rubiaceae.

Nowadays, more and more taxonomists start using computers. Modern research in the grass family (Watson, Clifford & Dallwitz 1985; Watson, Dallwitz & Johnston 1986), using DELTA for the storing of data in an automated bank, and accounting for the two first handicaps discussed above, may certainly serve as model for the assemblage, analysis and interpretation.

Appendix 1

SURVEY OF THE PROPOSED CLASSIFICATION

Bibliographical references to tribes and subtribes are only mentioned when not given in Darwin (1976a). Critical notes are especially included when no useful treatments of the tribes are available.

"Useful treatments" are papers with a bearing at tribal or subtribal level.

1 **Cinchonoideae** Raf.

Plants mostly woody, frequently very large trees. Stipules mostly entire (bifid or fimbriate in Ise.). Raphides mostly absent, present in tribes 9-10. Corolla aestivation variable, valvate or imbricate, rarely contorted. Placentas with numerous ovules. Fruits mostly dry and dehiscent (capsules), sometimes fleshy. Seeds numerous, often winged. Exotestal cells always with thickenings along inner tangential walls.
Heterodistyly frequent; stylar pollen presentation rare.

Note: The distinction between the tribes of this subfamily is not easy. A few arbitrary characters have been used to separate the Cinchoneae (vertically imbricate ovules and seeds mostly winged) from the Condamineeae (horizontal ovules, seeds mostly not winged, aestivation valvate) and Rondeletieae (as Condamineeae but aestivation contorted or imbricate). An in depth study of the tribal delimitation is much needed.

1 1 **Cinchoneae** DC.

Stipules interpetiolar, mostly entire, rarely bifid. Raphides absent (?). Inflorescences terminal, many-flowered. Ovary 2-locular, each axile placenta with many ovules. Capsules with many winged seeds. Exotestal cells with reticulate thickenings along the inner tangential wall.
Pollen frequently 3-colporate.

Useful treatment: Ehrendorfer 1988.

Cinchoninae DC.

Syn.: ? Coptosapelteae Bremek. ex Darwin
? Manettieae Bremek.

Trees or shrubs. Inflorescences lax. Corolla aestivation contorted, imbricate or valvate. Ovules pendulous, vertically imbricate.
Flower biology diverse (as well heterostyly as stylar pollen presentation occurring).

Distribution: pantropical.

Genera: *Alseis, Balmea, Blepharidium, Calycophyllum, Capirona, Cephalodendron, Cinchona, Corynanthe, Cosmibuena, Coursiana, Coutarea, Crossopteryx, Dolicholobium, Duidiana, Emmenopterys, Exostema, Ferdinandusa, Greeniopsis, Hymenodictyon, Joosia, Ladenbergia, Lecanosperma, Luculia, Macrocnemum P. Browne, Maguireocharis, Molopanthera, Mussaendopsis, Paracorynanthe, Pausinystalia, Pimentelia, Remijia, Schizocalyx, Stilpnophyllum, Suberanthus, Syringantha, Wittmackanthus.*

Genera often transferred to Hedyotideae because of presence of raphides (position to reconsider): *Bouvardia, Cigarilla, Danais, Dunnia, Heterophyllaea, Hindsia, Manettia, Merumea, Neohymenopogon, Schismatoclada.*

Tentatively included: *Coptosapelta, Wernhamia.*

Mitragyninae Haviland

Trees (Mitragyna), or climbers with fang hooks (Uncaria). Flowers clustered in spherical heads. Corolla aestivation valvate. Ovules basally attached, upwardly imbricate.

Stylar pollen presentation present.

Distribution: pantropical.

Useful treatments: Leroy 1975; Ridsdale 1978a.

Genera: *Mitragyna, Uncaria.*

Note: Bremekamp (1966) was the first to suggest a subtribe in the Cinchoneae for a number of genera previously included in the Naucleeae. Ridsdale's revisions have confirmed this. I provision-ally adopt here his Mitragyninae with only two genera. He indicated that the subdivision of the Cinchoneae as a whole needs reinvestigation, and that *Corynanthe, Pausinystalia* and possibly *Hymenodictyon* have the same insertion of ovules and seeds as the two genera placed here.

12 **Naucleeae** DC. ex Miq.

Trees, shrubs or lianas. Stipules interpetiolar, rarely somewhat intrapetiolar. Raphides absent. Flowers clustered in spherical heads. Ovary 2-locular, with numerous ± vertical, pendulous or predominantly pendulous ovules in each cell. Fruits free or connate into a syncarp or pseudosyncarp. Exotestal cells with thickenings along inner tangential wall.

Stylar pollen presentation present.

Pollen ? generally 3-colporate.

Useful treatments: Bakhuizen van den Brink 1970, Ridsdale 1975b, 1978b.

Note: Ridsdale (1978b), when proposing the subdivision followed here, believed "that the subtribes ... recognized are relatively homogeneous but ... have only a rather low level of relationship with each other". He associated the Naucleinae and "Anthoce-phalinae" with the Cinchoneae, and considered the Adininae as more distinct, probably deserving tribal recognition. Because of the low number of pendulous ovules in the Adininae, their transfer to the Antirheoideae needs consideration.

Adininae Ridsdale, Blumea **24**: 319 (1978)

Corolla aestivation imbricate, rarely valvate. Stigma ± globose. Placenta small, with the shape of an obovoid boss, attached to upper third of septum. Seeds flattened, ± winged.

Distribution: paleotropical.

Genera: *Adina, Adinauclea, Breonadia, Breonia, Diyaminauclea, Gyrostipula, Haldina, Janotia, Khasiaclunea, Ludekia, Metadina, Myrmeconauclea, Neobreonia, Neonauclea, Pertusadina, Sinoadina.*

Neolamarckiinae Robbrecht nom. nov.

Syn.: Anthocephalinae Ridsdale, Blumea **24**: 361 (1978)

Corolla aestivation imbricate. Stigma spindle-shaped. Placenta large, variously shaped (but not as in Nau.-Ad.), attached to upper third of septum. Seeds angular.

Distribution: tropical Asia.
Genus: *Neolamarckia*.
Note: Bosser (1984) forwarded arguments that *Anthocephalus* is synonymous with *Breonia*, and provided the name *Neolamarckia* for Ridsdales intended genus. A new subtribal name is consequently needed.

Naucleinae DC.

Corolla aestivation imbricate. Stigma spindle-shaped. Placenta as in Nau.-An., or peltate and attached to middle of septum. Seeds variously shaped, somewhat angular, rarely flattened and ± winged.

Distribution: paleotropical.
Genera: *Burttdavya, Nauclea, Ochreinauclea, Sarcocephalus.*

13 Hillieae Bremek. ex Darwin

Epiphytic shrubs. Stipules interpetiolar, entire. Raphides present. Corolla aestivation contorted to the right. Ovary 2-locular, numerous ovules in each locule. Capsules with numerous plumose seeds. Exotestal cells bulging, radially elongate, with reticulate thickenings.
Flower biology ?
Pollen 3-colporate.

Distribution: neotropical
Genera: *Hillia, Ravnia.*

14 Henriquezieae Hook. f.

Syn.: Gleasonieae Bremek.

Trees or shrubs. Stipules intrapetiolar, entire (*Gleasonia*), or interpetiolar, bifid (*Henriquezia*) or entire (*Platycarpum*). Colleters absent. Raphides absent. Inflorescences terminal. Corolla ± zygomorphic, the lobes imbricate in bud. Ovary 2-locular, with 2-many ovules per locule. Capsules woody, loculicidal, flattened perpendicularly to septum, with flattened, ± winged seeds. Exotestal cells bulging, with reticulate thickenings. Embryo very large, with foliaceous cotyledons and short radicle. Endosperm reduced.
Flower biology ?
Pollen grains 3-colp(oid)orate (in *Gleasonia* in permanent tetrads); shape frequently oblate.

Distribution: neotropical.
Useful treatments: Rogers 1984 (and papers cited therein).
Genera: *Gleasonia, Henriquezia, Platycarpum.*

15 Rondeletieae DC. ex Miq.

Syn.: Simireae Bremek. ex Darwin

Trees or shrubs, rarely (Sipaneopsis) herbaceous. Stipules entire, rarely bifid. Further little differing from the Condamineeae: corolla-lobes imbricate or more rarely contorted. Flowers frequently heterostylous.
Pollen mostly 3-colporate.

Distribution: centred in the New World; a few genera in tropical Asia, one *Wendlandia* sp. reaching NE Africa.
Useful treatments: Borhidi 1982; Borhidi & Fernandez Zequeira 1983 (and papers cited therein).
Genera: *Acrobotrys, Acunaeanthus, Aleisanthia, Arachnothryx, Augusta, Bathysa, Blandibractea, Chalepophyllum, Cuatreca-sasiodendron, Dendrosipanea, Eizia, Elaeagia, Glionnetia, Gloneria, Greenea, Holstianthus, Javorkaea, Lindenia, Macbrideina, Maguireothamnus, Neblinathamnus, Pteridocalyx, Rogiera, Roigella, Rondeletia, Simira, Sipaneopsis, Spathichlamys, Standleya, Steenisia, Stevensia, Warszewiczia, Wendlandia.*
Tentatively included: *Habroneuron.*

16 **Sipaneeae** Bremek.

Distribution: neotropical.
Genera: *Limnosipanea, Sipanea, Steyermarkia.*
Note: I have provisionally maintained Bremekamp's segregate of Rondeletieae for these three genera with herbaceous habit and contorted aestivation, but a revision of the Rondeletieae/Condamineeae complex may well show that this is not justified.

17 **Condamineeae** Hook. f.

Trees or shrubs. Stipules mostly interpetiolar, entire, rarely bifid. Raphides absent. Inflorescences mostly terminal and many-flowered. Corolla aestivation valvate, rarely imbricate. Ovary 2-locular, with many horizontal ovules in each locule. Capsules with many horizontal seeds. Exotestal cells with pitted thickenings along the inner tangential walls.
Flower biology: no peculiar adaptation known.
Pollen mostly 3-colporate, rarely porate (Bikkia).

Distribution: Predominantly neotropical, with one genus (*Pinckneya*) in N America, and a few genera from Malesia to New Caledonia (*Badusa, Bikkia*) and the Solomon Islands.
Useful treatment: Aiello 1979.
Genera: *Badusa, Bikkia, Ceuthocarpus, Chimarrhis, Condaminea, Cubanola, Dioicodendron, Flexanthera, Isidorea, Kerianthera, Morierina, Nernstia, Osa, Parachimarrhis, Picardaea, Pinckneya, Pogonopus, Portlandia, Rustia, Stomandra, Thogsennia, Tresanthera.* Tentatively included: *Kajewskiella, Pseudomussaenda.*
Notes: 1.- Hooker (1873) distinguished three subtribes, the Condamineinae, Portlandiinae and Pinckneyinae, a division not accepted by Schumann (1891) or Bremekamp (1966). Verdcourt (1958) even included the whole tribe in the Rondeletieae.
2.- Wernham (1916) added the African genus *Pseudomussaenda* to the Condamineeae-Pinckneyinae. Verdcourt (1951) questioned its place in the Condamineeae, and later (Verdcourt 1958) included it in the Isertieae. F. Hallé (1961) regarded the genus intermediate between Isertieae and Hedyotideae. The position of *Pseudomussaenda* is one of the problems to be considered in the needed redelimitation of the tribes of the Cinchonoideae.

1 8 **Isertieae** A. Rich. ex DC.

Syn.: Acranthereae Bremek. ex Darwin
Heinsieae Verdc.
Mussaendeae Hook. f., nom. illeg.
Sabiceeae Bremek.

Shrubs, lianas or trees. Stipules interpetiolar, mostly bifid, rarely entire or fimbriate. Raphides absent. Flowers mostly in terminal many-flowered inflorescences (often "calycophyllous pseudanthia" with semaphylls; inflorescences rarely (*Sabicea*, *Stipularia*) axillary and paired at nodes. Corolla-lobes mostly valvate, in *Isertia* spp., *Heinsia* and *Yutajea* imbricate. Ovary 2-5(-6)-locular, each placenta with numerous ovules. Fruits fleshy, with many small, angular seeds. Exotestal cells with pitted thickenings along the inner tangential walls.
Flowers frequently heterostylous.
Pollen 3-5-aperturate, colporate or porate.

Distribution: pantropical.
Useful treatments: F. Hallé 1961, Garcia Kirkbride 1979.
Genera: *Acranthera, Amphidasya, Aphaenandra, Ecpoma, Gonzalagunia, Gouldia, Heinsia, Indopolysolenia, Isertia, Keenania, Lecananthus, Leucocodon, Mussaenda, Mycetia, Ophryococcus, Pseudosabicea, Raritebe, Sabicea, Schizostigma, Stipularia, Temnopteryx, Yuatajea.*
Tentatively included: *Aoranthe, Schizomussaenda, Streblosiopsis.*

1 9 **Urophylleae** Bremek. ex Verdc.

Shrubs or small trees, rarely tending to be herbaceous. Stipules interpetiolar, entire (bifid in Pleiocarpidia). Raphides present. Inflorescences axillary and paired at nodes. Corolla-lobes valvate. Stigmatic lobes spreading. Ovary plurilocular, each placenta with numerous seeds. Fruits fleshy, with many angular seeds. Exotestal cells with ± massive thickenings, with large pits or numerous narrow perforations, along radial and inner tangential walls.
Flowers unisexual.
Pollen ?

Distribution: tropical Asia
Useful treatment: Bremekamp 1940.
Genera: *Antherostele, Crobylanthe, Didymopogon, Lepidostoma, Leucolophus, Maschalocorymbus, Pleiocarpidia, Praravinia, Pravinaria, Rhaphidura, Stichianthus, Urophyllum.*

1 10 **Pauridiantheae** Bremek. ex Darwin

Differing in little from the previous tribe. Inflorescences rarely terminal. Stigmatic lobes not spreading, often ± coherent. Ovary 2-(5-)locular. Flowers hermaphrodite, heterostylous.
Pollen 3-colporate.

Distribution: tropical Africa.
Useful treatments: Bremekamp 1941; N. Hallé 1964.
Genera: *Commitheca, Pampletantha, Pauridiantha, Poecilocalyx, Rhipidantha, Stelechantha.*

2 Ixoroideae Raf.

Plants woody. Stipules mostly entire (fimbriate in *Rutidea* spp.). Raphides absent, except in *Argocoffeopsis*, Gar.-D. Corolla-lobes with contorted aestivation. Placentas mostly pluriovulate, sometimes with 1-few ovules. Seed number variable. Fruits fleshy (in Gar.-G. with ± dry wall and seeds in pulp). Exotestal cells rarely parenchyma-like, generally with thickenings, either along the radial and inner and outer tangential walls or along one of them.
Stylar pollen presentation general (very few exceptions, e.g. *Cladoceras*, Pav.); flowers in addition often unisexual.

Note: The delimitation of the Gardenieae and associated tribes was much debated in the past. For a discussion and clarification see Robbrecht & Puff (1986).

2 11 Gardenieae A. Rich. ex DC.

Plants woody. Stipules interpetiolar, entire.
Raphides absent (but one record in *Argocoffeopsis*).
Corolla-lobes contorted to the left, rarely to the right.
Stylar pollen presentation present.

Useful treatments: F. Hallé 1967; Tirvengadum 1978; Tirvengadum & Sastre 1979; Wong 1984; Keddam-Malplanche 1985; Robbrecht & Puff 1986.

Gardeniinae DC.

Syn.: Brachytomeae Tirvengadum, Bull. Mus. Nation. Hist. Nat., Paris, ser. 4, sect. B, Adansonia **3**: 292 (1986)
Cordiereae A. Rich. ex DC.

Shrubs, trees or lianas, very rarely geofrutices. Inflorescences terminal, rarely pseudo-axillary, very rarely truly axillary and paired at nodes. Ovary 2(-9)-carpellate, with axile or parietal placentas with (few-) many ovules. Fruits mostly large, with ± dry wall and (few-)many seeds embedded in placental pulp. Seeds often lenticular. Exotestal cells mostly with thickenings along radial and inner tangential walls, rarely also along outer tangential walls. Embryo-radicle with variable orientation.

Pollen grains in tetrads or monads, mostly 3-porate, more rarely colporate.

Distribution: pantropical.

Genera: *Aidia, Aidiopsis, Alibertia, Amaioua, Anomanthodia, Atractocarpus, Atractogyne, Benkara, Borojoa, Brachytome, Brenania, Burchellia, Byrsophyllum, Calochone, Casasia, Catunaregam, Ceriscoides, Coddia, Deccania, Didymosalpinx, Dioecrescis, Dolichodelphys, Duroia, Euclinia, Fagerlindia, Gardenia, Genipa, Glossostipula, Hyperacanthus, Ibetralia, Kailarsenia, Kochummenia, Kutchubaea, Macrosphyra, Mantalania, Massularia, Melanopsidium Colla, Mitriostigma, Monosalpinx, Morelia, Neofranciella, Oligocodon, Oxyanthus, Oxyceros, Pelagodendron, Phellocalyx, Pleiocoryne, Porterandia, Posoqueria, Preussiodora, Pseudaidia, Pseudogardenia, Pseudomantalania, Randia, Rhyssocarpus, Rothmannia, Schachtia, Schumanniophyton, Sherbournia, Sphinctanthus, Stachyarrhena, Sukunia, Sulitia, Tamilnadia, Tarennoidea, Tocoyena, Trukia.*

Diplosporinae Miq.

Syn.: Cremasporeae Bremek. ex Darwin p.p. quoad genus typicum

Shrubs, rarely trees or geofrutices. Inflorescences axillary and paired at nodes. Ovary 2-locular, each axile placenta with 1-many ovules. Fruits mostly small, placenta rarely developed into arilloid wholly or partly covering seeds. Seeds 1-several per locule. Exotestal cells with no or ± weak thickenings (only in *Cremaspora* with apparently thickened radial walls). Embryo- radicle inferior or lateral.

Pollen grains 3-colporate.

Distribution: paleotropical.

Useful treatment: Robbrecht 1988.

Genera: *Argocoffeopsis, Calycosiphonia, Cremaspora, Diplospora, Nostolachma, Petitiocodon, Sericanthe, Tricalysia, Xantonneopsis.*

2 12 **Pavetteae** A. Rich. ex Dum.

Syn.: Ixoreae Hook. f., nom. illeg. (incl. *Coffea*).

Shrubs, rarely climbing or geofrutescent. Stipules inter-petiolar, entire (fimbriate in *Rutidea* spp.). Raphides absent. Inflorescences mostly terminal. Corolla-lobes contorted to the left. Ovary 2(-7)-locular, each axile placenta with 1-many ovules. Fruits fleshy. Seeds 1-numerous per locule, frequently with adaxial excavation. Exotestal cells sometimes paren-

chyma-like, mostly with thickenings along outer tangential walls. Embryo-radicle inferior or lateral.
Stylar pollen presentation present.
Pollen grains 3-4(-5)-colporate.

Distribution: mainly paleotropical, but Ixora also occurring in the Neotropis.
Useful treatments: Robbrecht 1984, Bridson & Robbrecht 1985, Robbrecht & Puff 1986.
Genera: *Captaincookia, Cladoceras, Coleactina, Dictyandra, Doricera, Duperrea, Hitoa, Ixora, Leptactina, Myonima, Nichallea, Pachystylus, Pavetta, Rutidea, Tarenna, Tennantia, Versteegia.*
Tentatively included: *Homollea, Homolliella, Paracephaelis, Schizenterospermum.*

2 13 **Coffeeae** DC.

Shrubs. Stipules interpetiolar, entire. Raphides absent. Inflorescences axillary and paired at nodes. Corolla-lobes contorted to the left. Ovary 2-locular, each axile placenta 1-ovulate. Fruits fleshy, with (1-)2 seeds with deep ventral groove ("coffee-beans"). Exotesta comprised of thin elongated parenchymatic cells plus isolated fibers. Embryo-radicle inferior.
Stylar pollen presentation present.
Pollen grains 3-4-colporate.

Distribution: paleotropical.
Useful treatments: Leroy 1971, 1980; Bridson 1982, 1987a; Robbrecht & Puff 1986.
Genera: *Coffea, Psilanthus.*

2 14 **Aulacocalyceae** Robbrecht & Puff, Bot. Jahrb. Syst. **108**: 123 (1986)

Shrubs, rarely trees. Stipules interpetiolar, entire. Raphides absent. Inflorescences terminal. Corolla-lobes contorted to the left. Ovary 2-locular, each axile placenta with 1-2(-3) ovules. Fruits fleshy, containing (1-)2-4(-5) seeds embedded in placental pulp difficultly discernible from proper fruit wall. Seeds glossy, without seed-coat. Embryo-radicle superior.
Stylar pollen presentation present.
Pollen grains 3-colp(oid)orate.

Distribution: paleotropical.
Useful treatment: protologue.
Genera: *Alleizettella, Aulacocalyx, Heinsenia, Himalrandia.*
Tentatively included: *Belonophora, Gardeniopsis.*

2 15 **Hypobathreae** (Miq.) Robbrecht, Bull. Nat. Plantentuin Belg. **50**: 75 (1980)

Shrubs, rarely trees. Stipules interpetiolar, entire. Raphides absent. Inflorescences axillary and paired at nodes. Corolla-lobes contorted to the left. Ovary 2-locular with axile placentas, rarely (Villaria) unilocular with 2 parietal placentas; ovules (1-)many. Fruits with fleshy or rarely leathery wall, with 1-many pendulous or horizontal seeds.

Exotesta mostly folded with regard to endotesta, appearing fibrous, composed of elongated cells with thickenings along radial wall, sometimes also along inner and outer tangential walls; exotestal cells rarely ± isodiametric, parenchyma-like. Embryo-radicle superior, or oriented towards septum in horizontal seeds.
Stylar pollen presentation present.
Pollen grains 3-colporate.

Distribution: paleotropical.
Useful treatments: Tirvengadum & Robbrecht 1985; Robbrecht & Puff 1986.
Genera: *Canephora, Chapeliera, Cowiea, Feretia, Fernelia, Flagenium, Galiniera, Gallienia, Hypobathrum, Hyptianthera, Jovetia, Kraussia, Lamprothamnus, Maschalodesme, Morindopsis, Nargedia, Paragenipa, Polysphaeria, Pouchetia, Ramosmania, Rhadinopus, Scyphostachys, Villaria, Xantonnea, Zuccarinia* Blume.
Tentatively included: *Lemyrea, Pubistylus.*

3 **Antirheoideae** Raf.

Plants generally woody, rarely (Kno.) herbaceous. Stipules mostly entire (divided in Kno.). Raphides generally absent, present in Cra. and Kno. Corolla aestivation mostly valvate, rarely imbricate or contorted. Placentas generally with a single, pendulous ovule (two in Ret.). Generally one (often elongated) seed per fruit chamber. Fruits fleshy (drupes with individual pyrenes or with plurilocular stones). Exotestal cells parenchyma-like or with (mostly reduced) thickenings along the inner tangential wall. Endosperm soft and oily; embryo frequently very large, with superior radicle.
Stylar pollen presentation general and flowers in addition often unisexual, except in Cra. and Kno. (heterodistylous).

3 16 **Retiniphylleae** Hook. f.

Shrubs or trees. Stipules interpetiolar, entire. Raphides absent. Inflorescences terminal. Corolla-tube often ± curved and lobes contorted to the left. Stamens inserted in corolla-throat; anthers with apical and basal sterile appendage. Ovary 5-locular, each cell with 2 pendulous ovules. Fruits fleshy, with generally 5 unilocular, one-seeded pyrenes with apical preformed slit. Seeds with characteristic saddle-like central-adaxial appendage. Exotestal cells frequently parenchyma-like.
Stylar pollen presentation present.
Pollen 3-colporate.

Distribution: neotropical.
Genus: *Retiniphyllum.*
Tentatively included: *Botryarrhena.*

3 17 **Vanguerieae** A. Rich. ex Dum.

Shrubs, trees, geofrutices or climbers. Stipules interpetiolar, absent. Raphides absent (sometimes isolated needle-shaped crystals in endotesta). Inflorescences axillary, paired at nodes. Corolla-lobes valvate. Stamens inserted in corolla-throat. Ovary 2-12-locular, with a single, apically attached, pendulous ovule in each cell. Fruits fleshy, with several unilocular pyrenes with apical preformed slit(s). Seeds with characteristic saddle-like appendage. Endosperm oily, often blue. Embryos large. Exotesta frequently with intercellular openings; cells parenchyma-like or with delicate thickenings.

Stylar pollen presentation very characteristic, with cylindrical or capitate stigmata.

Pollen grains 3-porate or 3-colporate, mostly oblate.

Distribution: centred in tropical Africa and Madagascar, extending into tropical Asia and Australia.

Useful treatments: Robyns 1928; Capuron 1969; Bridson 1985, 1986, 1987b, 1987c; Verdcourt 1987.

Genera: *Ancylanthos, Canthium, Cuviera, Cyclophyllum, Eriosemopsis, Fadogia, Fadogiella, Hutchinsonia, Keetia, Lagynias, Meyna, Multidentia, Pachystigma, Peponidium, Perakanthus, Plectroniella, Psydrax, Pygmaeothamnus, Pyrostria, Robynsia, Rytigynia, Scyphochlamys, Tapiphyllum, Temnocalyx, Vangueria, Vangueriella, Vangueriopsis.*

3 18 **Guettardeae** DC.

Syn.: Machaonieae A. Rich. ex Dum.

Shrubs or trees. Stipules interpetiolar, entire. Raphides absent. Inflorescences terminal or axillary and paired at nodes. Corolla-lobes with valvate or more rarely imbricate aestivation. Ovary 2-many-locular, with a single, apically attached, pendulous ovule in each cell. Fruits fleshy, with several-many unilocular pyrenes or plurilocular endocarp; capsules in Machaonia. Seeds frequently elongated; endosperm little-developed, oily. Embryo large. Exotestal cells frequently with thickenings along radial wall.

Stylar pollen presentation present.

Pollen 3-4-aperturate, porate or colpate.

Distribution: pantropical, but almost absent in Africa (only *Guettarda speciosa* on the coasts of E Africa). Many species in coastal vegetation.

Useful treatments: Jansen 1984; Wong 1988.

Genera: *Antirhea, Bobea, Chomelia* Jacq., *Dichilanthe, Guettarda, Guettardella, Machaonia, Malanea, Neolaugeria, Ottoschmidtia, Pittonniotis, Timonius.*

Tentatively included: *Neoblakea* (stipules divided).

Note: See 2.3.4 for wood anatomical evidence suggesting the exclusion of *Machaonia*, *Timonius* and *Dichilanthe*. Darwin (1979), however, accepted that *Timonius* agrees well with other Pacific members of the Guettardeae.

3 19 **Chiococceae** Hook. f.

Shrubs or trees. Stipules interpetiolar, entire. Raphides absent. Inflorescences axillary and paired at nodes, rarely terminal. Corolla-lobes valvate or more rarely imbricate. Stamens inserted at base of corolla-tube, base of filaments mostly fused. Ovary 2-locular, with a single, apically attached, pendulous ovule in each cell. Fruits fleshy, often flattened perpendicularly to septum, with 1-2 unilocular pyrenes with apical preformed slits, or with a single plurilocular endocarp. Seeds frequently flattened or elongated. Endosperm oily. Exotesta frequently with intercellular openings; cells parenchyma-like or with delicate thickenings along radial and inner tangential walls.
Stylar pollen presentation present.
Pollen 3-colporate.

Distribution: neotropical, but one genus (*Hodgkinsonia*) in Australia.
Genera: *Allenanthus, Asemnantha, Ceratopyxis, Chiococca, Chione, Erithalis* P. Br., *Hodgkinsonia, Phialanthus, Placocarpa, Salzmannia, Scolosanthus, Shaferocharis*.
Tentatively included: *Mastixiodendron*.

3 20 **Alberteae** Hook. f.

Shrubs, trees, or (*Nematostylis*) semisucculent (sub)shrubs. Stipules interpetiolar, entire. Raphides absent. Flowers ± zygomorphic, with corolla-lobes contorted to the left. Ovary 2-locular, with a single, apically attached, pendulous ovule in each cell. Fruits ± dry, indehiscent or dehiscent into mericarps. Exotestal cells with delicate thickenings along inner tangential wall. Embryo small.
Stylar pollen presentation present.
Pollen 3-colporate.

Distribution: subendemic to Madagascar, only Alberta magna occurring in South Africa.
Useful treatment: Puff, Robbrecht & Randrianasolo 1984.
Genera: *Alberta, Nematostylis*.
Tentatively included: *Airosperma, Boholia, Octotropis*.

3 21 **Cephalantheae** Kunth ex Ridsdale, Blumea **23**: 179 (1976)

Shrubs. Stipules interpetiolar, entire. Raphides absent. Inflorescences terminal and axillary, in compact globose heads. Corolla-lobes imbricate. Stamens inserted in corolla-throat. Ovary 2-locular, with a single, apically attached, pendulous ovule in each cell. Fruits fleshy, with 2 one-seeded, unilocular pyrenes with apical-marginal preformed slits. Seeds elongated, with stony arilloid at tip. Embryo large, with superior radicle. Endosperm frequently oily. Exotestal cells with delicate thickenings along inner tangential wall.
Stylar pollen presentation present.
Pollen 3-4-colporate.

Distribution: disjunct (1 sp. S. Africa, 2 spp. SE Asia, 3 spp. N-S America).
Useful treatment: Ridsdale 1976; Ehrendorfer 1988.
Genus: *Cephalanthus*.

3 22 Craterispermeae Verdc.

Shrubs or trees, rarely geofrutices. Stipules interpetiolar, entire. Raphides present. Inflorescences axillary and paired at nodes, condensed and borne on stout short peduncle. Corolla-lobes valvate. Ovary 2-locular, with a single, apically attached, pendulous ovule in each cell. Fruits fleshy; mostly only one locule developing; solitary pyrene ± spherical, with fibrous lid. Seed ± spherical. Seed-coat absent.
Flowers heterostylous.
Pollen 3-colporate.

Distribution: tropical Africa (also Seychelles and Madagascar).
Genus: *Craterispermum*.

3 23 Knoxieae Hook. f.

Plants herbaceous, rarely geofrutescent or entirely woody. Stipules interpetiolar, generally fimbriate, rarely (*Calanda*) entire. Raphides present. Inflorescences terminal. Corolla-lobes valvate. Ovary 2-5-locular, with a single, apically attached, pendulous ovule in each cell. Fruits ± fleshy to dry, dehiscent or tardily dehiscent into mericarps supported by true or false carpophores, with well developed horny endocarp with apical preformed slits. Endosperm oily. Embryo medium-sized to large. Exotestal cells with delicate thickenings.
Flowers heterostylous.
Pollen 3-colporate.

Distribution: centred in tropical Africa, only Knoxia extending into tropical Asia and Australia.
Useful treatment: Puff & Robbrecht (in press).
Genera: *Calanda, Chlorochorion, Knoxia, Neopentanisia, Paraknoxia, Pentanisia*.

Antirheoideae incertae sedis

Trailliaedoxa, Scyphiphora.

4 Rubioideae

Plants woody or herbaceous. Stipules frequently bifid or fimbriate. Raphides generally present. Corolla aestivation mostly valvate, rarely imbricate or contorted. Placentas pluriovulate (tribes 24-29) or with a single (rarely two) erect ovule(s) (tribes 30-39). Seed number variable. Fruits dry or fleshy. Exotestal cells often parenchyma-like.
Heterodistyly very common.

4 24 **Hedyotideae** Cham. & Schlecht.

Syn.: Cruckshanksieae Hook. f. (see Puff 1988)
Oldenlandieae Schumann, nom. illeg.
Pomazoteae Bremek. ex Darwin (see Axelius 1987)
Virectarieae Verdc.

Plants mostly herbaceous, rarely (sub)woody. Stipules interpetiolar, generally fimbriate. Raphides present, rarely (*Virectaria*) absent. Inflorescences frequently terminal and lax, also axillary and paired at nodes, congested. Corolla-lobes valvate. Ovary 2-locular, each axile placenta with (1-2)-many ovules; placenta varying from peltate and (sub)sessile to ± isodiametric and borne on a stout stalk. Capsules many-seeded. Seeds mostly angular, rarely ± winged. Exotestal cells frequently parenchyma-like.
Flowers frequently heterostylous.
Pollen 3-(pluri-)colporate.

Distribution: pantropical.
Useful treatments: Bremekamp 1952; Verdcourt 1953a, b, c; Lewis 1965; Terrell 1975; Terrell & al. 1986; Puff 1982, 1988.
Genera: *Agatisanthemum, Amphiasma, Arcytophyllum Willd., Astiella, Batopedina, Bradea, Carphalea, Carterella, Chamaepentas, Conostomium, Coptophyllum, Cruckshanksia, Dentella, Dibrachio-nostylus, Dolichometra, Eionitis, Exallage, Hedyotis, Hedythyrsus, Hekistocarpa, Houstonia, Jainia, Kohautia, Lelya, Leptomischus, Leptoscela, Lerchea, Lucya, Manostachya, Mitrasacmopsis, Mouretia, Neanotis, Nesohedyotis, Oldenlandia, Oreopolus, Otiophora, Otomeria, Paedicalyx, Parapentas, Payera, Pentanopsis, Pentas, Pentodon, Phyllocrater, Placopoda, Pleiocraterium, Polyura, Pseudonesohedyotis, Rachicallis, Sacosperma, Siderobombyx, Stephanococcus, Synaptantha, Thecorchus, Virectaria, Xanthophytopsis, Xanthophytum*; see also genera of doubtful position in Cin.-C.
Tentatively included: *Hayataella, Siemensia.*

4 25 **Ophiorrhizeae** Bremek. ex Verdc.

Plants herbaceous to woody. Stipules interpetiolar, mostly fimbriate. Raphides present. Inflorescences terminal. Corolla-lobes valvate. Ovary 2-locular, each axile placenta with many ovules. Capsules laterally flattened, many-seeded. Exotestal cells (? thick verrucate walls).
Flowers frequently heterostylous.
Pollen 3-(4-)colporate.

Distribution: from Sri Lanka and E India through Malesia to Fiji and Society Islands.
Useful treatment: Darwin 1976b.

Genera: Ophiorrhiza, Spiradiclis.
Tentatively included: *Klossia*.

4 26 **Coccocypseleae** Bremek.

Creeping herbs. Stipules entire. Raphides present. Inflorescences terminal, subcapitate. Corolla-lobes valvate. Ovary 2-locular, each axile placenta with many ovules. Fruits fleshy. Exotestal cells ? thick-walled.
Flowers frequently heterostylous.
Pollen 3-colporate.

Distribution: neotropical.
Genus: *Coccocypselum*.

4 27 **Argostemmateae** Bremek. ex Verdc.

Monocaul dwarfs. Stipules interpetiolar, mostly divided, rarely entire. Raphides present. Inflorescences terminal. Corollas white, lobes valvate. Stamens inserted near corolla-base, anthers mostly adnate into a cone. Ovary 2-locular, each axile placenta on stout stalk, with many ovules. Fruits dry, indehiscent or opening with operculum. Exotestal cells ? with strongly thickened radial walls.
Flower biology: flowers monomorphic, no peculiar adaptation known.
Pollen 3-colporate.

Distribution: paleotropical, Asia-centred (only 2 *Argostemma* spp. in West and Central Africa).
Useful treatment: Bremer 1987.
Genera: *Argostemma, Neurocalyx*.

4 28 **Hamelieae** DC.

Syn.: Deppeeae Kirkbride, Brittonia **36**: 317 (1984)

Shrubs or small trees. Stipules interpetiolar, entire or divided. Raphides present. Inflorescences terminal. Corolla often yellow or yellowish, sometimes reddish; aestivation very variable, imbricate or contorted to the right. Stamens inserted near corolla-base; anthers free. Ovary 2- (5-) locular, each axile placenta with many ovules. Fruits fleshy or dry. Exotestal cells (? granulate to tuberculate outer walls).
Flower biology: flowers monomorphic, no peculiar adaptation known.
Pollen ?

Distribution: neotropical, essentially Central American.
Useful treatment: Bremer 1987.
Genera: *Deppea, Hamelia, Hoffmannia, Omiltemia, Pinarophyllon*.

4 29 **Schradereae** Bremek.

Scrambling shrubs or epiphytic climbers, with adhesive adventitious roots. Stipules interpetiolar, entire. Raphides present. Inflorescences terminal, ± congested. Corolla-lobes valvate. Ovary 2-4-locular, each axile placenta with many ovules.
Fruits fleshy, many-seeded. Exotestal cells ? thick-walled.

Flower biology: no peculiar adaptation known.
Pollen ?

Distribution: Malesia, South-America.
Genera: *Lucinaea, Schradera.*

4 30 **Psychotrieae** A. Rich. ex Dum.

Syn.: Gaertnereae Bremek. ex Darwin
Psathureae A. Rich. ex Dum.

Shrubs or trees, rarely geofrutices or herbs. Stipules inter- or intrapetiolar, mostly divided, rarely entire. Raphides present. Inflorescences terminal, rarely axillary and paired at nodes. Corolla-lobes valvate, rarely imbricate. Ovary 2-5-locular, with a single erect ovule in each locule.
Fruits fleshy; endocarp frequently consisting of unilocular, one-seeded pyrenes with basal preformed slits. Seeds with horny endosperm and small embryos. Exotestal cells frequently parenchyma-like.
Flowers frequently heterostylous.
Pollen very variable, grains 0-5-(pluri-)aperturate, colpate, colporate or porate.

Distribution: pantropical.
Useful treatments: Bremekamp 1960, 1961, 1963; Petit 1964a.
Genera: *Allaeophania, Amaracarpus, Aphanocarpus, Calycosia, Cephaelis, Chaetostachydium, Chasallia, Chazaliella, Chytropsia, Coccochondra, Coelopyrena, Coryphothamnus, Cremocarpon, Declieuxia, Gaertnera, Gamotopea, Geophila, Gillespiea, Hedstromia, Hydnophytum, Hymenocnemis, Hymenocoleus, Lecariocalyx, Litosanthes, Mapouria, Margaritopsis, Montamans, Myrmecodia, Myrmephytum, Naletonia, Nonatelia Aublet, Pagamea, Pagameopsis, Palicourea, Peripeplus, Petagomoa, Proscephaleium, Psathura, Psychotria, Pyragra, Readea, Ronabea, Rudgea, Saldinia, Saprosma, Squamellaria, Stachyococcus, Streblosa, Strempelia, Trigonopyren.*
Tentatively included: *Fergusonia, Tsiangia.*
Note: Huxley (1981 & in prep.) and Jebb (1985) recognize the Hydnophytinae for the genera associated with *Myrmecodia* (*Hydnophytum, Myrmephytum, Squamellaria*); while the geographical distribution of these four genera (all Malesian) supports their view, their great palynological diversity (in a yet eurypalynous tribe) points to parallellism.

4 31 **Triainolepideae** Bremek.

Shrubs or trees. Stipules interpetiolar, fimbriate. Raphides present. Inflorescences terminal. Corolla-lobes valvate. Ovary 2-10-locular, with 2 or 3 erect ovules in each locule. Fruits fleshy, with a single plurilocular stone. Exotestal cells ?
Flowers frequently heterostylous.
Pollen grains 3-colporate.

Distribution: Madagascar (+ Comoro and Aldabra Isl.), penetrating into East Africa.
Useful treatment: protologue.
Genera: *Paratriaina, Thyridocalyx, Triainolepis.*

4 32 **Lathraeocarpeae** Bremek.

Small shrubs. Stipules interpetiolar, truncate with 1-2 teeth. Raphides present. Flowers solitary, terminal on short shoots. Corolla-lobes valvate. Ovary 4-locular, with a single erect ovule in each locule. Fruits with a single 4-locular stone, locules one-seeded. Seeds with fleshy (? oily) endosperm. Exotestal cells ?
Flowers frequently heterostylous.
Pollen grains pluricolporate.

Distribution: Madagascar.
Useful treatment: protologue.
Genus: *Lathraeocarpa*.

4 33 **Morindeae** Miq.

Shrubs, trees or lianas. Stipules interpetiolar, entire or 2-lobed. Raphides present. Inflorescences terminal or axillary and paired at nodes. Corolla-lobes valvate. Ovary 2-12-locular, with 1(-2) erect ovules in each locule. Fruits fleshy, frequently connate into syncarps; endocarp generally consisting of several unilocural, one-seeded pyrenes. Exotestal cells ?parenchyma-like.
Flowers frequently heterostylous.
Pollen 3-6-colporate.

Distribution: pantropical.
Useful treatments: Petit 1963; Johansson 1987.
Genera: *Appunettia, Appunia, Caelospermum, Colletoecema, Damnacanthus, Didymoecium, Gynochtodes, Lasianthus, Morinda, Motleya, Pogonolobus, Prismatomeris, Rennellia, Sarcopygme, Trichostachys.*
Tentatively included: *Siphonandrium*.

4 34 **Coussareeae** Hook. f.

Shrubs or trees. Stipules interpetiolar, entire. Raphides present. Inflorescences terminal. Corolla-lobes valvate. Ovary 2-locular, with a single erect ovule in each locule; septum thin or incomplete, early disappearing. Fruits ± leathery, unilocular, one-seeded. Exotestal cells ?
Flowers frequently heterostylous.
Pollen 2-4-porate.

Distribution: disjunct (*Schizocolea* in tropical Africa, other two genera neotropical).
Useful treatment: Dwyer & Hayden 1966.
Genera: *Coussarea, Faramea, Schizocolea.*

4 35 **Paederieae** DC.

Syn.: Putorieae DC. ex Sweet

Shrubs, climbing shrubs, dwarf shrubs or herbs. Stipules interpetiolar, divided or entire. Raphides present. Corolla-lobes valvate. Stamens inserted in upper part of corolla-tube. Ovary 2-5-locular, with a single erect ovule in each locule. Fruits dry, dehiscent into mericarps or opening with operculum, or fleshy, indehiscent. Exotestal cells frequently parenchyma-like.

Flowers frequently heterostylous.
Pollen 3-colpate.

Distribution: mainly northern hemisphere and centred in tropical Asia, extending into tropical Africa, the Mediterranean Region (*Putoria*) and North America (*Kellogia* spp.); one genus in the southern hemisphere (*Crocyllis*, southern Africa).
Useful treatments: Puff 1982; Robbrecht 1982b; Léonard 1984.
Genera: *Aitchisonia, Choulettia, Crocyllis, Jaubertia, Kelloggia, Leptodermis, Neogaillonia, Paederia, Plocama, Pseudogaillonia, Pseudopyxis, Pterogaillonia, Putoria, Serissa, Spermadictyon.*

4 36 **Anthospermeae** Cham. & Schlecht.

Trees, shrubs or herbs. Stipules interpetiolar, entire or divided. Raphides present. Corolla-lobes valvate. Stamen insertion low, usually at base of corolla-tube. Ovary 2-
(5-)locular, with a single erect ovule in each locule. Exotestal cells parenchyma-like or thickened.
Flowers unisexual, anemophilous.
Pollen 3-colporate.

Distribution: tropical, subtropical and temperate parts of southern hemisphere.
Useful treatments: Fosberg 1982; Puff 1982, 1986a; Robbrecht 1982b.

Anthosperminae Benth.
Ovaries free. Fruits dry, mostly dehiscent.

Distribution: Canary Islands, Africa, Arabia and Madagascar.
Genera: *Anthospermum, Carpacoce, Galopina, Nenax, Phyllis.*

Coprosminae Fosberg, Acta Phytotax. Geobot. **33**: 75 (1982)

Syn.: Durringtonieae Henderson & Guymer, Kew Bull. **40**: 99 (1985) (see Puff & Robbrecht 1988)
Ovaries free. Fruits fleshy, with (1-)2(-5) unilocular one-seeded pyrenes.

Distribution: south temperate amphi-transpacific, reaching New Caledonia (*Normandia*), Australia (*Durringtonia*) and western South America (*Leptostigma*).
Genera: *Coprosma, Durringtonia, Leptostigma, Nertera, Normandia, Peratanthe.*

Operculariinae Benth.

Flowers with fused ovaries. Dry syncarps opening by means of an operculum.

Distribution: Australia and Tasmania.
Genera: *Eleutheranthus, Opercularia, Pomax.*

4 37 **Theligoneae** Wunderlich ex Darwin

Herbs; lower leaves opposite and upper alternate (extreme anisophylly). Stipules interpetiolar, sheathing. Raphides present. Inflorescences axillary. Corolla-lobes valvate. Male flowers with (2-)7-30 stamens. Ovary 1-locular, with a single

basal ovule. Fruits drupaceous; pericarp with elaiosome. Seeds solitary, curved, with large embryo. Exotestal cells parenchyma-like.
Flowers unisexual, anemophilous.
Pollen (3-)4-8-porate.

Distribution: Mediterranean region, China and Japan.
Useful treatment: Wunderlich 1971.
Genus: *Theligonum*.

4 38 Spermacoceae A. Rich. ex Dum.

Plants herbaceous, rarely (sub)woody. Stipules interpetiolar, fimbriate. Raphides present. Inflorescences terminal or axillary and paired at nodes. Corolla-lobes valvate. Ovary 2(-5-6)-locular, with a single erect ovule in each locule. Fruits dry, dehiscent into mericarps. Seeds with apparent adaxial groove(s). Exotestal cells ? mostly parenchyma-like.
Flowers frequently heterostylous.
Pollen (3-)plurizonocolpate or -colporate, rarely pantoporate.

Distribution: pantropical.
Useful treatment: Williams 1974.
Genera: *Crusea* Cham. & Schlecht., *Diacrodon, Diodella, Diodia, Emmeorhiza, Ernodea, Gomphocalyx, Hydrophylax, Micrasepalum, Mitracarpus, Nodocarpaea, Phylohydrax, Psyllocarpus, Richardia, Schwendenera, Spermacoce, Staelia, Tobagoa, Tortuella.*

4 39 Rubieae

Plants herbaceous, rarely (sub)woody. Leaves and leaf-like stipules "verticillate". Raphides present. Inflorescences terminal. Calyx rudimentary. Corolla-lobes valvate. Ovary 2-locular, with a single erect ovule in each locule. Fruits dry or somewhat fleshy, didymous. Exotestal cells ?
Flowers frequently heterostylous; very rarely (*Phuopsis*) stylar pollen presentation.
Pollen pluricolpate.

Distribution: cosmopolitan.
Useful treatments: Ehrendorfer 1971 (and literature cited therein).
Genera: *x Asperugalium, Asperula, Bataprine, Callipeltis, Crucia-nella, Cruciata, Didymaea, x Galiasperula, Galium, Mericarpaea, Microphysa, Phuopsis, Relbunium, Rubia, Sherardia, Valantia, War-burgina.*

Tribus incertae sedis

40 **Catesbaeeae** Hook. f.

Genera: *Catesbaea, Phyllacanthus.*

41 **Hippotieae** Garcia Kirkbride, Revta. Brasil. Bot. **4**: 119 (1981)

Genera: *Hippotis, Pentagonia, Sommera.*
Tentatively included: *Wiasemskya.*

42 **Tammsieae** Garcia Kirkbride, Revta. Brasil. Bot. **4**: 123 (1981)

Genus: *Tammsia.*

43 **Jackieae** Korthals, Ned. Kruidk. Arch. **2**: 196 (1851)

Genus: *Jackiopsis* (syn. *Jackia*).

44 **Perameae** Bremek. ex Darwin

Genus: *Perama.*

Genera incertae sedis

Bertiera, Bothriospora, Clarkella, Cosmocalyx, Coutaportla, Didymochlamys, Eosanthe, Hintonia, Mitchella, Oregandra, Pentaloncha, Phitopis, Phyllomelia, Pseudohamelia, Rhopalobrachium, Riqueuria, Schmidtottia, Striolaria, Strumpfia.

Dubious genera

Alleizettea, Ariadne, Bellermannia, Benzonia, Berghesia, Etericius, Gilipus, Henlea, Menestoria, Neobertiera, Otocalyx, Stylosiphonia.

Fossil genera (taxonomy not considered in present work)

Canthidium, Cinchonidium, Coprosmaephyllum, Mitragynaxylon, Morindidium, Naucleoxylon, Psychotriphyllum, Rubiaceaecarpum, Rubiaceocarpum, Rubioides, Rubioxylon.

Excluded genera (see appendix 2 and 4)

Antherma, Carlemannia, Craterianthus, Dialypetalanthus, Hemipogon, Hylacium, Plectronia L., *Quiducia, Silamnus, Silvianthus, Spirea, Webera* Cramer.

Apendix 2

INDEX NOMINUM GENERICORUM: ADDITIONS AND CORRECTIONS RELATING TO RUBIACEAE

This list of additions to Farr, Leussink & Stafleu (1979) is updated until October 1988. Inclusions in the supplement to "Index Nominum Genericorum" (Farr, Leussink & Zijlstra 1986) are indicated by "suppl. 1".

Acunaeanthus Borhidi, Jarai-Komlodi & Moncada, Acta Bot. Acad. Sci. Hung. 26: 282. 1980.
T.: *A. tinifolius* (Grisebach) Borhidi (*Rondeletia tinifolia* Grisebach)

Adinauclea Ridsdale; suppl. 1

Afroknoxia Verdcourt, Kew Bull. 36: 493. 1981.
T.: *A. manika* Verdcourt

Aidiopsis Tirvengadum, Bull. Mus. Nation. Hist. Nat., Paris, ser. 4, 8, sect. B, Adansonia 3: 287. 1986.
T.: *A. forbesii* (King & Gamble) Tirvengadum (*Randia forbesii* King & Gamble)

Aoranthe C. Somers, Bull. Nat. Plantentuin Belg. 58: 64. 30 June 1988.
T.: *A. nalaensis* (De Wild.) C. Somers (*Randia nalaensis* De Wild.)

Arachnothryx Planchon
LT.: *A. leucophylla* (Kunth) Planch. (vide Borhidi, Act. Bot. Acad. Sci. Hung. 28: 68. 1982)

Argocoffeopsis Lebrun
LT.: *A. subcordata* (Hiern) Lebrun (*Coffea subcordata* Hiern) (vide Robbrecht, Bull. Nat. Plantentuin Belg. 51: 363. 1981)

Benkara Adanson
Replace Melastomataceae with Rubiaceae (fide Tirvengadum, Taxon 32: 436. 1983). See also Parkinson, Taxon 36: 602. 1987: ?conservation needed).

Bikkia Reinwardt; suppl. 1

Breonadia Ridsdale; suppl. 1

Calycosiphonia Pierre ex Robbrecht, Bull. Nat. Plantentuin Belg. 51: 370. 31 Dec. 1981.
T.: *C. spathicalyx* (K. Schumann) Robbrecht (*Coffea spathicalyx* K. Schumann)

Captaincookia N. Hallé; suppl. 1

Carlemannia Bentham
Replace Rubiaceae with Carlemanniaceae/Caprifoliaceae

Carterella Terrell, Brittonia 39: 250. 1987.
T.: *C. alexanderae* (A. Carter) Terrell (*Bouvardia alexanderae* A. Carter)

Catunaregam Wolf; suppl. 1

Ceriscoides (J.D. Hooker) Tirvengadum, Bull. Mus. Nation. Hist. Nat., ser. 3, 521, Bot. 35: 13. 1978.
T.: *C. turgida* (Roxburgh) Tirvengadum (*Gardenia turgida* Roxburgh)

Ceuthocarpus Aiello, Journ. Arn. Arb. 60: 109. Jan. 1979.
T.: *C. involucratus* (Wernh.) Aiello (*Portlandia involucrata* Wernh.)

Chapelieria A. Richard: deserves ort. corr. Chapeliera ?

Chazaliella Petit ex Petit & Verdcourt; suppl. 1

Cigarrilla Aiello, Journ. Arn. Arb. 60: 109. Jan. 1979.
T.: *C. mexicana* (Zuccarini & Martius ex DeCandolle) Aiello (*Coutarea mexicana* Zuccarini & Martius ex DeCandolle)

Chlorochorion Puff & Robbrecht, Bot. Jahrb. Syst. (in press)

Coccochondra Rauschert, Taxon 31: 561. 1982.
T.: *C. laevis* (Steyermark) Rauschert (*Chondrococcus laevis* Steyermark)
Substitute name for *Chondrococcus* Steyermark

Coddia Verdcourt, Kew Bull. 36: 509. 1981.
T.: *C. rudis* (E. Meyer ex Harvey) Verdcourt (*Randia rudis* E. Meyer ex Harvey)

Cofeanthus A. Chevalier
Nom. invalid. (vide Robbrecht, Bull. Nat. Plantentuin Belg. 51: 360. 1981)

Coleactina N. Hallé, Fl. Gabon 17: 83. 1970.
T.: *C. papalis* N. Hallé

Craterianthus Valeton ex Heyne
Replace Rubiaceae with Rhizophoraceae (vide Van Steenis, Bull. Jard. Bot. Buitenzorg, ser. 3, 17: 457. 1948)

Cubanola Aiello, Journ. Arn. Arb. 60: 111. Jan. 1979.
T.: *C. daphnoides* (R. Graham) Aiello (*Portlandia daphnoides* R. Graham)

Deccania Tirvengadum, Nord. J. Bot. 3: 456. 1983.
T.: *D. pubescens* (Roth) Tirvengadum (*Gardenia pubescens* Roth)

Declieuxia Kunth; suppl. 1

Dentella J.R. Forster & J.G.A. Forster; suppl. 1

Dialypetalanthus Kuhlmann
Replace Rubiaceae with Dialypetalanthaceae

Dioecrescis Tirvengadum, Nord. J. Bot. 3: 456. 1983.
T.: *Dioecrescis erythroclada* (Kurz) Tirvengadum (*Gardenia erythroclada* Kurz)

Diplocrater J.D. Hooker
LT.: *Tricalysia coriacea* (Bentham) Hiern (*Randia coriacea* Bentham)
Rem.: Combination of type species under Diplocrater not available (vide Robbrecht, Bull. Nat. Plantentuin Belg. 57: 71. 1987)

Diyaminauclea (J.D. Hooker) Ridsdale; suppl. 1

Doricera Verdcourt, Kew Bull. 37: 554. 1983.
T.: *D. trilocularis* (Balf.f.) Verdcourt (*Pyrostria trilocularis* Balf.f.)

Dressleriopsis Dwyer, Ann. Miss. Bot. Gard. 67 (1): 153. 1980.
T.: *D. panamensis* Dwyer

Durringtonia R. Henderson & Guymer, Kew Bull. 40: 99. 1985.
T.: *D. paludosa* R. Henderson & Guymer

Duvaucellia Bowdich
Replace Oleaceae with Rubiaceae.
Vide Bot. Macar. 6: 61. 1980 & Taxon 33: 298. 1984.

Eleutheranthus F.H. Mueller
orth. var. of *Eleutranthes*

Eleuthranthes F.H. Mueller in Bentham, Fl. Austral. 3: 437. 1867.
T.: *E. opercularina* F.H. Mueller in Bentham, nom. illeg.
Rem.: Vide Bull. Nat. Plantentuin Belg. 52: 358 (1982)

Epitaberna K. Schumann
Replace Apocynaceae with Rubiaceae
Vide N. Hallé, Flore Gabon 12: 132. 1966.

Exostema (Persoon) L.C. Richard ex Humboldt & Bonpland
LT.: *E. caribaeum* (Jacquin) Roemer & Schultes (vide Rogers, Journ. Arn. Arbor. 68: 165. 1987)

Fagerlindia Tirvengadum, Nord. J. Bot. 3: 457. 1983.
T.: *F. fasciculata* (Roxburgh) Tirvengadum (*Posoqueria fasciculata* Roxburgh)

Fructesca A.P. de Candolle ex Meisner
Replace "Rubiaceae/Loganiaceae" with Rubiaceae

Gaertnera Lamarck; suppl. 1

Glionnetia Tirvengadum, Bull. Mus. Nation. Hist. Nat., Paris, ser. 4, 6, sect. B, Adansonia 2: 198. 1984.
T.: *G. sericea* (Baker) Tirvengadum (*Ixora sericea* Baker)

Globulostylis Wernham
LT.: *G. talbotii* Wernham (vide Verdcourt, Kew Bull. 42: 189. 1987)

Glossostipula Lorence, Candollea 41: 454. 1987.
T.: *G. concinna* (Standley) Lorence (*Randia concinna* Standley)

Gynochtodes Blume, Bijdr. 993. Oct. 1826-Mar. 1827.
T.: *G. coriacea* Blume

Gynochthodes J.D. Hooker in Bentham et J.D. Hooker, Gen. 2: 119. 1873 (ort. var.)
= *Gynochtodes* Blume (vide Smith & Darwin 1988, Fl. Vit. Nova 4: 341. 1988)

Gyrostipula Leroy; suppl. 1

Haldina Ridsdale; suppl. 1

Hallea Leroy; suppl. 1

Hedyotis Linnaeus
LT.: *H. auricularia* Linnaeus rather then *H. fructicosa* Linnaeus (vide Rogers, Journ. Arn. Arbor. 68: 147. 1987, and Smith & Darwin, Fl. Vit. Nova 4: 352. 1988)

Hemipogon Decaisne
Replace Rubiaceae with Asclepiadaceae

Holstianthus Steyermark, Ann. Missouri Bot. Garden 73: 495. 1986.
T.: *H. barbigularis* Steyermark

Hylacium Palisot de Beauvois
Replace Rubiaceae with Apocynaceae (vide Hepper, Kew Bull. 16: 338. 1962)

Hymenodictyon Wallich in Roxburgh, Fl. ind. ed. Carey 2: 128. 1824 (nom. cons.)
T.: *H. excelsum* Wallich (typ. cons.)

Hyperacanthus E. Meyer ex Bridson, Kew Bull. 40: 275. 1985.
T.: *H. amoenus* (Sims) Bridson (*Gardenia amoena* Sims)

Indopolysolenia Bennet, Indian Forester 107: 437. 1981.
T.: *I. wallichii* (J.D. Hooker) Bennet (*Polysolenia wallichii* J.D. Hooker)
Substitute name for *Polysolenia* J.D. Hooker

Jackiopsis Ridsdale, Blumea 25: 295. 1979.
T.: *J. ornata* (Wallich) Ridsdale (*Jackia ornata* Wallich)
Substitute name for *Jackia* Wallich

Jainia Balakrishnan, J. Bombay Nat. Hist. Soc. 77: 116. 1980.
T.: *J. nicobarica* Balakrishnan

Janotia Leroy; suppl. 1

Javorkaea Borhidi & J. Komlodi, Acta Botanica Hungarica 29: 16. 1983.
T.: *J. hondurensis* (Donnell-Smith) Borhidi & J. Komlodi (Rondeletia hondurensis Donnell-Smith)

Kailarsenia Tirvengadum, Nord. J. Bot. 3: 462. 1983.
T.: *K. tentaculata* (J.D. Hooker) Tirvengadum (*Gardenia tentaculata* J.D. Hooker)

Kerianthera Kirkbride, Brittonia 37: 109. 1985.
T.: *K. preclara* Kirkbride

Khasiaclunea Ridsdale; suppl. 1

Kochummenia Wong, Malay. Nat. J. 38: 31. 1984.
T.: *K. stenopetala* (King & Gamble) Wong (*Gardenia stenopetala* King & Gamble)

Leptactina J.D. Hooker
LT.: *L. mannii* J.D. Hooker (vide Robbrecht, Pl. Syst. Evol. 145: 106. 1984)

Ludekia Ridsdale; suppl. 1

Mantalania Capuron ex Leroy; suppl. 1

Mastixiodendron Melchior
Replace Rubiaceae/Cornaceae with Rubiaceae (vide Darwin, J. Arn. Arb. 58: 355. 1977)

Melachone Gilli, Ann. Naturhist. Mus. Wien 83: 459. 1980.
T.: *M. microphylla* Gilli

Mitrasacmopsis Jovet
Replace Rubiaceae/Loganiaceae with Rubiaceae (vide Bremekamp, Acta Bot. Neerl. 15: 7. 1966)

Monosalpinx N. Hallé
Replace Gardeniaceae with Rubiaceae

Montamans J.D. Dwyer, Ann. Missouri Bot. Garden 67: 284. 1980.
T.: *M. panamensis* J.D. Dwyer

Motleya [as **Motleyia**] J.T. Johansson, Blumea 32: 149. 1987.
T.: *M. borneensis* J.T. Johansson

Multidentia Gilli; suppl. 1

Nargedia Beddome ex J.D. Hooker, Fl. Brit. India 3: 122. 1880. Fl. Sylv. S. India: t. 328. 1873-74.
T.: *N. macrocarpa* (Thwaites) J.D. Hooker (*Hyptianthera macrocarpa* Thwaites)

Nauclea L.
Note: for lectotypification of *Cephalanthus orientalis,* vide Ridsdale, Blumea 23: 184-186. 1976.

Neleixa Rafinesque
Replace Rubiaceae with Rubiaceae/Convolvulaceae

Neobreonia Ridsdale; suppl. 1

Neogaillonia Linczevski; suppl. 1

Neohymenopogon Bennet, Indian Forester 107: 436. 1981.
T.: *N. parasiticus* (Wallich) Bennet (*Hymenopogon parasiticus* Wallich)
Substitute name for *Hymenopogon*

Neolamarckia J. Bosser, Bull. Mus. natur. Hist. Nat., Paris, ser. 4, 6, sect. B, Adansonia 3: 247. 1984.
T.: *N. cadamba* (Roxburgh) Bosser (*Nauclea cadamba* Roxburgh)

Neolaugeria Nicolson; suppl. 1

Neoleroya A. Cavaco; suppl. 1

Neonauclea Merrill
LT.: *N. obtusa* (Blume) Merrill (*Nauclea obtusa* Blume). Vide Bakhuizen van den Brink, Taxon 19: 476. 1970.

Neorosea N. Hallé, Fl. Gabon 17: 268. 1970.
T.: *N. jasminiflora* (Klotzsch) N. Hallé (*Rosea jasminiflora* Klotzsch)
Substitute name for *Rosea* Klotzsch 1853, non Fabricius 1759.

Nichallea Bridson; suppl. 1

Ochreinauclea Ridsdale & Bakhuizen van den Brink f.; suppl. 1

Osa Aiello, Journ. Arn. Arb. 60: 115. Jan. 1979.
T.: *O. pulchra* (D. Simpson) Aiello (*Hintonia pulchra* D. Simpson)

Oxyceros Loureiro
LT.: *O. horrida* Loureiro (vide Wong, Malayan Nat. J. 38: 36. Aug. 1984)

Pappostyles Pierre, Bull. Mens. Soc. Linn. Paris 2: 1268. 1897.
T.: *P. neuropetalum* Pierre
Rem. The name is printed *Pappostylum*, but on the copy in BR corrected by hand Pappostyles; the hand-correction was probably done before the distribution; at any event the copies in BR and L are corrected by the same hand. Handwritten documents (herbarium labels etc.) of Pierre also mention Pappostyles. As the two orth. var. are taken up in Index Kewensis, it may be assumed that the copy in K (all copies ?) was (were) corrected also.

Pappostylum Pierre, Bull. Mens. Soc. Linn. Paris 2: 1268. 1897.
orth. var. = *Pappostyles* Pierre

Paracorynanthe Capuron; suppl. 1

Pertusadina Ridsdale; suppl. 1

Petitiocodon Robbrecht, Bull. Nat. Plantentuin Belg. 58: 109. 30 June 1988.
T.: *P. parviflorum* (Keay) Robbrecht (*Didymosalpinx parviflora* Keay)

Phallaria Schumacher
LT.: *P. horizontalis* Schumacher (vide Bridson, Kew Bull. 40: 722. 1985)

Phellocalyx Bridson, Kew Bull. 35: 315. 1980.
T.: *T. vollesenii* Bridson

Phylohydrax Puff, Pl. Syst. Evol. 154: 362. 1986.
T.: *P. carnosa* (Hochstetter) Puff (*Diodia carnosa* Hochstetter)

Phytopis J.D. Hooker
Misspelled for Phitopis, where correct entry

Platycarpum Bonpland
Replace Bignoniaceae/Henriqueziaceae with Rubiaceae

Pleiocoryne Rauschert, Taxon 31: 561. 1982.
T.: *P. fernandense* (Hiern) Rauschert (*Gardenia fernandensis* Hiern)
Substitute name for *Polycoryne* Keay

Polysolen Rauschert, Taxon 31: 561. 1982.
T.: *P. wallichii* (J.D. Hooker) Rauschert (*Polysolenia wallichii* J.D. Hooker)
Substitute name for *Polysolenia* J.D. Hooker (superfluous at date of publication, vide Kirkbride & Robbrecht, Taxon 33: 103. 1984)

Polysphaeria J.D. Hooker
LT.: suppl. 1

Pomax Solander ex DeCandolle; suppl. 1

Porterandia Ridley
T.: *P. anisophylla* (Jack ex Roxburgh) Ridley (the lectotypification by Wong, Malay. Nat. J. 38: 44. 1984 is superfluous)

Pristidia Thwaites
Replace Loganiaceae/Rubiaceae with Rubiaceae

Pseudaidia Tirvengadum, Bull. Mus. Nation. Hist. Nat., Paris, ser. 4, 8, sect. B, Adansonia 3: 286. 1986.
T.: *P. speciosa* (Beddome) Tirvengadum (*Griffithia speciosa* Beddome)

Pseudogaillonia Linczevski; suppl. 1

Pseudomantalania Leroy; suppl. 1

Pterogaillonia Linczevski; suppl. 1

Quiducia Gagnepain
Replace Rubiaceae with Carlemanniaceae/Caprifoliaceae (vide Ridsdale, Blumea 24: 42. 1978)

Ramosmania Tirvengadum & Verdcourt, Nord. J. Bot. 2: 326. 1982
T.: *R. heterophylla* (Balf.f.) Tirvengadum & Verdcourt

Rogiera Planchon
LT.: *R. amoena* Planchon (vide Borhidi, Acta Bot. Ac. Sci. Hung. 28: 67. 1982)

Roigella Borhidi & Fernandez, Acta Bot. Acad. Sci. Hung. 27 (3-4): 310. 1981.
T.: *R. correifolia* (Grisebach) Borhidi & Fernandez (*Rondeletia correifolia* Grisebach)

Rosea Klotzsch
LT.: *R. jasminiflora* Klotzsch (vide N. Hallé, Fl. Gabon 17: 269. 1970)

Rothamannia Thunberg
Misspelling for *Rothmannia* where correct entry.

Saldinia A. Richard; suppl. 1

Sarcopygme Setchell & Christophersen
LT.: *S. pacifica* (Reinecke) Setchell & Christophersen (Sarcocephalus pacificus Reinecke). Vide Bakhuizen van den Brink, Taxon 19: 479. 1970

Sericanthe Robbrecht, Bull. Nat. Plantentuin Belg. 48: 27. 30 June 1978.
T.: *Sericanthe odoratissima* (K. Schumann) Robbrecht (*Tricalysia odoratissima* K. Schumann)

Silvianthus J.D. Hooker
Replace Carlemanniaceae/Rubiaceae with Carlemanniaceae/Caprifoliaceae

Sinoadina Ridsdale; suppl. 1

Spirea Pierre
Replace Rubiaceae with Asteraceae

Suberanthus Borhidi & Fernandez, Acta Bot. Acad. Sci. Hung. 27: 314. 1981.
T.: *S. neriifolius* (A. Richard) Borhidi & Fernandez (*Exostema neriifolium* A. Richard)

Sykesia Arnold
Replace Loganiaceae with Rubiaceae

Tamilnadia Tirvengadum & Sastre, Mauritius Inst. Bull. 8 (4): 84. 1979.
T.: *T. uliginosa* (Retzius) Tirvengadum & Sastre (*Gardenia uliginosa* Retzius)

Tarennoidea Tirvengadum & Sastre, Mauritius Inst. Bull. 8 (4): 90. 1979.
T.: *T. wallichii* (J.D. Hooker) Tirvengadum & Sastre (*Randia wallichii* J.D. Hooker)

Tennantia Verdcourt, Kew Bull. 36: 511. 1981.
T.: *T. sennii* (Chiov.) Verdcourt (*Tricalysia sennii* Verdcourt)

Thecagonum Babu; suppl. 1

Thogsennia Aiello, Journ. Arn. Arb. 60: 116. Jan. 1979.
T.: *T. lindeniana* (A. Richard) Aiello (*Gonianthes lindeniana* A. Richard)

Tsiangia But, Hsue & Li, Blumea 31: 311. 1986.
T.: *T. hongkongensis* (Seemann) But, Hsue & Li (*Gaertnera hongkongensis* Seemann)

Vangueriella Verdcourt, Kew Bull. 42: 189. 1987.
T.: *V. laxiflora* (K. Schumann) Verdcourt (*Plectronia laxifora* K. Schumann)
It is clear that Verdcourt intends this species to be the type; the designation

"*Vangueriella calycophila* (K. Schumann) Verdcourt" (inval. comb. ?; no unambiguous citation of basionym) is clearly a clerical error.

Vangueriopsis Robyns
LT.: *V. lanciflora* (Hiern) Robyns (*Canthium lanciflorum* Hiern) (vide Verdcourt, Kew Bull. 42: 187. 1987)

Varneria Linnaeus, Amoen. Acad. 4: 136. 1759 (status to be clarified)
T.: *V. augusta* Linnaeus [*Gardenia augusta* (Linnaeus) Merill]. Vide Smith, Am. J. Bot. 61: 113. 1974.

Vavanga Rohr; suppl. 1

Yutajea Steyermark, Ann. Missouri Bot. Garden 74: 676. 1987.
T.: Y. liesneri Steyermark

Appendix 3

INDICES TO TAXA

The following indices refer to four different sources, recognizable as follows :

first references: figures and pages of the present work

references preceded by

NP: pages (17-156) of Schumann's (1891) treatment in "Die natürlichen Pflanzenfamilien"; references preceded by (1) - (4): pages of the four "Nachträge" of this treatment (Schumann 1897, 1900; Krause 1908, 1915) [references are given only to the main place of treatment for the accepted genera, and to the page of mention for the synonyms; for subfamilies, "supertribes", tribes and subtribes equally the main place of treatment is referred to only]

V: pages (209-281) of Verdcourt (1958)

B: pages (1-32) of Bremekamp (1966)

Schumann (1891) is the only author using a suprageneric category, without indication of rank, between the subfamily and the tribe, and provided them with the suffix -inae. These taxa may be regarded as supertribes; I did not alter their unfortunately chosen suffix.

For tribes and subtribes, I altered the suffix of the taxa, if necessary, to the standardized one; e.g. tribe "Cinchonaceae" is listed as "Cinchoneae", subtribe "Euspermacoceae" as "Spermacocinae".

In the Index to the genera, the authorities to the generic names are added where confusion is possible. The arrangment of the four "Nachträge" to Schumann 1891 is not entirely similar. Schumann (1897 & 1900) not only added genera but also gave adaptations of his (tribal) keys to the genera; these tribes are referred to here. In the addenda prepared by Krause (1908 & 1915) only genera are added; I nevertheless included, in the index to tribes, references to those tribes to which genera are added.

References to figures, separated by a semicolon, preceed page references (bold: pages of main treatment).

INDEX TO SUBCLASSES

INDEX TO ORDERS

INDEX TO FAMILIES

INDEX TO SUBFAMILIES

INDEX TO SUPERTRIBES

INDEX TO TRIBES

INDEX TO SUBTRIBES

INDEX TO GENERA, SUBGENERA AND SPECIES

Appendix 4

GENERA RUBIACEARUM

AN INDEX TO THE GENERA AND THEIR SYNONYMY OR TRIBAL/SUBTRIBAL POSITION

Synonyms (in italics) are given with =; the tribal/subtribal position of (or other statements on) **accepted genera** (bold) is given between brackets. Authorities are only given when needed (as set out in 1.5), i.e. for nomina or in case of generic homonymy inside Rubiaceae.

The spelling of generic homonyms, under the present rules of the "International Code of Botanical Nomenclature", becomes an increasing source of nomenclatural trouble for practicing taxonomists. It is not clear whether one shoud spell *Coelospermum* or *Caelospermum*, *Gynochthodes* or *Gynochtodes*. In such instances, I tried to be consistent with recent use. Also, the "Committee for Spermatophyta" recently voted on four cases of parahomonymy (Brummitt 1988). As regards the Rubiaceae, *Gaillona* and *Gaillonia* should no longer be treated as homonyms. Such a decision has an unfortunate retroactive effect on many specific names, since a series of new combinations under *Gaillonia* are now needed. In the present work, I have maintained the name *Neogaillonia*, mainly for clerical reasons.

A

Abbottia = Timonius
Abramsia = Airosperma
Acmostigma = Pavetta
Acranthera (Ise.)
Acrobotrys (Ron.)
Acrodryon = Cephalanthus
Acrostoma Didr., nomen = Remijia
Acrosynanthus = Remijia
Acunaeanthus (Ron.)
Adenosacme Wallich, nomen = Mycetia
Adenothola Lemaire, nomen = Manettia
Adina (Nau.-Ad.)
Adinauclea (Nau.-Ad.)
Aeginetia = Bouvardia
Aetheonema Reichb., nomen = Gaertnera
Afrohamelia = Atractogyne
Afroknoxia = Knoxia
Agatisanthemum (Hed.)
Agylophora Necker, nomen = Uncaria
Aidia (Gar.-G.)
Aidiopsis (Gar.-G.)
Airosperma (Alb. ?)
Aitchisonia (Pae.)
Alberta (Alb.)
Aleisanthia (Ron.)
Alibertia (Gar.-G.)
Allaeophania (Psy.)
Alleizettea (gen. dub.; ? Pau)
Alleizettella (Aul.)
Allenanthus (Chi.)
Alseis (Cin.-C.)
Amaioua (Gar.-G.)
Amaiova ort. var. = Amaioua
Amajoa ort. var. = Amaioua
Amajoua ort. var. = Amaioua
Amaracarpus (Psy.)
Amaralia = Sherbournia
Ambraria = Anthospermum
Ammianthus Spruce ex Benth., nomen = Retiniphyllum
Amphiasma (Hed.)
Amphidasya (Ise.)
Anacylanthus ort. var. = Ancylanthos
Ancylanthos (Van.)
Ancylanthus ort. var. = Ancylanthos
Andersonia W., nomen = Gaertnera
Androtropis R. Br., nomen = Acranthera
Anisomeris = Chomelia Jacq.
Anistelma = Hedyotis
Anomanthodia (Gar.-G.)
Anonymos Walt., nomen = Houstonia
Anotis = Arcytophyllum
Antacanthus A. Rich. ex DC., nomen = Scolosanthus
Antherma (not rubiaceous; Apocynaceae)
Antherostele (Uro.)
Antherura = Psychotria
Anthocephalus = Breonia
Anthospermum (Ant.-A.)
Antirhea (Gue.)
Antirhoea ort. var. = Antirhea
Antirrhoea ort. var. = Antirhea
Antoniana = Faramea
Aoranthe (Ise. ?)
Aparinanthus = Galium
Aparine = Galium
Aparinella = Galium
Aphaenandra (Ise.)
Aphanocarpus (Psy.)
Apomuria = Psychotria
Appunettia (Mor.)
Appunia (Mor.)
Arachnimorpha = Rondeletia
Arachnothryx (Ron.; = Rondeletia ?)
Arariba = Simira
Arbulocarpus = Spermacoce
Arcytophyllum Willd. (Hed.)
Argocoffea (Pierre) Lebrun, nomen = *Argocoffeopsis*
Argocoffeopsis (Gar.-D.)
Argostema ort. var. = Argostemma
Argostemma (Arg.)
Argostemmella = Argostemma
Ariadne (gen. dub.; aff. Phyllomelia)
Asemanthia = Mussaenda
Asemnantha (Chi.)
Aspera = Galium
x Asperugalium (Rub.)
Asperula (Rub.)
Aspidanthera = Ferdinandusa
Assidora = Schumanniophyton
Asterophyllum = Asperula
Astiella (Hed.)
Atractocarpus (Gar.-G.)
Atractogyne (Gar.-G.)
Aucubaephyllum = Psychotria
Augusta (Ron.)
Augustea ort. var. = Augusta
Aulacocalyx (Aul.)
Aulacodiscus = Pleiocarpidia
Axanthes = Urophyllum
Axanthopsis Korth., nomen = Urophyllum
Axolus = Cephalanthus

B

Baconia = Pavetta subg. Baconia
Badusa (Con.; aff. Morierina)
Balfourina = Didymaea

Balmea (Cin.-C.; aff. Cosmibuena & Blepharidium)
Bamboga = Mitragyna
Bancalus (mixture: Nauclea + Diyaminauclea)
Bartlingia = Plocama
Basanacantha = Randia
Bataprine (Rub.; better included in Galium ?)
Bathysa (Ron.)
Bathysograya = Badusa
Batopedina (Hed.)
Baumannia DC. = Damnacanthus
Baumannia Schumann = Knoxia
Becheria (mixture = Ixora + Psychotria, type non des.)
Belicea = Morinda
Belilla = Mussaenda
Bellardia = Coccocypselum ?
Bellermannia (gen. dub.)
Bellilla = Mussaenda
Bellynkxia = Appunia
Belonophora (Aul. ?)
Bemsetia = Ixora
Benkara (Gar.-G.)
Benteca = Hymenodictyon
Benzonia (gen. dub.)
Berghesia (gen. dub.)
Berghias Sonn., nomen = Gardenia; see Piringa
Bergkias ort. var. = Gardenia subg. Bergkias
Berthiera ort. var. = Bertiera
Bertiera Aublet (inc. sed.; ?Cinchonoideae)
Bertiera Blume, nomen = Myrioneuron/Mycetia ?
Bertuchia Dennst., nomen = Gardenia
Bigelovia Sprengel = Spermacoce
Bigelowia = Spermacoce (ort. var. of Bigelovia)
Bikkia (Con.)
Bikkiopsis = Bikkia
Billardiera Vahl, nomen = Coussarea
Billiotia = Melanopsidium (ort. var.) Billiottia DC., nomen = Melanopsidium
Blandibractea (Ron.)
Blepharidium (Cin.-C.)
Blepharostemma = Asperula
Bobea (Gue.)
Boholia (Alb. ?)
Bonatia = Tarenna
Bonifacia S. Manso ex Steudel, nomen = Augusta
Borojoa (Gar.-G.)
Borrera = Spermacoce
Borreria = Spermacoce
Bothriospora (inc. sed.; not retained in Ham.)
Botryarrhena (Ret. ?)
Bouvardia (Cin./Hed.)
Brachytome (Gar.-G.)
Bradea (Hed.)
Brenania (Gar.-G.)
Breonadia (Nau.-Ad.)
Breonia (Nau.-Ad.)
Brignolia = Isertia
Bruinsmania = Isertia
Bubalina Raf., nomen = Burchellia
Buchia = Perama
Buchozia L'Hér. ex Juss., nomen = Serissa
Buena Cavanilles = Gonzalagunia
Buena Pohl = Cosmibuena
Bunburya = Tricalysia
Bunophila = Machaonia
Bupleuroides = Phyllis
Burchellia (Gar.-G.)
Burneya = Timonius
Burttdavya (Nau.-N.)
Buseria = Coffea
Byrsophyllum (Gar.-G.)

C

Cadamba = Guettarda
Caelospermum (Mor.)
Cafe = Coffea
Calanda (Kno.)
Calderonia = Simira
Callicocca = Psychotria ?
Callipeltis (Rub.)
Calochone (Gar.-G.)
Calycodendron = Psychotria
Calycophyllum (Cin.-C.)
Calycosia (Psy.)
Calycosiphonia (Gar.-D.)
Campanocalyx = Keenania
Camptophytum = Tarenna
Camptopus = Psychotria (? worth distinction)
Campylobotrys = Hoffmannia
Canephora (Hyp.)
Canthidium (fossil)
Canthiopsis = Tarenna
Canthium (Van.)
Canthopsis = Catunaregam
Capirona (Cin.-C.)
Caprosma ort. var. = Coprosma
Captaincookia (Pav.)
Caquepiria = Gardenia
Caranda = Psydrax
Carapichea = Cephaelis

Carinta = Geophila
Carlemannia (not rubiaceous; Carlemanniaceae/Caprifoliaceae)
Carmenocania = Pogonopus
Carpacoce (Ant.-A.)
Carphalea (Hed.)
Carpothalis E. Mey., nomen = Tricalysia
Carterella (Hed.)
Caruelina = Chomelia Jacq.
Caryococca Willd. ex Schult. & Schult., nomen = Gonzalagunia
Casasia (Gar.-G.)
Cascarilla R. ex Steudel, nomen = Cinchona
Cascarilla (Endl.) Wedd. = Ladenbergia
Cassupa = Isertia
Catesbaea (Cat.)
Catesbya ort. var. = Catesbaea
Catsjopiri Rumph. nomen = Gardenia
Cattutella Reichb., nomen = Wendlandia (sphalm. pro *Calutekka*)
Catunaregam (Gar.-G.)
Censcus Gaertner, nomen = Catunaregam
Cephaelis (Psy.) = Psychotria ?
Cephalanthus (Cep.)
Cephaleis ort. var. = Cephaelis
Cephalidium = Breonia
Cephalina = Sarcocephalus
Cephalodendron (Cin.-C.)
Ceratites Miers, nomen = Rudgea
Ceratopyxis (Chi.)
Ceriscoides (Gar.-G.)
Ceriscus Gaertner ex Nees, nomen = Catunaregam
Ceuthocarpus (Con.)
Chaenocarpus = Spermacoce
Chaetostachydium (Psy.; = Psychotria ?)
Chaetostachys = Chaetostachydium
Chalazocarpus = Schumanniophyton
Chalepophyllum (Ron.)
Chamaedaphne nom. rej. = Mitchella
Chamaepentas (Hed.)
Chamisme = Houstonia
Chapeliera (Hyp.)
Chapelieria ort. var. = Chapeliera
Charpentiera = Pavetta
Chasalia ort. var. = Chasallia
Chasallia (Psy.)
Chazalia ort. var. = Chasallia
Chazaliella (Psy.)
Chenocarpus = Spermacoce (ort. var. of Chaenocarpus)
Chesnea = Cephaelis
Chimarhis ort. var. = Chimarrhis
Chimarrhis (Con.)
Chiococca (Chi.)
Chione (Chi.)
Chlorochorion (Kno.)
Chlorostemma = Asperula
Chomela ort. var. = Chomelia Jacq.
Chomelia Jacq. (Gue.)
Chomelia L. = Tarenna
Chondrococcus = Coccochondra
Choristes = Deppea
Choulettia (Pae.)
Chrysoxylon = Pogonopus
Chytropsia (Psy.; = Psychotria ?)
Cigarilla (Cin./Hed.)
Cinchona (Cin.-C.)
Cinchonidium (fossil)
Cladoceras (Pav.)
Clarkella (inc. sed.; excluded from Arg.)
Clavenna = Lucya
Clavennaea = Lucya
Cleisocratera = Saprosma
Clusiophyllea = Canthium
Coccochondra (Psy.)
Coccocipsilum ort. var. = Coccocypselum
Coccocypselum (Coc.)
Coccosipsilum ort. var. = Coccocypselum
Codaria = Lerchea
Coddia (Gar.-G.)
Coelopyrena (Psy.; aff. Psychotria)
Coelospermum ort. var. = Caelospermum
Cofeanthus A. Chev., nomen = Psilanthus
Coffea (Cof.)
Coleactina (Pav.)
Colladonia = Palicourea
Colletoecema (Mor.)
Commianthus = Retiniphyllum
Commitheca (Pau.)
Condalia = Coccocypselum
Condaminea (Con.)
Congdonia = Declieuxia
Conosiphon = Sphinctanthus
Conostomium (Hed.)
Conotrichia = Manettia
Coprosma (Ant.-C.)
Coprosmaephyllum (fossil)
Coptophyllum (Hed.)
Coptosapelta (Cin.-C.)
Coptospelta ort. var. = Coptosapelta
Coptosperma = Tarenna
Cordia Neck, nomen = Spermacoce
Cordiera = Alibertia
Cormigonus Raf., nomen = Bikkia
Corynanthe (Cin.-C.)
Corynula = Leptostigma
Coryphothamnus (Psy.)
Cosmibuena (Cin.-C.)
Cosmocalyx (inc. sed.; aff. Phyllomelia)
Coupoui = Duroia

Coupouia = Duroia (ort. var. of *Coupoui*)
Coupuia Raf., nomen = Duroia (ort. var. of *Coupoui*)
Coupuya = Duroia (ort. var. of *Coupoui*)
Coursiana (Cin.-C.)
Coussarea (Cou.)
Coutaportla (inc. sed.; excluded from Con.)
Coutarea (Cin.-C.)
Cowiea (Hyp.)
Craterianthus (not rubiaceous; = Pellacalyx, Rhizophoraceae)
Craterispermum (Cra.)
Creaghia = Mussaendopsis
Creatantha = Isertia
Cremaspora (Gar.-D.)
Cremocarpon (Psy.)
Crinita = Pavetta
Crobylanthe (Uro.)
Crocyllis (Pae.)
Crossopteryx (Cin.-C.)
Crucianella (Rub.)
Cruciata (Rub.)
Cruckshanksia (Hed.)
Crusea Cham. & Schlecht. (Spe.)
Crusea A. Rich. = Chione
Cryptospermum = Opercularia
Cuatrecasasia Standley, nomen = Cuatrecasasiodendron
Cuatrecasasiodendron (Ron.)
Cubanola (Con.)
Cuncea = Knoxia
Cunina = Nertera
Cunninghamia = Malanea
Cupi = Tarenna
Cupia = Aidia/Anomanthodia
Cupirana Miers, nomen = Duroia
Cupuia = Duroia (ort. var. of Coupoui)
Cussarea ort. var. = Coussarea
Cuviera (Van.)
Cyclophyllum (Van.)
Cymelonema = Urophyllum
Cynanchica Fourr., nomen = Asperula
Cyrtanthus = Posoqueria

D

Damnacanthus (Mor.)
Danais (Cin./Hed.)
Darluca (? not rubiaceous; ? Convolvulaceae)
Dasus = Lasianthus
Dasycephala = Diodia
Dasys = Lasianthus (ort. var. of Dasus)
Daun-contu = Paederia
Decameria Welw., nomen = Gardenia
Decapenta = Diodia
Deccania (Gar.-G.)
Declieuxia (Psy.)
Delpechia = Mapouria
Democritea = Serissa
Dendrosipanea (Ron.; aff. Chalepophyllum)
Dentella (Hed.)
Dentillaria = Knoxia
Deppea (Ham.)
Diacrodon (Spe.)
Dialypetalanthus (not rubiaceous; Dialypetalanthaceae)
Dibrachionostylus (Hed.)
Dichilanthe (Gue.)
Dichrospermum = Spermacoce
Dicrobotryum = Guettarda
Dictyandra (Pav.)
Dictyospora = Hedyotis (ort. var. of *Dyctiospora*)
Didymaea (Rub.)
Didymochlamys (inc. sed.; excl. from Ise.)
Didymoecium (Mor.)
Didymopogon (Uro.)
Didymosalpinx (Gar.-G.)
Dillenia = Sherardia
Dinocanthium = Pyrostria
Diodella (Spe.; = Diodia ?)
Diodia (Spe.)
Diodioides Loefl., nomen = Spermacoce
Diodois Pohl, nomen = Psyllocarpus
Dioecrescis (Gar.-G.)
Dioicodendron (Con.; aff Chimarrhis)
Dioneidon = Diodia (ort. var. of *Dioneiodon*)
Dioneiodon = Diodia
Diotocarpus = Pentanisia
Diotocranus = Mitrasacmopsis
Diphragmus = Spermacoce
Diplocrater = Tricalysia
Diplophragma Meissner, nomen = Hedyotis
Diplospora (Gar.-D.)
Diplosporopsis = Belonophora
Dirichletia = Carphalea
Discocoffea = Tricalysia
Discospermum = ? Diplospora (? worth distinction)
Disodea = Paederia
Disodia ort. var. = Paederia (ort. var. of *Disodea*)
Disperma = Mitchella
Diyaminauclea (Nau.-Ad.)
Dolianthus = Amaracarpus
Dolichanthera = Morierina
Dolichodelphys (Gar.-G.)
Dolicholobium (Cin.-C.)
Dolichometra (Hed.)

Dondisia = Canthium
Donidsia ort. var. = Canthium
Donkelaaria = Guettarda
Doricera (Pav.)
Dorisia = Mastixiodendron
Dorothea = Aulacocalyx
Douarrea = Psychotria
Dressleriopsis = Lasianthus
Duggena Vahl, nomen = Gonzalagunia
Duhamelia = Hamelia
Duidiana (Cin.-C.)
Dukea = Raritebe
Dunalia = Lucya
Dunnia (Cin./Hed.)
Duperrea (Pav.)
Duroia (Gar.-G.)
Durringtonia (Ant.-C.)
Duvaucellia nom. rej. prop. = Kohautia
Dychotria = Psychotria
Dyctiospora = Hedyotis
Dysoda = Serissa
Dysodidendron = Saprosma
Dysosmia = Saprosma

E

Ebelia = Diodia
Echinodendrum = Scolosanthus
Ecpoma (Ise.)
Edechia = Guettarda
Edithea = Omiltemia
Edrastima = Oldenlandia
Ehrenbergia = Amaioua
Einsteinia = Kutchubaea
Eionitis (Hed.; = Oldenlandia ?)
Eizia (Ron.)
Elaeagia (Ron.)
Elattospermum = Breonia
Eleutheranthus (Ant.-O.)
Eleuthranthes ort. var. = Eleutheranthus
Emeorhiza ort. var. = Emmeorhiza
Emmenopterys (Cin.-C.)
Emmenopteryx ort. var. = Emmenopterys
Emmeorhiza (Spe.)
Empogona = Tricalysia subg. Empogona
Encopea = Faramea
Endlichera = Emmeorhiza
Endolasia = Manettia ?
Endolithodes Bartl., nomen = Retiniphyllum
Endopogon = Diodia
Enkylista = Calycophyllum (ort. var. of *Eukylista*)
Enterospermum = Tarenna
Eosanthe (inc.sed.; aff. Phyllomelia)
Epidendroides Soland., nomen = Myrmecodia
Epitaberna = Heinsia
Epithinia = Scyphiphora
Ereicoctis Kuntze, nomen = Arcytophyllum
Eresimus = Cephalanthus
Eriosemopsis (Van.)
Eriostoma Baillon, nomen = Tricalysia
Erithalis P. Browne (Chi.)
Erithalis Forster = Timonius
Ernestimeyera = Alberta
Ernodea (Spe.)
Erosmia = Hoffmannia (ort. var. of *Evosmia*)
Erythrodanum = Nertera
Etericius (gen. dub.)
Eteriscus ort. var. = Etericius
Euathrania Nutt. ex A. Gray, nomen = Coprosma
Euclinia (Gar.-G.)
Eukylista = Calycophyllum
Eumachia = Psychotria
Eumorphanthus = Psychotria
Euosmia = Hoffmania (ort. var. of Evosmia)
Eupyrena = Timonius
Eurhotia Neck, nomen = Cephaelis
Eurynome DC., nomen = Coprosma
Evea = Cephaelis
Evosmia = Hoffmania
Exallage (Hed.; = Hedyotis ?)
Exandra = Simira
Exechostylus = Pavetta
Exostema (Cin.-C.)
Exostemma ort. var. = Exostema
Exostemon ort. var. = Exostema
Eyselia Neck., nomen = Galium

F

Fadogia (Van.)
Fadogiella (Van.)
Fagerlindia (Gar.-G.)
Famarea ort. var. = Faramea
Faramea (Cou.)
Ferdinandea = Ferdinandusa
Ferdinandusa (Cin.-C.)
Fereiria = Hillia
Feretia (Hyp.)
Fergusonia (Psy.; or Spe. ?)
Fernelia (Hyp.)
Ferretia ort. var. = Feretia
Figuierea = Caelospermum
Flagenium (Hyp.)

Flemingia = Tarenna
Flexanthera (Con.; aff. Rustia)
Foscarena = Randia ? (ort. var. of *Foscarenia*)
Foscarenia = Randia ?
Franchetia = Breonia
Franciella = Neofranciella
Froelichia = Coussarea
Fructesca = Gaertnera
Frutesca = Gaertnera (ort. var. of *Fructesca*)
Fuchsia Sw., nomen = Schradera

G

Gaertnera (Psy.)
Gaillionia = Neogaillonia (ort. var. of *Gaillonia*)
Gaillonia = Neogaillonia (see p. 235)
Galianthe = Spermacoce
x Galiasperula (Rub.)
Galiniera (Hyp.)
Galium (Rub.)
Gallienia (Hyp.)
Gallion ort. var. = Galium
Gallium ort. var. = Galium
Galopina (Ant.-A.)
Galvania = Psychotria
Gamotopea (Psy.; = Psychotria ?)
Ganguebina Vell., nomen = Manettia
Garapatica = Alibertia
Gardena ort. var. = Gardenia
Gardenia (Gar.-G.)
Gardeniola = Alibertia
Gardeniopsis (Aul. ?)
Genipa = (Gar.-G.)
Genipella L. C. Rich., nomen = Alibertia
Geocardia = Geophila
Geoherpum = Mitchella
Geophila (Psy.)
Gerontogea Cham. & Schlechtd. = Oldenlandia
Gilipus (gen. dub.)
Gillespiea (Psy.)
Gleasonia (Hen.)
Glionnetia (Ron.; aff. Lindenia)
Globulostylis = Cuviera subg. Globulostylis
Gloneria (Ron.)
Glossostipula (Gar.-G.)
Gomezia = Nertera (ort. var. of Gomozia)
Gomosia = Nertera (ort. var. of Gomozia)
Gomoza = Nertera (ort. var. of Gomozia)
Gomozia = Nertera
Gomphocalyx (Spe.)
Gomphosia = Ferdinandusa
Gonianthes = Cubanola
Gonotheca = Oldenlandia
Gonyanera = Acranthera
Gonzalagunia (Ise.; aff. Isertia)
Gonzalea = Gonzalagunia
Gouldia (Ise.)
Greenea (Ron.)
Greeniopsis (Cin.-C.)
Griffithia = Benkara
Grisia = Bikkia
Gruhlmannia = Spermacoce
Grumilea = Psychotria
Grundlea Poiret ex Steudel, nomen = Psychotria
Grunilea = Psychotria (ort. var. of *Grumilea*)
Guagnebina = Manettia
Guettarda (Gue.)
Guettardella (Gue.)
Gutenbergia = Morinda (ort. var. of *Guttenbergia*)
Guttenbergia = Morinda
Gynaecopachys = Aidia (ort. var. of *Gynopachys*)
Gynochthodes ort. var. = Gynochtodes
Gynochtodes (Mor.)
Gynopachis = Aidia sect. Gynopachis
Gynopachys = Aidia (ort. var. of *Gynopachys*)
Gyrostipula (Nau.-Ad.)

H

Habroneuron (Ron. ?)
Habsia Steudel, nomen = Guettarda
Haldina (Nau.-Ad.)
Halesia = Guettarda
Hallea = Mitragyna (? or distinct)
Hallesia = Guettarda (ort. var. of *Halesia*)
Hamela ort. var. = Hamelia
Hamelia (Ham.)
Hamellia ort. var. = Hamelia
Hamiltonia = Spermadictyon
Hayataella (? Hed.; ? aff. Hedyotis or Ophiorrhiza)
Hecistocarpus ort. var. = Hekistocarpa
Hedstromia (Psy.)
Hedyotis (Hed.)
Hedythyrsus (Hed.)
Heinsenia (Aul.)
Heinsia (Ise.)
Hekistocarpa (Hed.)
Heliospora Hook. f., nomen = Timonius
Helospora = Timonius

Hemidiodia = Diodia
Hemipogon (not rubiaceous; Asclepiadaceae)
Henisia ort. var. = Heinsia
Henlea (gen. dub.)
Henriquezia (Hen.)
Herrera = Erithalis
Heterophyllaea (Cin./Hed.)
Hexactina Willd. ex Schlechtd., nomen = Amaioua
Hexasepalum = Diodia
Hexepta = Coffea
Hexodontocarpus = Sherardia
Heymia Dennst., nomen = Dentella
Higgensia = Hoffmannia (ort. var. of *Ohigginsia*)
Higginsia = Hoffmannia (ort. var.)
Hilla ort. var. = Hillia
Hillia (Hil.)
Himalrandia (Aul.)
Hindsia (Cin./Hed.)
Hintonia (inc. sed.; excluded from Con.)
Hippotis (Hip.)
Hitoa (Pav.; = Ixora ?)
Hodgkinsonia (Chi.)
Hoffmannia (Ham.)
Holocarpa = Pentanisia subg. Holocarpa
Holocarya = Pentanisia (ort. var. of *Holocarpa*)
Holostyla = Caelospermum (ort. var. of *Olostyla*)
Holostylis = Caelospermum (ort. var. of *Olostyla*)
Holstianthus (Ron.)
Holtonia = Simira ?
Homaloclados = Faramea
Homollea (Pav. ?)
Homolliella (Pav. ?)
Hondbesseion = ? Canthium (ort. var. of *Hondbessen*)
Hondbessen = ? Canthium
Houstona ort. var. = Houstonia
Houstonia (Hed.)
Howardia = Pogonopus
Hutchinsonia (Van.)
Hydnophytum (Psy.)
Hydrophylax (Spe.)
Hydrophyllax ort. var. = Hydrophylax
Hydrophytum ort. var. = Hydnophytum
Hylacium (not rubiaceous; Apocynaceae)
Hymendocarpum = Nostolachma
Hymenocnemis (Psy.)
Hymenocoleus (Psy.)
Hymenodictyon (Cin.-C.)
Hymenodyction ort. var. = Hymenodictyon
Hymenopogon = Neohymenopogon
Hyperacanthus (Gar.-G.)
Hypobathrum (Hyp.)
Hypodematium = Spermacoce
Hyptianthera (Hyp.)

I

Ibetralia (Gar.-G.; = Alibertia ?)
Imantina = Morinda
Indopolysolenia (Ise.)
Ipecacuanha = Cephaelis
Isartia ort. var. = Isertia
Iserta ort. var. = Isertia
Isertia (Ise.)
Isidorea (Con.)
Ixora (Pav.)

J

Jackia = Jackiopsis
Jackiopsis (Jac.)
Jainia (Hed.; aff. Coptophyllum)
Jangaraca = Hamelia (ort. var. of *Tangaraca*)
Janotia (Nau.-Ad.)
Jaubertia (Pae.)
Javorkaea (Ron.)
Jocayena ort. var. = Tocoyena
Jontanea = Coccocypselum (ort. var. of *Tontanea*)
Joosia (Cin.-C.)
Jovetia (Hyp.)
Jurgensia = Spermacoce
Justenia = Bertiera

K

Kadua = Hedyotis
Kailarsenia (Gar.-G.)
Kajewskiella (Con. ?)
Karamyschewia Fisch. & Mey., nomen = Oldenlandia
Katoutheka Adans., nomen = Wendlandia
Keenania (Ise.)
Keetia (Van.)
Kelloggia (Pae.)
Kerianthera (Con.)
Kerstingia = Belonophora
Khasiaclunea (Nau.-Ad.)
Kinkina ort. var. = Cinchona
Klossia (Oph. ?; aff. Ophiorrhiza ?)
Knoxa ort. var. = Knoxia
Knoxia (Kno.)

Kochummenia (Gar.-G.)
Koehneago = Hoffmannia
Kohautia (Hed.)
Kotchubaea ort. var. = Kutchubaea
Kraussia (Hyp.)
Kumbaya Endl. ex Steudel, nomen = Gardenia
Kurria = Hymenodictyon
Kutchubaea (Gar.-G.)
Kyrtanthus = Posoqueria (ort. var. of *Cyrtanthus*)

L

Lachnastoma Korth. = Nostolachma
Lachnosiphonium = Catunaregam
Lachnostoma Hasskarl = Nostolachma (ort. var. of *Lachnastoma*)
Ladenbergia (Cin.-C.)
Lagotis E. Mey., nomen = Carpacoce ?
Lagynias (Van.)
Lamprothamnus (Hyp.)
Landia = Mussaenda
Lasianthus (Mor.)
Lasionema = Macrocnemum
Lasiostoma Benth. = Hydnophytum
Lathraeocarpa (Lat.)
Laugeria L. = Guettarda (ort. var. of *Laugieria* Jacq.)
Laugeria Vahl ex Hook. f. = Neolaugeria
Laugieria Jacq. = Guettarda
Lawia = Mycetia
Laxmannia Gmel. ex Trin., nomen = Phuopsis
Lecananthus (Ise.)
Lecanosperma (Cin.-C.)
Lecariocalyx (Psy.)
Lecontea = Paederia
Leiochilus = Coffea
Lelya (Hed.)
Lemyrea = Hyp ?
Lepidostoma (Uro.)
Lepipogon = Catunaregam
Leptactina (Pav.)
Leptactinia ort. var. = Leptactina
Leptodermis (Pae.)
Leptomischus (Hed.)
Leptopetalum = Hedyotis
Leptoscela (Hed.)
Leptoskela ort. var. = Leptoscela
Leptostigma (Ant.-C.)
Leptunis = Asperula (? or distinct)
Lerchea (Hed.)
Leroya = Pyrostria
Leucocodon (Ise.)
Leucolophus (Uro.)
Lightfootia = Rondeletia
Limnosipanea (Ron.)
Lindenia (Ron.)
Lipostoma = Coccocypselum
Lippaya = Dentella
Listeria = Oldenlandia
Lithosanthes ort. var. = Litosanthes
Litosanthes (Psy.)
Lonicera Adans., nomen = Hamelia
Loretoa = Capirona
Lucianea ort. var. = Lucinaea
Lucinaea (Sch.)
Luculia (Cin.-C.)
Lucya (Hed.)
Ludekia (Nau.-Ad.)
Lycioserissa = Canthium
Lygistum = Manettia
Lygodisodea = Paederia

M

Macbrideina (Ron.)
Machaonia (Gue.)
Macrandria Meissner, nomen = Oldenlandia
Macrocnemum P. Browne (Cin.-C.)
Macrocnemum Vell., nomen = Remija ?
Macrosiphon Miq., nomen = Hindsia
Macrosphyra (Gar.-G.)
Maguireocharis (Cin.-C.)
Maguireothamnus (Ron.)
Malanea (Gue.)
Mallostoma = Arcytophyllum
Mamboga = Mitragyna
Manetta ort. var. = Manettia
Manettia (Cin./Hed.)
Manostachya (Hed.)
Mantalania (Gar.-G.)
Mapouria (Psy.; = Psychotria ?)
Mappia = Crucianella
Mapuria ort. var. = Mapouria
Margaris DC., nomen = Chiococca
Margaris Griseb., nomen = Margaritopsis
Margaritopsis (Psy.)
Marquisia = Coprosma
Martha = Posoqueria
Maschalanthe = Urophyllum
Maschalocorymbus (Uro.)
Maschalodesme (Hyp.)
Massularia (Gar.-G.)
Mastixiodendron (Chi. ?)
Mathiola ort. var. = Guettarda (ort. var. of *Matthiola*)
Matthiola = Guettarda
Mattuschkaea = Perama

Mattuschkea Batsch, nomen = Perama
Mattuskea = Perama (ort. var. of *Mattuschkaea*)
Mazaea = Neomazaea
Megacarpha = Oxyanthus
Megalopus = Psychotria
Megaphyllum Spruce, nomen = Pentagonia
Meionandra = Valantia
Melachone = Amaracarpus
Melanea ort. var. = Malanea
Melanopsidium Colla (Gar.-G.)
Melanopsidium Poit. ex DC., nomen = Alibertia
Menestoria (gen. dub.; Mussaenda or Mycetia, see Farr, Leussink & Stafleu 1979)
Mephitidia = Lasianthus
Mericarpaea (Rub.)
Mericocalyx = Otiophora
Merismostigma = Caelospermum
Merumea (Cin./Hed.)
Mesoptera = Psydrax
Metabolos = Hedyotis
Metabolus ort. var. = Metabolos
Metadina (Nau.-Ad.)
Meyna (Van.)
Meynia ort. var. = Meyna
Micrasepalum (Spe.)
Microphysa (Rub.)
Microsplenium Hook. f., nomen = Machaonia
Mirmecodia ort. var. = Myrmecodia
Mitchella (inc. sed.)
Mitracarpum ort. var. = Mitracarpus
Mitracarpus (Spe.)
Mitragyna (Cin.-M.)
Mitragynaxylon (fossil)
Mitragyne ort. var. = Mitragyna
Mitrasacmopsis (Hed.)
Mitrastigma = Psydrax
Mitratheca = Oldenlandia
Mitreola = Ophiorrhiza
Mitriostigma (Gar.-G.)
Molopanthera (Cin.-C.)
Monadelphanthus = Capirona
Monosalpinx (Gar.-G.)
Montamans (Psy.)
Morelia (Gar.-G.)
Morierina (Con.)
Morinda (Mor.)
Morindidium (fossil)
Morindopsis (Hyp.)
Motleya (Mor.)
Motleyia ort. var. = Motleya
Mouretia (Hed.)
Multidentia (Van.)
Mungos = Ophiorrhiza
Mussaenda (Ise.)
Mussaendopsis (Cin.-C.)
Mycetia (Ise.)
Myonima (Pav.)
Myrioneuron R.Br. ex Kurz, nomen = Keenania ?
Myristiphyllum = Psychotria (ort. var. of *Myrstiphyllum*)
Myrmecodia (Psy.)
Myrmecoides ort. var. = Myrmecodia
Myrmeconauclea (Nau.-Ad.)
Myrmedoma = Myrmephytum
Myrmephytum (Psy.)
Myrstiphylla = Psychotria (ort. var. of *Myrstiphyllum*)
Myrstiphyllum = Psychotria

N

Nacibaea = Manettia (ort. var. of *Nacibea*)
Nacibea = Manettia
Naletonia (Psy.; = Psychotria ?)
Narega = Catunaregam
Nargedia (Hyp.)
Natalanthe = Tricalysia
Nauclea (Nau.-N.)
Naucleoxylon (fossil)
Neanotis (Hed.)
Neblinathamnus (Ron.)
Neleixa = Darluca
Nelitris Gaertner, nomen = Timonius
Nematostylis (Alb.)
Nemostylis = Phuopsis
Nenax (Ant.-A.)
Neobaumannia = Knoxia
Neobertiera (gen. dub.; aff. Bertiera ?)
Neoblakea (Gue. ?)
Neobreonia (Nau.-Ad.)
Neofranciella (Gar.-G.)
Neogaillonia (Pae.; see p. 235)
Neohymenopogon (Cin./Hed.)
Neolamarckia (Nau.-An.)
Neolaugeria (Gue.)
Neoleroya = Pyrostria ?
Neomazaea = Mazaea
Neonauclea (Nau.-Ad.)
Neopentanisia (Kno.)
Neorosea = Tricalysia
Neosabicea = Manettia
Neoschimpera = Psychotria
Nernstia (Con.)
Nertera (Ant.-C.)
Nerteria ort. var. = Nertera

Nescidia = Coffea
Nesohedyotis (Hed.)
Nettlera = Cephaelis
Neurocalyx (Arg.)
Neurocarpaea R. Br., nomen = Pentas
Nichallea (Pav.)
Nobula = Phyllis
Nodocarpaea (Spe.)
Nonatelia Aublet (Psy.; = Palicourea ?)
Nonatelia Kuntze, nomen = Lasianthus
Normandia (Ant.-C.)
Nostolachma (Gar.-D.)
Nothocarpus Post & Kuntze, nomen = Nodocarpaea
Nothophlebia = Pentagonia
Notodontia = Ophiorrhiza
Notopleura = Psychotria
Novatilea ort. var. = Nonatelia

O

Obbea = Bobea
Ochreinauclea (Nau.-N.)
Octavia = Lasianthus
Octodon = Spermacoce
Octomeria ort. var. = Otomeria
Octotropis (Alb. ?)
Ohigginsia = Hoffmannia
Oldenlanda ort. var. = Oldenlandia
Oldenlandia (Hed.)
Oligocodon (Gar.-G.)
Olostyla = Caelospermum
Omalocladus = Faramea (ort. var. of *Homaloclados*)
Omiltemia (Ham.)
Opercularia (Ant.-O.)
Ophiorhiza ort. var. = Ophiorrhiza
Ophiorrhiza (Oph.)
Ophryococcus (Ise.)
Oregandra (inc. sed.; ? aff. Simira)
Oreocaryon Kuntze ex Schumann, nomen = Cruckshanksia
Oreopolus (Hed.; = Cruckshanksia ?)
Oribasia = Nonatelia
Orthostema Wall., nomen = Pentas
Osa (Con.)
Otiophora (Hed.)
Otocalyx (gen. dub.)
Otocephalus = Calanda
Otomeria (Hed.)
Ottoschmidtia (Gue.)
Ourouparia = Uncaria
Outarda = Coutarea
Oxyanthus (Gar.-G.)
Oxyceros (Gar.-G.)
Oxyspermum = Galopina

P

Pacheya Scop. = Coussarea
Pachysanthus = Rudgea
Pachystigma (Van.)
Pachystylus (Pav.)
Paedera ort. var. = Paederia
Paederia (Pae.)
Paederiopsis = Paederia ? (ort. var. of *Poederiopsis*)
Paedicalyx (Hed.)
Pagamea (Psy.)
Pagameopsis (Psy.)
Paiva = Sabicea
Palicourea (Psy.)
Palicurea ort. var. = Palicourea
Palicuria ort. var. = Palicourea
Pallasia = Wittmackanthus
Pampletantha (Pau.)
Pancheria = Ixora (ort. var. of *Panchezia*)
Panchezia = Ixora
Panetos = Houstonia
Paolia = Coffea
Pappostyles = Cremaspora
Pappostylum = Cremaspora (ort. var. of *Pappostyles*)
Paracephaelis (Pav. ?)
Parachimarrhis (Con.)
Paracoffea = Psilanthus subg. Paracoffea
Paracorynanthe (Cin.-C.)
Paradina = Mitragyna
Paragenipa (Hyp.)
Paragophyton = Spermacoce
Paraknoxia (Kno.)
Parapentas (Hed.)
Paratriaina (Tri.)
Paravinia ort. var. = Praravinia
Patabea = Ixora
Patima = Sabicea
Patsjotti = Strumpfia
Pauridiantha (Pau.)
Pausinystalia (Cin.-C.)
Pavate = Pavetta
Pavetta (Pav.)
Payera (Hed.)
Pecheya = Coussarea
Peckeya = Coussarea (ort. var. of *Pecheya*)
Pegamea ort. var. = Pagamea
Pelagodendron (Gar.-G.)
Pelaphia Banks & Sol., nomen = Coprosma
Peltospermum = Sacosperma

Pentacarpaea = Pentanisia
Pentacarpus = Pentanisia (ort. var. of *Pentacarpaea*)
Pentagonia (Hip.)
Pentaloncha (inc. sed.)
Pentanisia (Kno.)
Pentanopsis (Hed.)
Pentas (Hed.)
Pentodon (Hed.)
Peponidium (Van.)
Perakanthus (Van.)
Perama (Per.)
Peratanthe (Ant.-C.)
Perdicesca = Mitchella
Peripeplus (Psy.)
Pertusadina (Nau.-Ad.)
Petagomoa (Psy.)
Peteria = Rondeletia (ort. var. of Petesia)
Petesia = Rondeletia
Petitiocodon (Gar.-D.)
Petunga = Hypobathrum
Phallaria = Psydrax subg. Phallaria
Phellocalyx (Gar.-G.)
Phialanthus (Chi.)
Phitopis (inc. sed.)
Phosanthus Raf., nomen = Isertia
Phuopsis (Rub.)
Phylanthera Nor., nomen = Hypobathrum
Phyllacantha ort. var. = Phyllacanthus
Phyllacanthus (Cat.)
Phyllis (Ant.-A.)
Phyllocrater (Hed.)
Phyllomelia (inc. sed.)
Phylohydrax (Spe.)
Phyteumoides Smeathm. ex DC., nomen = Virectaria
Picardaea (Con.)
Pimentelia (Cin.-C.)
Pinarophyllon (Ham.)
Pinckneya (Con.)
Pinknea ort. var. = Pinckneya
Piringa = Gardenia
Pittierothamnus = Amphidasya
Pittonniotis (Gue.)
Placocarpa (Chi.)
Placodium B. & H., nomen = Plocama
Placoma ort. var. = Plocama
Placopoda (Hed.)
Plastolaena Pierre ex A. Chev., nomen = Schumanniophyton
Platanocarpum = Nauclea
Platanocarpus = Nauclea (ort. var. of *Platanocarpum*)
Platanocephalus = Neolamarckia
Platycarpum (Hen.)
Platymerium = Hypobathrum
Plectronia L. (not rubiaceous; = Olinia, Oliniac.)
Plectronia auct. Rubiac. = Canthium s.l.
Plectroniella (Van.)
Pleimeris = Gardenia
Pleiocarpidia (Uro.)
Pleiocoryne (Gar.-G.)
Pleiocraterium (Hed.)
Pleotheca Wall., nomen = Spiradiclis
Plethyrsis = Richardia
Pleureia = Psychotria
Pleurocarpus = Cinchona
Pleurocoffea = Coffea
Pliocarpidia ort. var. = Pleiocarpidia
Plocama (Pae.)
Plo caniophyllon = Deppea
Poecilocalyx (Pau.)
Poederiopsis = Paederia ?
Pogonanthus = Morinda
Pogonolobus (Mor.)
Pogonopus (Con.)
Poiretia = Houstonia
Polycoryne = Pleiocoryne
Polycyliska = Lerchea
Polyozus Loureiro (mixture: Psydrax + *Psychotria*)
Polyozus Miq., nomen = Chasallia
Polyphragmon = Timonius
Polysolen = Indopolysolenia
Polysolenia = Indopolysolenia
Polysphaeria (Hyp.)
Polyura (Hed.)
Pomangium = Argostemma
Pomatium = Bertiera
Pomax (Ant.-O.)
Pomazota = Coptophyllum
Pontaletsje ort. var. = Poutaletsje
Porocarpus = Timonius
Porterandia (Gar.-G.)
Porterandia auct. Afric. = Aoranthe
Portlanda ort. var. = Portlandia
Portlandia (Con.; aff. Isidorea)
Posoqueria (Gar.-G.)
Posoria = Posoqueria
Potima = Faramea
Pouchetia (Hyp.)
Poutaletsje = Hedyotis ?
Praravinia (Uro.)
Pravinaria (Uro.)
Preussiodora (Gar.-G.)
Princea = Triainolepis
Prismatomeris (Mor.)
Pristidia = Gaertnera
Probletostemon = Tricalysia sect. Probletostemon
Proscephaleium (Psy.)

Psathura (Psy.)
Psathyra ort. var. = Psathura
Pseudaidia (Gar.-G.)
Pseudixora = Anomanthodia
Pseudochimarrhis = Chimarrhis
Pseudocinchona = Corynanthe
Pseudogaillonia (Pae.)
Pseudogardenia (Gar.-G.)
Pseudohamelia (inc. sed.; ? aff. Bertiera)
Pseudomantalania (Gar.-G.)
Pseudomussaenda (Con ?)
Pseudonesohedyotis (Hed.)
Pseudopeponidium = Pyrostria
Pseudopyxis (Pae.)
Pseudorachicallis Post & Kuntze, nomen = Arcytophyllum
Pseudorhachicallis Benth. & Hook., nomen = Arcytophyllum
Pseudosabicea (Ise.)
Pseudrhachicallis Korth., nomen = Arcytophyllum
Psilanthopsis = Coffea
Psilanthus (Cof.)
Psilobium = Acranthera
Psilostoma = Canthium s.l.
Pstathura ort. var. = Psathura
Psychothria ort. var. = Psychotria
Psychotria (Psy.)
Psychotriphyllum (fossil)
Psychotrophum = Psychotria
Psydax ort. var. = Psydrax
Psydrax (Van.)
Psyllocarpus (Spe.)
Pteridocalyx (Ron.)
Pterogaillonia (Pae.)
Pterostephus = Spermacoce
Ptychodea Willd., nomen = Sipanea
Ptychostigma = Galiniera (see Farr, Leussink & Stafleu 1979)
Pubeta = Duroia
Pubistylus (Hyp. ?)
Punophila = Machaonia (ort. var. of *Bunophila*)
Putoria (Pae.)
Pygmaeothamnus (Van.)
Pyragra (Psy.)
Pyrostria (Van.)

Q

Quiducia (not rubiaceous; Carlemanniaceae/Caprifoliaceae)
Quinquina ort. var. = Cinchona

R

Rachicallis (Hed.)
Ramosmania (Hyp.)
Ramspekia = Posoqueria
Randa ort. var. = Randia
Randia (Gar.-G.)
Rangia ort. var. = Randia
Raritebe (Ise.)
Ravnia (Hil.)
Readea (Psy.)
Relbunium (Rub.)
Remijia (Cin.-C.)
Rennellia (Mor.)
Restiaria = Uncaria
Retiniphyllum (Ret.)
Reussia Dennst., nomen = Paederia
Rhabdostigma = Kraussia
Rhachicallis ort. var. = Rachicallis (ort. var. of *Rachicallis*)
Rhadinopus (Hyp.)
Rhaphidura (Uro.)
Rhipidantha (Pau.)
Rhodostoma = Palicourea
Rhombospora = Greenea
Rhopalobrachium (inc. sed.; Antirheoideae)
Rhyssocarpus (Gar.-G.; = Melanopsidium ?)
Rhytidotus = Bobea (ort. var. of *Rytidotus*)
Ricardia ort. var. = Richardia
Richarda ort. var. = Richardia
Richardia (Spe.)
Richardsonia = Richardia
Rikarda ort. var. = Richardia
Riqueria ort. var. = Riqueuria
Riqueuria (inc. sed.)
Robynsia (Van.)
Rogiera (Ron.; Rondeletia ?)
Roigella (Ron.)
Rojoc = Morinda
Ronabea (Psy.; = Psychotria ?)
Ronabia ort. var. = Ronabea
Rondeleta ort. var. = Rondeletia
Rondeletia (Ron.)
Rosea = Tricalysia sect. Rosea
Rosenbergiodendron = Randia
Rotheria = Cruckshanksia
Rothmannia (Gar.-G.)
Rubeola J. Hill = Sherardia
Rubeola P. Miller = Crucianella
Rubia (Rub.)
Rubiaceaecarpum (fossil)
Rubiaceocarpum (fossil)
Rubina ort. var. = Rubia
Rubioides (fossil)
Rubioxylon (fossil)

Rudgea (Psy.)
Rustia (Con.)
Rutidea (Pav.)
Rytidea ort. var. = Rutidea
Rytidotus = Bobea
Rytigynia (Van.)

S

Sabicea (Ise.)
Sacconia = Chione
Sacosperma (Hed.)
Sahlbergia Neck., nomen = Gardenia
Saldanha = Hillia
Saldinia (Psy.)
Salzmannia (Chi.)
Samama Kuntze, nomen (mixture: Breonia + Anthocephalus)
Santalina = Tarenna
Santia = Lasianthus
Saprosma (Psy.)
Sarcocephalus (Nau.-N.)
Sarcopygme (Mor.)
Sardinia = Guettarda
Sarissus = Hydrophylax
Scepseothamnus = Alibertia
Scepsothamnus = Alibertia (ort. var. of *Scepseothamnus*)
Schachtia (Gar.-G.; = Duroia ?)
Schenckia = Deppea
Scherardia ort. var. = Sherardia
Schetti = Ixora
Schiedea A. Rich. = Machaonia
Schiedea Bartl., nomen = Richardia
Schismatoclada (Cin./Hed.)
Schizangium Bartl., nomen = Mitracarpus
Schizenterospermum (Pav. ?)
Schizocalyx (Cin.-C.)
Schizocolea (Cou.)
Schizomussaenda (Ise. ?)
Schizospermum Boiv. ex Baill., nomen = Cremaspora
Schizostigma (Ise.)
Schmidtottia (inc. sed.; excluded from Con.)
Schoenleinia = Bathysa
Schradera (Sch.)
Schreibersia = Augusta
Schumanniophyton (Gar.-G.)
Schwendenera (Spe.)
Schwenkfelda = Sabicea
Schwenkfeldia = Sabicea (ort. var. of *Schwenkfelda*)
Sclerococcus Bartl., nomen = Hedyotis
Scleromitrium Wight & Arn., nomen = Hedyotis
Scolosanthus (Chi.)
Scyphiophora ort. var. = Scyphiphora
Scyphiphora (inc. sed.; Antirheoideae)
Scyphochlamys (Van.)
Scyphostachys (Hyp.)
Seemannia Hook., nomen = Pentagonia
Sericanthe (Gar.-D.)
Serissa (Pae.)
Sestinia Boiss. & Hohen., nomen = Wendlandia
Shaferocharis (Chi.; aff. Phialanthus)
Sherarda ort. var. = Sherardia
Sherardia (Rub.)
Sherbournia (Gar.-G.)
Sicelium = Coccocypselum
Sickingia = Simira
Siderobombyx (Hed.)
Siderodendron = Ixora (ort. var. of *Siderodendrum*)
Siderodendrum = Ixora
Sideroxyloides = Ixora
Siemensia (Hed. ?; excluded from Con.)
Silambus ort. var. = Silamnus
Silamnus (not rubiaceous; ? Verbenaceae)
Silvianthus (not rubiaceous; Carlemanniaceae/Caprifoliaceae)
Simira (Ron.)
Sinoadina (Nau.-Ad.)
Sipanea (Sip.)
Sipaneopsis (Ron.)
Sipania Seemann, nomen = Limnosipanea
Siphomeris = Paederia
Siphonandra = Chiococca
Siphonandrium (Mor. ?)
Siphonia = Lindenia
Solena = Posoqueria
Solenandra = Exostema
Solenixora = Coffea
Solenocera Schumann, nomen (not rubiaceous; = Cynoctonum, Loganiaceae)
Sommera (Hip.)
Spallanzania = Mussaenda
Spathichlamys (Ron.)
Spermacoce (Spe.)
Spermacoceodes = Spermacoce
Spermacon = Spermacoce
Spermadictyon (Pae.)
Sphaerophora = Morinda
Sphinctanthus (Gar.-G.)
Spicillaria = Hypobathrum
Spiradiclis (Oph.)
Spirea (not rubiaceous; = Aspilia, Asteraceae)

Sprucea = Simira
Squamellaria (Psy.)
Stachyarrhena (Gar.-G.)
Stachyococcus (Psy.)
Staelia (Spe.)
Standleya (Ron.)
Stannia = Posoqueria
Staurospermum = Mitracarpus
Steenisia (Ron.)
Stelechantha (Pau.)
Stellix Nor., nomen = Psychotria
Stelmanis = Hedyotis
Stelmotis = Hedyotis
Stenaria Raf., nomen = Houstonia
Stenostomum = Antirhea
Stephanium = Palicourea
Stephanococcus (Hed.)
Stephegyne = Mitragyna
Steudelago = Exostema
Stevensia (Ron.)
Steyermarkia (Sip.)
Stichianthus (Uro.)
Stigmanthus = Morinda
Stigmatanthus = Morinda (ort. var. of *Stigmanthus*)
Stilpnophyllum (Cin.-C.)
Stipularia (Ise.)
Stomandra (Con.)
Straussia = Psychotria
Streblosa (Psy.)
Streblosiopsis (Ise. ?)
Strempelia (Psy.; = Rudgea ?)
Striolaria (inc. sed.)
Strumpfa ort. var. = Strumpfia
Strumpfia (inc. sed.)
Sturmia Gaertner f., nomen = Antirhea
Stylocoryna Cav. = Aidia (many included taxa belong to Tarenna)
Stylocoryne Wight & Arn., nomen = Aidia
Stylosiphonia (gen. dub.; ? Ron.)
Suberanthus (Cin.-C.)
Sukunia (Gar.-G.)
Sulcarinx Raf., nomen = Geophila/Psychotria ?
Sulipa = Gardenia
Sulitia (Gar.-G.)
Sulzeria Roem. & Schult., nomen = Faramea
Suteria = Cephaelis
Sykesia = Gaertnera
Symphyllarion = Hedyotis
Synaptantha (Hed.)
Synisoon = Retiniphyllum
Syringantha (Cin.-C.)

T

Tamatavia = Chapeliera
Tamilnadia (Gar.-G.)
Tammsia (Tam.)
Tangaraca = Hamelia
Tapesia Gaertner f., nomen = Hamelia
Tapinopentas = Otomeria
Tapiphyllum (Van.)
Tapogomea = Cephaelis
Taramea ort. var. = Faramea
Tardavel = Spermacoce
Tarenna (Pav.)
Tarennoidea (Gar.-G.)
Tatea = Bikkia
Teinosolen = Heterophyllaea
Temnocalyx (Van.)
Temnopteryx (Ise.)
Tennantia (Pav.)
Tepesia = Hamelia
Terebraria = Neolaugeria
Tertrea = Machaonia
Tessiera = Spermacoce
Tetralopha = Gynochthodes
Tetramerium = Faramea
Tetraplasia = Damnacanthus
Tetrastigma = Schumanniophyton
Thecagonum = Oldenlandia
Thecorchus (Hed.)
Theligonum (The.)
Theyodis = Oldenlandia
Thieleodoxa = Alibertia
Thiersia = Faramea
Thiollierea = Bikkia
Thogsennia (Con.)
Thouarsiora = Ixora
Thunbergia = Gardenia
Thyridocalyx (Tri.)
Thysanospermum = Coptosapelta
Timonius (Gue.)
Tobagoa (Spe.)
Tocoyena (Gar.-G.)
Tontanea = Coccocypselum
Tortuella (Spe.)
Tournefortiopsis = Guettarda
Trailliaedoxa (inc. sed.; Antirheoideae)
Tresanthera (Con.)
Trevirania Heynh., nomen = Psychotria
Triainolepis (Tri.)
Tribrachya = Rennellia
Tricalysia (Gar.-D.)
Trichogalium = Galium
Trichostachys (Mor.)
Trigonopyren (Psy.)

Triodon = Diodia
Trisciadia = Caelospermum
Trukia (Gar.-G.)
Tsiangia (Psy. ?)

U

Ucriana = Tocoyena or Augusta
Uncaria (Cin.-M.)
Uncariopsis = Schradera
Uncinaria Reichenb., nomen = Uncaria
Uragoga = Cephaelis
Urceolaria = Schradera
Urophyllum (Uro.)
Uruparia = Uncaria (ort. var. of *Ourouparia*)

V

Vaillantia ort. var. = Valantia
Valantia (Rub.)
Vanessa = Manettia
Vangueria (Van.)
Vangueriella (Van.)
Vangueriopsis (Van.)
Vanguiera ort. var. = Vangueria
Vanguieria ort. var. = Vangueria
Vanqueria ort. var. = Vangueria
Varnera ort. var. = Gardenia
Varneria = Gardenia
Vavanga Rohr, nomen = Vangueria
Versteegia (Pav.)
Verulamia = Pavetta
Vignaldia = Pentas
Vignaudia = Pentas (ort. var. of *Vignaldia*)
Villaria (Hyp.)
Virecta L. f. = Sipanea
Virecta Smith = Virectaria
Virectaria (Hed.)
Viscoides Jacq., nomen = Psychotria
Vissadali = Knoxia
Viviana Colla = Melanopsidium
Viviana Rafin. = Guettarda
Voigtia = Bathysa

W

Wahlenbergia = Tarenna
Wallichia = Urophyllum
Warburgina (Rub.)
Warnera Ellis, nomen = Gardenia
Warszewiczia (Ron.)
Watsonamra = Pentagonia
Webera Cramer (not rubiaceous; Azima or Plectronia)
Webera Schreber = Tarenna
Wendlandia (Ron.)
Wernhamia (Cin.-C. ?)
Wiasemskya (? Hip.; ? aff. Sommera)
Wiegmannia = Hedyotis
Wigmannia = Hedyotis (ort. var. of *Wiegmannia*)
Willdenovia = Rondeletia
Williamsia = Praravinia
Wittmackanthus (Cin.-C.)
Wittmannia = Vangueria

X

Xanthophytopsis (Hed.)
Xanthophytum (Hed.)
Xantonnea (Hyp.)
Xantonneopsis (Gar.-D.)
Xerococcus = Hoffmannia
Xeromphis = Catunaregam

Y

Yangapa = Gardenia
Yangapa Raf., nomen = Gardenia
Yutajea (Ise.)

Z

Zaluziana Comm. ex Gaertner, nomen = Bertiera
Zamaria Raf., nomen = Rondeletia
Zamavia Raf., nomen = Rondeletia
Zeuxanthe = Prismatomeris
Zuccarinia Blume (Hyp.)
Zuccarinia Spreng. = Jackiopsis
Zwaardekronia = Psychotria
Zygoon = Tarenna

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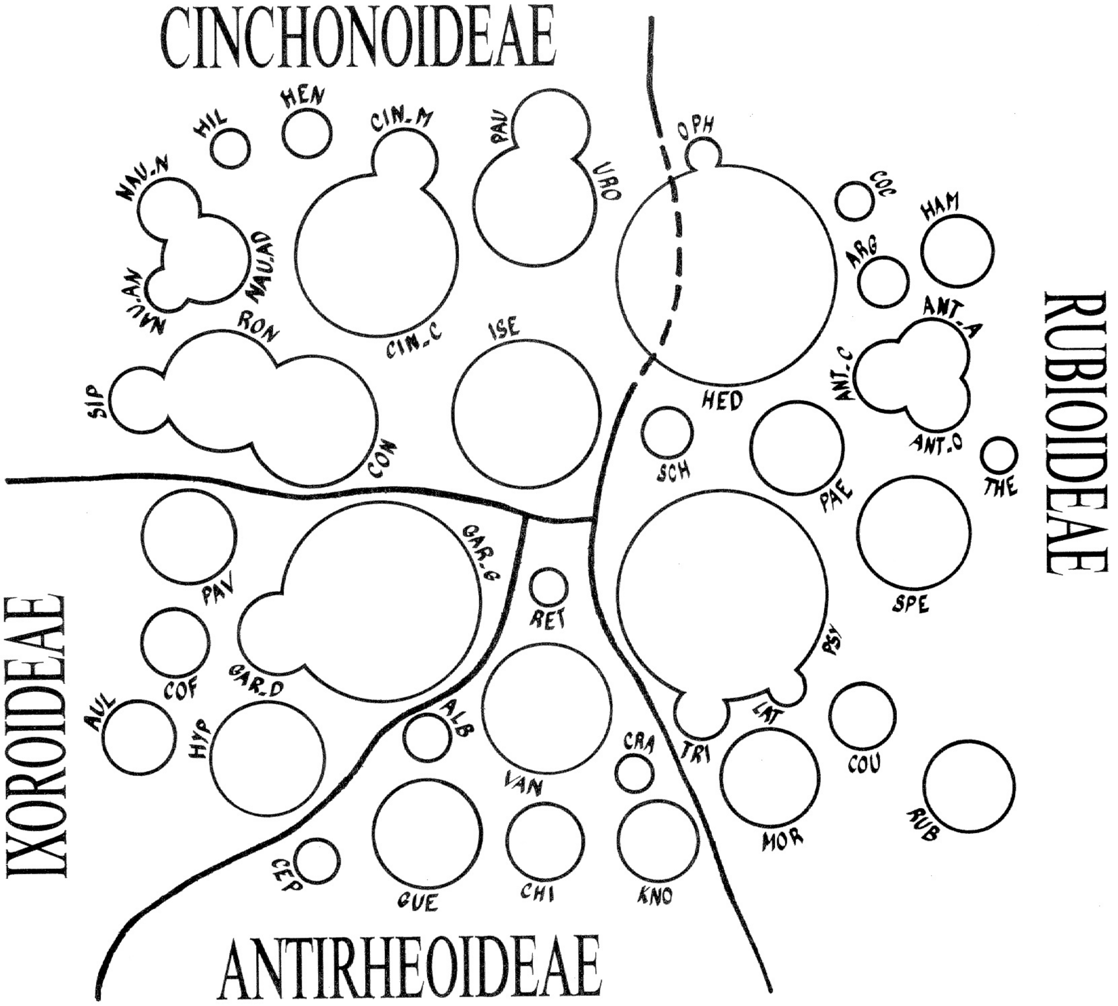

Mnemonic abbreviations for tribes and subtribes
(***:**taxa of uncertain position not taken up in diagram)

Alb.	Alberteae
Ant.	Anthospermeae
-A.	Anthosperminae
-C.	Coprosminae
-0.	Operculariinac
Arg.	Argostemmateae
Aul.	Aulacocalyceae
*Cat.	Catesbaeeae
Cep.	Cephalantheae
Chi.	Chiococceae
Cin.	Cinchoneae
-C.	Cinchoninae
-M.	Mitragyninae
Coc.	Coccocypseleae
Cof.	Coffeae
Con.	Condamineeae
Cou.	Coussarecae
Cra.	Craterispermeae
Gar.	Gardenieae
-D.	Diplosporinae
-G.	Gardenlinae
Gue.	Guettardeae
Ham.	Hamelleae
Hed.	Hedyotideae
Hen.	Henriquezieae
Hil.	Hillieae
*Hip.	Hippotleae
Hyp.	Hypobathreae
Ise.	Isertieae
*Jae.	Jackleae
Kno.	Knoxieae
Lat.	Lathraeocarpeae
Mor.	Morindeae
Nau.	Naucleeae
-Ad.	Adininae
-An.	Neolamarckiinae
-N.	Naucleinae
Oph.	Ophiorrhizeae
Pae.	Paederieae
Pav.	Pavetteae
Pau.	Pauridiantheae
*Per.	Perameae
Psy.	Psychotrieae
Ret.	Retiniphylleae
Ron.	Rondeletieae
Rub.	Rubieae
Sch.	Schradereae
Sip.	Sipaneeae
Spe.	Spermacoceae
*Tam.	Tammsieae
The.	Theligoneae
Tri.	Triainolepideae
Uro.	Urophylleae
Van.	Vanguerleae