A

SYSTEMATICS AND BIOGEOGRAPHY OF RETINIPHYLLUM (RUBIACEAE)

by

Rocio Cortés

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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Abstract

SYSTEMATICS AND BIOGEOGRAPHY OF RETINIPHYLLUM (RUBIACEAE)

by

Rocio Cortés

Advisor: Piero G. Delprete

Retiniphyllum consists of shrubs and small trees that grow mostly in white-sand soils of the Guayana and Brazilian Shields, with few species extending into the Amazon Region. The delimitation of the genus has been clear throughout history because of its two collateral and pendulous ovules per locule, a condition unique in the Rubiaceae. However, for the same reason, its placement within the family has been controversial. The monographic treatment of Retiniphyllum is presented, in which twenty two species and two varieties are recognized, including one newly described species. A key for the identification of the species is provided. Each species is described, typified, and mapped, supplemented by phenological and ecological observations. The position of the genus in the subfamily Ixoroideae is discussed based on a cladistic analysis of the trnL-F intergenic spacer and the rps16 intron. The tribe Retiniphylleae is monophyletic and monotypic, and is sister to two clades that include the Ixoroideae sensu Bremekamp. The three sections proposed by

Müller Argoviensis are shown to be paraphyletic, and no sections are here recognized in the genus. Botryarrhena and Scyphiphora, tentatively included in the Retiniphylleae by previous authors, are shown to be related to other tribes of the Ixoroideae. The phylogenetic relationships of Retiniphyllum are studied based on morphological and ITS sequence data. In the phylogenies obtained, Retiniphyllum secundiflorum was sister to the rest of the species, which were found in three main clades: one with species characterized by racemose inflorescences, long-tubular, white corollas, and supposedly butterfly-pollinated; another by species with racemose or umbellate inflorescences, long-tubular, red corollas, and hummingbird pollinated; and another formed by species with spicate inflorescences, red or white corollas, and hummingbird- or bee-pollinated, respectively. The phylogenies obtained indicated that the hummingbird-pollination syndrome evolved at least two times in the genus, while the bee- and supposed butterfly-pollination syndromes arose once each, independently. The historical biogeographical study showed that the ancestral area of distribution for Retiniphyllum was the Southern Guayana Region, and from there many dispersals and a few vicariant events are necessary to explain the current distribution of most species.

To my mother

To the memory of my father

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1. MORPHOLOGY AND TAXONOMY OF RETINIPHYLLUM

1.1. Taxonomic History

Retiniphyllum Bonpl. was established by Aimé Bonpland (1806) based on the type species R. secundiflorum Bonpl., from specimens collected in his travel with Alexander von Humboldt on the Río Orinoco in Venezuela. The generic name was derived from the Greek words ρητινη [retion=resin] and øνλλον [phillon=leaf] because of the copious resin secreted by colleters located inside stipules, bracteoles, and involucels. Bonpland placed Retiniphyllum in the Class Pentandria Monogynia, according to the Linnean System. This genus was described in Plantae aequinociales (Bonpland, 1806), the first of the six publications coordinated by Alexander von Humboldt where he intended to publish the results of his five-year expedition in the New World. Although the authority of the new taxa has been cited in most taxonomic literature as Humboldt & Bonpland, there is enough evidence (e.g. Stafleu & Cowan, 1976; Delprete, 2001) to consider Bonpland as the sole author of the taxa published in the Plantae aequinociales.

The third publication in the series coordinated by Humboldt was Nova Genera et Species Plantarum, which was written by Carl S. Kunth (1818) and edited by Humboldt and Bonpland. Kunth placed Retiniphyllum with Guettarda L. and Nonatelia Aubl. in the section VIII (Guettardeae), being characterized by having multilocular fruits, single-seeded locules, and five stamens. Although Retiniphyllum, Guettarda, and Nonatelia have fruits with single-seeded locules, the number of ovules in each locule differs in Retiniphyllum. Guettarda and Nonatelia have ovaries with a single ovule in each locule while Retiniphyllum has two ovules per locule and, due to the abortion of one, produce fruits with five single-seeded locules. Kunth's system was largely influenced by A. L. de Jussieu (1789), who founded the Rubiaceae and proposed the first system of classification for the family. Jussieu used fruit characteristics such as the number of locules and number of seeds per locule as cardinal characters in his system of classification. Therefore, Kunth placed Retiniphyllum close to unrelated genera due to the limitations of the family classification available at that time, and overlooking the bi-ovulated locules in Retiniphyllum. Subsequently, Roemer and Schultes (1818), following the Linnean system, included Retiniphyllum in the Pentandria Monogynia (Class V).

Antoine L. de Jussieu (1820) treated Retiniphyllum as synonymous with Nonatelia, and placed the latter in the fourth section of his classification, which included genera with baccate or drupaceous, multilocular fruits, with single-seeded locules. Jussieu considered that Retiniphyllum and Nonatelia shared characters such as exserted stamens, single stigma, and 5-seeded, globose berries. Once again, and ignoring the bi-ovulate ovaries of Retiniphyllum, this genus was believed to be related to a taxon with which it shares no evolutionary affinities. Although Jussieu synonymized Retiniphyllum with Nonatelia, he did not make the necessary combination. It was Sprengel (1825) who, following Jussieu's conclusions, published the combination Nonatelia secundiflora (Bonpl.) Spreng., the sole species of Retiniphyllum known at that time. Nonatelia, with a total of eight species, was placed in the Linnean Pentandria Monogynia by Sprengel.

Achille Richard (1830) presented a second system of classification for the Rubiaceae. It was highly influenced by Jussieu's system, dividing the family in eleven tribes grouped in two sections: seven tribes bearing fruits with single-seeded locules and four tribes bearing fruits with many-seeded locules. He returned Nonatelia secundiflora to Retiniphyllum and included the genus in the Guettardeae [as

"Guettardacées"], a tribe that included genera with fleshy drupes and several to single-seeded locules. Richard stated that Retiniphyllum differed from Nonatelia in having a tubular or campanulate calyx, recumbent corolla lobes, and exerted stamens. Although Richard observed some differences between both genera, it is clear from his description that he was unaware that Retiniphyllum has two ovules per locule while Nonatelia has just one ovule per locule.

Alphonse P. de Candolle (1830) almost entirely reproduced Richard's system (see Delprete, 1999: 5-6). He maintained Retiniphyllum in the tribe Guettardeae [as "Guettardaceae"], and placed it in his subtribe Guettardineae [as "Guettardeae"], which included the genera with simple inflorescences. At the end of the generic description, Candolle stated the differences between Retiniphyllum and Nonatelia reiterating the characters proposed by Richard (1830). In addition, Candolle differentiated Retiniphyllum by its racemose inflorescence (vs. thyrsoid, paniculate, or corymbose in Nonatelia), single stigma, and bony pyrenes (vs. bilobed stigma and coriaceous pyrenes in Nonatelia). The first two characters were stated in the descriptions of both genera (Richard, 1830). The observation about the pyrenes consistency is the only original contribution that might be attributed to

Candolle for the delimitation of Retiniphyllum. Candolle's system was widely used by botanists at that time, as for example George Don (1834), who placed Retiniphyllum as it was stated by Candolle.

Stephan Endlicher (1838), also followed Candolle's classification, and maintained Retiniphyllum in the subtribe Guettardineae [as "Euguettardeae"] of the tribe Guettardeae, in the subfamily Coffeoideae [as "Coffeaceae"].

Bentham (1841) described the second species of the genus, Retiniphyllum scabrum Benth., from Robert Schomburgk's collections in Guyana. In addition, he described the new genus Commianthus Benth., based on the type species C. schomburgkii Benth. He placed both genera in the tribe Cordiereae, a tribe founded by Richard (1830) and characterized by fleshy, multi-locular fruits with one- or two-seeded locules. Although Bentham did not discuss the affinity of the new genus with Retiniphyllum, the spicate inflorescence of Commianthus is the most obvious difference between the genera. A very important contribution made by Bentham was to report for the first time the presence of two ovules per locule in both taxa. In the same publication, Bentham described Patima laxiflora Benth., admitting that the position of this new species in the genus Patima was tentative, due to the incomplete type specimens. He observed only a few badly preserved flowers (which he thought to be "male"), three immature fruits, and produced an inaccurate description. According to Bentham, Patima laxiflora had unisexual flowers and numerous seeds, a mistake that was later corrected by Brown (1901).

In the second supplement of the Genera Plantarum, Endlicher (1842) included Commianthus in the tribe Cordiereae of the subfamily Coffeoideae [as "Coffeaceae"], with the genera Cordiera A. Rich. and Tricalysia A. Rich., while maintaining Retiniphyllum in the tribe Guettardeae, subfamily Coffeoideae, without acknowledging Bentham's placement of Retiniphyllum in the same tribe with Commianthus.

Walpers (1843, 1846) did not follow Bentham's treatment either, and kept the genera in two different tribes of the subfamily Coffeoideae [as "Coffeaceae"], Retiniphyllum in the Guettardeae (Walpers, 1843) and Commianthus in the Cordiereae (Walpers, 1843; 1846).

Several years after, Bentham (1853) maintained Commianthus in the Cordiereae and described four additional species from Spruce's collections in the Amazon basin, namely C. discolor Benth., C. concolor Benth., C. pilosus

Benth., and C. speciosum Benth. At that time, Commianthus had a total of five species, and Retiniphyllum two.

Carl Müller (1858) wrote a synopsis of Commianthus, and following previous treatments of the genus, placed it in the Cordiereae, subfamily Coffeoideae [as "Coffeaceae"]. He included a description of the genus, and a description of the five known species.

Joseph D. Hooker (1873) proposed the first Rubiaceae classification influenced by the theory of evolution proposed by his friend Charles Darwin (1859). He divided the family in three Series: A. with pluri-ovular locules; B. with collateral ovules; and C. with uni-ovular locules. He was the first author to use corolla aestivation as a cardinal character for the subdivision of the Rubiaceae at tribal level. He established the tribe Retiniphylleae Hook. f. and placed it in the Series B with the tribe Cruckshanksieae (incl. Cruckshanksia Hook. f. & Arn. and Oreopolus Schltdl.). At the end of the description of Series B, Hooker included two genera in the Genera Ovulis gemina dubiae affinitatis: Jackia Wall. and Scyphiphora Gaertn. f.

Hooker (1873) defined the tribe Retiniphylleae as having corollas with contorted aestivation, a 5-7-locular ovary, two ovules per locule, drupaceous fruits with 5-7 pyrenes, and pyrenes containing one seed (by abortion of one ovule). In the Retiniphylleae, he included only the genera Retiniphyllum and Kutchubaea Fisch. ex DC. The inclusion of Kutchubaea in the tribe Retiniphylleae was due to an incorrect description of Kutchubaea fruits. While in the original description of Kutchubaea, Candolle (1830) did not describe the fruits, Hooker (1873) erroneously described the fruits of this genus from Patima laxiflora, a species that was later transferred to Retiniphyllum by Brown (1901). Kutchubaea has large, leathery berries with many seeds immersed in a gelatinous pulp, typical of the tribe Gardenieae and quite clearly different from those of the Retiniphylleae. Another important contribution of Hooker was to treat Commianthus as a synonym of Retiniphyllum. Although he did not justified his decision, apparently he realized that the different inflorescence architecture (racemose or umbellate in Retiniphyllum vs. spicate in Commianthus) did not justify the separation of the two genera. Nevertheless, Hooker did not make the necessary combinations. Finally, after the description of Retiniphyllum, he described Ammianthus, with the intention to validate an unpublished name annotated by Spruce on one of his specimen label (Spruce 2248), which is the type of Commianthus pilosum Spruce ex Benth. It is clear that

Spruce considered his collection number 2248 a new genus, although he did not publish it. Hooker was uncertain if Ammianthus could be a new subgenus or a new genus, by writing "subgenus v. novum genus efficit". Taking into account that the status was not clearly established, I consider Ammianthus Spruce ex Hook. f. as an invalid name with status confusum.

Baillon (1879) established the genus Synisoon Baill., based on the type species S. schomburgkianum Baill. from a collection of Robert Schomburgk in Guyana. He considered that the aril was diagnostic for the foundation of his new genus. Although Baillon noticed the affinity of Synisoon with Retiniphyllum, he stated that the inflorescence and ovule position of S. schomburgkianum were sufficient characters to keep his new genus separated from Retiniphyllum. This incorrect observation was later rectified by Brown (1901), by realizing that Synisoon schomburgkianum had already been described as Patima laxiflora by Bentham, and these were in turn synonymous with Retiniphyllum laxiflorum.

Baillon (1880), in his Natural History of Plants, divided the Rubiaceae in 15 tribes, and included Retiniphyllum in the "Morinda Series" or tribe Morindeae. However, Baillon pointed out that Retiniphyllum "forms an abnormal subseries and has nothing in common with most of the preceding genera, except that there are in each cell two collateral ascending ovules with micropyle inferior and exterior". In addition to his unusual taxonomic placement, Baillon was also incorrect about the position of the ovules, which are descending instead of ascending.

The first partial revision of Retiniphyllum was published by Müller Argoviensis (1881) in Martius' Flora Brasiliensis. Müller Argoviensis maintained only Retiniphyllum in the Retiniphylleae, the only tribe placed in the Series A, defined by two collateral ovules in each locule. In agreement with Hooker's conclusions, Müller Argoviensis transferred all the species of Commianthus to Retiniphyllum and made the corresponding combinations. In addition, he divided the genus into three sections: Ammianthus Hook. f. ex Muell. Arg. (validating Hooker's Ammianthus) by having tri-alate, excavated pyrenes, sessile flowers, long-sheathing and scarious stipules; Retiniphyllum [as "Euretiniphyllum"] by having tri-carinate pyrenes, non-scarious stipules, and pedicellate flowers; and Commianthus (Benth.) Muell. Arg. by having tri-carinate pyrenes, non-scarious stipules, and sessile flowers. Finally, Müller Argoviensis described four new species: Retiniphyllum martianum Muell. Arg., R. pallidum Muell.

Arg., R. rhabdocalyx Muell. Arg., and R. truncatum Muell. Arg., for a total of ten species treated in Flora Brasiliensis, and a grand total of 12 species known in Retiniphyllum.

Luerssen (1882) published a handbook of medicinal plants in which he presented a little known system of classification of the Rubiaceae, which was overlooked by most botanists. He included his subfamilies Retiniphylloideae [as "Retiniphylleae"] and Cruckshanksioideae [as "Cruckshanksieae"] in a group characterized by having locules with two collateral ovules. In the Retiniphylloideae, he included the genera Retiniphyllum, Jackia, and Scyphiphora and in the Cruckshanksioideae only the genus Cruckshanksia.

Schumann (1891) published a system of classification of the Rubiaceae, where he divided the family in two subfamilies and 21 tribes. Schumann's classification was strongly influenced by Hooker's system (1873). Schumann departed from previous classifications by repositioning all the genera that had been included in the Hooker's Series B, in his subfamily Cinchonoideae. He transferred the Retiniphylleae to the tribe Gardenieae, probably misinterpreting the ovule position of Retiniphyllum. He also transferred the tribe Cruckshanksieae to the Oldenlandieeae.

Krause (1908a) published Retiniphyllum angustiflorum K. Krause and R. pauciflorum Kunth ex K. Krause, validating an unpublished name annotated by Kunth on a Humboldt and Bonpland collection preserved at the Berlin Herbarium (Humboldt 934). In the same year, Krause (1908b) published Retinipyllum fuchsioides K. Krause from a collection by Ule in Cerro Escalero, Perú. Jacques Huber (1914) later described Retiniphyllum schomburgkii var. angustiflorum Huber from a Ducke collection from Pará, Brazilian Amazon. In 1931, Standley published three new species of Retiniphyllum: R. adinanthum Standl., R. kuhlmannii Standl. (Standley, 1931a) and R. erythranthum Standl. (Standley, 1931b). A few years later, Standley (1936) transferred R. adinanthum to his new genus Stachyococcus Standl. According to him, the absence of fruits in the original description of R. adinanthum made him place this species in Retiniphyllum, a genus "with which actually it has no affinities" (Standley, 1936), a conclusion that found later workers in agreement. While Stachyococcus adinanthum (Standl.) Standl. has flowers grouped in glomerules along spicate inflorescences, valvate aestivation, and 1-ovulate, bilocular ovaries, alternatively, Retiniphyllum has spicate (not grouped in glomerules), racemose or umbellate inflorescences, contorted aestivation, and 2-ovulate, (4-)5(-8) locular ovaries.

In the following years, Standley and Ducke described four species of Retiniphyllum: R. cearense Standl. (Standley, 1937), R. cataractae Ducke (Ducke, 1938), R. chloranthum Ducke (Ducke, 1943) and R. maguirei Standl. (Standley, 1948), bringing the number of species in this genus to 22.

In a new classification, Verdcourt (1958) kept for the first time only Retiniphyllum in the tribe Retiniphylleae, in the subfamily Cinchonoideae, based on contorted aestivation, fleshy fruits composed of 5-7 pyrenes, collateral ovules, and the absence of raphides.

Steyermark (1965) published the most recent and comprehensive taxonomic treatment of Retiniphyllum. He neither used nor mentioned the former infrageneric classification of Retiniphyllum proposed by Müller Argoviensis, and maintained the genus in the tribe Retiniphylleae. In addition, he described three new species: R. glabrum Steyerm., R. guianense Steyerm., and R. tepuiense Steyerm.; two varieties of R. laxiflorum, one variety of R. scabrum, one variety of R. maguirei, one subspecies and one variety of R. schomburgkii, and one variety of R. truncatum. Steyermark treated R. erythranthum as a variety of R. scabrum., and he also synonymized R. angustiflorum with R. martianum, R. rhabdocalyx with R. speciosum, and R. schomburgkii var. angustiflorum Huber with R. schomburgkii var. schomburgkii.

Bremekamp (1966) proposed a system of classification dividing the Rubiaceae in eight subfamilies. Although he criticized previous placements of Retiniphyllum, he did not proposed any placement for it, and simply called it an "aberrant" genus. He pointed out that Retiniphyllum cannot be placed near to Nonatelia, as stated by Richard, because of its absence of raphides. He also indicated Schumann's (1891) had erroneously placed Retiniphyllum in the tribe Gardenieae. According to Bremekamp (1966), the absence of secondary pollen presentation (as well as fruit morphology), a defining character of the tribe Gardenieae and his subfamily Ixoroideae are not present in Retiniphyllum. The system proposed by Bremekamp is considered one of the most important in the 20th century, which influenced later classifications.

Steyermark (1974) published a treatment of Retiniphyllum in the Flora of Venezuela, in which he presented detailed descriptions of the 10 species occurring in this country. He also published two new species of

Retiniphyllum: R. longiflorum Steyerm. and R. parvifolium Steyerm., bringing the genus to a total of 27 published names (Steyermark, 1974).

Robbrecht (1988, 1993) published the most recent, comprehensive classification of the Rubiaceae, using morphological, anatomical, and palynological evidence. He divided the family in four subfamilies: Antirheoideae, Cinchonoideae, Ixoroideae, and Rubioideae. He maintained Retiniphyllum in the tribe Retiniphylleae in the subfamily Anthirheoideae, and included tentatively the genus Botryarrhena in the tribe. He positioned the tribe Retiniphylleae in the subfamily Antirheoideae. According to Robbrecht (1988), the tribe Retiniphylleae often has a curved corolla-tube, contorted aestivation, stylar pollen presentation, 5-locular ovaries, two collateral ovules per cell, ovule attachment to placenta in the middle of the septum (but clearly pendent), and drupaceous fruits with five one-seeded pyrenes.

Molecular phylogenies revolutionized the classifications previously proposed for most plant families, and the Rubiaceae is not an exception. Starting in the 1990's, the monophyly of the family, subfamilies and tribes has been tested using mainly molecular data (Bremer & Jansen, 1991; Bremer & Struwe, 1992; Bremer et al., 1995;

Bremer, 1996; Rova et al., 2002). While the family was shown to be clearly monophyletic, the definition and position of the subfamilies and tribes remains in a state of flux. The Antirheoideae, where Robbrecht placed Retiniphyllum, is not supported by molecular data, and the Rubiaceae is better treated as three subfamilies; Ixoroideae, Cinchonoideae, and Rubioideae (Bremer & Jansen, 1991; Bremer & Struwe, 1992; Bremer et al., 1995; Bremer, 1996; Rova et al., 2002). Additionally, according to the phylogenies presented by Anderson & Rova (1999) using rps16 and Rova et al. (2002) based on trnL-F, Retiniphyllum is placed within the subfamily Ixoroideae.

A summary of the history of the position of Retiniphyllum in the Rubiaceae is presented in Table 1.

Table 1: Summary of the position of Retiniphyllum in the Rubiaceae. Tribe names are abbreviated as follows: Cor.= Cordiereae, Gar.= Gardenieae, Gue.= Guettardeae, Mor.= Morindeae, Ret.= Retiniphylleae.

Author	**Family subdivision**	**Tribe**	**Characters used**
Bonpland, 1805	Pentandria-Monogynia		One ovary and five stamens
Kunth, 1818	Section VII Guettardeae		Multilocular fruits, single seeded locules and five stamens
Roemer & Schultes, 1818	Class V Pentandria-Monogynia		Tri- to penta-seeded fruits
Antoine L. de Jussieu, 1820	Section IV		Baccate or drupaceous, multilocular fruits and single-seeded locules
Sprengel, 1825	Pentandria-Monogynia		One ovary and five stamens
Richard, 1830	Section I	Gue.	Fleshy drupes with several single-seeded locules
Candolle, 1830	Group A	Gue.	Drupaceous fruits, pyrenes 2-10, and terete seeds
Endlicher, 1838 Retinipyllum	Subfamily Coffeoideae	Gue.	Fleshy fruits with several single- or two-seeded locules
Bentham, 1841 [Commianthus & Retiniphyllum]	Section I (Richard's system)	Cor.	Fleshy fruits with several single- or two-seeded locules

Endlicher, 1842 [Commianthus]	Subfamily: Coffeoideae	Cor.	
Walpers, 1843 [Retiniphyllum]	Subfamily Coffeoideae	Gue.	
Walpers, 1843 [Commianthus]	Subfamily Coffeoideae	Cor.	
Walpers, 1846 [Commianthus]	Subfamily Coffeoideae	Cor.	
Müller, 1858 [Commianthus]	Subfamily Coffeoideae	Cor.	
Hooker, 1873	Series B	Ret.	Corolla with contorted aestivation, 5-7 locular ovary, two ovules per locule, drupaceous fruits with 5-7 one-seeded pyrenes
Baillon, 1880		Mor.	Two collateral "ascending" ovules
Müller Argoviensis, 1881	Series A	Ret.	Two collateral ovules per locule
Schumann, 1891	Subfamily Cinchonoideae	Gar.	Fleshy fruits with several to many seeds and flowers with contorted aestivation
Verdcourt, 1958	Subfamily Cinchonoideae	Ret.	Absence of raphides, contorted aestivation, fleshy fruits with 5-7 pyrenes, collateral ovules
Steyermark, 1965, 1974		Ret.	
Robbrecht,	Subfamily	Ret.	Absence of

1988, 1993	Antirheoideae		raphides, fleshy fruits with individual pyrenes, parenchyma-like exotestal cells, stylar pollen presentation
Andersson & Rova, 1999	Subfamily Ixoroideae	Ret.	RPS16 CPDNA sequence variation
Rova et al., 2002	Subfamily Ixoroideae	Ret.	TRNL-F CPDNA sequence variation

1.2. General Morphology

Habit

Retiniphyllum species are shrubs or small trees commonly 1 to 6 m tall, rarely to 10 m tall. The tree architecture has not been studied in detail; however, according to personal observations, R. chloranthum, R. concolor, R. truncatum, and R. speciosum follow the Fagerlind's Model (Hallé et al., 1978). In this model, the trunk produces tiers of modular branches, each one sympodial and plagiotropic by apposition. The modular branches are occasionally seen on herbarium specimens, indicating that perhaps most of the species in the genus conform to this pattern.

Leaves

Leaves of *Retiniphyllum* are opposite, decussate, and petiolate, with the exception of some individuals of *R. concolor* where leaves are sessile. Petioles are mostly adaxially flattened, glabrous or pubescent, and very variable in size, ranging from 2.5 mm long in *R. cataractae* to 30 mm long in *R. chloranthum*.

Blades are elliptic, ovate, obovate, and oblong, and chartaceous to coriaceous. The smaller leaves have been recorded in *R. parvifolium*, i.e., 2.2-4.2 x 1.1-2.7 cm, while the largest leaves were observed in *R. concolor*, i.e., 8.5-37.5 x 3-12.5 cm. Leaf surfaces vary from totally glabrous to densely pubescent, but in some species there is only a marginal row of strigose hairs at the blade margins. Although the secondary venation is mostly broquidodromous, there are species (e.g., *R. glabrum*, *R. laxiflorum*) in which the blades are basally eucamptodromous and distally broquidodromous. The tertiary venation is random-reticulate in all the species. Domatia are mostly absent on the leaves, although some species (e.g., *R. chloranthum*, *R. concolor*) occasionally have pocket domatia.

Stipules

Stipules are interpetiolar, connate at base, sheathing, and truncate (cup-shaped, e.g., R. truncatum), triangular (e.g., R. secundiflorum), or splitting on one side in some species (e.g., R. pilosum, R. fuchsioides). Stipules are persistent in most species, but they can also be caducous in some species (e.g., R. pauciflorum). The margin is entire, or rarely lobulate, serrulate or laciniate. Stipules are coriaceous in most species, or papyraceous in a few species (e.g., R. pilosum). The external indument varies from strigose, hirsute, or puberulent, or lacking (glabrous). They are mostly glabrous on the internal side, and always with colleters, these present throughout or only at base.

Stipules are commonly uniform in shape within the same species, but are usually dimorphic in R. cataractae and R. pauciflorum. In these species they can be both short, cup-shaped, or foliose, long sheathing and splitting on one side. The foliose stipules are up to 16 mm long in R. cataractae and up to 9 mm long in R. pauciflorum. Both kind of stipules might be found in sterile or fertile branches. In R. cataractae, foliose stipules are the most common type, and only few nodes have cup-shaped stipules. Whereas in R. pauciflorum cup-shaped stipules occur in most nodes, occasionally foliose ones occur only in some nodes.

Retiniphyllum scabrum has dimorphic stipules, according to the developmental stage of the branches. Branches bearing reproductive structures have cup-shaped stipules up to 4 mm long, while sterile branches have triangular and deeply laciniate stipules, up to 15 mm long.

Colleters

Species of Retiniphyllum are characterized by the copious resin that cover their buds, branches, flowers, and fruits (hence the name of the genus). This substance is produced by colleters located inside stipules, bracteoles, involucels, and calyces (Figs. 1A-D). In Rubiaceae, where the presence of stipular colleters is almost universal, the standard colleter type is finger-like with elongate axial cells and a palisade epidermis (Lersten, 1974; Robbrecht, 1988). Although the standard type is found in Retiniphyllum, brush-like colleters are the most common type (Fig. 1A-C). Brush-like colleters have a longitudinal axis covered with distinct epidermal cells (Fig. 1C), while the standard type is covered by a palisade epidermis (Fig. 1D) (Lersten, 1974; Robbrecht, 1988).

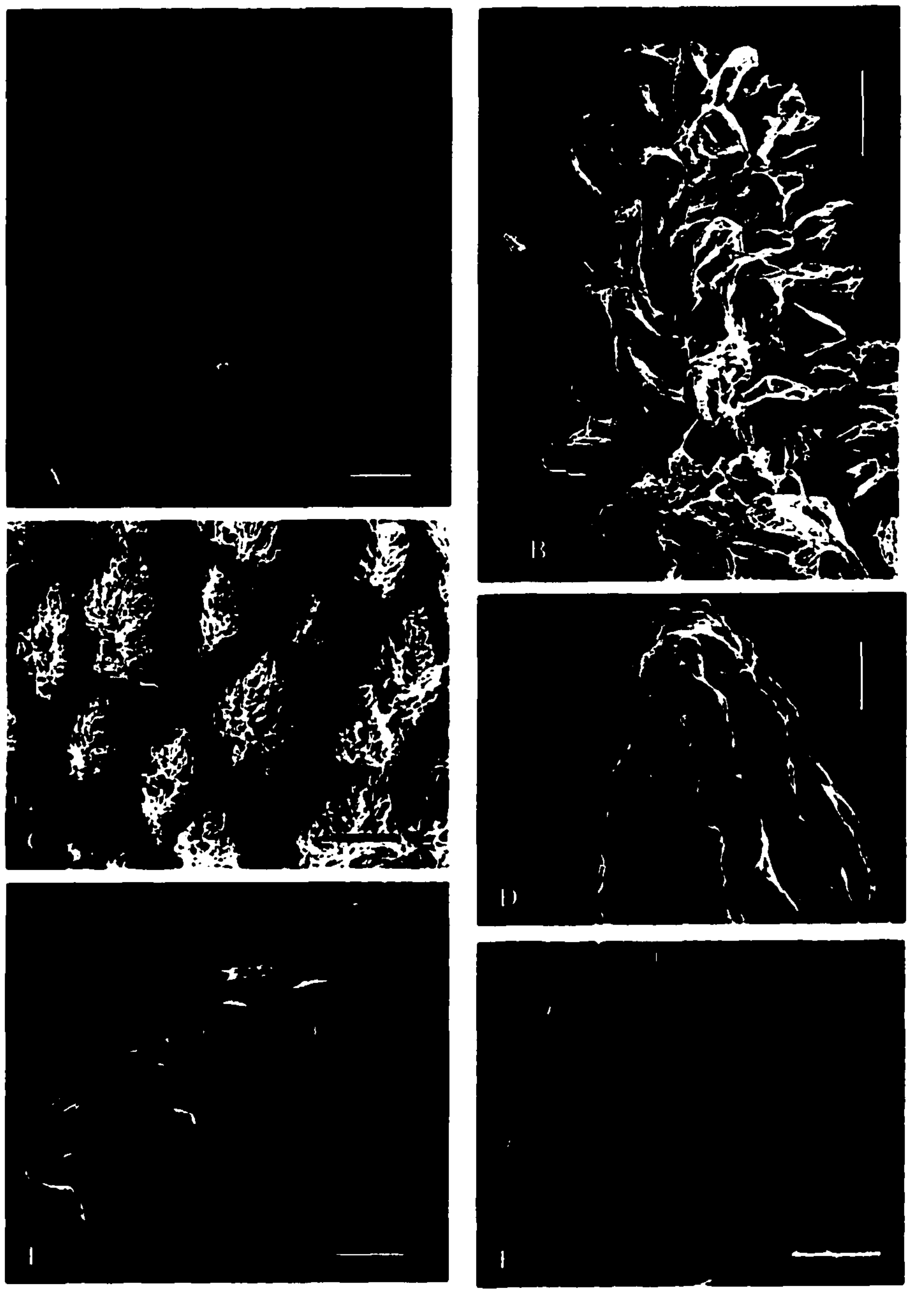
Colleters inside cup-shaped stipules are distributed throughout in the abaxial side, while those inside large triangular stipules are inserted in a single row at the base. Colleters are present in reduced bracteoles, and absent in the foliose ones. All the species have colleters inside involucels, except for R. fuchsioides and R. pilosum. Six species have colleters inside the calyces: R. cataractae, R. chloranthum, R. concolor, R. guianense, R. longiflorum, and R. secundiflorum. The presence or absence of colleters inside bracteoles, involcels, and calyces is constant within species, indicating that they have systematic value.

Indument

In most species of Retiniphyllum the presence, type, and abundance of vestiture is constant, and taxonomically useful, while in the widespread species, is variable and not diagnostic. Examples of the first case are R. pilosum and R. glabrum, as it is indicated by their names. On the other hand, R. concolor, might have most of its organs either glabrous or pubescent.

Verdcourt (1958), in an extensive study about trichomes of Rubiaceae, found that the trichomes inside the

Fig. 1: SEM photomicrographs of colleters and hairs of Retiniphyllum. **A-C.** R. chloranthum (Clark 6599, NY). **A.** Dendroid stipular colleters. **B.** Close up of the colleter tip. **C.** colleters inside involucel. **D.** R. fuchsioides (Wolfe 12222), tip of standard stipular colleter. **E.** R. secundiflorum (Huber 3413), filament indument. **F.** R. francoanum (Cárdenas 6929) leave indument. Scale bars: A 200 µm; B,D 20µm; C,E 100µm; F 500µm.



flower are unicellular, thin-walled, and ribbon-like. He also found that in other parts of the plant, trichomes presented more variation. In agreement with Verdcourt's observations, trichomes inside the flowers in Retiniphyllum are ribbon-like (Fig. 1E), while those associated to leaves (Fig. 1F) correspond to the cylindrical type (Robbrecht, 1988). In this type, the outer hair walls are thickened, and the individual cells are not distinguishable on the outline.

Inflorescences

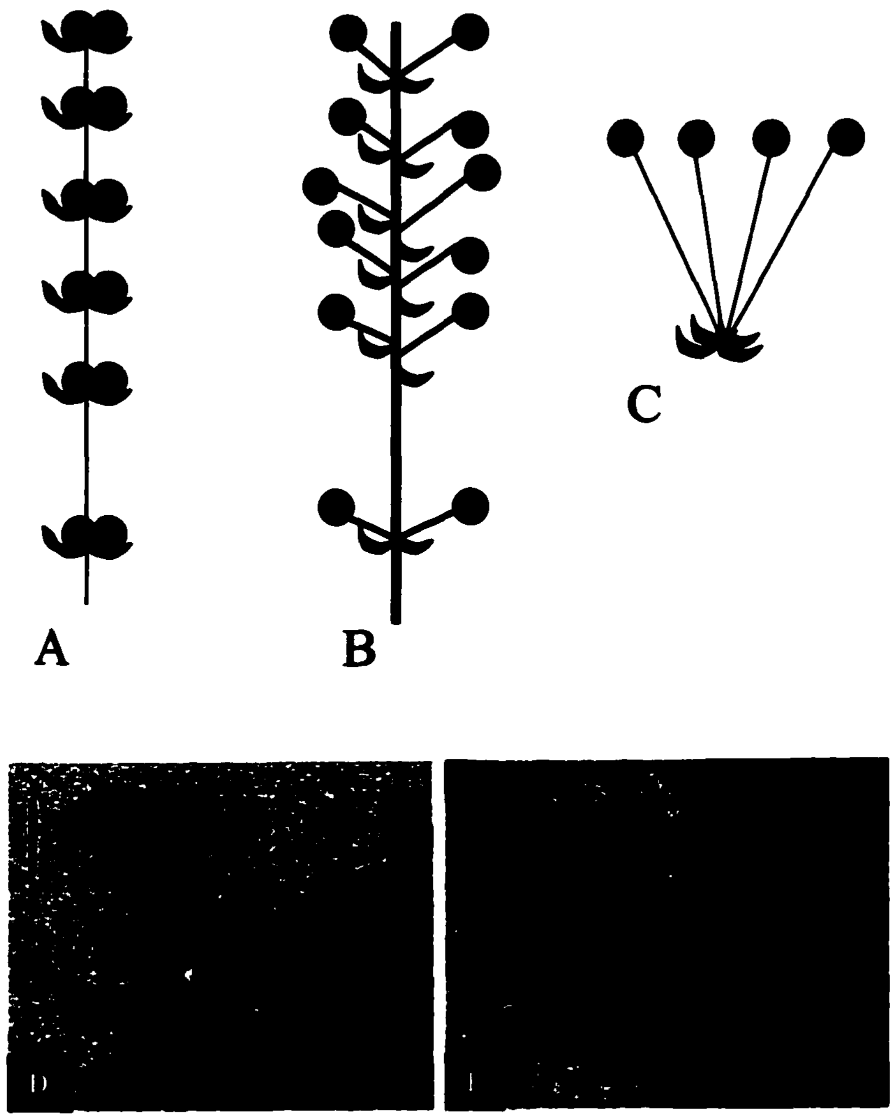
Inflorescences of Retiniphyllum are terminal in most species, and axillary in R. secundiflorum and R. francoanum Cortés-Ballén. In these two species, the inflorescences are inserted in pairs at the axils of the distal nodes of the branches. In these cases, the inflorescences are truly axillary, considering that they are never present on short shoots, as in some Rubiaceae genera.

Inflorescences are spicate (Fig. 2A) or racemose (Fig. 2B) in most species, or umbellate (Fig. 2C) in R. pauciflorum and R. scabrum. In R. cataractae, the rachis is extremely reduced and the inflorescence seems to be umbellate, but instead two verticils of flowers are inserted on a reduced rachis.

According to Weberling (1992), the order in which flowers open in racemose, spicate and umbellate inflorescences usually corresponds to the order in which the flowers are developed, starting with the lowermost flower and continuing upwards. Flowers development in Retiniphyllum does not correspond entirely to this order. Instead, it is common to find opened flowers in the center of the inflorescence, and young buds at basal and distal portions of the inflorescence.

The length of the inflorescence rachis is variable, and it ranges from 1 to 30 cm. The rachis might be ridged, laterally compressed, or occasionally terete, glabrous or pubescent, and green. In the species with racemose or spicate inflorescences, each basal pair of flowers might be subtended by a bract, either very reduced and inconspicuous, or leaf-like, expanded and with leaf-like venation. The portion of the rachis above the basal pair of flowers is elongated, separating the basal pair of flowers from the rest of the inflorescence (Figs. 2A,B). The peduncle of the racemose or spicate inflorescences, defined as the portion between the last pair of leaves and the

Fig. 2. Inflorescences and bracteoles variation in Retiniphyllum. A. spicate. B. racemose. C. umbellate. D. R. concolor, (Clark 6599) reduced bracteole. E. R. fuchsioides (Cornejo 2685), foliose bracteole. Scale bars: D,E 1 mm.


A
B
C

first pair of flowers, is variable in size, and might be glabrous or pubescent.

Bracteoles

Bracteoles (the smaller bracts subtending the flowers) may be very reduced and inconspicuous (Fig. 2D), or foliose (Fig. 2E). Reduced bracteoles are present in most species, (up to 2 mm long), and are either glabrous or pubescent outside, and glabrous and with colleters inside. Foliose bracteoles are found only in R. fuchsioides, R. pilosum and R. secundiflorum. In these species, bracteoles are up to 6 mm long, lanceolate, pubescent outside, glabrous or pubescent inside, and without colleters. Size, indument, and presence of colleters are useful characters in differentiating species of Retiniphyllum.

Involucels

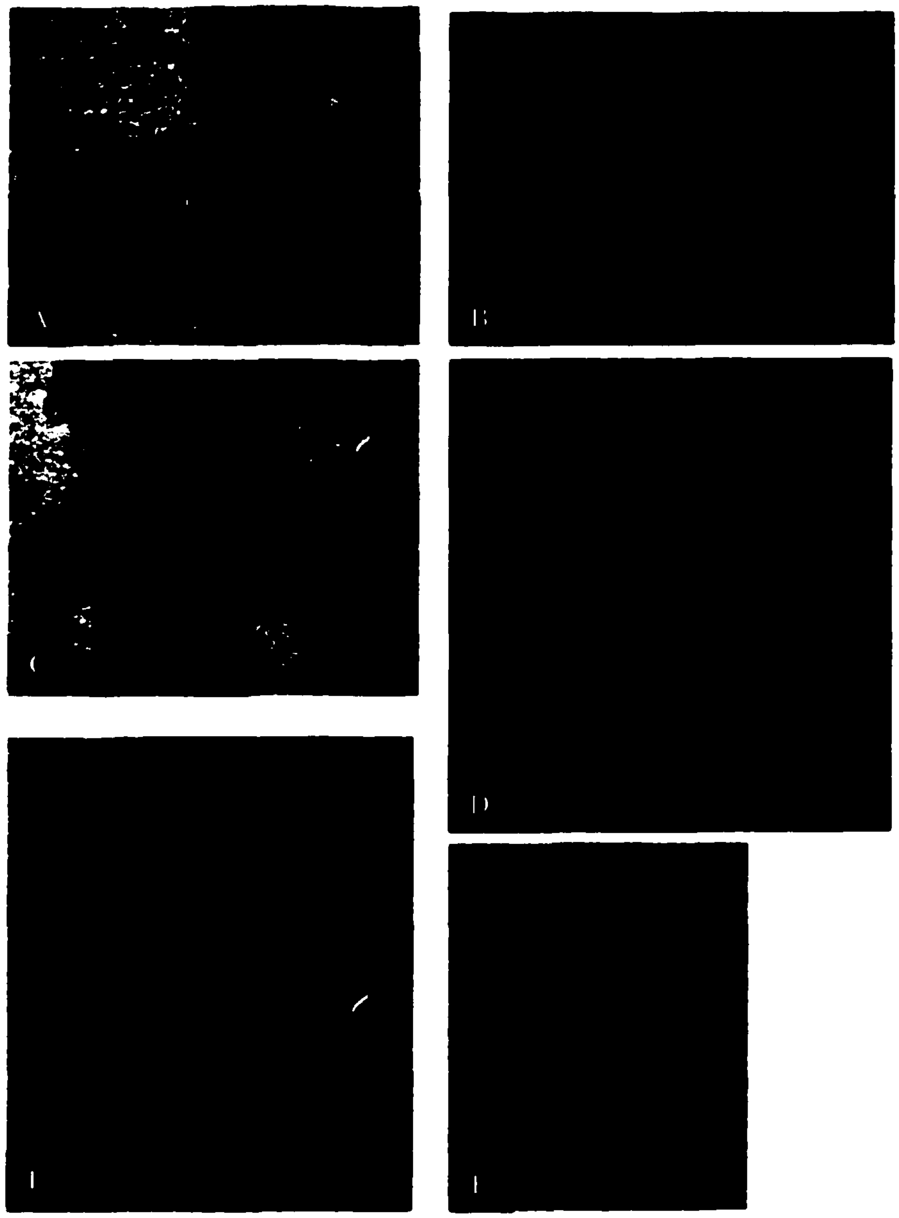
In all the species of Retiniphyllum, each flower is subtended by an involucel that might be sessile (Fig. 3A,C) or pedicellate (Figs. 2E, 3B). In most of the species, the involucels are truncate, but in few species they are lobulate. In R. chloranthum (Fig. 3B) and R. pilosum (Fig.

3C) the lobes are broadly triangular, while in R. fuchsioides (Fig. 2E) they are narrowly triangular. Involucels in R. secundiflorum and R. francoanum are unique in having one half of the involucel truncate and the other half with three lobes. Involucels might be glabrous or pubescent outside, and glabrous or pubescent inside, and with or without colleters. When present, colleters are distributed throughout the internal surface of the involucel. The persistence of involucels is an important character, perhaps correlated with fruit dispersal. In most species the involucels are persistent to the rachis of the infrutescences when the fruits fall, in R. secundiflorum and in R. francoanum the involucels remain attached to the fruit, and are dispersed as a unit. The taxonomic value of involucels is remarkable considering that they vary in shape, size, presence of pedicel, margin, consistency, colleters, indument, and kind of persistence.

Calyces

Calyces of Retiniphyllum are actinomorphic, 5-merous, either tubular or cupular. In most species the calyx is tubular (longer than wide) (Figs. 3D,E), and may be truncate or lobulate. Whereas, in a few other species (R.

Fig. 3. Involucel and calyx variation in Retiniphyllum. **A.** R. kuhlmannii (Irwin 16561), sessile involucel. **B.** R. chloranthum (Aymard 5812), pedicellate and lobulate involucel. **C.** R. pilosum (Berry 5633), sessile and lobulate involucel. **D.** R. pilosum (Schultes 18202), tubular calyx. **E.** R. pauciflorum (Maguire 41892). **F.** R. chloranthum (Delascio 16112), cupulate calyx. Scale bars: A,D 1 mm; B,C,E,F 2 mm.



chloranthum, R. concolor and R. longiflorum), the calyx is cupular (wider than long) and truncate or lobulate (Figs. 3B,F). In R. speciosum the calyx is distally tubular and inflated at medial portion, having five conspicuous vascular bundles running along its distal portion, each ending in a tooth.

The size of the calyx varies moderately. In the species with tubular calyces, the shortest are found in R. schomburgkii (1.8-5.2 mm long), and the longest are found in R. rhabdocalyx (6.3-10 mm long). The cupular calyces are smaller, and vary from 0.8 to 1.5 mm long.

The lobes in the species with tubular calyces are mostly triangular up to 2 mm long, or subulate and up to 4 mm long only in R. pilosum. In the species with cupular calyces the lobes are triangular, very reduced, and up to 1 mm long.

Calyces of Retiniphyllum may be glabrous or pubescent outside or inside. The type and density of calyx pubescence varies from dense and pilose in R. pilosum (Fig. 3D) to sparse and puberulent in R. parvifolium.

The calyx is usually green in most species with white corollas, or reddish to totally red in some of the red-flowered species (e.g. R. rhabdocalyx).

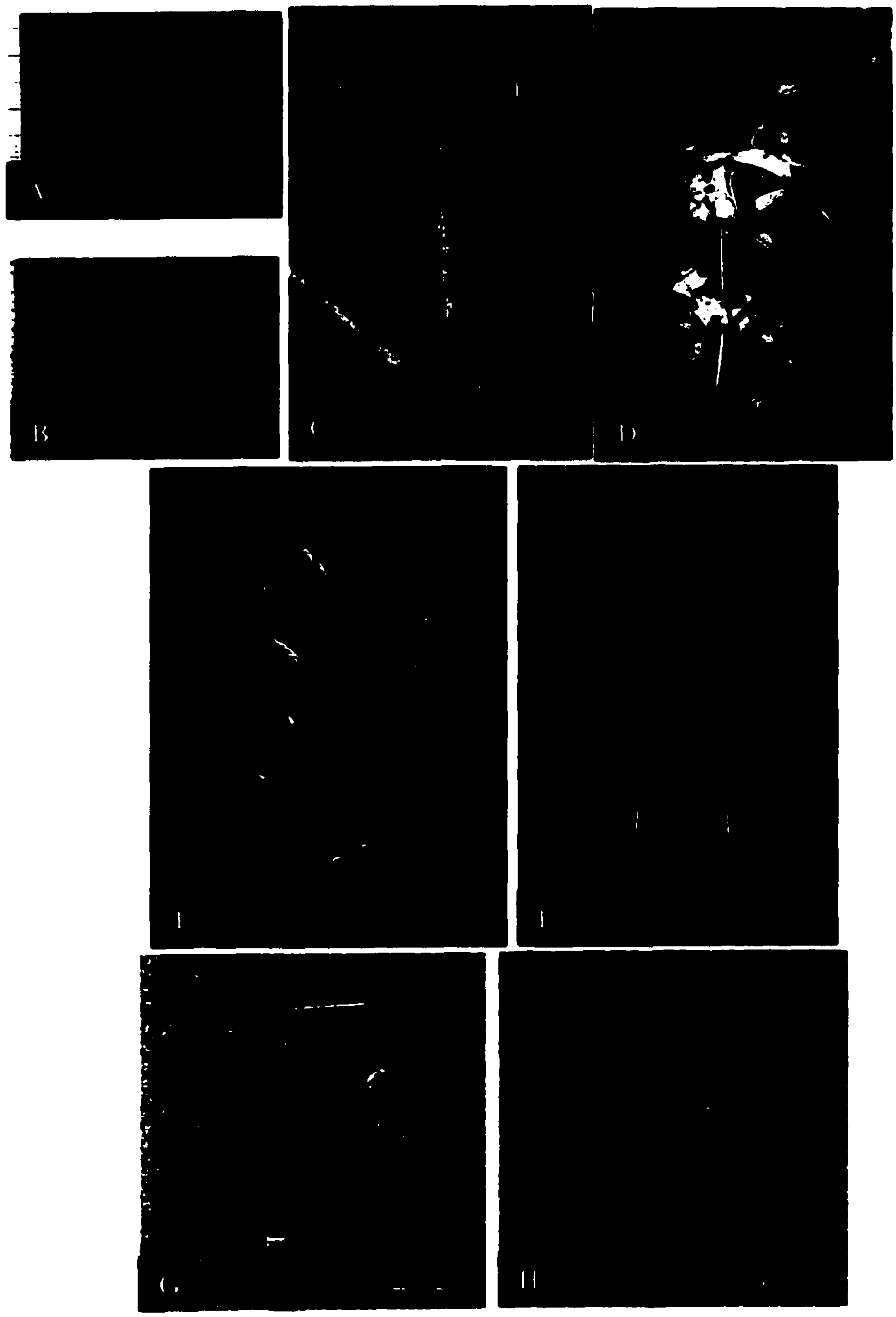
Colleters may be present or absent inside of the calyx. Species with cupular calyces have short colleters spread throughout the internal surface of the calyx; while species with tubular calyces usually do not have colleters, except for R. cataractae, R. guianense, and R. secundiflorum, in which colleters are present in a single row at the basal portion of the calyx.

The calyx is persistent to the fruit in all the species of Retiniphyllum and remains of approximately the same size in mature fruit.

Corollas

Corollas of Retiniphyllum are 5-merous, although 6-merous corollas are exceptionally found in some individuals of R. schomburgkii. Corolla shape is uniformly hypocrateriform, and the aestivation of the corolla lobes is always contorted to the left. Corollas are actinomorphic in some species (Figs. 4A,E,F), or in some others zygomorphic (Figs. 4B-D). In zygomorphic corollas, either the tube or the lobes are bent commonly downwards (exceptionally upwards), and the degree of curvature is stronger at the bud stage in anthesis. This is specially true in R. rhabdocalyx and R. speciosum in which the

Fig. 4. Corolla diversity in Retiniphyllum. **A.** R. pauciflorum (Maguire 41892), actinomorphic flowers. **B.** R. truncatum (Schultes 17230), zygomorphic flowers. **C.** R. concolor. **D.** R. schomburgkii. **E.** R. rhabdocalyx. **F.** R. laxiflorum. **G.** R. scabrum (Steyermark 989), anther in frontal view. **H.** R. fuchsioides (Cornejo 2685), anther in dorsal view. Scale bars: A,B 1 cm; G,H 1 mm.



curvature is slight in bud and almost imperceptible at full anthesis.

Corolla size ranges from 12 mm long in R. schomburgkii to 46 mm long in R. rhabdocalyx. Corolla tubes of Retiniphyllum may be cylindrical, infundibuliform, or narrowly infundibuliform. In R. chloranthum and R. concolor the tube is tubular in most of its length and slightly narrower at the middle portion. In species with infundibuliform corollas, the tube is inflated at base or straight. Corolla tube ranges from 3.8 mm long in R. schomburgkii to 33 mm long in R. longiflorum. Tubes may be glabrous, strigose, or puberulent outside. An internal ring or hairs is located at or near the mouth of the tube. While the portion of tube below the ring of hairs is glabrous, the tube is either tomentose or sericeous above the ring of hairs.

Corolla lobes are oblong or spatulate, acute or rounded at apex, and reflexed or coiled at anthesis. They range from 6 mm long in R. truncatum to 14 mm long in R. schomburgkii and R. speciosum. The length of the lobes in zygomorphic flowers varies only a few millimeters. Lobes are heavily tomentose or sericeous inside and outside, except for R. longiflorum with lobes sparsely puberulent throughout. The ratio of lobes/tube length is very variable in the genus and represents a significant character in distinguishing species. Corolla lobes may be shorter, longer or same size than tube. When shorter than the tube, corolla lobes range from slightly shorter to four times shorter in R. longiflorum. When longer, they range from slightly longer to 2 1/2 times longer in R. schomburgkii.

Corolla color is variable and consistent among the species of Retiniphyllum, ranging from white, greenish-white, pinkish-white, deep pink to red. In about half of the species the tube is white, greenish white or tinged with pale pink, and the lobes may be totally white, greenish white, tinged with pale pink, or with the left half of the lobe light pink and right half white. In the last case, the pink portion is the exposed part of the lobes when they are in bud, and the white part is the portion covered by the adjacent lobe. When the flowers are in anthesis, the vascular bundles of the filaments turn pink, and considering that fade few days after anthesis, they might function as pollinator guides. In the rest of the species the corolla is deep pink to red throughout.

In order to facilitate further discussions (e.g. pollination biology, phylogeny), I divided the species in three main types of corolla:

1. Corolla white or greenish-white, short-tubular corollas (less than 10 mm long), present in R. cataractae, R. guianense, R. kuhlmannii, R. parvifolium, R. pilosum, R. schomburgkii (Fig. 4D), R. tepuiense, and R. truncatum (Fig. 4B).

2. Corolla white or greenish-white, long-tubular corollas (more than 10 mm long), present in R. chloranthum and R. concolor (Fig. 4C).

3. Corolla red or dark pink, long tubular corollas (more than 10 mm), present in R. discolor, R. francoanum, R. fuchsioides, R. glabrum, R. laxiflorum (Fig. 4F), R. longiflorum, R. maguirei, R. rhabdocalyx (Fig. 4E), R. pauciflorum, R. scabrum, R. secundiflorum, and R. speciosum.

Androecium

Stamens are always five, inserted near the mouth, alternating with the corolla lobes. Stamens are totally reflexed in anthesis, with the anthers positioned at the same level than corolla lobes.

The anthers are dorsifixed near the base, and are lanceolate, oblong or narrowly oblong, ranging from 1.1-2.5 mm long in R. schomburgkii to 2.5-3.5 mm long in R.

rhabdocalyx. Anthers have translucent or whitish sterile appendages at apex and at base (Figs. 4G,H). The apical appendages are narrowly triangular to lanceolate and apiculate, and vary in length from 0.2 to 1 mm. The basal appendages are truncate, and exceptionally bilobed only in R. parvifolium, and range from 0.3 to 1 mm long. No important variation in the length or shape of anther appendages were discovered among species of Retiniphyllum. For a discussion about the probable function of anther appendages see the Floral Biology section.

The filaments are basally flattened or throughout the entire length, and range from 4 to 8.8 mm long. They are glabrous at basal and distal portion, and pilose, hirsute, or puberulent along most of their length. In some species the indument is restricted to the lateral edges of the flat portion of the filaments.

Gynoecium

The ovary of Retiniphyllum is commonly pentalocular (Fig. 5A); however, in R. secundiflorum either five or six locules are found, and R. francoanum has ovaries with seven or eight locules. Another exception is R. laxiflorum var. brasiliense, having six-locular ovaries. Exceptionally, in some rare individuals of R. tepuiense, four locules are found (Fig. 5B).

The locules are separated by a massive and complete septum. At the ovary stage, each locule includes, without exception, two collateral ovules (Fig. 5C). The ovules are pendulous and attached along the septa either at distal (Figs. 5D-F), medial (Figs. 5G-H), or basal portion (Figs. 6A-D). The two collateral ovules are attached to a large obturator, which is considered an outgrowth of the funiculus (Puff, 1986). The ovules are attached to the obturator either distally (and therefore pendulous) (Figs. 5C-H), or along most of the ventral side and therefore vertical (Fig. 6C).

Ovaries (4-)5(6-8)-locular, with two collateral pendulous ovules per locule is a unique combination of characters in the Rubiaceae, a family in which number of locules and ovules have been used as cardinal characters in the historical classifications proposed. Consequently, Retiniphyllum has been considered "abnormal" by Baillon (1880) and "aberrant" by Bremekamp (1966), and has been historically segregated either with a few other aberrant genera, or isolated in its own tribe.

Ovaries are very variable in shape, from globose, to narrowly obconical, ellipsoid, turbinate, transversally

Fig. 5. Gynoecium morphological variation in Retiniphyllum. **A.** R. fuchsioides (Wolfe 12222), ovary. **B.** R. tepuiense (Nee 31111), ovary. **C.** R. maguirei, collateral ovules. **D, E.** R. fuchsioides (Vasquez 24668), ovary and ovules. **F.** R. scabrum (Huber 10166), ovules. **G, H.** R. speciosum (Romero-Castañeda 3514), ovary with ovules. **OB**=obturator. Scale bars: A,B 500 µm; C,E,F,H 100 µm; D,G 1 mm.

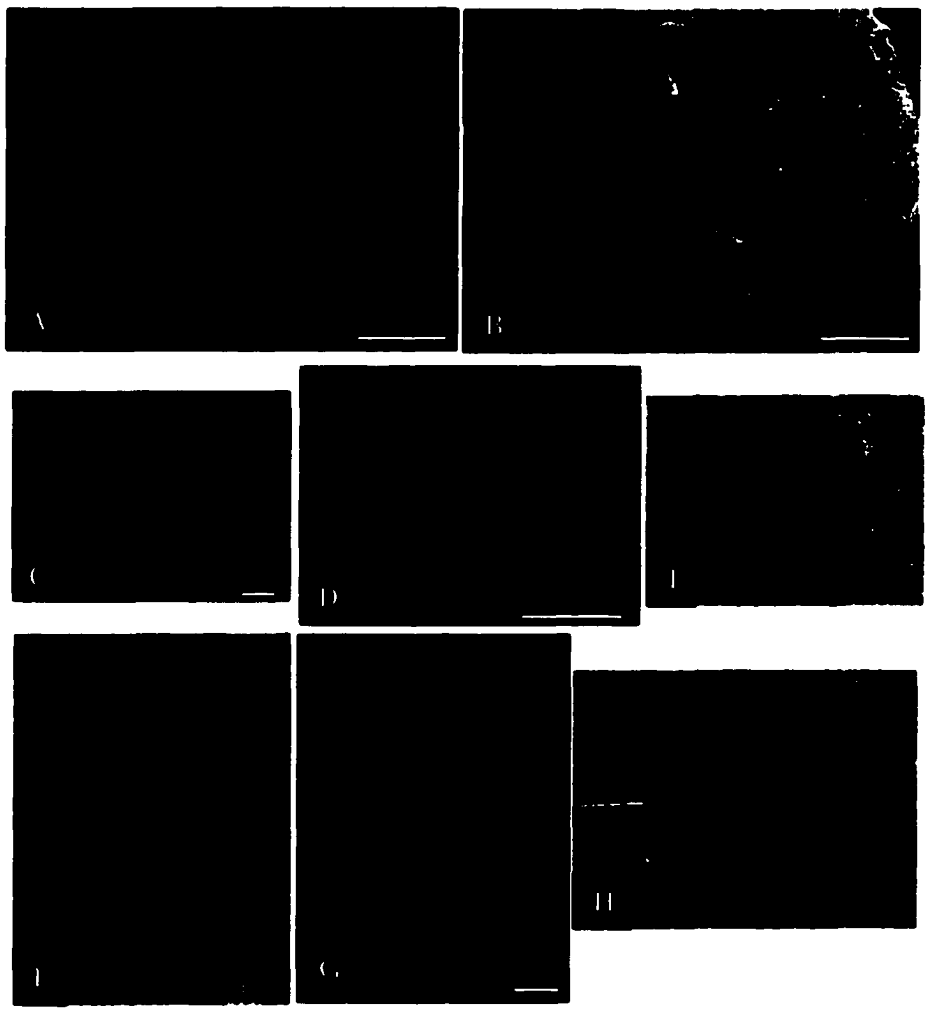
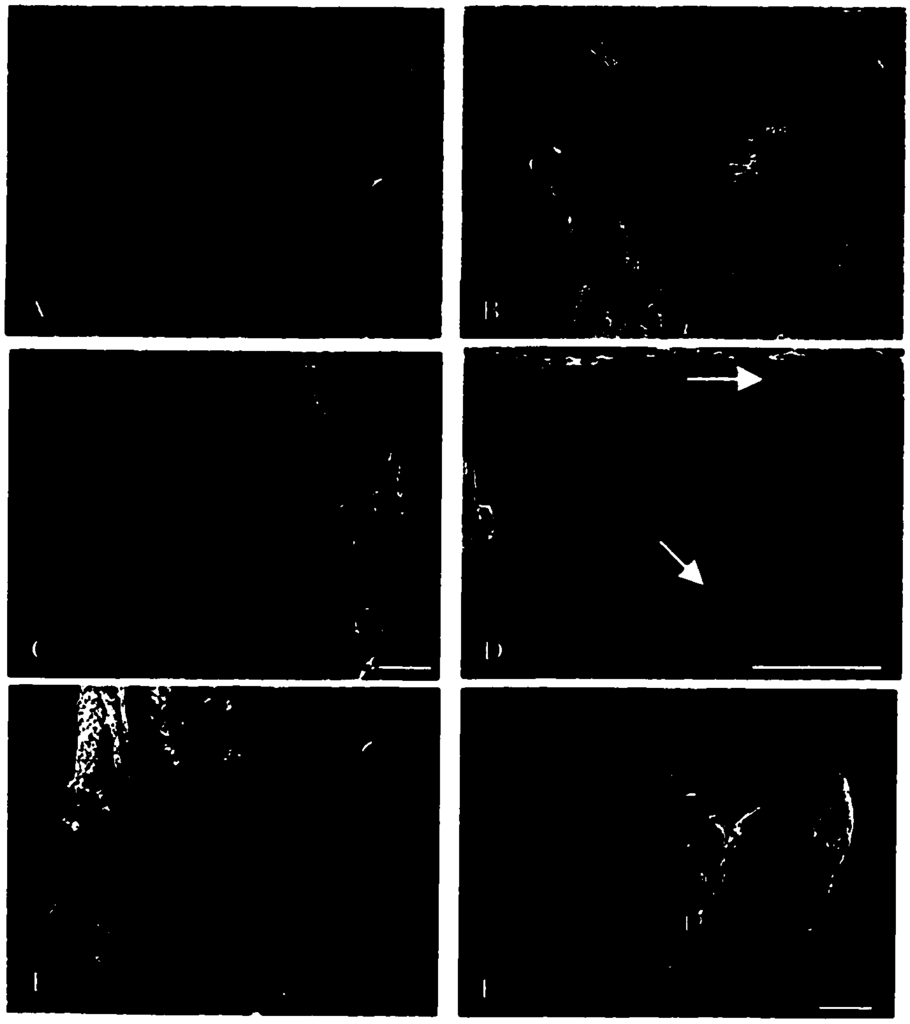


Fig. 6. **A, B.** R. parvifolium (Kirkbride 2978), ovules. **C,** R. kuhlmannii (Irwin 16561), ovules. **D.** R. discolor (Prance 15539), disk with stomata. **E.** R. tepuiense (Maguire 27870) capitate portion of the style. **F.** R. cataractae (Huber 3388), stigma at maturity. Scale bars: A-D,F 100 µm; E 500 µm.



ellipsoid (compressed at both ends), or rarely cylindrical or oblate. Ovaries are commonly glabrous, although there are few species (e.g., R. pilosum), with hirsute or hirsutulous ovaries.

The disk of Retiniphyllum is annular, and located at the top of the ovary. It is fleshy, glabrous, persistent and up to 2 mm long, and commonly with sparse stomata (Fig. 6D).

The styles are exserted well beyond the corolla, and are slender and terete for most of their length, although they may be slightly carinate at distal portion. The shortest styles are found in R. schomburgkii (11-17.5 mm long), and the longest in R. rhabdocalyx (32-45 mm long). Although the styles are glabrous at distal and basal portions, they are commonly hirsute, hirsutulous, or pilose for most of their length. In the species observed in the field, styles are of the same color of the corolla lobes, and this might be true in all species of the genus.

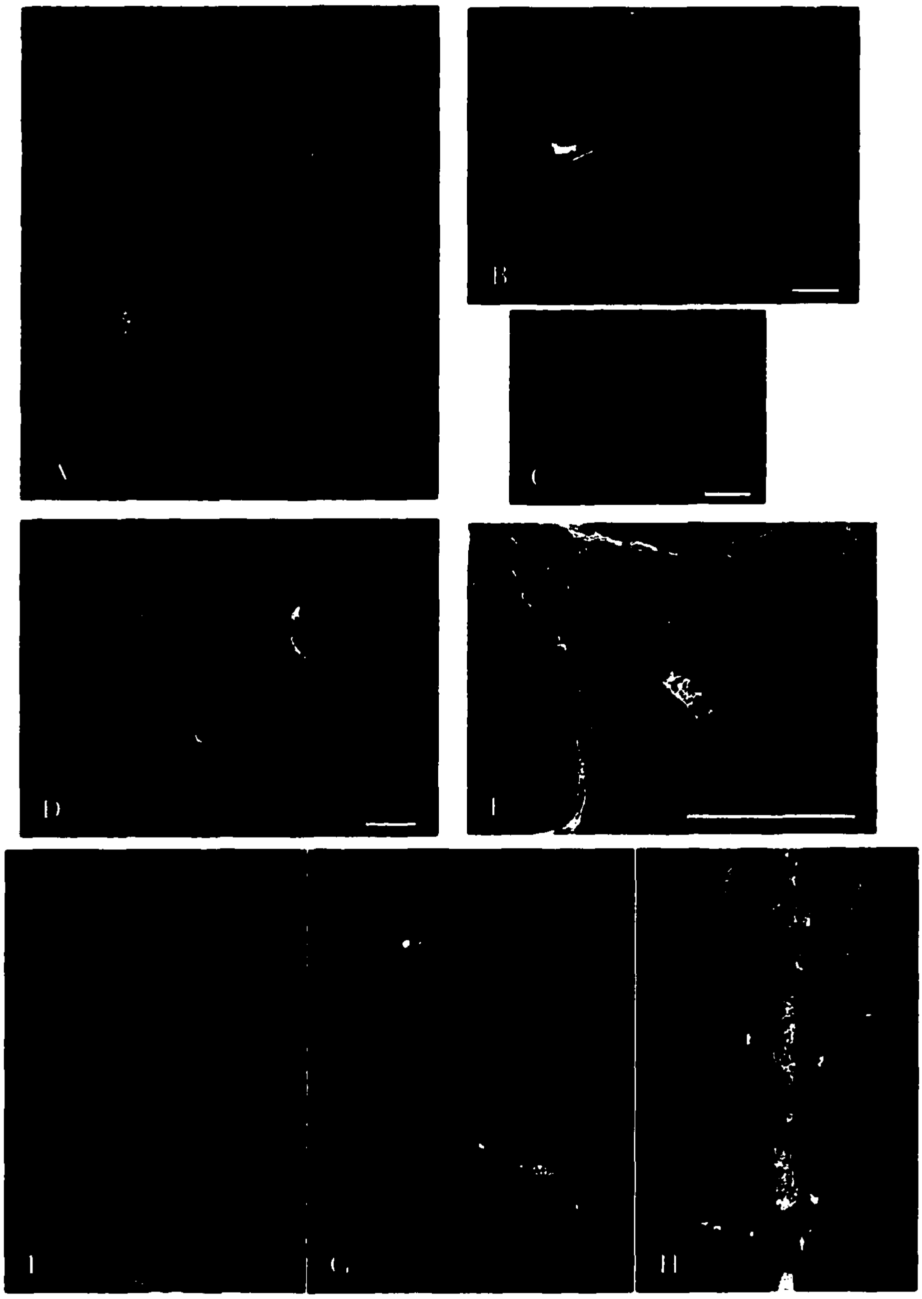
The style has five stigmatic branches at distal portion. Before the opening of the style lobes, the capitate portion of the style is either globose (Fig. 6E) or ellipsoid. When they open, the lobes are initially straight, and later recurving or coiling outward, so that the adaxial receptive surfaces come into contact with the abaxial sides of the stigmatic lobes (Fig. 6F). The lobes are narrowly triangular, and up to 2 mm long.

Fruits

Fruits of Retiniphyllum are drupaceous, with a thin exocarp, a fleshy mesocarp, and woody endocarps (pyrenes). Fruits are mostly pentalocular (Fig. 7A), but exceptionally they have four, six or eight locules (Fig. 7B,D). They are globose or transversally or longitudinally ellipsoid, and they range from 3 mm long in R. parvifolium to 12 mm long in R. scabrum. The sizes mentioned do not include the persistent calyx, which maintains approximately the same size in mature fruits.

The exocarp is thin, glossy, and the mesocarp is fleshy. The fruits generally pass from green to red during maturation and eventually turn to deep purple at full maturity (Fig. 7F-H). The pyrenes are woody and fill up most of the fruit. Each locule contains a pyrene that is attached to a massive vertical septum in the middle of the fruit. In most of the species the fruits are glabrous, but they are pilose in R. pilosum and occasionally hirsute in R. schomburgkii.

Fig. 7. Fruits diversity in Retiniphyllum. **A.** R. chloranthum, (Liesner 19713) transversal section of pentalocular fruit. **B, C.** R. secundiflorum (Foldats 3628). **B.** section of fruit with six locules. **C.** close-up of a locule with two seeds. **D. E.** R. francoanum (Cárdenas 6929). **D.** section of fruit with eight locules. **E.** close-up of a locule with two seeds. **F.** R. chloranthum, flowers and fruits. **G.** R. laxiflorum, immature fruits. **H.** R. schomburgkii, fruits. Scale bars: A 5 mm; B,D 1 mm; C,E 0.5 mm.



Pyrenes

The woody endocarps of the drupaceous fruits of the Rubiaceae are variable in shape and opening mechanisms. The early studies of Petit (1964) in the Psychotrieae showed their taxonomic value of these characters at the generic level. His ideas were followed, among others, by Robbrecht (1975, 1989), who has used pyrene morphology as a cardinal character in the study of African Psychotrieae. More recently, Piesschaert (2001) studied in detail pyrenes of the Psychotrieae, the largest tribe in the Rubiaceae (about 50 genera and 2000 species), and demonstrated their taxonomic significance. He found that the morphological variation of pyrenes is larger that had been considered in the past, and that they may be valuable characters not only at the generic level, but also at species level. For example, in Chassalia, a paleotropical genus with about 42 species, he found four different types of pyrenes.

Pyrenes of Retiniphyllum have not been previously studied in detail. Rodriguez (1976), in her study of the fleshy fruits and seeds of Venezuelan Rubiaceae, included the fruits of eight species of Retiniphyllum. Although she pointed out that the shape of the pyrenes differed among species of the genus, as can be seen in the illustrations, she did not describe them in detail.

The goals of this study are to describe the morphological variation of pyrenes in Retiniphyllum, to evaluate their taxonomic value, and to search for characters that might be used in assessing phylogenetic relationships among Retiniphyllum species.

Pyrenes were separated from the fleshy mesocarp, and cleaned with a brush under the microscope. They were placed on stubs and gold-coated using a Hummer 6.2 sputter coater, and then observed with a JEOL S410LV scanning electron microscope.

General Shape and size:

Pyrenes have a ventral and a dorsal ridge with sharp or acute margins. The ridges divide the pyrene in two halves, these with an external surface either smooth or verrucate (Fig. 8A-F), and with wings variable absent or present, and at different positions (Fig. 9A-F). Pyrenes are elliptic in dorsal view, reniform in lateral view, longer than wide, glabrous and bright yellow. The smallest pyrenes are found in R. parvifolium (2.5-3.8 mm long), and the largest in R. scabrum (4.5-8 mm long).

Opening mechanism:

Pyrenes in Retiniphyllum present a germination mechanism consisting in a perforation in the ventral side (Figs. 8C, 9B), and a preformed germination slit along their outline (Fig. 9F). When pressure is exerted on the perforation, the pyrene splits in two halves. The perforation may be located at the basal, medial or apical portion of the ventral side of the pyrene. The germination slit may run partially or totally around the pyrene outline.

Five main types of pyrenes have been detected in Retiniphyllum, based on the presence, consistency and position of the wings. Table 2 summarizes the characteristics of each species.

Type 1: Pyrenes without wings (Fig. 8A-F). They are narrowly elliptic in dorsal view, and generally reniform in lateral view, always longer than wide. The dorsal margin is convex and may exhibit a narrow depression near the distal end. The ventral margin is straight, or slightly concave (Fig. 8A) and may be homogeneous in size throughout or becoming narrower near the perforation. The base may be acute, round or truncate, and the distal end may be acute or round. The surface is smooth or verrucose throughout, or only verrucose near the dorsal margin and smooth near the ventral margin. The perforation is located at the medial

Fig. 8. Pyrenes without wings in Retiniphyllum. **A.** R. concolor (Urrego 1498). **B.** R. guianense (Tillet 44824). **C.** R. truncatum (Clark 6821), arrow indicates the perforation. **D.** R. rhabdocalyx (Cortés 1648). **E-F.** R. speciosum (Spruce 2340). Scale bars: A 1.5 mm; B-F 2 mm.

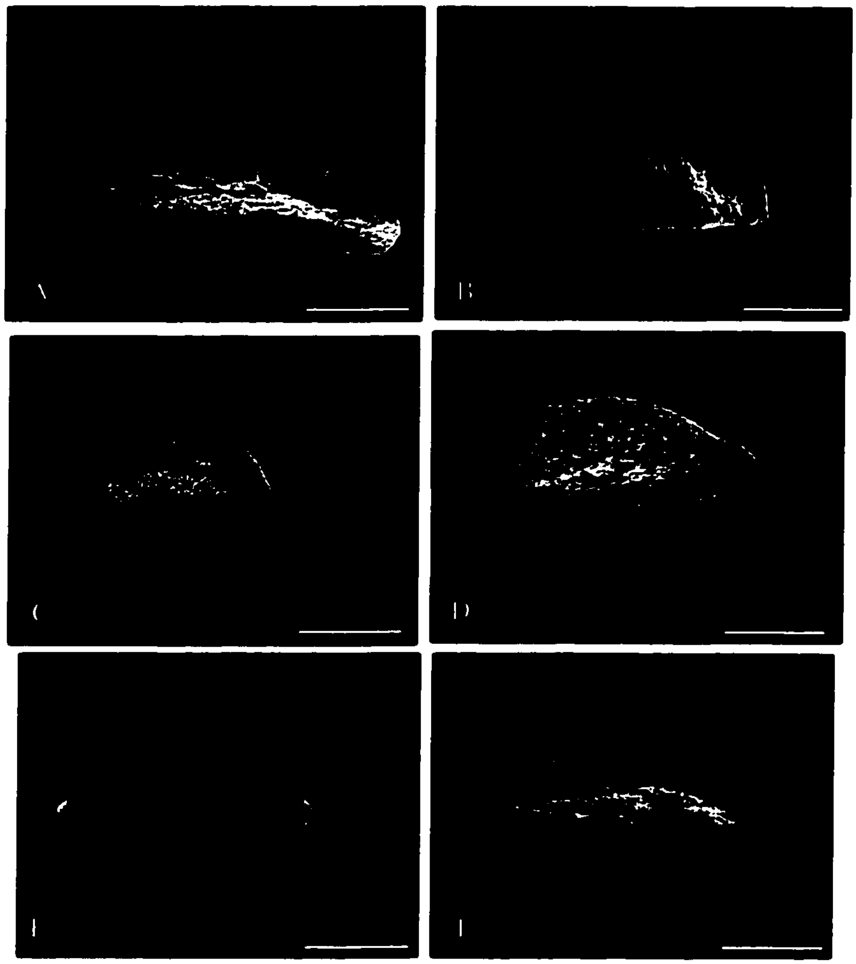


Fig. 9. Winged pyrenes in Retiniphyllum. **A.** R. francoanum (Cárdenas 6929). **B.** R. pilosum (Pabón 422), arrow indicates the perforation. **C.** R. chloranthum (Pipoly 7616). **D.** R. fuchsioides (Knapp 8526). **E.** R. laxiflorum (Maguire 24373). **F.** R. scabrum (Huber 10166). Scale bars: A-D,F 2 mm; E 2.5 mm.

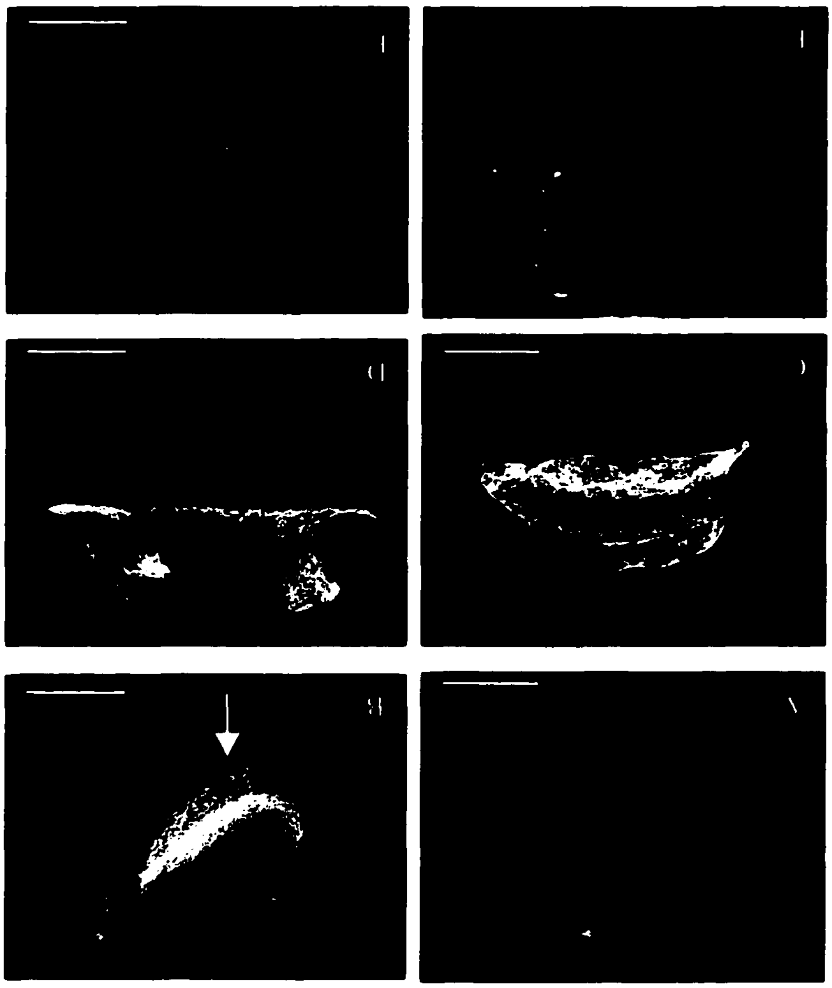


Table 2: Pyrenes morphological characters evaluated on the species of Retiniphyllum.

	Type	Dorsal margin: Irre-gular, Entire	Dorsal Depre-ssion: Absent Present	Ventral Margin: Homoge-neous, Hetero-geneous	Base: Acute Truncate Round	Apex: Acute Round	Surface: Verrucate Dorsally verrucate Smooth
R. cataractae	I	I	A	He	A	A	V
R. chloranthum	IV	E	A	He	A	A	S
R. concolor	I	E	A	He	A	A	S
R. discolor	I	E	A	He	A, R	R	D
R. francoanum	III	E	A	He	R	R	V
R. fuchsioides	IV	E	A	He	R	A	S
R. glabrum	I	E	P	He	A	R	D
R. guianense	I	E	A	Ho	T	A	S
R. kuhlmannii	I	E	A	He	A	A	D
R. laxiflorum	IV	E	A	He	R	R	D

Cont. Table 2

	Type	Dorsal margin: Irregular, Entire	Dorsal Depression: Absent Present	Ventral Margin: Homogeneous, Heterogeneous	Base: Acute Truncate Round	Apex: Acute Round	Surface: Verrucate Dorsally verrucate Smooth
R. parvifolium	I	E	A	He	R	R	D
R. pauciflorum	I	I	A	Ho	A	A	V
R. pilosum	III	E	A	Ho	R	A	S
R. rhabdocalyx	I	E	P	He	R	R	D
R. scabrum	IV	E	A	He	R	R	D
R. schomburgkii	I	E	A	He	A	A	D
R. secundiflorum	II	E	A	Ho	R	R	V
R. speciosum	I	E	P	He	A	R	D
R. tepuiense	III	E	P	He	A	A	V
R. truncatum	I	E	A	He	R	A	D

Cont. Table 2

	Wings: Absent Present	Ribs Wings	Consis-tency Charta-ceous Horny	Direction Parallel Perpendi-cular	Cavity Absent Present	Perfora-tion Base Center Apex
R. cataractae	A	-	-	-	-	B
R. chloranthum	P	W	H	P	A	C
R. concolor	A	-	-	-	-	C
R. discolor	A	-	-	-	-	B
R. francoanum	P	W	C	Pa	A	B
R. fuchsioides	P	W	H	P	P	C
R. glabrum	A	-	-	-	-	C
R. guianense	A	-	-	-	-	C
R. kuhlmannii	A	-	-	-	-	B
R. laxiflorum	P	W	H	P	P	C
R. parvifolium	A	-	-	-	-	C
R. pauciflorum	A	-	-	-	-	C
R. pilosum	P	W	C	Pa	A	B
R. rhabdocalyx	A	-	-	-	-	C
R. scabrum	P	W	C	P	P	A
R. schomburgkii	A	-	-	-	-	C
R. secundiflorum	P	R	C	P	A	C
R. speciosum	A	-	-	-	-	C
R. tepuiense	P	W	C	Pa	A	B
R. truncatum	A	-	-	-	-	B

portion or near the base of the dorsal margin. The preformed germination slit runs around the pyrene outline. Species included: R. cataractae, R. concolor, R. discolor, R. glabrum, R. guianense, R. kuhlmannii, R. parviflorum, R. pauciflorum, R. rhabdocalyx, R. schomburgkii, R. speciosum and R. truncatum.

Type 2: Pyrenes with a very reduced rib at each side of the dorsal margin, almost imperceptible in some specimens. Pyrenes are oblong in dorsal and lateral views, and almost as long as wide. The dorsal margin is convex, and the ventral margin is straight. The base and apex are round, and the surface is verrucose throughout. The perforation is located at the medial portion of the ventral margin. The preformed germination slit is located at the basal end of the pyrene. Species included: R. secundiflorum.

Type 3: Pyrenes with two wings parallel to the pyrene body, inserted near the ventral margin, and upward (Fig. 9A,B). The wings may be chartaceous or horny. Pyrenes are obovate in dorsal view, elliptic or oblong in lateral view, and longer than wide. The dorsal margin is convex, and the ventral margin may be straight or convex. Both ends are either round or acute. The surface may be smooth or verrucate throughout. The perforation is located at the base of the ventral margin. The preformed germination slit is located at the base of the pyrene. Species included: R. pilosum, R. tepuiense and R. francoanum.

Type 4: Pyrenes with two wings perpendicular to the pyrene body, inserted near the dorsal margin (Fig. 9C). The wings are horny. Pyrenes are elliptic in dorsal view, reniform in lateral view, and longer than wide. The dorsal margin is convex, and the ventral margin is concave. Both ends are acute, and the surface is smooth throughout. The perforation is located at the medial portion of the ventral margin. The preformed germination slit is located at the base of the pyrene. Species included: Retiniphyllum chloranthum.

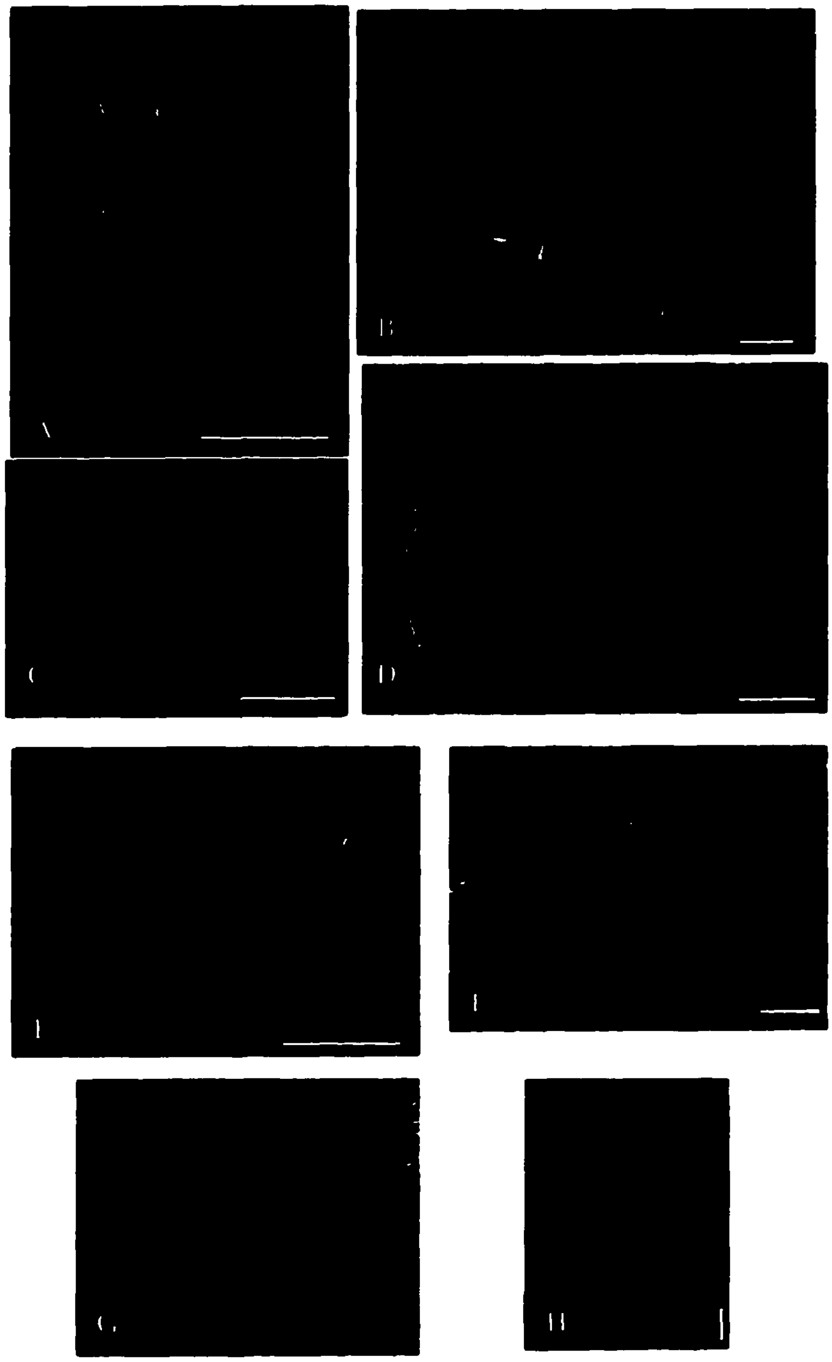
Type 5: Pyrenes with two wings perpendicular to the pyrene body, inserted near the dorsal margin of the pyrene (Fig. 9D-F). Each wing has a tubular cavity inside, with a round opening at the base of the pyrene. The wings may be horny or chartaceous. Pyrenes are oblong in dorsal view, elliptic in lateral view, and longer than wide. The dorsal margin is convex, and the ventral margin is straight. Both ends are either round or acute, and the surface is smooth throughout. The perforation is located at the apex or medial portion of the ventral margin. The preformed germination slit runs completely around the pyrene's outline. Species included: R. fuchsioides, R. laxiflorum and R. scabrum.

Seeds

In most of the species of Retiniphyllum, one of the two collateral ovules inside each locule is aborted, and each pyrene includes only one seed at fruit maturity. In this case, the aborted ovule remains undeveloped and attached to the mature seed (Figs. 10A-D,G). Exceptions to this trait are found in R. secundiflorum and R. francoanum in which both ovules develop into two seeds per pyrene (Figs. 10 E,F). This exceptional feature was observed in Retiniphyllum for the first time in this study.

Seeds may have two main shapes: either reniform, (ventrally concave and dorsally convex), or cylindrical. Most species have reniform seeds (Fig. 10C), and only R. francoanum, R. laxiflorum (Fig. 10B), R. scabrum (Fig. 10A,G), and R. secundiflorum (Fig. 10E,F) have cylindrical seeds. Cylindrical seeds are mostly attached to the placenta near the top of the septum (Fig. 10A,B,G), while reniform seeds are mostly attached to the placenta at the middle of the septum. Both ends of the seeds might be either round or acute. Seeds range in size from 1.8 to 5 mm

Fig. 10. Seeds of Retiniphyllum. **A.** R. scabrum (Huber 10166), seed with aborted ovule attached. **B.** R. laxiflorum (Steyermark 59464), seed with aborted ovule attached. **C,D.** R. kuhlmannii (Irwin 16561), seed with aborted ovule and obturator remnant. **E, F.** R. secundiflorum (Huber 3396), two seeds inside a pyrene. **G.** R. scabrum (Cardona 2636) single seed inside pyrene with aborted ovule attached. **H.** R. cataractae (Ducke 35007), seed with obturator remnant covering the aborted ovule. Scale bars: A,C,E 1 mm; B,D,F,H 200 um, G 2 mm.



long, and up to 1 mm wide. Seeds are characterized by having an appendage attached to the hilum, that correspond to the remanent of the obturator (Fig. 10H).

Pollen and orbicules Morphology

The most common type of pollen in the Rubiaceae family is tricolporate and with reticulate sexina. In the subfamily Ixoroideae (sensu Bremer et al., 1995; Andreasen & Bremer, 1996; Andreasen et al., 1999; Rova et al., 2002), tricolporate pollen characterizes whole tribes, as for instance Pavetteae and Hypobathreae (Robbrecht, 1988). A remarkable exception is found in the tribe Gardenieae, where there are genera with porate, colporate or pororate pollen grains with 3 to 10 apertures (Persson, 1993).

The most common sexine patterns in Rubiaceae is reticulate, perforate and microreticulate (Endress et al., 1996). However, sexine pattern may be very variable within the same tribe. For instance, Persson (1993) reported six sexine patterns in the tribe Gardenieae: tectate, semitectate, reticulate, foveolate, rugulate, perforate, and psilate.

Because of the variation found in number and type of apertures, and sexine pattern, these characters have demonstrated systematic value at subfamilial, tribal, and generic levels, and have been widely used (Andersson, 1993; Persson, 1993; Huysmans et al., 1994; Delprete, 1999; Huysmans et al., 2000). However, palynological studies at species level are scarce in the Rubiaceae and in many genera there is no variation among species. In fact, pollen morphology of Retiniphyllum is here studied for the first time, and below it is shown to be of taxonomic value at subgeneric level.

Orbicules are sporopollenin particles found on the tapetum surface. Although their function is still unclear, orbicules occur in most major groups of Angiosperms (for a review, see Huysmans et al., 1998). Orbicules have been found in the three subfamilies of the Rubiaceae, and a total of 35 genera have been reported to have orbicules so far (Igersheim, 1993a; Huysmans et al., 1997, Huysmans et al., 1998; Huysmans et al., 2000; Vinckier et al., 2000). The surveys made in the subfamilies Cinchonoideae (sensu Robbrecht, Huysmans et al., 1997), and Ixoroideae (sensu Robbrecht, Vinckier et al., 2000) suggest that orbicules may have systematic value at tribal and generic levels.

However, there are no studies of Rubiaceae orbicules that indicate a possible systematic value at the species level.

This study presents a survey of pollen and orbicules of Retiniphyllum, and focuses on the search for characters of systematic value that might contribute to produce a robust phylogenetic hypothesis for the genus.

Materials and methods

Pollen was processed and acetolyzed following Huysmans' (1998) protocol. Flower buds were rehydrated in photoflo for 30 minutes. The anthers were macerated and separated from debris using a fine mesh, and transfered to glacial acetic acid. After centrifugation, the pollen was acetolyzed in a mixture (9:1) of acetic acid anhydride and sulphuric acid, and warmed on a heating block for 10 minutes. After rinsing with distilled water, the sample was divided in two parts. One part was centrifuged with glicerin-water and mounted on slides to be observed in the light microscopy (LM), and the other part was centrifuged and stored in ethanol 70% to be observed in the scanning electron microscopy (SEM). Pollen preserved in ethanol was placed on stubs and gold-coated using a Hummer 6.2 Sputter coater, and then observed with a JEOL S410LV scanning electron microscope.

Measurements of polar and equatorial length were made on ten pollen grains per sample with LM under oil immersion at a x 1000 magnification. All other measurements were made on pictures taken at the SEM.

For the observation of orbicules, flower buds were extracted from herbarium specimens and rehydrated for 30 minutes in Agepon wetting agent. The anthers were extracted from the flower buds and dissected removing pollen grains from the tapetum. The anthers were placed on stubs and air dried for 24 hours. The stubs were sputter coated and then observed at the SEM. Measurements were made on pictures taken at the SEM.

This study was based on 25 herbarium specimens of 21 species from NY herbarium. The vocuher specimens are listed in Appendix A.

Pollen terminology follows that of Punt et al. (1994). Shape classes in equatorial view were based on the relation between the length of the polar axis and the equatorial diameter of the pollen grain (Erdtman, 1971). In addition to Erdtman's shape classes, the shape delineated by the pollen grain in outline was also used.

Results

Pollen Morphology

Pollen grains of Retiniphyllum are medium-sized, as the polar axis (P) ranges from 26.6 to 52.2 μm and the equatorial diameter (E) from 22.2 μm to 42.2 μm. The smallest grains are found in Retiniphyllum secundiflorum (P=30 μm, E=24.5 μm), and the largest pollen grains are found in R. chloranthum (P=46.6 μm, E=38.7 μm). Table 3 summarizes the pollen characters of the species examined.

In equatorial view, the shape of the pollen grains is mostly prolate-spheroidal or subprolate, and rarely prolate. Pollen grains are oblong in outline only in R. chloranthum (Fig. 11A) and R. concolor, and elliptic in the rest of the species (e.g. R. kuhlmannii; Fig. 11B). In most of the species, the grains are round at polar view (Amb) [e.g. R. scabrum (Fig. 11C), R. truncatum (Fig. 11D)], and exceptionally slightly sub-angular in R. fuchsioides (Fig. 11E) and R. glabrum.

All the species of Retiniphyllum have tricolporate pollen grains. The ectoaperture is a colpus with distinct

Table 3: Pollen morphological characters evaluated on the species of Retiniphyllum. All measurements are in µm.

	R. cataractae	R. chloranthum	R. concolor	R. discolor
P	32.2(34.9)36.6	40(44.2)52.2	40(44.5)50	32.2(39.9)44.4
E	26.6(28)30	28.9(34.8)42.2	33.3(36.7)41.1	25.5(32.7)38.9
P/E	1.18(1.24)1.26	1.08(1.27)1.46	1.11(1.2)1.33	1.09(1.21)1.36
Shape	subprolate	Prolate spheroidal, subprolate	prolate spheroidal, subprolate	subprolate, prolate, prolate sph.
Amb	-	Circular	circular, semi-angular	semi-angular
Apo. Index	-	0.5-0.55	0.69	0.33-0.35
Width ecto.	3.6-4	5-6.1	4-6.6	4.5-8.5
Ends of ectoaperture	obtuse, trucate	Obtuse, acute	acute, obtuse	obtuse, truncate
Mesoaperture	la-longate,	lalongate	lalongate	lalongate
Width meso.	3.0-3.9	4-6	4-6.5	3.8-6.5
Height mes.	3.5-4	2-4.1	2.8-5	2.5-5.3
Aspis	absent	Absent	absent	Absent,present
Sexine	Microreticu-late	Reticulate to microreticu-late.	reticulate to microreticu-late.	Microreticulate, tectate-perforate
Max. Ø lumina apo.	0.6	2.5	1.2	1
Max. Ø meso.	1	1.9	1.9	1
Lumina shape	round	Round	round	round
Width muri	0.2-0.9	0.4-1.1	0.5-1.4	0.3-0.7
Type	V	I	I	V

Cont. Table 3

	R. fuchsioides	R. glabrum	R. guianense	R. kuhlmannii
P	33.3(38.5)41.1	-	34.4(38)40	31.1(33.4)35.5
E	30(31.4)33.3	-	30(31.7)33.3	26.6(28.2)30
P/E	1.13(1.22)1.28	-	1.1(1.19)1.28	1.03(1.18)1.33
Shape	Prolate spheroidal, subprolate	-	prolate spheroidal, subprolate	prolate spheroidal, subprolate
Amb	Semi-angular	Circular	circular	circular
Apo. Index	0.48	-	0.46	0.35
Width ecto.	4.6	-	4.5-5.6	4-4.5
Ends of ectoaperture	Acute	Obtuse, truncate	obtuse	obtuse
Mesoaperture	Lolongate		lalongate, lolongate	lalongate
Width mesoaperture	4.2		4.5-5	4-4.5
Height mesoaperture	6		4.6-4.8	2.5-3.5
Aspis	Absent		absent	absent
Sexine	Tectate-perforate	Microreticu-Late.	Microreticu-late.	Microreticu-late.
Max. Ø lumina apo.	0.5		0.9	0.8
Max. Ø meso.	0.3		1.4	1
Lumina shape	Round	Round	angular	angular
Width muri	-	-	0.3-0.6	0.3-0.6
Type	IV	V	V	V

Cont. Table 3

	R. laxiflorum	R. longiflorum	R. maguirei	R. parvifolium
P	31.1(33.8)36.6	35.5(37.0)40	-	32.2(35.7)41.1
E	26.6(28.7)31.1	28.9(31.5)33.3	-	27.8(30)32.2
P/E	1.11(1.17)1.23	1.13(1.17)1.26	-	1.1(1.18)1.32
Shape	prolate spheroidal, subprolate	Prolate spheroidal, subprolate	-	prolate spheroidal, subprolate
Amb	circular	-	circular	circular
Apo. Index	0.42	-	0.52	0.42
Width ectoaperture	3-4.5	5.5	4.2-5.2	4.2-5.2
Ends of Ect.	acute	Obtuse	obtuse	obtuse
Mesoaperture	lalongate, lalongate	-	lolongate	lalongate
Width mesoaperture	3-4.5	-	3.5-4.5	4-5
Height mesoaperture	3-3.5	-	4.2-5	3.2-3.5
Aspis	absent	Absent	present	absent
Sexine	tectate-perforate	Tectate-perforate	tectate-perforate	Tectate-perforate
Max. Ø lumina apo.	0.6	-	1	0.8
Max. Ø meso.	0.6	0.3	1.1	0.8
Lumina shape	round	Round	round	round
Width muri	-	-	-	-
Type	III	III	III	III

Cont. Table 3

	R. pauciflorum	R. pilosum	R. scabrum	R.schomburgkii
P	34.4(36.7)38.9	34.4(38)40	30(38)45.5	34.4(38.7)43.3
E	28.9(31.1)34.4	30(33.3)37.7	24.4(31.15)37.7	32.2(34.3)35.5
P/E	1.12(1.17)1.23	1.06(1.13)1.22	1.04(1.21)1.34	1.03(1.13)1.21
Shape	prolate spheroidal, subprolate	prolate spheroidal, subprolate	subprolate	prolate spheroidal, subprolate
Amb	circular	Circular	circular	-
Apo. Index	0.42	0.45	0.48	-
Width ectoa.	4	4.2-4.5	3.2-5.8	4-5
Ends ectoap.	obtuse	Acute	truncate	obtuse
Mesoaperture	lalongate	Lalongate	-	lalongate, lolongate
Width mesoaperture	3.4-4	4-4.2	2.8-5	3-4.5
Height mesoaperture	2.8-3.2	3.2-3.8	3.5-5.5	3.5-4
Aspis	present	Present	present	absent
Sexine	microreticulate	Microreticulate	Microreticulate	microreticulate
Max. Ø lumina apo.	0.5	0.9	0.9	1.5
Max. Ø lumina meso.	1.1	1.5	1.5	1.4
Lumina shape	angular	Angular	angular	round
Width muri	0.3-0.4	0.4-0.7	0.3-0.7	0.3-0.6
Type	II	V	II	V

Cont. Table 3

	R.secundifloru	R. rhabdocalyx	R. tepuiense	R. truncatum
P	26.6(30)32.2	34.4(37.1)40	40(40.9)43.3	34.4(37.9)40
E	22.2(24.5)26.6	27.8(29.7)32.2	33.3(34.7)36.6	30.0(32.8)35.5
P/E	1.16(1.21)1.33	1.21(1.33)1.46	1.12(1.17)1.22	1.06(1.15)1.33
Shape	Subprolate	Subprolate, prolate	Prolate spheroidal, subprolate	prolate spheroidal, subprolate
Amb	-	Circular	Circular	Circular
Apo. Index	-	0.54	0.55	0.33
Width ectoaperture	3.8	5.8-6.2	2.5-3	4-6.5
Ends of ect.	Acute	Obtuse	obtuse, truncate	Obtuse
Mesoaperture	Lalongate	-	lolongate	lalongate, lolongate
Width mesoaperture	3.8	4.4-4.8	2.5-3	2.5-5.5
Height mesoaperture	3	4.3-4.7	4-5	3-4.2
Aspis	Absent	Present	absent	Absent
Sexine	Tectate-perforate	Tectate-perforate	Microreticulate	Microreticulate
Max. Ø lumina apo.	-	0.7	1.8	0.6
Max. Ø meso.	0.6	1	1.1	1.6
Lumina shape	Round	Round	round	Angular
Width muri	-	-	0.3-1.1	0.2-0.7
Type	III	III	V	V

margins. The width of the ectoaperture ranges from 2.5 μm in R. tepuiense (Fig. 11F) to 6.6 μm in R. discolor (Fig. 11G). The ends of the ectoaperture are obtuse (e.g. R. discolor; Fig. 11G), acute (e.g. R. pilosum; Fig. 11H), or truncate (e.g. R. tepuiense; Fig. 12A). The length of the colpi, indirectly evaluated by the Apocolpium Index, ranges from 0.33 in R. truncatum (Fig. 11D) to 0.69 in R. concolor (Fig. 12B). The colpus membrane is coarse, and is beset with sexinous elements.

The mesoaperture is located at the equator of the ectocolpus. Most species have a rectangular mesoaperture (e.g. R. kuhlmannii; Fig. 12C) that is commonly called porus, for lack of a better term. Most likely this porus is just the hole in the sporoderm caused by the overlap of both the ecto- and endocolpus. Circular mesoapertures occur only in R. scabrum and R. speciosum (Fig. 12D). The porus is lalongate in more than half of the species (e.g. R. truncatum; Fig. 12E), and lolongate in some species (e.g. R. tepuiense; Fig. 12F). In R. cataractae, R. guianense, R. laxiflorum, R. schomburgkii and R. speciosum the length and breadth of the porus is more or less identical (circular) (e.g. R. speciosum; Fig. 12D). In R. discolor, R. maguirei, R. pauciflorum, R. pilosum, R. scabrum and R. speciosum, a

Fig. 11. SEM photomicrographs of pollen grains of Retiniphyllum. A. R. chloranthum (Colella 1895), equatorial view. B. R. kuhlmannii (Maguire 56447), equatorial view. C. R. scabrum, (Steyermark 104202), polar view. D. R. truncatum (Murça-Pires 742), polar view. E. R. fuchsioides (Dudley 13175), polar view. F. R. tepuiense (Maguire 37030), equatorial view. G. R. discolor (Huber 6119), equatorial view. H. R. pilosum (Wurdack 43270), equatorial view. Scale bars: 5 μm.

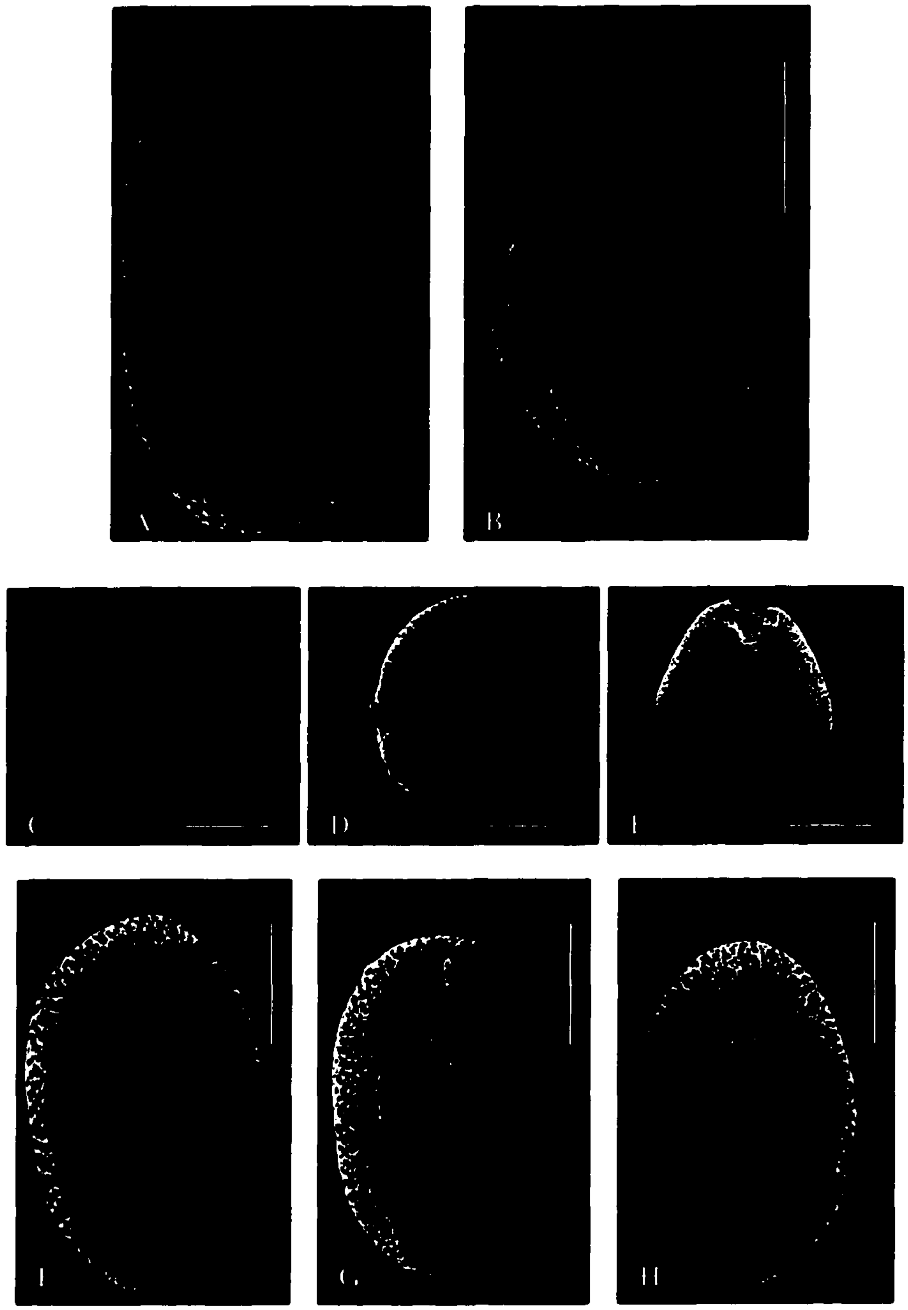
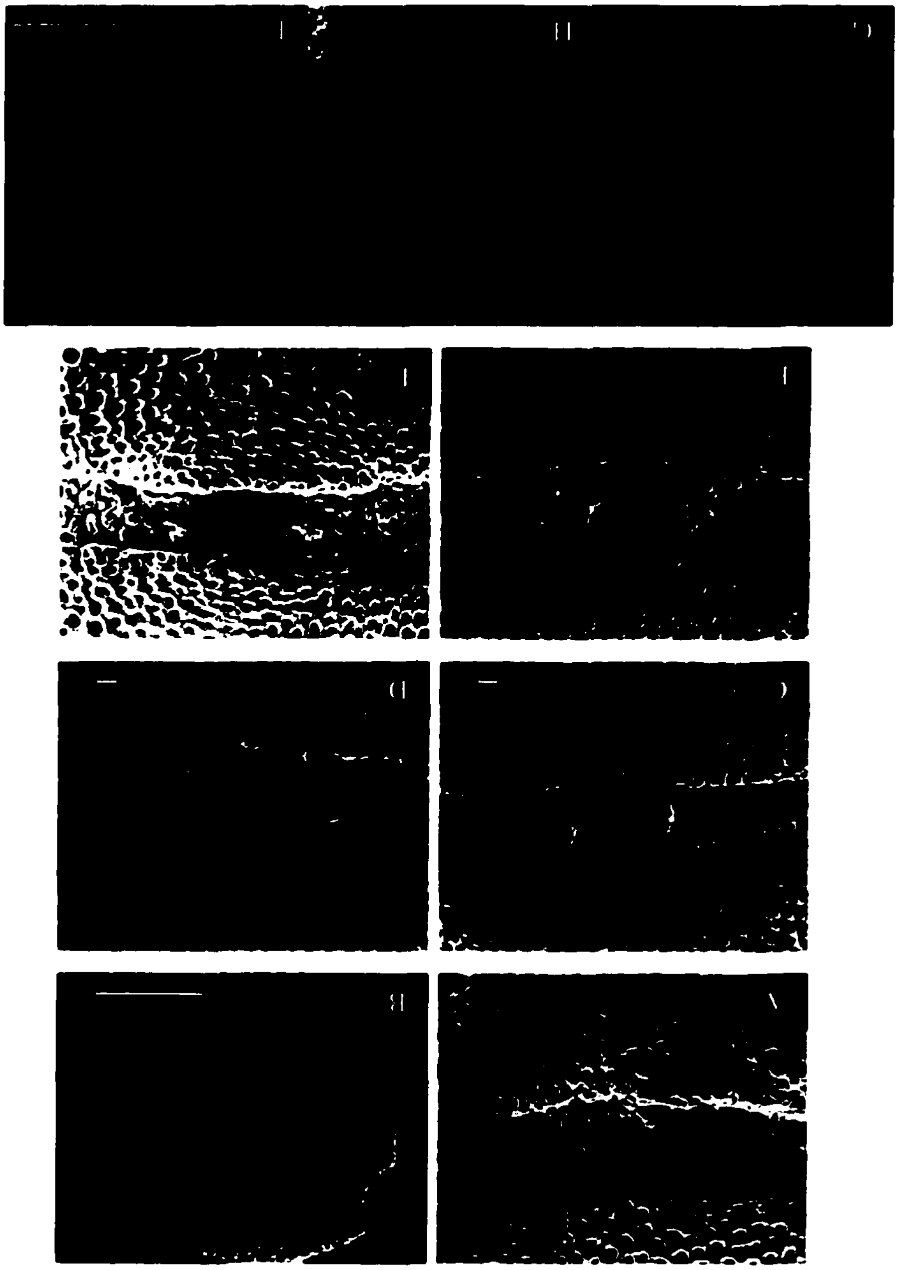


Fig. 12. SEM photomicrographs of pollen grains of Retiniphyllum. **A.** R. tepuiense (Maguire 37030) equatorial view. **B.** R. concolor (Cortés 1611), polar view. **C.** R. kuhlmannii (Maguire 56447), equatorial view. **D.** R. rhabdocalyx (Cortés 1648), equatorial view. **E.** R. truncatum (Murça-Pires 742), equatorial view. **F.** R. tepuiense (Maguire 37030) equatorial view. **G.** R. fuchsioides (Dudley 13175), endoaperture. **H.** R. scabrum (Steyermark 104202), endoaperture. **I.** R. truncatum (Murça-Pires 742), endoaperture. Scale bars A-C: 1 μm; D-H: 5 μm.



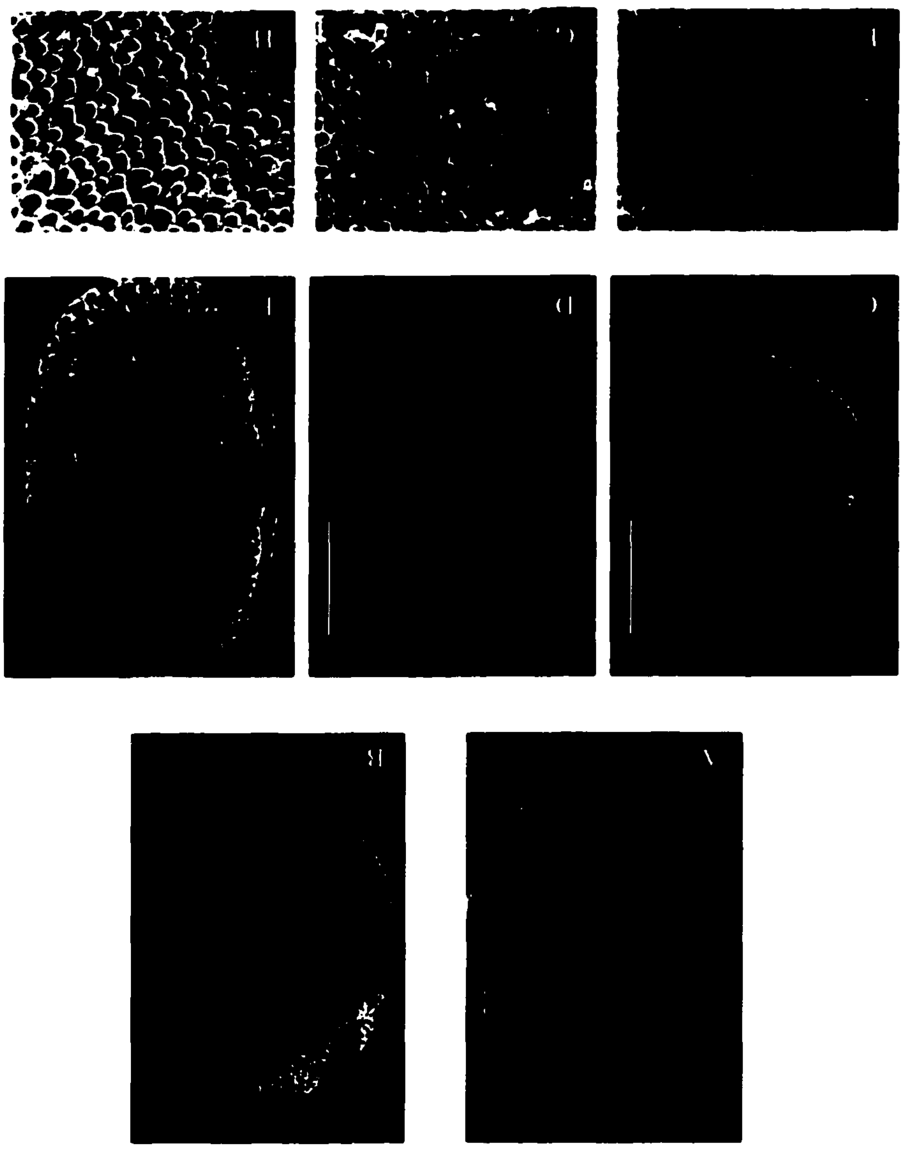
protruding thickening of the exine around the mesoaperture (aspis) is found (Fig. 11G, 12D).

The endoaperture is a colpus with smooth margins and acute ends, perpendicular to the ectocolpus. The inner nexine surface is granular as in most Rubiaceae. The endoaperture was observed in all the species of Retiniphyllum at the LM, and in R. fuchsioides (Fig. 12G), R. scabrum (Fig. 12H), and R. truncatum (Fig. 12I), from broken pollen grains at the SEM.

The sexine ornamentation varies in Retiniphyllum. A microreticulate tectum is the most common sexine pattern and occurs in half of the species (e.g. R. schomburgkii; Fig. 13A, R. scabrum; Fig. 13B). A tectum perforatum is found in seven species (e.g. R. laxiflorum, Fig. 13C; R. fuchsioides, Fig. 13D), and a reticulate pattern occurs only in R. concolor (Fig. 13E) and R. chloranthum. In all species, the sexine is smooth without any supratectal processes.

In most species the lumina, that is the space enclosed by the muri, are quite uniform throughout the mesocolpium and decrease in diameter towards the proximity of the ectocolpus. However, in R. pauciflorum and R. scabrum (Fig. 13B), the lumina tend to be larger in the center of the mesocolpium and decrease in size towards the poles.

Fig. 13. SEM photomicrographs of pollen grains of Retiniphyllum. **A.** R. schomburgkii (Maguire 30901) equatorial view. **B.** R. scabrum (Steyermark 104202), equatorial view. **C.** R. laxiflorum (Maguire 28707), equatorial view. **D.** R. fuchsioides (Dudley 13175), equatorial view. **E.** R. concolor (Cortés 1611), equatorial view. **F.** R. guianense (Tillet 44824) equatorial view. **G.** R. pilosum (Wurdack 43270), equatorial view. **H.** R. discolor (Huber 6119), equatorial view. Scale bars A-E: 5 µm; F-H: 1 µm.



Instead, in R. chloranthum (Fig. 11A) and R. concolor (Fig. 13E) the lumina are smaller in the equatorial portion of the mesocolpium and increase in diameter towards the poles.

The shape of the lumina varies from angular to round. The lumina are angular in eight species (e.g. R. guianense, Fig. 13F; R. pilosum, Fig. 13G), and round in the rest of the species of the genus (e.g. R. discolor, Fig. 13H).

Five types of pollen grains have been detected in Retiniphyllum, based on shape on outline, sexin ornamentation and lumina size and shape, which are described below.

Type I: Grains prolate-spheroidal, or subprolate [P/E 1.08(1.2)1.32]; P 40(46.05)52.2 μm and E 31.1(37.9)42.4 μm, oblong in outline; amb circular; apocolpium index 0.5-0.57; ectoaperture 4-5.5 μm wide; obtuse ends; mesoaperture lalongate, 2.8-5.2 x 2-5.5 μm, aspis absent or present; sexine micro- or reticulate, maximum Ø lumina apocolpia 2.5 μm, mesocolpia 1.9 μm, lumina round, muri 0.4-1.1 μm wide.

Pollen grain Type I is found only in R. chloranthum (Fig. 11A) and R. concolor (Fig. 13E). It exhibits a unique character within the genus such as the shape in outline and the lumina being shorter in the centre of the mesocolpium and increasing in diameter towards the poles. It is the largest pollen grain found in the genus. Within

Retiniphyllum, these species with this pollen type are distinct in having white long-tubular corollas, and therefore suggesting a correlation between pollen and floral morphology.

Type II: Grains prolate-spheroidal, or subprolate [P/E 1.04(1.2)1.34]; P 30(37.4)45.1 μm and E 24.4(31.2)37.7 μm, elliptic in outline; amb circular; apocolpium index 0.42-0.48; ectoaperture 3.2-5.8 μm wide, obtuse or truncate ends; mesoaperture lalongate, 2.8-5 x 2.8-5 μm, aspis present; sexine microreticulate, maximum Ø lumina apocolpia 0.9 μm, mesocolpia 1.5 μm, lumina angular, muri 0.3-0.7 μm wide.

Pollen grain Type II is found in R. pauciflorum and R. scabrum (Fig. 13B). It is unique in the genus by having lumina larger at the equatorial portion of the mesocolpium and decreasing in size towards the poles. It is found in the only species of the genus with umbellate inflorescences, and therefore indicating a correlation between pollen features and inflorescence architecture.

Type III: Grains prolate, prolate-spheroidal, or subprolate [P/E 1.11(1.22)1.46]; P 26.6(34.22)41.1 μm and E 22.2(28.22)32.2 μm, elliptic in outline; amb circular; apocolpium index 0.38-0.54; ectoaperture 3-6.2 μm wide, acute or obtuse ends; mesoaperture la- or lolongate, 3-5 x 3-5 μm, aspis absent or present; sexine tectate-perforate, maximum Ø lumina apocolpia 1.1 μm, mesocolpia 1.1 μm, lumina round.

Pollen grain Type III has a tectate-perforate sexine and it is found in R. laxiflorum (Fig. 13C), R. longiflorum, R. maguirei, R. parvifolium, R. secundiflorum and R. rhabdocalyx (Fig. 12D). Except for R. parvifolium (with short-tubular, white corollas) species of this group have long-tubular, red corollas.

Type IV: Grains elliptic-prolate, spheroidal, or subprolate [P/E 1.13(1.22)1.28]; P 33.3(38.5)41.1 μm and E 30(31.4)33.3 μm, elliptic in outline; amb semi-angular; apocolpium index 0.48; ectoaperture 4.6 μm wide, acute ends; mesoaperture lolongate, 4.2 x 6 μm, aspis absent; sexine tectate-perforate, maximum Ø lumina apocolpia 0.5 μm, mesocolpia 0.3 μm, lumina round.

Pollen grain Type IV is found only in R. fuchsioides (Fig. 13D). The character that distinguish this type from the other types is the extremely reduced lumina size, (puncta 0.2 μm), which is the smallest in the genus.

Type V: Grains prolate-spheroidal, or subprolate [P/E 1.03(1.18)1.36]; P 31.1(37.67)44.4 μm and E 25.5(31.65)37.7 μm, elliptic in outline; amb circular; apocolpium index

0.33-0.55; ectoaperture 2.5-8.5 μm wide, acute, obtuse or truncate ends; mesoaperture la- or lolongate, 2.5-6.5 x 2.5-5.3 μm, aspis absent or present; sexine microreticulate, maximum Ø lumina apocolpia 1.5 μm, mesocolpia 1.6 μm, lumina round or angular, muri 0.2-1.1 μm wide.

Pollen Type V is found in R. cataractae, R. discolor (Fig. 11G, 13H), R. glabrum, R. guianense (Fig. 13F), R. kuhlmannii, (Fig. 11B, 12C), R. pilosum (Fig. 11H), R. schomburgkii (Fig. 13A), R. speciosum, R. tepuiense (Fig. 11F, 12A, 12F), and R. truncatum (Fig. 11E, 12I, 12E). This is the most common type of pollen in Retiniphyllum, but apparently not correlated with any macromorphological character, and perhaps originated several times within the genus.

Discussion

Retiniphyllum posses 3-zonocolporate pollen, which is the most common type in the Rubiaceae (Robbrecht, 1988). Consequently, pollen characters have limited utility to postulate the subfamilial affinities of the tribe Retiniphyllae; however, they may be of some value when combined with additional morphological characters.

Pollen morphological variability in Retiniphyllum is considerable. Although type and number of apertures are stable in all species, features such as size and ends shape of ectoapertures, shape of mesoapertures, presence of aspis, sexine ornamentation and lumina shape and size are variable, and of some taxonomic value.

Retiniphyllum chloranthum (Fig. 11A) and R. concolor (Fig. 13E) exhibit a combination of characters that distinguish them from the rest of the species. They have the largest pollen grains in the genus. In addition, their lumina are smaller in the centre of the mesocolpium and increase in diameter towards the poles, a character unique within the genus. They also have a short ectoaperture (Amb <0.5), lalongate mesoaperture and round lumina. Within Retiniphyllum, these species form a distinct monophyletic group that possess white long-tubular flowers, indicating a direct correlation between pollen and floral morphology. Another example is found in R. scabrum (Fig. 13B) and R. pauciflorum, two very similar species difficult to differentiate without flowers, that have pollen with larger lumina in the center of the mesocolpium that decrease in size towards the poles and the ectocolpus.

The correlation between pollination syndromes in Retiniphyllum and pollen morphology suggests that some pollen characters have systematic value, and that they will contribute to support phylogenetic hypothesis constructed with molecular and morphological data.

Orbicules Morphology

Orbicules occur on the inner wall of the anther locules, in all species of Retiniphyllum. They are variable in shape, aggregation, size and surface characteristics among species (Table 4). In this genus, it is possible to identify two main orbicule types: doughnut-shaped and disk-shaped. Although in both types the orbicules are more or less circular and flattened, the doughnut-shaped orbicules have a round depression in the middle (Fig. 14A), and the disk shaped ones are without depression (Fig. 14B). In both types the borders of the orbicule vary from regular to irregular within the same specimen (Fig. 14C).

The most common type of orbicule in Retiniphyllum is the doughnut shaped one, which is found in 14 species. The disk-shaped orbicules occur exclusively in R. parvifolium (Fig. 14D). The rest of the species have both types of orbicules. In R. kuhlmannii (Fig. 14E, 14F) for instance, a transition between doughnut-shaped and disk-shaped orbicules is present: instead of a single central cavity,

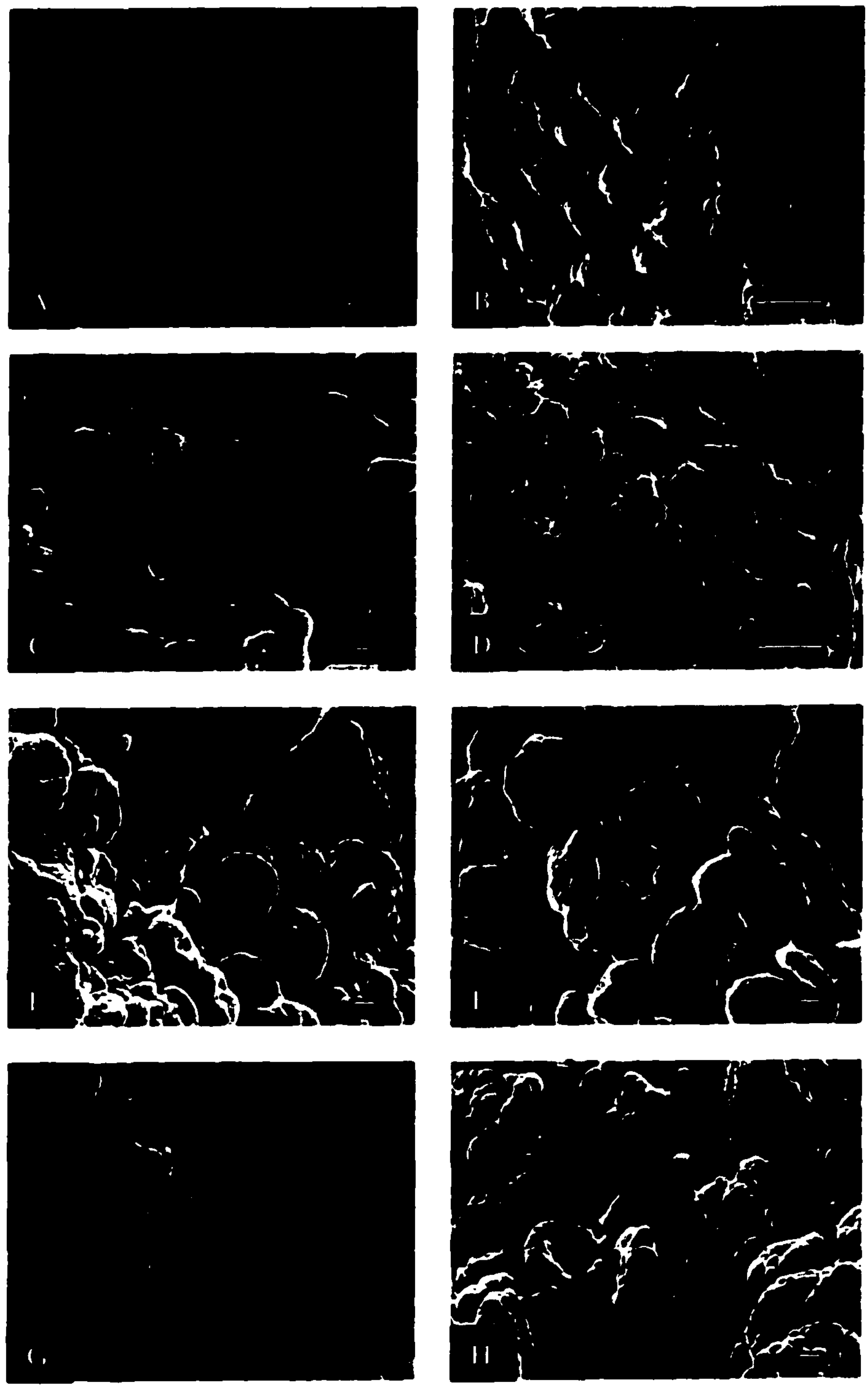
Table 4. Orbicules characteristics found in species of Retiniphyllum.

Species	Shape	Type of aggregation	Size µm	Surface
R. cataractae	Doughnut-shaped	not fused	1.4-2.7	Smooth
R. chloranthum	Doughnut- and Disk-shaped	mostly separated or a few fused	1.9-4	Rough
R. concolor	Doughnut-shaped	mostly separated or a few fused	1.8-3.3	Smooth
R. discolor	Doughnut-shaped	fused often in pairs	1.8-3.0	Smooth
R. fuchsioides	Doughnut-shaped	mostly separated or a few fused	2.8-3.8	Rough
R. guianense	Mostly doughnut-shaped, few disk-shaped	mostly fused, few separated	1.4-2.8	Rough
R. glabrum	Doughnut-shaped	mostly separated or a few fused	2-3.5	Smooth
R. kuhlmannii	Doughnut- and disk-shaped	mostly fused or a few separated	1.3-3.4	Rough
R. laxiflorum	Doughnut-shaped	mostly fused or separated	2.0-2.6	Smooth
R. longiflorum	mostly disk-shaped	separated	2.6-4.1	Smooth

Cont. Table 4

Species	Shape	Type of aggregation	Size µm	Surface
R. maguirei	doughnut-shaped	mostly fused or separated	1.9-3.5	Rough, granulate
R. parvifolium	disk-shaped	mostly fused or separated	1.5-4.3	Smooth
R. pauciflorum	doughnut-shaped	mostly separated or a few fused	1.0-3.3	Smooth
R. pilosum	doughnut-shaped	mostly fused or a few separated	1.0-2.2	Rough
R. rhabdocalyx	doughnut-shaped	mostly separated, and few fused	2.3-4.0	Smooth
R. scabrum	doughnut- and disk-shaped	mostly fused few separated	1.5-2.4	Rough
R. schomburgkii	doughnut-shaped	mostly separated or a few fused	2.8-4.3	Smooth
R. secundiflorum	doughnut-shaped	mostly separated or a few fused	2.6-4.3	Striate
R. speciosum	doughnut-shaped	mostly separated or a few fused	-	Rough, granulate
R. tepuiense	doughnut- and disk-shaped	mostly separated and few fused	1.5-3.3	Smooth
R. truncatum	doughnut-shaped	mostly separated or a few fused	1.6-3.8	Smooth

Fig. 14. SEM photomicrographs of orbicules of Retiniphyllum. **A.** R. cataractae (Ducke 35067), orbicules. **B.** R. concolor (Cortés 1611), orbicules. **C.** R. schomburgkii (Maguire 30901), orbicules. **D.** R. parvifolium (Prance 25239), orbicules. **E, F.** R. kuhlmannii (Maguire 56447), orbicules. **G.** R. rhabdocalyx (Cortés 1648), orbicules. **H.** R. maguirei (Maguire 24220), orbicules. Scale bars: A, B, D: 10 μm; C, E-H: 1 μm.

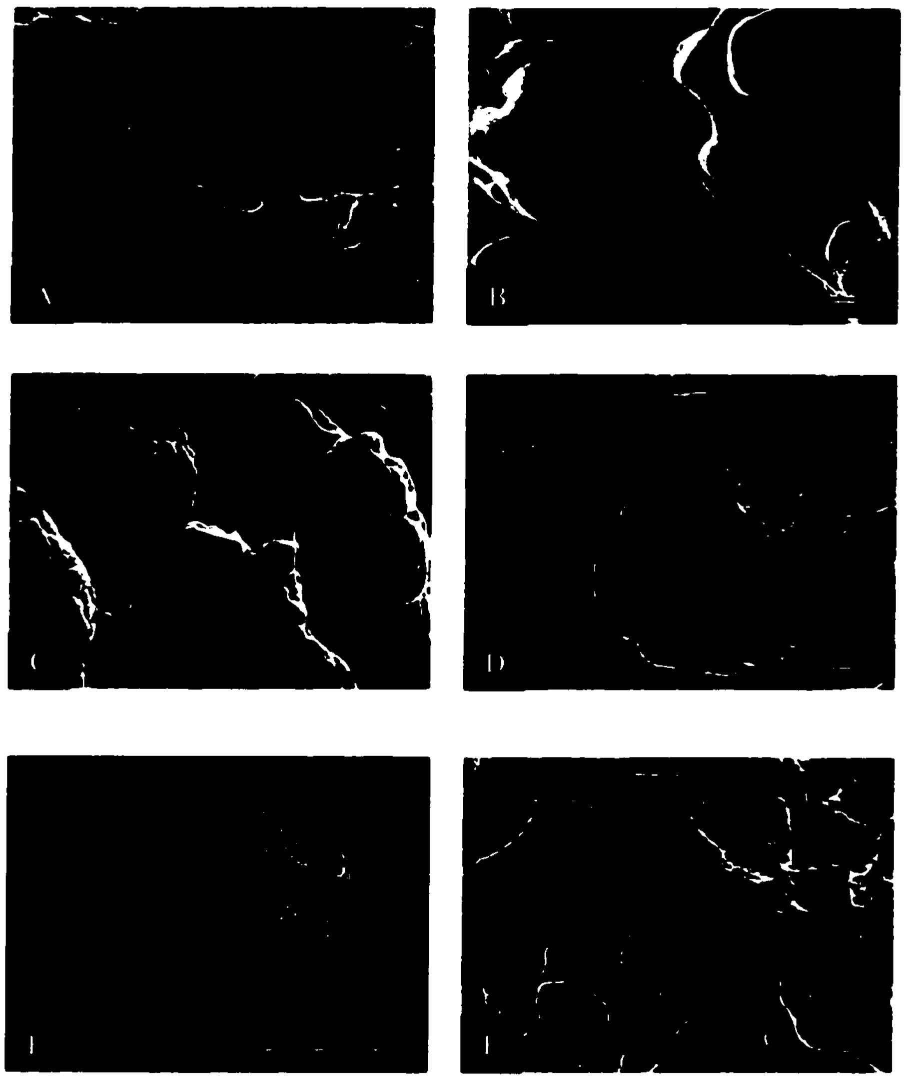


there are several small perforations in the orbicular wall. Since intermediate forms were observed in several species (e.g., R. kuhlmannii) the distinction between the two types is blurred.

The doughnut-shaped type corresponds to the orbicules reported by Huysmans et al. (1997) in Luculia gratissima (Wall.) Sweet (Cinchoninae, Rubiaceae), and by Vinckier et al. (2000) in Leptactina Hook. f., Pavetta L., and Tarenna Gaertn. (Pavetteae, Rubiaceae); however, orbicules in Retiniphyllum are larger. While in Retiniphyllum orbicules size ranges from 1.0 to 4.3 µm, in Luculia they are less than 0.5 µm (Huysmans et al., 1997), and the maximum size reported by Vinckier et al. (2000) in Leptactina, Pavetta and Tarenna is 1.66 µm.

The depression of the doughnut-shaped orbicules might be empty (e.g. R. rhabdocalyx, Fig. 14G) or might contain lipidic droplets of tapetal origin (e.g. R. maguirei, Fig. 14H). The size of the depression varies from a very small hole of 0.1 µm to a large depression of 2 µm; however, both types might occur in the same anther (Fig. 15A). The surface of the orbicules is smooth in most species (e.g. R. concolor, Fig. 15B) or minutely granular in some species (e.g. R. fuchsioides, Fig. 15C), and R. secundiflorum, Fig. 15D). No correlation was found between the

Fig. 15. SEM photomicrographs of orbicules and pollen grains of Retiniphyllum. **A.** R. laxiflorum (Maguire 28707), orbicules. **B.** R. concolor (Cortés 1646), orbicules. **C.** R. fuchsioides (Dudley 13175), orbicules. **D.** R. secundiflorum (Huber 3413), orbicules. **E.** R. pauciflorum (Wurdack 42752), pollen grain with an orbicule attached. **F.** R. discolor (Huber 6119), orbicules. Scale bars: A-D, F: 1 µm; E: 5 µm.



ornamentation of the pollen sexine and the surface texture of the orbicules (Fig. 15F).

The size of the orbicules in Retiniphyllum ranges from 1.0 to 4.3 μm. The smallest orbicules are found in R. pilosum (1.0-2.2 μm), and the largest in R. parvifolium, R. schomburgkii and R. secundiflorum, with orbicules up to 4.3 μm. Orbicule size might varies extensively in a single specimen as, for instance, in R. parvifolium (1.5-4.3 μm). Orbicules can be separated or fused. When fused, they might be in pairs or in aggregates of three or more orbicules (Fig. 15G).

Discussion

The presence of orbicules in all the species of Retiniphyllum confirms the hypothesis that orbicules are common in the Rubiaceae, although they have been usually overlooked in palynological studies (Huysmans et al., 1997). The survey of orbicules in the subfamilies Cinchonoideae (sensu Robbrecht, Huysmans et al. 1997), and Ixoroideae (sensu Robbrecht, Vinckier et al., 2000) found that most of the species evaluated possessed orbicules, and suggest that they may be systematically useful at the generic and tribal levels. However, at species level, as in

Retiniphyllum, the systematic value of orbicule morphology is limited and sometimes even variable within the same species.

1.3 Floral Biology

Secondary Pollen Presentation

One of the main characters used by Bremekamp (1934) used to define his subfamily Ixoroideae was what he called "ixoroid pollen mechanism", a phenomenon commonly known as secondary pollen presentation (SPP), or more specifically stylar pollen presentation. According to this mechanism, pollen is deposited from the anthers on the external portion of the unopened stigma and/or style before anthesis, and once the stigma elongates and the flower opens, pollinators transport the pollen to flowers with opened, receptive stigmas (Robbrecht, 1988). Usually this kind of flowers are two-day flowers, with the male stage on the first day (pollen presented on the stigma), and the female stage (receptive stigma) on the second day.

Robbrecht (1988) suggested SPP in the tribe Retiniphylleae, but Puff et al. (1996), in their detailed study of SPP in the Rubiaceae, did not confirm its presence because of a lack of direct observations. Only Rosero & Sazima (2002), in their study about the pollination biology of R. rhabdocalyx, confirmed the presence of SPP in the genus. They found that three species of hummingbirds forced-open the flower buds when looking for nectar, receiving a great quantity of pollen from the immature stigma, and depositing it onto the receptive stigmas of nearby plants. Rosero and Sazima (2002) found that the nectar is available from pre-anthesis to the third day of anthesis, and the stigma is receptive only starting from the second day of anthesis. They also reported that the life-span of the flowers of R. rhabdocalyx is of five days, and self-pollination test showed that the flowers of this species are self-incompatible.

According to my observations, when opening flower buds close to anthesis, the capitate portion of the style is at intimate contact with the anthers and heavily covered with pollen, while its medial portion is often sinuous and compressed within the flower bud. I observed this phenomenon in herbarium specimens of R. tepuiense, R. parvifolium, R. fuchsioides, and R. laxiflorum (Delprete, pers. comm.). Taking into account that the two first species have white flowers with short tubular corollas (probably bee-pollinated) and the two last species have red flowers with long-tubular corollas (hummingbird-pollinated), it seems that the mechanism of SPP might be present in most, if not in all, the species of Retiniphyllum.

Retiniphyllum is one of the few genera in Rubiaceae with apical and basal appendages. Igersheim (1993b) suggested that the apical appendages present in Vangueria Comm. ex Juss. and other genera in the tribe Vanguerieae, could be involved in reducing the chances of self-pollination. Genera in the Vanguerieae have prominent and specialized "stylar heads" acting as pollen presenters for the SPP mechanism. Igersheim observed that at bud stage, some species of Vanguerieae had early exposition of the stigmatic surfaces, and considered that the apical appendages created a protective cover. Considering that in R. rhabdocalyx the stigma is receptive only starting from the second day of anthesis, and that flowers are self-incompatible (Rosero & Sazima, 2002), the appendages clearly do not have the protective function suggested by Igersheim. Most likely, the role of the appendages is to create a chamber in which the capitate portion of the style is in close contact with the anthers when pollen is released. This chamber would have similar advantages of "stylar heads", hairs, ridges and grooves on the style, observed in genera of the Rubiaceae with SPP.

Agents of Pollination

Species with white and short- or long-tubular corollas are probably pollinated by insects, as indicated by the pollinator guides running through their tubes. The short-tubular corollas are most likely pollinated by bees. I have observed Euglossine bees visiting flowers of R. truncatum. At anthesis, the style curves slightly upwards and functions as a landing surface for the bees to visit each flower. Bees land on the well-exserted style and walk toward the corolla tube to gather the nectar produced by the disk. Because the pollen is transferred from style in male stage to style in receptive stage, it is not necessary for the bees to touch the anthers, which are fully reflexed over the corolla lobes at anthesis. Gunter Gerlach (per. comm.) observed Euglossine bees with this behaviour for the flowers of R. schomburgkii (Fig. 4D).

Species with long-tubular corollas are probably pollinated by butterflies, but this remains as an open question. This syndrome is present only in the sister species R. chloranthum and R. concolor. These species have pollen type I in which the pollen grains are oblong in outline and the lumina being shorter in the centre of the mesocolpium and increasing in diameter towards the poles. These characters are unique in the genus, and represent two synapomorphies for this clade. In addition, these species have the largest pollen grains found in the genus.

Species with red or dark pink and long-tubular corollas are more likely pollinated by hummingbirds. Rosero & Sazima (2002) recorded three species of hummingbirds pollinating R. rhabdocalyx: Phaethornis bourcieri, Thalurania furcata, and Chlorostilbon olivaresi. In addition, Delprete (pers. comm.) observed that flowers of R. laxiflorum were visited by Thalurania furcata.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

Retiniphyllum is a Neotropical genus with sixteen species endemic to the Guayana Shield, two endemic to the Brazilian Shield, and three that are widespread in both shields, and sporadically reaching the Amazon Region. The Guayana and Brazilian Shields are the oldest part of the South American continent, and they are divided by the geologically young Amazon basin. The Shields consist of a rock basement that was formed during Archean and Proterozoic times, while the Amazon Region was formed during the Cenozoic (Fig. 16). A species occurring outside the Shields is R. fuchsioides, found in Perú in uplands West of the Amazon region, near the Andean moutain range.

Most species of Retiniphyllum are restricted to lowlands (<500 m), while some are also found in uplands (500-1500 m), and two species occur in the highlands of the Guayana region above 1500 m (Pantepui Province). More than half of the species of Retiniphyllum grow in Río Negro caatinga forests, a formation widespread along the Río Negro basin (Huber, 1995) and dominant in the states of Guainía and Vaupés in Colombia, Amazonas in Venezuela, and North of the state of Amazonas in Brazil.

1.4. Systematic Treatment

Retiniphyllum Bonpl. in Humb. & Bonpl., Pl. aequin. 1:86, pl. 25. "1805" [1808]; Muell. Arg. in Mart., Fl. Bras. 6(5):6-14. 1881; Standl., Field Mus. Nat. Hist., Bot. Ser. 13: 113-114. 1936; Steyerm., Mem. New York Bot. Gard. 12(3): 178-285. 1965; Steyerm. in Lasser & Steyerm., Fl. Venez. 9:741-772. 1974. Type species. Retiniphyllum secundiflorum Bonpl.

Commianthus Benth., J. Bot. (Hooker) 3: 223. 1841.

Retiniphyllum sect. Commianthus (Benth.) Muell. Arg. in Mart., Fl. Bras. 6(5): 6. 1881. Type species. Commianthus schomburgkii Spruce ex Benth.

Retiniphyllum sect. Ammianthus Spruce ex Muell. Arg. in Mart., Fl. Bras. 6(5): 6. 1881. Ammianthus Spruce, nomen. (stat. confusum). Type species: Retiniphyllum pilosum Muell. Arg.

Shrubs or small **trees**. **Stipules** interpetiolar, connate at base, sheathing, truncate or triangular, splitting at one side or not; margin entire, rarely lobulate, serrulate or laciniate; coriaceous or papyraceous; glabrous or pubescent outside, glabrous and with colleters throughout or at base inside, persistent or caducous, sometimes dimorphic. **Leaves** petiolate, rarely sessile; blades elliptic, ovate, obovate, lanceolate or oblanceolate; cuneate, attenuate or acute at base; caudate, acuminate, apiculate, mucronulate, obtuse, acute, rounded or retuse at apex; coriaceous, chartaceous or papyraceous; pubescent or glabrous; secondary venation brochido- or eucamptodromous; tertiary veins random reticulate; domatia absent or ocasionally pocket-shaped. **Inflorescences** terminal or axillary, erect or exceptionally pendulous; racemose, spicate or umbellate, with or without bracts subtending the most basal pair of flowers. **Bracteoles** subtending flowers, reduced or foliose, glabrous or pubescent, with or without colleters inside. **Involucel** subtending each flower, falling off with the fruit or persistent on the rachis, discoid or cupular, margin lobulate, toothed, undulate or truncate; glabrous or pubescent, with or without colleters inside. **Flowers** 5-merous, bisexual, protandrous, sessile or pedicellate. **Calyx** cupular or tubular, actinomorphic, truncate or lobulate, glabrous or pubescent, with or without colleters inside, persistent, green, dark pink or red. **Corolla** hypocrateriform, actinomorphic or zygomorphic, white, greenish-white and tinged with light pink, dark pink or red; lobes reflexed at anthesis, shorter, longer or same size of corolla tube, oblong or lanceolate, acute or rounded at apex, sericeous throughout, aestivation contorted to the left; tube infundibuliform or cylindrical, pubescent or less often glabrous outside, with a ring of hairs near the base or at mouth inside, glabrous below and pubescent above. **Stamens** 5, exerted well above the corolla, reflexed on the lobes at anthesis, attached near the mouth of the corolla tube; filaments complanate, expanded at base, pubescent or rarely glabrous; anthers elliptic, lanceolate or oblong, dorsifixed near the base, dehiscing by longitudinal slits, with basal appendages oblong and truncate, with apical appendages narrowly triangular, with orbicules on the tapetum. **Pollen** 3-colporate; sexine reticulate, microreticulate or tectate-perforate. **Style** exserted well beyond the corolla, terete, rarely with ridges, pubescent at medial portion, glabrous basally and distally; distal portion capitate, ellipsoid, or globose before style branches opening; style branches 5, recurved at maturity. **Ovary** inferior, commonly 5-locular, rarely 4-, or 6-8-locular, turbinate, narrowly obconical, globose, cylindrical, rarely oblate or longitudinally ellipsoid, glabrous or pubescent, placentation axile; ovules two per locule, collateral, pendulous and attached along the septa either at distal, medial, or basal portion. **Fruits** drupaceous, globose, transversally or longitudinally ellipsoid, glabrous or pubescent, fleshy, red at maturity and aging in dark purple. **Pyrenes** commonly five, rarely four, six or eight, reniform, with or without wings, perforation in the ventral side, preformed germination slit along their outline. **Seeds** one per pyrene due the abortion of one ovule (the aborted ovule remaining attached to the mature seed), or rarely two per pyrene (both ovules develop), reniform or cylindrical, attached at top or at center of the septum.

The phylogenetic analysis using a combined data set of morphological and molecular (ITS) data showed that the three sections proposed by Müller Argoviensis (1881) are not monophyletic (Fig. 48). The three species of sect. Retiniphyllum (R. chloranthum, R. concolor, and R. secundiflorum) are placed in two different clades, and the single species of sect. Ammianthus (R. pilosum) is placed in the same clade with species of the sect. Commianthus. Two groups within Retiniphyllum are clearly delimited. One including the species with spicate inflorescences, and another including R. chloranthum and R. concolor. Until a better sampling inside the clade with racemose and umbellate inflorescences is performed, I prefer not to recognize any subgeneric or sectional ranks within Retiniphyllum in this study.

Distribution and Ecology: Retiniphyllum is a Neotropical genus, always associated to white-sand soils, with sixteen species endemic to the Guayana Shield, two endemic to the Brazilian Shield, and three present on both shields (Fig. 16). The widespread species are also found in the Amazon Region. A species occurring outside the shields is Retiniphyllum fuchsioides, found in Perú in the uplands West of the Amazon region. Most species of Retiniphyllum are restricted to lowlands (75-500 m), while some are also found in uplands (500-1500 m), and two species occur in the highlands of the Guayana region above 1500 m (Pantepui Province, sensu Berry et al., 1995). More than half of the species of Retiniphyllum grow in Río Negro caatinga forests, a formation widespread along the Río Negro basin (Huber, 1995) and dominant in the states of Guainía and Vaupés in Colombia, Amazonas in Venezuela, and northern portion of the Amazonas in Brazil.

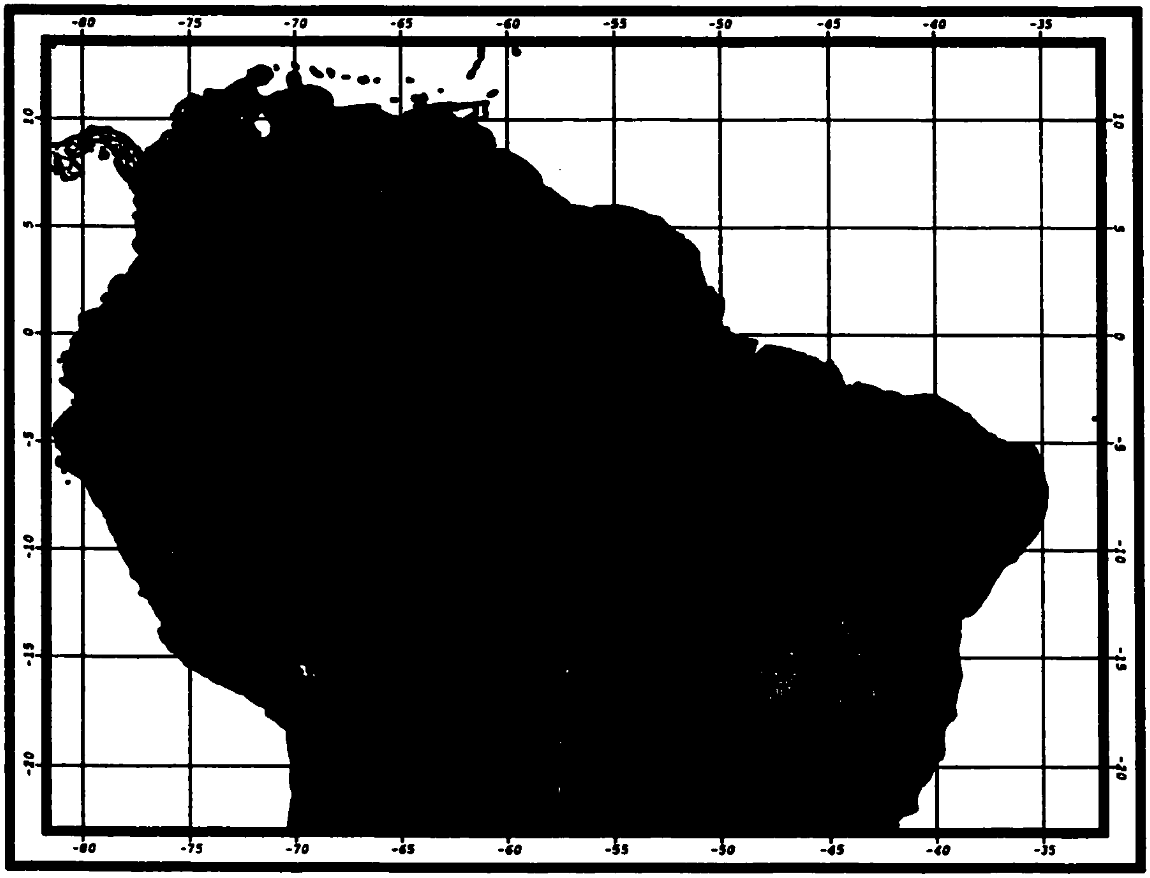


Fig. 16. Geologic map of South America with the geographical distribution of Retiniphyllum.

Key to the species of Retiniphyllum

1. Flowers pedicellate

    2. Inflorescence umbellate

        3. Involucel, pedicel and calyx pubescent; pyrenes with two lateral wings; seeds cylindrical, inserted at top of the septum............................17. R. scabrum

        3. Involucel, pedicel and calyx glabrous; pyrenes without wings; seeds reniform, inserted at the middle of the septum...........14. R. pauciflorum

    2. Inflorescence racemose

        4. Corolla white, greenish-white and sometimes tinged with light pink

            5. Calyx cupular, wider than long; corolla tube more than 10 mm long; pyrene surface smooth

                6. Involucel lobulate; pyrenes with two lateral wings.........2. R. chloranthum

                6. Involucel truncate; pyrenes without wings ....3. R. concolor

5. Calyx tubular, longer than wide; corolla tube less than 10 mm long; pyrene surface verrucate

7. Calyx hirsutulous or hispidulous; corolla lobes more than 4/5 of tube length; fruit globose; pyrenes with two lateral wings..........21. R. tepuiense

7. Calyx glabrous; corolla lobes less than 4/5 of tube length; fruit transversally ellipsoid; pyrenes without wings..........1. R. cataractae

4. Corolla red or dark pink

8. Bracteoles foliose, more than 2 mm long

9. Stipules more than 7 mm long; inflorescences terminal, pendulous; involucel papyraceous; pyrenes smooth with two lateral wings.................................6. R. fuchsioides

9. Stipules less than 7 mm long; inflorescences axillary, erect; involucel coriaceous; pyrenes verrucate, with a very reduced longitudinal rib at each side..............19. R. secundiflorum

8. Bracteoles reduced, less than 2 mm long

10. Stipules triangular, more than 4 mm long; inflorescence axillary ....5. R. francoanum

10. Stipules truncate, less than 2 mm long; inflorescence terminal

11. Calyx cupular, less than 2 mm long; involucel discoid ....11. R. longiflorum

11. Calyx tubular, more than 2 mm long; involucel cupular

12. Pedicels less than 3.5 mm, lobes/tube ratio more than 4/5......12. R. maguirei

12. Pedicels more than 5 mm long; lobes/tube ratio less than 4/5....10. R. laxiflorum

1. Flowers sessile

13. Corolla red or dark pink, tube more than 10 mm long

14. Leaves less than 10 cm long; flowers actinomorphic

15. Corolla shorter than 28 mm long; fruit transversally ellipsoid.......4. R. discolor

15. Corolla longer than 29 mm long; fruit globose........................7. R. glabrum

14. Leaves more than 10 cm long; flowers zygomorphic

16. Corolla tube 15-20 mm long; calyx with conspicuous vascular bundles ....20. R. speciosum

16. Corolla tube 20-32 mm long; calyx without conspicuous vascular bundles ....16. R. rhabdocalyx

13. Corolla white, greenish-white and tinged with light pink, tube less than 10 mm long

17. Leaves, stipules and rachis pubescent

18. Stipules oblong or ovate, 15-30 mm long, papyraceous; bracteoles foliose, more than 4 mm long; involucel lobulate, papyraceous; pyrenes with two lateral wings, surface smooth..................15. R. pilosum

18. Stipules truncate, up to 3 mm long, coriaceous; bracteoles reduced, less than 2 mm; involucel truncate, coriaceous; pyrenes without wings, dorsally verrucate

19. Leaves pubescent below; petiole longer than 5 mm; calyx glabrous ....18. R. schomburgkii

19. Leaves glabrous below; petiole shorter than 5 mm; calyx pubescent ....13. R. parvifolium

17. Leaves, stipules and rachis glabrous

20. Calyx more than 4 mm, glabrous; pyrene surface smooth...............8. R. guianense

20. Calyx less than 4 mm, pubescent; pyrene surface dorsally verrucate

21. Rachis less than 2 mm thick; ovary globose, not costate; fruit globose ....9. R. kuhlmannii

21. Rachis more than 2 mm thick; ovary longitudinally ellipsoid, costate; fruit longitudinally ellipsoid ....22. R. truncatum

1.4.1. Retiniphyllum cataractae Ducke, Arq. Inst. Biol. Veg. 4(1): 62. 1938. Type. Brazil. Amazonas: Rio Curicuriary (affl. of Rio Negro), 21 Feb 1936 (fl, fr), Ducke s.n. (RB 35067) (holotype, RB-n.v.; isotypes, G, NY, U, US). Fig. 17

Shrubs up to 4.5 m tall. **Leafy branchlets** terete, 1.3-3.2 mm thick, strigose. **Stipules** sheathing, strigose outside, glabrous and with colleters throughout or at base inside, dimorphic, in some branches truncate or lobulate, 1.4-1.8 mm long, coriaceous, lobes broadly triangular up to 0.2 mm, persistent; on some other branches splitting on one side, broadly triangular, acute at apex, 6.5-16 mm long, papyraceous, subcaducous. **Leaves** petiolate; petioles 2.5-9 mm long, 1-1.5 mm thick, strigose; blades 3.5-8.3 x 1.3-2.6 cm, L/W 2.7:1-4.8:1, elliptic-lanceolate, oblanceolate, elliptic or subovate, cuneate at base, acute or rounded at apex, coriaceous, strigose throughout, brownish or olive green when dry; primary, secondary and tertiary veins strigose below; secondary venation weak broquidodromous, 8-12 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, short-racemose, 5-9 flowered, erect, 2-4 cm long; rachis terete, 0.2 mm thick, glabrous, with or without two foliose bracts at base, 7-13 mm. **Bracteoles** reduced, 0.2-0.3 mm, margin entire, glabrous, with colleters inside. **Involucel** discoid, 0.5 x 1.3 mm, with small teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers**

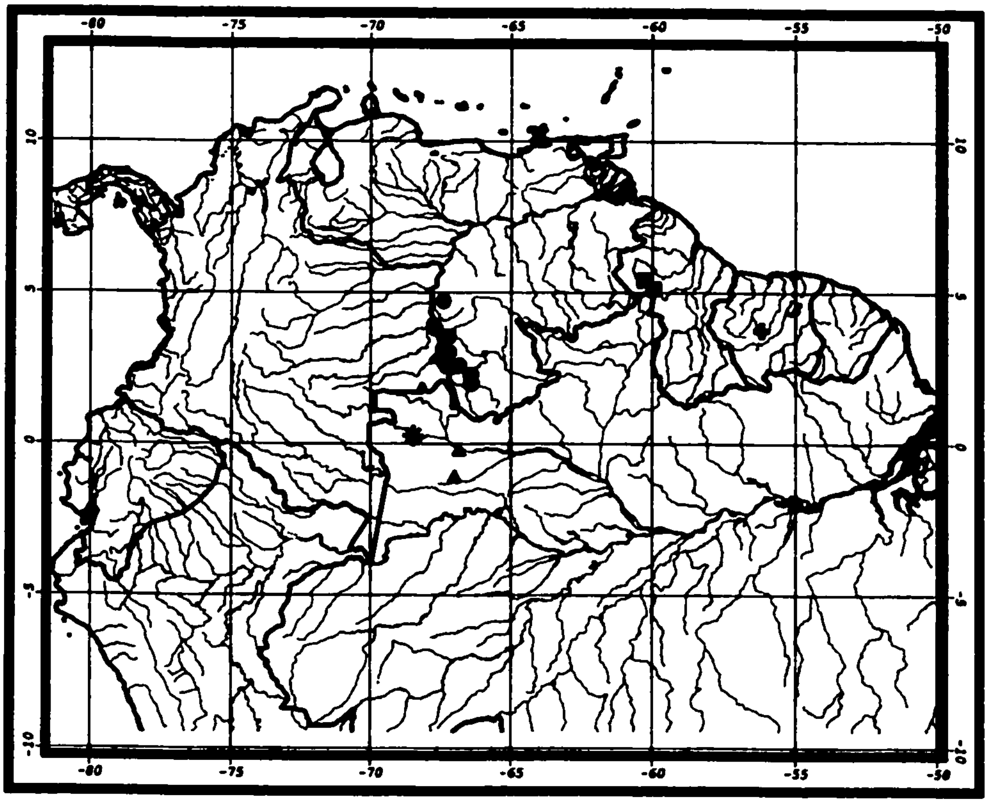


Fig. 17. Distribution of *Retiniphyllum cataractae* (▲) *R. guianense* (■), *R. longiflorum* (✱), *R. maguirei* (✚), and *R. pauciflorum* (●).

actinomorphic, pedicellate; pedicels 1-3.5 x 0.5-0.9 mm, glabrous. **Calyx** tubular, with small lobes, 2-4 x 2.5-3 mm, glabrous outside, rarely with few hairs distally, glabrous and with colleters inside; lobes up to 0.2 mm long, rounded at apex, with a colleter at tip, glabrous. **Corolla** 11.2-14 mm long; tube infundibuliform, 5.7-7 mm long, 2-2.5 mm wide at base, 1.5-1.8 mm wide at mouth, glabrous at base, sericeous above base outside, with a ring of hairs at distal portion, 1.2-1.5 mm wide at 3-3.5 mm from base, glabrous below ring, white; lobes 1/2-2/3 of tube length, 5.6-7.4 x 2-2.3 mm, oblong or lanceolate, acute or rounded at apex, sericeous throughout, white. **Filaments** 3.2-4.5 mm long, 0.2-0.3 mm wide, laterally compressed, expanded at base, sparsely pilose at edges or rarely throughout; anthers elliptic, 1.8-2.2 x 0.3-0.4 mm; basal appendages oblong, 0.2-0.3 mm long, truncate at base; apical appendages narrowly triangular, 0.2-0.3 mm long. **Pollen** subprolate; sexine microreticulate. **Style** 12-12.8 x 0.2-0.3 mm, sparsely pilose at basal and medial portions, glabrous distally, capitate portion ellipsoid before branches opening, style branches narrowly triangular, 0.2-0.3 x 0.1 mm. **Ovary** 5-locular, turbinate, 4-5.9 x 2.5-3.1 mm, glabrous. **Fruit** transversally elliptic, 4-7 x 3-4.6 mm, glabrous. **Pyrenes** 4.6 x 1.8 mm, surface verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.8-3.2 x 0.9-1.1 mm.

Distribution (Fig. 17) **and ecology.** Known only from two collections in NW Brazil, in the state of Amazonas.

According to Ducke (1938), this species is frequent in the "catingas" (Rio Negro caatinga forests sensu Huber, 1995) near cataracts, hence its specific epithet. Flowering and fruiting specimens were collected in February.

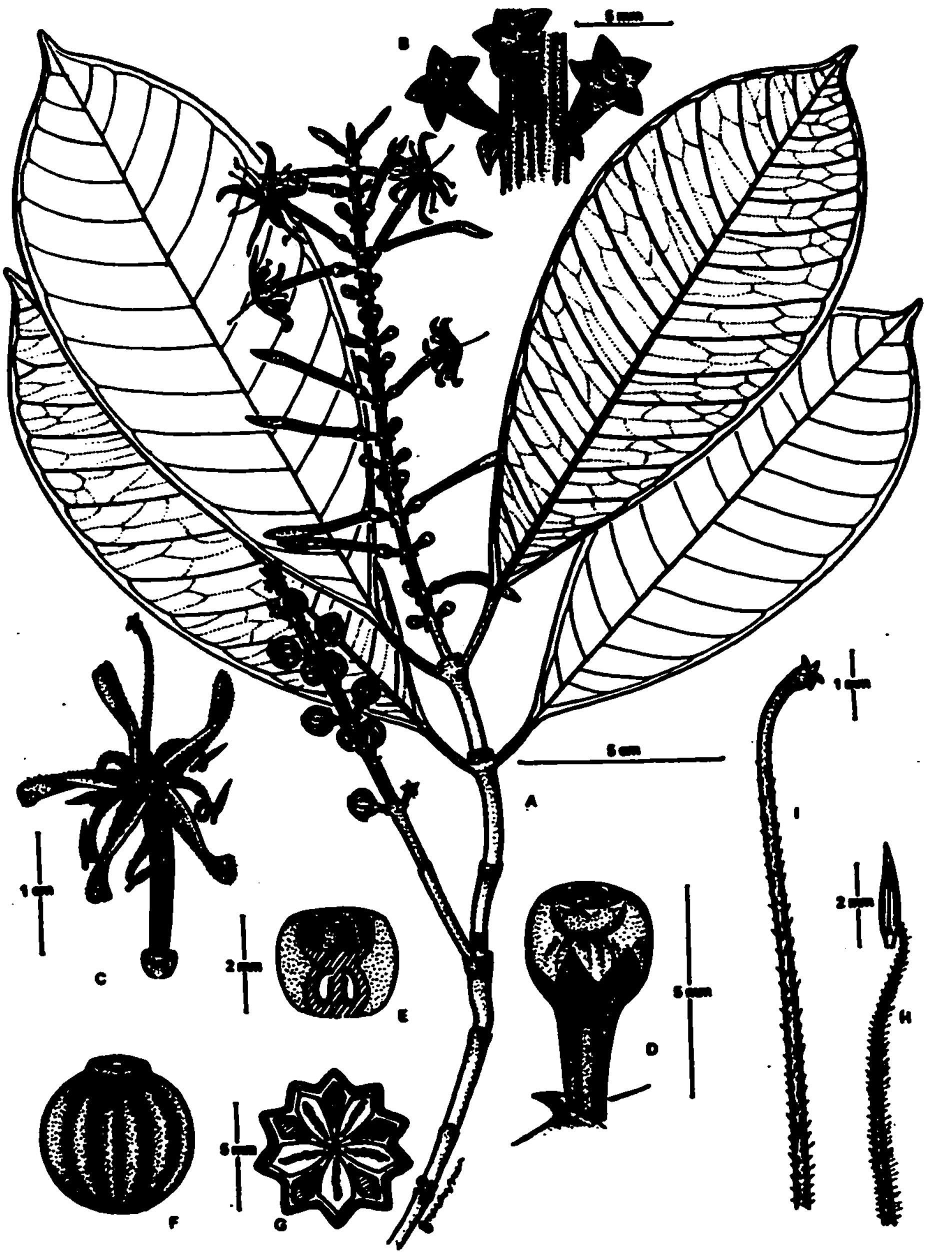
Additional specimen examined. BRAZIL. Amazonas: Rio Negro, Enuixy [Uneiuxi], Lago Dondona, 18 May 1947, Fróes 22349 (VEN).

Retiniphyllum cataractae is vegetatively similar to *R. pauciflorum*, and differs from it in having short-tubular, white corollas (vs. long-tubular, red corollas in *R. pauciflorum*), and shorter calyx, corolla, filaments and style. An additional difference is the inflorescence architecture: although apparently umbellate, the inflorescence of *Retiniphyllum cataractae* has a reduced rachis while in *Retiniphyllum pauciflorum* the rachis is absent.

1.4.2. Retiniphyllum chloranthum Ducke, Trop. Woods 76: 31. 1943. Type. Brazil. Amazonas: Mun. Manaus, Rio Tarumá-Mirim, 4 Jul 1941 (fl, fr), Ducke 1143 (holotype, RB-n.v.; isotypes, NY, R, US). Figs. 1A-C, 3B,F, 7A,F, 9C, 11A, 18, 19

Shrubs to **small trees** up to 10 m tall. **Leafy branchlets** terete, 3.5-4.8 mm thick, glabrous. **Stipules** sheathing, truncate, 2-4 mm long, coriaceous, glabrous outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate; petioles 13-30 mm long, 2-3 mm thick, glabrous; blades 13-30 x 6-14.5 cm, L/W 1.8:1-3:1, obovate or elliptic, cuneate or acute at base, short-acuminate at apex, with an acumen up to 1.2 cm long, coriaceous, glabrous above, margin with or without strigose hairs, hirtellous or glabrous below, dark green and opaque above, pale green and glossy or opaque below, brown or greenish when dry; primary and secondary veins hirtellous or glabrous below; secondary venation brochidodromous, 14-21 veins each side, tertiary veins random reticulate; domatia absent or rarely pocket-shaped. **Inflorescences** terminal, racemose, erect, 6-19 cm long; rachis ridged,

Fig. 18. Illustration of Retiniphyllum chloranthum. A. Habit of inflorescence with leaves. B. Bracteoles and involucels. C. Flower. D. Immature fruit covered with resin. E. Ovary and Calyx. F. Fruit. G. Transvesal seccion of a fruit showing five pyrenes.


5 mm
B
1 cm
5 cm
A
C
2 mm
E
5 mm
D
I
2 mm
H
F
5 mm
G

2-6.2 mm thick, glabrous, with a stipular collar and two bracts subtending the basal pair of flowers, 2-2.5 mm long, rarely resembling small leaves, up to 10 mm long, portion of rachis from first pair to next flowers 0.8-2 cm; peduncle 1.4-3.5(-5) cm long. **Bracteoles** reduced, 0.7-2 mm long, margin 3-lobate, glabrous, verrucose, with colleters inside. **Involucel** discoid, 1.2-2 x 2.2-3 mm, 5-lobulate, lobes broadly triangular, 0.5-2.5 x 0.8-1.5 mm, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, portion with lobes bent downward. **Flowers** zygomorphic, pedicellate; pedicels 1.4-3 x 0.6-1.5 mm, glabrous. **Calyx** cupular, truncate, with small teeth or small lobes, 0.8-1 x 1.8-2.9 mm, glabrous or hirtellous, verrucose outside, glabrous and with colleters throughout inside, lobes 0.2-0.3 x 0.9-1 mm, broadly triangular, glabrous or hirtellous, greenish. **Corolla** 16-27 mm long; tube cylindrical, (8.5-)10-19 mm long, 0.7-1.3 mm wide at base, 1.8-2 mm wide at mouth, glabrous or minutely puberulent outside, with a ring of hairs at basal portion, 0.5-1 mm wide at 4-4.5 mm from base, glabrous below ring, tomentose above ring inside, white throughout with five longitudinal lines pale pink; lobes 2/5-3/4 of tube length, 5.5-8.5 x 1.5-2 mm, narrowly oblong, round at apex, sericeous throughout, left half of the lobe light pink, and right half white. **Filaments** 5-6.2 mm long, 0.25-0.4 mm wide, expanded at base, hirsute throughout; anthers lanceolate, 1.5-2.2 x 0.3-0.5 mm; basal appendages oblong, 0.3-0.5 mm long, truncate at base; apical appendages narrowly triangular, 0.2-0.3 mm long. **Pollen** subprolate or prolate; sexine reticulate. **Style** 18-25 x 0.3-0.4 mm, hirsutulous at base and medial portion, glabrous distally; capitate portion globose before branches opening, style branches narrowly triangular, 0.2-0.5 mm long. **Ovary** 5-locular, narrowly obconical, 0.8-0.9 x 1-1.2 mm, glabrous. **Fruit** globose, 10-ribbed, 5-9.2 x 4.2-7 mm, glabrous, red. **Pyrenes** 5.2-5.5 x 1.8-3.0 mm, surface smooth, with two perpendicular wings inserted near the dorsal margin. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 3.1-4.3 x 0.7-1.4 mm.

Distribution (Fig. 19) **and ecology.** Widespread in the Guayana Region, commonly found in caatinga forests and shrublands throughout the Rio Negro basin, at low elevations, in Brazil, Colombia and Venezuela. Found also in basimontane and submontane forests of Cerro Duida (from 120 to 1000 m) and Cerro La Neblina (from 140 to 780 m) in the state of Amazonas in Venezuela. Widespread in the state of Bolívar, Venezuela, it is found from the Gran Sabana

(500 m), to the summit of Guaiquinima (730 m). In the Chimantá Massif, it is found from uplands (400-1100 m) to highlands at the summit of Apacará. There is no indication of the elevation of the Apacará-tepui collection, but considering that its maximum elevation is at 2450 m, the collection was probably made at ca. 2000 m. This species is also found in uplands between 450-650 m at The Pakaraima Mountains in Guyana, in the Venezuela-Guyana border. Flowering specimens were collected in all the months of the year. Fruiting specimens were collected in all the months, except for January and July.

Additional specimens examined. BRAZIL. Amazonas: Between Rio Marié and Morro Ximaio, 0°45-50'S, 60°50'W, 07 Jul 1979 (fl), Poole 1908 (GH, NY); Rio Negro, Tapuruquara-mirim, L margin of Rio Marié, 17 Oct 1978 (fl, fr), Nascimento 615 (NY); left margin of Rio Negro, Tapuruquara-mirim, Rio Marié, 16 Oct 1978 (fl), Nascimento 662 (NY); Rio Negro, caatinga at mouth of Rio Marié, 16 Oct 1978 (fr), Madison et al. 6329 (US); Rio Negro, Río Curicuriari, 18 May 1973, Silva et al. 1689 (US); Coari, 21 Sep 1976 (fl, fr), Bahia 123 (NY); Jaú National Park, Campina do Pataué, 29 Jun 1997 (fr), Ferreira 66 (INPA); Manacapuru, margin of Lago Grande, 08 Oct 1976 (fl), Bahia 209 (US); Manaus-Caracaí rd, km 125, 20 Feb 1979 (fl), Coêlho et al. 929 (BM, NY).

COLOMBIA. Amazonas: Mun. Leticia, Río Caquetá, Inspección Santa Isabel, 12 km NE of Santa Isabel, 300-400 m, 09 Apr 1994 (fr), Cárdenas & Gangi 4628 (MO); Río Miritiparaná, Cerro de la Gente Chiquita, headwaters of Quebrada Guacayá, 18-19 May 1952 (fl, fr), Schultes & Cabrera 16494 (GH, US); Río Miritiparaná, Cerro de la Gente Chiquita, headwaters of Quebrada Guacayá, 18-19 May 1952 (fr), Schultes & Cabrera 16537 (F, GH). **Guainía:** Cerro Caño

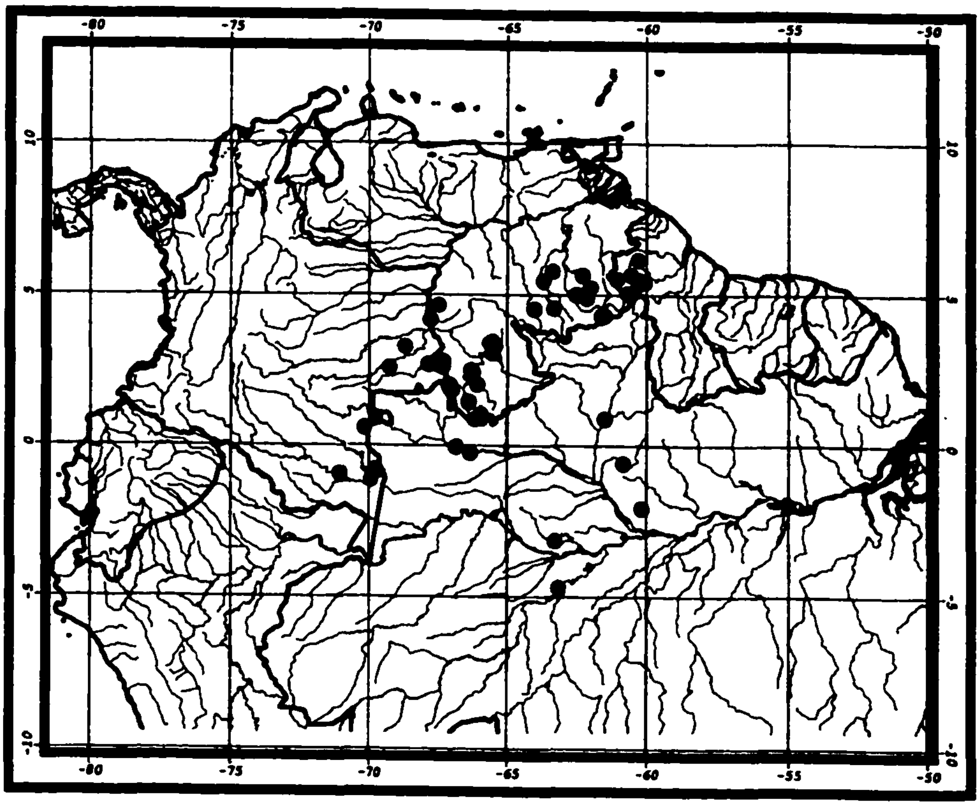


Fig. 19. Distribution of *Retiniphyllum chloranthum*

Minas, 2°38'N, 69°14'W, 300 m, Córdoba et al. 126 (COL); Río Inírida, Chorro Bocón, 01 May 1980 (fr), Triana 106 (COL). **VAUPÉS:** Río Guainía, Caño del Caribe (between Isla del Venado and San José) and vicinity, 2°45'N, 67°50'W, 259-274 m, 2 Nov 1952 (fr), Schultes et al. 18255 (GH, US); Río Negro, San Felipe and vicinity (below confluence of Río Guainía and Río Casiquiare), 1°50'N, 67°0'W, 183 m, without date (fl), Schultes et al. 18244 (F, US); Río Paca (tributary of Río Papurí), Wacaricuara and vicinity, 0°30'N, 70°10'W, 198 m, 1-3 Jun 1953 (fr), Schultes & Cabrera 19560 (US); Serrania de Taraira, 10 km NW of Raudal de la Libertad, 0°53'N, 69°45'W, 250 m, 23 Aug 1993 (fr), Rodríguez 133 (COL); Serrania de Taraira, 10 km NW of Raudal de la Libertad, 0°58'S, 69°45'W, 250 m, 31 Jul 1993 (fl), Cortés & Rodríguez 668 (COL, NY); trail from Río Vaupés to Cerro Mitú, 200-300 m, 31 Mar 1970 (fr), Soejarto & Lockwood 2483 (COL).

GUYANA. Along Waruma trail, 5-10 km upstream of Kako River, 5°18'N, 60°40'W, 650 m, 12 Feb 1989 (fr), Hahn & Gopaul 5311 (MO); Karowrieng River, between Maipuri Falls and 4 km downstream, 5°40'N, 60°15'W, 550-570 m, 27 Dec 1989 (fr), Gillespie & Smart 2899 (MO, NY, US); Pakaraima Mts., 0.5 km SW of upper Mazaruni River, at rapids near gorge opening, 5°37'N, 60°17'W, 600-650 m, 11 Oct 1992 (fr), Hoffman et al. 2900 (MO); Pakaraima Mts., base camp 8.6 km NE Imbaimadai on Partang River tributary, 0.5 km E, 5°46'N, 60°15'W, 600 m, 20 May 1992 (fr), Hoffman et al. 1742 (MO); Pakaraima Mts., upper Mazaruni River Basin, Karowrieng River, above Maipuri Falls, 5°42'N, 60°03'W, 550 m, 12 Jun 1986 (fr), Pipoly & Alfred 7616 (MO, NY, US); Mt. Membaru, 5°57'N, 60° 33-34'W, 450 m, 12 Nov 1979 (fl), Maas & Westra 4272 (K[2], MO, NY); Paruima Falls to Paruima Mission, 600 m, 08 Nov 1951 (fr), Maguire & Fanshawe 32464 (NY); low bog-forest bordering Maokay-dai savannah near mouth Mokay River, 490 m, 09 Sep 1960 (fl, fr), Tillet & Tillet 45349 (NY).

VENEZUELA. AMAZONAS: 2 km E of San Carlos de Río Negro. Ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 120 m, 07 Apr 1979 (fl), Liesner 6360 (MO, VEN); 2 km E of San Carlos de Río Negro. Ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 120 m, 07 Apr 1979 (fr), Liesner 6326 (MO, VEN); along Caño San Miguel, just above Limoncito, 15 km from Río Guainía, 100-140 m, 28 Jun 1959 (fl, fr), Wurdack & Adderly 43234 (G, NY, US); along the rd. between Yavita and Pimichín, 1 km from Yavita, 2°55'N, 67°25-30'W, 125 m, 21 Apr 1970 (fl), Steyermark & Bunting 102875 (K, US); around Remo Campament, May 1989 (fl), Foldats & Velazco 9596 (NY); ca. 1 km E of Colón by the Río Guainía, 2°2'13"N, 67°6'14"W, 120 m, 30 Mar 2000 (fr), Berry & Aymard 7422 (MO); Capihuara, upper Río Casiquiare, 120 m, 26 May 1942 (fr), Williams 15556 (F[2], US); Cerro de La Neblina, Río Yatua, 650-700 m, 23 Dec 1953 (fl, fr), Maguire et al. 36824 (NY); Cerro Duida, southeastern-facing slopes along Caño Negro (tributary of Caño Iguapo), 305-1095 m, 25 Aug 1944 (fr), Steyermark 57947 (F, NY); Dpto. Atabapo, 15 km N from Esmeralda, between Río Iguapo and SE side of Cerro Duida, 3°19'N, 65°31'W, 300 m, 08 Mar 1980 (fl), Huber 5067 (NY, VEN); Dpto. Atabapo, between Duida and Marahuaca, near base of Duida, 3°34'N, 65°32'W, 1000 m, 27 Oct 1988 (fr), Liesner 25490 (MO); Dpto. Atabapo, La Esmeralda, 5 km N of village, 3°10'N, 65°33'W, 106 m, (fl), Coomes 209 (K); Dpto. Atabapo. Río Negro Forest, affluent of Cunucunuma, N side of Duida, 01 Apr 1990 (fl), Fernandez 7638 (MO); Dpto. Atures, 110 km up from Río Guayapo, 01 May 1989 (fr), Foldats & Velazco 9317 (NY); Dpto. Atures, L margin of Caño Cabeza de Manteco, affluent of Río Autana, in Raudal Manteco, 4°52'N, 67°27'W, 100-120 m, 10 Nov 1984 (fr), Guanchez & Melgueiro 3470 (MO, VEN); Dpto. Atures, edge of Lagoon below Raudal de Ucata, above town of San Juan de Ucata, 4°20'25"N, 67°44'12"W, 120-150 m, 20 Jun 1992 (fr), Berry et al. 5164 (MO); Dpto. Casiquiare, Río Casiquiare, Laguna del Paciba and vicinity, 08 Feb 1991 (fl), Collela et al. 1895 (NY); Dpto. Río Negro, 0.5-1.5 km SE of Cerro de la Neblina Base Camp which is in Rio Mawarinuma, 0°50'N, 66°10'W, 140 m, 21 Feb 1984 (fl), Liesner 16164 (MO, NY, US, VEN); Dpto. Río Negro, Cerro de la Neblina Camp. IV, 15 km NNE of Pico Phelps, 0°51'N, 65°57'W, 780 m, 15-18 Mar 1984 (fl), Liesner 16714 (MO, NY, US); Dpto. Río Negro, lower Río Guainia, raudal lombríz. 2 km of mouth of Río Casiquiare, 2°2'N, 66°05'W, 140 m, 26 Nov 1992 (fr), Aymard et al. 9753 (MO); Dpto. Río Negro, Río Varía, 1°25'N, 66°24'W, 90 m, 01 Apr 1991 (fl, fr), Velazco 1761 (MO); Dto. Alto Orinoco, La Esmeralda, forest between La Esmeralda and the Cerro Duida, approx. 2 km from La Esmeralda, 3°10'N, 65°33'W, 120 m, 12 Feb 1995 (fr), Zimmermann et al. 78 (MO, VEN); IVIC study area, 4 km E of San Carlos de Río Negro, 1°56'N, 67°4'W, 120 m, 10 Nov 1977 (fr), Liesner 3279 (MO, VEN); Maroa, Río Guainía, 127 m, 02 Sep 1942 (fl), Williams 14192 (F); Río Guainia, just S of Maroa, 120-140 m, 28 Nov 1953 (fl), Maguire et al. 36454 (NY, US, VEN); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 06 Apr 1978 (fl, fr), Clark 6599 (NY, VEN); San Carlos de Río Negro, vicinity of airport, 125 m, 17-18 Apr 1970 (fr), Steyermark & Bunting 102758 (MO, NY, US); San Carlos de Río Negro., ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, IVIC main study site, 4.3 km NNE on Solano rd, 1°56'N, 67°03'W, 119 m, 25 Aug 1981 (fl), Clark & Maquirino 8191 (COL, MO); Savanna at Budare on S of Río Temí, above Yavita, 2°52'15"N, 67°18'30"W, 110 m, 25 Nov 1995 (fr), Berry et al. 5635 (MO); vicinity of Cerro Neblina base camp on Río Mawarinuma, 0°50'N, 66°10'W, 140 m, 26 Nov 1984 (fr), Croat 59328 (MO). BOLIVAR: 17 km E of El Pauji by rd., 64 km W of Santa Elena by rd., 4 km N of highway, Río Las Ahallas, 4°30'N, 61°30'W, 850 m, 28 Oct 1985 (fr), Liesner 19059 (MO); 3 km S of El Pauji, 4°30'N, 61°30'W, 900 m, 08 Nov 1985 (fl, fr), Liesner 19713 (VEN); 4 Km W of El Pauji, 2 to 5 km N of rd., Río Chaberu, 4°30'N, 61°36'W, 750-900 m, 12 Nov 1985 (fr), Liesner 19922 (MO, NY); Chimantá Massif, along Río Tirica (Río Aparuren) just above Techine-Meru, 427 m, 16 Jan 1955 (fl), Steyermark & Wurdack 128 (F[2], NY[2], US, VEN); Chimantá Massif, along trail between camp 2 and camp 3, NW of Abacapa-tepui, 750-1100 m, 05 Apr 1953 (fr), Steyermark 74845 (COL, F[2], NY[2], VEN); Dto. Heres, central base of Guaiquinima-tepui, along quebrada El Trueno, 90 km S of Paragua, 6°4'N, 63°22'W, 500 m, 12 May 1987, Aymard 5812 (MO, NY, VEN); Dto. Piar, 2 to 5 Km W of Amaruay-tepui, Guarumo, 5°56'N, 62°17'W, 470 m, 04 May 1986 (fl), Liesner & Holst 20600 (MO, NY); Gran Sabana, W side, Canaima National Park, Isla Raton, Junction Río Auyán and Río Churum, 500 m, 26-31 Aug 1994 (fl), Delascio 16112 (VEN); Río Caura, ca. 2 km down Caño Guacamaya (Guaya), 4°44'N, 64°01'W, 13 Apr 1988 (fl), Stergios 12076 (NY); Sierra Ichun, N of salto Maria Espuma (Salto Ichun), along Río Ichun, 4°46'N, 63°18'W, 625-725 m, 27 Dec 1961 (fr), Steyermark 90254 (NY, VEN); summit of Cerro Apacará, Río Canorí, 08 Jul 1946, Cardona 1602 (US, VEN); summit of Cerro Guaiquinima, along the affluent of Río Carapo, 1 km up the river of Salto Szczerbanari, SE side of the mountain, 5°44'4"N, 63°41'8"W, 730-750 m, 23-24 May 1978 (fr), Steyermark et al. 117217 (MO, VEN).

Local names. Colombia: o-ñó-ka (Tanimuka, Schultes & Cabrera 16494), ka-hoon-chá (Yukuna, Schultes & Cabrera

16494). Venezuela: Kitak-yei (Delascio 16112), palo de cogollo de piedra (Velazco 1761), palo de galleneta (Coomes 209), peramán de vieja (Foldats & Velazco 9596).

Retiniphyllum chloranthum is sympatric with R. concolor with which is commonly confused, and from which it differs in having involucels 5-lobulated and winged pyrenes (vs. involucels truncate and unwinged pyrenes in R. concolor). When dry, the fruits of R. chloranthum have ten ribs: five correspond to the dorsal margins of each pyrene, and the other five to the ribs created by the contact of the wings of adjacent pyrenes (Fig. 7F).

Retiniphyllum chloranthum and R. concolor have a flowers type that is unique within the genus in having zygomorphic, long corollas, tube white with five, light pink longitudinal lines, lobes either totally white or half white and half pale pink, and style slightly bent at anthesis. I have observed Euglossine bees visiting the flowers of R. concolor using the style as a landing platform.

1.4.3. Retiniphyllum concolor (Spruce ex Benth.) Muell. Arg. in Mart., Fl. Bras. 6(5): 8. 1881, emend. Cortés.

Commianthus concolor Spruce ex Benth. in Hook. f., Hooker's J. Bot. Kew Gard. Misc. 5: 235. 1853. Type. Brazil. Amazonas: Uananaca, borders of an elevated sandy campo, Dec 1851 (fl, fr), Spruce 2028 (lectotype, K, here selected; photo-K at NY; isolectotypes, BM, F, G[2], K, M; photo-M at F, NY). The lectotype specimen has a handwritten label by Spruce reporting the collection locality of Uananaca, as reported by Bentham. The dubious isolectotypes have a typed label with the same collection number but indicating the collection locality of São Gabriel de Cachoeira. Figs. 2D, 4C, 8A, 12B, 13E, 14B, 15B, 20

Retiniphyllum martianum Muell. Arg. in Mart., Fl. Bras. 6(5): 9. 1881. Type. Colombia. Vaupés: Cataracts of Cupatí, near Rio Japurá, (fl, fr), Martius s.n. (lectotype, G, here selected; isolectotype, M; photo-M at F, NY).

Retiniphyllum angustiflorum Krause, Bot. Jahrb. Syst. 40: 326. 1908. Type. Perú. Loreto: near Rioja, W of Moyobamba, 800-900 m, Oct 1906 (fl, fr), Weberbauer 4695 (B*; lectotype, G, here selected; photo-B at F, G, GH, NY; frag. at F).

Shrubs to **small trees** up to 6 m tall, 5 cm dbh. **Leafy branchlets** terete or slightly quadrangular, 3-6.5 mm thick, glabrous or hirtellous. **Stipules** sheathing, truncate, 1.5-5 mm long, coriaceous, glabrous or strigose outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate, rarely sessile; petioles 5-20 mm long (rarely absent), 1.5-2.5 mm thick, glabrous or hirtellous; blades 8.5-37.5 x 3-12.5 cm, L/W 2.8:1-3.6:1, obovate, oblanceolate or elliptic, cuneate or acute at base, apiculate or acuminate at apex, the acumen up to 2 cm long, coriaceous, glabrous above, margin with strigose hairs, dark green and opaque above, pale green and glossy or opaque below, brown when dry; primary, secondary and tertiary veins hirtellous or hispidulous below; secondary venation brochidodromous, 11-31 veins each side, tertiary veins random reticulate; domatia pocket-shaped. **Inflorescences** terminal, racemose, erect, (2.5-)4-10(-18) cm long; rachis ridged, 1.4-10 mm thick, glabrous or rarely hirtellous or hispidulous, with a stipular collar and two bracts subtending the basal pair of flowers, 1.5-12 mm long, rarely resembling small leaves, 0.3-19 cm long, portion of rachis from first pair to next flowers 0.9-1.6(-5) cm; peduncle 0.2-1(-6.5) cm long. **Bracteoles** reduced, 0.3-0.6 mm long, margin truncate or 3-lobate, glabrous, with colleters inside. **Involucel** discoid, 0.6-0.8 x 0.7 mm, truncate or with small teeth up to 0.1 mm long, coriaceous, glabrous or rarely hispidulous or hirsute outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, portion with lobes bent downward. **Flowers** zygomorphic, pedicellate; pedicels 1-2.5(-4) x 0.8-1.7 mm, glabrous or rarely hirsute or hispidulous. **Calyx** cupular, either truncate or with teeth or lobes, 0.8-2 x 2-2.6 mm, glabrous, rarely hispidulous, smooth or verrucose outside, glabrous and with colleters throughout inside, lobes broadly triangular, up to 0.1 mm long, greenish. **Corolla** 15.8-39 mm long; tube cylindrical, 10-24 mm long, 1.3-2 mm wide at base, 1.8-3 mm wide at mouth, glabrous or minutely puberulent outside, with a ring of hairs at basal portion, 0.8-1.5 mm wide at 4.5-6.5 mm from base, glabrous below ring, tomentose above ring inside, white with five longitudinal, pale pink lines; lobes 2/5-3/5 of tube length, 4-10.5 x 1.6-2.5 mm, narrowly oblong, acute at apex, sericeous throughout, left half of the lobe pale pink and right half white. **Filaments** 4.5-7 mm long, 0.3-0.4 mm wide, expanded at base, hirsute throughout or only at edges; anthers lanceolate, 2-2.9 x 0.3-0.7 mm; basal appendages oblong, 0.3-0.5 mm long, truncate at base; apical appendages narrowly triangular, 0.5-0.7 mm long.

Pollen prolate-spheroidal or subprolate; sexine microreticulate. **Style** 20-29 mm long, hirsutulous at base and medial portion, glabrous distally, capitate portion globose before branches opening, style branches narrowly triangular 0.2-0.5 mm long. **Ovary** 5-locular, narrowly obconical, 1.4-2 x 1-2 mm, glabrous or rarely hispidulous. **Fruit** globose, 5-ribbed, 7-9 x 4.5-5 mm, glabrous, rarely hirsutulous, red. **Pyrenes** 4.8-6.2 x 1.8-2 mm, surface smooth, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 3.4-3.5 x 0.6-0.8 mm.

Distribution (Fig. 20) **and ecology.** Widespread in the area of distribution of the genus. Commonly found in the Rio Negro caatinga forests and shrublands at low elevations in Brazil, Colombia and Venezuela. Found also growing in white-sand soils at low altitudes (<500 m) in Brazil (Acre), Colombia (Amazonas) and Perú (Loreto), and in uplands in the state of San Martin, Perú (800-1000 m). This species occurs also in a disjunct area in the Serra do Cachimbo, Pará, Brazil, at 430 m. Flowering specimens were collected in all months of the year. Fruiting specimens were collected in all months, except for August and December.

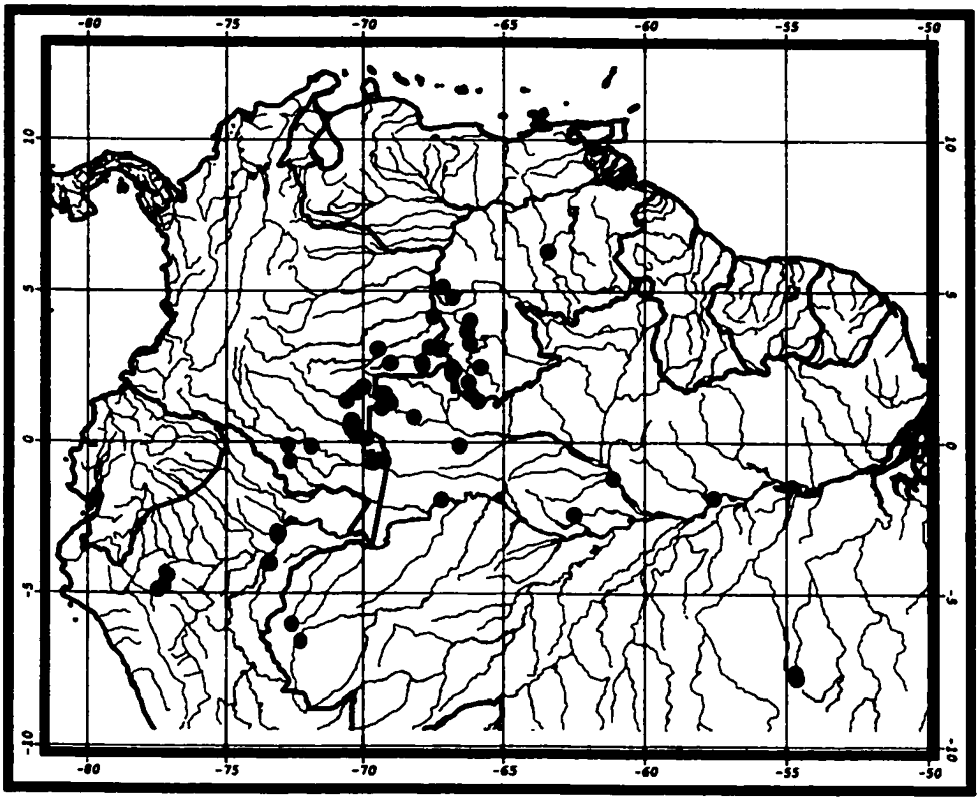


Fig. 20. Distribution of Retiniphyllum concolor

Additional specimens examined. BRAZIL. ACRE: Cruzeiro do Sul, 10 Feb 1976 (fl, fr), Monteiro & Damiao 275 (INPA); Cruzeiro do Sul, 10 Feb 1976 (fl), Monteiro & Damiao 274 (US); Cruzeiro do Sul, near new airport, 10 Feb 1976 (fl), Monteiro & Damiao 260 (INPA, US); Mun. Cruzeiro do Sul, N of Rio Ipixuna, 7°4'S, 72°51'W, 30 Sep 1987 (fl), Ferreira & Araujo 35 (INPA). **AMAZONAS:** Japuré ["Japurensis"], Sep (fl), Martius s.n. (M); between Rio Marié and Morro Ximaio, 0°45'S, 66°50'W, 07 Jul 1979 (fl), Poole 1908 (MO); between Rio Marié and Morro Ximaio, 0°45'S, 66°50'W, 07 Jul 1979 (fr), Poole 1913 (NY); Camanaus, 31 Oct 1971 (fr), Prance et al. 15892 (MO, NY, US[2]); Mun. Itapiranga, left side of Rio Uatuma, behind Igarapé Catitu, 18 Jul 1979 (fl, fr), Cid et al. 469 (MO, NY); near Igarapé Lages, Km 130, 15 Feb 1974 (fr), Steward et al. P20295 (MO, NY); Parque Nacional do Jaú, 02 Sep 1998 (fr), Vicentini et al. 1364 (INPA); Río Negro, Camanaos, 30 Nov 1929 (fl), Ducke 22900 (G, US); Rio Negro, Taracuá, 28 Feb 1959 (fl), Rodrigues 143 (NY); Yútica, left margin of Río Vaupés, 15 Nov 1952 (fr), Romero-Castañeda 3533 (COL). **PARÁ:** Paraensis, Sep (fl), Martius s.n. (M); Mun. Itaituba, estrada Santarém-Cuiabá, Serra do Cachimbo, 8°45'S, 54°57'W, 06 May 1983 (fl, fr), Silva 258 (NY, US); Serra do Cachimbo, km 858 Río Escorpião, 430 m, 08 Nov 1977 (fr), Prance et al. 25037 (NY, US).

COLOMBIA. AMAZONAS: Margen izquierda del Río Caquetá frente a la Isla de Mariñame, 01 Mar 1990 (fl, fr), Urrego et al. 1498 (NY); Río Apaporis, raudal de Jirijirimo. Sabana al lado sur del raudal, 150 m, 11-12 Sep 1986 (fl), Bernal et al. 1232 (NY); Río Caquetá (left side) in front of Isla Mariñame, Jun 1989 (fr), Urrego et al. 630 (NY); Río Caquetá, in front of Isla Mariñame, 120-180 m, 26 Apr 1986 (fr), Galeano et al. 1177 (NY); Río Caquetá, Isla San Pablo, La Pedrera, 160 m, 05 Jun 1984 (fl), Jaramillo et al. 8093 (COL); Río Igará-Paraná, Bella Vista, plateau summit, 08 Sep 1973 (fl), Sastre 2159 (COL, G, US); Río Igará-Paraná, La Chorrera, 13 Sep 1973 (fr), Sastre 2193 (COL, G); Río Igaraparaná, Puerto Buenaventura, 17 km from La Chorrera, 09 Oct 1973 (fl), Sastre 2438 (COL[2], G). **GUAINÍA:** 1°47'N, 67°6'W, 120 m, 06 Apr 1984 (fl, fr), Gentry & Stein 46417 (COL, MO); Cerro Puavi or Cerro Mañoco, near Sejal, Río Guainía, 190 m, 17 Oct 1977 (fr), Pabón et al. 395 (COL); raudal Alto, Río Inírida, 120 m, 10 Nov 1978 (fr), Espina 318 (COL); Río Guainía, Puerto Colombia, , 250-260 m, Oct 31-Nov 2 1952 (fr), Schultes et al. 18155 (F); Serrania de Naquén, Caño Culebra, near Helipuerto 16, 2°6'N, 68°11'W, 300 m, 02 Apr 1993 (fr), Madriñán & Barbosa 854 (COL, MO); Serrania de Naquén, rd. to Cerro minas, Maimachi, 2°12'N, 68°13'W, 455 m, 09 Apr 1993 (fr), Madriñán & Barbosa 964 (COL); Serrania de Naquén. Mun. de Maimachi, Caño Ima, 2°12'N, 68°12'W, 350 m, 26 Jul 1992 (fr), Cortés et al. 145 (COL, MO); Río Guainía, Pto. Colombia and vicinity, 2°40'S, 67°30'W, 250-260 m, 31 Oct-2 Nov 1952 (fr), Schultes et al. 18156 (GH, US). VAUPÉS: Cerro de La Pedrera, 02 May 1952 (fr), Schultes & Cabrera 16295 (F, GH, US); Cerro Yupati, La Pedrera, 350 m, 08 Mar 1990 (fl), Galeano et al. 1980 (NY); Cerro Yupati, La Pedrera, 240-580 m, 30 Sep 1952 (fl, fr), García-Barriga 14524 (COL); Cerro Yupati, La Pedrera, 200-250 m, 08 Mar 1990 (fl), Galeano et al. 1981 (COL); Circasia, Río Vaupés, 200 m, 10 Sep 1939 (fl), Cuatrecasas 7165 (COL, F, US); Mun. La Pedrera, rd. to Cerro Yupatí, 1°16'S, 69°38'W, 500 m, 15 Jun 1993 (fr), Cortés 484 (COL); Mun. Mitú, around Mitú, rd. to Monfort, 13 Jan 2000 (fl), Cortés 1625 (NY); Mun. Mitú, around Santa Cruz, 12 Jan 2000 (fl), Cortés 1619 (COL, NY); Mun. Mitú, around Santa Cruz, 12 Jan 2000 (fl), Cortés 1618 (NY); Mun. Mitú, around Santa Cruz, 12 Jan 2000 (fl), Cortés 1618 (COL); Mun. Mitú, around Santa Cruz, Km 5.5, 12 Jan 2000 (fl, fr), Cortés 1620 (COL, NY); Mun. Mitú, rd. from Bogotá cachivera to Acaricuara, 16 Jan 2000 (fl), Cortés 1645 (NY); Mun. Mitú, rd. from Bogotá cachivera to Acaricuara, 16 Jan 2000 (fl), Cortés 1646 (NY); Mun. Mitú, rd. from Yararaca to Santa Cruz, km 11, 10 Jan 2000 (fl), Cortés 1604 (NY); Mun. Mitú, rd. from Yararaca to Santa Cruz, km 11, 10 Jan 2000 (fl), Cortés & Rubiano 1603 (COL, NY); Mun. Mitú, rd. from Yararaca to Santa Cruz, km 11, 10 Jan 2000 (fl), Cortés & Rubiano 1605 (NY); Mun. Mitú, Rd. between Yararaca to Santa Cruz, Km 5.5, 11 Jan 2000 (fl, fr), Cortés 1609 (COL, NY); Mun. Mitú, Rd. between Yararaca to Santa Cruz, Km 5.5, 11 Jan 2000 (fl), Cortés 1611 (COL, NY); Mun. Mitú, Rd. between Yararaca to Santa Cruz, Km 5.5, 11 Jan 2000 (fl, fr), Cortés 1610 (COL, NY); Piracuara, 27 Nov 1952 (fl), Romero-Castañeda 3766 (NY); Río Apaporis, cachivera de Jirijirimo, 250 m, 12 Aug 1951 (fl), Schultes & Cabrera 13519 (COL, US); Río Apaporis, cachivera de Jirijirimo, 250 m, 13 Jun 1951 (fr), Schultes & Cabrera 12451 (GH); Río Apaporis, cachivera de Jirijirimo, 250 m, 11 Jun 1951 (fr), Schultes & Cabrera 12358 (COL); Río Apaporis, cachivera de Jirijirimo, 250 m, 16 Sep 1951 (fl, fr), Schultes & Cabrera 14059 (F, US); Río Apaporis, cachivera de Jirijirimo, 250 m, 10 Jun 1951 (fl, fr), Schultes & Cabrera 12501 (F, GH, US); Río Apaporis, cachivera de Jirijirimo (below mouth of

Río Kananarí), 0°5'N, 70°40'W, 275 m, 15 Mar 1952 (fr), Schultes & Cabrera 15930 (US[2]); Río Apaporis, Jirijirimo, 250 m, 25-26 Nov 1951, García-Barriga 13755 (COL); Río Apaporis, Jirijirimo, 250 m, 25-26 Nov 1951 (fl), García-Barriga 13730 (COL, NY, US); Río Apaporis, raudal de Jirijirimo, Mar 1951 (fr), Schultes 12110 (COL, GH); Río Apaporis, raudal Yayacopi (La Playa), 0°5'S, 70°30'W, 250 m, 18 Aug 1952 (fl), Schultes & Cabrera 16923 (F, GH, NY, US); Río Inírida (left margin), raudal Guacamayo, 69°45'W, 180 m, 04 Feb 1953 (fr), Fernández 2130 (COL, US); Río Paca (tributary of Río Papurí), Wacaricuara and vicinity, 0°30'S, 70°10'W, 200 m, 1-3 Jun 1953 (fl), Schultes & Cabrera 19558 (US); Río Papurí, ca. Yapú, 200 m, 15 Feb 1977 (fr), Patmore & Dufour 32 (COL, K); Río Papurí, Teresita, 27 May 1953 (fr), Schultes & Cabrera 19447 (F, GH, US[2]); Río Papurí. Teresita, 27 May 1953 (fr), Schultes & Cabrera 19446 (F, US); Río Piraparaná (tributary of Río Apaporis), caño Teemeeña, savannah O-koó-me-gwa, 0°15-25'S, 70°30'W, 200 m, 06 Sep 1952 (fr), Schultes & Cabrera 17220 (US[2]); Río Piraparaná, basin of the Apaporis river, loma Buc-chia, 250-600 m, 28-31 Aug 1952, García-Barriga 14290 (COL); Río Piraparaná, environs of catholic mission San Miguel, 24 Oct 1976 (fl, fr), Davis 157 (COL, GH); Río Piraparaná, environs of catholic mission San Miguel, 24 Oct 1976 (fl, fr), Davis 157A (F); Río Vaupés, Caño Pacú, 06 Mar 1944 (fl), Schultes 5821 (F); Río Vaupés, Javareté, 14-24 May 1953 (fl), Schultes & Cabrera 19414 (US); Río Vaupés, Mitú and vicinity, 27 Sep-20 Oct 1966 (fl, fr), Schultes et al. 24413 (GH, MO); Río Vaupés, Mitú and vicinity, summit of Cerro Mitú, 09 Oct 1966 (fr), Schultes et al. 24345 (COL, MO).

PERÚ. AMAZONAS: Bagua Province. Dto. Imaza. Comunidad Aguaruna de Wanás (Km 92 Carretera Bagua-Imacita. Cerros Chinim, 800-850 m, 31 Aug 1996 (fl), Díaz et. al. 8091 (MO, NY). **LORETO:** Maynas Province, Dto. Iquitos, El Dorado-Inia, 3°57'S, 73°24'W, 140 m, 30 Apr 1997 (fl), Vásquez & Soto 23781 (MO); Maynas Province, vicinity of Iquitos, (fr), Revilla 3087 (G); Maynas, 4 km from Mishana, Río Nanay, Callicebus Biological Station, 150 m, 10 Jan 1976 (fl), Gentry et al. 15791 (MO); Maynas, Dto. Iquitos, Rd. Peña Negra, km 5.5 from Quisto Cocha to caserio Varillal, 150 m, 19 Feb 1986 (fl), Rimachi 8144 (US); Prov. Maynas, Distr. Iquitos, Puerto Almendras, 130 m, 28 Jul 1988 (fl), Van der Werff et al. 9830 (MO); Prov. Maynas, Iquitos, Nina rumi-Río Nanay, 3°48'S, 73°25'W, 122 m, 05 Mar 1987 (fl, fr), Vásquez et al. 8901 (F, MO); Prov. Maynas, Río Nanay, caserio Mishana, 4-6 Sep 1974 (fl), Foster & Foster 4034 (MO, US); Prov. Requena, Jenaro Herrera, 4°55'S, 73°40'W, 140 m, 07 Aug 1988 (fl), Van der Werff et al. 9996 (F, MO, NY); Prov. Requena, Jenaro Herrera, Río Ucayali, 4 55'S, 73 45'W, 21 Feb 1987 (fl), Gentry et al. 56247 (F, MO, NY); Prov. Requena, Jenaro Herrera, Río Ucayali, 4°55'S, 73° 40'W, 03 Aug 1984 (fl), Mejia 328 (US); Provincia Requena, Dto. Sapuena, vicinity of Genaro Herrera, 1 km S of rd. Genaro Herrera-Brazil at km 5, 200 m, 21 Apr 1987 (fl), Acevedo & 1611 (NY, US); Ucayali Province, Sapuena, Jenaro Herrera, 4°55'S, 73°45'W, 130 m, 13 Mar 1989 (fl, fr), Vásquez & Soto 11893 (MO); vicinity of Iquitos, 120 m, (fl), Revilla 3514, 3752 (F, MO), 4275 (MO). **San Martín:** Along rd. between Moyobamba and Chachapoyas; vicinity of km markers 430-431, just E of village of Naranjos, 5°21'S, 77°20'W, 770 m, 12 Apr 1984 (fr), Croat 58154A (MO); Prov. Rioja, Naranjillo, along rd. Rioja-Pedro Ruiz, 5°44'S, 77°28'W, 950 m, 22 Mar 1998 (fr), Van der Werff et al. 15455 (MO); Prov. Rioja, Rioja, 1000-1100 m, 03 Sep 1974 (fl), Ferreyra 18459 (MO, US); Rioja, 56 km N of Rioja, 2 km E of Naranjos, 5°51'S, 77°40'W, 980 m, 01 Jun 1986 (fr), Knapp et al. 7448 (F, MO).

VENEZUELA. Amazonas: 0.5 km NE of San Carlos de Río Negro, 1°55'N, 67°5'W, 120 m, 17 Nov 1977 (fl), Liesner 3574 (MO, VEN); 1 km N of San Carlos de Río Negro, ca. 20 km S of confluence of R. Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 120 m, 18 May 1979 (fr), Liesner 7534 (MO); 4 km from San Carlos de Río Negro, 1°55'N, 67°02'W, 120 m, 23 Mar 2000 (fl), Berry & Aymard 7000 (MO); 4 km from San Carlos de Río Negro, 1°55'N, 67°02'W, 120 m, 24 Mar 2000 (fr), Berry & Aymard 7093 (MO); 4 km NE of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 120 m, 04 Apr 1979 (fr), Liesner 6167 (MO); ca. 1 km E of Colón, Río Guainía, 2°2'N, 67°06'W, 120 m, 30 Mar 2000 (fl, fr), Berry & Aymard 7426 (MO); ca. 5 km W of Yavita, along Yavita-Maroa rd., 2°53'N, 66°27'W, 110 m, 23 May 1996 (fl, fr), Aymard & Gómez 10985 (MO); carretera San Carlos-Solano 1-2 km, 120 m, 06 Feb 1977 (fl), Morillo & Villa 5328 (VEN); carretera San Carlos-Solano, 12 km N of San Carlos, 120 m, 06 Feb 1977 (fl), Morillo & Villa 5427 (VEN); Depto. Río Negro, middle part of the Río Baria, 1°05'N, 66°25'W, 80 m, 29 Jun 1984 (fl), Davidse & Miller 26817A (MO); Dpto. Atabapo, Río Caname, 1 km from its confluence with Río Atabapo, 3°41'N, 66°27'W, 95 m, Nov 1989 (fr), Yanez 38 (MO, NY); Dpto. Atabapo; Río Puruname, affluent of Río Orinoco, 1 km S of

San Juan de Puruname, 3°18'N, 66°33'W, 100 m, 03 Jun 1982 (fl), Huber & Tillett 6419 (INPA, NY, US); Dpto. Atures, left margin of caño Cabeza de Manteco, affluent of Río Autana, 4°52'N, 67°27'W, 100-120 m, 11 Oct 1984 (fr), Guanchez & Melgueiro 3464 (MO); Dpto. Atures, Río Sipapo, 3-4 km up to mouth of Guayaco, 4°30'N, 67°05'W, 80-150 m, 17 Feb 1985 (fl), Carnevali et al. 1575 (MO); Dpto. Casiquiare, 20 km S-E of San Fernando de Atabapo, 3°50'N, 67°47'W, 110 m, 10-16 Jan 1988 (fl), Aymard et al. 6535 (MO); Dpto. Casiquiare, between Yavita and Maroa, 125-140 m, 6-9 Jul 1969 (fl, fr), Bunting et al. 3919 (VEN); Dpto. Río Negro, Río Pasimoni, 1°30'N, 66°30'W, 80 m, Apr 1990 (fr), Velazco 1942 (MO); Dpto. Río Negro, Río Pasimoni, near (desembocadura) of Yatua, 1°30'N, 66°30'W, 80 m, Apr 1990 (fr), Velazco 2934 (MO); Dpto. Río Negro. Bajo Río Guainía, Raudal Lombriz, 2 km from mouth of Río Casiquiare, 2°2'N, 66°05'W, 26 Jan 1992 (fl), Aymard et al. 9764 (MO, NY); Dto. Río Negro, 0.5-1.5 km SE of Cerro de La Neblina, 0°50'N, 66°10'W, 140 m, 21 Feb 1984 (fr), Liesner 16161 (MO, US); Maroa, Río Guainía, 127 m, (fl), Williams 14192a (F); Maroa, Río Guainía, 127 m, (fr), Williams 14192 (F, US); Maroa, Río Guainía, 127 m, 09 Feb 1942, Williams 14228 (F, US); San Carlos de Río Negro, 26 Jan 1992 (fr), Berry 1371 (MO); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 28 Apr 1978 (fr), Clark 6769 (NY); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 10 Jan 1979 (fl), Clark 6464 (NY); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare. 4.3 km NNE on Solano rd., 1°56'N, 67°03'W, 119 m, 28 Dec 1978 (fl), Clark 6916 (NY, VEN). **Bolívar:** Río Paragua, around of Minas de Manaima, 6°7'N, 63°45'W, 300 m, 13 May-13 Jun 1987, Stergios 10285 (MO).

Local names. Venezuela: Aji de morrocoy (Liesner 6167), palo ojo de picure (Clark 6916).

Retiniphyllum concolor is similar to R. chloranthum, and easily distinguishable by its truncate involucel and for the non-winged pyrenes. When dry, the fruits of Retiniphyllum concolor are five-ribbed, while those of R. chloranthum are ten-ribbed. Because these species have a similar geographic distribution, grow in the same habitats, and their morphological similarities, they are occasionally collected together and mounted as mixed collections. Due to this problem, Retiniphyllum concolor has been often erroneously identified as R. martianum.

Bentham (1853) described Commianthus concolor from a Spruce's collection near the Rio Negro, Brazil. Although Bentham did not indicate the type, the locality that he cited corresponds to that of Spruce 2028. There are at least seven duplicates of Spruce 2028, and two of them are preserved at K. The specimen with the Herbarium Benthamianum seal preserved at K has a label with Spruce's handwriting reporting the locality Uananaca, and it is here designated as the lectotype of Commianthus concolor. The other specimens, with the same collection number, have labels indicating the collection locality of "São Gabriel da Cachoeira" and are here treated as isolectotypes.

Müller Argoviensis (1881) transferred Commianthus concolor to Retiniphyllum, citing Spruce 2028 and Spruce 3535. His description of Retiniphyllum concolor was based on both collections; unfortunately, Spruce 3535 is a mixed collection, and one duplicate is R. concolor, while the other (one of the two housed at BR, sheet No. 2) corresponds to a species of Retiniphyllum undescribed at that time. While Retiniphyllum concolor has truncate involucel and fruits with five ribs, the undescribed species has a lobulate involucel and fruits with ten ribs. Because of this, Müller Argoviensis (1881) described the fruits of Retiniphyllum concolor as 5-ribbed in the full description, and as 10-ribbed in the diagnostic description. In the same publication, he described Retiniphyllum martianum, pointing out its similarities with R. concolor. He differentiated them by the 10-ribbed fruits and involucel minutely denticulate in R. concolor, and by the 5-ribbed fruits and a truncate involucel in R. martianum. As a consequence, Müller Argoviensis amended Bentham's description, but unfortunately using a mixed collection. Because of Müller's incorrect description, the name Retiniphyllum concolor has been thereafter erroneously used to refer the species with 10-ribbed fruits.

Retiniphyllum angustiflorum was described by Krause (1908) based on a Weberbauer's collection from Loreto, Perú. He mentioned the resemblance between this species and Retiniphyllum concolor, and pointed out that R. angustiflorum has narrower leaves, tetragonal and thicker inflorescences, and shorter calyx. Retiniphyllum angustiflorum was treated as synonymous with R. martianum by Steyermark (1965). According to my observations, Retiniphyllum angustiflorum should be included within the morphological variation of R. concolor, and it is here treated as synonymous with it.

1.4.4. **Retiniphyllum discolor** (Spruce ex Benth.) Muell. Arg. in Mart., Fl. Bras. 6(5): 11. 1881. Commianthus discolor Spruce ex Benth. in Hook. f., Hooker's J. Bot. Kew Gard. Misc. 5: 234. 1853. "Ammianthus discolor" Spruce, in herb. Type. Brazil. Amazonas: Rio Negro, Uananaca, between Barcellos and São Gabriel da Cachoeira, Dec 1851 (fl), Spruce 2010 (lectotype, K, here selected; photo-K at NY; isolectotypes M, NY; photo-M at F). Figs. 6D, 11G, 13H, 15F, 21

Shrubs to **small trees** up to 3 m tall. **Leafy branchlets** terete, 1.8-3.1 mm thick, glabrous. **Stipules** sheathing, truncate, 1-1.5 mm long, coriaceous, glabrous outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate; petioles 9.5-11.8 mm long, 0.9-1.4 mm thick, glabrous; blades 4.6-9.6 x 2.2-4.1 cm, L/W 1.8:1-

2.7:1, elliptic or ovate, cuneate or acute at base, slightly acuminate to acute at apex, coriaceous, glabrous throughout, brown or green when dry; secondary venation brochidodromous, 8-13 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect, 6.1-14.8 cm long; rachis decussately compressed, 1.5-2.2 mm thick, glabrous; peduncle 1.1-2.4 cm long. **Bracteoles** reduced, 0.6-0.8 mm long, margin with small teeth, glabrous, with colleters inside. **Involucel** discoid, 0.5-0.9 x 3-3.6 mm, with small teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, sessile. **Calyx** tubular, lobulate, 8.1-8.5 x 3.2-3.8 mm, glabrous and verrucose outside, glabrous, and without colleters inside; lobes 0.6-1.4 x 0.1-0.6 mm, narrowly triangular or deltoid, glabrous or verrucose. **Corolla** 25.5-27.8 mm long; tube narrowly infundibuliform, 14.5-15.8 mm long, 1.5-2 mm wide at base, 3.3-3.4 mm wide at mouth, glabrous at base, strigose at middle part and at mouth outside, with a ring of hairs at basal portion, at 2.5-2.7 mm from base, glabrous below ring inside, red; lobes 3/4-4/5 of tube length, 10.3-12 x 1.4-2.2 mm, lanceolate, acute at apex, sericeous throughout, red. **Filaments** 6.9-7.9 mm long, 0.5 mm wide, expanded at base, hirsute throughout; anthers narrowly oblong, 2.6-3 x 0.4-0.7 mm; basal appendages oblong, 0.4-0.5(-1) mm long, truncate at base; apical appendages narrowly triangular, 0.7-0.9 mm long. **Pollen** subprolate or prolate; sexine microreticulate. **Style** 20-25.2 mm long, pilose at base and medial portion, glabrous distally; capitate portion ellipsoid before branches opening, style branches narrowly triangular, 0.5-0.8 mm. **Ovary** 5-locular, globose, 1.7-2.2 x 2-2.9 mm, glabrous. **Fruit** transversally ellipsoid, 5.5-7 x 4.2-7.1 mm, glabrous throughout, red. **Pyrenes** 5.9-6 x 2.5 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.7 x 0.5 mm.

Distribution (Fig. 21) **and ecology**. A lowland species occurring in the caatingas of the in Rio Negro in Brazil and Venezuela. Flowering specimens were collected in February, March, May and October. Fruiting specimens were collected in February and July.

Additional specimens examined. BRAZIL. AMAZONAS: Between Barcellos and São Gabriel da Cachoeira, Spruce 2063 (M); N margin of Rio Aracá, just above Igarapé Sauadaua, 0°13'N, 63°8'W, 80 m, 26 Jul 1985 (fr), Prance et. al. 29865 (F, NY, US); Rio Uneiuxi, 200-300 km above mouth, 22 Oct 1971

Fig. 21. Distribution of <u>Retiniphyllum discolor</u> (✱), and <u>R. glabrum</u> (●).

(fl), Prance et al. 15539 (NY, US, VEN). **Roraima:** São José do Anauá, Campina do Seu Antônio, Lavrado da Perdida, 1°29'5"N, 60°58'19"W, 26 Mar 1999 (fl), Vicentini & Carneiro 1455 (INPA).

VENEZUELA. Amazonas: Dpto. Atabapo, 4°6'N, 66°31'W, 180 m, 01 May 1990 (fl), Marin 1125 (MO); Dpto. Atabapo, lower Río Ventuarí, 10 km NE of Caño Marueta mouth, 4°18'N, 66°16'W, 110 m, 18 Feb 1981 (fl, fr), Huber 6119 (COL, NY, US, VEN).

Retiniphyllum discolor, occurring in Brazil and Venezuela, is similar to R. glabrum, known only from Brazil; both species have flowers in spicate inflorescences with long-tubular, red corollas. However, R. discolor has larger calyx and longer filaments, shorter corolla (25.5-27.8 mm long in R. discolor vs. 29-33 mm long in R. glabrum), shorter style, and fruit transversally ellipsoid (vs. globose in R. glabrum).

Richard Spruce annotated his collection 2010 with "Ammianthus discolor", a name that remained unpublished. Bentham (1853) published Spruce's specific epithet in the genus Commianthus.

1.4.5. Retiniphyllum francoanum R. Cortés, sp. nov. Type. Colombia. Caquetá: Sierra de Chiribiquete, South camp, left side of river, upriver of major waterfall, 300 m, 6 Dec 1990 (fl, fr), Estrada, Fuertes, Franco & Palacios 646 (holotype, COL; isotypes, COL, K, MO, NY). Figs. 1F, 7D,E, 9A, 22

Shrubs up to 3 m tall. Stipules tubular, broadly triangular. Inflorescences axillary, racemose, erect, 4-11 flowered. Bracteoles reduced. Involucel cupular, 3-6 lobulate, unequal lobes, persistent to the fruits. Ovaries turbinate, 7-8-locular. Fruits with two cylindrical seeds per locule. Pyrenes verrucate, winged.

Shrubs up to 3 m tall. **Leafy branchlets** terete, 2.5-3.5 mm thick, minutely hirtellous. **Stipules** tubular, broadly triangular, 4.8-9.2 x 3.4-5 mm, acute, acuminate or rarely bilobed at apex, margin entire or serrulate, coriaceous, strigose outside, glabrous and with colleters from base to middle portion inside, caducous or sub-caducous. **Leaves** petiolate; petioles 5-11 mm long, 1.1-2 mm thick, hispidulous; blades 3.1-8.8 x 0.9-4.5 cm, L/W 2:1-3.4:1, elliptic, oblong-elliptic or obovate, cuneate at base, acute or round at apex, coriaceous, hispidulous, with strigose hairs at margin and along primary vein above, canescent below, brownish or olive green when dry; primary, secondary and tertiary veins strigose below; secondary venation eucamptodromous, 11-12 veins each side, tertiary veins random reticulate; domatia absent or pocket. **Inflorescences** axillary, racemose, erect, 4-11 flowered; 0.7-4.2 cm long; rachis slightly ridged or terete, 0.5-1 mm wide, hirtellous, with or without a stipular collar subtending the basal pair of flowers, portion of rachis from first pair to next flowers 3.5-8 mm long; peduncle 2-12 mm long, hirtellous. **Bracteoles** reduced, margin with minute teeth up to 0.6 mm long, glabrous, with colleters inside. **Involucel** cupular, lobulate, 1-2.5 x 1.8-2.6 mm, 3-6 lobes of different sizes, two major lobes narrowly triangular, 0.8-1.5 x 0.3-0.4, one to four minor lobes, deltoid, 0.3 x 0.3 mm, strigose outside, hispid and with colleters at base inside, persistent to the fruit. **Flower buds** cylindrical, tube straight or rarely slightly bent. **Flowers** actinomorphic, pedicellate; pedicels 2-2.7 x 0.5-0.6 mm, hirsute. **Calyx** tubular, lobulated, 2.6-4.3 x 1.9-2.4 mm, strigose outside, hispid and with colleters inside; lobes 1.2-2.5 x 0.3-0.5 mm, narrowly triangular, strigose, diminutely verrucose, green. **Corolla** 21-28 mm long; tube infundibuliform, 16-21 mm long, 2-3.5 mm wide at the orifice, 1-1.5 mm wide at base, sericeous outside, with a ring of hairs at base, 1-1.5 mm wide at 2.5-4.3 mm from base, glabrous below ring, strigose above ring inside, red; lobes 1/3-1/4 of tube length, 5-7 x 0.7-1.6 mm, lanceolate, acute at apex, throughout; fuchsia. **Filaments** 3.3-4.2 mm long, 0.1-0.3 mm wide, slightly expanded at base, pilose throughout; anthers elongate, 1.7-2 x 0.2-0.5 mm; basal appendages oblong, 0.3 mm long, truncate at base; apical appendages narrowly triangular, 0.1-0.2 mm long. **Style** 24-26 x 0.3-0.6 mm, pilose at base and medial portion, glabrous distally; capitate portion oblong before branches opening, style branches narrowly triangular, up to 0.2 mm long. **Ovary** 7-8-locular, turbinate, 1-1.3 x 1.4-1.5 mm, pubescent; disk up to 0.8 mm long. **Fruit** longitudinally ellipsoid, 3.8-4.5 x 4.1-6 mm, glabrous, only apically strigose. **Pyrenes** 2.9-3 x 1.8 mm, surface verrucate, with two parallel wings inserted near the ventral margin. **Seeds** two per locule, cylindrical, attached at distal portion of the septum, 2.5 x 1 mm.

Distribution (Fig. 22) **and ecology**. Found only in the Escarpe de Araracuara and in the Serrania de Chiribiquete in the Departments of Caquetá and Guaviare (respectively), Colombia, at elevations of 100-350 m. Flowering specimens were collected in January, April, July, November and December. Fruiting specimens were collected in December

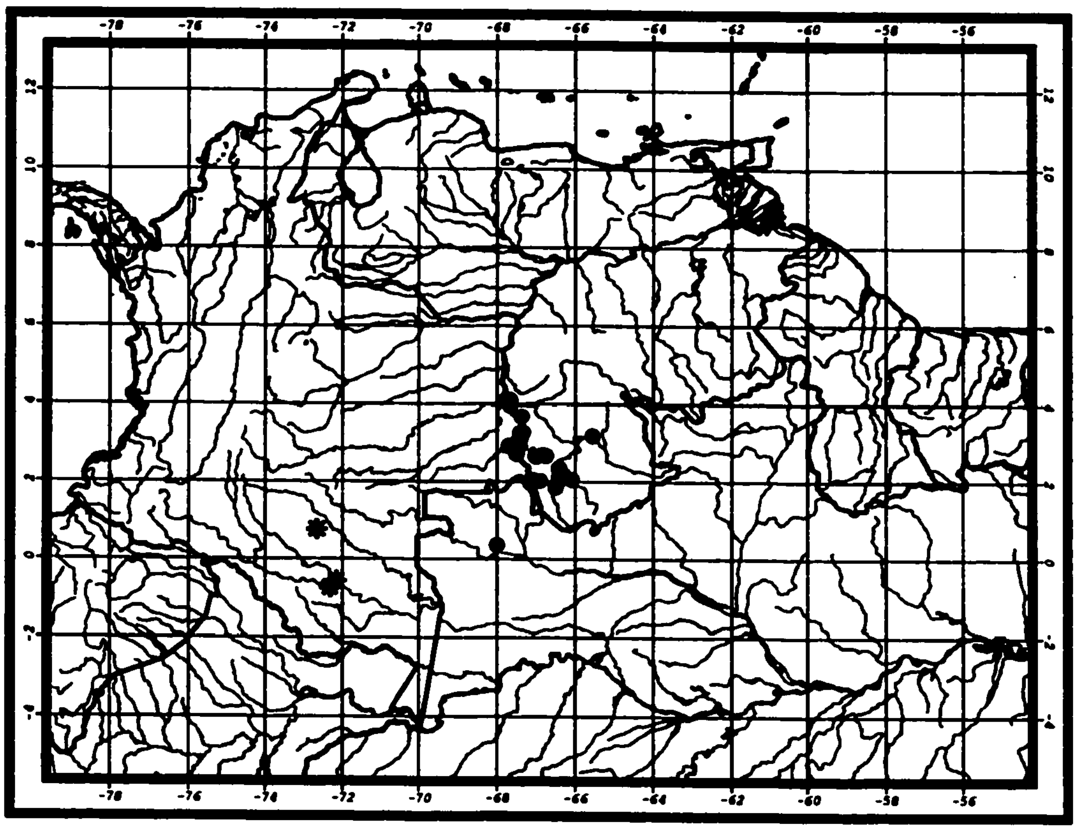


Fig. 22. Distribution of Retiniphyllum francoanum (✱), and R. secundiflorum (●).

Additional specimens examined. COLOMBIA. CAQUETÁ: Río Caquetá, Araracuara, 01 Apr 1976 (fl), Sastre & Reichel 5133 (COL); Mun. Solano, L margin of Río Caquetá, Paujil (Caño Paujil), 190 km NW from Araracuara, 0°45-48'S, 72°20-25'W, 100-350 m, 24 Jul 1992 (fl), Arbeláez & Sueroque 167 (MO); Parque Nacional Natural Chiribiquete, raudal del Río Sararamano, cerro cercano, 29 Jan 1992 (fl), Puerto Rastrojo CHI-35 (NY); Serrania de Chiribiquete, sector nororiental Río Cuñare, raudal El Tubo, 28 Nov 1995 (fl), Cárdenas et al. 6929 (MO).

Retiniphyllum francoanum is unique in the genus by having ovaries with 7-8-locules. Most of the species of the genus have 5-locular ovaries, and 5 or 6-locular ovaries are common in Retiniphyllum secundiflorum, closely related to this species. Retiniphyllum francoanum and R. secundiflorum are unique in the genus by having axillary inflorescences, fruits with two seeds per locule, and involucels persistent to the fruits. This species differs from Retiniphyllum secundiflorum in having reduced bracteoles (vs. foliose), winged pyrenes (vs. slightly ribbed), bracteoles with colleters (vs. without colleters), turbinate ovaries (vs. ellipsoid), shorter pyrenes, shorter inflorescences, narrower rachis, and longer corolla tube. In addition, Retiniphyllum francoanum has corolla lobes 1/3-1/4 of the tube length, which are 1/2-2/3 in R. secundiflorum.

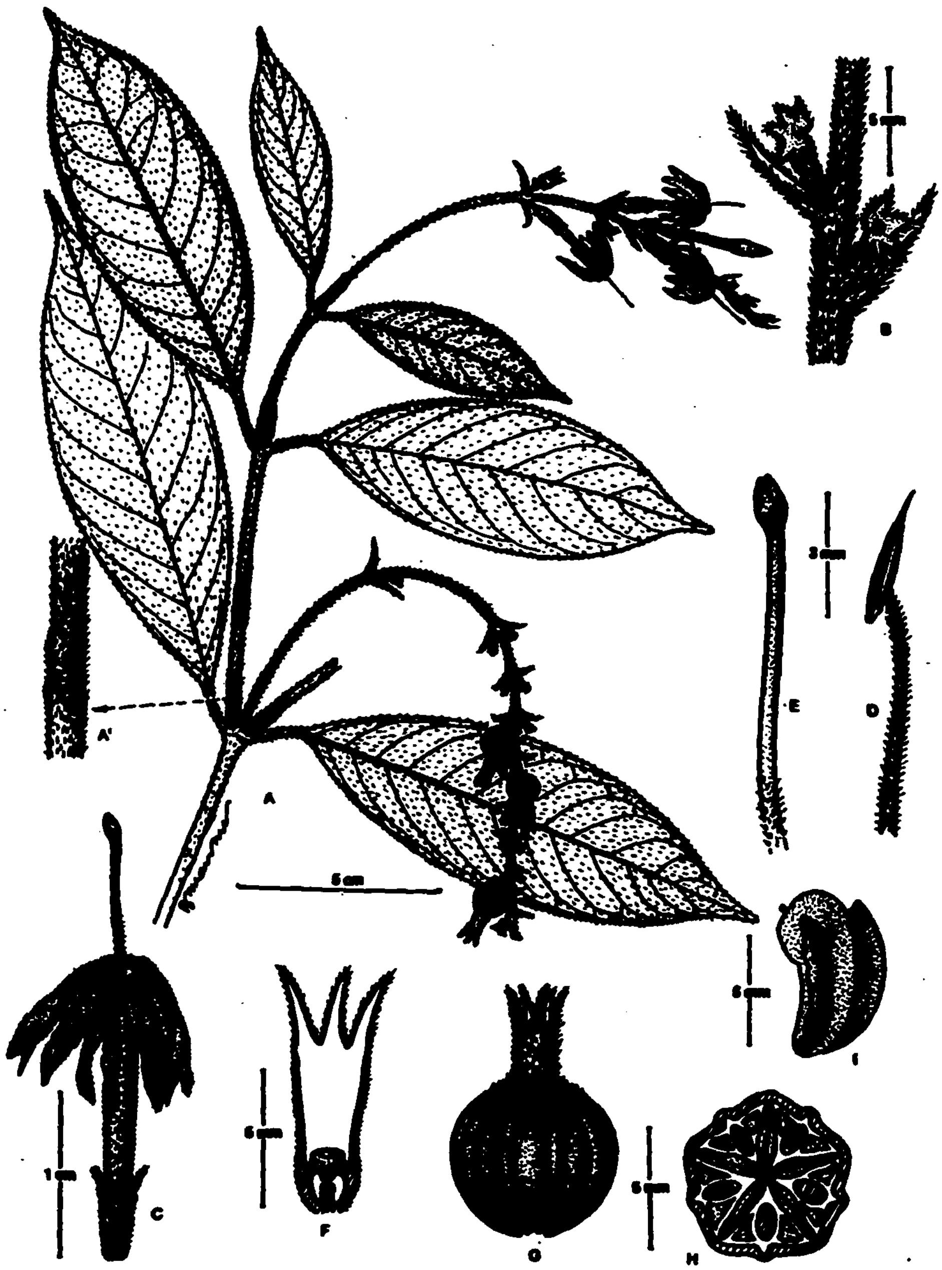
This species is named in honor of my professor Pilar Franco (1950-2000), who was part of the team that collected the type specimens. The specific epithet intends to commemorate Pilar's memory after her tragic death while collecting in Villavicencio, Meta, Colombia.

1.4.6. Retiniphyllum fuchsioides K. Krause, Verh. Bot. Vereins Prov. Brandenburg 50: 101. 1908. Type. Peru. Loreto: Cerro de Escalero, 1100 m, Nov 1902 (fl), Ule 6544 (B*; lectotype, F, N. 895700 (fragment), here selected; isolectotype, F, N. 607336 (fragment); photo-B at F, GH, NY). Figs. 1D, 2E, 4H, 5A,D,E, 9D, 11E, 12G, 13D, 15C, 23, 24

"Retiniphyllum spruceanum" Muell. Arg., nom. nud., in Mart., Fl. Bras. 6(5): 7. 1881.

Shrubs to **small trees** to 7 m tall. **Leafy branchlets** terete, 1.7-4 mm thick, tomentose. **Stipules** sheathing, splitting in one side, broadly triangular, acuminate or rarely bilobed at apex, margin entire, serrulate at apex, 7.5-18 x 3.6-5.5 mm, chartaceous, strigose outside, verrucose and with colleters at base inside, persistent. **Leaves** petiolate; petioles 5-13(-22) mm long, 1-1.8 mm thick, strigose; blades 6.9-16 x 2.2-5 cm, L/W 2.2:1-4.2:1, lanceolate, elliptic, rarely oblanceolate, acute or cuneate at base, acuminate at apex, acumen 6-15 mm long, chartaceous or papyraceous, strigose, with strigose hairs at margin and along primary vein above, strigose below, dark brown or olive green when dry; primary, secondary and tertiary veins strigose below; secondary venation eucamptodromous or weak broquidodromous, 9-17 veins each side, tertiary veins alternate percurrent; domatia absent. **Inflorescences** terminal, racemose, pendulous, 8.2-30 cm long; rachis canaliculate, 1-2.1 mm thick, tomentose, with or without two bracts subtending the basal pair of flowers, 5.5-14 mm long, portion of rachis from first pair to next flowers 2.8-3.6 cm long; peduncle 3-11 cm long, tomentose. **Bracteoles** foliose, 5.2-9.5 x 0.8-2 mm, margin entire, glabrous or hirsute, without colleters inside. **Involucel** cupular, 0.8-1.5 x 2-2.5 mm, 5-7-lobate, lobes of different sizes, 0.2-1.5 mm long, with or without colleters at apex, rarely 1/3-1/4 of the cup does not develop lobes, papyraceous, strigose or hirsute outside, glabrous and without colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, pedicellate, pedicels 2.5-9 x 0.5-0.8 mm, hirsute. **Calyx** tubular, lobulate, 2.4-5 x 2-3.1 mm, pubescent or hirsutulous outside, glabrous or strigose and without colleters inside, lobes 1-3.5 x 0.6-1.1 mm, triangular or

Fig. 23. Illustration of <u>Retiniphyllum fuchsioides</u>. A. Habit of inflorescence showing stipule. B. Bracteoles and involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Ovary and calyx. G. Fruit. H. Fruit in transversal section. I. Pyrene



narrowly triangular, hirsutulous. **Corolla** 23-40 mm long; tube narrowly infundibuliform, 16-25 mm long, 1.1-2 mm wide at base, 2.5-4.2 mm wide at the orifice, sericeous outside, with a ring of hairs at basal portion, 1.5-1.7 mm wide at 2.5-3 mm from base, glabrous below ring, sericeous above ring inside, red; lobes 1/3-3/4 of tube length, 6-17 x 1.5-3 mm, lanceolate, rarely obovate, acute at apex, sericeous throughout, red. **Filaments** 4.6-6.2 mm long, 0.3-0.6 mm wide, expanded at base, pilose throughout; anthers lanceolate, 2.6-3.9 x 0.6-0.8 mm; basal appendages obconical, 0.7-0.9 mm long, truncate at base; apical appendages narrowly triangular, 0.9-1.2 mm long. **Pollen** prolate-spheroidal or subprolate; sexine tectate-perforate. **Style** 26-35 x 0.2-0.5 mm, pilose at base and medial portion, glabrous distally; capitate portion ellipsoid before branches opening, style branches triangular, 0.2-0.8 mm long. **Ovary** 5-locular, narrowly obconical, 1.7-2.6 x 1.7-2.8 mm, puberulent. **Fruit** globose, 5.5-8.5 x 5.5-8 mm, puberulent, deep purple. **Pyrenes** 5-7.4 x 2.4-3.3 mm, surface smooth, with two perpendicular wings inserted near the dorsal margin. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.5-3.4 x 0.8-1.1 mm.

Distribution (Fig. 24) **and ecology**. This species has an unusual distribution and ecology in the genus. Known only from Perú, mainly at uplands from 600-1120 m in the states of Loreto, Amazonas, San Martín, Pasco, Huanuco and Puno. Habitats include mainly montane forest on rocky soils with abundant organic matter, but not white-sand soils, as in the rest of the species. Flowering specimens were collected in January, and from June to October. Fruiting specimens were collected in January, June, July, October and November.

Additional specimens examined. PERÚ. AMAZONAS: Prov. Bagua, Dto. Imaza, community Aguaruna Putuim (Annex of Yamayakat), high colines, 5°3'20"S, 78°20'23"W, 760 m, 24 Sep 1994 (fl), Díaz et al. 7225 (MO); Prov. Bagua, Dto. Imaza, community Aguaruna Putuim, Annex of Yamayakat, high zones of Putuium, 5°3'20"S, 78°20'23"W, 700 m, 18 Jan 1996 (fr), Díaz et al. 7685A (MO); Bagua Province, Dto. Imaza, Cerros de Putuim, 5°3'20"S, 78°20'23"W, 350 m, 15 Jun 1996 (fr), Vásquez et al. 21190 (MO); Bagua Province. Dto. Imaza, Tayu Mujaji, community of Wawas, 5°15'56"S, 78°22'07"W, 900 m, 23 Oct 1997 (fl), Vásquez et al. 24668 (MO). **HUANUCO:** Prov. Pachitea, region of Pucallpa, W part of the Sira Mountains and adjacent lowland, ca. 24 km SE, ca. 26 km ESE of Puerto Inca, from the beginning of the mountain rain forest next to the Campamento Pato Rojo, 9°27'S, 74°46'W, 1000 m, 27 Jan 1988 (fl, fr), Morawetz & Wallnöfer 11-27188 (K); S slope of the Rio Llullapichis watershed, on the ascent of Cerros del Sira, 9°27'S, 74°46'W, 1000 m, 23 Jul 1969 (fl), Dudley 13175 (MO, NY, VEN); S slope of the Rio Llullapichis watershed, on the ascent of Cerros del Sira, 9° 28'S, 74°46'W, 1080 m, 02 Jul 1969 (fl, fr), Wolfe 12222 (MO); **LORETO:** Pumayacu, between Balsapuerto and Moyobamba, 6°S, 76°45'W, 600-1200 m, Aug-Sep 1933 (fl), Klug 3168 (F, GH, MO, NY, US). **PASCO:** Oxapampa Province, W side of Cordillera de San Matias

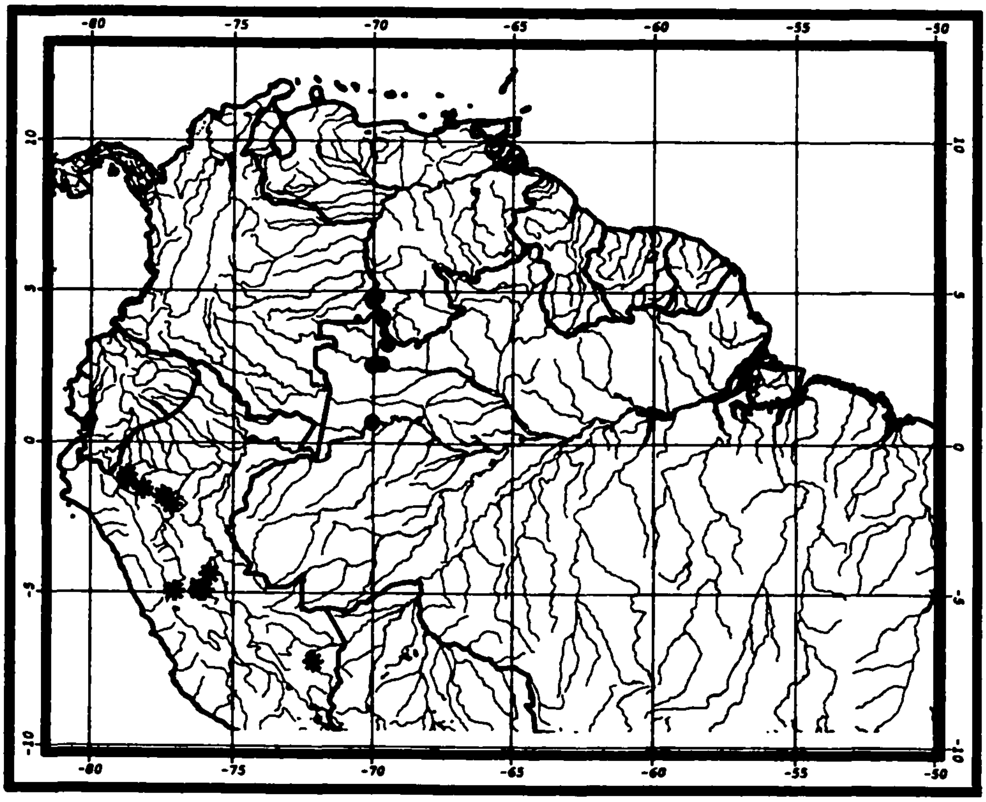


Fig. 24. Distribution of Retiniphyllum fuchsioides (✱), and R. pilosum (●).

between Iscosacin and summit, 10°11'S, 75°12'W, 910 m, 22 Jun 1982 (fl), Smith 2048 (MO); Prov. Oxapampa, Serrania de San Matias W of Puerto Bermudez, 10°11'S, 75°12'W, 900-1050 m, 15 Jun 1983 (fl, fr), Gentry et al. 42013 (MO[2]); Prov. Oxapampa, Valle del Palcazu, Cordillera de San Matias, rd. of Loma Linda, 10°11'S, 75°W, 640 m, 22 Jul 1981 (fl), Foster 4500 (MO). PUNO: Carabaya Province, headwaters of Río Candamo, 13°18'S, 70°07'W, 800-850 m, 14 Nov 1996 (fr), Cornejo & Balarezo 2685 (MO[2]). SAN MARTIN: Lamas, old trail from Yumbatos to San Antonio de cumbasa, S of Shapajilla, upper slopes of Cerro Isco, 6°22'S, 76°23'W, 600-800 m, 05 Oct 1986 (fl, fr), Knapp et al. 8526 (F, MO, NY[2]); Prov. Rioja, Dto. Pardo Miguel, between Poblado Aguas Verdes and Paraiso, up to Río Serrano Yacu, 5°40'S, 77°38'W, 1120 m, 15 Jun 1998 (fl, fr), Sánchez Vega et al. 9341 (NY). UNKNOWN STATE: Chicoplaya, 1978 (fl), Ruíz & Pavón 7/96 (F, fragment); without locality, Ruíz & Pavón s.n. (BM[2]).

Retiniphyllum fuchsioides has foliose bracteoles and cupular involucels with unequal lobes, a condition found only also in R. pilosum, which is also similar by having winged pyrenes. However, Retiniphyllum fuchsioides have pyrenes with wings inserted near the dorsal margin and bent downwards, while those of R. pilosum have wings inserted near the ventral margin and bent upwards. Retiniphyllum pilosum has spicate and erect inflorescences, white, short-tubular corollas, while R. fuchsioides has racemose and pendulous inflorescences, red, long-tubular corollas.

The type specimen of Retiniphyllum fuchsioides, Ule 6544, preserved at the Berlin herbarium (B) was destroyed during the Second World War. This specimen was photographed by Macbride (negative No. 288) and the photographs were distributed to F, GH and NY (and probably other institutions). Unfortunately, only a fragment of the type is preserved at F, with four open flowers. No other type specimens have been found. Consequently, I have designated the fragment specimen preserved at F as the lectotype of Retiniphyllum fuchsioides.

Although Spruce annotated his collection 4254 (collected at Tarapoto, Perú), as Retiniphyllum peruvianum, this binomial remained unpublished. In addition, the fragment of this collection at F is annotated as "Retiniphyllum spruceanum Muell. Arg., nomen ined.". The name Retiniphyllum spruceanum Muell. Arg. was published in Flora Brasiliensis in the description of Section Euretiniphllym, but without any description, and therefore it should be treated as a nomen nudum.

1.4.7. **Retiniphyllum glabrum** Steyerm., Mem. New York Bot. Gard. 12: 243. 1965. Type. Brazil. Amazonas: Rio Uaupes, between Inaporé and confluence with Rio Negro, 14-15 Nov 1947 (fl, fr), Schultes & Pires 9100 (holotype, US; photo-US at NY[2]). Fig. 21

Shrubs. **Leafy branchlets** terete, 1-2 mm thick, glabrous. **Stipules** sheathing, truncate, 1-1.6 mm long, coriaceous, glabrous outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate; petioles 6-11 mm long, 0.7-1 mm thick, glabrous; blades 5.4-7.2 x 1.6-2.4 cm, L/W 2.8:1-3.9:1, elliptic, cuneate at base, slightly acuminate to acute at apex, chartaceous, glabrous throughout, brown or olive green when dry; secondary venation basally eucamptodromous, distally broquidodromous, 10-13 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect; 7.8-11.5 cm long, rachis terete, 0.8-2 mm thick, glabrous, with two bracts up to 1 mm long, subtending the first pair of flowers; peduncle 1-2.2 cm long. **Bracteoles** reduced, 0.4-0.5 mm long, margin entire, glabrous, with colleters inside. **Involucel** discoid, 0.5-0.6 x 2.5-4 mm, margin entire or with small teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, sessile. **Calyx** tubular, lobulate, 5.3-6 x 3-3.4 mm, glabrous outside, glabrous and without colleters inside, lobes 1-1.6 x 0.5-1 mm, narrowly triangular or deltoid, glabrous. **Corolla** 29-33 mm long; tube narrowly infundibuliform, 17-21 mm long, 1-1.2 mm wide at base, 3-

3.2 mm wide at mouth, glabrous at base, sericeous at middle part and mouth outside, with a ring of hairs at basal portion, 0.9-1 mm wide at 2.2-2.7 mm from base, glabrous below ring, and strigose above ring inside, red; lobes 1/2 of tube length, 10.5-11 x 1.6-2 mm, oblong, acute at apex, sericeous throughout, red. **Filaments** 4-5.2 mm long, 0.2-0.4 mm wide, expanded at base, hirsute throughout; anthers lanceolate, 2.5-2.7 x 0.5 mm; basal appendages oblong, 0.3-0.4 mm long, truncate at base; apical appendages apiculate, 0.3-0.8 mm long. **Pollen** with sexine microreticulate. **Style** 25-32 x 0.3-0.5 mm long, ridged, hirtellous from base to medial portion, glabrous distally; capitate portion ellipsoid before branches opening, style branches deltoid, 0.5 x 0.1-0.2 mm. **Ovary** 5-locular, globose, 2-2.3 x 1.8-2.8 mm, glabrous. **Fruit** globose, 6-6.5 x 5-6.5 mm, glabrous throughout. **Pyrenes** 5.5-5.6 x 2-2.3 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 4-4.3 x 0.9-1 mm.

Distribution (Fig. 21) **and ecology**. Known only from two collections in NW Brazil at lowlands. Although there is no indication of the kind of vegetation on the collection labels, it seems most likely that the species grows in Rio

Negro caatinga forest or shrublands. Collected with flowers and fruits in November.

Additional specimen examined. BRAZIL. Amazonas: Igarapé da Chuva, Taracuá, Rio Vaupés, between Ipanoré and confluence with Rio Negro, 0°6'N, 68°28'W, 84 m, 12 Nov 1947 (fl, fr), Schultes & Pires 9073 (US).

Retiniphyllum glabrum is most similar to R. discolor, both having spicate inflorescences and long-tubular, red corollas; however, R. glabrum has shorter calyx and filaments, longer corolla (29-33 mm long in R. glabrum vs. 25.5-27.8 mm long in R. discolor), longer style, and globose fruit (vs. transversally ellipsoid).

1.4.8. **Retiniphyllum guianense** Steyerm., Mem. New York Bot. Gard. 12: 242. 1965. Type. Guyana: Trail along SE side of Merumé Mtn., Partang River, Upper Mazaruni River Basin, 1140 m, 5 Jul 1960 (fr), Tillet, Tillet & Boyan 44824 (holotype, NY). Figs. 8B, 13F, 17

Shrubs up to 2 m tall. **Leafy branchlets** aristate or terete, 2.4-5 mm thick, glabrous. **Stipules** sheathing, truncate, 1.5-2.1 mm long, coriaceous, glabrous outside, glabrous and with colleters throughout inside, persistent.

Leaves petiolate; petioles 9-11 mm long, ca. 1-2 mm thick, glabrous; blades 6.2-13.4 x 3.2-4.6 cm, L/W 1.9:1 to 2.9:1, elliptic, oblanceolate or obovate, cuneate at base, acute to acuminate at apex, the acumen 0.3-0.5 cm long, coriaceous, glabrous throughout, brown or olive green when dry; secondary venation broquidodromous, 9-11 each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect; 1.5-6.5 cm long; rachis terete, 1.5-3 mm thick, glabrous, without bracts; peduncle 0.6-1.1 cm long. **Bracteoles** reduced, 0.2-0.4 mm long, margin entire, glabrous, with colleters inside. **Involucel** discoid, 0.5-0.8 x 2.2-2.5 mm, margin entire, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** unknown. **Flowers** zygomorphic, sessile. **Calyx** tubular, truncate, 4.5-5.3 x 2.8-3.5 mm, glabrous outside, glabrous and with colleters inside. **Corolla** 14.6-15 mm long; tube infundibuliform, 7-9 mm long, 1.5 mm wide at the base, 2.6 mm wide at mouth, basally glabrous, the rest sericeous outside, with a ring of hairs at distal portion, 1 mm wide at 4.8 mm from base, glabrous below ring and sericeous above ring inside, white; lobes about same size than tube, 7-9 x 1.9-2.2 mm, oblong, acute at apex, sericeous throughout; white or cream-white. **Filaments** 5-5.5 mm long, 0.4 mm wide, expanded at base, hirsute throughout; anthers oblong, 2.3-3.4 x 0.4-0.6 mm; basal appendages obovate, 0.3-0.4 mm long; apical appendages narrowly triangular, 0.5-0.8 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 18.5 x 0.3-0.4 mm, pilose basally, distally glabrous; capitate portion ellipsoid before opening, style branches triangular, 0.2 mm long. **Ovary** 5-locular, narrowly obconical, 2.2 x 1.9-2.5 mm, glabrous. **Fruits** transversally ellipsoid, 9-11.6 x 6-8, glabrous. **Pyrenes** 5-5.1 x 3-3.5 mm, surface smooth, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 3.6-3.9 x 1.8-2.3 mm.

Distribution (Fig. 17) **and ecology.** Endemic to Guyana, this species is only known from two collections, one from uplands (1140 m) in Merumé Mountains, and the other from highlands (1500 m) in Pakaraima Mountains. In the last locality, the species was found growing in a swamp scrub. A flowering specimen was collected in October. Fruiting specimens were collected in July and October.

Additional specimen examined. GUYANA: Pakaraima Mts., northeastern plateau of Mount Ayanganna, 5°23'N, 59°58'W, 1500 m, 30 Oct 1992 (fl, fr), Henkel & Hoffman 54 (MO, US).

Retiniphyllum guianense is unique in the genus in having a coriaceous calyx, in which the distinction between calyx and ovary is not evident externally. Its spicate inflorescences with short-tubular, white corollas could be confused with the widespread R. schomburgkii; the former differs from the latter in having shorter inflorescences (1.5-6.5 cm in R. guianense vs. 6-18.5 cm in R. schomburgkii), longer styles, and larger fruits.

1.4.9. Retiniphyllum kuhlmannii Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 356. 1931. Type. Brazil. Mato Grosso: Rio Verde, Chapadão, Apr 1918 (fl), Kuhlmann 2343-K (B*, lectotype, F, here selected; isolectotype, R). Figs. 3A, 6C, 10C,D, 11B, 12C, 14E,F, 25

Shrubs or **small trees** up to 4 m tall, 8 cm dbh. **Leafy branchlets** terete or decussately compressed, 2.3-3.5 mm thick, glabrous. **Stipules** sheathing, truncate, 1.2-2.1 mm long, coriaceous, glabrous outside, glabrous and with colleters inside, persistent. **Leaves** petiolate; petioles 9-14 mm long, 1-1.8 mm thick, glabrous; blades 5.1-12.5 x 3-6.7 cm, L/W 1.2:1-2.4:1, elliptic or obovate, cuneate or acute at base, short-acuminate to acute at apex, the acumen up to 0.8 mm long, coriaceous, glabrous throughout, brown or olive green when dry; secondary venation brochidodromous, 9-16 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect, 1.5-17.5 cm long; rachis terete or laterally compressed, 1.4-2 mm thick, glabrous, rarely with a stipular collar subtending the basal pair of flowers, portion of rachis from first pair to next flowers 12-24 mm; peduncle 1.5-5.5(-9) cm long. **Bracteoles** reduced, 0.3-0.5 mm long, margin entire, glabrous, with colleters inside. **Involucel** discoid, 0.3-0.7 x 2-4 mm, truncate or with small teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. Flower buds cylindrical, portion with lobes bent downward. **Flowers** zygomorphic, sessile. **Calyx** tubular, truncate or lobulate, 3.2-4 x 1.9-3.3 mm, strigose throughout or strigose only basally outside, glabrous and without colleters inside, with teeth or lobes, 0.2-0.5 x 0.2-1 mm, narrowly triangular, verrucose, green. **Corolla** 14.7-18.3 mm long; tube infundibuliform, 6.7-9.5 mm long, 1-1.9 mm wide at base, 0.5-1.8 mm wide at middle part, 3 mm wide at mouth, swollen or not at base, glabrous from base to middle part, strigose at mouth outside, with a ring of hairs at distal portion inside, at 2.3-4.5 mm from base, glabrous below ring inside, white or cream-white; lobes 2/3-1 of tube length, 6.4-9.2 x 1-2.2 mm, lanceolate, acute at apex, sericeous throughout, white or cream-white. **Filaments** 5-5.6 mm long, 0.3-0.5 mm wide, hirsute mainly at edges; anthers narrowly oblong, 1.9-2 x 0.3-0.4 mm; basal appendages oblong, 0.4 mm long, truncate at base; apical appendages narrowly triangular, 0.3-0.5 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 14.5-16.5 x 0.2-0.5 mm, pilose retrorsely from base to medial portion, glabrous apically; capitate portion globose before branches opening, style branches narrowly triangular, 0.3 mm long. **Ovary** 5-locular, globose, 1.2-2 x 1.8-2.7 mm, glabrous. **Fruit** globose, 3.5-4.5 x 3.7-5.4 mm, glabrous throughout, reddish. **Pyrenes** 3.8-4.4 x 1.9-2.2 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the basal portion of the septum, 2.1-2.7 x 0.7-0.9 mm.

Distribution (Fig. 25) **and ecology**. Found only in Brazil, from lowlands (< 500 m) to 900 m in the states of Bahia, Mato Grosso, Pará and Rondonia. Flowering specimens were collected in March, April, June, August and September. Fruiting specimens were collected in June, August and September.

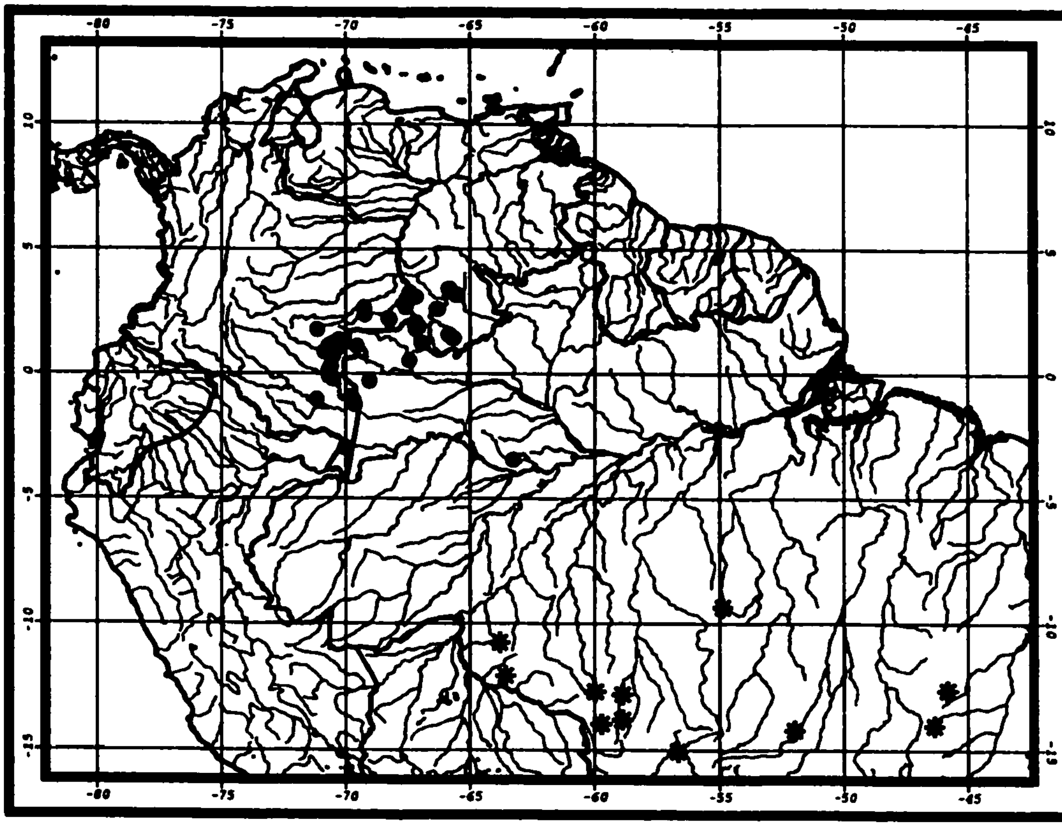


Fig. 25. Distribution of Retiniphyllum kuhlmannii (✱), and R. truncatum (●).

Additional specimens examined. BRAZIL. BAHIA: Espigão Mestre, ca. 100 km WSW of Barreiras, 12°40'S, 45°50'W, 750 m, 05 Mar 1972 (fl), Anderson et al. 36622 (NY). **MATO GROSSO:** 76 km E of Vilhena, 25 Sep 1963 (fl, fr), Maguire et al. 56820 (MO, NY); Juruena, Apr 1909 (fl), Hoehne 1785 (R); Rio Verde, Chapadão, Apr 1918 (fl), Kuhlmann 2343-K (F, R); Sararé, 13°50'S, 58°55'W, 04 Aug 1978 (fr), Pires & Santos 16394 (F, NY); Serra do Parecis, Brasilia-Acre highway, 700-900 m, 31 Aug 1963 (fl), Maguire et al. 56447 (NY); Serra do Roncador, ca. 94 km N of Xavantina, 550 m, 04 Jun 1966 (fl, fr), Irwin et al. 16561 (F, NY, US). **PARÁ:** Mun. Itaituba, Serra do Cachimbo, rd Santarém-Cuiabá, km 794, margin of Rio Braço-Norte, affluent of Curuá, 9°22'S, 54°54'W, 26 Apr 1983 (fl), Amaral et al. 967 (K, MO, NY, US). **RONDONIA:** Mun. Costa Marques, 123 km from Costa Marques, 12°05'S, 63°35'W, 24-25 Mar 1987 (fl), Cid 8666 (MO); S. Pacas Novos, 10°46'S, 63°49'W, 15 Aug 1976 (fl), Rosa et al. 885 (MO, NY).

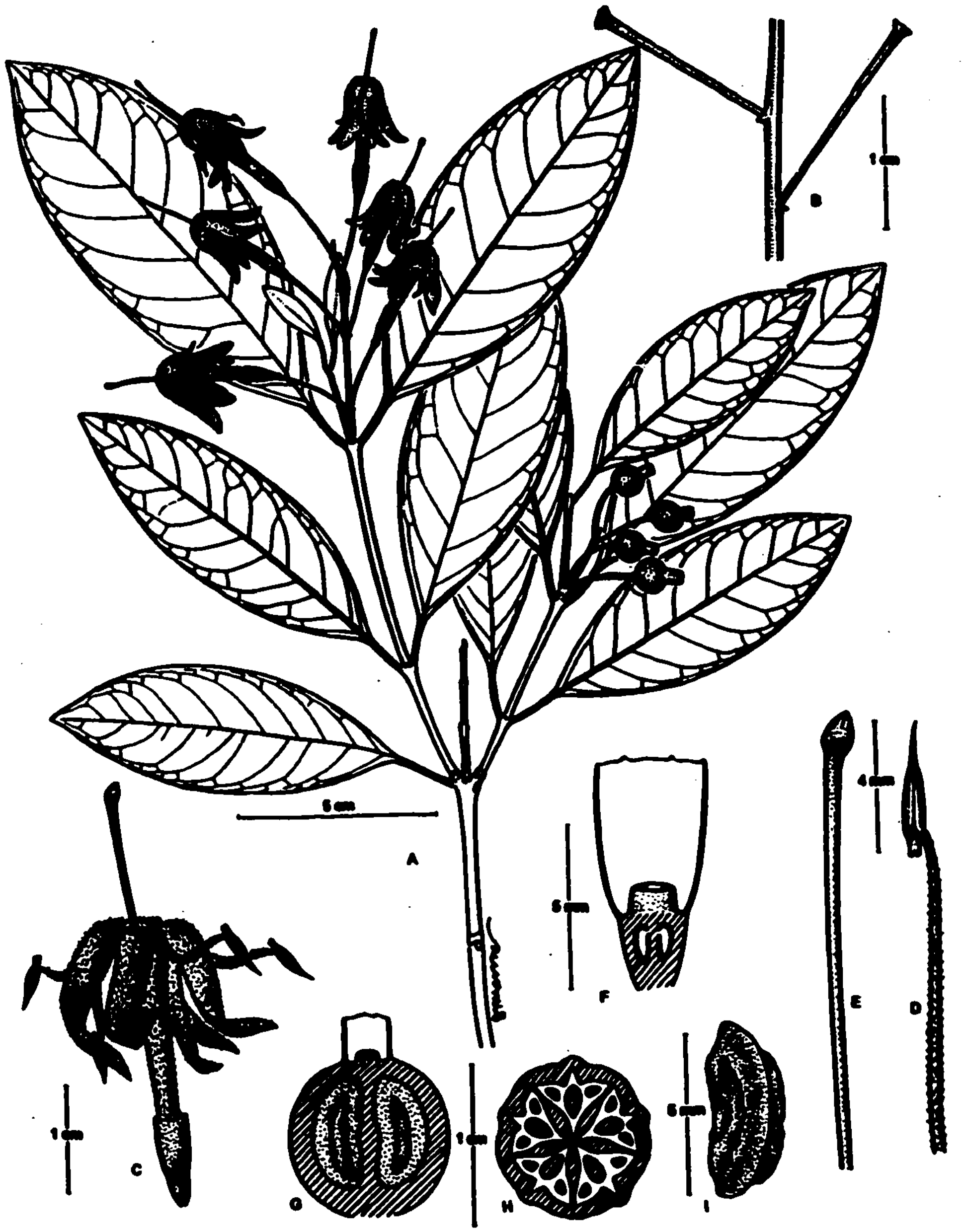
Retiniphyllum kuhlmannii is similar to R. truncatum, both having spicate inflorescences, short-tubular, white corollas and glabrous leaves. The former differs from the latter in having thinner rachis, ovary and fruit globose and not costate (vs. longitudinally ellipsoid and costate in R. truncaum). Also, Retiniphyllum kuhlmannii occurs in in the Brazilian states of Bahia, Goiás, Mato Grosso, Pará and Rondonia, while R. truncatum is widespread in the Guayana region, and occurs in the Brazilian state of Amazonas, and in Colombia and Venezuela.

Standley (1931a) selected the specimen of Retiniphyllum kuhlmannii preserved at B as the holotype, which was destroyed during WWII. From the isotypes deposited at F and R, I selected the specimen preserved at F as the lectotype, because it has eight open flowers, while the specimen at R has only one open flower and several floral buds.

1.4.10. Retiniphyllum laxiflorum (Benth.) N. E. Br., Trans. Linn. Soc. London, Bot. 6: 36. 1901. Synonymy and types cited under varieties. Figs. 4F, 7G, 9E, 10B, 13C, 15A, 26, 27

Shrubs to **small trees** up to 4 m tall. **Leafy branchlets** terete or quadrangular, 1.3-3 mm thick, glabrous or hirtellous. **Stipules** sheathing, truncate, margin entire or with small teeth, 1-2.5 mm long, coriaceous, puberulent or glabrous outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate; petioles 4-17 mm long, 1-1.5 mm thick, glabrous; blades 4.1-11.3 x 1.5-5.5 cm, L/W 1.9:1-3.1:1, elliptic, oblanceolate or rarely lanceolate, cuneate at base, acute or obtuse at apex, chartaceous or subcoriaceous, glabrous above and below, brownish or olive green when dry; secondary venation eucamptodromous and distally broquidodromous, 8-12 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, racemose, pendant, 6-8 flowers per inflorescence, (0.85-)1.5-7(-8.7) cm long; rachis decussately compressed or terete, 0.6-1.8 mm thick, glabrous, with a stipular collar up to 1 mm long subtending the basal pair of flowers; peduncle 0.1-2.3 cm long. **Bracteoles** reduced, 0.3-0.8 mm, margin with small teeth, glabrous, with colleters inside. **Involucel** discoid, 0.4-1 x 1.5-2 mm, with small teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, pedicellate, pedicels (5-)10-26 x 0.4-0.8 mm, glabrous. **Calyx** tubular, truncate, with small teeth or small lobes, (3.2-)3.9-5.5 x 2.1-3.7 mm, glabrous or diminutely hirtellous outside, glabrous and without colleters inside; lobes 0.6-1.5 mm long, widely triangular, glabrous or diminutely hirtellous, green tinged with red. **Corolla** (23-)27-44 mm long; tube narrowly infundibuliform, 13-22 mm long, 1.2-2 mm wide at base, 3.5-4 mm wide at mouth, sericeous outside, with a ring of hairs at basal portion, 1-1.5 mm wide at 2.5-3.9 mm from base, glabrous below ring, sericeous above ring inside, red; lobes 1/2-4/5 of tube length, rarely as long as corolla tube, 8-20 x 1.8-3.7 mm, oblong or lanceolate, acute or rarely obtuse at

Fig. 26. Illustration of Retiniphyllum laxiflorum. A. Habit of inflorescence showing stipule. B. Bracteoles and involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Ovary and calyx. G. Fruit. H. Fruit in transversal section. I. Pyrene


1 cm
B
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apex, sericeous throughout, red. **Filaments** (6-)8-11 mm long, 0.5-0.8 mm wide, expanded at base, pilose throughout; anthers elliptic, 2.6-3.5 x 0.6-0.8 mm; basal appendages obovate or oblong, 0.7-1 mm long, truncate at base; apical appendages narrowly triangular, 0.7-0.9 mm long. **Pollen** prolate-spheroidal or subprolate; sexine tectate-perforate. **Style** (20-)28-35 x 0.3-0.6 mm, pilose at base and medial portion, glabrous distally; capitate portion globose before branches opening, style branches triangular, up to 1 mm long. **Ovary** 5- or 6-locular, turbinate or narrowly obconical, 1.7-4 x 1.7-2.3 mm, glabrous. **Fruit** globose, (6-)7-9.7 x 5.5-8.5 mm, stipitate or sessile, stipe up to 2 mm long, glabrous, red. **Pyrenes** (3.8-)5-6.2 x 2.5-2.8 mm, surface dorsally verrucate, with two perpendicular wings, inserted near the dorsal margin. **Seeds** one per locule, cylindrical, attached at the distal portion of the septum, 2.6-2.7 x 0.7-0.9 mm.

Retiniphyllum laxiflorum is recognizable for its long and slender pedicels with pendulous flowers, and its long-tubular, red corollas. This species is most similar to Retiniphyllum maguirei, from which it differs in having longer corolla (27-44 mm in R. laxiflorum, vs. 20.5-27.3 mm

R. maguirei), longer pedicels, and lobes 1/2-4/5 of tube length (vs. 4/5-1 1/5 of tube length in R. maguirei).

George Bentham (1841) described Patima laxiflora Benth, and Baillon (1879) described Synisoon schomburgkianum Baill, both based on Schomburgk's collections in British Guyana. Brown (1901), noticed their similarities, and synonymized both taxa under his new combination Retiniphyllum laxiflorum.

Steyermark (1965) subdivided Retiniphyllum laxiflorum into three varieties, based mainly on the length of the corolla lobes: var. laxiflorum, with lobes 11-16 mm long, var. longilobum, with lobes 17-20 mm long, and var. brasiliense, with lobes 10-10.5 mm long. The ranges reported by Steyermark for each variety are not clear-cut, being variable even among the flowers of the type specimens. For instance, Maguire 3514, the paratype of var. longilobum, has lobes 14-16 mm long. In addition, Maguire 28707, cited by Steyermark in the typical variety, has lobes 17-19 mm long, a range that would belong to var. longilobum. Because the lobe size is a continuous gradient among var. laxiflorum and var. longilobum, and there is no correlation with other characters, these two varieties are here treated as synonymous. On the other hand, in Retiniphyllum laxiflorum var. brasiliense, endemic to the

Atlantic forest of the state of Bahia, Brazil, flowers and fruits are much smaller and this variety is here maintained as such.

Key to the varieties of Retiniphyllum laxiflorum

1. Pedicels 13-26(-9.5) mm long; corolla lobes 11-20 mm long; filaments 8-11 mm long; style 28-35 mm long; pyrenes 5-6.2 mm long; fruits 7-9.7 mm long. (Guyana, Surinam, and Venezuela) . . . . 10a. var. laxiflorum

1. Pedicels 5-12 mm long; corolla lobes 10-10.5 mm long; filaments 6-8 mm long; style 20-28 mm long; pyrenes 3.8-4.2 mm long; fruits up to 6 mm long. (Serra Sincorá, Bahia, Brazil) . . . . 10b. var. brasiliense

1.4.10.a. Retiniphyllum laxiflorum (Benth.) N. E. Br. var. **laxiflorum.** Retiniphyllum laxiflorum (Benth.) N. E. Br., Trans. Linn. Soc. London, Bot. 6: 36. 1901. Patima laxiflora Benth., J. Bot. (Hooker) 3: 220. 1841. Type. Guyana: Without locality, 1842-1843 (fl, fr), Rob.

Schomburgk 158 (lectotype, K, N. 2138, here selected; isolectotype, K, N. 2139).

Synisoon schomburgkianum Baill., Bull. Mens. Soc. Linn. Paris 208. 1879. Type. Guyana. Roraima, 1843 (fl, fr), Rob. Schomburgk 724 (815B) (lectotype, K, N. 2142, here selected; isolectotype, BM).

Retiniphyllum laxiflorum (Benth.) N. E. Br. var. longilobum Steyerm., Mem. New York Bot. Gard. 12: 233. 1965. Type. Venezuela. Amazonas: Cerro Sipapo (Paráque), infrequent in forest along N escarpment, 1400 m, 23 Dec 1948 (fl), Maguire & Politi 27869 (holotype, NY; isotype, US; photo-US at NY).

Distribution (Fig. 27) **and ecology**. Widespread in the Guayana Region, from uplands to highlands. Commonly found in escarpments or summits in most of the mountains of the region in Brazil, Guyana, Surinam and Venezuela. Although most often found from 500-1500 m, Retiniphyllum laxiflorum var. laxiflorum is also found in the Pantepui Province (>1500 m) in Mount Roraima (Guyana), Cerros Sipapo and Aratitiyope (Amazonas, Venezuela) and Ptari-tepui (Bolivar,

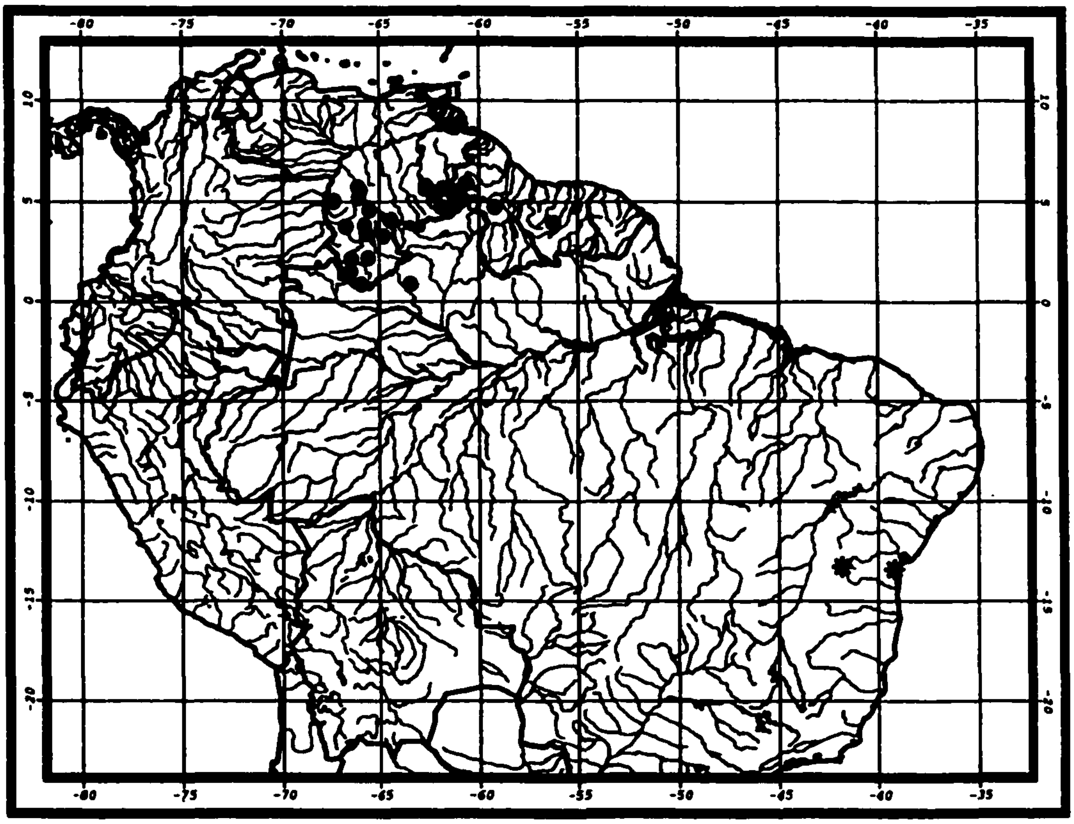


Fig. 27. Distribution of Retiniphyllum laxiflorum. var. laxiflorum (●), and R. laxiflorum var. brasiliense (✱).

Venezuela). This species is found in shrublands, and submontane and montane forest, often at margins of streams. Flowering and fruiting specimens were collected throughout the year, except in June.

Specimes examined. BRAZIL. Amazonas: Plato da Serra Araca, parte SE da Serra Norte, 0°51'N, 63°22'W, 1150-1250 m, 24 Feb 1984 (fl), Tavares et al. 135 (F, K, MO, NY, US); Mun. Barcelos, Plato da Serra Araca, Serra Norte, 6 horas W do campo de pouso, 0°51'N, 63°22'W, Alt. 1150 m, 20 Feb 1984 (fl), Amaral 1636 (F, INPA, GH, MO, NY); Serra Araca, 03 Feb 1978 (fl-fr), Rosa & Lira 2361 (INPA, NY). **Roraima:** Auaris Mission, Rio Auaris, 800 m, 06 Dec 1973 (fl), Prance et al. 20030 (NY, US); near summit of Serra Parima, S of Auaris airstrip, 1200 m, 30 Jul 1974 (fr), Prance et al. 21557 (INPA, GH, MO, NY, US); vicinity of Auaris, 4°3'N, 64°22'W, 760-800 m, 05 Feb 1969 (fl), Prance et al. 9607 (F, NY, R, US); vicinity of Auaris, 64°25'W-4°6'N, 800 m, 28 Jul 1974 (fl), Prance et al. 21452 (NY, US); vicinity of Auaris, upper slopes of Serra Parima, S of Auaris, 4°3'N, 64°22'W, 1400-1520 m, 10 Feb 1969 (fl-fr), Prance et al. 9802 (G, MO, NY, R); S Roraima, Arabapu creek bank edging the savannah on clay soil, 08 Dec 1957 (fl), Field No. RB107 NY.

GUYANA: Arabupu R., Mt. Roraima, 1300 m, 18 Nov 1938 (fl, fr), FDBG 2805 (K); Cuyuni-Mazaruni Region, Utshe camp, 5°45'N, 61°08'W, 975 m, 22 May 1990 (fr), McDowell & Gopaul 2731 (NY); Cuyuni-Mazaruni, Utshi R. to Great Falls trail, on Kamarang River, 5°40'N, 61°06'W, 910 m, 30 Jan 1996 (fl, fr), Clarke 890 (MO, NY, US); Kamarang River crossing, Kamarang head, 900 m, 05 Mar 1952 (fl), Maguire 33260 (NY); Mt. Roraima, on the great sandstone boulders, Philipp camp., 1600-1800 m, 08 Nov 1927 (fl), Tate 318 (NY); southern Pakaraima mountains, Chimapu savanna, 1200 m, 09 Sep 1961 (fl), Maguire et al. 46151 A NY, US; southern Roraima, 08 Dec 1957 (fl), FDBG 7931 (K, NY).

SURINAM: Summit of Tafelberg, between Lisa Creek waterfall over W rim of the tepui and upper Augustus, 3° 55'25"N, 56°11'20"W, 675 m, 03 Jul 1998 (fr), Evans et al. 3038 (NY); Tafelberg, Savanna No. 1, vicinity Camp No. 1, 03 Aug 1944 (fl), Maguire 24220 NY, US; Tafelberg, Savanna No. 4, 552 m, 15 Aug 1944 (fl-fr), Maguire 24373 (F, GH, MO, NY, US); Tafelberg, Savanna No. 7, 495 m, 17 Sep 1944 (fl-fr), Maguire 24787 NY; Tafelberg, Savanna No. 7, 495 m, 17 Sep 1944 (fl-fr), Maguire 24786 (NY); Tafelberg, Savanna No. 8, 776 m, 22 Aug 1944 (fl-fr), Maguire 24439 (F, GH, NY, US).

VENEZUELA. Amazonas: Río Ventuari, Río Manapiare, Caño Guaviarito, campo Verado and campo M. perez, Caño Verado, 900-1100 m, 30 Jan 1951 (fl), Maguire et al. 31645 (NY); Cerro Sipapo (Paraque), above lower escarpment, Caño Grande, 1500 m, 21 Jan 1949 (fl-fr), Maguire & Politi 28515 (GH, NY, US); Cerro Yavi, 1450 m, Mar 1-2 1947 (fl-fr), Phelps & Hitchcock 10 (NY, US); Depto. Atabapo, Serrania del Paru, sector centro-NE de la serrania, al S del Río Paru, 4°33'N, 65°31' W, 710 m, 5-6- Oct 1979 (fl-fr), Huber 4372 (NY, US); Cerro de la Neblina, Río Yatua, W escarpment slopes of Caño Grande E of cumbre camp, 1100-1300 m, 25 Nov 1957 (fl-fr), Maguire et al. 42229 (NY, US); Cerro Duida, 1000 m, (fl, fr), Farinas et al 427 (NY[2], VEN); Cerro Guanay, 5°50'15"N, 66°25'58"W, 1150 m, 28 Feb 1995 (fr), Michelangeli, F. 204 (MO); Cerro Sipapo (Paraque), near intermediate camp, 600 m, 02 Feb 1949 (fl), Maguire & Politi 28707 (NY, US); Cerro Sipapo (Paraque), N escarpment, 1400 m, 25 Dec 1948 (fr), Maguire & Politi 27925 (NY, US); Cerro Yapacana, 3°45'N, 66°45'W, 550-825 m, 07 May 1970 (fl), Steyermark & Bunting 103087 (NY, US); Cerro Yapacana, summit, 3°45'N, 66°45'W, 1000-1200 m, 5-7 May 1970(fl), Steyermark & Bunting 103141 (NY); Cerro Yapacana, Río Orinoco, 02 Jan 1951 (fl-fr), Maguire et al. 30626 (NY); Depto. Atabapo, between Río Ocamo and Río Matacumi, 3 16'N, 64 45'W., 850-870 m, 16 Feb 1981 (fl), Guanchez 605 (VEN); Depto. Atabapo, Cerro Duida, 3°32'N, 65°32'W, 865 m, 02 Mar 1992 (fl), Dezzeo & Fernández 338 (VEN); Depto. Atabapo, E slope of Huachamacari, 3°49'N, 65°42'W, 600-700 m, 03 Nov 1988 (fl), Liesner 25761 (MO, NY); Depto. Atabapo, N of Duida, 3°45'N, 65°40'W, 750 m, 16 Nov 1982 (fr), Guanchez 2307 (MO); Depto. Atabapo, slope of Huachamacari, 3°39'N, 65°42'W, 850 m, 06 Mar 1985 (fl-fr), Liesner 18348 (MO, NY); Depto. Atabapo, altiplanicie del Cerro Paru, 4°34'N, 65°31'W, 590 m, 01 Feb 1992 (fl, fr), Chaviel 306 (MO, NY); Depto. Atabapo, altiplanicie del Cerro Paru, 4°34'N, 65°31'W, 590 m, 01 Feb 1992 (fl), Chaviel 181 (MO, NY); Depto. Atabapo. Serrania de Paru, sector N, 4°32'N, 65°31'W, 800 m, 03 Mar 1979 (fl-fr), Huber 3618 (COL, K, NY); Depto. Atures. Río Coro-Coro, W of

Serrania de Yutaje, 8 km N of settlement of Yutaje, 5°41'30"N, 66°07'30"W, 650 m, 21 Feb 1987 (fl-fr), Holst & Liesner 3103 (MO, NY, US); Depto. Río Negro, Cerro Aratitiyope, 2°10'N, 65°34'W, 990-1670 m, 24-28 Feb 1984 (fl), Steyermark et al. 130057 (MO, NY); Depto. Río Negro, Cerro de la Neblina Camp IV, 15 km NNE of Pico Phelps, N branch of river in canyon, 780 m. 0°51'N, 65°57'W, (fr), Liesner 16622 (MO, NY); Dto. Roscio, 3 km S of El Pauji, 4°90'N, 61°35'W, 900 m, 19 Oct 1985 (fl-fr), Holst & Liesner 2337 (MO); Río Casiquiare, Farinas et al. 674 (NY); Río Orinoco, Río Cuao, along Cuao Creek, 125 m, 27 Nov 1948 (fl), Maguire & Politi 27471 (NY, US); Río Siapa, below Raudal Gallineta (about 110 river Km from mouth), 900 m, 21 Jul 1959 (fl-fr), Wurdack & Adderly 43551 (GH, NY, US); Serrania Yutaje, Río Manapiare, Caño Yutaje, 1250 m, 12 Feb 1953 (fl,fr), Maguire & Maguire 35184 (NY); Serrania Yutaje, Río Manapiare, Caño Yutaje, 1200 m, 25 Feb 1953 (fl), Maguire & Maguire 35414 NY; Serrania Yutaje, Río Manapiare, Caño Yutaje, 1300-1400 m, 15 Feb 1953 (fl), Maguire & Maguire 35241 (GH, NY, US). BOLIVAR: 17 km E of El Pauji by rd. and 64 km W of Santa Helena, Río Las Ahallas, 4°30'N, 61°30'W, 850 m, 29 Oct 1985 (fl), Liesner 19072 (MO); 17 km E of El Pauji by rd. and 64 km W of Santa Helena, Río Las Ahallas, 4°30'N, 61°30'W, 850 m, 29 Oct 1985 (fl, fr), Liesner 19103 (MO); 3 km S of El Pauji, 4°30'N, 61°35'W, 900 m, 19 Oct 1985 (fl, fr), Liesner & Holst 18814 (MO); 4 km W of El Pauji, 2 to 5 km N of rd., Río Chaberú, 4°30'N, 61°36'W, 750-900 m, 12 Nov 1985 (fl, fr), Liesner 19907 (MO); Auyantepui, terraza de Guayaraca, 1100 m, Apr 1956, Vareschi & Foldats 4662 (F); Chimantá Massif, along Río Sarven 1 km downstream from camp 9, 1200 m, 08 Feb 1953 (fr), Wurdack 34340 (NY); Dto. Piar/Sifontes, altiplanicie of Río Uaiparu, aprox. 50 km NNW de Ikabaru, 4°42'N, 61°49'W, 900 m, 18 Feb 1986 (fr), Huber & Fernandez 11327 (NY[2]); Dto. Roscio, 2 km SW of Peray-tepui, 55 km from Sta. Helena on rd. to Icabarú, 4°33'N, 61°30'W, 1050 m, 26 Jul 1983 (fl), Huber & Aalarcón 7885 (VEN); Dto. Roscio. Altiplanicie entre San Francisco de Yuruani y Chirimata, aprox. 10-15 km al ENE de San Ignacio de Yuruani, 5°02'N, 61°00'W., 1100 m., 02 Mar 1984 (fl), Huber 9165 (NY); Dto. Piar, Guayaraca, between escarpment and Río Guayaraca S base of Auyan-tepui, 5°44'N, 62°32'W, 950 m, 25-27 Nov 1982 (fl, fr), Davidse & Huber 22672 (MO, NY)); Dto. Piar, Guayaraca, at top of Salto Aicha near E base of Uaipan-tepui, 5°38'N, 62°32'W, 1100 m, 27-28 Nov 1982, Davidse & Huber 22924 (MO); Gran Sabana, Uarí, 15 Mar 1946 (fl, fr), Tamayo 3131 (F, G, US); Gran

Sabana, Ilu-tepui, at NW base of mountain, 1000 m, 07 Feb 1952 (fl-fr), Maguire 33209 (NY); Gran Sabana, ca. 10 km SW of Karaurin-tepui at junction of Rio Karaurin and Rio Asadon (Río Sanpa), 5°19'N, 61°03'W, 900-1000 m, 23 Apr 1988 (fl-fr), Liesner 23707 (MO, NY); Gran Sabana, ca. 10 km SW of Karaurin-tepui at junction of Río Karaurin and Río Asadon (Rio Sanpa), 5°19'N, 61°03'W, 900-1000 m, 21 Apr 1988 (fl-fr), Liesner 23551 (MO); Kavanayen, 28 May 1946 (fl), Lasser 1799 (F, K, NY, US); La Gran Sabana, Chirimata, rd. to Monte Roraima, 1040 m, 04 May 1988 (fl), Sastre et al. 8483 (MO); Lueoa-San Francisco de Yuruani rd. Km 210, Gran Sabana, 5°20'N, 61°13'W, 1150 m, 22 Nov 1997 (fl-fr), Luteyn et al. 15271 (NY); Mount Roraima District, vicinity of Arabupu, 1300 m, 18 Nov 1938 (fl), Pinkus 44 (F, G[2], GH, MO, NY[2], US); Mun. Gran Sabana, Parupa, 5°42'N, 61°38'W, 1200 m, 05 May 1996 (fl), Diaz et al. 2638 (MO); Mun. Raúl Leoni, upper Río Túriba and Caño La Miel, 6°34'N, 66°23'W, 800 m, Jun 1989 (fl), Fernández & Delgado 5864 (MO); Mun. Raúl Leoni, upper Río Túriba and Caño La Miel, 6°34'N, 66° 23'W, 800 m, Jun 1989 (fl), Fernández 5636 (MO, NY); Mun. Urdaneta, Dto. Roscio, 5°0'N, 61°0'W, 1120 m, 19 Feb 1986 (fr), Hernández 180 (MO); Ptari-tepui, vicinity of Misia Kathy Camp, Alt. 1585 m., 28 Oct 1944 (fl), Steyermark 59463 (F, NY[2]); Quebrada O-paru-má, between Santa Teresita de Kavanayén and Río Pacairo, 1065-1220 m, Nov 20-21 1944 (fl), Steyermark 60353 (F[2], US); Río Purpur, valle Uriman, Alto Caroni, camino al Auyan-tepui, 800 m, 01 Jan 1949 (fl-fr), Cardona 2593 (NY); Uaipan-tepui, above Salto Hacha, on plateau at SE of the peaks of Uaipan, 1000 m, 02 Mar 1967 (fl-fr), Koyama & Agostini 7425 (NY[2], US).

Local name. Guyana: Tukwoinauku (Arekuna, Forest Department of British Guiana, 2805).

1.4.10.b. Retiniphyllum laxiflorum (Benth.) N. E. Br. var. **brasiliense** Steyerm., Mem. New York Bot. Gard. 12: 234. 1965. Type. Brazil. Bahia: Gorge of Zesuserra, Serra

Sincorá, rocky soil, 1000 m, 9 Oct 1942 (fl, fr), Krukoff 3 (holotype, NY).

Distribution (Fig. 27) **and ecology.** Endemic to Serra Sincorá, Bahia, Brazil, from 1000 to 1650 m. Flowering and fruiting specimens were collected in October and December.

Additional specimens examined. BRAZIL. Bahia: Mucugé, Serra do São Pedro, 1100-1280 m, 17 Dec 1984 (fr), Lewis 7041 (K[2]); Mun. Abaira, Agua Limpa, 13°18'N, 41°52'W, 1350-1650 m, 21 Dec 1991 (fl), Harley et al. 50250 (NY).

1.4.11. Retiniphyllum longiflorum Steyerm., Brittonia 33: 396. 1981. Type. Brazil. Amazonas: Rio Uaupés, Taracuá, catinga, 1 Mar 1959 (fl), P. Cavalcante 712 (holotype, VEN). Fig. 17

Shrubs 2 m tall. **Leafy branchlets** aristate, 2-3 mm thick, glabrous. **Stipules** sheathing, truncate, 1.2-1.6 mm long, coriaceous, glabrous outside, glabrous and with colleters inside, persistent. **Leaves** petiolate; petioles 9-16 mm long, ca. 1-2 mm thick, minutely puberulent; blades 11.4-13.5 x 2.6-3 cm, L/W 4.4:1 to 4.5:1, oblanceolate, attenuate at base, acuminate at apex, the acumen 6 mm long, chartaceous, glabrous above, brown when dry; primary, secondary and tertiary veins minutely puberulent below; secondary venation broquidodromous, 10-12 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, racemose, erect, 3.5 cm long, rachis ridged, 1.2-1.6 mm thick, glabrous, minutely verrucose, without bracts. **Bracteoles** reduced, 0.4-0.5 mm long, margin crenate, with colleters inside. **Involucel** discoid, 0.5-0.8 x 1.5-2 mm, margin crenate, coriaceous, minutely puberulent and verrucose outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, pedicellate; pedicels 3.8-4 mm long, minutely puberulent and verrucose;. **Calyx** cupular, lobulate, 1.1-1.5 x 2-2.2 mm, minutely puberulent and verrucose outside, glabrous and with colleters inside; lobes 0.1 x 1.2 mm, broadly triangular, with irregular margins. **Corolla** 39.5-42.5 mm long; tube narrowly infundibuliform, 32-33 mm long, 1.8-2.3 mm wide at base, 3.5-5.7 mm wide at mouth, minutely puberulent outside, with a ring of hairs at basal portion, 1 mm wide at 6.7 mm from base, glabrous below ring and puberulent above ring inside, reddish; lobes 1/4 of tube length, 7.8-9 x 1.9-2.2 mm, oblong, acute at apex, densely puberulent at mouth and sparsely puberulent throughout, reddish. **Filaments** 4-4.5 mm long, expanded at base, densely puberulent at base; anthers narrowly elliptic, 2.5-3.2 x 0.6-0.8 mm; basal appendages oblong or elliptic, 0.4-0.5 mm long; apical appendages narrowly triangular, 0.5-0.7 mm long. **Pollen** prolate-spheroidal or subprolate; sexine tectate-perforate. **Style** 42-44 x 0.3-0.4 mm, sparsely puberulent; capitate portion ellipsoid before branches opening, style branches triangular, 0.8-0.9 x 0.2-0.3 mm. **Ovary** 5-locular, cylindrical, 2.5-2.8 x 1.8-2 mm, puberulent. **Fruits** unknown.

Distribution (Fig. 17) **and ecology**. Only known from the type locality from the Rio Uaupés, Brazil. Flowering specimens were collected in March.

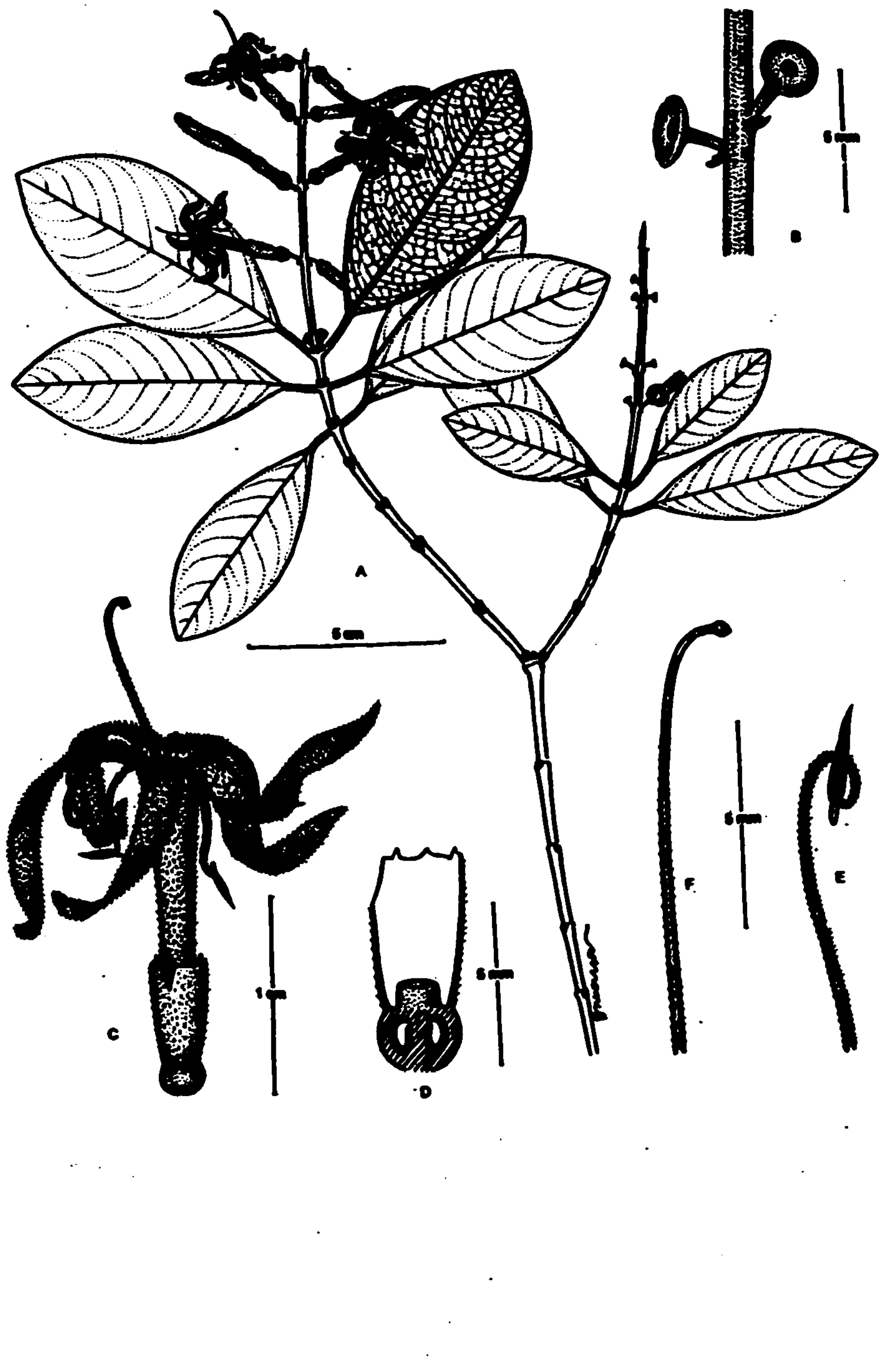
Retiniphyllum longiflorum is similar to *R. chloranthum* and *R. concolor* in having pedicellate flowers, long-tubular corollas, and cupular calyces. Nevertheless, *Retiniphyllum longiflorum* is easily recognizable from the other two species by its oblanceolate leaves, red corollas, and corolla lobes 1/4 of tube length.

1.4.12. Retiniphyllum maguirei Standl., Bull. Torrey Bot. Club 75: 571. 1948. *Retiniphyllum maguirei* var. *maguirei*, Mem. New York Bot. Gard. 12: 239. 1965. Type. Surinam: Tafelberg, Savanna No. 4, 552 m, 15 Aug 1944 (fl), Maguire 24374 (holotype, F, N. 1170997; isotypes, F, NY, US, VEN; photo-US at NY). Figs. 5C, 14H, 17, 28

Retiniphyllum maguirei Standl. var. reticulatum Steyerm., Mem. New York Bot. Gard. 12: 239. 1965. Type. Surinam: Tafelberg, Savanna No. 1, 565 m, 13 Aug 1944 (fl), Maguire 24361 (holotype, VEN; isotypes, F, GH, MO, NY, US).

Shrubs up to 4 m tall. **Leafy branchlets** terete, 1.5-3 mm thick, hirsute. **Stipules** sheathing, truncate, margin entire or irregular, 1.2-2 mm long, coriaceous, strigose outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate; petioles 8-14 mm long, 1.5-1.6 mm thick, pubescent; blades 4.9-9.2 x 2.3-3.9 cm, L/W 2.1:1-2.9:1, oblanceolate or elliptic, acute at base and at apex, subcoriaceous or chartaceous, glabrous above, glabrous or scarcely hirsutulous below, brownish or olive green when dry; primary, secondary and tertiary veins strigose or hirsute below; secondary venation eucamptodromous, 8-11 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal,

Fig. 28. Illustration of Retiniphyllum maguirei. A. Habit of inflorescence showing stipule. B. Bracteoles and involucels. C. Flower in anthesis. D. Ovary and calyx. E. Stamen, anther with basal and apical appendages. F. Style and stigmatic surfaces.


A
B
C
D
E
F
5 cm
5 mm
1 cm

racemose, erect, 4.2-11.3 cm long; rachis decussately compressed, rarely angulate, 1.5-1.8 mm thick, glabrous or pubescent, without bracts; peduncle 1.2-2.3 cm long, glabrous or pubescent. **Bracteoles** reduced, 0.4-0.7 mm long, with small teeth, glabrous, with colleters inside. **Involucel** discoid, 0.7-0.8 x 2-2.3 mm, with small teeth, coriaceous, glabrous or strigose basally outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, subsessile or pedicellate, pedicel size decreases toward apex; pedicels 0.3-5 x 0.6 mm, glabrous or distally strigose. **Calyx** tubular, with small teeth or lobes, 4-6 x 2.3-3.3 mm, hirsutulous outside, glabrous and without colleters inside; lobes 0.2-0.75 x 0.7-1 mm, triangular, hirsutulous or glabrous. **Corolla** 20.5-27.3 mm long; tube narrowly infundibuliform, 11-14.5 mm long, 1.2-2 mm wide at base, 3-3.7 mm wide at mouth, sericeous outside, with a ring of hairs at basal portion, 1.7-2.2 mm wide at 3.7-4.9 mm from base, glabrous below ring, sericeous above ring inside, red; lobes 4/5-1 1/5 of tube length, 10-15 x 1.2-2.2 mm, lanceolate, acute at apex, sericeous outside and inside, red. **Filaments** 7-10 mm long, 0.3-0.6 mm wide, expanded at base, pilose throughout or only at edges; anthers lanceolate, 1.5-3 x 0.4-0.6 mm; basal appendages obovate, 0.5-0.7 mm long; apical appendages narrowly triangular, 0.6-1 mm long. **Pollen** with sexine tectate-perforate. **Style** 19-27 x 0.3-0.5 mm, pilose at base and medial portion, and glabrous distally; capitate portion globose before branches opening, style branches narrowly triangular, up to 0.3 mm long. **Ovary** 5-locular, globose or subglobose, 1.6-2.1 x 1.7-2.8 mm, glabrous. **Fruit** globose, 5.5-5.8 x 5.5-6.5 mm, basally glabrous, distally hirsutulous, blackish. **Pyrenes** 4-4.8 x 2-2.6 mm, surface dorsally verrucate, with two perpendicular wings inserted near the ventral margin. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.5-2.6 x 0.6-0.8 mm.

Distribution (Fig. 17) **and ecology**. Only known from Mount Tafelberg, Surinam, at about 500 m. Flowering and fruiting specimens were collected in August and September.

Additional specimens examined. SURINAM: Mt. Tafelberg, Savanna No. 1, vicinity camp No. 1, 03 Aug 1944 (fl, fr), Maguire 24220 (F[1171014], GH, MO, NY, US); Mt. Tafelberg, Savanna No. VII, 495 m, 17 Sep 1944 (fl, fr), Maguire 24787 (F, GH, MO, NY, US).

Retiniphyllum maguirei is unique in the genus in having racemose inflorescences with pedicels that decrease in length toward the distal end, and the uppermost flowers subsessile. This species is similar to Retiniphyllum laxiflorum, by having long tubular, red corollas. Retiniphyllum laxiflorum has longer corollas, pedicels two to five times longer than in R. maguirei, and corolla lobes 1/2-4/5 of tube length (vs. 4/5-1 1/5 in R. maguirei.

Standley (1948) suggested that this species might be of hybrid origin, from a cross between R. laxiflorum and R. schomburgkii. The latter species has spicate inflorescences with short tubular, white corollas, while the former has racemose inflorescences with long tubular, red corollas. Because no population studies of this species where undertaken, Standley's hypothesis remains to be tested.

Standley (1948) described Retiniphyllum maguirei from two collections made by Maguire at Mount Tafelberg, Surinam. Steyermark (1965) emended Standley's original description adding, among other characters, that the pedicels are 1-7 mm long (vs. 3-5 mm long in Standley's description), and the calyx 6-9 mm long (vs. 6-7 mm). However, according to my observations, Steyermark's emendation is incorrect, and Standley's original description is here maintained. The flowers of Retiniphyllum maguirei range from subsessile to pedicellate in the same inflorescence. The basal flowers have pedicels up to 5 mm long, and the other pedicels gradually decrease in size toward the distal end, where they are subsessile. The calices of Retiniphyllum maguirei range from 4 to 6 mm long, in agreement with Standley's description (6-7 mm) considering that he included ovary length.

Maguire 24220 was cited among the paratypes of R. maguirei, but the duplicate specimen preserved at F is instead Retiniphyllum laxiflorum, with longer pedicels. This specimen is perhaps what caused Steyermark's erroneous emendation in describing the pedicels of Retiniphyllum maguirei as much longer than what they really are.

In the same publication, Steyermark (1965) described Retiniphyllum maguirei var. reticulatum, differentiating it from the typical variety by its prominently reticulate leaves, pedicels 1-4.5 mm long (vs. 2-7 mm), calyx 8.5-9 mm long (vs. 6-7 mm), with triangular lobes up to 0.75 mm (vs. with only minute protuberances). Steyermark stated that the type collection (Maguire 24374) is a mixture of the two varieties. According to him, the holotype at F and the isotype preserved at VEN correspond to the typical variety, while the isotype at NY would correspond to Retiniphyllum maguirei var. reticulatum. In my observations, the pedicels of Retiniphyllum maguirei are up to 5 mm long, the calyces are up to 6 mm long and with minute protuberances (Maguire

24220) or small lobes (Maguire 24374 at F and VEN), therefore not supporting the characters used by Steyermark to differentiate between these varieties. Therefore, no varietal ranks are recognized in R. maguirei.

1.4.13. **Retiniphyllum parvifolium** Steyerm., Brittonia 33: 397. 1981. Type. Brazil. Pará: Serra do Cachimbo, 425 m, 12 Dec 1956 (fl), Murça Pires, Black, Wurdack & Silva 6063 (holotype, NY; isotype, VEN). Figs. 6A,B, 14D, 29

Shrubs up to 2.5 m tall. **Leafy branchlets** terete or decussately compressed, 1.1-2 mm thick, hirsutulous, diminutely verrucose. **Stipules** sheathing, truncate, margin entire or irregular, 1-2 mm long, coriaceous, hirsutulous outside, glabrous and with colleters throughout inside, subcaducous or persistent. **Leaves** petiolate; petioles 2.2-5 mm long, 0.8-1 mm thick, hirsutulous; blades 2.2-4.2 x 1.1-2.7 cm, L/W 1.3:1-2.3:1, obovate, elliptic or ovate, acute at base, rounded, retuse or acute at apex, chartaceous, glabrous, with a row of hirsute hairs at margin above, glabrous below, brownish or olive green when dry; primary vein sparsely hirsute below, secondary and tertiary veins glabrous below; secondary venation broquidodromous, 5-9 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect, 4-18 cm long; rachis grooved, rarely ridged, 1-2.2 mm wide, hirsutulous, with or without a stipular collar and two bracts subtending the basal pair of flowers, bracts 2.7 mm long, portion of rachis from first pair to next flowers 0.6-1.9 cm; peduncle 0.9-10.6 cm long, hirsutulous. **Bracteoles** reduced, 0.2-0.6, margin entire, glabrous or hirsutulous, with colleters inside. **Involucel** discoid, 0.3-1 x 0.2-0.6 mm, truncate, coriaceous, hirsutulous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, bent downward. **Flowers** zygomorphic, sessile. **Calyx** tubular, truncate with small teeth, 3.1-4 x 2.2-3 mm, hirsute outside, glabrous and without colleters inside. **Corolla** 14-18.8 mm long; tube infundibuliform, 5.5-7.8 mm long, 0.7-1.5 mm wide at base, 2-3 mm wide at mouth, sericeous outside, with a ring of hairs at distal portion, 1.5 mm wide at 4-4.2 mm from base, glabrous below ring, white to cream-white; lobes 1-1 4/5 of tube length, 7.5-11.5 x 1.3-3.1 mm, oblong or oblanceolate, acute or rounded at apex, sericeous throughout, white to cream-white. **Filaments** 4.5-7.2 mm long, 0.2-0.7 mm wide, expanded at base, pilose throughout or at edges; anthers narrowly elliptic or lanceolate, 2-3 x 0.3-0.7 mm; basal appendages bilobed, each lobe narrowly triangular or oblong, 0.4-0.7 mm long; apical appendages narrowly triangular, 0.4-0.7 mm long. **Pollen** prolate-spheroidal or subprolate; sexine tectate-perforate. **Style** 11.5-16 x 0.2-0.3 mm, glabrous throughout; capitate portion ellipsoid before branches opening, style branches narrowly triangular, up to 0.2 mm long. **Ovary** 5-locular, globose or longitudinally ellipsoid, 0.9-1.5 x 1-2 mm, glabrous. **Fruit** globose or longitudinally ellipsoid, 3.3-4 x 3.6-4.8 mm, glabrous. **Pyrenes** 2.5-3.8 x 1.7-2 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the basal portion of the septum, 2-2.6 x 0.8-0.9 mm.

Distribution (Fig. 29) **and ecology**. Endemic to the Serra do Cachimbo, ranging across the states of Para and Mato grosso, at lowlands from 300-400 m. Found in grassy savannas on sandstone, and in campinas. Flowering specimens were collected in February, April, May, November and December. Fruiting specimens were collected in February, April, May and September.

Additional specimens examined. BRAZIL. Mato Grosso: Fazenda Cachimbo, Projeto RADAM BR 165, rd. Santarém Cuiabá, km 877, Salto de Curuá, 01 Dec 1976 (fl), Cordeiro 1269 (F, NY, US). **Pará:** N slope of Serra do Cachimbo, cachoeira de Curuá, 300 m, 11 Nov 1977 (fl), Prance et al.

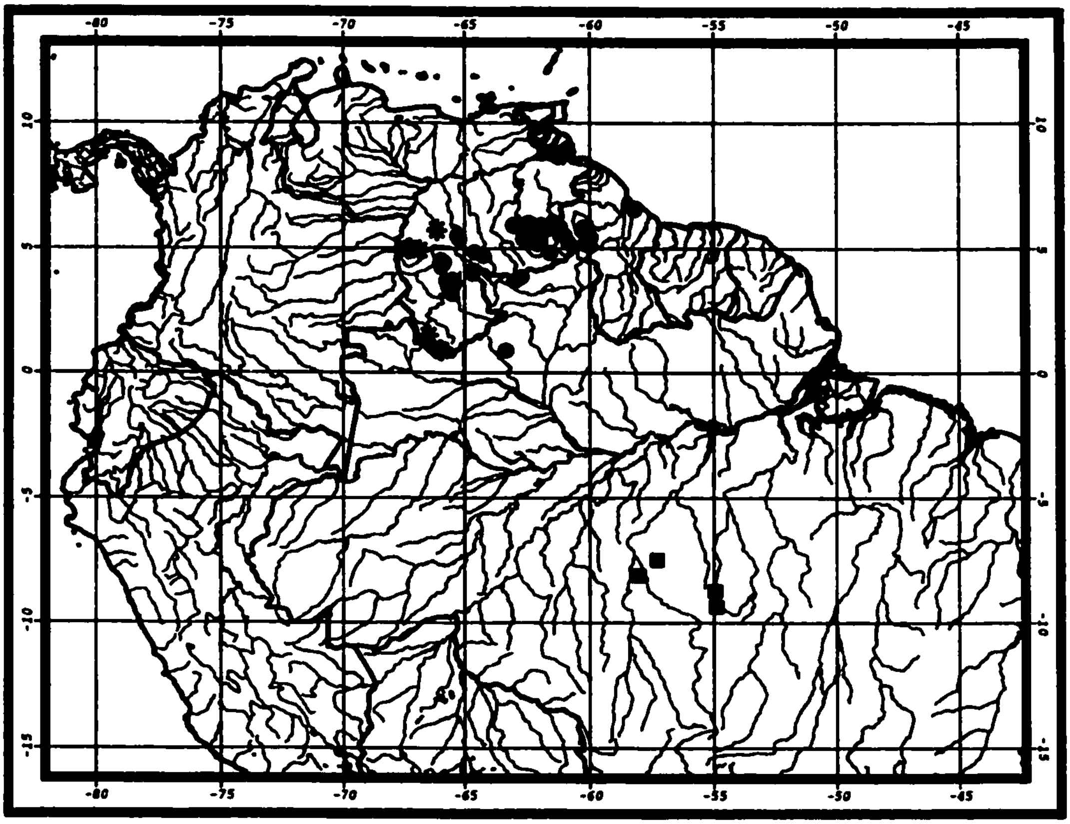


Fig. 29. Distribution of Retiniphyllum parvifolium, R. scabrum, and R. tepuiense

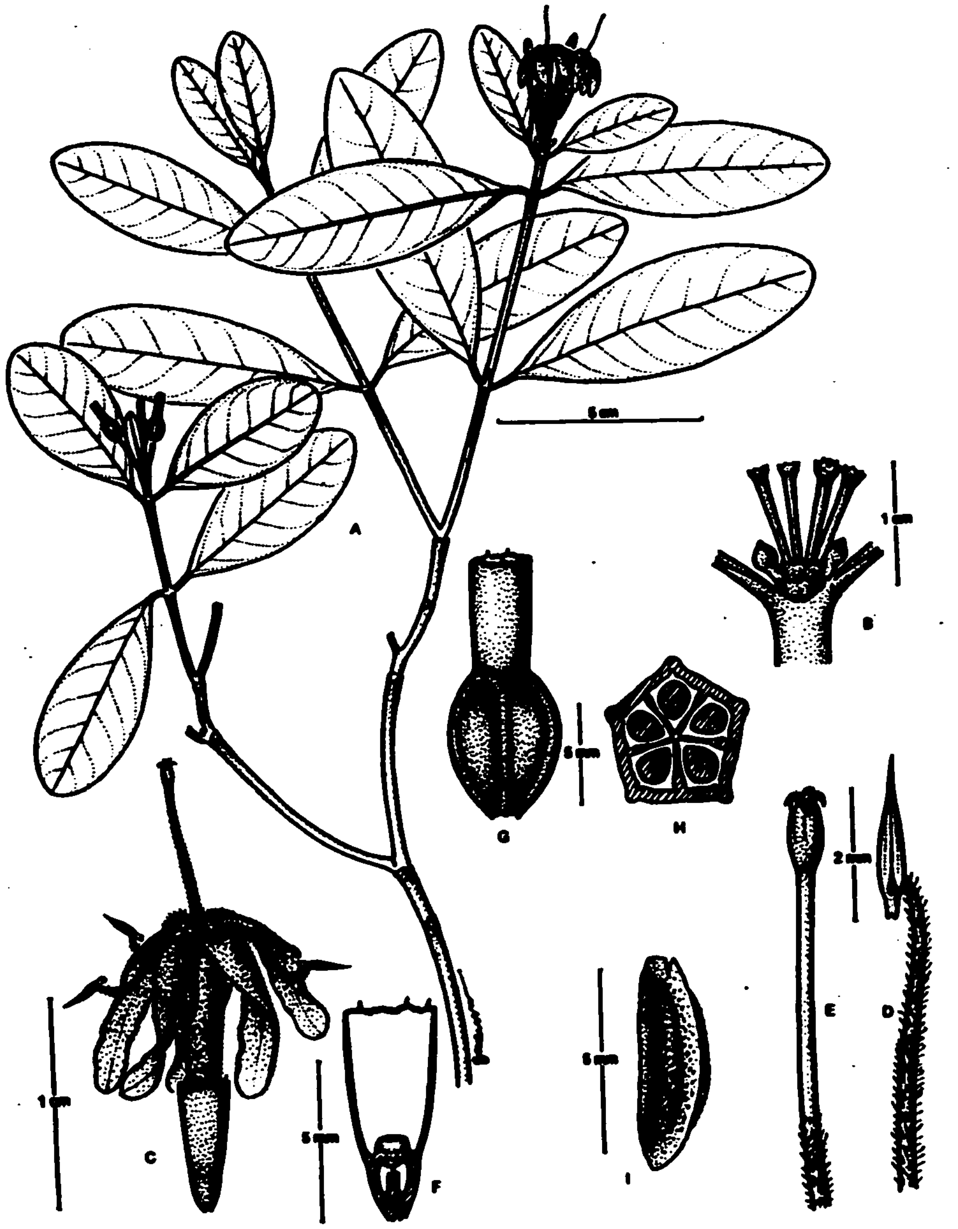
24847 (NY, US[3]); Serra do Cachimbo, 8°7'S, 58°01'W, 22 Sep 1977 (fr), Vaz s.n. (RB 197681) (NY); Serra do Cachimbo, along BR-163, Cuiaba-Santarem rd., at Corrego São Bento, 21 Feb 1977 (fl), Kirkbride & Lleras 2978 (BR, F, K, NY, US); Serra do Cachimbo, along BR-163, Cuiaba-Santarem rd., km 879, 290 m, 20 Feb 1977 (fl, fr), Kirkbride & Lleras 2934 (NY, US); Serra do Cachimbo, along BR-163, Cuiaba-Santarem rd., km 879, 20 Feb 1977 (fl), Kirkbride & Lleras 2974 (NY); Serra do Cachimbo, km 798, vicinity of Cachimbo Airport, 11 Nov 1977 (fl), Prance et al. 25239 (GH, MO, NY, US); Serra do Cachimbo, Mun. Itaituba, rd Santarém-Cuiabá BR-163, km 749, Cachoeira da Luz, rio Curuá, 9°22'S, 54°54'W, 25 Apr 1983 (fl, fr), Amaral et al. 944 (MO, NY, US); Serra do Cachimbo, Mun. Itaituba, rd Santarém-Cuiabá BR-163, km 877, Cachoeira da Luz, rio Curuá, 8°45'S, 54°57'W, 03 May 1983 (fl, fr), Amaral et al. 1118 (NY, F); Serra do Cachimbo, NW edge, 25 km by foot NE of Missão Velha, on Rio Cururú, 7°30'S, 57°15'W, 400 m, 14 Feb 1974 (fl, fr), Anderson 10960 (NY, US).

Retiniphyllum parvifolium is an elegant shrub easily recognizable for its small leaves. Its flowers are similar to those of R. schomburgkii, which are different by having hirsute calyx, glabrous style, and anthers with bilobed basal appendages.

1.4.14. **Retiniphyllum pauciflorum** Kunth ex K. Krause, Bot. Jahrb. Syst. 40: 326. 1908. Type. Venezuela. Amazonas: Near San Baltazar, Río Atabapo, May 1800 (fl), Humboldt & Bonpland 934 (B*; lectotype, F, N. 606657 (fragment), here selected; photo-B at F, GH, MO, NY). Figs. 3E, 4A, 15E, 17, 30

Shrubs 1-4 m tall. **Leafy branchlets** decussately compressed or rounded, 1-3 mm thick, glabrous, hirsutulous or hirsute. **Stipules** sheathing, with colleters throughout inside, dimorphic, in some branches truncate or rarely lobulate, 1-2 mm long, coriaceous, glabrous outside, persistent; in some other branches splitting in one side, acute, 6-9 mm long, papyraceous, strigose outside, glabrous inside, caducous. **Leaves** petiolate; petioles 5-12 mm long, 1-1.5 mm thick, glabrous; blades 4.3-8.7 x 1.5-3.4 cm, L/W 2.1:1 to 3.2:1, oblanceolate, elliptic, subovate or suboblong, acute or cuneate at base, round, acute or retuse at apex, coriaceous, glabrous, brown or olive green when dry; primary vein hispidulous above, glabrous or strigose below; secondary venation weak broquidodromous, 9-12 each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, umbellate, erect, 4 flowers per inflorescence, with or without two bracts at base, 0.8-2.5 cm long; peduncle reduced, 1.3-2 mm long, glabrous. **Bracteoles** reduced, 0.5-1 mm long, truncate, with small teeth, coriaceous, glabrous, with colleters inside. **Involucel** discoid, 0.2-0.5 x 1-1.3 mm, margin with small

Fig. 30. Illustration of Retiniphyllum pauciflorum. A. Habit of inflorescence. B. Bracteoles and involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Ovary and calyx. G. Fruit. H. Fruit in transversal section. I. Pyrene.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teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the stem. **Flower buds** cylindrical, straight, or rarely bent up or downward. **Flowers** actinomorphic, pedicellate, pedicels 3-12 mm long, glabrous. **Calyx** tubular, lobulated, 4.5-7.5 x 3-3.8 mm, glabrous outside, glabrous and without colleters inside; lobes round with a tooth at apex or triangular, 0.1-0.7 x 1-1.2 mm, green. **Corolla** 23-36 mm long; tube very narrowly infundibuliform, 15-18 mm long, 1.7 mm wide at base, 3.5-5 mm wide at mouth, sericeous outside, with a ring of hairs at basal portion, 2-2.4 mm wide at 2.4-2.5 mm from base, glabrous below ring and pilose above ring inside, red; lobes 2/5-4/5 of tube length, 7-12 x 1.8-3.5 mm, oblong, acute or round at apex, sericeous throughout; red. **Filaments** 6.5-7.5 x 0.2-0.8 mm, expanded at base, pilose at edges; anthers oblong, 2.2-3 x 0.3-0.5 mm; basal appendages oblong, 0.5-0.6 mm long, truncate at base; apical appendages narrowly triangular, 0.3-0.6 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 23-28 x 0.3-0.7 mm, distally inflated and grooved, pilose; capitate portion ellipsoid before branches opening, style branches narrowly triangular, 0.2-0.4 x 0.1 mm. **Ovary** 5-locular, turbinate, 4.3 x 1.9-3 mm, glabrous. **Fruit** transversally ellipsoid, 6.5 x 4.8-5, glabrous.

Pyrenes without wings, 5-5.8 x 1.6-2.5, surface verrucate. **Seeds** one per locule, reniform, attached at medial portion of the septum, 3.1 x 1 mm.

Distribution (Fig. 17) **and ecology**. Found in seasonally inundated forests throughout the Rio Negro basin, at low elevations, in the Venezuelan state of Amazonas. Flowering specimens were found in all the months of the year, except for July and December.

Additional specimens examined. VENEZUELA. AMAZONAS: 1 km W of La Ceiba, Caño San Miguel, 2 km above Limoncito, 120-140 m, 14 Oct 1957 (fl), Maguire et al. 41892 (F, NY, US[2], VEN); 20 km above San Fernando de Atabapo, sabana Cumare, R bank of Caño Cumare, 125-140 m, 03 Jun 1959 (fl), Wurdack & Adderley 42752 (F, G, NY, VEN); along lower Río Guasacavi, 1 km upstream of Gallineta, 3°12'44"N, 67°26'04"W, 100 m, 2-3 Mar 1996 (fl), Berry et al. 5822 (MO); banks of black-water Río Temi from Sejal to mouth of river, 110 m, 29 Nov 1995 , Berry et al. 5764 (MO); Depto. Atabapo, Caño Caname, Sabanas de Cucurital, aprox. 20 km E of mouth, 100 m, 29 Apr-4 May 1979 (fl), Huber et al. 3699 (NY, VEN); Depto. Atabapo, lower part of Caño Caname, ca. 3 km W of Mavacal, 3°41'N, 67°23'W, 95 m, 02 May 1979 (fl), Davidse et al. 17094 (MO, NY, VEN); Depto. Atabapo, upper portion of Caño Caname, 3°40'N, 67°13'W, 100 m, 03 May 1979 (fl), Davidse et al. 17148 (MO); Depto. Casiquiare, Caño San Miguel, 2°40'N, 66°50'W, 160 m, 21 Apr 1991 (fl), Aymard 9110 (MO, NY); Depto. Casiquiare, Caño San Miguel, 2°37'N, 67°07'W, 160 m, 18 Apr 1991 (fl), Aymard 8941 (MO); Depto. Casiquiare, near Yavita, along Río Temi, 3°0'N, 67°25'W, 110 m, 25 Aug 1978 (fl), Huber 2619 (NY, VEN); Depto. Casiquiare, S of Caño San Miguel, 30 km from its junction with Río Guainía, 2°38'N, 67°16'W, 90 m, 24 Feb 1979 (fl), Huber 3388 (NY, US, VEN); Caño Momoni. Cuenca del Río Casiquiare, 10-22 Feb 1989, Stergios et al. 13240 (NY); Casiquiare, Caño Monomi, 02 Nov 1962 (fl), Vareschi

7782 (COL); laja Suiza, 3.5 km SSW of Santa Cruz, 3°14'18"N, 67°24'30"W, 100 m, 03 Mar 1996 (fl), Berry et al. 5865 (MO[2]); left bank of Caño Hechimoni, 8 km above mouth, 100-130 m, 09 Feb 1954 (fl), Maguire et al. 37634 (NY, VEN); lower Río Guasacavi, 0-1 km W of mouth of Río Temi, 3°14'00"N, 67°23'38"W, 100 m, 06 Mar 1996 (fl), Berry et al. 5996 (MO); mouth of Caño Chimoni, R side going up, 2°2'N, 66°24'W, 200 m, 17-20 Sep 1986, Stergios et al. 9435 (MO); N bank of Caño Cumare, close to mouth at the Río Atabapo, 3°58'N, 67°41'W, 110 m, 25 May 1993 (fl), Berry et al. 5502 (MO); Reserva Forestal El Sipapo, R side of Río Sipapo, May 1971 (fl), Blanco 1201 (NY, VEN); Río Atacavi, central portion, 09 Sep 1960 (fl), Foldats 3789 (NY, US, VEN); Río Casiquiare, Jan-Feb 1969 (fl), Fariñas et al. 674 (MO, NY[2], VEN); Río Temi, 1-2 km above Yavita, 2°55'04"N, 67°24'29"W, 110 m, 18 Nov 1996 (fl), Berry & Rosales 6405 (MO); Yavita, 128 m, 28 Jan 1942 (fl), Williams 14044 (F, US).

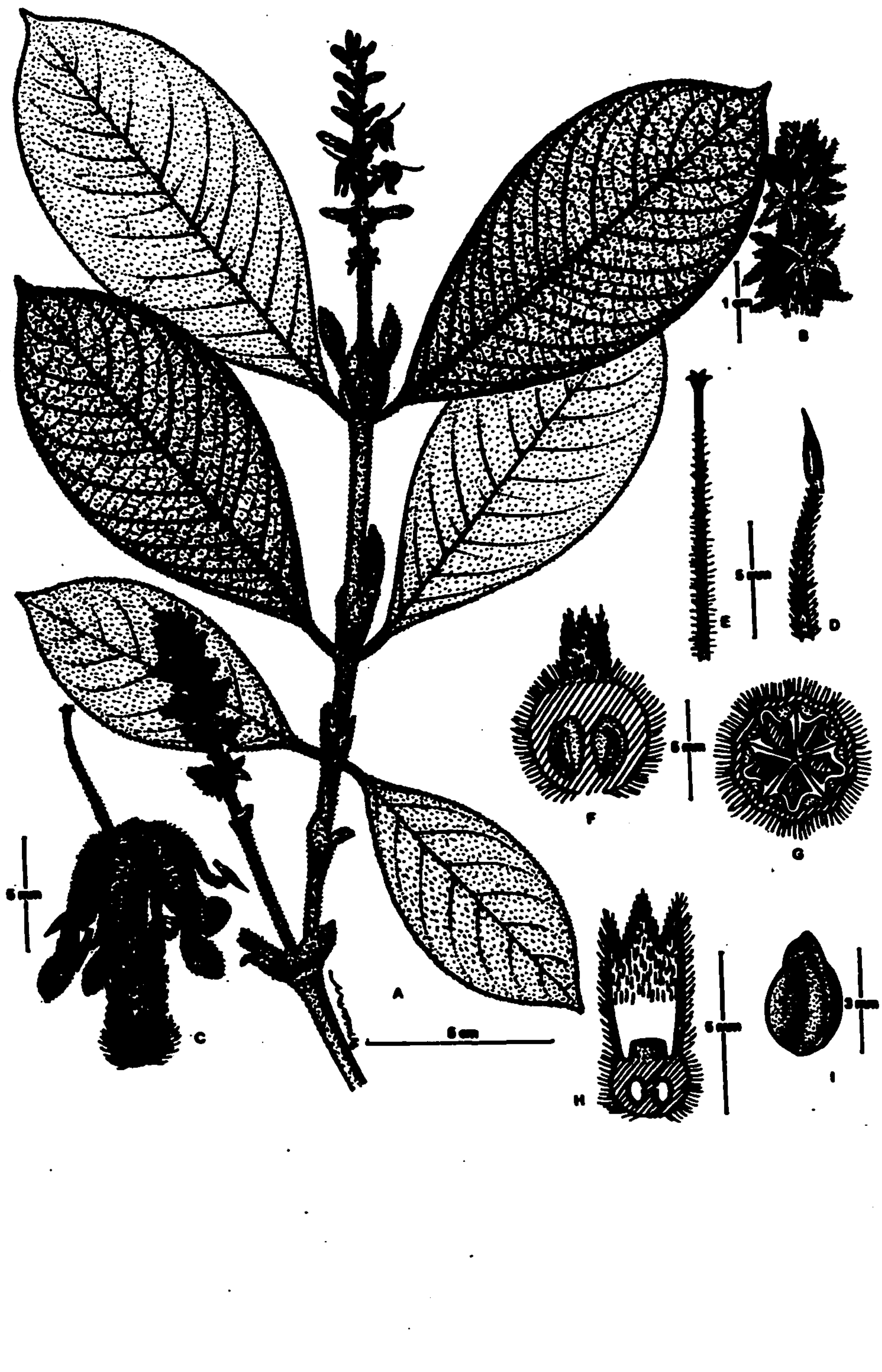
This species is vegetatively similar to Retiniphyllum cataractae, from the Amazonas state of Brazil. While Retiniphyllum pauciflorum has long-tubular, red corollas, R. cataractae has short-tubular, white corollas. In addition, Retiniphyllum pauciflorum has umbellate inflorescences, and longer calyx, corolla, filaments and style, while R. cataractae has short-racemose inflorescences and a very reduced rachis.

The holotype of Retiniphyllum pauciflorum was destroyed at the Berlin herbarium during World War II, and no isotypes were found at P. The single isotype specimen known to me is a fragment preserved at F, consisting of a bract and a flower. Without further options, I select the fragment preserved at F as the lectotype of Retiniphyllum pauciflorum.

1.4.15. Retiniphyllum pilosum (Spruce ex Benth.) Muell. Arg. in Mart., Fl. Bras. 6(5): 7. 1881. Commianthus pilosus Spruce ex Benth. in Hook. f., Hooker's J. Bot. Kew Gard. Misc. 5: 233. 1853. Type. Brazil. Amazonas: Rio Negro, São Gabriel da Cachoeira, caatingas, Jan-Aug 1852 (fl, fr), Spruce 2248 (lectotype, K, here selected; photo-K at NY; isolectotypes, B*, BM, G[3], GH, K, M, NY; photo-B at F, GH, MO, NY). Figs. 3C,D, 9B, 11H, 13G, 24, 31

Shrubs to **small trees** 0.5-4 m tall. **Leafy branchlets** terete or ridged, 3-6.5 mm thick, hirsute. **Stipules** sheathing, splitting in one side, oblong or ovate, acute or round at apex, 15-30 mm long, papyraceous, hirsute outside, glabrous or rarely scarcely hirsute and with colleters at base inside, persistent. **Leaves** petiolate; petioles 6-22 mm long, 0.8-4 mm thick, hirsute; blades 7.6-18 x 3.5-7 cm, L/W 1.9:1-2.6:1, obovate or oblanceolate, cuneate at base, acuminate at apex, acumen up to 6 mm long, sub-coriaceous or papyraceous, abundantly hirsute above and below, brownish or olive green when dry; primary, secondary and

Fig. 31. Illustration of Retiniphyllum pilosum A. Habit of inflorescence. B. Bracteoles and involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Fruit. G. Fruit in transvesal section. H. Ovary and calyx. I. Pyrene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tertiary veins hirsute below; secondary venation eucamptodromous, 7-12 veins each side, tertiary veins random reticulate; domatia absent or pocket-shaped. **Inflorescences** terminal, spicate, erect; 5.5-12.5 cm long; rachis ridged, 1-3 mm thick, hirsute, with or without a stipule up to 6 mm long and two foliose bracts subtending the basal pair of flowers, 11.5-39 mm long, portion of rachis from first pair to next flowers 1-2 cm long; peduncle 2-5.5 cm long, hirsute. **Bracteoles** foliose, lanceolate, 4.3-5.5 x 0.7-1.5 mm, margin entire, hirsute, without colleters inside. **Involucel** cupular, 2.4-3.5 x 3-4.5 mm, lobulated, lobes 7-9, narrowly or broadly triangular, with a colleter at apex, 1.2-3.2 x 0.4-1.8 mm, papyraceous, hirsute outside, glabrous or rarely hirsute and without colleters inside, persistent to the rachis. **Flower buds** cylindrical, tube bent downward. **Flowers** zygomorphic, sessile. **Calyx** tubular, lobulate, 2.8-4.2 x 2.1-3.5 mm, hirsute and verrucose outside, hirsute and without colleters inside; lobes 1-1.5 x 0.8-0.9 mm, triangular, hirsute, green. **Corolla** 13.3-15.1 mm long; tube infundibuliform, 6.8-8.3 mm long, 0.6-1.5 mm wide at base, 1.5-2.6 mm wide at mouth, rarely inflated at base, sericeous outside, with a ring of hairs at distal portion, 2 mm wide at 4-4.5 mm from base, glabrous below ring inside, white or cream white with lines pale pink; lobes 3/4-1 of tube length, 6-9 x 1.3-2.7 mm, lanceolate, oblong or lanceolate, acute at apex, sericeous outside and inside, white or cream white. **Filaments** 4-6.5 mm long, 0.1-0.5 mm wide, slightly expanded at base, pilose throughout; anthers elliptic, 1.8-2.2 x 0.5 mm; basal appendages oblong, 0.4-0.5 mm long, truncate at base; apical appendages narrowly triangular, 0.6 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 13.5-15 x 0.2-0.4 mm, pilose at base and medial portion, glabrous distally; capitate portion globose before branches opening, style branches triangular, up to 0.1 mm long. **Ovary** 5-locular, globose, 1.6-2.2 x 2-2.4 mm, hirsute. **Fruit** longitudinally ellipsoid or rarely globose, 5-6 x 4.5-7.8 mm, hirsute, red. **Pyrenes** 3.9-5.2 x 2.1-2.8 mm, surface smooth, with two parallel wings inserted near the dorsal margin. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.5-3.4 x 0.8-1.1 mm.

Distribution (Fig. 24) **and ecology**. This species grows in the caatinga forests of the Rio Negro basin, along the Guainia and Negro Rivers, at low elevations (75-140 m), in the Colombian-Venezuelan border and in NW Brazil. Flowering specimens were collected most of the year, except by May, June and December. Fruiting specimens were collected for most of the year, except for May, June, September and December.

Additional specimens examined. BRAZIL. Amazonas: Between Rio Marié and Morro Ximaio, 00°45-50'N, 66°50'W, 07 Jul 1979 (fr), Poole 1914 (NY); Rio Curicuriary, Rio Negro, 27 Nov 1929 (fl), Ducke 22901 (US); Rio Negro, São Gabriel da Cachoeira, airport, 20 Oct 1978 (fr), Madison et al. 6519 (F, K, US); São Gabriel, Uaupés, next to the airport, 20 Oct 1978 (fr), Nascimento 699 (NY).

COLOMBIA. Guainía: Puerto Colombia, Río Negro, 75 m, 27 Oct 1977 (fr), Pabón et al. 422 (COL); Río Guainía, Puerto Colombia and vicinity, 2°40'N, 67°30'W, 250-260 m, Oct 31-Nov 2 1952 (fr), Schultes et al. 18155, 18237 (F, GH, US); (fr), Schultes et al. 18202 (NY, US).

VENEZUELA. Amazonas: 1 km E of Maroa, 100-140 m, 01 Jul 1959 (fl, fr), Wurdack & Adderley 43270 (F, G, GH, NY, US, VEN); 1 km E of Maroa, 120-140 m, 07 Oct 1957 (fl, fr), Maguire et al. 41742 (NY[2], US, VEN); 4 km E of San Carlos de Río Negro, 1°56'N, 67°4'W, 120 m, 11 Nov 1977 (fr), Clark 3357 (MO); 4 km from San Carlos de Río Negro off rd. to Solano, 120 m, 22 Sep 1975 (fl), Berry & Brunig 1486 (VEN); 4 km NE of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, IVIC study site, 1°56'N, 67°03'W, 120 m, 09 Apr 1979 (fl, fr), Liesner 6414 (MO, VEN); budare on S side of black water Río Temi above Yavita, 2°52'15"N, 67°18'30"W, 110 m, 25 Nov 1995 (fr), Berry et al. 5633 (MO); Dep. de Río Negro, between San Carlos de Río Negro and Solano, 11-17 Mar 1979 (fr), Marcano-Berti & Salcedo 125-979 (VEN); Dpto. Rio Negro, 2 km E and SE of San Carlos de Río Negro, 1°51'N, 67°03'W, 120 m, 12 Nov 1987 (fl, fr), Liesner & Carnevali 23021 (MO, NY, VEN); Dpto. Rio Negro, Río Pasimoni, 1°30'N, 66°30'W, 80 m, Apr 1991 (fr), Velazco 1961 (MO); Maroa, Río Guainía, 127 m, 19 Feb 1942 (fl, fr), Williams 14432 (F, G[2], NY, US, VEN); Río Negro, Jucabi (at mouth of Río Curicuriari) and vicinity, 17 Jan 1948 (fl), Shultes & López 9633 (GH, NY, US); rd. San Carlos de Río Negro-Solano, 2 km E from

San Carlos, 1°55'17"N, 67°02'46"W, 120 m, 03 Apr 2000 (fl), Berry & Aymard 7565 (MO); rd. San Carlos de Río Negro-Solano, 2-3 km from San Carlos, 1°54'N, 67°02'W, 120 m, 25 Mar 2000 (fl), Berry & Aymard 7229 (MO); rd. to San Carlos to Solano, 12 km N of San Carlos, 100-120 m, 06 Feb 1977 (fl), Morillo & Villa 5426 (VEN); San Carlos, Aug 1853 (fl, fr), Spruce 3048 (K); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 10 Jan 1978 (fr), Clark 6461 (NY); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 06 Mar 1979 (fr), Clark 7170 (NY); savanna at Budare on S side of black-water Río Temí above Yavita, 2°52'15"N, 67°18'30"W, 110 m, 25 Nov 1995 (fr), Berry et al. 5633 (VEN); Yavita, 130 m, 19 Oct 1950 (fl, fr), Maguire 29301 (NY[2], VEN).

Local Names. Venezuela: borrajon (Liesner 6414), palo de peluza (Clark 3357).

Retiniphyllum pilosum is easily recognizable for the abundant indument present in branches, leaves, flowers, and fruits. Its foliose bracteoles and cupular involucel are similar to those of R. fuchsioides; however, the latter has long-tubular, red corollas, while R. pilosum has short-tubular, white corollas.

Bentham (1853) did not cite any type specimen in the original description of Commianthus pilosus. However, the collection locality of Spruce 2248 corresponds to that cited in the original publication; in addition, the specimen was cited by Müller Argoviensis (1881) when he transferred Commianthus pilosus to Retiniphyllum. Although Müller Argoviensis misread Spruce's handwriting, and wrote

"Spruce n. 2243", it is clear that he was referring to Spruce 2248. The specimen Spruce 2248 preserved at K has the seal of the Herbarium Benthamianum and it is here selected as the lectotype of Commianthus pilosus. The name Ammianthus pilosus was handwritten by Spruce on the label of the lectotype, but it was never published.

1.4.16. **Retiniphyllum rhabdocalyx** Muell. Arg. in Mart., Fl. Bras. 6(5): 10. 1881. Type. Colombia [cited as "Brazil"]. Caquetá: Sierra de Araracuara, near Japurá, Feb (fl), Martius s.n. [Herb. Mart. 3148] (holotype G-DC-n.v.; photo-M at F, MO, NY[2]). Figs. 4E, 8D, 12D, 14G, 32

Shrubs or **small trees** up to 6 m tall. **Leafy branchlets** terete, 4-4.5 mm thick, glabrous. **Stipules** sheathing, truncate, 2-2.5 mm long, coriaceous, glabrous outside, glabrous and with colleters inside, persistent. **Leaves** petiolate; petioles 8-20 mm long, 1-2 mm thick, glabrous 10-21 x 4-11 cm, L/W 1.7:1-3.1:1, oblong, elliptic or obovate, decurrent or acute at base, caudate at apex, coriaceous, glabrous above and below, dark or light brown when dry; secondary venation brochidodromous, 15-24 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect, 8.5-23.5 cm long; rachis ridged, 2-4 mm thick, glabrous or hirtellous, with or without two foliose bracts subtending the basal pair of flowers, rarely resembling leaves, 0.4-11 cm long, portion of rachis from first pair to next flowers 1.8-3 cm; peduncle 1.5-7 cm long. **Bracteoles** reduced, 0.6-1 mm long, margin entire or with small teeth, glabrous, with colleters inside. **Involucel** discoid, 0.5-0.9 x 2.1-2.8 mm, truncate or with small teeth, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** zygomorphic, sessile. **Calyx** tubular, lobulate or with small teeth, 6.3-10 x 3-4.2 mm, glabrous at medial and distal portions, hirtellous at base outside, glabrous and without colleters inside, inflated at base for an extent of 1 mm; lobes 0.8-2.1 x 0.6-1.6 mm, broadly triangular or deltoid, red. **Corolla** 28-46 mm long; tube narrowly infundibuliform, 20-32 mm long, 1.1-2 mm wide at base, 3.9-4.3 mm wide at mouth, glabrous at base, strigose at middle part and at mouth outside, with a ring of hairs at basal portion, at 2.4-4.5 mm from base, glabrous below ring inside, sericeous above ring inside, red throughout; lobes 1/3-1/2 of tube length, 8.5-13.5 x 2.2-4 mm, lanceolate, round or acute at apex, sericeous throughout, red. **Filaments** 7.5-8.8 mm long, 0.3-0.5 mm wide, expanded at base, hirsute throughout; anthers narrowly oblong, 2.5-3.5 x 0.3-0.5 mm; basal appendages oblong, 0.3-0.6 mm long, truncate at base; apical appendages narrowly triangular, 0.5-0.6 mm long. **Pollen** subprolate or prolate; sexine tectate-perforate. **Style** 32-45 mm long, sparsely hirsutulous, glabrous basally and distally; capitate portion oblong before branches opening; style branches narrowly triangular, 0.4-0.5 mm long, not rolled at maturity. **Ovary** 5-locular, globose or cylindrical, 1.5-2.5 x 2.2-2.7 mm, glabrous. **Fruit** globose or transversally ellipsoid, 5-6.2 x 4-7 mm, glabrous throughout, red. **Pyrenes** 5-6.5 x 2-2.2 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 3.9 x 1 mm.

Distribution (Fig. 32) **and ecology**. This species has a punctuated distribution scattered throughout NW Brazil and SE Colombia, occurring at low elevations (100-500 m), in forests and shrublands on white-sand areas. Flowering specimens were collected from September to February, June, and July. Fruiting specimens were collected in January, September, October, and December.

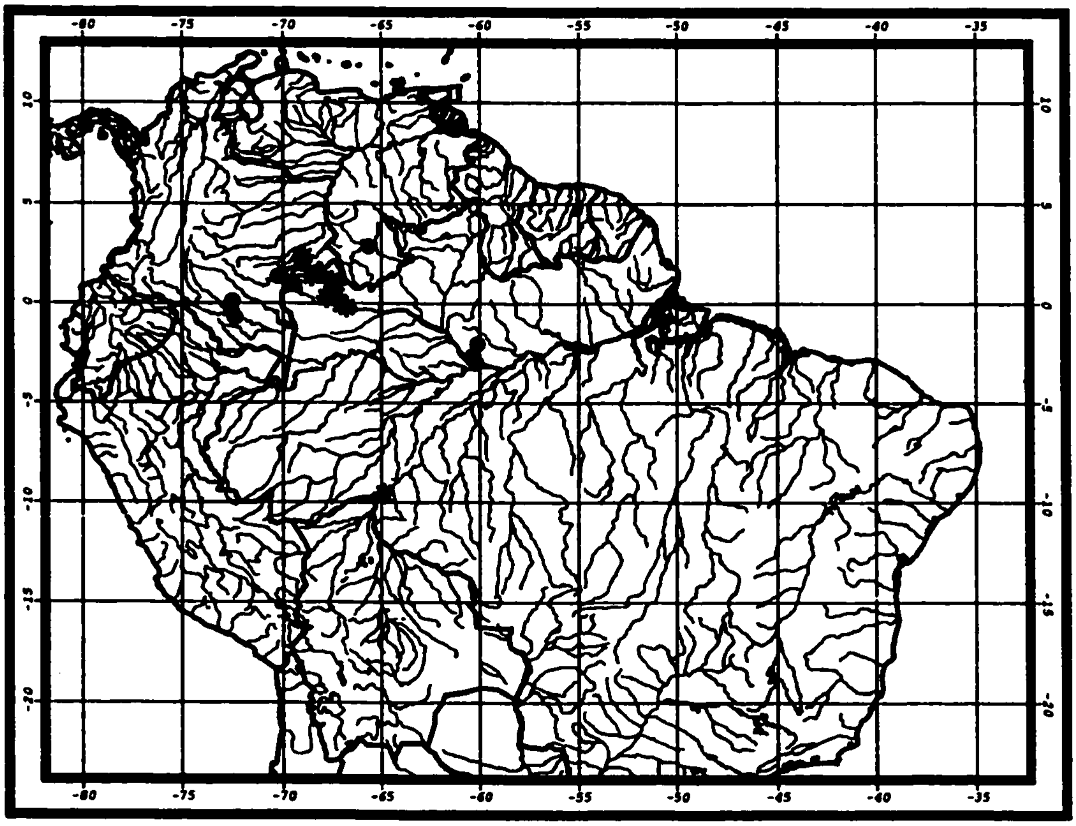


Fig. 32. Distribution of Retiniphyllum rhabdocalyx (●), and R. speciosum (✱).

Additional specimens examined. BRAZIL. AMAZONAS: Along Manaus-Caracarai rd., km 130, 2°5'S, 60°5'W, 13 Nov 1973 (fl), Berg et al. P19524 (NY); Manaus, Rio Tarumá-miry, 14 Jan 1941 (fl), Ducke 789 (F, GH, MO, NY[2], R, US); Manaus-Caracarai rd, km 130, 2°5'S, 60°5'W, 27 Sep 1974 (fl), Conant et al. 1112 (INPA); Rio Cuieras, near Jarada, 17 Sep 1973 (fl, fr), Prance et al. 18048 (BR[2], MO, NY, US); Rio Negro, s.d.(fl), Martius s.n. (M).

COLOMBIA. CAQUETÁ: Araracuara, Balcón del Diablo, near airstrip, 13 Dec 1983 (fl, fr), Forero & Pabón 9818 (COL[2], MO, NY); Araracuara, around airstrip, 0°25'S, 72°30'W, 200-300 m, 04 Nov 1991 (fl), Restrepo & Matapi 342 (NY); Araracuara, around airstrip, 0°25'S, 72°20'W, 250 m, 23 Oct 1990 (fr), Restrepo et al. 171 (MO, NY); Araracuara, Isla de las Mercedes, Río Caquetá, 14 Sep 1977 (fl), Aguirre-Galviz 1131 (COL); Araracuara, Japura, (fl), Martius s.n. (G); Araracuara, near airport, 0°25'S, 72°19'W, 250 m, 25 Jan 1989 (fl, fr), Gentry & Sanchez 65180 (MO); Araracuara, Río caquetá, Angostura, 400 m, 21 Dec 1951 (fl), García-Barriga & Schultes 14161 (GH, US); Araracuara, Río caquetá, Angostura, 400 m, 21 Dec 1951 (fr), García-Barriga & Schultes 14132 (COL, US); Araracuara, rd between airstrip and Guácharos cave, Puerto Arturo, 01 Sep 1977 (fl), Aguirre-Galviz 936, 992 (COL); Around Araracuara, Río Caquetá, 22 Oct 1982 (fl), Idrobo et al. 11244 (COL); Mun. Solano, Araracuara, rd. Araracuara-airstrip-Guácharos cave, 0°35'S, 72°24'W, 300 m, 14 Nov 1993 (fl), Cárdenas et al. 4015 (COL, MO); Mun. Solano, left margin of Río Caquetá, Paujil, 10 km NO of Araracuara, 0°45'-0°48'S, 72°20'-72°25'W, 100-350 m, 02 Dec 1993 (fl), Arbeláez & Sueroque 502 (MO); Solano, Río Mesay, Puerto Abeja Station, 0°04'27"N, 72°27'05"W, 24 Jul 1999 (fl), Rosero 90 (COL). **GUAINÍA:** Nabuquen trail, 2°51'127"N, 65°38'339"W, 500 m, 25 Feb 1995 (fl), Córdoba et al. 513 (COL). **VAUPÉS:** Mun. Mitú, rd between Bogotá cachivera and Acaricuara, 16 Jan 2000 (fl, fr), Cortés 1648 (COL, NY).

This species has beautiful, long-tubular, dark pink corollas that are pollinated by hummingbirds (Rosero Lasprilla & Sazima, 2002). Steyermark (1965) treated

Retiniphyllum rhabdocalyx as synonymous with R. speciosum because he concluded that both taxa have similar calyx ribs and lobes/tube ratio. According to my observations, the calyx of Retiniphyllum rhabdocalyx is 6.3-10 mm long, and basally inflated; whereas, the calyx of Retiniphyllum speciosum is 4-6.5 mm long, inflated for most of its length, and with conspicuous vascular bundles at the non-inflated portion. In addition, the corolla tube, style and pyrenes are larger in Retiniphyllum rhabdocalyx than in Retiniphyllum speciosum. In conclusion, because of the morphological differences that characterize these taxa, R. rhabdocalyx should be treated as a distinct species.

1.4.17. **Retiniphyllum scabrum** Benth., J. Bot. (Hooker) 3: 222. 1841. Retiniphyllum scabrum var. scabrum, Mem. New York Bot. Gard. 12: 235. 1965. Type. Guiana: Between Roraima and Esmeralda, [Journey from Roraima to Esmeralda and Fort São Joaquim (Nov 1838-Jun 1839)] 1839 (fl), Rob. Schomburgk 156.S (lectotype, K, here selected). Figs. 4G, 5F, 9F, 10A,G, 11C, 12H, 13B, 29, 33

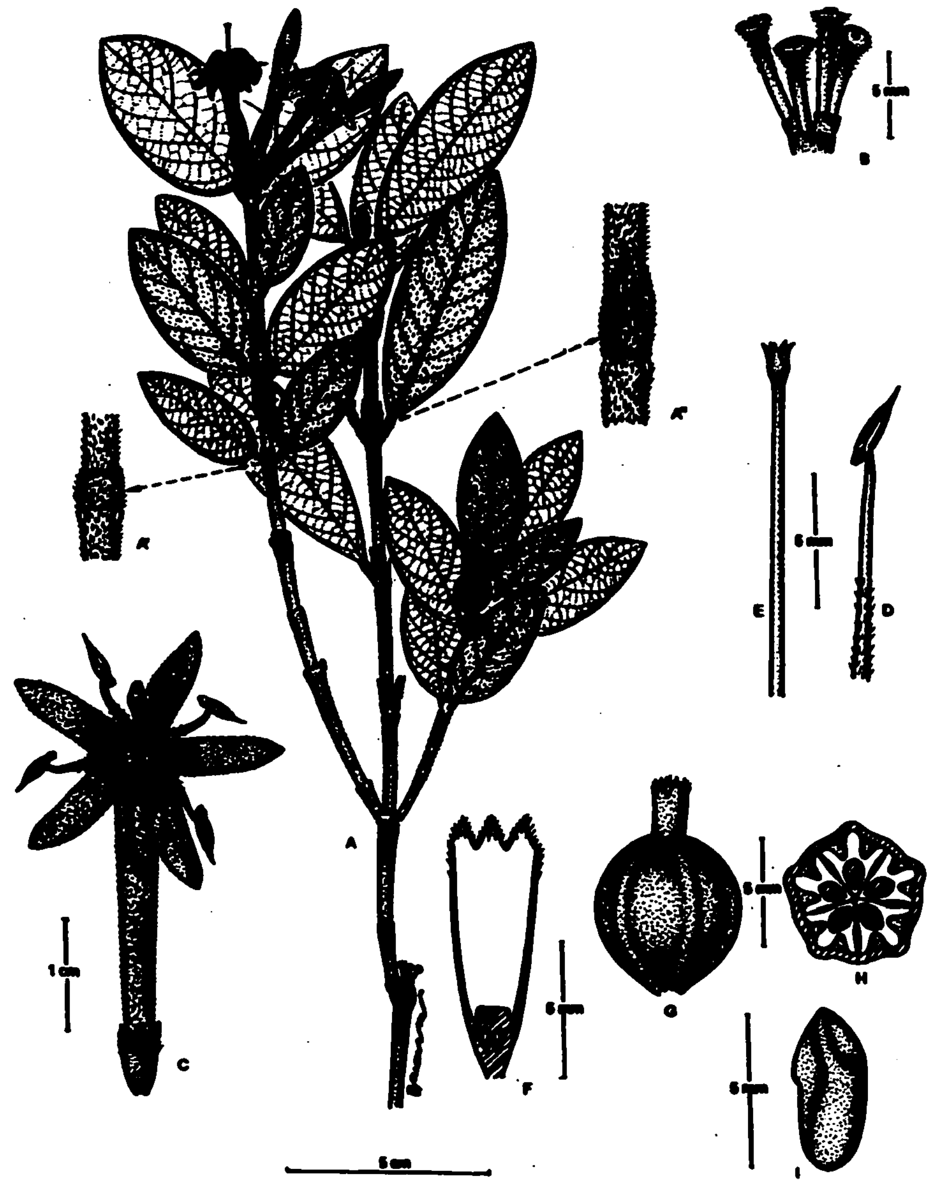
Retiniphyllum scabrum var. erythranthum (Standl.) Steyerm., Mem. New York Bot. Gard. 12: 236. 1965. Retiniphyllum erythranthum Standl., Field Mus. Nat. Hist., Bot. Ser. 7: 399. 1931. Type. Venezuela. Amazonas: Summit of Mount Duida, slopes at central camp, 1600 m, 28 Dec 1928-1 Jan 1929 (fl), Tate 561 (holotype, NY, frag.-NY at F; photo-NY at F, G).

Retiniphyllum scabrum var. ayangannense Steyerm., Mem. New York Bot. Gard. 12: 236. 1965. Type. Guyana: Mount Ayanganna, shoulder of E flank above Thompson Camp, scrub and low forest, 1370-1525 m, 8 Aug 1960 (fl), Tillet, Tillet & Boyan 45194 (holotype, NY; isotype, US).

Retiniphyllum cearense Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 220. 1937. Type. Guiana: Between Roraima and Esmeralda, [Journey from Roraima to Esmeralda and Fort São Joaquim (21 Nov 1838-20 Jun 1839)] 1839 (fl), Schomburgk 156 [as "Gardner 156"] (holotype, G-DEL, frag.-F; isotype, BM). The holotype specimen of Retiniphyllum cearense has the label: "Bresil: Province de Ceara. M. Gardner (Août-Novembre 1858). Envois reçus en janvier wt avril 1840". On this label, it has been glued a small label with the number "156" Rob. Schomburgk's handwriting, the same number and handwriting found in the label of the type specimen of R. scabrum. It is obvious that the label with "156" was erroneously glued on Gardner's label of R. scabrum. Therefore, no collections of Retiniphyllum have ever been made in the state of Ceará.

Shrubs up to 3 m tall. **Leafy branchlets** terete or decussately compressed, 1.2-3.7 mm thick, hirsute. Stipules sheathing, hirsute or strigose outside, glabrous and with colleters throughout or at base inside, dimorphic, in some branches truncate, 1-4 mm long, entire, coriaceous, persistent; in some other branches broadly triangular, 9.5-15 mm long, margin deeply laciniate, chartaceous, persistent. **Leaves** petiolate; petioles 2.5-10 mm long, 1.3-3 mm thick, hirsute or strigose; leaves dimorphic, blades in fertile shoots 1.7-7.4 x 1.2-4.2, L/W 1.4:1-2.8:1, ovate or elliptic, acute or rounded at base, acute, mucronulate, or obtuse at apex, coriaceous, scarcely strigose or hirtellous throughout with abundant strigose hairs at margin and along primary vein above, heavily hirsute or strigose below, brown or olive green when dry; primary, secondary and tertiary veins hirsute below; secondary venation weak broquidodromous, 5-9 veins each side, tertiary veins random reticulate; domatia absent; blades in

Fig. 33. Illustration of Retiniphyllum scabrum. A. Habit of inflorescence. B. Involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Ovary and calyx. G. Fruit. H. Fruit in transversal section. I. Pyrene


A
A'
A"
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1 cm
5 cm

sterile shoots 5.3-12.4 x 1.9-3.8, L/W 2.3:1-3.3:1, elliptic or rarely obovate, cuneate or acute at base, acute at apex, coriaceous, strigose, hirsute or hirtellous throughout with abundant strigose hairs at margin and along primary vein above and below, brown or olive green when dry; secondary venation weak broquidodromous, 9-10 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, fasciculate, 4-flowered, rarely 5-9-flowered, erect; peduncle reduced, up to 2.5 mm long, glabrous. **Bracteoles** discoid, up to 0.4 mm, margin with small teeth, glabrous, with colleters inside. **Involucel** discoid, with small teeth, 0.2-0.5 x 1.3-2.2 mm, coriaceous, hirsutulous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, pedicellate; pedicels 0.8-3(-4.8-5.5) x 0.8-1.2(-2.8) mm, hirsutulous. **Calyx** tubular, margin subtruncate, with small teeth or lobulate, 3-6.5(-8) x 2.8-4.2 mm, hirsute outside, mostly glabrous but scarcely strigose near margin and without colleters inside, lobes 0.6-2 x 0.9-1.2 mm, deltoid, narrowly or broadly triangular, hirsutulous, red. **Corolla** 30-38 mm long; tube narrowly infundibuliform, 22-27 mm long, 1.3-2 mm wide at base, 3.5-5 mm wide at mouth, sericeous outside, with a ring of hairs at basal portion, 1-2 mm wide at 2.8-4 mm from base, glabrous below ring, and sericeous above ring inside, red; lobes 1/4-2/5(-3/5) of tube length, 6.8-10.5 x 1.7-4.9 mm, oblong, lanceolate, ovate or elliptic, acute or rounded at apex, sericeous throughout, red. **Filaments** 4.6-6.2 mm long, 0.3-0.7 mm wide, expanded at base, pilose at lateral edges or throughout; anthers narrowly elliptic, 2.4-3.5 x 0.4-0.8 mm; basal appendages obovate or oblong, 0.5-0.8 mm long, truncate at base; apical appendages narrowly triangular, 0.4-0.9 mm long. **Pollen** subprolate; sexine microreticulate. **Style** 25-35.5 x 0.2-0.3 mm, mostly pilose but glabrous basally and distally, rarely glabrous throughout; capitate portion ellipsoid before branches opening, style branches broadly triangular, up to 2 mm long. **Ovary** 5-locular, turbinate or narrowly obconical, sometimes stipitate, 2-4.5 x 1.5-3 mm, hirtellous. **Fruit** transversally ellipsoid or globose, sometimes stipitate, 6-11 x 6-9 mm, glabrous, black purple or dark blue. **Pyrenes** 4.5-8 x 2.5-3.5 mm, surface dorsally verrucate, with two perpendicular wings inserted near the dorsal margin. **Seeds** one per locule, cylindrical, attached at the distal portion of the septum, 2.9-4 x 0.9-1 mm.

Distribution (Fig. 29) **and ecology**. Widespread in uplands and highlands in the Guayana Region, in the Sierra Parima, in the Paru and Duida-Marahuaka massifs in the state of Amazonas, Venezuela, and in most of the mountains in the state of Bolivar. Outside Venezuela, it is found in Guyana along the Pakaraima Mountains range, and in Brazil in the Serra Araça. This is the most common species of Retiniphyllum found in the Pantepui Province (above 1500 m). Flowering and fruiting specimens were collected throughout the year.

Additional specimens examined. BRAZIL. AMAZONAS: N massif of Serra do Aracá, 0°51-57'N, 63°21-22'W, 1200 m, 15 Feb 1984 (fl), Prance et al. 29084 (MO, NY).

GUYANA. CUYUNI-MAZARUNI: Ayanganna Plateau, 3 km N of Koatse, 5°38'N, 60°04'W, 650-670 m, 27 Feb 1987 (fl), Pipoly 10720 (NY, US); Ayanganna Plateau; N of central portion, 5°28'N, 60°-04'W, 650-700 m, 01 Mar 1987 (fl), Pipoly & Gharbaran 10895 (NY, US); Mt. Ayanganna, easternmost peak, 5°25'N, 59°57'W, 1350-1380 m, 11 Mar 1987 (fl), Pipoly 11138 (NY, US[2]); Mt. Ayanganna, easternmost peak, 5°38'N, 60°04'W, 1350-1380 m, 11 Mar 1987 (fl), Pipoly 11105 (MO, NY, US); Pakaraima Mts., 12.7 km NE Imbaimadai, 5°48'N, 60°14'W, 700 m, 25 May 1992 (fl), Hoffman & Henkel 1884 (MO, NY, US); Pakaraima Mts., NE plateau of Mt. Ayanganna, 5°23'N, 59°58'W, 1500-1650 m, 01 Nov 1992 (fl), Hoffman & Henkel 3150 (MO, US); Pakaraima Mts.; between Koatse River and Chenoweing village, 05°27'N, 60°04'W, 700-800 m, 12 Nov 1992 (fl), Hoffman & Henkel 3334 (MO, NY, US); Paruima, 15 km W, 0.25 km W of camp near eastern summit of Waukauyengtipu, 5°49'N, 61°12'W, 1525 m, 15 Jul 1997 (fr), Clarke et al. 5706 (MO); Paruima, 20 km W, Waukauyengtipu, 5°49'N, 61°14W, 1430 m, 19 Jul 1997 (fl, fr), Clarke et al. 5894 (MO). **MAZARUNI-POTARO:** upper Mazaruni River basin, N of Karowrieng River, Pakaraima Mts. Peak, 5°43'N, 60°8'W, 1385 m, 14 Jun 1986 (fr), Pipoly & Alfred 7832 (US); upper Mazaruni River basin, N of Karowrieng River, Pakaraima Mts. Peak, 5°43'N 60°8'W, 1385 m, 14 Jun 1986 (fl, fr), Pipoly & Alfred 7779 (MO); upper Mazaruni River basin, Ayanganna Plateau, savannah near G.S. Camp 1 on trail to Ayanganna, Tillet 44916 (NY). **POTARO-SIPARUNI:** Pakaraima Mts., Sukabi River, above Aando Falls, 5°10'N, 60°10'W, 800 m, 19 Oct 1994 (fl), Henkel et al. 5935 (INPA, MO, US); Pakaraima Mts.; Ireng River at Kurutuik Falls, 05°05'N, 59°59'W., 670 m, Mutchnick 186 (MO, NY, US); Pakaraima Mts., Mt. Kukuinang, Kukuinang savanna, 2-3 km SSW from mountain peak, 5°04'N, 59°57'W., 950-1050 m, 27 Feb 1993 (fl), Henkel et al. 1605 (MO, NY, US); Pakaraima Mts., N of Imbaimadai airstrip, 5°43'N, 60°18'W, 511 m, Pipoly 7832 (NY).

VENEZUELA. AMAZONAS: Depto. Atabapo, plateau of Duida above Culebra, 3°36'N, 65°42'W., 1250 m, 02 Mar 1985 (fl), Liesner 18160 (MO); Depto. Atabapo, slope of Cerro Marahuaca Río Yameduaka arriba, 3°38'N, 65°28'W., 1225 m, 17-18 Feb 1985 (fl, fr), Liesner 17610 (MO, NY); Sierra Parima, headwaters of Río Matacuni, 4°5'N, 64°40'24"W., 1500 m, 19 May 1973 (fl), Steyermark 107498 (F, MO, NY, US); summit of Mount Duida, dry slopes of savanna hills, 1400 m, Aug-Apr 1929 (fl), Tate 756 (F, NY); summit of Mount Duida, summit of ridge 25, 1800 m, 26 Nov-16 Dec 1928 (fl), Tate 465 (NY); along of the Orinoco, 2100 m, Jan-Feb 1969 (fl), Farinas 543 (VEN); along of the Orinoco, Jan-Feb 1969, Farinas 370 (NY[2]); Cerro Duida, N of Esmeralda, 3°10"N 65°31'W, 1350 m, 29 Jan-11 Feb 1975 (fl), Tillet et al. 751-43 (K, VEN); Cerro Duida, Río Cunucunuma, 2000-2300 m, 23 Nov 1950 (US), Maguire et al. 29674 (F, R, US); Cerro Duida, Río Cunucunuma, along N escarpment above Culebra, 1400 m, 20 Nov 1950 (fl), Maguire 29598 (NY); Cerro Duida, Río Cunucunuma, in upper drainage of Culebra Creek, 1500-1600 m, 21 Nov 1950 (fr), Maguire et al., 29617 (NY); Cerro Duida, Río Cunucunuma, near Culebra Creek, 1500 m, 19 Nov 1950 (fl), Maguire 29555 (NY); Cerro Duida, southeastern-facing slopes along Caño Negro (tributary of Caño Iguapo), 305-1095 m, Aug 25-26 1944 (fl), Steyermark 58034 (F, NY); Cordillera Parima, summit of Cerro Cayenama, 3°58'N, 64°40'W, 1750 m, Mar 1971 (fl), Cardona 3087 (VEN); Depto. Atabapo, Cerro Duida, 3°32'N, 65°40'W, 1380 m, 29 Mar 1992 (fr), Dezzeo & Fernández 351 (VEN); Depto. Atabapo, Cerro Duida, summit, near E escarpment, 3°25'N, 65°40'W, 1230 m, 10 Feb 1982 (fl), Steyermark 126376 (COL, K, MO, NY, US);

Depto. Atabapo, Cerro Marahuaca, above branch of Caño Negro, S-central portion of meseta, downstream from Sima Camp, 3°43'N, 65°31'W., 1220-1350 m, 23-24 Feb 1985 (fl), Steyermark & Holst 130638 (MO, NY); Depto. Atabapo, Cerro Marahuaca, SE slopes, 3°35'N, 65°23'W, 1500-1600 m, 20 Oct 1988 (fl), Liesner 25118 (MO); Depto. Atabapo, Serrania del Parú (Aroko), 4°31'N, 65°35'W, 1100 m, 3-4 Oct 1979 (fl), Huber 4282 (NY, US, VEN); Depto. Atures, Sierra Maigualida, NW sector, small valley along an upper tributary of Caño Iguana, 5°30'N, 65°15'W., 2000 m, 28 Feb-3 Mar 1991 (fl), Berry 4838 (MO, NY, VEN); Dpto. Atabapo, Cerro Duida, summit, E-central portion, 3°40'N, 65°45'O., 1500 m, 16 Feb 1981 (fr), Steyermark 124580 (MO, NY[2]); Dpto. Atabapo, Río Ventuarí, 4°14N 65°58', 1250 m, Feb 1992 (fl), Chaviel 398 (MO); Dpto. Atabapo, Río Yudi, 5°29'N, 65°18'W, 1600 m, Mar 1992 (fl), Delgado 1710 (NY); Dpto. Atabapo, summit of Cerro Marahuaca, 3°43'N 65°30'w, 1200 m, 16 Oct 1988 (fl), Liesner 24298 (MO); Dpto. Atures, Serranía Uasadi, sector NW, 5°21N 65°12W, 1850 m, 22 Nov 1988 (fl), Huber 12846 (VEN); Laguna Asisa, Cerro Asisa (La Momia), Serrania Parú, 4°14'N 65°56'W, 1310 m, 07 May 1973 (fl), Hoyos & Morillo, 73 (VEN); region of Duida and Marahuaca, Apr-Jun 1950 (fl), Barnes 81 (VEN); Serrania Paru, Caño Asisa, Río Ventuari, 2000 m, 02 Feb 1951 (fl, fr), Cowan & Wurdack 31147 (NY, US); Serrania Paru, Caño Asisa, Río Ventuari, summit along W rim 1-6 km N of camp Caño head, 2000 m, 04 Feb 1951 (fl), Cowan & Wurdack 31232 (GH, NY); Serrania Paru, Caño Asisa, Río Ventuari, summit along W rim 1-6 km N of camp Caño head, , 2000 m, 31 Jan 1951 (fl, fr), Cowan 31105 (NY); Serrania Paru, Río Ventuari, Río Paru, Caño Asisa, 1600 m, 13 Feb 1949 (fl), Phelps 505 (NY); summit of Cerro Duida, along valley forest between Central Camp and Brocchinia hills, 2100 m, 31 Aug 1944 (fl), Steyermark 58129 (F, NY, US); summit of Cerro Duida, Brocchinia hills, 1700-1980 m, 01 Nov 1944 (fl), Steyermark 58150 (F, GH). BOLIVAR: Aaprada-tepui, Urimán, 900-1000 m, 18 Aug 1953 (fl), Bernardi 800 (VEN); plateau of Auyan-tepui, SW sector, along small river, headwaters of the Rio Churun, 5°48.02'N, 62°33.82'W., 1850 m, 23-25 Apr 1996 (fl), Anderson 13874 (NY, VEN); alto Río Cuyuni, above escarpment of La Escalera, 850 m, 20-21 Aug 1962 (fl, fr), Maguire 46830 (NY); arriba del Salto Angel, 14-22 Dec 1984 (fl), Oliva & Michelangeli 51 (VEN); Auyan-tepui, summit SE, near the cave, NW of Oso Woods Camp, 2200 m, 01 May 1964 (fl), Steyermark 93204 (F, NY); Auyan-tepui, 1850 m, Tate 1173 (NY); Auyan-tepuy, Salto La Catira, E of Río Churúm, 1750 m, 27-28 Dec 1977, Brewer-Carias s.n. (VEN); Auyantepui, central portion, 1800 m, Apr 1956 (fl), Foldats 2628 (F); Cerro Auyantepuy, Alto Caroni, Jan 1949 (fl), Cardona 2636 (NY, US); Cerro Uaipan, Rio Canori, 1500 m, Feb 1948 (fl), Cardona 2396 (MO, VEN); Cerro Uaipan, Rio Canori, Guayana, 1800 m, 26 Nov 1946 (fl), Cardona 2066 (G, NY, US); Cerro Venamo SW, 1400-1450 m, Steyermark 92506 (NY); Cerro Venamo, N slopes, between rd. camp. 125 and beginning of dwarf forest, 1100-1300 m, 14 Apr 1960 (fl), Steyermark & Nilsson 156 (NY); Chimantá Massif, NW part of summit of Abacapa-tepui, 2125-2300 m, 13 Apr 1953 (fr), Steyermark 74950 (F, NY); Chimantá Massif, Torono-tepui, savanna and stream margin along Caño E of high part of Torono-tepui, 1975 m, 20 Feb 1955 (fl), Steyermark & Wurdack 989 (F, NY, US); Dto. Piar, Auyan-tepui summit, edge of massif, 5°53'N, 62°62'W, 1740 m, 27 May 1986 (fl, fr), Holst 3014 (MO); Dto. Piar, Macizo del Chimantá, sector centro meridional NE of Torono-tepui, 5°16'N, 62°09'W., 2100 m, 11-15 Feb 1985 (fr), Pipoly 7262 (MO, NY); Dto. Piar, Macizo del Chimantá, sector SE, NE of Acopan-tepui, 5°12'N, 62°05'W., 1950 m, 8-11 Feb 1985 (fl, fr), Pipoly et al. 7158 (MO, NY); Dto. Piar, Macizo del Chimantá, sector SSE, SE of Acopan-tepui, headwaters of Río Aarauac, 5°11'N, 62°00'W., 1920 m, 13-16 Feb 1984, Huber et al. 9034 (NY); Dto. Piar, Meseta del Auyan-tepui, sector SW, aprox. 10 km SW of Churun-Meru (Salto Churun), 5°49'N, 62°35'W, 1900 m, 10 Dec 1983 (fl), Huber & Medina 8486 (MO, NY, US); Dto. Piar, plateau of Auyan-tepui, sector centro-W, aprox. 15 km WSW of Salto Angel (Churun-Meru), Huber 11223 (NY); Dto. Piar, plateau S of Terekeyuren-tepui, aprox. 40 km NE of Mision de Kamarata, 5°51'N, 62°03'W., 1780 m, Huber 11121 (NY); Dto. Piar. Camarcaibarai-tepui, W slope shoulder, 5°52'N, 62°01'W, 1800 m, 22 May 1986 (fl, fr), Holst et al. 2869 (MO, NY); Dto. Piar. Macizo del Chimantá, sector centro meridional, NE of Torono-tepui and central section of Chimantá-tepui, 5°16'N, 62°09'W, 2100 m, 11-15 Feb 1985 (fl), Huber et al. 10166 (MO, NY); Dto. Piar. Macizo del Chimantá, sector SSE, plateau SE of Acopan-tepui, headwaters of Río Aarauac, 5°11'N, 62°00'W., 1920 m, 14-16 Feb 1984 (fr), Luteyn et al. 9476 (M, NY, US); Dto. Piar. Macizo del Chimantá, sector SSE, plateau SE of Acopan-tepui, headwaters of Río Aarauac, 5°11'N, 62°00'W., 1920 m, 14-16 Feb 1984 (fl), Steyermark et al. 129966 (NY); Dto. Piar. Macizo del Chimantá, farallones superiores del Amuri-tepui, 5°10'N, 62°07'W., 1850 m, 2-5 Feb 1983, Steyermark et al. 128578 (F, MO, NY, US); Dto. Sifontes, Cerro Kukenan, 05°12'N, 60°50'W., 1500 m, 06 Sep 1986 (fl), Huber 11787 (NY); Distr. Piar, Macizo del Chimantá, sector SSE, plateau SE of Acopán-tepui, headwaters of Río Arauác, 5°11'N, 62°00'W, 1920 m, 14-16 Feb 1984, Luteyn et al. 9476 (NY); Dto. Heres, Cerro Marutani, summit, along Río Carla, 3°50'N, 62°45'W, 1200 m, 11-14 Jan 1981 (fl), Steyermark et al. 123909 (MO, NY); Dto. Piar, Cerro Auyantepuy, between the first and second wall, Río Churum, 1750-1800 m, 27-28 Mar 1987, Delascio 13195 (MO, VEN); Dto. Piar, Murisipan-tepui, 5°51'N, 62°2'W., 1700 m, 26 May 1986 (fl), Steyermark et al. 132109 (MO, NY); fila de la Danta at km 132-132.5, between Luepa and Cerro Venamo, 1200 m, 18 Apr 1960 (fl), Steyermark & Nilsson 300 (NY); Gran Sabana, plateau, drainage of Rio Aponguao headwaters, near Km 147 S of El Dorado, 1350-1400 m, 21 Dec 1970 (fl), Steyermark 104202 (NY, VEN); Ilu-tepui, Gran Sabana, 1000-1300 m, 08 Feb 1952 (fl), Maguire 33249 (M, NY, US), Maguire 33325 A (NY), Maguire 33345 (NY, US); km 133 S of El Dorado, 1300 m, 16 Mar 1974 (fl, fr), Gentry et al. 10564 (MO); Macizo de Chimantá, sector SE, Acopantepui, 2000 m, Jan 1991 (fl), Delascio 14649 (VEN); Meseta del Jaua, summit of Cerro Jaua, 4°48'50"N, 64°34'10"W, 1750-1800 m, 22-28 Feb 1974, Steyermark 109297 (US, VEN); Meseta del Jaua, summit of Cerro sarisariñama, 4°41'40"N, 64°13'20"O, 1410 m, 10 Feb 1974 (fl), Steyermark 108867 (VEN); Meseta del Jaua, summit of Cerro Sarisariñama, 4°41'40"N, 64°13'20"O, 1380 m, 11-12 Feb 1974 (fl), Steyermark 108957 (F, K, MO); Mun. Gran Sabana, Chimantá Massif, SSE sector, SE summit of Acopan-tepui, headwaters of Rio Arauak, 5°11'N, 62°W., 1920 m, 6-8 Apr 1989, Pruski & Huber 3684 (NY); N-facing slope forest, Sororopan, 1500 m, 17 Dec 1952 (fl), Maguire & Wurdack 33914 (NY, US); P. N. Canaima, Auyantepui, meandro lagunoso Río Churum, 1500 m, 19 Apr 1996 (fl, fr), Delascio 17039 (VEN); plateau at base of SW del Aprada-tepui, 05°23'N, 62°27'W, 1200 m, 05 May 1987 (fr), Huber 12094 (NY); Plateau of Auyan-tepui, central N section of E branch, 5°57'N, 62°25'W, 1940 m, 27 Aug 1983 (fl), Prance & Huber 28274 (K, NY, US); Ptari-tepui, vicinity of Misia Kathy Camp, 1585 m, 28 Oct 1944 (fl), Steyermark 59463 (F); Ptari-tepui, vicinity of Misia Kathy Camp, 1585 m, 28 Oct 1944 (fr), Steyermark 57464 (GH); Ptari-tepui, vicinity of Misia Kathy Camp, 1585 m, 28 Oct 1944 (fr), Steyermark 59464 (F[2], US); Ptari-tepui, vicinity of Ptari-tepui Cave rock camp, 1600-2000 m, 12-13 Aug 1970, Moore 9756 (VEN); Río Tehuanen camp between Kavanayén and Ptari-tepui, 1240 m, 12-13 Aug 1970 (fl), Moore et al. 9697 (NY, US, VEN); Río Uiri-yuk, escarpment of La Escalera, 850 m, 21 Aug 1962 (fr), Maguire et al. 46830 (NY); rd. El Dorado-Sta. Helena de Uairen, near Río Aponguao, 12 Dec 1969 (fr), Marcano

Berti & Bautista 2480 (US, VEN); Sierra Pakaraima, headwaters of Río Paragua (Aguapira), along the Venezuela-Brazil border, 3°40'N, 63°00'O, 1400 m, 4-5 May 1973 (fr), Steyermark 107335 (F, MO, NY); summit of Auyan-tepui, E side, N of Mision de Camarata, 5°50'N, 62°30'W, 1940 m, 27 Feb 1978 (fl), Steyermark et al. 116102 (NY, VEN); summit of Auyantepui, 2000-2200 m, Sep 1937 (fl), Cardona 213 (US, VEN); summit of Cerro Auyantepuy, 1800 m, 05 Feb 1988 (fl), Delascio & López 13671 (MO, VEN); summit of Cerro Auyantepuy, 1800 m, 05 Feb 1988 (fl), Delascio & López 13195 (MO); Uaipan-tepui, summit, 1900 m, Phelps 385 (NY); Uaipan-tepui, W peak, ca. 50 m below the summit, 1900 m, 04 Mar 1967 (fl), Koyama & Agostini 7479 (NY).

Retiniphyllum scabrum is most similar to R. laxiflorum by having showy, long-tubular, red corollas, and the same kind of pyrenes, and easily distinguishable by their inflorescences, which are umbellate in Retiniphyllum scabrum and racemose in R. laxiflorum.

Bentham (1841) described Retiniphyllum scabrum Benth., from a Robert Schomburgk's collection from the Guayana Region. This collection was made in the journey from Roraima to Esmeralda and Fort São Joaquim from 21 November 1838 to 20 June 1839 (Van Dam, 2002), but the exact locality and date is unknown. As explained above, the type specimen Retiniphyllum cearense Standl. was not collected by Gardner in Ceará, but by Robert Schomburgk in the Guayana Region instead. Standley (1937), not knowing about the erroneous label of the specimen, stated that

Retiniphyllum cearense is related to R. erythranthum "in which the leaves have only a sparse pubescence of closely appressed hairs". Although he did not mention additional differences between both taxa, he described the flowers of R. cearense as sessile. However, the specimen has flowers with pedicels ranging from 2 to 4 mm long. Based on Standley's description, Steyermark (1965), having observed only the fragment specimen housed at F (a leaf and a flower without involucel), was unable to observe the pedicels of the flowers and maintained R. cearense as a separate species.

Steyermark (1965) reduced Retiniphyllum erythranthum at the varietal rank under R. scabrum. According to Steyermark, the typical variety of Retiniphyllum scabrum has elliptic, obovate to lanceolate-oblong leaves, with scabrid-hirsutulous indument below, calyx lobes 0.75-2 mm long, and it is restricted to the Bolívar State of Venezuela, while R. scabrum var. erythranthum has ovate or broadly elliptic-ovate leaves, usually glabrous or with less abundant (not scabrid) trichomes, calyx lobes 0.75 mm long, and it is confined to Cerro Duida and other mountains in the State of Amazonas, Venezuela. However, as Steyermark (1974) pointed out, individuals with intermediate characters between the two varieties are often found, as leaf shape and indument and calyx lobes length vary considerably in Retiniphyllum scabrum. The distinction between the two varieties was apparently based on a gradation of morphological characters. For instance, some specimens have the typical features of Retiniphyllum scabrum var. scabrum, except for the leaves shape and indument (e.g. Anderson 13874, Delascio & López 13671), or except by the leaves shape and indument, and the calyx lobes (Pipoly et al. 7158; Luteyn et al. 9476) that resemble var. erythranthum. The morphological plasticity of Retiniphyllum scabrum becomes evident when studying individuals from Serra Araça, Brazil (Prance et al. 29084), in which leaf shape resembles that of var. erythranthum, leaves indument and calyx lobes resemble that of the typical variety.

Steyermark (1965) described Retiniphyllum scabrum var. ayangannense Steyerm. from a specimen collected at Mount Ayanganna, Guyana, distinguishing it by a sub-truncate or repand-denticulate calyx, (vs. lobulate with ovate to broadly triangular lobes in the other two varieties). Although most specimens from Mount Ayanganna have a non-lobulate calyx, one recent collection (Pipoly et al. 10720) has calyx with well developed, triangular lobes up to 1 mm long. Another collection (Hoffman & Henkel 3334) from

Pakaraima Mountains, to which Mount Ayanganna is included, has calyx with very reduced teeth (0.2 mm long), and also well developed lobes up to 1.2 mm long. Therefore, the collections of Retiniphyllum scabrum from Mount Ayanganna show the range of morphological variation of calyx shape in the species. In conclusion, due to the lack of morphological characters related to geographic distribution, no varietal ranks are recognized in Retiniphyllum scabrum.

1.4.18. **Retiniphyllum schomburgkii** (Benth.) Muell. Arg. in Mart., Fl. Bras. 6(5): 12. 1881. Commianthus schomburgkii Benth., J. Bot. (Hooker) 3: 223. 1841. Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. schomburgkii, Mem. New York Bot. Gard. 12: 240. 1965. Type. Guyana: Precise locality unknown [ascent of the Rivers Courantyne and Berbice (2 Sep 1836-Mar 1837), or expedition to the source of he Essequibo River and Mount Roraima (12 Sep 1837-9 Nov 1838)], 1837 (fl, fr) Rob. Schomburgk 179 (lectotype, K, here selected; isolectotypes, BM, BR[2], F, G[2], NY, US, W; photo-G at F, GH). Figs. 4D, H7, 13A, 14C, 34, 35

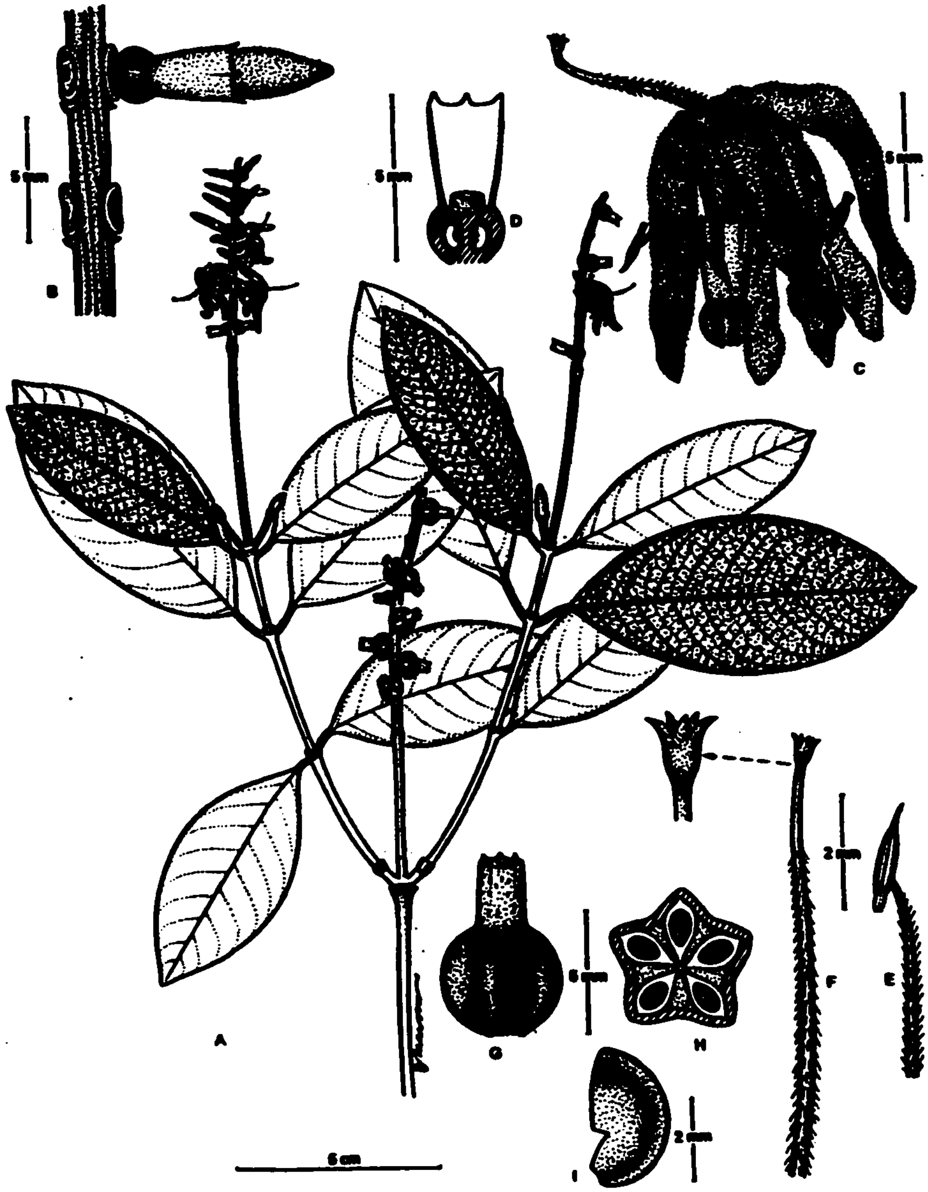
Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. occidentale Steyerm., Mem. New York Bot. Gard. 12: 240. 1965. Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. occidentale var. occidentale, Mem. New York Bot. Gard. 12: 240. 1965. Type. Venezuela. Amazonas: Cerro Yapacana, NW base, edge of Savanna No. 3, 150 m, 17 Mar 1953 (fl), Maguire & Wurdack 34531 (holotype, NY; isotype, US).

Retiniphyllum schomburgkii (Benth.) Muell. Arg. subsp. occidentale Steyerm. var. hirticalyx Steyerm., Mem. New York Bot. Gard. 12: 241. 1965. Type. Colombia. Guainia: 0.5-1.5 km N of Puerto Colombia (opposite Maroa), sabanita, 130 m, 12 Oct 1957 (fl), Maguire, Wurdack & Keith 41860 (holotype, NY; isotype, US).

Retiniphyllum schomburgkii (Benth.) Muell. Arg. var. angustiflorum J. Huber, Bull. Soc. Bot. Genève 6: 209. 1914. Type. Brazil. Pará: Rio Trombetas, Campos de l'Ariramba, 20 Dec 1906 (fl) Ducke 8022 (lectotype, RB-n.v.; isolectotypes, BM, G).

Shrubs to **small trees** up to 5 m tall, and 4 cm dbh. **Leafy branchlets** terete, 1.8-4 mm thick, glabrous or hirsute. **Stipules** sheathing, truncate, 1.5-2.5 mm long, coriaceous, hirsute or glabrous outside, glabrous and with colleters inside. **Leaves** petiolate; petioles 5-20 mm long, 1-2 mm thick, glabrous or hirsutulous; blades 3.3-12.1 x (1.6-)2.2-5.3 cm, L/W 1.4:1-3.2:1, elliptic, oblong-elliptic, oblanceolate or obovate, cuneate, acute or round at base, mucrunulate, acuminate, acute, obtuse or round at apex, coriaceous, hirsutulous or hirsute below, glabrous above except for the midvein that is strigose, rarely hirsutulous above, rarely midvein glabrous, brown or greenish when dry; secondary venation brochidodromous, 9-14 veins each side, tertiary veins random reticulate; domatia absent or rarely pocket. **Inflorescences** terminal, spicate, erect, 6-18.5 cm long; rachis terete, 1-4 mm thick, hirsutulous, sinuous or straight at distal portion, with or without two foliose bracts subtending the basal pair of flowers, 1-2.5 mm long, rarely resembling small leaves, 8.5-35 mm, portion of rachis from first pair to next flowers 0.8-3 cm; peduncle 1.7-8.5 cm long. **Bracteoles** reduced, 0.5-1 mm long, margin entire or rarely 3-lobate, glabrous or hirsute, with colleters inside. **Involucel** discoid, 0.2-0.9 x 2-3.2 mm, truncate, coriaceous, glabrous or hirsute outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, tube bent downward. **Flowers** zygomorphic, sessile, rarely with a pedicel 0.4-0.7 mm long. **Calyx** tubular, truncate or with five or six teeth, 1.8-5.2 x 2-3.1 mm, papillose outside, glabrous and without colleters inside, teeth (-0.3)0.5-1.6 mm long, greenish-yellow. **Corolla** 12.1-23 mm long; tube infundibuliform, 3.8-10 mm long, 0.5-2.2 mm wide at base, 1.3-3.5 mm wide at the orifice, strigose outside, with a ring of hairs inside at distal portion, 3-4.5 mm from base, glabrous below ring inside, white or greenish-white, with five longitudinal light pink lines; lobes five, rarely six, 1-2 1/2 of tube length, 6.5-14 x 1.2-2.8 mm, narrowly oblong or lanceolate, acute or round at apex, sericeous throughout, white. **Filaments** (4.5-)6.2-8 mm long, 0.2-0.6 mm wide, expanded at base, hirsute; anthers narrowly oblong, 1.1-2.5 x 0.3-0.7 mm; basal appendages oblong, 0.3-0.8 mm long, truncate at base; apical appendages narrowly triangular, 0.2-0.5 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 11-17.5 mm long, pilose retrorsely at base and medial portion, glabrous distally; capitate portion globose before branches opening, style branches narrowly triangular, 0.3-0.5 mm. **Ovary** 5-locular, globose, cylindrical or longitudinally ellipsoid, rarely turbinate, 0.7-2.3 x 1.6-3 mm, glabrous or hirsute. **Fruit** globose, transversally or longitudinally ellipsoid,

Fig. 34. Illustration of Retiniphyllum schomburgkii. A. Habit of inflorescences. B. Bracteoles and involucels. C. Flower in anthesis. D. Ovary and calyx. E. Stamen, anther with basal and apical appendages. F. Style and stigmatic surfaces. G. Fruit. H. Fruit in transversal section. I. Pyrene.


A
B
C
D
E
F
G
H
I
5 mm
2 mm
5 cm

3.5-5.5 x 4-7 mm, glabrous or hirsute throughout, reddish. **Pyrenes** 3.1-5 x 1.5-2.5 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.2-3 x 0.6-1.4 mm.

Distribution (Fig. 35) **and ecology**. Widespread in the area of distribution of the genus. This species is found from Surinam to Colombia, and from the Río Orinoco in Venezuela to Serra do Cachimbo in Pará, Brazil. Although Retiniphyllum schomburgkii is found more often in lowlands, it has been collected in high elevations. For instance, it has been collected at base (300 m) and summit (2300 m) of Mount Duida in Amazonas, Venezuela. Flowering and fruiting specimens were collected throughout the year.

Selected specimens examined. BRAZIL. AMAZONAS: Mun. Barcelos, Rio Jauari, 0°42'N, 63°22'W, 07 Feb 1985 (fl), Silva 223 (NY); vicinity of Manaus, Ponta Negra, 18 Dec 1968 (fl), Prance et al. 9094 (NY); Rio Uatuma, Mun. Itaperanga, 18 Jul 1979 (fl), Cid et al. 485 (NY); rd. Humaitá-Itaituba, 8°7'S, 61°49'W, 24 Nov 1979 (fr), Vieira et al. 125 (MO); Serra Aracá, 0°48'N, 63°8'W, 140 m, 04 Mar 1984 (fl, fr), Pipoly & Cress 6787 (US); Temendaui, between Manaus and São Gabriel, 0°35'S, 64°40'W, 30 Jun 1979 (fr), Alencar 250 (NY); vicinity of Ponta Negra, Rio Negro, 18 Dec 1968 (fl), Prance et al. 9094 (F). **PARÁ:** E of Tucurí and Rio Tocantins, 3°30'S, 49°32'W, 28 Oct 1981 (fr), Daly et al. 979 (MO); Gurupá, campina do Jacopi, 7°35'S, 57°31'W, 140 m, 07 Feb 1974 (fl, fr), Silva & Rosario 5039 (US);

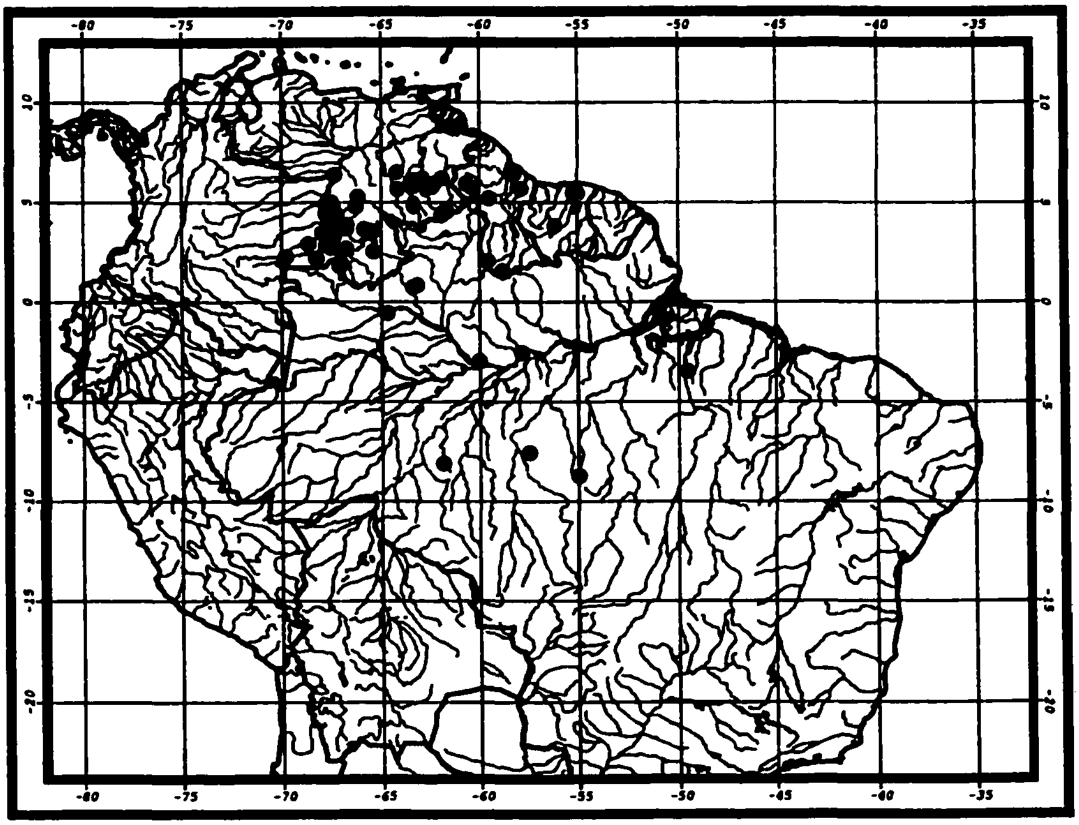


Fig. 35. Distribution of Retiniphyllum schomburgkii

Serra do Cachimbo, Km 873 Cuiabá-Santarem, 460 m, 06 Nov 1977 (fr), Prance et al. 24929 (US).

COLOMBIA. GUAINÍA: Morroco trocha Nabuquén, 2°52'550"N, 68°39'363"W, 24 Feb 1995 (fl), Córdoba et al. 608 (COL); Morroco, trocha Nabuquén, 2°52'N, 68°39'W, 24 Feb 1995 (fr), Córdoba et al. 608 (COL); near San Felipe airport, 1°47'N, 67°6'W, 120 m, 06 Apr 1984 (fr), Gentry & Stein 46379 (COL, MO, NY); Puerto Colombia, close to Maroa, 19 Feb 1965 (fl), Fernández-Pérez 6923 (COL); Puerto Huesito, Alto de la Cruz, between Caño Chaquita (affluent of Río Atabapo) and Caño Gente, 200 m, 18-20 Aug 1975 (fl, fr), García-Barriga 20913 (COL, F, GH, US); Río Negro, Puerto Colombia, 75 m, 27 Oct 1977 (fr), Pabón et al. 433 (COL); Río Negro, San Felipe and vicinity (below confluence of Río Guainía and Río Casiquiare), 1°50'N, 67°0'W, 183 m, 25 Oct 1952 (fl), Schultes et al. 17985 (US), (fl, fr), Schultes et al. 17997 (BM, F, GH, NY, US); San Felipe, 1°47'N, 67°6'W, 120 m, 06 Apr 1984 (fr), Gentry & Stein 46379 (COL); Serranía de Naquén, around Maimachi and Mina Vieja, 02°09'N, 68°14'W, 115 m, 12 Apr 1993 (fr), Barbosa & Madriñán 8424 (COL, F, MO, NY); Serrania de Naquén, Maimachi, 2°9'N, 68°14'W, 115 m, 12 Apr 1993 (fr), Barbosa & Madriñán 8424 (COL). **VAUPÉS:** Raudal Guacamayo, 2°15'N, 69°45'W, 180 m, 04 Feb 1955 (fr), Fernández 2152 (F); Río Inírida, left margin of Raudal Guacamayo, 69°45'W, 180 m, 04 Feb 1953 (fl, fr), Fernández 2152 (COL, F, US).

GUYANA: Kamoa River, 1°32'N, 58°50'W, 260 m, 17 Sep 1989 (fl), Jansen-Jacobs et al. 1644 (NY); Rupununi Savanna, 1°60'N, 59°34'W, 290 m, 07 Sep 1997 (fl), Jansen-Jacobs et al. 5395 (MO); Kuroba, E of Mazaruni River, 5°54'N, 60°36'W, 550-620, 24 Jan 1996 (fl), Clarke 804 (NY); Berbice River; Warnibo Creek, 5°39'N, 57°53'W, 60 m, 28 Jun 1995 (fl), Chanderbali 116 (NY); along Linden Highway, 6 km S of Kuru-Kuru Creek, 23'N, 58 14'W, 10-20 m, 03 Jan 1992 (fl), Hoffman et al. 701 (MO); vicinity of Yarowakabra Housing, 6°28'N, 58°12'W, 50 m, 13 Sep 1986 (fr), Pipoly & Williams 8448 (NY); Pakaraima Mountains, 5°42'N, 60°18'W, 500 m, 22 Jun 1986 (fl), Pipoly & Alfred 7973 (MO); Kaieteur National Park, 5°11'N, 59°30'W, 500 m, 19 Jul 1993 (fl), Henkel & Williams 2301 (MO).

SURINAM: Tafelberg Mountain, savanna No. 4, 552 m, 15 Aug 1944 (fl), Maguire 2437a (GH); vicinity of Zanderij, 45-50 km S of Paramaribo, 19 Sep 1976 (fr), Mori et al. 8346 (NY).

VENEZUELA. AMAZONAS: NE of caserio Munduapo, 20 km from Río Sipapo mouth, 4°53'N, 67°47'W, 90 m, 17 Feb 1979 (fl), Huber 3152 (NY); rd. San Carlos de Río Negro-Solano, 1° 55'N, 67°2'W, 120 m, 03 Apr 2000 (fr), Berry & Aymard 7567 (MO); 1-1.7 km W of Laguna Uquira, 4.5 km SSW from mouth of Río Temi, 3°11'43"N, 67°24'03"W, 100 m, 06 Mar 1996 (fl), Berry et al. 6027 (MO); 110 km up of Río Guayapo, 4°18'N, 67°28'W, 120 m, May 1989 (fr), Foldats & Velazco 9320 (NY); 25 km SW La Esmeralda, 3°30'N, 65°25'W, 280 m, 17 Feb 1990 (fl), Aymad & Delgado 7937 (NY); 3 km E of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 120 m, 23 Apr 1979 (fl, fr), Liesner 6910 (MO); 3 km NE of San Carlos de Río Negro along rd. to Solano, 120 m, 09 Apr 1984 (fl, fr), Stein 1494 (MO, NY, US); 4 km W of Serrania del Cuao, 4°59'N, 67°32'W, 100 m, 14 Jul 1980 (fr), Huber & Tillet 5287 (NY); Cerro Duida, N slopes of Caño Negro, 2000-2300 m, 23 Nov 1950 (fl), Maguire et al. 29704 (NY); Cerro Moriche, Río Ventuarí, 150 m, 17 Jan 1951 (fl), Maguire et al. 30997 (GH, NY); Cerro Moriche, Río Ventuarí, 800 m, 14 Jan 1951 (fl), Maguire et al. 30901 (US); Cerro Morrocoy, Valle del Río Camani, 5°15'N, 66°09'W, 130 m, 20 Aug 1978 (fr), Huber 2357 (VEN); Cerro Yapacana, 3°45'N, 66°45'W, 550-825 m, 07 May 1970 (fr), Steyermark & Bunting 103094 (NY); Depto. Atabapo, sabanita a 5 km al ESE de la punta E del Cerro Yapacana, 3° 40'N, 66°44'W, 120 m, 28 Jun 1979 (fr), Huber 3892 (VEN); Dpto. Atabapo, 44 km SE from Sta. Barbara del Orinoco, 3°50'N, 66°44'W, 130 m, may 1990 (fl), Marin 1192 (MO); Dpto. Atabapo, Caño Caname, Cucurital, 3°40'N, 67°22'W, 100 m, 29 Apr-4 May 1979 (fl), Huber et al. 3735 (NY, VEN); Dpto. Atabapo, Río Cunucunuma, Raudal Mapaco, 3°37'N, 65° 51'W, 170 m, Apr 1990 (fl, fr), Fernández 7802 (MO, NY); Dpto. Atures, 2 km upstream of San Juan de Ucata, 4°20'25"N, 67°14'12"W, 120-150 m, 19 Jun 1992 (fl, fr), Berry et al. 5118 (MO, NY); Dpto. Atures, 3 km N of Santa Rosa de Ucata, east of Río Orinoco, 4°23'33"N, 67°44'27"W, 120 m, 22 Jun 1992 (fl, fr), Berry et al. 5207 (MO); Dpto. Atures, 4 km W from Serranía del Cuao, 4°59'N, 67°32'W, 100 m, 14 Jul 1980 (fr), Huber & Tillett 5287 (NY); Dpto. Atures, Santa Rosa de Ucata, 4°24'N, 67°46'W, 80-85 m, 19 Apr 1989 (fl), Romero et al. 1845 (GH, MO, NY); Dpto. Casiquiare, Caño San Miguel, Las Tinajas, 2°39'N, 66°45'W, 160 m, 22 Apr 1991 (fr), Aymard 9241 (NY); Dpto. Río Negro, vicinity and N of Cerro Vinilla, 30 km SSW of Ocamo, affluent of Río Orinoco, 2 31'N, 65 23'W, 440-600 m, 1-2 Mar 1984 (fl, fr), Steyermark et al. 130365 (MO); La Esmeralda, Jan-Feb 1969 (fl, fr), Fariñas et al. 595 (VEN);

near San Carlos de Río Negro, 1°55'N, 67 W, 125 m, 17 Jan 1968 (fl, fr), Wessels 2264 (NY); Raudal Maturín, Río Asa, 6°22'N, 67°19'W, 13 May-13 Jun 1987 (fl), Stergios 11244 (NY); Río Caname, 36 km from Río Aatabapo, 3°37'N, 67°07'W, Nov 1989 (fr), Yanez 164 (MO); Río Casiquiare, Jan-Feb 1969 (fl, fr), Fariñas et al. 695 (NY); Río Guainia, Caño Pimichín, 128 m, 01 Jan 1942 (fl), Williams 14929 (NY); Río Guainia, Río Negro, confluence with Casiquiare, 1854 (fl), Spruce 3557 (C); Sabana de Moyo, on S bank of Río Ventuarí, 15 km above mouth, 150 m, 05 May 1954 (fl), Silverio-Level 32 (NY); Sabana de Moyo, R bank of Orinoco, 10 km above mouth of Río Ventuarí, 125-150 m, 31 Jul 1959 (fl, fr), Wurdack & Adderley 43703 (G, NY); San Carlos de Río Negro, 100 m, 28 Feb 1942 (fl), Williams 14519 (F[2], G[3], US); San Carlos de Río Negro, 3-4 km N of Sa Carlos on rd. to Solano, 09 Apr 1984 (fl, fr), Plowman 13535 (F, K, NY); San Carlos de Río Negro-Solano rd., 1-4 km NE of San Carlos, 1°56'N, 67°02'W, 100 m, 24 Apr 1974 (fr), Morillo et al. 3901 (VEN); San Carlos de Río Negro-Solano rd., 2 km E of San Carlos, 1°55'17"N, 67°02'46"W, 120 m, 03 Apr 2000 (fr), Berry & Aymard 7567 (MO); San Juan de Ucata, Caño Ucata, affluent fo the Río Orinoco, 4°20'N, 67°44'W, 120-150, 19 Jun 1992 (fr), Berry et al. 5118 (NY); SE of Cerro Autana, 4°48'N, 67°26'W, 110 m, 16 Jul 1980 (fr), Huber & Tillet 5345 (NY); Yavita, 128 m, 01 Jan 1942 (fl), Williams 13891 (F[2], G, GH, NY, US). BOLIVAR: 3 km S of El Pauji, 4°30'N, 61°35'W, 900 m, 08 Nov 1985 (fr), Liesner 19712 (VEN); alto Río Cuyuní, Río Chicanán, 2 km south of Río Chibau, 100 m, 01 Sep 1962 (fl), Maguire et al. 53549 (NY); alto Río Cuyuní, Río Chicanán, between Salto Pitón and Quebrada Franela, Cerro Pitón, Cordillera Epicara, 400 m, 9-11 Sep 1962, Maguire et al. 53691 (NY); Cerro Guaiquinima, SW portion, 5°38'N, 64°08'W, 830 m, 01 Sep 1988 (fl), Fernandez 4714 (NY); Dto. Heres, upper Río Aza, 6°5'N, 63°17'W, 370 m, 21 Mar 1985 (fr), Huber 10299 (US); Dto. Piar, Auyan-tepui, 5°42'N, 62°37'W, 900 m, 11 Dec 1984 (fl), Huber et al. 9891 (NY); Dto. Piar, Río Aparamán, 5°55'N, 62°13'W, 500 m, 07 May 1986 (fl), Holst & Liesner 2808 (MO); Dto. Roscio, Ikabaru, 4°20'N, 61°51'W, 400 m, 29 Nov 1982 (fl), Steyermark et al. 127299 (MO); La Gran Sabana, ca. 3 km NW of Kamarata, 450 m, 23 Feb 1967 (fl, fr), Koyama & Agostini 7264 (NY); Mun. Raul Leoni, Río Ichun, 5°47'N, 63°20'W, 460 m, Mar 1988 (fr), Delgado 139 (MO); Mun. Sucre, 6°28'N, 64°12'W, 293 m, Jun 1989 (fr), Fernandez & Yanez 450 (NY); Mun. Gran Sabana, sector occidental, Parque Nacional Canaima Isla Raton, intersección Río Auyán y Río Churum, 500 m, 26-31 Aug 1994 (fl), Delascio 16083 (VEN); Sierra Ichún, Salto Maria Espuma, 4°46'N, 63°18'W, 625-725 m, 27 Dec 1961 (fl), Steyermark 90290 (NY).

Two species are similar to Retiniphyllum schomburgkii in having spicate inflorescences with white and short-tubular corollas: R. parvifolium, endemic to Serra do Cachimbo in Brazil, with reduced leaves (2.2-4.2 x 1.1-2.7 cm), and R. guianense, endemic to Mt. Merumé in Guyana, with reduced inflorescences (1.5-6.5 cm), and fruits about twice the size of R. schomburgkii.

The name Retiniphyllum sericeum was found in a handwritten note on the specimen Poeppig D. 2948, and this name remained unpublished.

1.4.19. Retiniphyllum secundiflorum Bonpl. in Humb. & Bonpl., Pl. aequin. 1: 86. 1806. Nonatelia secundiflora (Bonpl.) Spreng., Syst. Veg. 1: 751. 1825. Type. Venezuela. Amazonas: San Baltazar, between Río Orinoco and Río Negro, Humboldt & Bonpland s.n. (lectotype, P-n.v., N. 135095, here selected; photo-P at NY; isolectotype, B*; photo-B at F, GH, MO). Figs. 1E, 7B,C, 10E,F, 15D, 22, 36

Shrubs to **small trees** 1-5 m tall. **Leafy branchlets** terete or decussately compressed, 2-4 mm thick, glabrous or strigose. **Stipules** sheathing, deltoid or broadly triangular at apex, 4-7 x 3-5 mm, coriaceous, strigose outside, glabrous and with colleters throughout inside, caducous. **Leaves** petiolate; petioles 3-16 mm long, 1-2 mm thick, strigose at edges; blades 3.6-11.5 x 2-5.6 cm, L/W 1.5:1-2.7:1, obovate, oblanceolate, elliptic or oblong, acute or rounded at base, rounded, retuse, or rarely slightly acuminate at apex, coriaceous, glabrous or hispidulous, with strigose hairs at margin and along primary vein above, canescent below, brownish or olive green when dry; primary, secondary and tertiary veins strigose below, secondary venation eucamptodromous, 11-16 veins each side, tertiary veins random reticulate, rarely percurrent close to the margin; domatia absent or pocket. **Inflorescences** axillary, racemose, erect, 5-16 cm long; rachis terete, laterally compressed, rarely angulate, 0.9-1.8 mm thick, hirsute or hirsutulous, with a stipular collar up to 1.5 mm long and two bracts subtending the basal pair of flowers, bracts 9-11 mm long, portion of rachis from first pair to next flowers 1.2-3.5 cm long; peduncle 0.9-5.8 cm long, hirsute or hirsutulous. **Bracteoles** foliose, 1.8-4 x 0.6-0.8 mm, margin entire, glabrous, without colleters inside.

Fig. 36. Illustration of *Retiniphyllum secundiflorum*. A. Habit of inflorescences showing stipules. B. Bracteoles and involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Ovary and calyx. G. Fruit. H. Fruit in transversal section. I. Pyrene.


A'
B
5 mm
A
5 cm
1 mm
E
D
5 mm
F
1 cm
C
G
5 mm
H
4 mm
I

Involucel cupular, 0.5-1.5 x 2.1-2.7 mm, half entire, the other half with four lobes of different sizes, the shortest 0.7-1.4 mm long, the largest 2-4.5 mm, coriaceous, hispidulous outside, hispid and with colleters inside, persistent to the fruit. **Flower buds** cylindrical, straight. **Flowers** actinomorphic, pedicellate; pedicels 0.5-2.3 x 0.5 mm, hirsutulous. **Calyx** tubular, lobulate, 3-7.5 x 2.5-3.3 mm, hispidulous or hirsutulous outside, hispid and with colleters inside, lobes 2-3.9 x 0.5-0.8 mm, narrowly triangular, hirsutulous, green. **Corolla** 17-34 mm long; tube infundibuliform, 0.9-1.8 mm wide at base, 11-17.5 mm long, 2-3 mm wide at the orifice, sericeous outside, with a ring of hairs at basal portion, 0.6-1.5 mm wide at 2.3-3.8 mm from base, glabrous below ring, sericeous above ring inside, red; lobes 1/2-2/3 of tube length, 5.5-10 x 1-1.5 mm, lanceolate, acute at apex, sericeous throughout, red. **Filaments** 3-6.5 mm long, 0.05-0.1 mm wide, slightly expanded at base, scarcely pilose at lateral edges; anthers elliptic to narrowly elliptic, 1.4-2 x 0.3-0.6 mm; basal appendages oblong, 0.4-0.5 mm long, truncate at base; apical appendage narrowly triangular, 0.2-0.3 mm long. **Pollen** prolate-spheroidal or subprolate; sexine tectate-perforate. **Style** 18-27 x 0.2-0.4 mm, pilose at base and medial portion, glabrous distally; capitate portion globose before branches opening, style branches narrowly triangular, up to 1 mm long. **Ovary** 5- or 6-locular, longitudinally ellipsoid, 1.2-1.5 x 1.5-2.1 mm, hispidulous. **Fruit** longitudinally ellipsoid, 3-6.7 x 3.8-6.7 mm, hirsute, hirsutulous or glabrous, red. **Pyrenes** 4 x 2.1-2.7 mm, surface verrucate, with two very reduced ribs near the dorsal margin, almost imperceptible in some individuals. **Seeds** two per locule, cylindrical, attached at distal portion of the septum, 2.2-2.4 x 0.9-1 mm.

Distribution (Fig. 22) **and ecology**. Found almost exclusively in the lowlands caatinga forests and shrublands of the Río Negro basin, along the Venezuelan-Colombian border, sometimes in seasonally inundated areas. Flowering specimens were collected most of the year, except August and December. Fruiting specimens were collected most of the year, except January, August, November and December.

BRAZIL. Amazonas: Near Igarapé Jurapary, affluent of Rio Uaupés, 2 Nov 1932 (fl), Ducke s.n. [RB24021] (G, K, US); near Igarapé Jurapary, affluent of Rio Uaupés, 10 Feb 1936 (fl), Ducke 222 (NY[2]).

COLOMBIA. Guainía: 1-2 km W of Río Guainía, along caño, 0.5 km N of mouth of Casiquiare (where Ríos Negro, Guainía and Casiquiare join), 1°57'N, 67°08'W, 120 m, 05 Feb 1980 (fl), Liesner & Clark 9108 (COL, MO).

VENEZUELA. Amazonas: 1 km W of La Ceiba, Caño San Miguel, 2 km above Limoncito, 120-140 m, 14 Oct 1957 (fl, fr), Maguire et al. 41914 (NY, US); 15 km above San Fernando de Atabapo, 100 m, 17 Oct 1950 (fr), Maguire 29262 (COL, NY); along Río Casiquiare, 300 m below mouth of Río Pacimoni, 120 m, 19 Apr 1953 (fr), Maguire & Wurdack 35726 (M, NY); Caño Momoni, up to the mouth, 10-20 Feb 1989 (fl), Stergios et al. 13172 (NY); Caño Mononi, Casiquiare, before the mouth of Río Pasiba, 18 Feb-4 Mar, 1986, Stergios & Aymard 9128 (MO, VEN); Casiquiare, Laja de Caraca, 04 Oct 1928 (fl, fr), Luetzelburg 22577 (M); Depto. Atabapo, nearly opposite Cucurital de Caname, N of Caño Caname, 3°40'N, 67°22'W, 95 m, 02 May 1979 (fl), Davidse et al. 17058 (K, MO, NY); Depto. Atabapo, Caño Caname (affluent of Río Atabapo), Sabanas de Cucurital, 20 km E of mouth, 3°4'N, 67°22'W, 100 m, 29 Apr-4 May, 1979 (fr), Huber et al. 3657 (K, NY); Depto. Atabapo, Caño Caname, Sabanas de Cucurital, 20 km E of mouth, 3°40'N, 67°22'W, 100 m, 29 Apr-4 May 1979, Huber et al. 3701 (NY); Depto. Atabapo, Cucurital de Caname, Caño Caname, 3°40'N, 67°22'W, 100 m, 30 Apr-1 May, 1979 (fl), Davidse et al. 16902 (K, MO, NY, US); Depto. Casiquiare, Caño San Miguel, 2°39'N, 66°50'W, 160 m, 24 Apr 1991 (fl, fr), Aymard 9011 (MO); Depto. Casiquiare, Caño San Miguel, 2°40'N, 66°50'W, 160 m, 22 Apr 1991 (fr), Aymard 9129 (NY); Depto. Casiquiare, Caño San Miguel, 30 km E of Río Guainía, 2 38'N, 67 16'W, 90 m, 24 Feb 1979 (fl, fr), Huber 3389 (COL, NY, US); Depto. Casiquiare, Caño San Miguel, between Las Tinajas and Caño Iqueven, 2°39'N, 66°45'W, 160 m, 25 Apr 1991 (fr), Aymard 9201 (MO, NY); Depto. Casiquiare, W side of Caño Pimichín, S of Caserio Pimichín, 2°50'N, 67°33'W, 110 m, 24 Feb 1979 (fl, fr), Huber 3396 (NY); Depto. Casiquiare, Caño Pimichín, 128 m, 6-9 Jul 1969 (fl, fr), Bunting et al. 4080 (F, VEN); Depto. Casiquiare, edge of upper Caño Pimichín, 2°54'N, 67°42'W, 100 m, 01 Mar 1980 (fl), Huber 4900 (NY); Depto. Casiquiare, Río Temi, 1-2 hours from Yavita, 100-140 m, 6-19 Jun 1969 (fl), Bunting et al. 3664 (VEN); Depto. Casiquiare, W of Río Temí, 5 km from the river, 2°57'N, 67°29'W, 100 m, 24 Feb 1979 (fl, fr), Huber et al. 3413 (NY); Depto. Río Negro, lower Río Siapa, close to its junction with Río casiquiare, 2°05'N, 66°25'W, 125 m, 07 Feb 1981 (fl), Huber & Medina 5796 (NY); Depto. Río Negro, lower Río Siapa, close to its junction with Río casiquiare, 2°05'N, 66°25'W, 125 m, 07 Feb 1981 (fl), Huber & Medina 5826 (COL, NY); Dpto. Río Negro, bajo Río Guainia, Raudal Lombríz, 2 km from mouth of Río casiquiare, 2°2'N, 66°05'W, 140 m, 26 Jan 1992 (fl), Aymard et al. 9760 (MO, NY); Dpto.

Río Negro, Antiguo caserio Yanomami, Río Siapa, 2°8'45"N, 66°17'30"W, 12 Oct 1987 (fl, fr), Delascio & Liesner 13437 (MO, VEN); Esmeralda, Dec 1853 (fl), Spruce 3247 (NY); laja Jabua, granitic outcrop on E bank of Río Temi, several km from mouth, 3°12'33"N, 67°22'29"W, 100 m, 23 Nov 1995 (fl), Berry et al. 5561 (MO, NY, VEN); laja Suiza, from mouth of Río Guasacavi on N side, 3.5 km SSW of Santa Cruz, 3°14'18"N, 67°24'30"W, 100 m, 03 Mar 1996 (fl, fr), Berry et al. 5860 (MO); left bank of Caño Hechimoni, 8 km above mouth, 100-130 m, 09 Feb 1954 (fl), Maguire et al. 37626 (NY); left bank of Caño Hechimoni, 8 km above mouth, , 100-130 m, 09 Feb 1954 (fl, fr), Maguire et al. 37667 (G, NY[2], R); North-facing bank of Caño Cumare several km from its mouth at the Río Atabapo, 3°57'N, 67°40'W, 110 m, 25 May 1993 (fl, fr), Berry et al. 5462 (MO); Raudal Lombríz, Río Guainía, 2°2'13"N, 67°06'14"W, 120 m, 30 Mar 1900 , Berry & Aymard 7457 (MO); R bank of Caño Cumare, 20 km above San Fernando de Atabapo, 125-140 m, 03 Jun 1959 (fl, fr), Wurdack & Adderley 42753 (G, NY, US); Río Casiquiare, up to Solano, 100 m, 08 Apr 1970 (fr), Steyermark & Bunting 102449 (NY); Río Casiquiare, Vasiva and Pacimoni, Apr 1853 (fl, fr), Spruce 3413 (BM, BR, C, F, G[3], GH, NY[2]); Río Guainía, Caño Pimichín below Pimichín, 125-135 m, 14 Apr 1953 (fl, fr), Maguire & Wurdack 35607 (F, NY); Río Guainía, lower San Miguel, Caño Ichana, 125 m, 25 Mar 1942 (fr), Williams 14886 (F[2], G[2], GH, NY[2], US[2]); Río Guainía, Maroa, 125 m, 13 Feb 1942 (fl, fr), Williams 14320 (F, G, GH, NY, US); Río Temi, 14 km S of mouth Río Temi, 3°06'37"N, 67°23'22"W, 100 m, 08 Mar 1996 (fl), Berry et al. 6098 (MO); Río Temi, downstream from Yavita, 2°56'14"N, 67°26'21"W, 110 m, 29 Nov 1995 (fl), Berry et al. 5751 (VEN); San Fernando, Río Atabapo, playa Tigre, 01 Feb 1971 (fl), Medina 551 VEN; Santa Cruz, margen del Río Atabapo, cerca del Río Atacavim, 03 Sep 1960 (fl), Foldats 3628 (NY, VEN); Sta. Cruz, village on the Río Atabapo, 1 km N of confluence of Ríos Temeni and Atacavi, 17-18 Nov 1979 (fl), Thomas & Rogers 2673 (NY); up to the mouth of Caño Chimoni, 2°2'N, 66°24'W, 200 m, 17-20 Sep 1986 (fl, fr), Stergios et al. 9434 (MO); Yavita, 128 m, 1942 (fl), Williams 14043 (F, G[2], GH, MO, NY[2], US).

Local names. Venezuela: peramancito (Williams 14320).

Retiniphyllum secundiflorum is similar to R. francoanum, endemic to Sierra de Chiribiquete, Colombia, by having axillary inflorescences, fruits with two seeds per locule, and involucel persistent to the fruit. Retiniphyllum secundiflorum differs from R. francoanum by having foliose bracteoles (vs. reduced), ovaries 5- or 6-locular (vs. 7- or 8-locular), pyrenes without wings (vs. winged), and larger inflorescences and pyrenes.

Retiniphyllum secundiflorum is the type species of the genus, and was described by Jaimé Bonpland (1806) from a specimen collected on his travels with Alexander von Humboldt, on the Río Orinoco, Venezuela (Delprete, 2001). Antoine L. de Jussieu (1820) treated Retiniphyllum as synonymous with Nonatelia Aubl., and Sprengel (1825), following Jussieu's conclusion, made the combination Nonatelia secundiflora (Bonpl.) Spreng. Five years later, Achille Richard (1830) returned Nonatelia secundiflora to its original placement in Retiniphyllum.

1.4.20. Retiniphyllum speciosum (Spruce ex Benth.) Muell. Arg. in Mart., Fl. Bras. 6(5): 10. 1881. Commianthus speciosus Spruce ex Benth. in Hook. f., Hooker's J. Bot. Kew Gard. Misc. 5: 234. 1853. Type. Brazil. Amazonas: Rio

Negro, near São Gabriel da Cachoeira, small sandy campo scarcely 100 feet by 10 in the midst of the forest, Jan-Aug 1852 (fl, fr), Spruce 2340 (lectotype, K, here selected; photo-K at NY; isolectotypes, B*, BM, G[2], M, NY, frag.-F; photo-B at F, GH, MO, NY). Figs. 5H, 8E,F, 32

Shrubs to **small trees** up to 6 m tall. **Leafy branchlets** terete, 3.2-4.5 mm thick, glabrous. **Stipules** sheathing, truncate, 2-2.5 mm long, coriaceous, glabrous outside, glabrous and with colleters inside, persistent. **Leaves** petiolate; petioles 12-18 mm long, 1.5-2.6 mm thick, glabrous; blades 12.5-20.5 x 4.3-8 cm, L/W 2.2:1-3.7:1, oblong, elliptic or ovate, decurrent at base, caudate or apiculate at apex, apiculus up to 10 mm long, coriaceous, glabrous above and below, brown or greenish when dry; secondary venation brochidodromous, 17-24 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect, 9.1-23.5 cm long; rachis ridged, 2-3.5 mm thick, glabrous, with or without two foliose bracts subtending the first pair of flowers, rarely resembling small leaves, 55 mm long, portion of rachis from first pair to next flowers 1-4 cm; peduncle 0.7-7 cm long. **Bracteoles** reduced, 0.5-0.8 mm long, margin entire, glabrous, with colleters inside. **Involucel** discoid, 0.7-0.9 x 2.5-2.8 mm, truncate, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** zygomorphic, sessile. **Calyx** ovate, with teeth at margin, 4-5(-6.5) x 2.1-3.7 mm, glabrous outside, glabrous and without colleters inside, medial portion inflated, vascular bundles conspicuous in the non-inflated portion of the calyx, 2-3 mm long, ending in teeth, 0.2-10 mm long. **Corolla** 16.9-34 mm long; tube narrowly infundibuliform, 15-20 mm long, 0.8-1.6 mm wide at base, 2.2-2.4 mm wide at the orifice, glabrous at base, strigose at medial portion and mouth outside, with a ring of hairs at basal portion, 3-4 mm from base, glabrous below ring inside, sericeous above ring inside, red; lobes 1/2-3/4 of tube length, 6.9-14 x 1.5-3.3 mm, lanceolate, round or acute at apex, sericeous throughout, red. **Filaments** 7.8-9 mm long, 0.3-0.8 mm wide, expanded at base, hirsute throughout; anthers narrowly oblong, 2.2-2.8 x 0.4-0.7 mm; basal appendages oblong, 0.4-0.6 mm long, truncate at base; apical appendages triangular, 0.3-0.5 mm long. **Style** 28-31 mm long, scarcely hirsutulous, glabrous basally and distally; capitate portion oblong before branches opening; style branches narrowly triangular, 0.5-2 mm long. **Ovary** 5-locular, globose or oblate, 1.5-2 x 1.8-3.3 mm, glabrous. **Fruit** transversally ellipsoid, 5-6 x 4-5.5 mm, glabrous throughout, red. **Pyrenes** 4.5-4.9 x 2-2.2 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 3.7-4.1 x 1.2-1.5 mm.

Distribution (Fig. 32) **and ecology**. This species occurs mostly in the caatinga forests and shrublands of the Rio Negro basin, in NW Brazil, and in the state of Guainía, Colombia, at low elevations, with a disjunct distribution in the state of Rondonia, Brazil. Flowering specimens were collected in May, and from September to December, and fruiting specimens only in September.

Additional specimens examined. BRAZIL. AMAZONAS: without locality, s.d., (fl), Koch 52 (F); Arary-pirá, Rio Aiary, near Rio Negro, 05 Nov 1945 (fl), Fróes 21341 (GH, K, NY); Ayari, Uapuy, 20 Oct 1914 (fl), Luetzelburg 22597 (M); foothills of Serra Curicuriari, 06 Nov 1971 (fl), Prance et al. 16159 (MO, NY, R, U); Icana, Tumiry, 27 Oct 1928 (fl), Luetzelburg 22413 (M); Rio Curicuriary, near Cataractam Cajú, 20 Oct 1932 (fl), Ducke 24020 (G, U, US); Rio Negro, Igarapé Tourí, São Felipe, 27 Sep 1952 (fl), Fróes 28762 (U); Rio Uaupés, near Serra dos Tucanos, 05 Dec 1947 (fl), Pires 864 (NY, U[2]); São Felipe, Rio Içana, 21 Sep 1952 (fl), Fróes & Addison 28674 (U[2]); São Gabriel do Cachoeira, Rio Negro, 1852 (fl), Spruce s.n. (C); Serra do Tunuí, 15 May 1948 (fl), Black 48-2670 (U); Serra Wabeesee, below Bela Vista, Río Uaupés, between Inaporé and confluence with Rio Negro, 17 Nov 1947 (fl), Schultes & Pires 9139 (GH, NY, US); Rio Uaupés, 14 Nov 1928 (fl), Luetzelburg 22515 (M); Rio Uaupés, Yutica, 28 Nov 1915 (fl), Luetzelburg 23608 (M, W); Upper Rio Negro, 1907-1908 (fl), Weiss & Schmidt s.n. (F, NY); Yútica, left margin of Río Uaupés, 15 Nov 1952 (fl), Romero-Castañeda 3524, 3514 (COL).

RONDONIA: Porto Velho, 17 Sep 1975 (fr), Mota & Coêlho 182 (US). **STATE UNKNOWN:** Without locality (fl), Spruce 2360 (G).

COLOMBIA. GUAINÍA: Caño Guarinuma, Río Guainía, 150 m, 10 Oct 1977 (fl), Espina et al. 136 (COL); Karanacoa, Río Guainía, 150 m, 12 Oct 1977 (fl), Espina et al. 190 (COL).

Retiniphyllum speciosum is similar to R. rhabdocalyx, by having spicate inflorescences, and long-tubular, dark pink dark pink corollas. These species were treated as synonymous by Steyermark (1965); however, they are here treated as separate because Retiniphyllum speciosum has a calyx inflated for most of its length, with conspicuous vascular bundles in the non-inflated portion. Additionally, the corolla tube, the styles are shorter, and the pyrenes are smaller in R. speciosum than in R. rhabdocalyx.

Bentham (1853) did not cite any type specimen in the original description of Commianthus speciosus. However, Spruce 2340 corresponds to the locality cited in Bentham's publication, and it was mentioned by Müller Argoviensis (1881) when he transferred Commianthus speciosus to Retiniphyllum. The specimen Spruce 2340 preserved at K has the seal of the Herbarium Benthamianum as is here selected as the lectotype of Commianthus speciosus. The name

Ammianthus speciosus was handwritten by Spruce on the specimen label, and the specific epithet was published by Bentham.

1.4.21. Retiniphyllum tepuiense Steyerm., Mem. New York Bot. Gard. 12: 237. 1965. Type. Venezuela. Amazonas: Cerro Sipapo (Paráque), upper E basin, along water course, 1600-1800 m, 20 Jan 1949 (fl), Maguire & Politi 28458 (holotype, NY; isotypes, U, US; photo-US at NY). Figs. 5B, 6E, 11F, 12A,F, 29

Shrubs up to 4 m to **small trees** up to 8 m tall. **Leafy branchlets** terete or decussately compressed, 1.8-3 mm thick, hirsutulous. **Stipules** tubular, truncate or rarely broadly triangular, 1-4.5 mm, with small teeth, coriaceous, hirsute outside, glabrous and with colleters throughout inside, persistent. **Leaves** petiolate; petioles 5-15 mm long, 1-2 mm thick, hirsutulous or glabrous 3-10.5 x 1.4-4, L/W 2:1-2.9:1, obovate, oblanceolate or elliptic, acute or cuneate at base, acute or rounded at apex, coriaceous, glabrous, with hirtellous hairs at margin, glabrous below, primary vein glabrous or hirtellous below, brownish or olive green when dry; secondary veins weak broquidodromous, 8-13 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, racemose, erect, up to 36 flowers per inflorescence, 4.5-11.6 cm long; rachis ridged, 0.7-3 mm thick, glabrous or hirtellous, basal pair of flowers subtended by a stipular collar up to 1.5 mm long, rarely with two foliose bracts 4 mm long, portion of rachis from first pair to next flowers 1.3-2.5 cm long; peduncle 0.7-2.8 cm long, hirtellous or glabrous. **Bracteoles** reduced, 0.5-1 mm, with small teeth, glabrous, with colleters inside. **Involucel** discoid, 0.5-0.8 x 1.6-2 mm, coriaceous, glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, straight. **Flowers** zygomorphic, pedicellate; pedicels 2.5-7.2 x 0.9-1.5 mm, glabrous or hirsutulous. **Calyx** tubular 2.5-3 x 2.8-3.2 mm, glabrous, hirsutulous or hispidulous outside, hispidulous and without colleters inside, with small teeth or lobes up to 2 mm, broadly triangular, hirsutulous. **Corolla** 12.9-17.7 mm long; tube infundibuliform, 4.3-7.2 mm long, 1.6-2 mm wide at base, 2.8-3 mm wide at the orifice, sericeous outside, with a ring of hairs at distal portion, 1-2 mm wide at 3.8-4.5 mm from base, glabrous below ring, cream-white tinged with pink; lobes 1 1/2- 2 of tube length 8-10.5 x 1.3-2.8 mm, spatulate or lanceolate, round at apex, sericeous throughout, cream-white tinged with pink. **Filaments** 4.5-6.5 mm long, 0.2-1.5 mm wide, laterally compressed, expanded at base, pilose throughout, rarely only at lateral edges; anthers lanceolate, 2.2-3 x 0.4-0.8 mm, basal appendages oblong, 0.5-0.8 mm long, truncate at base or obovate with rounded margin; apical appendages narrowly triangular, 0.5-0.6 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 8.5-13.5 x 0.2-0.6 mm, clavate, pilose from base to medial portion, and glabrous distally; capitate portion globose before branches opening, style branches narrowly triangular, up to 0.2 mm long. **Ovary** 5-locular, rarely 4-locular, globose, 2-2.8 x 2-3.3 mm, glabrous or hirsutulous. **Fruit** globose, 6-7 x 6-7.5 mm, glabrous, dark purple. **Pyrenes** 4.7-5.5 x 2.3-3 mm, surface verrucate, with two parallel wings inserted near the ventral margin. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 2.5 x 0.8 mm.

Distribution (Fig. 29) **and ecology**. This species occurs only at high elevations (1300-1900 m), in the westernmost mountains of the Guayana Region, in the state of Amazonas, Venezuela. It has been collected from Cerro de la Neblina to the South to Cerros Sipapo, Cuao, and Serrania Yutage in the North, in upper montane forests.

Found mostly in the Pantepui Province of the Guayana Region, Retiniphyllum tepuiense is not sympatric with R. scabrum, the other highland species of the genus. Flowering specimens were collected from January to March, and from October to December. Fruiting specimens were collected in February, November, and December.

Additional specimens examined. VENEZUELA. AMAZONAS: Cerro de la Neblina, 1-2 km N of Cumbre Camp, 1700-1800 m, 10 Jan 1954 (fl), Maguire et al. 37163 (NY); Cerro de la Neblina, 12.5 km NNW of Pico Phelps, 16.25 km NE of Base Camp, 0°54'30"N, 66°02'30"W, 1670-1690 m, 12 Feb 1985 (fl), Boom et al. 5796 (BR, MO, NY, US, VEN); Cerro de la Neblina, Camp XI, 6.2 km NNE of Pico Phelps, 0°51'45"N, 65°58'50"W, 1500 m, 26 Feb 1985 (fr), Nee et al. 31111 (F, NY, US, VEN); Cerro de la Neblina, Río Yatua, 1700 m, 04 Jan 1954 (fl), Maguire et al. 37030 (NY, US); Cerro de la Neblina, Río Yatua, 1800-1900 m, 17 Nov 1957 (fl, fr), Maguire et al. 42129 (GH, NY, US); Cerro de la Neblina, headwaters of Caño Grande, 1900 m, 16-17 Oct 1970, Steyermark 103935 (NY, US); Cerro Sipapo (Paráque), 1800 m, 20 Dec 1948 (fr), Maguire & Politi 27784, 28025 (NY), 27870 (NY, US), (fl, fr), 27578 (NY, US), 27680 (NY); Depto. Atures, cumbre centro-oriental del Macizo del Cuao, 4°58'N, 67°19'W, 1800 m, 10 Feb 1993 (fl), Huber 13507 VEN; Dpto. Atures, Caño Piedra, 115 km al SE de Pto. Ayacucho, 4°54'N, 66°54'W, 1500 m, Sep 1989 (fl), Fernández et al. 5928 (MO); Dpto. Atures, Valley of Río Coro-Coro, W of Serrania de Yutaje, 5°42'30"N, 66°10'W, 1300 m, 07 Mar 1987 (fl), Holst & Liesner 3371 (MO, NY, VEN).

Retiniphyllum tepuiense is exceptional in the genus by having racemose inflorescences and short-tubular, white corollas. In the rest of the species of Retiniphyllum, those with short-tubular, white corollas are always sessile, and therefore found only in spicate inflorescences. Retiniphyllum chloranthum and R. concolor have racemose inflorescences and long-tubular, white corollas.

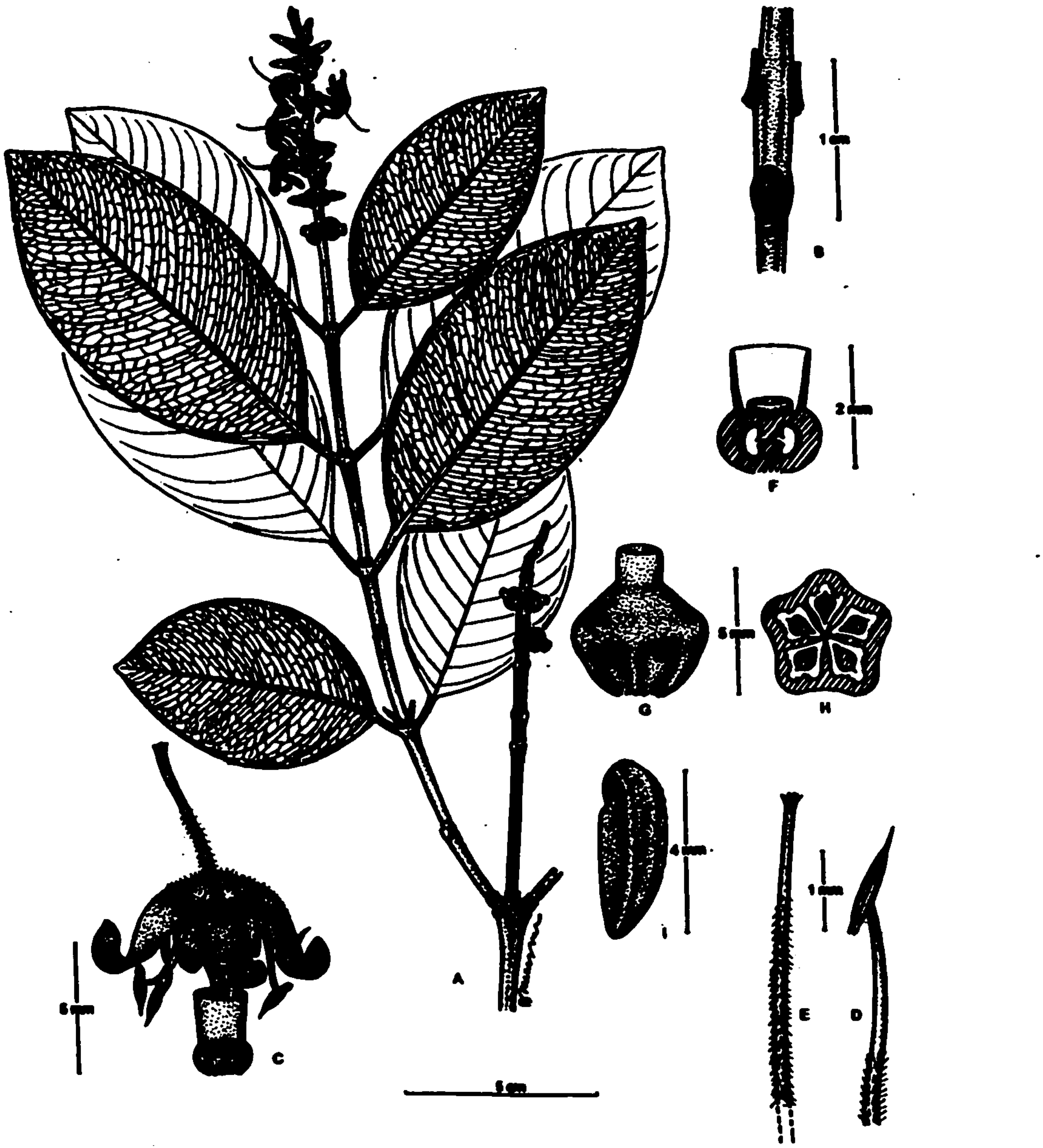
22. Retiniphyllum truncatum Muell. Arg. in Mart., Fl. Bras. 6(5): 11. 1881. Retiniphyllum truncatum Muell. Arg. var. truncatum, Mem. New York Bot. Gard. 12: 241. 1965. Type. Venezuela. Amazonas: Tomo, along Río Guainía, Jun 1854 (fl, fr), Spruce 3131 (lectotype, K, here selected; photo-K at NY; isolectotypes, B*, BM, BR, C-n.v., F[2], G[3], NY, W[2]; photo-B at F, GH, MO, NY; photo-C at F, GH, MO, NY). Figs. 4B, 8C, 11D, 12E,I, 25, 37

Retiniphyllum pallidum Muell. Arg. in Mart., Fl. Bras. 6(5): 12. 1881. Type. Colombia. Vaupés: Rio Negro Province, Cupati, Jan (fl), Martius s.n. (lectotype M, N. 26368, here selected; photo-M at F).

Retiniphyllum truncatum Muell. Arg. var. angustifolium Steyerm., Mem. New York Bot. Gard. 12: 242. 1965. Type. Colombia. Amazonas: Picada Cotuhé, 8 Nov 1946, Schultes & Black 46-375 (holotype, US; photo-US at NY[2]).

Shrubs to **small trees** up 4 m tall, and 4 cm dbh. **Leafy branchlets** terete, 2-4.8 mm thick, glabrous. **Stipules** sheathing, truncate, 1.1-2 mm long, coriaceous, glabrous outside, glabrous and with colleters throughout inside. **Leaves** petiolate; petioles 8-15 mm long, 1.2-2 mm thick, glabrous; blades 4.5-12.7 x 2.3-6.7 cm, L/W 1.5:1-3.2:1, elliptic, oblong-elliptic, ovate or obovate, cuneate or acute at base, short-acuminate to acute at apex, the acumen up to 0.3 mm, coriaceous, glabrous above and below, blade dark green above, pale green below, brown or green when dry; secondary venation brochidodromous, 9-17 veins each side, tertiary veins random reticulate; domatia absent. **Inflorescences** terminal, spicate, erect; 7.2-19.3 cm long; rachis decussately compressed, 2.1-3.6 mm thick, glabrous, rarely with two foliose bracts subtending the basal pair of flowers, 2.2-9 mm long, rarely resembling small leaves, 30 mm long, portion of rachis from first pair to next flowers 1.1-3.3 cm; peduncle 1.7-4.7(-6.6) cm long. **Bracteoles** reduced, 0.2-0.7 mm long, margin with small teeth, glabrous, with colleters inside. **Involucel** discoid, 0.3-0.6 mm long, truncate, with small teeth or repand, coriaceous,

Fig. 37. Illustration of Retiniphyllum truncatum. A. Habit of inflorescences showing stipules. B. Bracteoles and involucels. C. Flower in anthesis. D. Stamen, anther with basal and apical appendages. E. Style and stigmatic surfaces. F. Ovary and calyx. G. Fruit. H. Fruit in transversal section. I. Pyrene.


A
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5 cm

glabrous outside, glabrous and with colleters inside, persistent to the rachis. **Flower buds** cylindrical, tube or portion with lobes bent downward. **Flowers** zygomorphic, sessile. **Calyx** tubular; truncate, with small teeth or lobes, 2-3.8 x 2-3 mm, strigose outside, glabrous and without colleters inside, lobes 0.3-0.5 x 0.8-1 mm, broadly triangular, green. **Corolla** 13-17.5 mm long; tube infundibuliform, 5.5-7.5 mm long, 0.8-1.6 mm wide at base, 1.3-1.8 mm wide at medial portion, 1.7-3.7 mm wide at the orifice, inflated or not at base, glabrous from base to medial portion and strigose at mouth outside, with a ring of hairs at distal portion, at 3.1-4.6 mm from base, glabrous below ring inside, white or greenish-white with five longitudinal light pink lines; lobes 1-1 2/5 of tube length, 6-11 x 1.2-2.8 mm, narrowly oblong or lanceolate, round to acute at apex, sericeous outside and inside, white or white tinged with light pink. **Filaments** 4.5-7.5 mm long, 0.2-0.5 mm wide, slightly expanded at base, hirsute mainly at lateral edges; anthers narrowly oblong, 1.5-2 x 0.3-0.5 mm; basal appendages oblong, 0.3-0.5 mm long, truncate at base; apical appendages narrowly triangular, 0.4-0.5 mm long. **Pollen** prolate-spheroidal or subprolate; sexine microreticulate. **Style** 13-20.5 mm long, pilose from base to medial portion, glabrous distally; capitate portion globose before branches opening, style branches narrowly triangular, 0.1-0.5 mm. **Ovary** 5-locular, longitudinally ellipsoid, costate, 1-1.7 x 2.5-3.5 mm, glabrous. **Fruit** longitudinally ellipsoid, 2.6-4.5 x 3.5-6.5 mm, glabrous throughout or strigose at top, red when mature, aging in deep purple. **Pyrenes** 3.2-3.5 x 1.5-1.9 mm, surface dorsally verrucate, without wings. **Seeds** one per locule, reniform, attached at the medial portion of the septum, 1.8-2.1 x 0.5-0.9 mm.

Distribution (Fig. 25) **and ecology**. Found mostly in the Rio Negro caatinga forests and shrublands in the states of Amazonas, of both Venezuela and Brazil, and in the departments of Amazonas, Guainía and Vaupes in Colombia. Although mostly present at low elevations (100-500 m), this species is found in uplands as well. For instance, it has been collected in Venezuela at 1500-1600 m, at Cerro Duida, and at Macizo Aracamuni at 650-700 m, and in Colombia at 730 m on Serrania de Naquen and at 700 m at Cerro Isibukuri. Flowering specimens were collected throughout the year. Fruiting specimens were collected most of the year except for March and May.

Additional specimens examined. BRAZIL. AMAZONAS: Yútica, left margin of Río Vaupés, 15 Nov 1952 (fl), Romero-Castañeda 3521 (COL); Jaú National Park, Campina do Patauá, 29 Jun 1997 June 29, 1997 (fl), Ferreira & Ramos 81PNJ (INPA); Jaú National Park, Campina do Patauá, quadrante K8, 31 Aug 1998 (fl), Vicentini et al. 1331 (INPA); path between headwaters of Ira-Igrapé and headwaters of Igarapé Abiú, affluent of Río Taraira, 4-6 Jul 1948 (fl), Schultes & López 10188 (US); upper Río Negro basin, Río Içana, Tunuí, base of Serra, Nov 1947 (fl, fr), Murça-Pires 742 (NY[3], US).

COLOMBIA. AMAZONAS: Santa Isabel, sabanas de Solarte, 1° 05'S, 71°10'W, 4-6 Dec 1996 (fl, fr), Arbeláez et al. 653 (COL); trapecio Amazónico, between Amazon and Putumayo watersheds, 100 m, Nov 1945 (fr), Schultes 6903 (COL, US). **GUAINÍA:** 1°47'N, 67°6'W, 120 m, 04 Jun 1984 (fl), Gentry & Stein 46401 (COL, MO, NY); Caserio Santa Rita, Río Guainía, 100 m, 15 Oct 1977 (fl), Pabón et al. 356 (COL); Cerro Caño Minas, 2°38'137"N, 69°14'387"W, 300 m, 16 Feb 1995 (fr), Córdoba et al. 107 (COL); Maimachi, Serrania de Naquén, on trail to Caño Minas, 2°12'N, 68°13'W, 455 m, 04 Sep 1993 (fl), Madriñán & Barbosa 964 (MO); Mun. Maimachi, Serrania de Naquén, near airstrip 15, 2°13'N, 68°14'W, 730 m, 17 Jul 1992 (fl), Cortés et al. 106 (COL, MO, NY[2]); Puerto Colombia and vicinity, Río Guainía, 244-259 m, 31 Oct-2 Nov 1952 (fl), Schultes et al. 18170 (F, GH, NY, US); Raudal Pilón, Río Guainía, 145 m, 10 Aug 1977 (fl), Pabón et al. 283 (COL); Río Negro, vicinity of Piedra de Cocui, 27 Dec 1947 (fr), Schultes & López 9513 (GH, US). **VAUPÉS:** Bacaricuara, 09 Jun 1943 (fl), Allen 3100 (COL, MO); La Pedrera, Río Caquetá, Cerro Yupatí, 350 m, 03 Aug 1990 (fl), Galeano et al. 1993 (COL, NY); Mitú and vicinity, along Río Vaupés at Circasia, 13 Sep 1976 (fl), Zarucchi 2039 (COL, F, US); Mitú and vicinity, lower Río Paraná-pichuna, 09 Jun 1976 (fl), Zarucchi 1966 (GH, MO, US); Mun. Mitú, Río Vaupés, Los Cerros, 570 m, 25 Jul 1993 (fl), Galeano et al. 1123 (COL); Mun. Mitú, trail from Bogotá Cachivera and Acaricuara, 16 Jan 2000 (fr), Cortés 1647 (COL, NY); Mun. Mitú, trail from Mitú to Monfort, rd. between Timbó and Bogotá Cachivera, 15 Jan 2000 (fr), Cortés 1642 (COL); 1640 (COL, NY); (fl, fr), Cortés 1641 (COL, NY); Río Apaporis, Cachivera de Jirijirimo, 0°5'N, 70°40'W, 274 m, 08 Dec 1951 (fl), Schultes & Cabrera 13502 (F, US); 12453 (GH, US); 14009 (GH, NY, US); 14057 (F, GH, NY, US); (fl, fr), 12464 (BM, GH[2], US); Río Apaporis, Jirijirimo, 250 m, 25-26 Nov 1951 (fl, fr), García-Barriga

13753 (COL, NY[2], US); Río Apaporis, near confluence with Río Cananarí, 28 Feb 1952 (fl), Mora & Van der Hammen APA-164 (COL[2]); Río Apaporis, Raudal de Jirijirimo, Mar 1951 (fl), Schultes 12111 (COL, GH, US); Río Apaporis, Raudal de Jirijirimo, 150 m, 11-12 sep 1986 (fl), Bernal et al. 1246 (COL, NY); Río Apaporis, Raudal de Jirijirimo, 27 Nov 1951 (fl, fr), Schultes & Cabrera 14628 (GH, US); Río Apaporis, Raudal de Jirijirimo, 27 Nov 1951 (fr), Schultes & Cabrera 14631 (BM, F, GH, US); Río Apaporis, Raudal de Jirijirimo, below of Río Kananarí, 0°5'N, 70°40'W, 274 m, 21 Jan 1952 (fr), Schultes & Cabrera 14958 (F, US); Río Caquetá, La Pedrera and vicinity, 10 Dec 1952 (fr), Schultes & Cabrera 17802 (F, US); Río Caquetá, La Pedrera and vicinity, Cerro de La Pedrera, 05 Feb 1952 (fl), Schultes & Cabrera 16314 (US); Río Caquetá, La Pedrera and vicinity, Cerro de La Pedrera, 10 Feb 1952 (fl, fr), Schultes & Cabrera 17681 (F, GH, US); Río Kananarí, Cerro Isibukurí, 0°15'N, 70°35'W, 23-25 Jan 1952, Schultes & Cabrera 15702 (US[2]); Río Kananarí, Cerro Isibukurí, 762 m, 12 Apr 1951 (fl), Schultes & Cabrera 14731 (COL, GH[2]); Río Kananarí, summit of Cerro Isibukurí, 700 m, 29-30 Nov 1951 (fl), García-Barriga 13815 (COL, US); Río Kubiyú, Cerro Kañendá, 15 miles upstream from mouth, 1°0'N, 70°15'W, 244-274 m, 11 Oct 1952 (fr), Schultes & Cabrera 18367 (F, GH, US); Río Negro, San Felipe (El Castillo), 12 Dec 1947 (fl, fr), Schultes & López 9327 (COL, K, US[2]); Río Negro, San Felipe and vicinity, 1°50'N, 67°0'W, 183 m, 25 Oct 1952 (fr), Schultes & Cabrera 17989 (F, GH, US); Río Negro, San Felipe and vicinity, 1°50'N, 67°0'W, 183 m, 25 Oct 1952 (fl, fr), Schultes et al. 18023 (COL, F, GH, US); Río Paraná Pichuna, tributary of Río Vaupés, 1°10'N, 70°30'W, 213 m, Jun 1953 (fl), Schultes & Cabrera 19943 (GH); Río Piraparaná, environs of the catholic mission of San Miguel, trail beyond airstrip to the chacra of captain Rufino Vendaño Morris, 24 Oct 1976 (fl), Davis 157b (F); Río Piraparaná, Raudal Ma-hoó-gaw-he, 30 Aug 1952 , Schultes & Cabrera 17112 (BM, F, GH, US); Río Piraparaná, tributary of Río Apaporis, Caño Teemeña, 0°15'S-0°25'N, 70°30'W, 15 Sep 1952 (fl), Schultes & Cabrera 17473 (F, GH, US); Río Piraparaná, tributary of Río Apaporis, Caño Teemeña, 0°15'S-0°25'N, 70°30'W, 09 Jun 1952 (fl), Schultes & Cabrera 17253a (US); Río Piraparaná, tributary of Río Apaporis, Caño Teemeña, Savannah O-koó-me-gwa, 0°15'S-0°25'N, 70°30'W, 09 Jun 1952 (fl), Schultes & Cabrera 17230 (F, GH, NY, US); Río Piraparaná, tributary of Río Apaporis, Cerro E-ree-eé-ko-mee-o-kee, 0°15'S-0°25'N, 70°30'W, 18 Sep 1952 (fl), Schultes & Cabrera 17502 (F, GH, US); Río

Vaupés, Caño Aceite, 12 Jun 1975 (fr), Roa 272 (COL); Río Vaupés, Cerro Circasia, between Río Tí and Ñamú, 380-450 m, 30 Oct 1952 (fl), García-Barriga 15034 (COL); Río Vaupés, Circasia, R margin of the river, 200 m, 10 Sep 1939 (fl), Cuatrecasas 7167 (COL, F, US); Río Vaupés, falls of Yuruparí, 04 Dec 1953 (fl), Schultes & Cabrera 19011 (COL); Río Vaupés, Raudal de Yuruparí, 0°40'N, 70°30'W, Nov 1951 (fl), Schultes & Cabrera 19721 (F, US); Río Vaupés, Raudal de Yuruparí, 0°40'N, 70°30'W, Nov 1951 (fl), Schultes & Cabrera 19751 (BM, F, GH, US); rd. to Monfort, km 4, Cucura, 07 Mar 1993 (fl), Martínez 51 (COL); Serrania de Taraira, 10 km NW from Raudal de la Libertad, Río Apaporis, 0°58'S, 69°45'W, 250 m, 25 Jul 1993 (fr), Cortés & Rodriguez 582 (COL); Serrania de Taraira, 10 km NW from Raudal de la Libertad, Río Apaporis, 0°58'S, 69°45'W, 250 m, 23 Jul 1993 (fl), Cortés & Rodriguez 529 (COL); Yapobodá, near maloca of Yararacá, upper Cuduyarí, 12 Oct 1943 (fl, fr), Allen 3187 (COL, MO, US); Yuruparí, 350 km from Mitú, 220 m, 24 Sep 1939 (fl, fr), Cuatrecasas 6962 (COL, F, NY, US).

VENEZUELA. Amazonas: Río Guainía and Río Negro confluence, Casiquiare, 1854 (fl), Spruce 3131 (C); 10 km from san Carlos going to Solano, Bana de Mary, 27 Aug 1982 (fl), Ruiz et al. 4022 (NY); 10 km NE of San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 120 m, 04 Jul 1979 (fl), Liesner 6301 (MO); 12 km NE of San Carlos de Río Negro, Bana de Mary, 1°57'N, 67°03'W, 120 m, 20 Sep 1983 , Kapos & Tanner 109 (MO); 4 km E of San Carlos de Río Negro, 1°56'N, 67°04'W, 120 m, 11 Nov 1977 (fl, fr), Liesner 3363 (MO); 4 km E of San Carlos de Río Negro, 1 56'N, 67 04'W, 120 m, 11 Oct 1977 (fr), Liesner 3289 (MO); along rd. between Yavita and Pimichín, 1 km from Yavita, 2°55'N, 67°25-30'W, 125 m, 21 Apr 1970 (fl), Steyermark & Bunting 102887 (NY); Barra de Mari, rd. to Solano from San Carlos de Río Negro, 27 Aug 1982 (fl), Hernandez 52 (F); between Esmeralda and SE base of Cerro Duida, 200 m, 22 Aug 1944 (fl), Steyermark 57818 (F, NY); Casiquiare, Capihuara, 10 Mar 1942 (fl), Williams 16181 (US); Cerro Duida, along Río Orinoco, Jan-Feb 1969 (fr), Fariñas et al. 381 (MO, NY); Cerro Duida, Culebra Creek, 1600 m, 22-24 Apr 1949 (fr), Maguire & Maguire Jr. 29089 (NY); Cerro Duida, Río Cunucunuma, near Culebra Creek, 1500 m, 19 Nov 1950 (fl), Maguire et al. 29534 (NY, US); Dpto. Atabapo, Cerro Duida, 3°23'N, 65°48'W, 360 m, 11 Oct 1982 (fl, fr), Guanchez 2160 (VEN); Dpto. Atabapo, El Almidón, on the border between Dptos.

Atabapo and Casiquiare, 03°04'N, 67°06'W, 80 m, Nov 1989 (fr), Velazco 865 (NY); Dpto. Atabapo, La Esmeralda, 5 km N of village, 3°10'N, 65°33'W, 106 m, 25 May 1993 (fl), Coomes 213 (K); Dpto. Atabapo, near Cerro Duida, 3°23'N, 65°48'W, 360 m, 11 Oct 1982 (fr), Guánchez 2160 (MO); Dpto. Río Negro, around San Carlos de Río Negro on the rd. to Solano, 23-29 Jul 1982 (fl), Stergios & Aymard 6786 (MO); Dpto. Río Negro, E side of Macizo Aracamuni, 1°32'N, 65°48'W, 750 m, 02 Oct 1981 (fl), Huber & Medina 5899 (COL, NY, US, VEN); Dpto. Río Negro, km 11 NE of San Carlos de Río Negro along the rd. to Solano, 1°53'N, 67°02'W, 75 m, 24 Jun 1984 (fl), Davidse & Miller 26553 (MO, NY); Dpto. Río Negro, km 11 of San Carlos-Solano rd. (IVIC study area), 1°56'N, 67°03'W, 120 m, 16 Sep 1980 (fl), Huber et al. 5660 (NY); Dpto. Río Negro, San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 25 Jan 1985 (fr), Boom et al. 5370 (INPA, NY, VEN); Dpto. Río Negro, slope of Cerro Aracamuni, 1°24'N, 65°38'W, 600 m, 20 Oct 1987 (fl), Liesner & Delascio 22229 (MO, NY); Río Atabapo, Río Orinoco, Caño Temi, 3°00'N, 67°27'W, 120 m, 18 Oct 1950 (fl), Maguire 29294 (NY); Río Guainía, 1 km E of Maroa, 2°43'N, 67°32'W, 120-140 m, 10 Jul 1957 (fl), Maguire et al. 41743 (NY); Río Guainía, N of Maroa, 130 m, 10 Jul 1957 (fl), Maguire et al. 41754 (NY); Río Guainía, Raudal Lombriz, 2°2'13"N, 67°06'14"W, 120 m, 30 Mar 19200 , Berry & Aymard 7456 (MO); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 1°56'N, 67°03'W, 119 m, 1986 (fl), Uhl 473 (MO); San Carlos de Río Negro, ca. 20 km S of confluence of Río Negro and Brazo Casiquiare, 10.8 km NE of San Carlos on Solano rd., 1°56'N, 67°03'W, 119 m, 30 Sep 1978 (fl, fr), Clark 6821 (NY); Santa Cruz, margin of Río Atabapo, near mouth of Río Aatacavi, 3°15'N, 67°20'W, 09 Apr 1960 (fl), Foldats 3663 (NY, US, VEN); south of Yavita, 2°55'16"N, 67°26'17"W, 110 m, 28 Nov 1995 (fr), Berry et al. 5714 (NY, VEN).

Retiniphyllum truncatum is similar to R. kuhlmannii in having short-tubular, white corollas; however, the fruit of R. truncatum is longitudinally ellipsoid and conspicuously costate, while that of R. Kuhlmannii is globose and not costate. In addition, Retiniphyllum truncatum has thicker inflorescence rachis, and shorter pyrenes than those of R. Kuhlmannii.

Müller Argoviensis (1881), distinguished Retiniphyllum pallidum from R. truncatum by having paler leaves and branches, longer calyx and ovary, calyx five-denticulate (vs. truncate in R. truncatum), corolla lobes about the same size of the corolla tube (vs. lobes longer than tube), and corolla with a ring of hairs below middle portion of tube (vs. ring of hairs at middle portion of tube). Detailed observations of numerous specimens, including many recent collections, of R. truncatum showed that this species has a wider range of morphological variation than those observed by Müller Argoviensis. For instance, Retiniphyllum truncatum has a truncate, denticulate or lobate calyx, a variation that was noted by Steyermark (1965). According to my observations, the pale tone of the leaves and the shorter corolla lobes (5.5-6.7 in R. pallidum vrs. 6.5-11 in R. truncatum) are the only differences between the two taxa. These morphological variation are here treated as a morphological gradation, and Retiniphyllum pallidum is here treated as synonymous with R. truncatum.

Steyermark (1965) distinguished Retiniphyllum truncatum var. angustifolium from the typical variety because of its narrower leaves (2-3.2(-4)). A close examination demonstrated that there are specimens with narrow leaves throughout the range of distribution of the species. Taking into account that there is no correlation between leaf shapes and geographic distribution of this species, no varietal ranks are recognized in Retiniphyllum truncatum.

The specimen here designated as lectotype of Retiniphyllum truncatum has three labels reporting different collection localities. The first label reads "fl. Guainia, secus Tomo. Previously called casiquiarensis but inappropriately for I never see it in the true Casiquiarian affluent, June, 1854" the second reads "fl. Guainia," and the third reads "Commianthus casiquiarensis. Inter San Carlos et Solano, Oct, 1853". In addition, the labels of all the isolectotypes read "ad flumen Guainia v. Rio Negro supra ostium fluminis Casiquiare, 1854". According to Spruce's travel diary (Spruce, 1909), he arrived at Tomo, a Mission on the Río Guainía, on the 4^{th} of June of 1854. Because this date agrees with the month and year of the first label, I regard Tomo as the most accurate locality for the lectotype specimen.

As mentioned above, one of the labels attached to the lectotype bares the name "Commianthus casiquiarensis" in

Spruce's handwriting, that was never published. The name "Commianthus breviflorus" was written in the labels of the isolectotypes and in one of the labels of the lectotype, that also remained unpublished.

2. PHYLOGENY AND BIOGEOGRAPHY OF RETINIPHYLLUM

2.1. The genus Retiniphyllum and its placement in the subfamily Ixoroideae

2.1.1. Introduction

Due to its peculiar morphology, the genus Retiniphyllum has been variously included or associated with members of the three subfamilies currently recognized in the Rubiaceae. In the earliest systems of classification (Kunth, 1818; Roemer and Schultes, 1818; Jussieu, 1820; Richard, 1830; Candolle, 1830; Bentham, 1841), the bi-ovulated locules of Retiniphyllum were misinterpreted, resulting in its association with tribes that currently belong to the subfamily Rubioideae. Hooker (1873) founded the tribe Retiniphylleae, and placed it in the Series B with the tribe Cruckshanksieae, whose members are now included in the subfamily Rubioideae (Robbrecht, 1988; Bremer & Manen, 2000). Hooker (1873) included the genera Retiniphyllum and Kutchubaea Fisch. ex DC. (see details in pages 8-9) in the tribe Retiniphylleae, and he also mentioned that the genera Jackia Wall. and Scyphiphora

Gaertn. f. had dubious affinities with the tribes Retiniphylleae and Cruckshanksieae. Schumann (1891) did not recognize the tribe Retiniphylleae, but placed Retiniphyllum in the tribe Gardenieae, subfamily Cinchonoideae. On the contrary, Verdcourt (1958) kept Retiniphyllum in the tribe Retiniphylleae of the subfamily Cinchonoideae, based on the absence of raphides, contorted aestivation, fleshy fruits with 5-7 pyrenes and collateral ovules. Robbrecht (1988) included Retiniphyllum in the tribe Retiniphylleae, of the subfamily Antirheoideae, based on the curved corolla-tube, contorted aestivation, stylar pollen presentation, 5-locular ovaries with two collateral ovules, and drupaceous fruits with five pyrenes, each one-seeded. He pointed out the similarities of the tribes Retiniphylleae and Vanguerieae, such as the preformed germination slit of the pyrenes, and the appendage attached to the hilum of the seeds. Robbrecht (1988) included only Retiniphyllum in the tribe Retiniphylleae, and tentatively included Botryarrhena, perhaps because of the racemose inflorescences and perfect flowers with two ovules per locule, and Scyphiphora because of its peculiar placentation (two ovules per locule, one at top of the other).

Retiniphyllum has (4-)5(-6-8)-locular ovaries with two collateral pendulous ovules per locule, a unique combination of characters in the Rubiaceae, and the reason for its controversial relationships and ambiguous position within the family. Consequently, the use of exclusively morphological data is a limitation when attempting to position taxa with an uncommon morphology, as is the case of this genus. Therefore, molecular data provide a suitable alternative to study the phylogenetic relationships of Retiniphyllum.

Andersson and Rova (1999), in their phylogenetic study focused on the subfamily Rubioideae using rps16, sampled Retiniphyllum for the first time, and placed it within the subfamily Ixoroideae. This placement was supported by Rova et al. (2002), in their study of the Condamineeae-Rondeletieae-Sipaneeae complex, using trnL-F spacer sequence data. Retiniphyllum was located in an isolated clade of the Ixoroideae, among members of the tribes Mussaendeae, and sister to a clade with members of the tribes Coffeeae, Gardenieae, Octotropideae, Pavetteae, Rondeletieae, and Vanguerieae.

Considering that Rova et al. (2002) sampled mostly Neotropical genera, and that Retiniphyllum was included in a clade with largely Paleotropical or Pantropical representatives, the sampling in my study was expanding to include more paleotropical genera of the Ixoroideae.

The goals of this study are: 1) test the monophyly of the tribe Retiniphylleae, 2) test the monophyly of the genus Retiniphyllum, and 3) Position the Retiniphylleae within the subfamily Ixoroideae.

2.1.2. Materials and Methods

2.1.2.1. Taxon sampling and characters:

In order to obtain a better sampling throughout the subfamily, I decided to include additional genera to those sampled by Persson (2000a, 2000b), and Rova et al. (2002). Leaf samples were in part collected in the Botanical Gardens of Bruxelles (BR), Leiden (L), and Wageningen (W) by Piero Delprete, or obtained from herbarium material preserved at NY.

The characters used were chloroplast DNA (cpDNA) sequences of two molecular markers: the trnL-F intergenic spacer and the rps16 intron.

Using all the trnL-F sequences deposited in GenBank by Persson (2000a, 2000b), and Rova et al. (2002), and the sequences generated in this project, an initial analysis was performed including a total of 122 taxa, 89 of which were obtained from GenBank, and 33 were new.

In order to be able to use the two molecular markers in a combined analysis, and because I had fewer rps16 intron sequences available, a subset of the trnL-F spacer data matrix was selected, keeping the genera for which both data sets were available. Few additional genera with only trnL-F sequence data were selected in order to have representatives of all the clades formed in the initial trnL-F analysis. Information of voucher specimens is presented in Table 5.

Members of the two other subfamilies of the Rubiaceae were selected as outgroups, Psychotria sp. and Amphidasya colombiana (Standl.) Steyerm. from the Rubioideae, and Cinchona pitayensis Wedd., Portlandia platantha Hook. f., Rondeletia inermis (Spreng.) K. Krause & Urb., Gonzalagunia kallunkii Dwyer, and Ottoschmidtia sp. from the Cinchonoideae.

Table 5. Taxa used in the phylogenetic analyses of trnL-F spacer and rps16. Acronyms of the Botanical Gardens where some samples were obtained are BR= Bruxelles, L= Leiden, and W= Wageningen. Sequences originally published in *Rova et al., 2002; **Persson, 2000b; ***Struwe et al., 1998.

Taxa	Voucher	GenBank Accession numbers trnL-F	rps16
Aidia micrantha	Delprete 7371 (NY)	TBA	TBA
Aleisanthia rupestris	Tange 45171 (AAU)*	AF152660	-
Alibertia sp.	Alves 2251 (NY)	TBA	TBA
Amphidasya colombiana	Stahl 3542 (GB)*	AF152624	-
Bertiera guianensis	Andersson et al. 2029 (GB)*	AF152670	-
Borojoa patinoi	Persson et al. 2194 (GB)**	AF201034	AF200984
Botryarrhena pendula	Campos 29 (NY)	TBA	-
Calochone redingii	Chase 3355 (K)**	AF201036	AF200986
Calycophyllum spruceanum	Hatschbach 62777 (NY)	TBA	TBA
Catunaregam spinosa	Delprete 7411 (NY)	TBA	TBA
Ceriscoides sessiliflora	Maxwell 87-967 (AAU)**	AF201039	AF200989
Cinchona pitayensis	Andersson et al. 2109 (GB)*	AF152684	TBA
Coffea liberica	Delprete 7357 (NY) Bot. Gard., BR 19391724	TBA	TBA
Condaminea corymbosa	Rova et al. 2084 (S)***	AF102406	TBA
Cremaspora triflora	De Block 111 (BR)**	AF201040	AF200990
Deccania pubescens	Fisher 29 (K)**	AF201041	AF200991
Duperrea pavettifolia	Delprete 7373	TBA	TBA

	Bot. Gard. BR 00-5173		
Dyalipetalanthus fuscecens	Nee 34472 (NY)	TBA	TBA
Didymosalpinx norae	Delprete 7366 (NY)	TBA	TBA
Euclinia longiflora	Delprete 7386 (NY)	TBA	-
Fadogia audruana	Fay 8901 (NY)	TBA	TBA
Ferdinandusa sp.	Alves 2267 (NY)	TBA	TBA
Feretia aeruginescens	Mwanyambo 154 (NY)	TBA	TBA
Fernelia buxifolia	Delprete 7370 (NY)	TBA	TBA
Gardenia taitensis	Struwe & Albert 1208 (NY)***	AF102426	TBA
Genipa sp.	Delprete 6522 (NY)*	AF152665	TBA
Gleasonia prancei	Amaral 1568 (NY)*	AF152682	TBA
Gonzalagunia rosea	Rova and Sundbaum 2404 (GB)*	AF152723	-
Heinsia crinita	Nemba 221 (NY)	TBA	-
Hippots brevipes	Woytkowski 5620 (NY)*	AF152636	TBA
Hippotis scarlatina	-		AF331650
Ibetralia surinamensis	Persson 1930 (GB)**	AF201048	AF201000
Ixora finlaysoniana	Delprete 7344 (NY)	TBA	TBA
	Bot. Gard., L		
Kailarsenia ochreata	Wrigley & Telford 1488 (CBG)**	AF201049	AF201002
Keetia multiflora	Delprete 7384,	TBA	-
	Bot. Gard. BR 94-1491-37		
Kutchubaea sp.	Rodriguez 59 (NY)	TBA	TBA
Leptacina leopoldi-secundi	Delprete 7364 (NY)	TBA	TBA
	Bot. Gard. BR 95-0049-59		
Limnosipanea erythraeoides	Macedo 5537 (US)	TBA	TBA
Macrosphyra longistyla	Bagshawe 1457 (BM)**	AF201051	AF201004
Maguireothamnus speciosus	Steyermark 75781 (NY)*	TBA	-
Mussaenda pubescens	Delprete 7399,	TBA	TBA
	Bot. Gard., BR 99-1119-01		
Ottoschmidtia sp.	Delprete 7580 (NY)	TBA	TBA

Oxyanthus formosus	Delprete 7333 (NY)	TBA	TBA
Pentagonia sp.	Tuberquia 490 (S)*	AF152633	-
Pavetta stenosepala	Delprete 7387 (NY)	TBA	TBA
	Bot. Gard. BR 98-1822-16		
Platycarpum acreanum	Cid Ferreira 10407 (NY)	TBA	-
Polysphaeria sp.	Groves 529 (K)**	AF152655	AF201011
Portlandia platantha	Bot. Gard., Inst. f. Botanik,	AF102469	TBA
Posoqueria latifolia	Persson et al. 1950 (GB)*	AF152680	-
	Vienna, cult. no. RR-1039***		
Pouchetia baumanniana	Delprete 7359(NY)	TBA	TBA
	Bot. Gard. BR 87-1145	TBA	-
Pseudomussaenda flava	Andrews 857 (S)*	AF152652	TBA
Psilanthus mannii	Delprete 7349 (NY)	TBA	-
	Bot. Gard. L 24637		
Psychotria sp.	Araújo s.n. (EAC 21465)	TBA	TBA
Psydrax schimperiana	Delprete 7388 (NY)	TBA	TBA
Pyrostria media	Zarucchi 7424 (NY)	TBA	TBA
Randia nitida	Delprete 7358 (NY)	TBA	TBA
	Bot. Gard. BR 64-0516		
Retiniphyllum concolor	Berry 7093 (NY)	TBA	TBA
Retiniphyllum laxiflorum	Luteyn 15271 (NY)	TBA	TBA
Retiniphyllum maguirei	Evans 3230 (MO)	TBA	TBA
Retiniphyllum rhabdocalyx	Cortés 1648 (NY)	TBA	TBA
Retiniphyllum schomburgkii	Berry 7567 (MO)	TBA	TBA
Rondeletia inermis	Acevedo-Rodriguez et al. 7691 (NY)*	AF152745	-
Rosenbergiodendron densiflorum	Jansen-Jacobs et al. 3977 (GB)**	AF201061	-
Rothmannia manganjae	Delprete 7346 (NY)	TBA	-
	Bot. Gard. L 950231		

Rutidea orientalis	Salubeni 6225 (NY)	TBA	TBA
Schumanniophyton magnificum	Delprete 7352 (NY)	TBA	TBA
	Bot. Gard. W-C71PT00832		
Scyphiphora hydrophyllacea	Larsen 43134 (NY)	TBA	TBA
Sherbournia sp.	Cable 1049 (K)**	AF201064	AF201017
Simira cf. rubescens	Silveira 1132 (NY)	TBA	TBA
Sipanea acinifolia	Hatsbach 60916 (NY)	TBA	TBA
Sipanea biflora	Rova et al. 2005 (GB)*	AF152675	TBA
Sipanea wilson-brownei	Mori 25056 (NY)	TBA	TBA
Sipaneopsis rupicola	Wurdack and Adderley 43253 (NY)*	AF152678	TBA
Sphinctanthus microphyllus	Persson & Gustafsson 353 (GB)**	AF201066	AF201020
Stachyarrhena harley	Thomas 12032 (NY)	TBA	TBA
Sukunia longipes	Kiehn MK-940807-3/3 (WU)**	AF201068	AF201022
Tamilnadia uliginosa	Tirvengadum 2006 (AAU)	AF201069	AF201023
Tarenna drummondii	Delprete 7406 (NY)	TBA	TBA
	Bot. Gard. BR 98-1836-30		
Tocoyena williamsii	Stahl 3028 (GB)**	AF201071	TBA
Tricalysia junodoi	Delprete 7375 (NY)	TBA	TBA
Vangueria madagascarensis	P. Delprete 7383,	TBA	TBA
	Bot. Gard. BR 95-1161-07		

2.1.2.2. DNA extraction, amplification, and sequencing

Leaf samples were collected either on silica gel or from herbarium specimens. Genomic DNA was extracted from approximately 1 cm^2 of dried leaf tissue using a modified CTAB methodology (Struwe et al., 1998). See table 6 for chemical abbreviations used in the description of the DNA extraction, amplification, and sequencing methods. Leaf material was ground in a Lysing Matrix tube (Bio 101, Vista, CA) and pulverized for 15 seconds in a Bio 101 Fastprep machine at speed 5. Subsequently, 500 μl of Carlson Lysis Buffer (2 g CTAB, 8.18 g NaCl, 0.745 g EDTA, 10 ml 1 M Tris/HCl pH 7.0, nanopure water to 100 ml, verified to pH 9.5, autoclaved, then 1 g PEG 4000 added when cool) and 75 μl of β-mercaptoethanol (100%) were added to each tube. Tubes were incubated at 74°C with occasional shaking for 60-90 min. Next, 575 μl of SEVAG (24:1 Chloroform:iso-amylalcohol) were added to each tube which were placed on a tipping board for 30 min at room temperature. Tubes were then centrifuged at 14,000 rpm for 1 min, and 350 μl of supernatant were added to new tubes containing 1050 μl of NaI solution, 20 μl Glassmilk, and 4 μl TBE modifier (Bio 101, Vista, CA). These tubes were placed on a tipping board for 30 min at room temperature.

Afterwards, tubes were centrifuged at 14,000 rpm for 1 min and all of the supernatant was discarded. Next, each Glassmilk pellet was washed three times with 800 μl and once with 150 μl of ice cold New Wash solution (Bio 101, Vista, CA). After the final wash, all of the New Wash was aspirated from the Glassmilk pellet and 50 μl of 10mM Tris-Cl pH 8.5 elution buffer were added to resuspend the DNA. Tubes were incubated at ~55°C for ~10 min and then centrifuged for 1 min at 14,000 rpm. The supernatant containing the DNA was transferred to new tubes for storage at -20°C.

DNA was amplified using the polymerase chain reaction (PCR). A negative control was used in each PCR reaction in order to check for contamination. PCR reactions were performed in a 25 μl mixture consisting of 2.5 μl 10x buffer (Boehringer Mannheim, Ingelheim, Germany), 2.5 μl 25 mM $MgCl_2$ (Perkin Elmer, Foster City, CA) 2.5 μl, 2.5 μl 0.04% BSA (New England Biolabs, Bevery, MA), 2.5 μl 2.5 mM dNTPs (Boehringer Mannheim, Ingelheim, Germany), 5.8 μl autoclaved nanopure water, 1 μl each of two 10 μl primers, 5 μl 5 M betaine (Q-solution), 0.2 μl Taq polymerase 5000 units (Qiagen Inc.), and 2 μl of genomic DNA. All PCR and cycle sequencing reactions were run on a Gene Amp PCR system 9600 (Perkin Elmer, Foster City, CA).

For amplification of the trnL-F spacer, the primers "e" (5'-GGTTCAAGTCCCTCTATCCC-3') and "f" (5'-ATTTGAACTGGTGACACGAG-3') of Taberlet et al. (1991) were used. The rps16 intron was amplified using the primers rpsF (5'-GTGGTAGAAAGCAACGTGCGACTT-3')and rpsR2 (5'-TCGGGATCGAACATCAATTGCAAC-3') designed by Oxelman et al. (1997). The PCR conditions were: hold 94°C for 3 min, 32 cycles of 94°C for 45 sec, 52°C for 30 sec, 72°C for 1 min 30 sec, and hold 74°C for 7 min, hold 4°C. To detect successfully amplified products and the possible contamination of negative controls, PCR products were examined on 1% agarose LE (low electroendosmosis) gel (Roche), tracking dye (bromophenol blue and xylene cyanol) were added to 2 μl DNA template, runned with 1x TBE buffer pH 8 on Owl EasyCast model B-1 30 min at 120 V, stained in ethidium bromide bath (50 μl EtBr per 500 ml deionized water) 10 min, destain in deionized water bath 5 min, and visualized under ultraviolet light at 302 nm. Amplified products were purified with spin columns from the QIAquick PCR purification kit (Qiagen, Valencia, CA) following protocols provided by the manufacturer and examined on 1% agarose gel in the same way than the PCR products. Purified products were cycle sequenced using 1.5 μl Big Dye (Applied Biosystems Inc.), 1.25 μl dilution buffer, 2.75 μl water, 0.5 μl DMSO, 1 μl of 10μl primer, and 3 μl purified amplified PCR product. Primers for cycle sequencing were the same as those used in the PCR reactions. Cycle sequencing conditions were: hold 95°C for 1 min, 32 cycles of 96°C for 10s, 50°C for 5 sec, 60°C for 3 min, hold 4°C. The reactions were cleaned using hydrated Sephadex G-50 DNA Grade F (Amersham Pharmacia Biotech Inc, Piscataway, NJ) 2.7 gr/40 ml water, after spinned the columns 2 min at 2600 rpm, the samples were added, spinned again 2 min at 2600 rpm and dried in Speed Vac. Cycle sequencing fragments were separated on 29:1 Acrylamide gels 4.5% 50 ml (Amresco Inc., Solon, OH). Gels were prepared with a mixture consisting of 18 g Urea ultrapure grade (Amresco Inc.), 0.5 g Amberlite mixed bed resin MB-150 (Sigma-Aldrich, Milwaukee, WI), 27 ml nanopure water, and 5.6 ml Acryl/Bis (Amresco Inc.). The samples were resuspended in 5:1 Formamide 100% (Amresco, Inc.): blue-dextran loading dye. The two strands of DNA were sequenced on 36-lane gels using 1x TBE Powder-Disodium, ultrapure grade (Amresco Inc.). Sequences were run on an ABI Prism 377 DNA sequencer (Applied Biosystems) during 4 or 9 hours and edited in Sequencher version 3.1.2 (Gene Codes Corporation, Ann Arbor, MI).

Table 6: Abbreviations used in the description of the DNA extraction, amplification, and sequencing methods.

5S-NTS: 5S nontranscribed region

BSA: bovine serum albumin.

CTAB: Cetyl-trimethylammonium bromide.

DMSO: dimethyl sulfoxide.

dNTP: PCR nucleotide mix (dATP, dCTP, dGTP, dTTP).

EDTA: Ethylene diaminetetraacetic acid.

ITS: internal transcribed spacer.

nrDNA: nuclear ribosomal DNA.

rps16: ribosomal protein, 30S, S16, intron

SEVAG: 24:1 Chloroform: iso-amyl alcohol.

TBE: Tris-borate-EDTA

Tris: Tris-(hydroxymethyl)-aminomethane.

trnL-F: intergenic spacer between the trnL (UAA) 3' exon and the trnF (GAA) gene.

Taq polymerase: Thermus aquaticus DNA polymerase.

2.1.2.3. Alignment and gap coding

The sequences were first edited in Sequencher 3.0 (Gene Codes Corporation, Ann Harbor, MA), and preliminary aligned with ClustalX (Thompson et al., 1997) using the default settings. Then, they were manually aligned using BioEdit (Hall, 1999), following two of the criteria presented by Oxelman et al. (1997): Indels were placed so as to keep the number of substitutions within an aligned region to a minimum, and indels of the same length were coded as the same event when their interpretation was not ambiguous. Accordingly, presence (1) or absence (0) of indels were coded as an additional character, and placed in the position preceeding the indel in the data matrices (Appendixes C & D).

2.1.2.4. Phylogenetic analysis

Parsimony analyses with equal character weights and unordered characters were performed with Nona (Goloboff, 1993) in concert with WinClada (Nixon, 2002). In the analyses, gaps were treated as missing values. Five heuristic searches were performed holding a maximum of 10,000 trees per search. In each search, 500 replications were carried out, keeping five trees per replication under the option mult*max*. Additionally, multiple parsimony ratchet searches were performed in order to check if the heuristic search found the most pasimonious trees. The ratchet searches used the default settings (200 replicates and 5-25% characters) that have worked well in the past with diverse data sets (Nixon, per. comm.). The trees obtained were used to calculate a strict consensus tree. In order to evaluate the relative support of the clades, bootstrap analyses were executed using 1000 replicates.

2.1.3. Results

2.1.3.1. The trnLF analysis

The aligned data matrix of the preliminary trnL-F analysis, including all the sequences available, had a total of 122 taxa, and 461 characters, 270 of which were variable, and 158 parsimony-informative. The heuristic search hit the maximum number of trees to hold (10,000). The trees were 429 steps long, with a consistency index (CI) of 0.68 (0.59 when excluding uninformative characters), and a retention index (RI) of 0.87. Several ratchet searches yield trees of equal length (429 steps) and, compared to the heuristic search, with the same three main clades. Figures 38 and 39 show the strict consensus tree obtained in the heuristic search with bootstrap values (BO) above the branches.

This analysis resulted in three main clades with lack of resolution at the base (Figs. 38 and 39). Clade A (Fig. 38) is supported in 71% of the bootstrap replicates, and contains the genera Maguireothamnus Steyerm., Limnosipanea Hook. f., Neobertiera Wernham, Sipaneopsis Steyerm. and Sipanea Aubl. (Fig. 38). Clade B (Fig. 38) is weakly supported (BO=59%), and includes 24 genera that had been placed in the subfamily Cinchonoideae in Robbrecht's system (1988). Clade C is shown in Fig. 39. It is weakly supported (BO=53%), and correspond to the tribes of the subfamily Ixoroideae sensu Robbrecht (1988), with the addition of the tribes Mussaendeae (sensu Bremer & Thulin, 1998), Retiniphylleae, and Vanguerieae (sensu Robbrech, 1988). It is important to note that, although the relationships among the tribes in clade C are not strongly supported, the monophyly of each of the three clades is well supported (91%, 100%, and 87%, respectively).

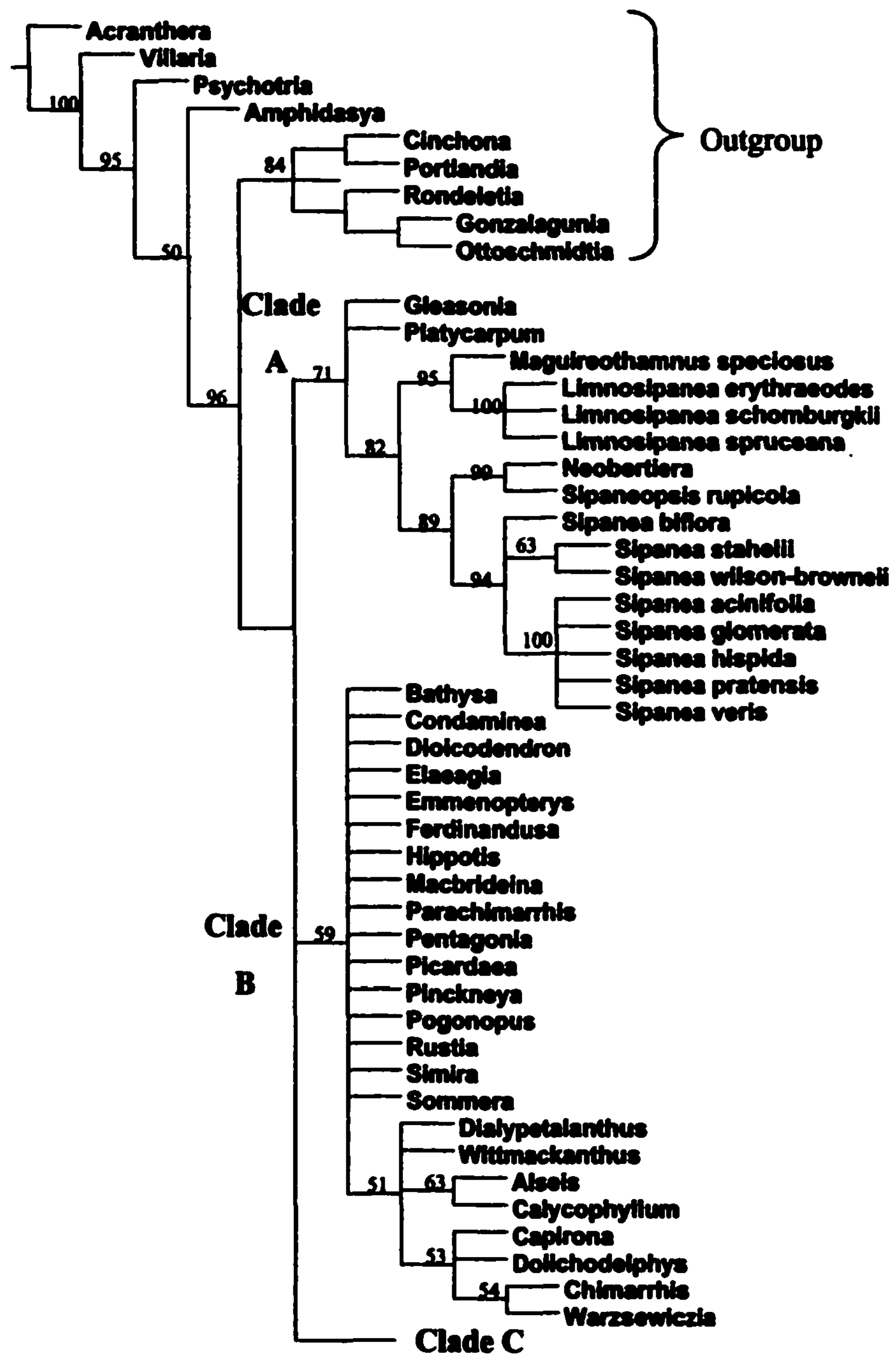

Fig. 38. Strict consensus tree of the 10,000 most parsimonious trees from the trnL-F analysis, with all the sequences available. Bootstrap values are indicated above branches.

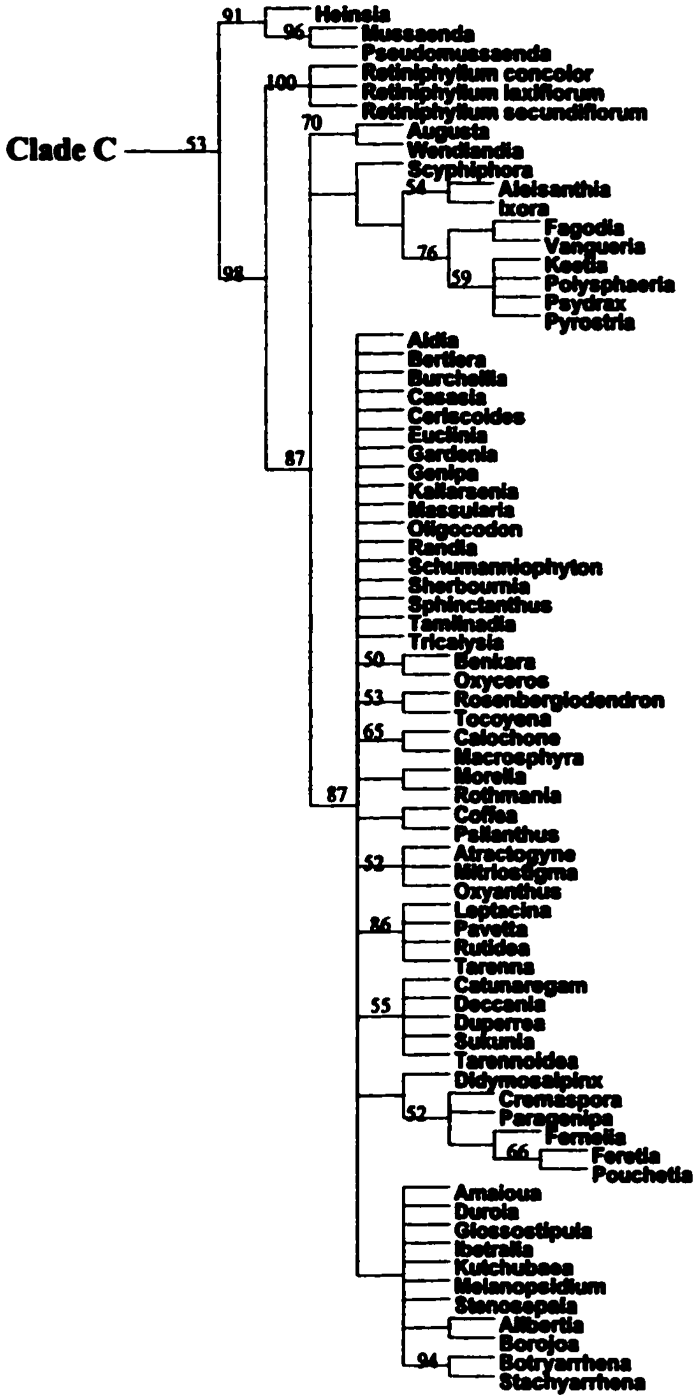

Fig. 39. Clade C of Figure 38. Bootstrap values are indicated above branches.

Based on these results, I selected a sample of the data set with representatives of all the clades formed, giving preference to those with both trnL-F spacer and rps16 intron sequences.

The subset of the trnL-F spacer data matrix had a total of 80 taxa and 445 characters, of which 243 were variable, and 122 were parsimony-informative. The aligned data matrix is showed in appendix B. The shortest trnL-F spacer sequence was found in Psydrax Gaertn. (316 bp), and the largest in Stachyarrhena Hook. f. (374 bp). In Retiniphyllum, the length varied from 332 bp in R. rhabdocalyx to 361 bp in R. maguirei and R. schomburgkii. The heuristic search hit the maximum number of trees to hold (10,000). The trees were 297 steps long, with a CI=0.72 (0.60 when excluding uninformative characters), and a RI=0.85. Several ratchet searches yield trees of equal length (297 steps) and, compared to the heuristic search, with the same three main clades. Figure 40 shows the strict consensus tree obtained in the heuristic search with bootstrap values above the branches.

Comparing the analysis including all the taxa (Figs. 38 & 39) to the one that includes a subset of the data (Fig. 40), the same topology was maintained. Considering that the basic composition of the clades was not altered by

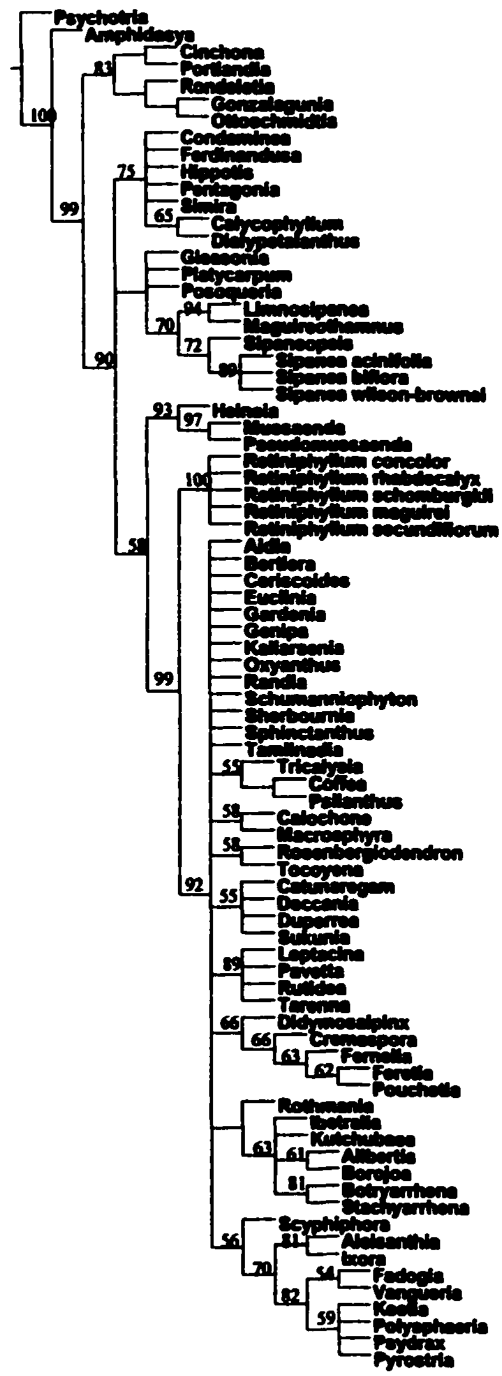

Fig. 40. Strict consensus tree of the 10,000 most parsimonious trees from the trnL-F analysis, subset of the data matrix. Bootstrap values are indicated above branches.

the reducing of the sampling, the subset of the trnL-F spacer data matrix was used in order to combine it with the rps16 intron sequence data.

2.1.3.2. The rps16 analysis

A total of 62 taxa were included in the rps16 intron analysis, 24 of them were new sequences, and 38 were downloaded from GenBank. The aligned data matrix had a total of 1013 characters, after the exclusion of 28 ambiguous positions. Approximately half of the characters were variable (496), and 224 were parsimony-informative. The length of the rps16 intron sequences varied from 746 bp in Simira Aubl. to 807 bp in Schumanniophyton Harms. Within Retiniphyllum, the sequences were of comparable length, with the shortest found in R. concolor (766 bp), and the largest in R. secundiflorum (784 bp). The aligned data matrix is presented in appendix C.

The heuristic search yield a total of 384 trees, 560 steps long, with a CI=0.73 (0.57 when excluding uninformative characters), and a RI=0.80. The strict consensus tree obtained in this analysis is shown in Fig. 41, with bootstrap values located above the branches.

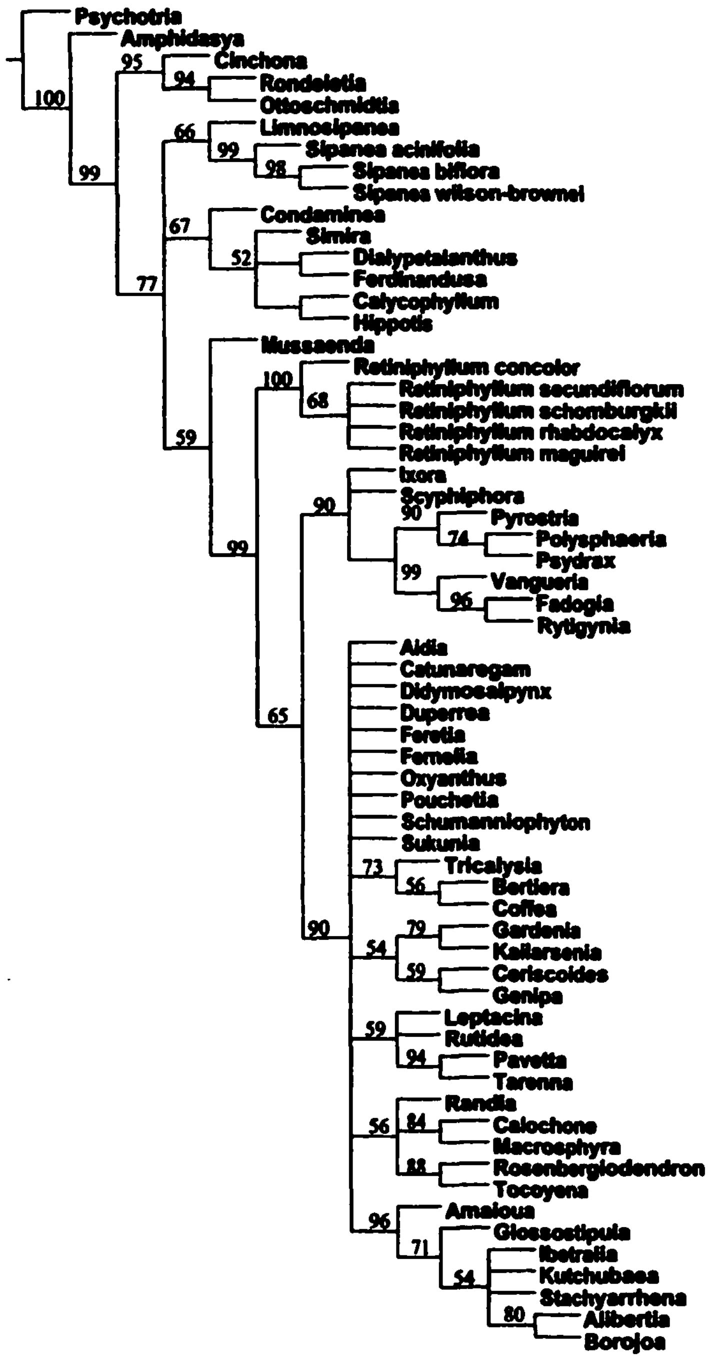

Fig. 41. Strict consensus tree of the 384 most parsimonious trees from the <u>rps16</u> analysis. Bootstrap values are indicated above branches.

This analysis resulted in three main clades with lack of resolution at the base, and congruent to the clades formed in the trnL-F analysis. The tribe Retiniphylleae was supported in 100% of the bootstrap replicates in both analyses.

2.1.3.3. The combined analysis

The combined analysis was used to formulate the conclusions, because it provides the greatest "explanatory power" for the data (Nixon & Carpenter, 1996). This analysis hit the maximum number of trees to hold (10,000). The trees obtained were 871 steps long, with a CI=0.72 (0.58 when excluding uninformative characters), and a CI=0.82. Several ratchet searches yield trees of equal length (871 steps) and, compared to the heuristic search, with the same three main clades. The strict consensus tree obtained in the heuristic search is presented on Fig. 42, with bootstrap values indicated above the branches.

The combined data analysis produced the same three clades obtained in the analyses using trnL-F and rps16 separately. However, the clades were supported by higher bootstrap values. In this analysis the tribe Mussaendeae is sister to the Retiniphylleae which is sister to the

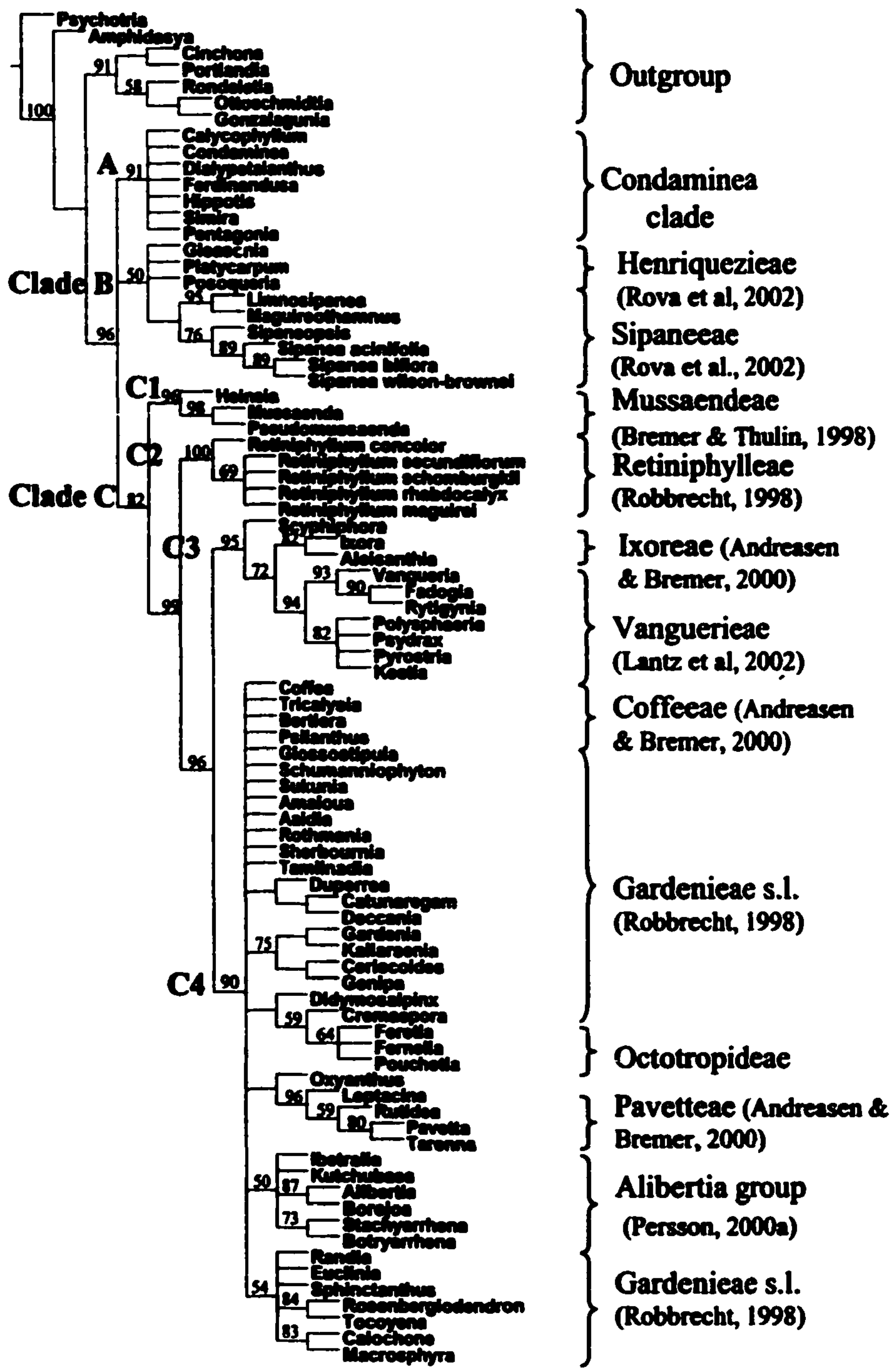

Fig. 42. Strict consensus tree of the 10,000 most parsimonious trees from the combined analysis. Bootstrap values are indicated above branches.

Ixoreae, Vanguerieae, Coffeeae, Octotropideae, Pavetteae, the "Alibertia group", and Gardenieae s.l.

2.1.4. Discussion

2.1.4.1. The monophyly and position of Retiniphyllum and the Retiniphylleae

In all the analyses performed (trnL-F, Figs. 38-40; rps16, Fig. 41; the combined analysis, Fig. 42), the genus Retiniphyllum formed a well supported monophyletic lineage (BO=100%). These results strongly support the monophyly of Retiniphyllum and its place as the only genus in the tribe Retiniphylleae. The analyses included members of almost all the tribes of the subfamily Ixoroideae sensu Robbrecht (1988). The only tribe not included is the Aulacocalyceae, a small group of four genera (Robbrecht and Puff, 1986), in which at least one genus, Heinsenia K. Schum., belongs to the Gardenieae as circumscribed by Andreasen and Bremer (2000). Additionally, the sequences used in these analyses nearly doubled the number of genera compared to Rova et al. (2002). While Rova's et al. analysis comprised 52 genera, my initial trnL-F analysis, included 112 DNA sequences, representing 99 genera.

Because of the isolated position of Retiniphyllum, it was decided that this genus should be maintained in the tribe Retiniphylleae.

Within the subfamily Ixoroideae, Retiniphyllum has the largest branch lengths, as shown in the phylogram of one of the most parsimonious trees of the combined analysis (Fig. 43). The high number of character state changes of Retiniphyllum is perhaps comparable to the unusual morphological characters found in the genus and supports its distinctiveness from the other tribes.

Retiniphyllum was positioned in the largest clade of the subfamily Ixoroideae (clade C) (Fig. 42). In clade C, the tribe Mussaendeae (C1), is sister group to the rest of the clades, and the Retiniphylleae (C2) is sister to the remaining members of the clade. This placement of the Retiniphylleae confirms the results found by Rova et al. (2002). The clade sister to the Retiniphylleae contains two groups: Clade C3, with members of the tribes Ixoreae, Vanguerieae, plus the genus Scyphiphora, and the clade C4, that includes members of the tribes Coffeeae, Gardenieae, Pavetteae, and Octotropideae.

According to these results, the closest relatives to the tribe Retiniphylleae are the members of the clades C3 and C4. From a morphological perspective, Retiniphylleae is

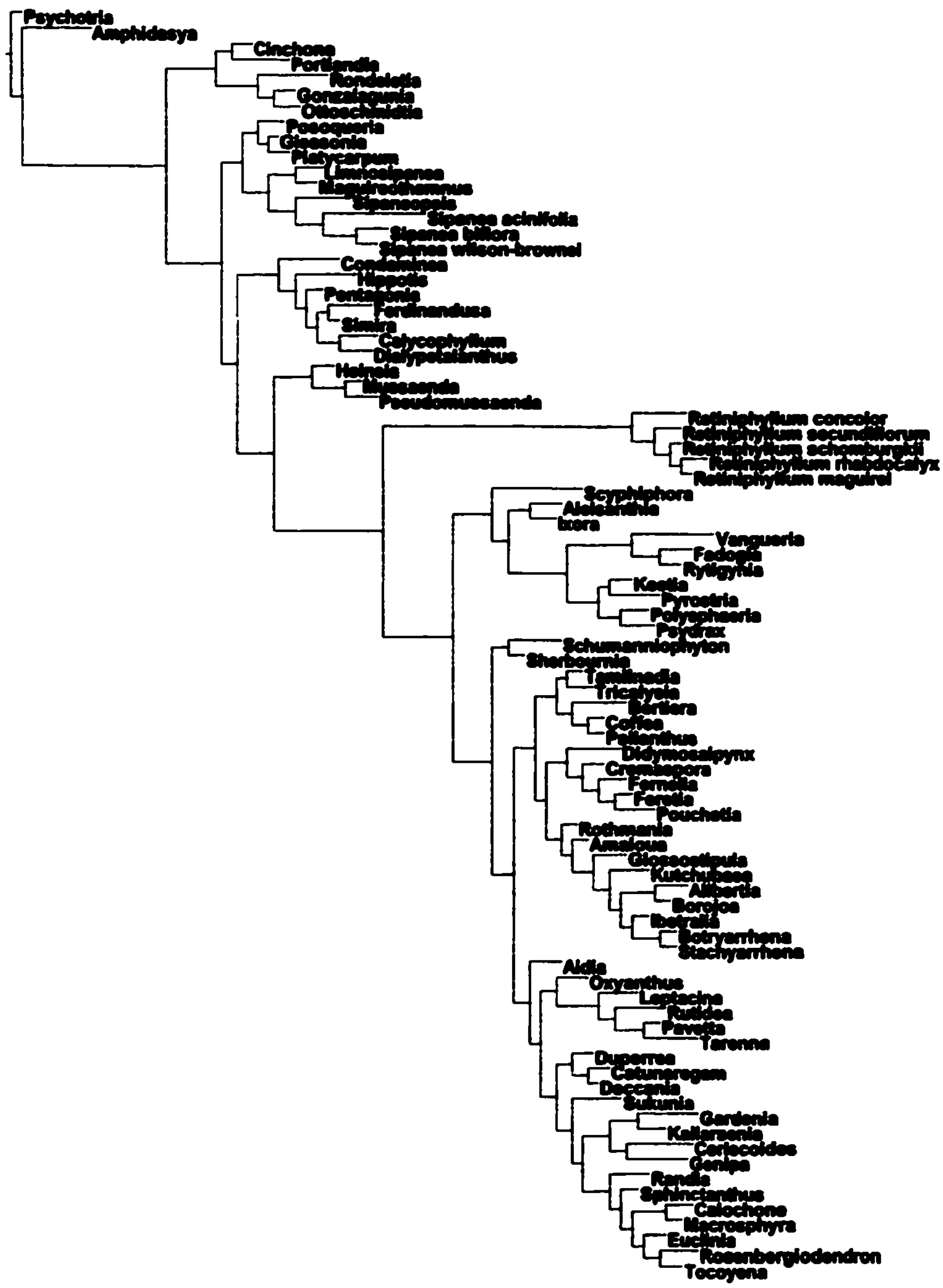

Fig. 43. Phylogram of one of the most parsimonious trees from the combined analysis.

more similar to the Vanguerieae than to the taxa of the other two clades. Members of the Vanguerieae have 2--12-locular ovaries, pyrenes with apical preformed slits, seeds with saddle-like appendages, and stylar pollen presentation. Robbrecht (1988) pointed out these morphological similarities, and placed both tribes together in the subfamily Antirheoideae, although they are shown to belong to the Ixoroideae.

2.1.4.2. The placement of Botryarrhena

Robbrecht (1988) tentatively included the Neotropical genus Botryarrhena in the tribe Retiniphylleae. This genus comprises two, tree species, distributed in the Amazon basin and in the Guayana Region. Ducke (1932) founded the genus, and placed it in the tribe Gardenieae. He pointed out the resemblance of Botryarrhena with Retiniphyllum by having bisexual flowers, terminal and racemose inflorescences, and two (rarely three or four) ovules per locule. At that time, the fruits of Botryarrhena were unknown. The genus Botryarrhena has bilocular, berry-like fruits, a common condition in many genera in the subfamily Ixoroideae, but not in Retiniphyllum.

Ducke (1932) also suggested an affinity between the genera Botryarrhena and Stachyarrhena in having racemose inflorescences, but differing because of the dioecious flowers of Stachyarrhena. This last genus is placed within the "Alibertia group", a clade within the tribe Gardeniaeae that has been studied in detail by Persson (2000a, 2000b), using 5S-NTS and ITS sequences. Persson (2000a) placed Stachyarrhena in an uncertain position within the "Alibertia group". While in the ITS analysis Stachyarrhena was placed at the base of two clades including Alibertia species, in the 5S analysis it was placed in an unresolved position at the base of the "Alibertia group". Unfortunately, Persson did not include Botryarrhena in his analysis.

The results presented here represent the first attempt in positioning Botryarrhena in the Rubiaceae. In this analysis, the genus was placed within the "Alibertia group" (BO=72%), sister to Stachyarrhena, and with the genera Ibetralia Bremek., Kutchubaea, Amaioua Aubl., Glossostipula Lorence, Alibertia A. Rich. in DC., and Borojoa Cuatrec. (Fig. 42). The bootstrap value supporting the Botryarrhena-Stachyarrhena clade is 65% in the combined analysis, and 80% in the trnL-F analysis. The discrepancy in the bootstrap values might be due to the lack of the rps16 intron sequence for Botryarrhena in the combined analysis. Botryarrhena is unique within the "Alibertia group" by having bisexual flowers, while the other genera are clearly dioecious, and usually with solitary female flowers and male flowers in inflorescences. The inclusion of Bothryarrhena inside the "Alibertia group", previously characterized by having unisexual flowers, indicates that the bisexual flowers originated at least once in this clade.

2.1.4.3. The placement of Scyphiphora

The Asiatic genus Scyphiphora comprises a single species, S. hydrophyllacea Gaertn. f., that is the only mangrove species in the family. It is unique in having two ovules per locule in which one is pendulous and the other is erect. Robbrecht (1988) thought that this peculiar ovules morphology is perhaps derived from a similar condition in Retiniphyllum (two pendulous, collateral ovules). Puff and Rohrhofer (1993) studied in detail the morphology of Scyphiphora and stated that there are no characters suggesting a close relationship to Retiniphyllum. They tentatively placed Scyphiphora the subtribe Diplosporinae, in the Gardenieae s.l. He based this on the presence of traqueidal idioblasts in Scyphiphora, which are comparable to the mesophyll sclereids of the Gardenieae. Bremer et al. (1999) and Andreasen and Bremer (2000), using morphological and molecular characters, placed Scyphiphora as a sister taxon to the tribe Ixoreae, and they tentatively included it in the Ixoreae. According to the results presented here, Scyphiphora is sister to a clade that includes not only the tribe Ixoreae, but also the Vanguerieae (Fig. 42). Although the rps16 intron analysis placed Scyphiphora in an unresolved position with Ixora and the tribe Vanguerieae (Fig. 41), this is probably due to the lack of at least one more genus of the tribe Ixoreae in that analysis. In both the trnL-F spacer (Fig. 40), and combined analyses (Fig. 42), Scyphiphora was positioned on the same strongly supported clade. These results indicate that Scyphiphora is neither included in the tribe Gardenieae s.l., as Puff and Rohrhofer (1993) stated, nor in the tribe Ixoreae, as Andreasen and Bremer (2000) suggested. Furthermore, Retiniphyllum and Scyphiphora are in two different clades, indicating that the biovulated condition of these taxa evolved independently.

2.1.4.4. Phylogeny of the subfamily Ixoroideae

2.1.4.4.1. The Condaminea clade

The clade A in Fig. 42 includes members of different tribes included in the subfamily Cinchonoideae by Robbrecht (1988): Condamineeae (Condaminea DC.), Cinchoneae (Calycophyllum DC., Ferdinandusa Pohl), Hippotideae (Hippotis Ruíz & Pav., Pentagonia Benth.), and Rondeletieae (Simira). These genera are characterized by 2-locular ovaries, peltate placenta attached to the entire length of the septum, and capsular fruits. The member tribes of this clade confirms the results presented by Rova et al. (2002).

The genus Dialypetalanthus Kuhlmann is included here in the clade A. Its placement has been historically controversial due to the presence of free petals and numerous stamens in two rows, characters unique in the Rubiaceae. Although Dialypetalanthus was treated as Rubiaceae (Kuhlmann, 1925), it was later transferred to its own family, the Dialypetalanthaceae by Rizzini and Occhioni (1949), a family believed to be related to Myrtaceae or Melastomataceae. Piesschaert et al. (1997), in a detailed morphological and anatomical study maintained Dialypetalanthus in its own family and suggested a close relationship with the Rubiaceae. Recently, Fay et al. (2000) found that Dialypetalanthus is a member of the Rubiaceae as indicated by rbcL data. They placed this genus in the subfamily Ixoroideae, in a clade with Calycophyllum, Capirona Spruce, Condaminea, Hippotis, Pentagonia and Pogonopus Klotzsch. Due to the low bootstrap values supporting the clade, they recommended the use of additional loci to clarify the placement of the genus in the subfamily. Indeed, trnL-F spacer and rps16 intron data support that Dialypetalanthus is a member of the Rubiaceae family, and it is placed in the subfamily Ixoroideae in a strongly supported clade with genera characterized by valvate or imbricate aestivation, 2-locular ovaries, many seeds inserted on the entire length of the septum, and capsular fruits.

2.1.4.4.2. The Sipaneeae-Henriquezieae clade

Clade B is composed by the tribes Sipaneeae and Henriquezieae (Fig. 42). The Sipaneeae (Bremekamp, 1934, 1966; Robbrecht, 1988) included only the genera Limnosipanea, Sipanea, and Steyermarkia Standl., and it was placed in the subfamily Cinchonoideae. Rova et al. (2002), using trnL-F spacer data, placed this tribe in a strongly supported clade inside the Ixoroideae. According to Rova's phylogeny, the genera Maguireothamnus, Neobertiera, Sipanea, and Sipaneopsis were also included in the Sipaneeae. Based on these results, Delprete and Cortés (submitted) expanded the sampling within this tribe, and using ITS and trnL-F spacer sequences, added Chalepophyllum Hook. f. Based on overall morphological similarity, Dendrosipanea Ducke, Neblinathamnus Steyerm., and Pteridocalyx Wernham were tentatively included into the Sipaneeae.

The tribe Henriquezieae was placed in the subfamily Cinchonoideae by Robbrecht (1988), including the genera Gleasonia Standl., Henriquezia Spruce ex Benth., and Platycarpum Bonpl. Gleasonia was positioned by Rova et al. (2002) in a clade sister to the tribe Sipaneeae with the genera Posoqueria Aubl., and Molopanthera Turcz. in the subfamily Ixoroideae. In the present analysis using trnL-F spacer and rps16 intron, the genus Platycarpum is placed for the first time with members of the tribe Henriquezieae.

2.1.4.4.3. The tribe Mussaendeae

According to Robbrecht (1988), the genera Heinsia DC. and Mussaenda were part of the tribe Isertia, and Pseudomussaenda Wernham was included in the Condamineeae. Bremer and Thulin (1998), re-established the Mussaendeae to include these three genera, and placed the tribe in the subfamily Ixoroideae. Bremer and Thulin (1998) found low support for the placement of the tribe within Ixoroideae; however, Rova et al. (2002) discovered it, along with Mussaenda and Pseudomussaenda to be one of the three Ixoroideae clades, sister to Retiniphyllum. This placement is confirmed by the combined analysis, as well as the inclusion of Heinsia in the Mussaendeae, in accordance with Bremer and Thulin's results (1998).

2.1.4.4.4. The Scyphiphora-Ixoreae-Vanguerieae clade

The tribe Ixoreae was recently re-defined by Andreasen and Bremer (2000) to include Ixora, Myonima Comm. ex Juss. and Versteegia Valeton. In Robbrecht's system (1988) these genera were considered part of the tribe Pavetteae, which was shown to be polyphyletic (Andreasen et al., 1999; Andreasen & Bremer, 2000). However, in the analysis presented by Rova et al. (2002), Ixora was positioned in a well supported clade with Aleisanthia Ridl., Aleisanthiopsis, and Greenea Wight & Arn. Because of this, a better circumscription of the tribe is necessary. In addition, Ixora is probably not monophyletic, as it was suggested by Andreasen and Bremer's (2000) study, in which the four species of Ixora included were placed in two different clades. The results presented here are in agreement with Rova et al. (2002), in which the tribe Ixoreae is sister to the Vanguerieae.

The tribe Vanguerieae is strongly supported in a clade sister to the tribe Ixoreae. Scyphiphora is sister to both tribes. Vanguerieae was considered part of the subfamily Antirheoideae by Robbrecht (1988); however, latter studies have shown to belong to the Ixoroideae (Bremer et al., 1995, Andersson & Rova, 1999). The first phylogeny of the tribe was recently proposed by Lantz et al. (2002), using ITS sequence data. They sampled 16 genera of the Vanguerieae and found several clades within the tribe. The results presented here support the monophyly of the tribe, using cpDNA. Robbrecht (1988) pointed out the similarities between the fruits and seeds of the Retiniphylleae and Vanguerieae, being one of the reasons to place the tribes in the subfamily Antirheoideae. Members of the tribe

Vanguerieae have ovary 2-12 locular, with a single and pendulous ovule, and drupaceous fruits. Although the fruits of the Vanguerieae are similar to those of most of the species of the Retiniphylleae, the development of a single-seeded pyrenes is the product of the abortion of one ovule in the latter, and in the former a product of single-celled locules.

2.1.4.4.5. The Gardenieae and allied tribes complex

Robbrecht (1988) circumscribed the tribe Coffeeae to include only Coffea L., and Psilanthus Hook. f.; however, Persson (2000b) and Rova et al. (2002) found Coffea in a clade with Tricalysia A. Rich. ex DC. and Bertiera Aubl.; and Andreasen and Bremer (2000) delimited the Coffeeae including all these genera. These four genera are placed in an unresolved position at the base of the Gardenieae s.l. (Fig. 42), the trnL-F spacer and rps16 intron characters being less informative than those used by Andreasen and Bremer (2000), using ITS, rbcL, and morphology.

The Gardenieae as circumscribed by Robbrecht (1988) included 77 genera divided in two subtribes. Persson (2000b) analyzed the phylogeny of this tribe using trnL-F spacer and rps16 intron, and discover two main clades. One clade included most of the genera that had been considered previously in the Gardenieae subtribe Gardeniinae, and the other clade comprised a group of Neotropical genera characterized by having unisexual flowers. The last clade had been proposed by Robbrecht and Puff (1986), and was informally called the "Alibertia group" by Persson (2000a). The "Alibertia group" was in an unresolved position with members of the tribes Coffeeae, Pavetteae, and Octotropideae in Persson's phylogeny. Andreasen and Bremer (2000) obtained a more resolved cladogram in which the two clades reported by Persson were positioned in a single clade that they re-circumscribed as the tribe Gardenieae. My results do not differ notably from Persson's (2000b) phylogenies. However, an interesting difference was the placement of the genus Botryarrhena in the "Alibertia group". Although similar in many respects, the bisexual flowers of Botryarrhena are exceptional in the "Alibertia group", where the rest of the genera have unisexual flowers.

The genera Leptacina Hook. f., Rutidea DC., Pavetta L., and Tarenna Gaertn. form a well supported clade. They are members of the Pavetteae, a tribe paraphyletic as had been defined by Robbrecht (1988). Andreasen and Bremer (2000) delimited the Pavetteae to include these genera, plus Dictyandra Welw. ex Hook. f. The results presented here give additional evidence to support Andreasen and Bremer's circumscription.

The members of the tribe Octotropideae (sensu Robbrecht, 1988) sampled here included the genera Feretia Delile, Fernelia Comm. ex Lam., and Pouchetia A. Rich. The monophyly of this tribe was supported by rbcL data (Andreasen and Bremer, 2000), and now by trnL-F and rps16, although a phylogenetic study including a better sampling of the nearly 30 genera is needed.

The genus Cremaspora Benth. is sister to the Octotropideae in a strongly supported clade. Based on their phylogenies, Andreasen and Bremer (2000) resurrected the Cremasporeae. This tribe was founded by Bremekamp (1934), but not recognized by Robbrecht (1988), who included Cremaspora in the Gardenieae. In the present analysis, the Cremasporeae-Octotropideae clade is sister to Didymosalpinx Keay, a genus considered a member of the Gardenieae by Robbrecht, and that was included with related-Gardenieae tribes by Persson (2000b). My results suggest that a better understanding of the phylogeny of the Octotropideae is required to clarify the relationships.

2.1.4.5. Biogeographic remarks

The present analysis allows some considerations about the biogeography of the subfamily from a phylogenetic perspective. By simply mapping the geographic distribution of the tribes on the combined analysis (Fig. 42), some observations can be made. First, clade A and B are almost strictly Neotropical. The only exception is the monotypic, Asiatic genus Emmenopterys Oliv. Clade C, in which the Retiniphylleae is included, comprises Pantropical (Ixoreae and Gardenieae), and Paleotropical (Mussaendeae, Vanguerieae, Coffeeae, Octotropideae, and Pavetteae) tribes. The tribe Retiniphylleae is the only strictly Neotropical tribe in this clade.

These results contrast with the ideas about the earliest lineages in the subfamily, and even in the family. The tribe Gardenieae has been considered one of the most primitive groups in the Rubiaceae (Hallé, 1967; Robbrecht & Puff, 1986), and it has been speculated that this tribe could have originated in Africa, from where it spread to Asia and then to Neotropics. While the sampling here was not designed to address this question, the phylogeny of the Ixoroideae presented here does not support this scenario. Although there is no resolution among the three basal clades, the tribe Gardenieae is in a derived position respect to most of the tribes of the Ixoroideae, and therefore in contrast with this hypothesis. The fact that two of the three clades of the Ixoroideae are almost strictly Neotropical, and the other is, with the exception of Retiniphylleae, Pan- or Paleotropical, suggests that the Neotropics could have played a more important role in the early history of diversification of the subfamily. However, it is better to reserve speculation about this issue until a more resolved phylogeny is obtained, and appropriate historical biogeographical studies can be performed.

2.1.5. Conclusions

The phylogenetic analysis of the trnL-F spacer and rps16 intron, strongly supported the monophyly of both the tribe Retiniphylleae and the genus Retiniphyllum.

The tribe Retiniphylleae is monotypic and is sister to two clades, one containing the tribes Ixoreae and Vanguerieae and the genus Scyphiphora, and the other is the core of the traditional members of the subfamily Ixoroideae.

Botryarrhena is not closely related to the tribe Retiniphylleae, and is instead placed within the "Alibertia group" of the tribe Gardenieae, and sister to the genus Stachyarrhena. Its bisexual flowers are unique and derived within a group with unisexual flowers.

The genus Scyphiphora is placed in a clade close to the tribe Retiniphylleae, sister to the clades that include the tribes Ixoreae and Vanguerieae. The biovulated condition in Retiniphyllum and Scyphiphora corresponds to two independent evolutionary events.

Major findings regarding the systematics of the subfamily Ixoroideae include:

- The three Ixoroid clades of Rova et al. (2002) are further supported by the addition of rps16 intron sequence data.
- The genus Dialypetalanthus is included in the Rubiaceae-Ixoroideae, in a clade containing genera that used to belong to the subfamily Cinchonoideae.
- The genus Platycarpum is placed in the Sipaneeae-Henriquezieae clade.
- The re-established the Mussaendeae by Bremer and Thulin (1998) is supported with new evidence.
- The tribe Vanguerieae is sister to the tribe Ixoreae, both sister to the genus Scyphiphora.

- The delimitation of the tribes Pavetteae and Octotropideae described by Andreasen and Bremer (2000) is here supported by new evidence.
- The tribe Cremasporeae, as circumscribed by Andreasen and Bremer (2000), is not supported.

2.2. Phylogeny of Retiniphyllum

2.2.1. Introduction

The genus Retiniphyllum comprises 22 species of shrubs or small trees, characterized by (4-)5(-6-8)-locular ovaries with two collateral pendulous ovules per locule. This combination of characters is unique in the Rubiaceae, and is the main reason for its isolation in the monotypic tribe Retiniphylleae. The monophyly of both the genus and the tribe was tested and confirmed in this study, using trnL-F spacer and rps16 intron sequence data (see previous section).

The morphological diversity within Retiniphyllum is noteworthy. For instance, involucels are rarely found in Rubiaceae genera, but are always associated with the flowers in this genus, and are diagnostic characters when delimiting species. Pyrene morphology is very variable when examined in detail, especially regarding the presence, consistency, and position of wings.

The flowers of Retiniphyllum show three pollination syndromes. Species with showy, dark pink to red corollas, are pollinated by hummingbirds, as confirmed in R. rhabdocalyx (Rosero Lasprilla & Sazima, 2002), and species with white corollas are probably pollinated by insects. Among the insect-pollinated species, those with short-tubular corollas are possibly bee-pollinated, while those with long-tubular corollas are probably pollinated by moths, butterflies, and perhaps bees.

Based on the variation in stipules, involucels, pedicels, and pyrenes Müller Argoviensis (1881) divided the genus in three sections: sect. Retiniphyllum [as "Euretiniphyllum"], sect. Commianthus, and sect. Ammianthus.

The primary objective in this study is to analyse the phylogenetic relationships among the species of Retiniphyllum using morphological data and nuclear ribosomal DNA sequence variation of the ITS region. The phylogenies obtained will provide a framework for the interpretation of the evolution of morphological characters in the genus. At the same time, the monophyly of the sections proposed by Müller Argoviensis will be tested.

2.2.2. Materials and Methods

2.2.2.1. Taxon sampling

Extracted DNA was from 12 species, eight from silica gel material and four from herbarium specimens. Five species that are known only from the type collection were not included. In addition, attempts at DNA extraction from herbarium specimens were largely unsuccessful in the remaining five species. Voucher information is presented in Table 7. Alternatively, all 22 species were included in the morphological analyses.

2.2.2.2. Characters

The morphological data matrix consisted of 38 characters that showed variation among species of the genus and were parsimony-informative. The character coding was fulfilled by direct observation of about 1500 herbarium specimens, and from field observations. The characters and character states used in this analysis are given in Table 8 (see the morphology chapter for a detailed description of character states). After plotting on stock charts all the potentially useful quantitative characters, only three of them showed clear discontinuities, and were incorporated in the cladistic analysis: lobes/tube ratio, pedicel, and calyx length.

Molecular data were obtained from nrDNA sequence variation of the internal transcribed spacer region ITS. Except for the primers and the program of the PCR reaction, the DNA extraction, amplification, and sequencing were performed using the same methodology described in the previous section. For amplification of the ITS region (ITS1, ITS 2, and 5.8S rDNA), the external primers [5'-TATGCTTAAAYTCAGCGGGT-3'] and [5'-AACAAGGTTTCCGTAGGTGA-3'] were used (Nickrent et al, 1994). The PCR conditions were: hold 97°C for 50 sec, 30 cycles of 97°C for 50 sec, 53°C for 50 sec, 72°C for 1 min 50 sec, hold 72°C for 7 min, hold 4°C.

Cross contamination was controlled by using negative controls in the PCR reactions and following the rules and protocols of the Cullman Laboratory. In addition, DNA of two individuals per species were extracted, amplified, and sequenced, when possible.

Table 7. Taxa used in the phylogenetic analyses of Retiniphyllum using ITS.

Taxa	Voucher	EMBL Accession number
Aidia micrantha	-	AJ224835
Coffea arabica	-	AJ224846
Cremaspora triflora	-	AJ224824
Gardenia thunbergia	-	AJ224833
Ixora coccinea	-	AJ224826
Ixora finlaysoniana	Delprete 7344 (NY)	TBA
Ixora parviflora	-	AJ224840
Leptactina platyphylla	-	AJ224825
Mussaenda erythrophylla	-	AJ224823
Oxyanthus pyriformis	-	AJ224837
Pavetta lanceolata	-	AJ224832
Psilanthus mannii	-	AJ224822
Posoqueria latifolia	-	AJ224828
Randia moorei	-	AJ224835
Retiniphyllum chloranthum	Berry 7422 (MO)	TBA
Retiniphyllum concolor	Cortés 1609 (NY)	TBA
Retiniphyllum discolor	Vicentini 1455 (NY)	TBA
Retiniphyllum laxiflorum	Luteyn 15271 (NY)	TBA
Retiniphyllum maguirei	Evans 3230 (MO)	TBA
Retiniphyllum parvifolium	Amaral 944 (NY)	TBA
Retiniphyllum pilosum	Berry 7665 (MO)	TBA
Retiniphyllum rhabdocalyx	Cortés 1648 (NY)	TBA
Retiniphyllum scabrum	Delascio 17039 (NY)	TBA
Retiniphyllum schomburgkii	Berry 7567 (MO)	TBA
Retiniphyllum secundiflorum	Berry 7457 (MO)	TBA
Retiniphyllum truncatum	Cortés 1640 (NY)	TBA
Sipanea hispida	Cortés 1593	TBA
Tricalysia cryptocalyx	-	AJ224827

Table 8. Characters and character states used in the morphological analysis.

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0. stipules dimorphism: dimorphic stipules = 0; a single type of stipules = 1.
1. stipules shape: truncate = 0; triangular = 1; splitting in one side, triangular or ovate = 2.
2. stipules external indument: glabrous=0; with indument=1.
3. leaf indument: glabrous = 0; with indument = 1.
4. leaf surface: smooth = 0; alveolate = 1.
5. inflorescence position: axillary = 0; terminal = 1.
6. inflorescence morphology: spike = 0; raceme = 1; umbel = 2; cyme = 3
7. inflorescence orientation: pendulous = 0; erect = 1.
8. inflorescences per node: two = 0; one = 1.
9. rachis indument: glabrous = 0; with indument = 1.
10. bracteoles colleters: without = 0; with = 1.
11. involucel shape: discoid = 0; cupular = 1.
12. involucel indument: glabrous = 0; with indument = 1.
13. involucel colleters: without = 0; with = 1.
14. involucel persistency: persistent to the fruits = 0; persistent to the rachis = 1. In most species the involucels are persistent to the rachis of the infrutescences when the fruits fall, but in few species the involucels remain attached to the fruit, and dispersed with it as a unit.
15. pedicel: sessile = 0; pedicellate = 1.
16. pedicel lenght: 5-26 mm = 0; 0.3-5 mm = 1; 0 mm = 2.
17. calyx morphology: cupular = 0; tubular = 1.
18. calyx indument outside: glabrous = 0; with indument= 1.
19. calyx indument inside: glabrous = 0; with indument = 1.
20. calyx colleters: without = 0; with = 1.
21. calyx length: less than 2 mm = 0; more than 2 mm = 1.
22. corolla symmetry: actinomorphic = 0; zygomorphic = 1.
23. corolla color: dark pink to red = 0; white to cream white with lines pale pink = 1.
24. tube shape: infundibuliform = 0; narrowly infundibuliform = 1; cylindrical = 2.
25. lobes/tube ratio: less than 4/5 = 0; more than 4/5 = 1.
26. tube inner ring of hairs: at distal portion = 0; at basal portion = 1.
27. pollen shape in outline: oblong = 0; elliptic = 1.
28. lumina size uniformity: decreasing toward the poles = 0; increasing toward the poles = 1; homogeneous throughout = 2.

29. fruit shape: transversally ellipsoid = 0; longitudinally ellipsoid = 1; globose = 2.
30. fruit indument: glabrous = 0; with indument = 1.
31. pyrene shape: without wings = 0; with a very reduced rib at each side of the dorsal margin = 1; with two parallel wings inserted near the ventral margin = 2; with two perpendicular wings inserted near the dorsal margin = 3.
32. pyrene surface: verrucate = 0; dorsally verrucate = 1; smooth = 2.
33. pyrenes outgrowths: absent = 0; present = 1.
34. pyrenes perforation: at basal portion = 0; at middle portion = 1; at distal portion = 2.
35. seeds shape: cylindrical = 0; reniform = 1; ovoid = 2.
36. seed insertion: at distal portion = 0; at middle portion = 1.
37. seeds per locule: 2 = 0; 1 = 1.

2.2.2.3. Alignment

The sequences obtained were first edited using Sequencher 3.0 (Gene Codes Corporation, Ann Harbor, MA, USA), preliminary aligned with ClustalX (Thompson et al., 1997), and then manually aligned using BioEdit (Hall, 1999) following two of the criteria presented by Oxelman et al. (1997): Indels were placed so as to keep the number of substitutions within an aligned region to a minimum, and indels of the same length were coded as the same event when their interpretation was not ambiguous. Accordingly, presence (1) or absence (0) of indels was coded as an additional character. The alignment of the ITS sequence data is shown in Appendix D.

2.2.2.4. Phylogenetic analysis

Parsimony analyses with equal character weights and unordered characters were performed with Nona (Goloboff, 1993) in concert with WinClada (Nixon, 2002). In the analyses, gaps were treated as missing values. Five heuristic searches were performed holding a maximum of 10,000 trees per search. In each search, 500 replications were carried out, keeping five trees per replication under the option mult*max*. The trees obtained were used to calculate a strict consensus tree. In order to evaluate the relative support of the clades, Bremer support was calculated, and bootstrap analyses were executed using 1000 replicates.

2.2.2.5. Outgroup

Although the alignment of the ITS region among species of Retiniphyllum was straightforward, the alignment with the outgroup was difficult. When trying to align several different genera of the tribes Gardenieae, Vanguerieae, and Ixoreae, some regions with multiple alternative alignments had to be discarded from the analysis, reducing the number of informative characters. Among the genera evaluated as outgroup, the sequence of Ixora was the only one that was unambiguously aligned with those of Retiniphyllum, and did not require the exclusion of any regions. Therefore, Ixora was the only taxon used as outgroup in all the analyses.

Although in theory it is not necessary to have more than one outgroup (Nixon and Carpenter, 1993), when possible, it is better to have several outgroups representing gradually more distant lineages rather than a single outgroup (Wensel, 2002). In order to test if the use of a single outgroup could affect the phylogeny of the ingroup, an additional analysis using optimization alignment was performed. Optimization alignment is a method in which alignment and tree search are combined in one step (Wheeler, 1996). This analysis was performed with the program POY (Wheeler et al., 2002), using 500 random addition sequences, followed by TBR branch swapping. Substitution and gap costs were set to maximize secondary homology (substitution costs 2, gap cost 1; De Laet, pers. Comm.). In this analysis, branch support was assessed by means of a jackknife analysis (Farris et al., 1996) using 200 pseudoreplicates. A total of 16 taxa were used as outgroups, and except for two taxa, the sequences were downloaded from GenBank.

2.2.3. Results

2.2.3.1. The morphological data analysis

Cladistic analysis of the morphological data matrix yielded 12 trees of 110 steps, with a consistency index (CI) of 0.50 and a retention index (RI) of 0.72. Figure 44 shows the strict consensus tree with bootstrap and Bremer support values above and below branches respectively.

According to morphological data, Retiniphyllum chloranthum and R. concolor are sister taxa in a well supported clade, as indicated by the bootstrap value (BO=75%), and the Bremer support (BR=5). This clade is sister to the remainder species of the genus. Among the three remaining clades, R. longiflorum forms a monotypic clade, sister to two larger clades. Although this clade has a low bootstrap support (values <50% are not indicated), Bremer support value is not low (5). One of the two large clades includes species characterized by having pedicellate flowers, the other, with the exception of R. tepuiense, includes species with sessile flowers. The clades formed in the morphological analysis had, with few exceptions, low

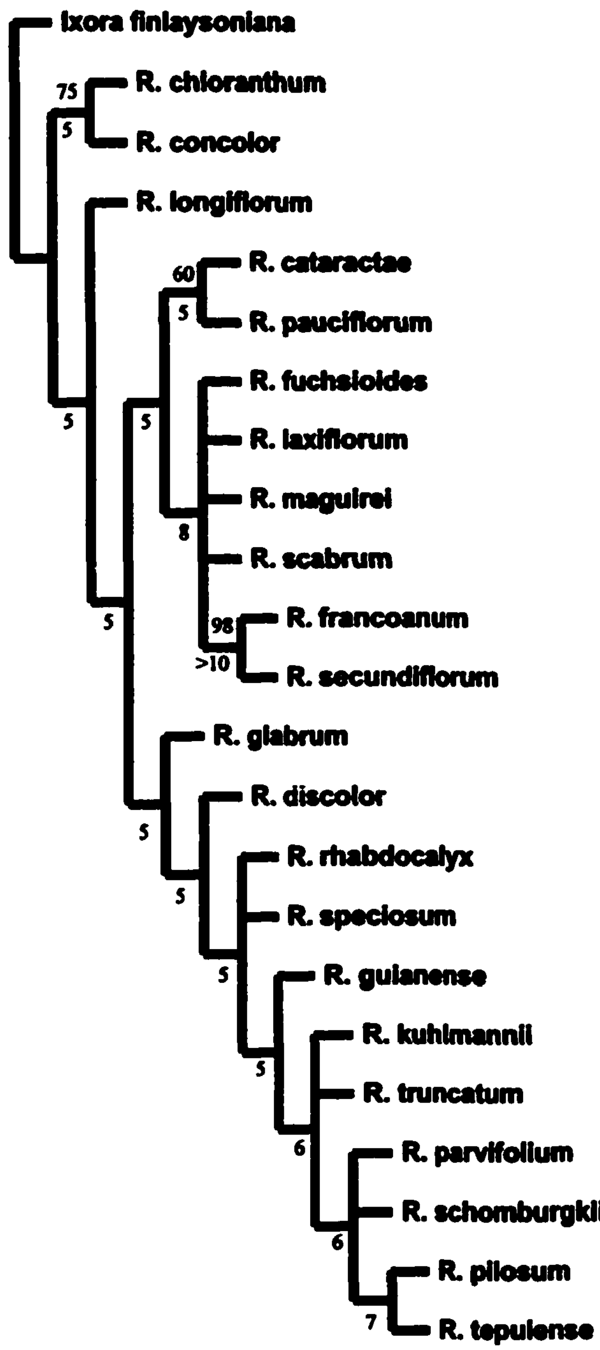

Figure 44. Strict consensus of 12 trees obtained in the analysis of morphological data. Bootstrap and Bremer support values are shown at the nodes (BO/BR)

bootstrap support. On the other hand, Bremer values better supported the clades.

2.2.3.2. The ITS analysis

The aligned data matrix with all the ITS sequences available, using Ixora as outgroup, had a total of 635 characters, of which 147 were variable, and only 46 were informative.

The heuristic search of the ITS sequence data yielded a single tree of 89 steps, with a CI=0.81 (0.58 when excluding uninformative characters), and a RI=0.59. Figure 45 shows the single most parsimonious tree with bootstrap and Bremer support values above and below branches respectively.

This analysis resulted with two main clades that are sister to R. secundiflorum. The shortest of these clades includes R. chloranthum and R. concolor. In the other clade, R. pilosum is sister to the six remaining species. The only clade supported by high bootstrap value (81%) is the one including R. laxiflorum and R. maguirei. Bremer support values are higher at the base of the tree (5 or 6) than in the less inclusive clades.

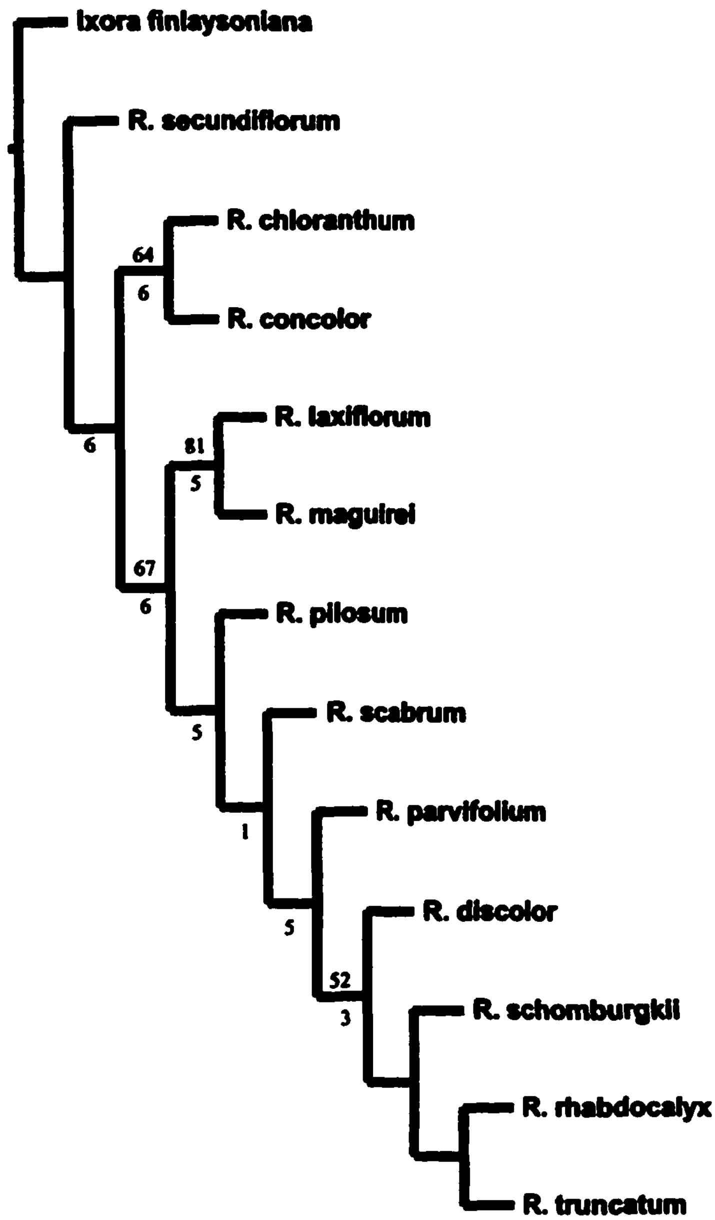

Figure 45. Single tree obtained in the analysis of ITS sequence data. Bootstrap and Bremer support values are shown at the nodes (BO/BR).

2.2.3.3. Outgroup test

The analysis of the ITS sequence data including 16 outgroups, and using optimization alignment, yielded a single most parsimonious tree of 1190 steps long. Figure 46 shows the tree with jackknife support values above branches. The topology of the tree is almost identical to the result using only Ixora as outgroup (Fig. 45). The single difference is the lack of resolution in the optimization alignment analysis of the clade formed by R. discolor, R. rhabdocalyx, R. schomburgkii, and R. truncatum. This difference is not significant, considering the lack of support inside this clade in the analysis using Ixora. The jackknife analysis showed higher support values for the clades supported in the single-outgroup analysis. In addition, the jackknife analysis supported two clades that were not supported in the analysis using only Ixora as outgroup.

Taking into account that the inclusion of several outgroups did not affect considerably the topology of the tree, I decided to continue using Ixora as the single outgroup.

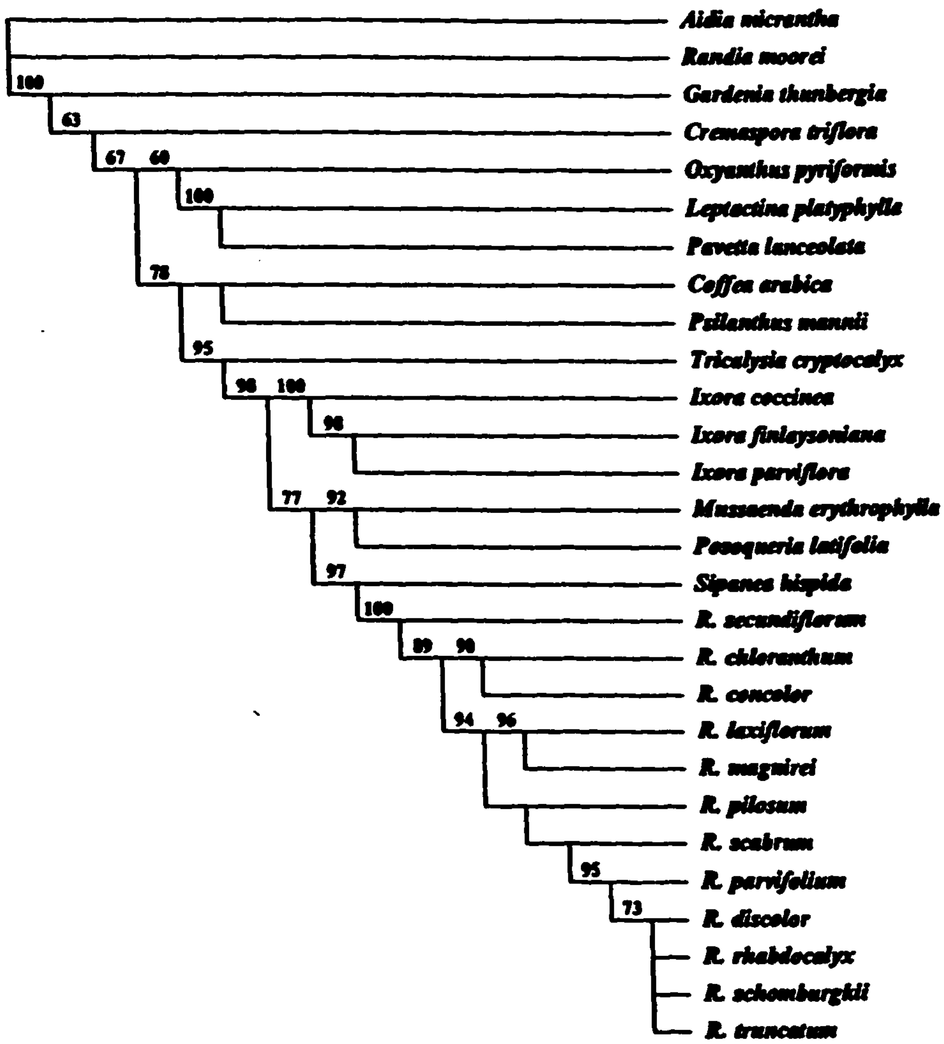

Fig. 46. Single tree obtained in the analysis of ITS sequence data using multiple outgroups with optimization aligment. Jacknife values are shown above branches.

2.2.3.4. The combined analysis

The heuristic search of the combined analysis including all the species yielded a single tree of 290 steps, with a CI of 0.64 (0.49 when excluding uninformative characters), and a RI of 0.61. Figure 47 shows the single tree obtained with bootstrap and Bremer support values (BO/BR) indicated above branches. This tree had low bootstrap support values in which only the R. chlorantum-R. concolor clade had a strong support value (85%). The large quantity of missing data in the molecular data set, and the reduced number of characters in the morphological data set are responsable for the low general support.

On the other hand, the heuristic search of the combined analysis including the 12 species for which molecular and morphological data were available, yielded a single tree of 281 steps, with a CI of 0.74 (0.62 when excluding uninformative characters), and a RI of 0.58. Figure 48 shows the single most parsimonious tree with character optimizations using the slow option from Winclada (Nixon, 2002). Only morphological characters are numbered, and correspond to those in the data matrix (Table 8). In addition, bootstrap and Bremer support values (BO/BR) are indicated above branches. This tree was better supported

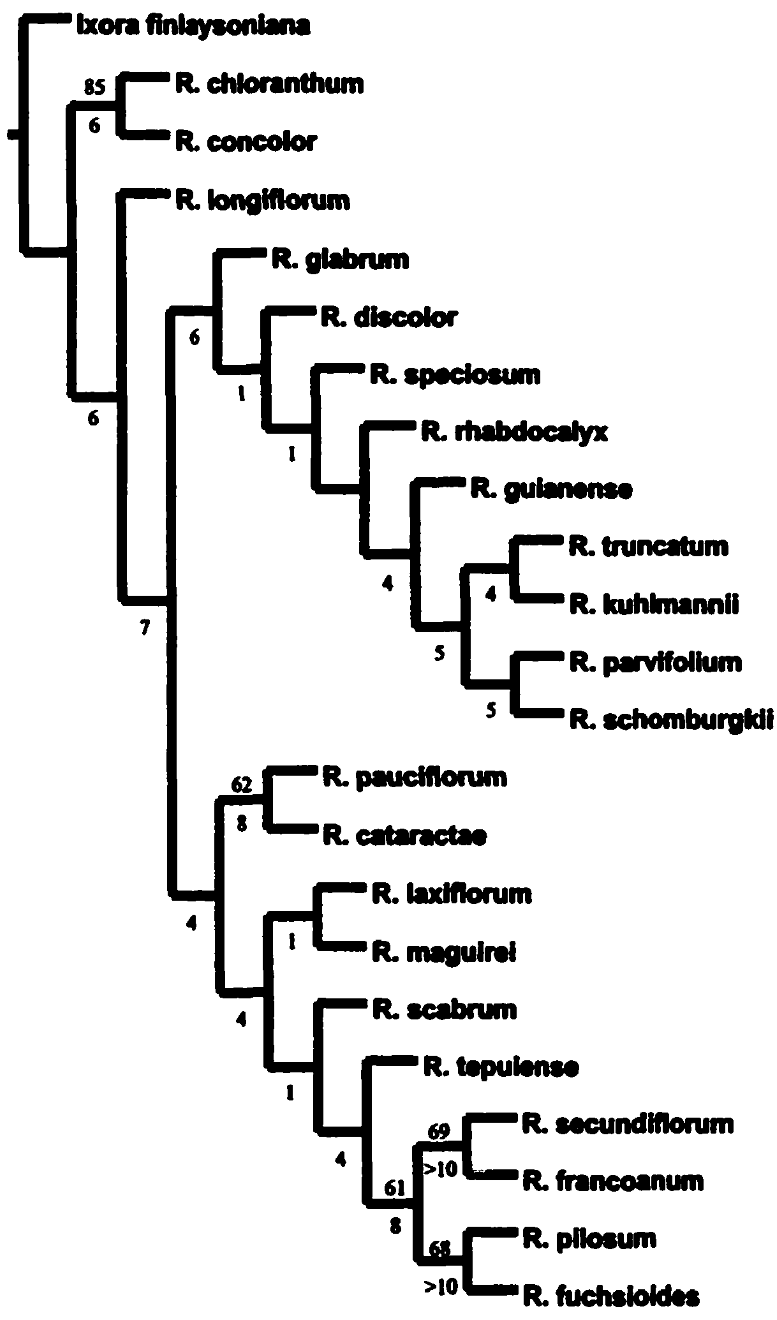

Figure 47. Single tree obtained in the combined analysis of ITS sequence data and morphology including all the species. Bootstrap and Bremer support values are shown at the nodes (BO/BR).

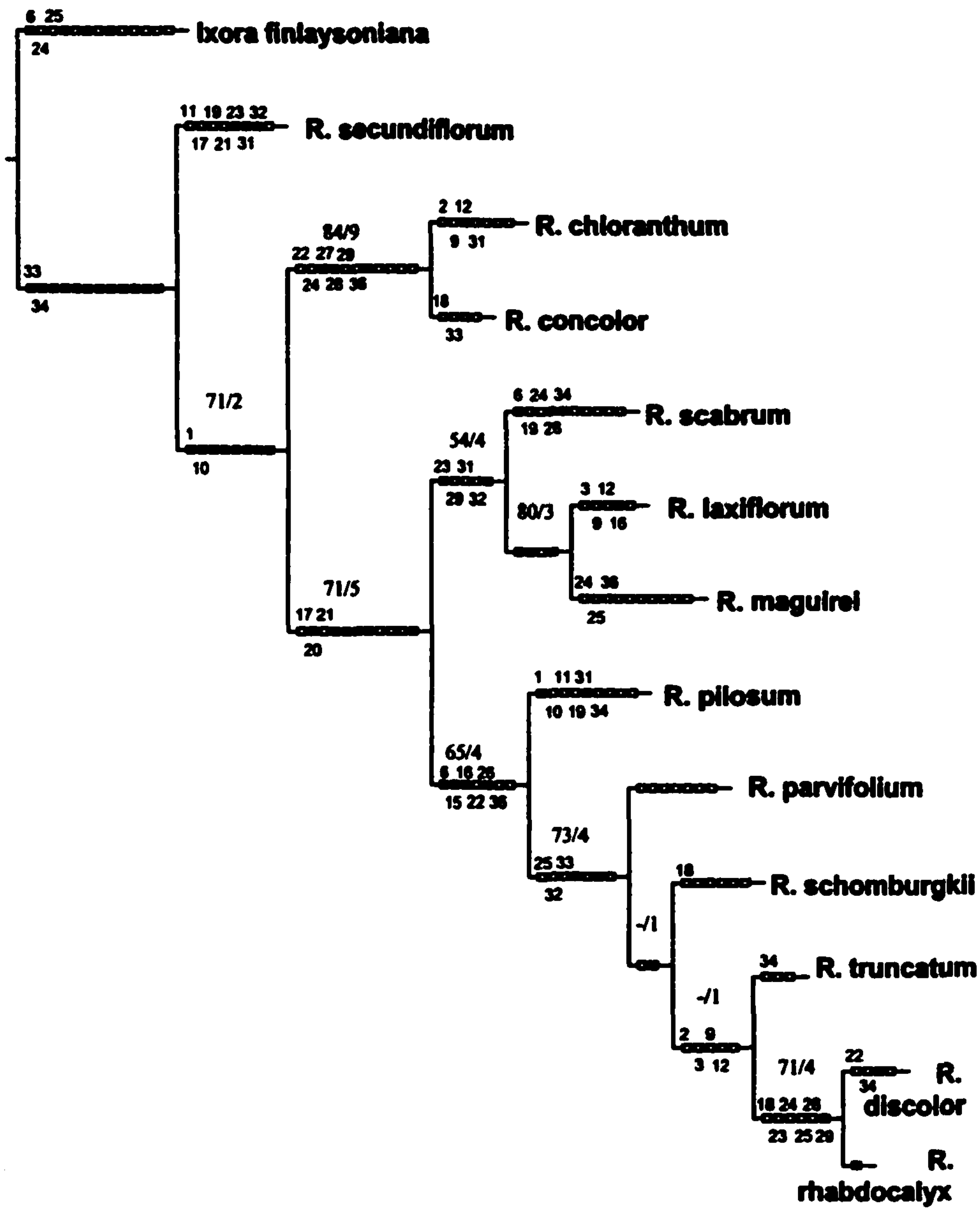

Figure 48. Single tree obtained in the combined analysis of ITS sequence data and morphology. Character optimizations were calculated using the slow option of WinClada. Black hashmarks indicate synapomorphies or autopomorphies, white hashmarks indicate homoplasies. Only morphological characters are numbered. Bootstrap and Bremer support values are shown above the nodes (BO/BR).

and because it includes representatives of the three main clades formed, it will be use in the following discussion.

In this tree (Fig. 48), the clade that includes the ingroup is supported by 12 synapomorphies, two of them from morphology: winged pyrenes, and pyrenes perforated at middle portion, and 10 from molecular characters.

Retiniphyllum secundiflorum is sister to a clade that comprises the rest of the species of the genus. This clade is supported by eight synapomorphies: truncate stipules and bracteoles with colleters, plus six molecular characters. This clade is well supported by the bootstrap analysis, although its Bremer support is low.

One of the two major clades is formed by R. chloranthum and R. concolor. This group is supported by six morphological and five molecular characters. While most of the characters are homoplasious, one molecular, and two morphological characters are synapomorphies: pollen oblong in outline, and pollen increasing in size toward the poles. This clade is well supported, as indicated by the bootstrap (84%), and the Bremer support value (9).

The clade that includes most of the species of Retiniphyllum is supported by eleven characters, five are synapomorphies, and six are homoplasious. Calyx without colleters is the single morphological synapomorphy for the group. This clade is well supported by the two parameters used (BO=71%, BR=5).

The clade including R. scabrum, R. laxiflorum and R. maguirei is supported by four morphological characters, all of them homoplasious, and by one molecular synapomorphy. This group is better supported by the Bremer analysis (BR=4), than by the bootstrap analysis (BO=54%). Retiniphyllum laxiflorum is sister species to R. maguirei, in a clade supported by four molecular characters, three of them synapomorphies, and one homoplasious. This group is better supported by the bootstrap analysis (BR=80), than by the Bremer analysis (BR=3).

The last clade includes all the species with spicate inflorescences. It is supported by one molecular, and six morphological characters. In addition to the characters associated to spicate inflorescences, the ring of hairs located at distal portion of the corolla tube, is a synapomorphy for the group. This group is better supported by the Bremer analysis (BR=4), than by the bootstrap analysis (BO=65%). This clade includes six species, and the only morphological synapomorphy found for any clade is the transversally ellipsoid fruits, present in the sister species R. discolor and R. rhabdocalyx.

2.2.4. Discussion

2.2.4.1. Infrageneric delimitation of Retiniphyllum

The three sections proposed by Müller Argoviensis (1881) were based on the type of stipules, involucels, pyrenes, and pedicels. In the section Ammianthus, Müller included only Retiniphyllum pilosum, which he characterized by the 3-winged pyrenes, sessile involucels, and long-sheathing, scarious stipules. He distinguished the other two sections by having 3-ribbed pyrenes, and non-scarious stipules. In section Retiniphyllum, characterized by "pedicellate involucel" with distinct lobes, he included R. secundiflorum, R. concolor sensu Müller (=R. chloranthum), R. martianum (=R. concolor), and R. spruceanum (=R. fuchsioides). In section Commianthus, characterized by a cupular, sessile involucel with truncate margin, he included Retiniphyllum discolor, R. rhabdocalyx, R. schomburgkii, R. speciosum, and R. truncatum.

The analysis performed using the combined data set produced a tree (Fig. 48) where the species of the same section are placed in different clades. For example, the three species of sect. Retiniphyllum are placed in two different clades, and the single species of sect. Ammianthus is placed in the same clade with species of the sect. Commianthus. While sect. Commianthus would be monophyletic with the inclusion of Retiniphyllum pilosum, sect. Retiniphyllum would be monophyletic only with the exclusion of: R. chloranthum, R. concolor, and R. fuchsioides, considering that R. secundiflorum is the type of the section. Therefore, the sections, as proposed by Müller Argoviensis (1881), are not monophyletic.

To date, two groups within Retiniphyllum are clearly delimited. One including the species with spicate inflorescences, and another including R. chloranthum and R. concolor. Until a better sampling inside the clade with racemose and umbellate inflorescences is done, I prefer not to establish sections inside the genus. Therefore, no subgeneric or sectional ranks are recognized within Retiniphyllum in this study.

2.2.4.2. Evolution of characters

2.2.4.2.1. Evolution of colleters

All the species of Retiniphyllum have colleters inside stipules; however, not all of them have colleters inside bracteoles, involucels, and calyces. The optimization of the colleters characters in Retiniphyllum (Figs. 49 & 50) indicate that their presence inside the bracteoles is a derived condition that originated once, and was lost again in R. pilosum (Fig. 49). On the other hand, the presence of colleters inside calyces is the plesiomorphic condition in Retiniphyllum, with a subsequent loss early in the diversification of the genus (Fig. 50). Involucel colleters is an uninformative character in the phylogenetic analysis of Retiniphyllum because all the species, except R. pilosum, have colleters inside involucels. It is of interest to note that R. pilosum completely lacks colleters.

Most of the species of the genus have colleters inside at least two structures at the same time, either calyx and involucel or bracteoles and involucel. The exceptions to this trend are the sister species R. chloranthum and R. concolor, with colleters inside the three structures at the same time, and R. pilosum without colleters. The former sister species are among the most widespread species in the genus, and considering that colleters are hypothesized to enhance the meristematic tissues' protection (Robbrecht,

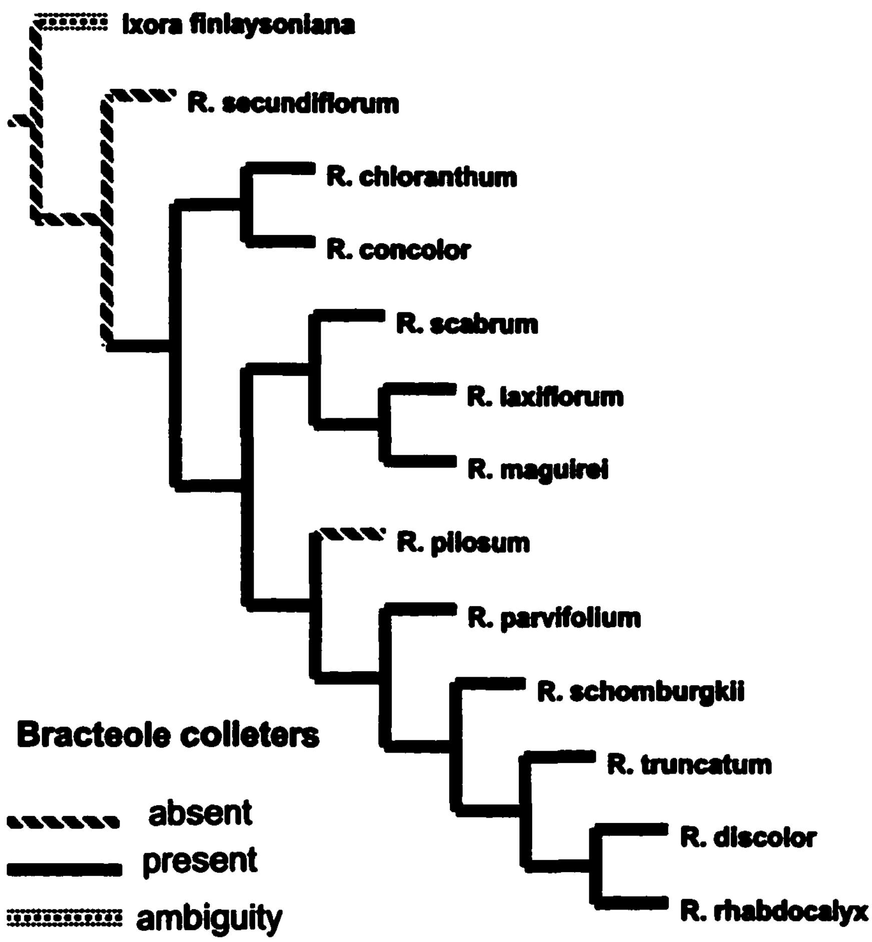

Figure 49. Character state optimization of bracteole colleters on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

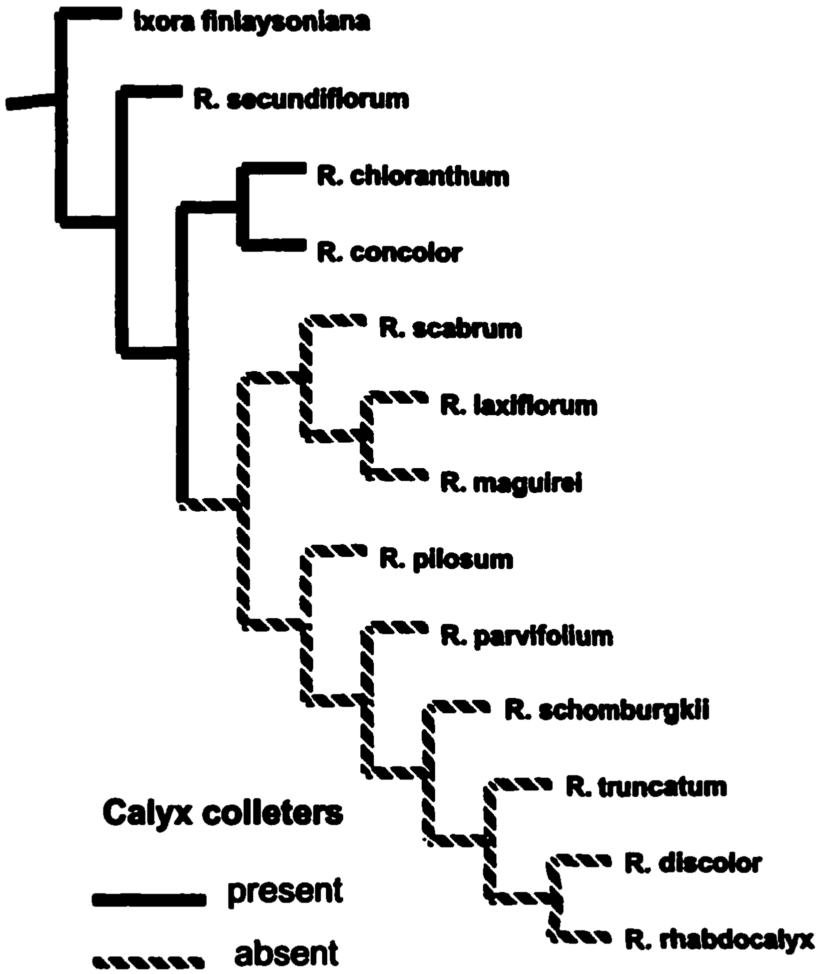

Figure 50. Character state optimization of calyx colleters on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

1988), perhaps colleters give a selective advantage for the colonization of new habitats perhaps represented and advantage. On the other hand, the great quantity of indument covering all the structures of R. pilosum perhaps represents an alternative source of protection, reducing the selective advantage of colleters in this species.

2.2.4.2.2. Evolution of Inflorescences architecture

The flowers of Retiniphyllum are organized in three types of inflorescences: Racemes, spikes, and umbels. Optimization of inflorescences morphology indicates that racemose inflorescences with pedicellate flowers is the ancestral character in Retiniphyllum (Fig. 51). Subsequently, this inflorescence evolved into two other architectures: Umbellate, through the extreme reduction of the rachis, and spicate, by the reduction of the pedicels. Although it seems to be clear that spicate inflorescences evolved once in Retiniphyllum, the same is not true for the umbellate condition. The combined analysis included only R. scabrum, one of the three species with umbellate inflorescences. The inclusion of R. cataractae and R. pauciflorum in the combined analysis will indicate if the umbellate condition evolved twice in the genus, because

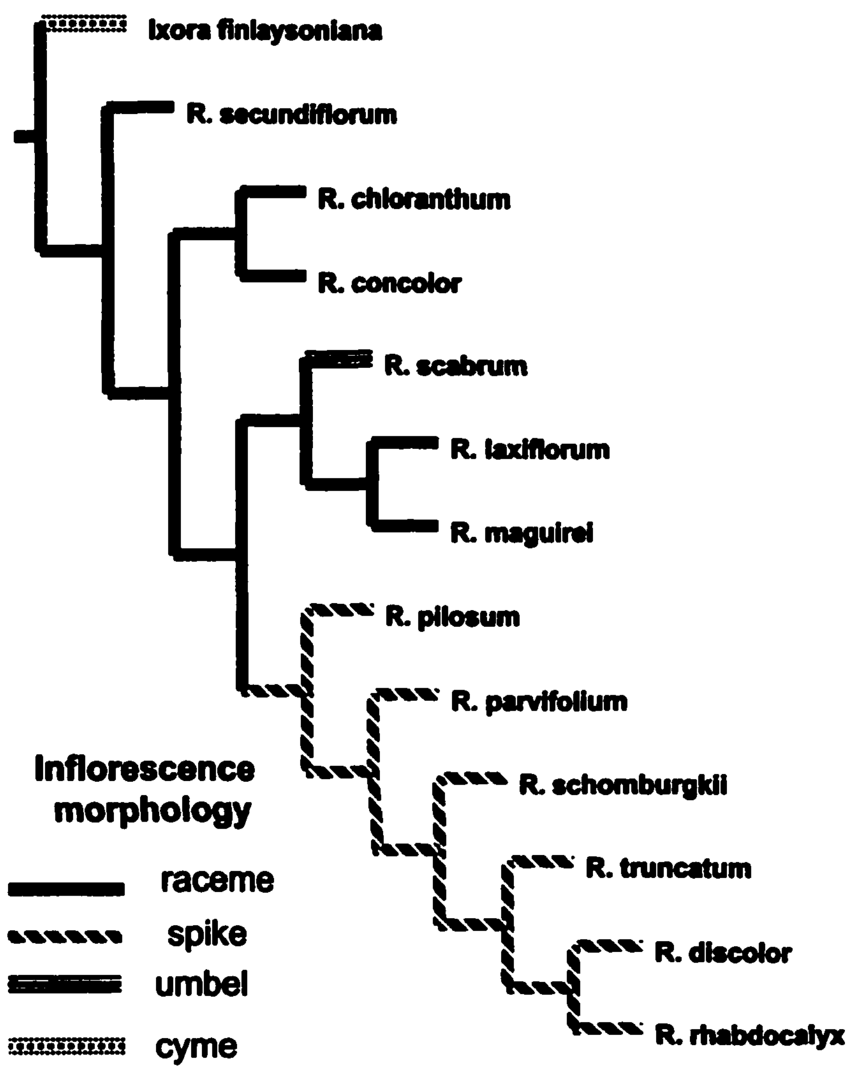

Figure 51. Character state optimization of inflorescence morphology on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

it is suggested in the analysis using only morphological data (Fig. 44).

2.2.4.2.3. Evolution of flowers morphology

Flower characters that have shown patterns of evolution are calyx morphology, corolla symmetry, corolla color, position of ring of hairs in the corolla tube, pollen shape in outline, and pollen lumina uniformity.

Most species of Retiniphyllum have tubular calyx (longer than wide), whereas a few species have cupular calyx (wider than long). The optimization of calyx morphology indicates that cupular calyx evolved once (Fig. 52). However, if the tubular calyx evolved one or two times depends on the optimization option used. Under the slow option of Winclada (Deltran in PAUP), tubular calyces evolved twice (Fig. 52), but under the fast option (Acctran in PAUP), tubular calyces evolved once (not shown). Therefore, there is an ambiguous interpretation for the evolution of the tubular condition of the calyx.

Corollas in Retiniphyllum might be zygo- or actinomorphic. Zygomorphic corollas is a derived condition, as indicated by the optimization of this character in the combined analysis (Fig. 53). This condition arose twice,

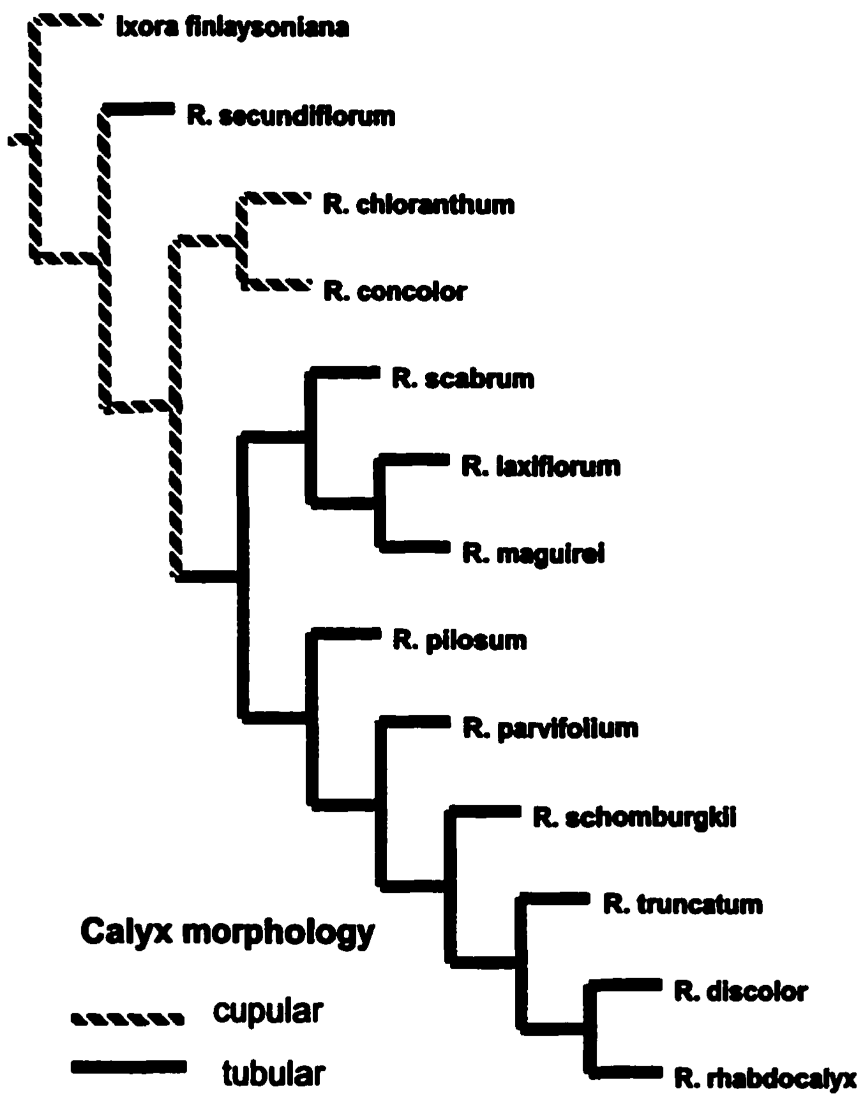

Figure 52. Character state optimization of calyx morphology on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

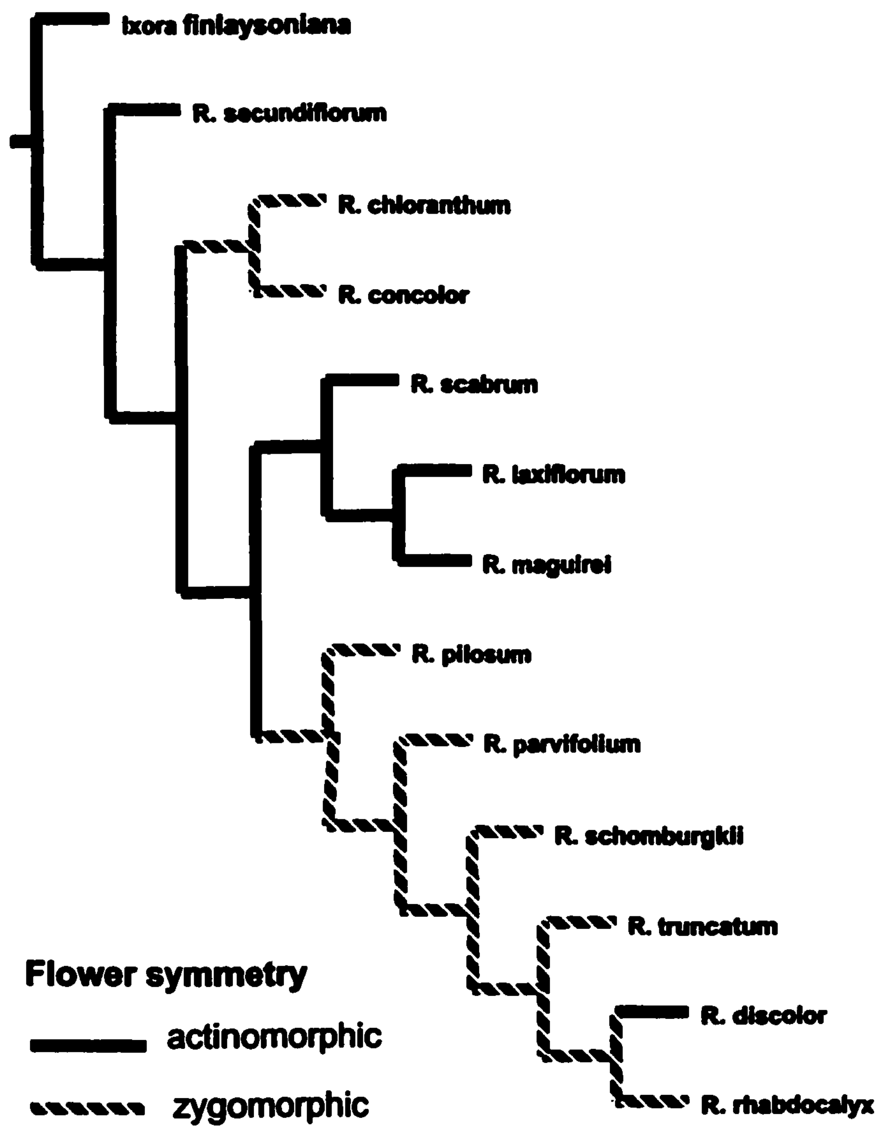

Figure 53. Character state optimization of flower symmetry on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

once in the Retiniphyllum concolor - R. chloranthum clade, and once in the spicate clade, with a subsequent reversal in R. discolor and R. rhabdocalyx to the ancestral condition.

Some species in Retiniphyllum have white to greenish-white corollas, while others have deep pink to red corollas (white vs. red corollas for abbreviation). According to the optimization of corolla color (Fig. 54), it seems that the ancestral condition was red-colored corollas. The white-colored corollas arose twice, with a reversal to the ancestral condition in the clade R. discolor - R. rhabdocalyx.

In Retiniphyllum, the ring of hairs in the corolla tube might be located at distal or basal portion of the tube. The ancestral condition seems to be the basal placement of the ring of hairs, when this character is optimized onto the cladogram (Fig. 55). The distal placement evolved once in the spicate group, with a reversal in the R. discolor - R. rhabdocalyx.

Retiniphyllum concolor and R. chloranthum have two pollen characters unique to the genus: pollen grains oblong in outline and lumina that increases in size toward the poles. These characters showed to be clear synapomorphies

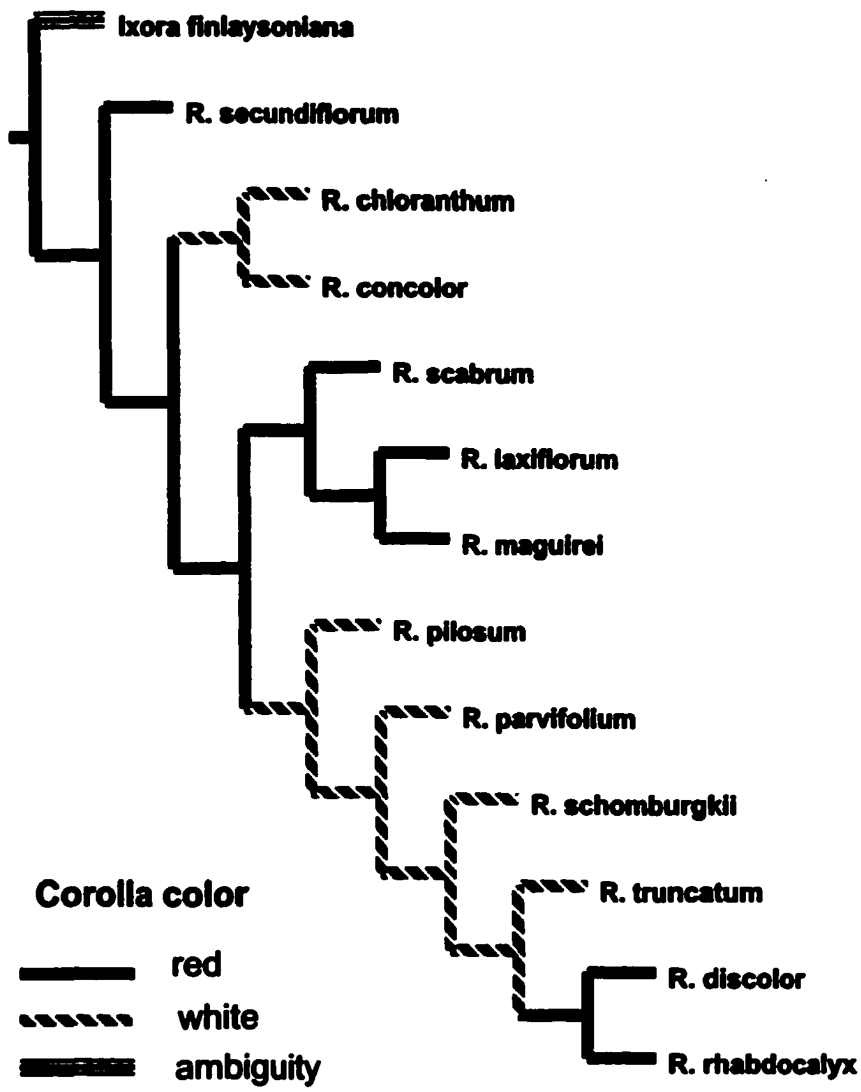

Figure 54. Character state optimization of corolla color on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

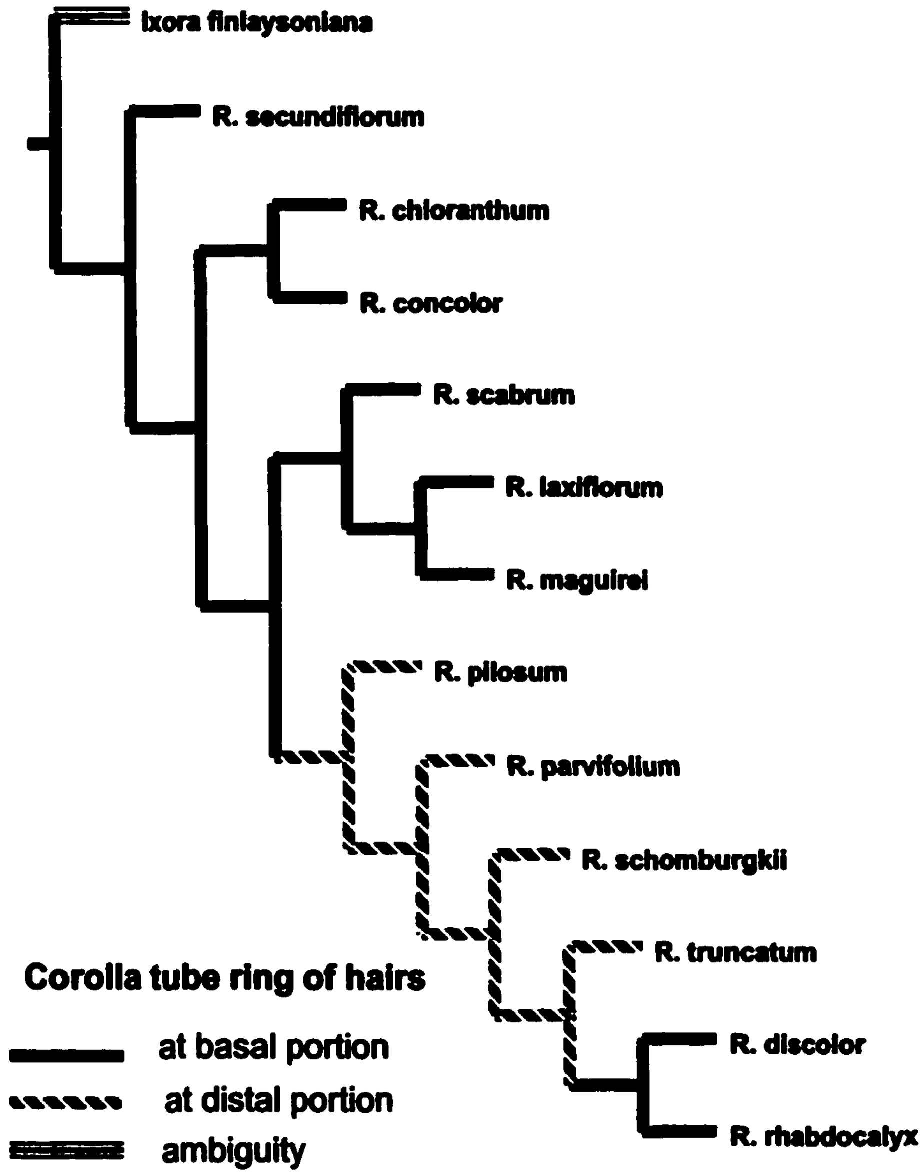

Figure 55. Character state optimization of corolla tube ring of hairs on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

for the clade, and derived conditions within <u>Retiniphyllum</u> when they were optimized (Figs. 56 & 57).

2.2.4.2.4. Evolution of pyrenes

Two characters related to pyrene morphology, the presence or absence of wings and the position of the perforation along the ventral side of the pyrene, were also analyzed to examine character evolution. Winged pyrenes appear to be an ancestral condition in <u>Retiniphyllum</u>, when this character is optimized onto the cladogram (Fig. 58). Pyrenes without wings evolved twice, one time in <u>R. concolor</u>, and another time in the spicate clade. Another ancestral condition in <u>Retiniphyllum</u> was resolved to be pyrene perforation located at median portion. Pyrenes perforated at basal portion arose two or three three times, while those perforated at distal portion arose only once in <u>R. scabrum</u> (Fig. 59).

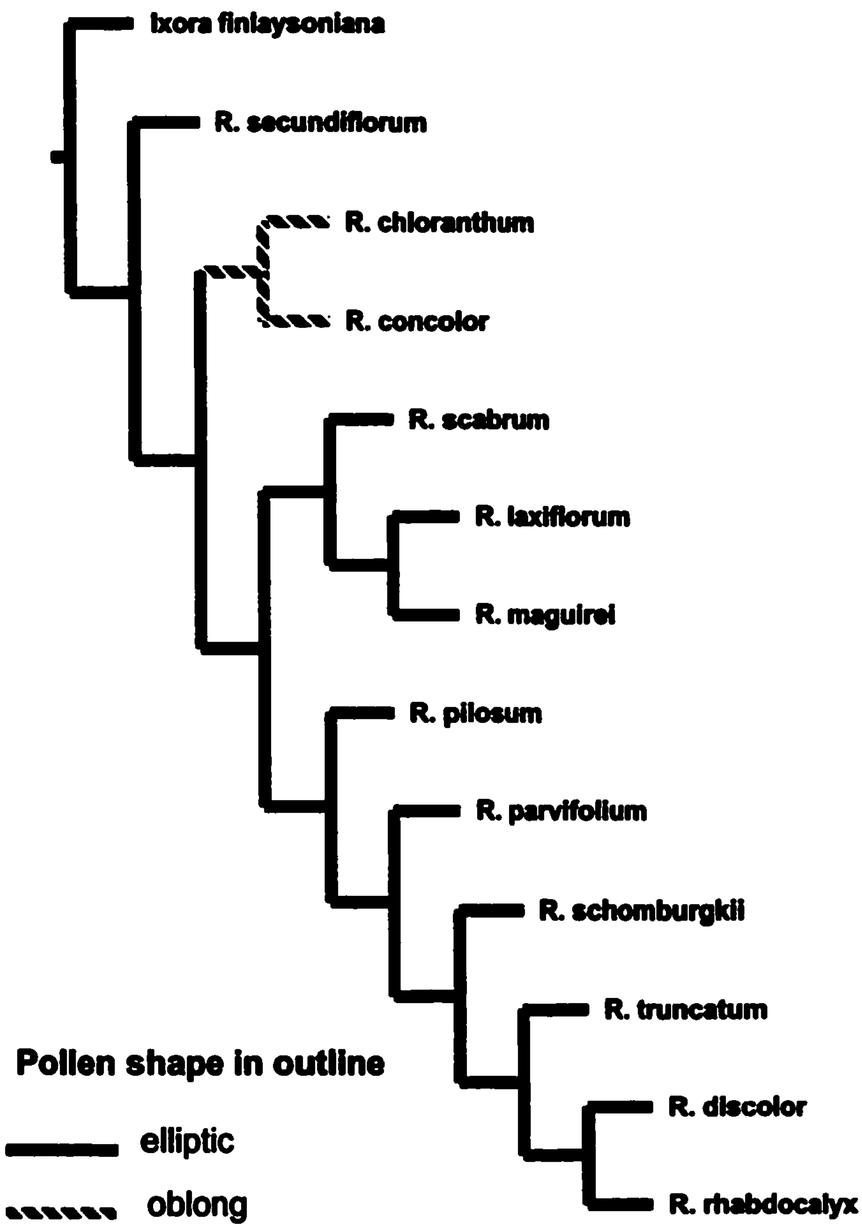

Figure 56. Character state optimization of pollen shape in outline on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

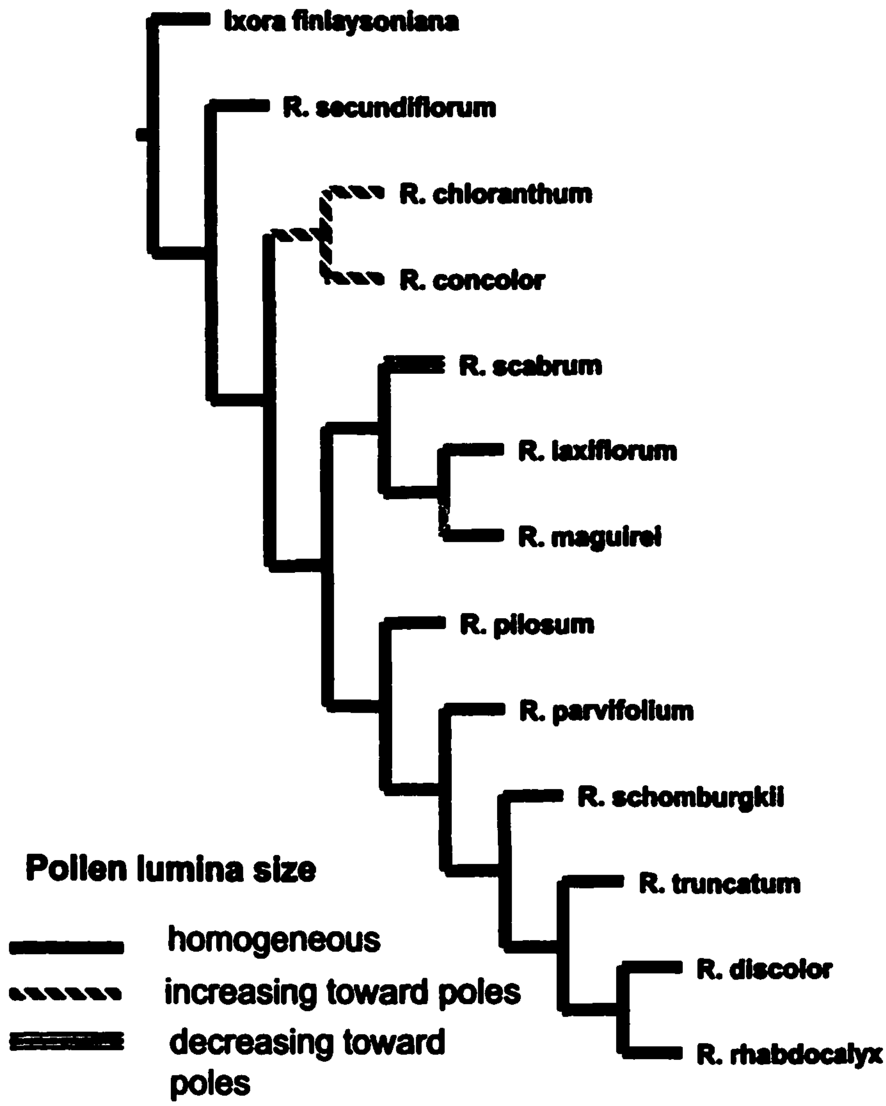

Figure 57. Character state optimization of pollen lumina size on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

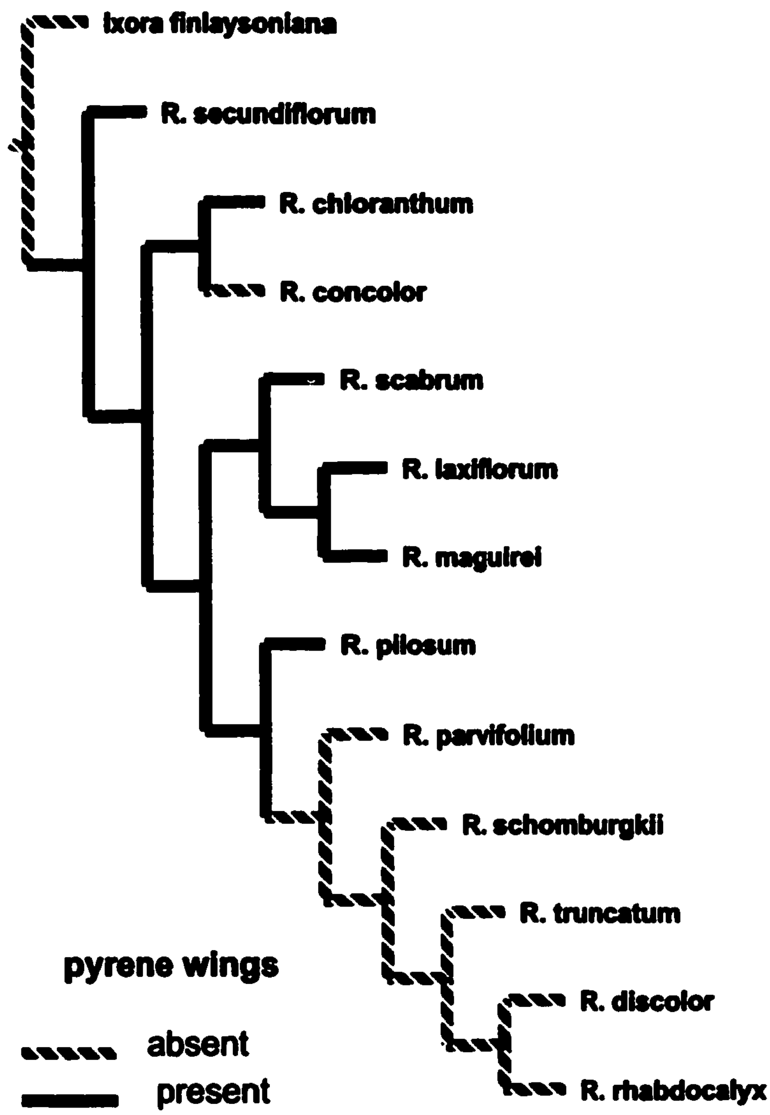

Figure 58. Character state optimization of pyrene wings on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

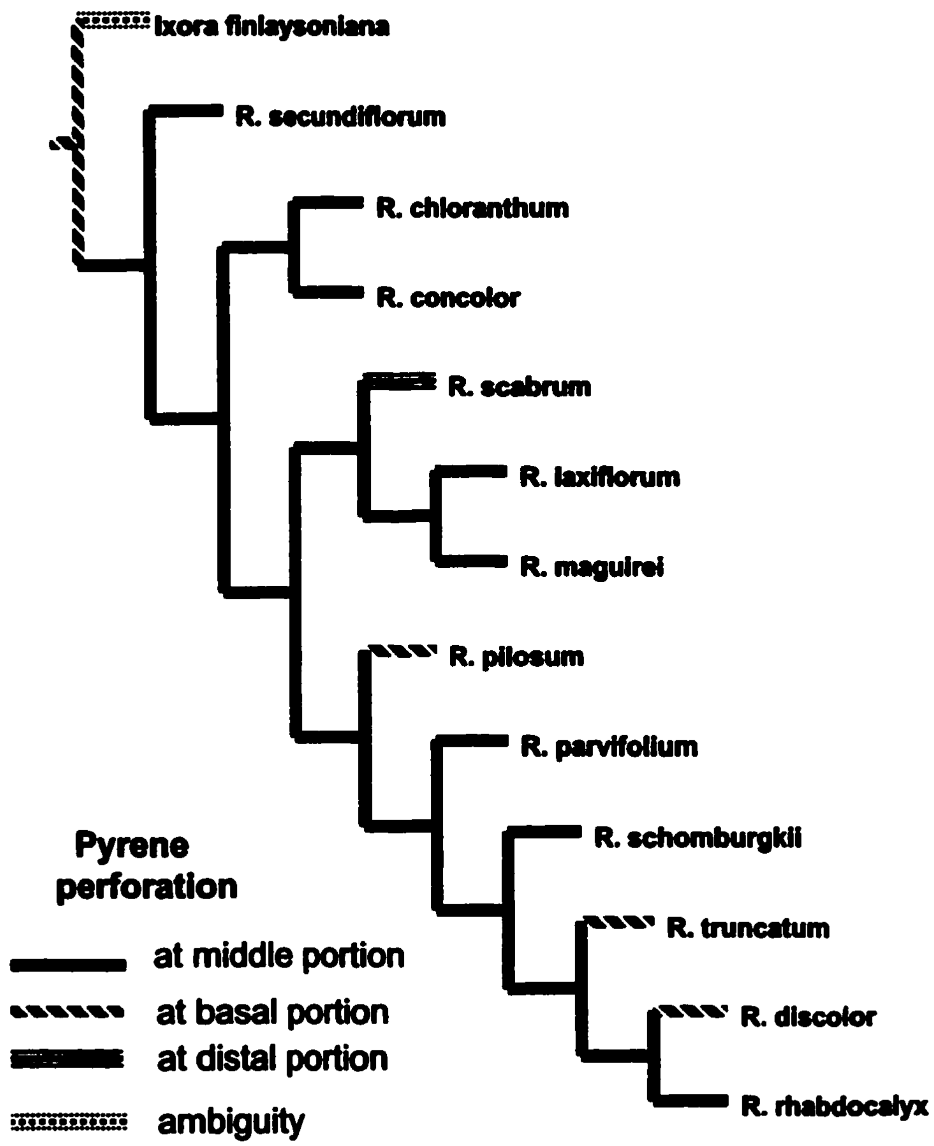

Figure 59. Character state optimization of pyrene perforation on the combined analysis of ITS sequence data and morphology, using the slow option of WinClada.

2.2.4.2.5. Evolution of pollination syndromes

The flowers of Retiniphyllum show three pollination syndromes, two related to insects and one to birds, particularly hummingbirds.

Retiniphyllum concolor and R. chloranthum can probably be assumed to be pollinated by insects, perhaps butterflies or bees, based on corolla morphology and field observations (Faegri and Van der Pijl, 1979). These species have long-tubular corollas, cylindrical tube with pollinator guides, and white to greenish-white corollas. According to the combined analysis, these species are sister taxa, and can be assumed that this pollination syndrome arose once (Fig. 48). White-colored corollas (Fig. 54) were shown to be derived conditions when optimized, suggesting that this syndrome was derived in Retiniphyllum.

Another pollination syndrome related to insects is found in R. parvifolium, R. pilosum, R. schomburgkii and R. truncatum. These species are assumed to be pollinated by insects, most likely bees, based on the morphology of the corollas and field observations (Faegri and Van der Pijl, 1979). They have short-tubular corollas, infundibuliform tube with pollinator guides, and white to greenish-white corollas. According to the combined analysis (Fig. 48), these species are members of a single clade, and can be assumed that this pollination syndrome arose once in the spicate clade. Another group of species are hummingbird pollinated, as is suggested by the corolla morphology, and has been confirmed for R. rhabdocalyx (Rosero Lasprilla & Sazima, 2000). In addition to this species, the syndrome of ornitophily is shown by R. discolor, R. scabrum, R. laxiflorum, R. maguirei and R. secundiflorum. These species have long tubular, mostly narrowly infundibuliform, and dark pink to red corollas. According to the combined analysis, these species are placed in three different clades. Considering that all the red-colored species share this syndrome, the optimization of corolla color would help to understand its evolution. Figure 54 shows that the red-colored condition is ancestral in the genus, and perhaps the syndrome of ornitophily can be interpreted as ancestral. If so, the syndrome evolved twice, and had a reversal to the ancestral condition in the R. discolor - R. rhabdocalyx clade.

2.2.5. Conclusions

The three sections proposed by Müller Argoviensis (1881) are not supported, and based on the lack of distinct definable clades an infrageneric classification for Retiniphyllum is not guaranteed at this time.

According to the optimization of morphological characters, it seems that some ancestral conditions in Retiniphyllum were: lack of colleters inside bracteoles, presence of colleters inside calyces, racemose inflorescences, actinomorphic corollas, dark pink to red corollas, ring of hairs at the base of the corolla tube, pollen elliptic in outline, pollen lumina homogeneous, and winged pyrenes perforated at medial portion.

It appears to be that the syndrome of ornitophily was the ancestral condition in Retiniphyllum, and evolved more than once during the diversification of the genus. Each of the two insect-pollinated syndromes arose once, independently one from the other.

2.3. Biogeography of Retiniphyllum

2.3.1. Introduction

The Guayana Region extends from southeastern Colombia to French Guiana, covering the Southern portion of Venezuela below the Orinoco River, northern Brazil, and Surinam and Guyana almost entirely. The Guayana Region was formally defined and divided into four provinces by Berry et al. (1995). The Western and Eastern Guayana Provinces include, with few exceptions, lowlands below 500 m. The Central Guayana Province includes areas from lowlands to highlands up to 1500 m, and the Pantepui region covers the highlands above 1500 m (Berry et al., 1995). The landscape of the region, especially in the Central and Pantepui Provinces, is characterized by flat-topped mountains, commonly known as tepuis.

Most species of Retiniphyllum (19 of 22) are distributed in the Guayana Region. While 13 species are endemic to this region, six species are distributed in the Amazon Region and/or in the Brazilian Shield. Although species of Retiniphyllum are found in the four provinces, the Western Guayana Province has the highest number of species (14 species) and the highest endemism for the genus (8 species). The Río Negro basin covers a large area inside the Western Guayana Province and is the richest area of Retiniphyllum species. The Río Negro basin, which was considered by Prance (1977) as part of the Amazon Region, contains a very peculiar flora with a high percentage of endemic species. The high level of endemism has been associated with the nutrient-poor, white-sand soils (Maguire, 1970; Huber, 1988; Kubitzki, 1989, 1990).

Three species of Retiniphyllum are not found in the Guayana Region: R. kuhlmannii, R. parvifolium and R. fuchsioides. While the first two are distributed in the Brazilian Shield, R. fuchsioides grows in several low mountains located near the Peruvian Andes (e.g. Cerros del Sira, Sierra de Putuim, Cordillera de San Matias) from 350 to 1200 m. Although the floristic composition and affinities of these mountains have not been studied, it seems that they have floristic affinities with the Guayanan flora.

After twenty years of botanical exploration in the Venezuelan Guayana, Maguire (1970) postulated a hypothesis by which there was a floristic exchange between the Guayana and Brazilian Shields, when both shields were contiguous, followed by biological diversification in isolation on tepui summits. According to Maguire, the longtime isolation of the tepui summits from one another and from the lowlands was the cause of the high levels of endemism on the tepui summits. However, a better understanding of the flora of the Guayana region has shown that diversification took place in both directions, from the upper regions downward and from the lowland upward, and the idea of long-lasting isolation is not valid anymore (Huber, 1988; Kubitzki, 1990). In contrast to Maguire's hypothesis, Kubitzki (1989) postulated that the lowlands were the center of diversification of the core elements of the Guyana flora, and from there radiated into surrounding lowland regions, upland regions, and highlands. He cited Retiniphyllum as one of the examples of taxa that supports his hypothesis.

One of the few methods in historical biogeography used to investigate the distributional history of individual taxa (taxon biogeography) is Dispersal-Vicariance Analysis (DIVA). This is a relatively new method developed by Ronquist (1997), to reconstruct the optimal ancestral distribution of each node on a cladogram. The optimal reconstructions minimize the number of dispersal and extinction events, and favor vicariance (Ronquist, 1997).

My objective in this part of the project was to hypothesize about the distributional history of the genus Retiniphyllum, and to test Kubitzki's hypothesis.

2.3.2. Materials and Methods

The historical biogeography of Retiniphyllum was studied using Dispersal-Vicariance analysis (DIVA). The ancestral distributions were reconstructed with the optimization method implemented in the computer program DIVA 1.0 (Ronquist, 1996). Dispersal and vicariance, the two alternative explanations for current distributions, were postulated for each node.

DIVA analysis requires a fully resolved phylogeny, and the areas of distribution of the terminals. Two phylogenies were used: the one obtained from the combined analysis including 12 species of Retiniphyllum (Fig. 48), and the one obtained from the combined analysis including all the species of the genus (Fig. 47). The two cladograms (Figs. 47 and 48) were presented in the last section (2.2.).

The areas of endemism were selected according to the major biogeographical areas in which Retiniphyllum is distributed: The Guayana Region, the Amazon Basin, the Brazilian Shield, and the Subandean Region. The Guayana

Region was divided, based on the level of endemism for the genus, in two areas. One area includes the Western Guayana province, as defined by Berry et al. (1995), and the other includes the three other provinces: Central Guayana, Eastern Guayana and Pantepui. These two areas are denominated here Southern and Northern Guayana Region respectively.

The genus Ixora, which was selected as outgroup, has a Pantropical distribution. It was coded as distributed in the same areas as the ingroup, plus a hypothetical additional area that represents the rest of the distribution of the genus.

2.3.3. Results

2.3.3.1. First DIVA analysis

This analysis included the 12 species of Retiniphyllum for which morphological and molecular data were available (Fig. 48). The Dispersal-Vicariance analysis produced five alternative reconstructions of the distribution history of Retiniphyllum. The optimal distributions at each ancestral node are presented in Fig. 60. The five reconstructions require two vicariant events, and while one of the

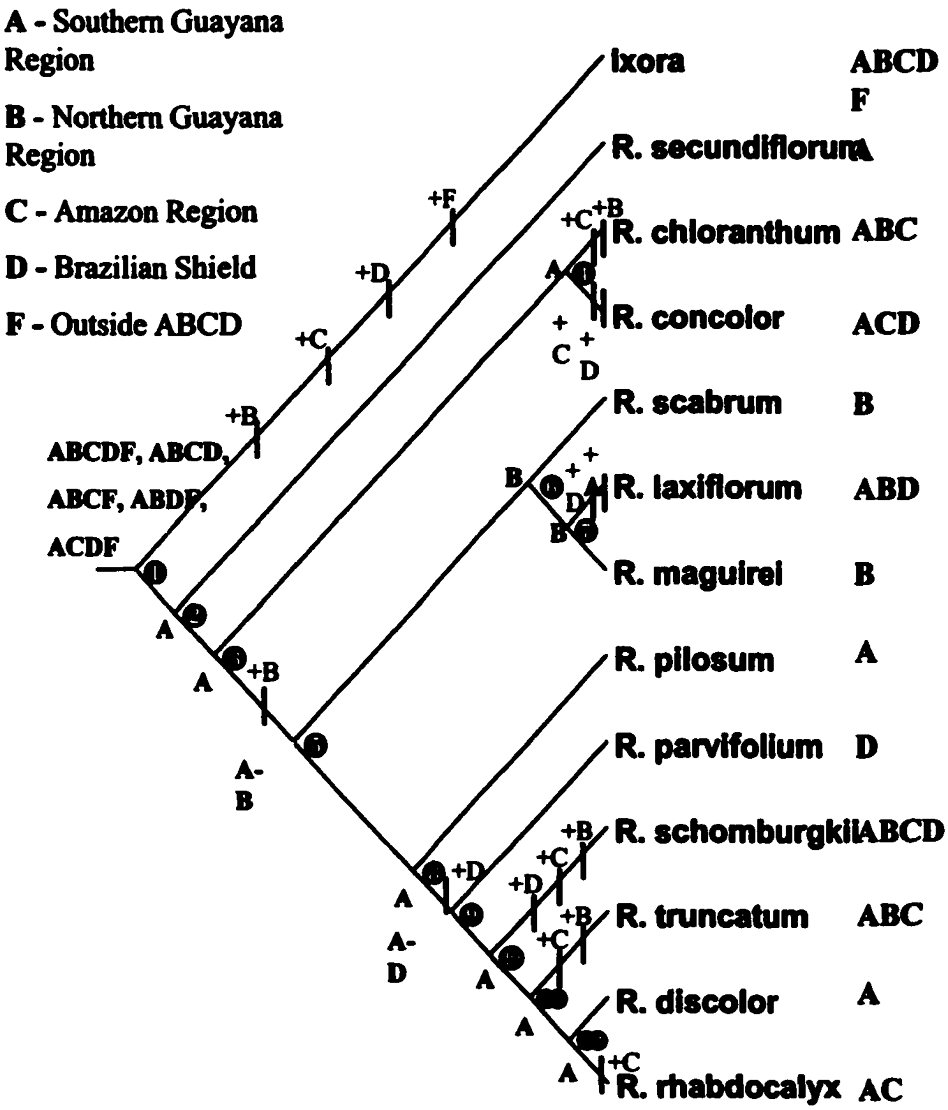

Fig. 60. Hypothetical biogeographical history of Retiniphyllum. Dispersal events are indicated on the branches, and ancestral distributions at the nodes. Vicariant events are inside rectangles. In front of each taxon, its current distribution is indicated.

reconstructions requires 14 dispersals, the other four require 15 dispersals.

The only difference between all the reconstructions is the optimization of the basal most event, that is the node of the outgroup. The first reconstruction postulates a widespread ancestor with the same distribution as Ixora. The other four reconstructions implied an ancestor distributed in all the areas, except one. For instance, the fourth reconstruction hypothesizes an ancestor distributed in the Southern Guayana Region, the Amazon Region, and the Brazilian Shield that dispersed from there to the Northern Guayana Region.

The five biogeographical reconstructions coincide in the optimizations of all the ingroup nodes. The ancestral distribution for R. secundiflorum (node 2) is postulated to be the Southern Guayana Region, the same area as its current location.

The Southern Guayana Region is also the ancestral distribution for node 3, and for the clade R. chloranthum - R. concolor (node 4). Four dispersal events have to be postulated in order to explain the current distribution of the two species at node 4. Both species dispersed from the Southern Guayana to the Amazon Region. In addition, R.

chloranthum dispersed to the Northern Guayana, and R. concolor to the Brazilian Shield.

It is postulated that a dispersal occurred from node 3 to 5, followed by a vicariant event that split the Southern Guayana from Northern Guayana. Accordingly, this vicariant event gave rise to two of the main lineages in Retiniphyllum: the spicate clade, and the R. scabrum-R. laxiflorum-R. maguirei clade.

The ancestral distribution for nodes 6 and 7 is postulated to be the Northern Guayana. Two dispersals are needed to explain the distribution of R. laxiflorum, one to the Southern Guayana, and the other to the Amazon Region.

The Southern Guayana Region is hypothesized to be the ancestral distribution for the clade with spicate inflorescences (node 8). It is postulated that a dispersal occurred from the Southern Guayana to the Brazilian Shield, followed by a vicariant event that divided the regions at node 9, and caused R. parvifolium to evolve in the Brazilian Shield.

It is postulated that the ancestors at nodes 10 to 12 were in the Southern Guayana, and subsequently dispersed to the Northern Guayana, the Amazon Region, and the Brazilian Shield, in the case of R. schomburgkii. R. truncatum dispersed to the Northern Guayana, and to the Amazon

Region. Finally, R. rhabdocalyx dispersed only to the Amazon Region.

2.3.3.2. Second DIVA analysis

This analysis included all the species of Retiniphyllum (Fig. 47). The Dispersal-Vicariance analysis produced 41 alternative reconstructions of the distribution history of the genus. The optimal ancestral distribution at each node is presented in Fig. 61. The high number of reconstructions is due to six nodes. Node I, that is the ancestral distribution for the outgroup, has 10 alternative optimal reconstructions. Nodes II, V, and VI have seven, node III has six, and node IV has nine alternative reconstructions.

The biogeographical reconstructions coincide in the optimizations of 16 of the ingroup nodes and require a minimum of 23 dispersal events.

The ancestral distribution for node 2, that divided the clade R. chloranthum-R. concolor from the rest of the species is postulated to be the Southern Guayana. The same is true for nodes 3 to 8. Four dispersal events have to be postulated in order to explain the current distribution of the two species at node 3. Both species dispersed from the

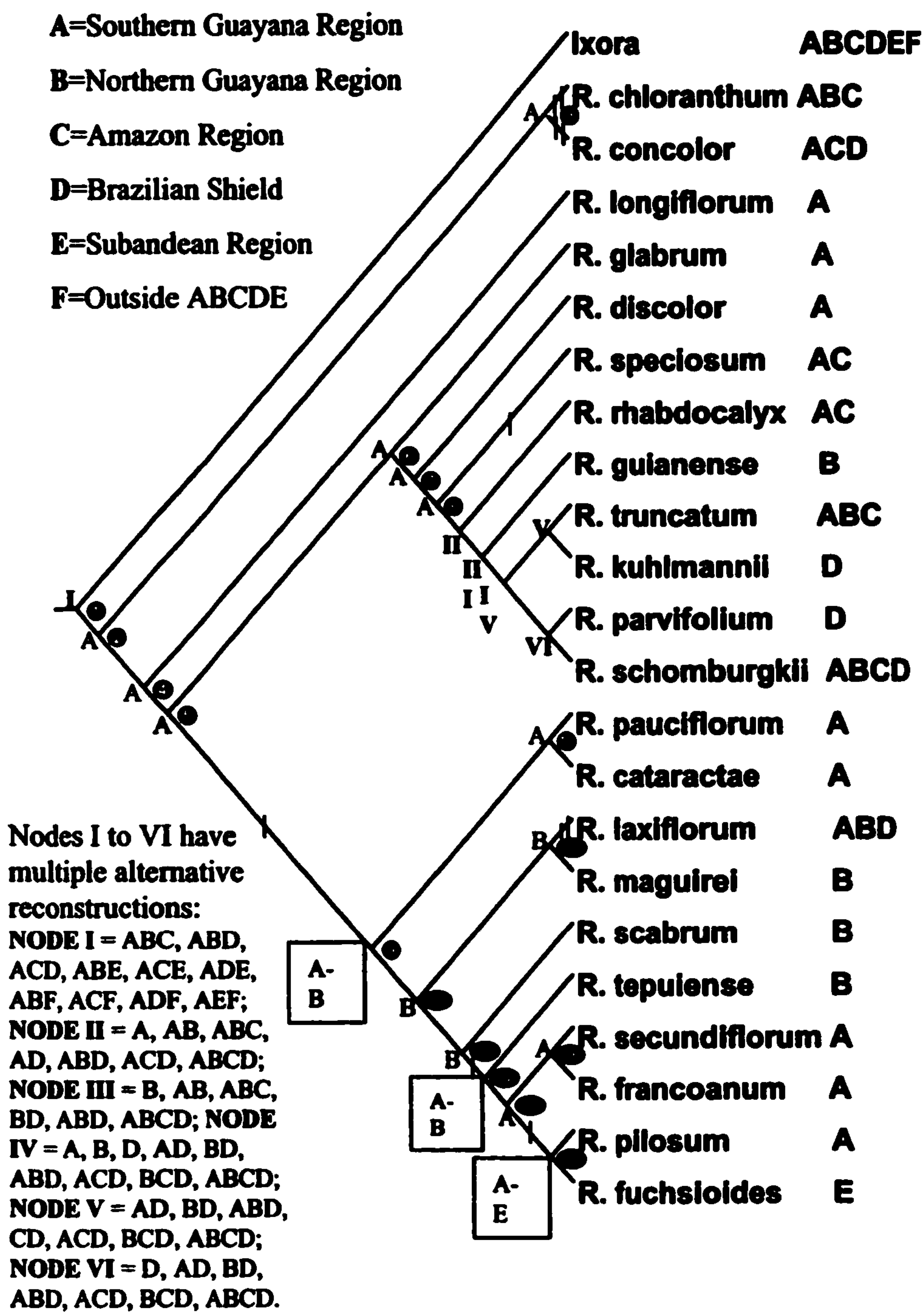

Fig. 61. Hypothetical biogeographical history of Retiniphyllum using all the species. Dispersal events are indicated on the branches, and ancestral distributions at the nodes. Vicariant events are inside rectangules. In front of each taxon, its current distribution is indicated.

Southern Guayana to the Amazon Region. Additionally, R. chloranthum dispersed to the Northern Guayana, and R. concolor to the Brazilian Shield. The current distribution of R. speciosum is explained by a dispersal event from the Southern Guayana to the Amazon Region.

It is postulated that a dispersal occurred from node 5 to 9, followed by a vicariant event that split the Southern from the Northern Guayana. Accordingly, the ancestral distribution for the R. pauciflorum-R. cataractae clade is postulated to be the Southern Guayana. The ancestral distribution for nodes 11 to 13 is postulated to be the Northern Guayana. Two dispersals are needed to explain the distribution of R. laxiflorum, one to the Southern Guayana, and the other to the Amazon region.

It is postulated that a dispersal occurred from node 13 to 14, followed by a vicariant event that split the Southern from the Northern Guayana and caused R. tepuiense to evolve in the latter. The ancestral distribution for nodes 15 and 16 is postulated to be the Southern Guayana. Finally, a dispersal occurred from the Southern Guayana to the Subandean Region and the vicariant event that divided these regions caused R. pilosum to evolve in the former and R. fuchsioides to evolve in the latter.

2.3.4. Discussion

2.3.4.1. The history of diversification of *Retiniphyllum*

DIVA analyses indicate that the history of diversification of *Retiniphyllum* started in the Southern Guayana Region. This region is postulated to be the ancestral distribution for: *R. secundiflorum*, *R. chloranthum*, *R. concolor*, and *R. discolor*. On the other hand, the Northern Guayana Region is postulated to be the ancestral distribution for: *R. scabrum*, *R. laxiflorum*, and *R. maguirei*.

It is not possible to postulate the ancestral distributions for *R. pilosum*, *R. parvifolium*, *R. schomburgkii*, *R. truncatum*, and *R. rhabdocalyx* because they have multiple reconstructions when all the species are include in the analysis (Fig. 61).

The Southern Guayana Region is tentatively postulated as the ancestral distribution for *R. longiflorum*, *R. glabrum*, *R. speciosum*, *R. pauciflorum*, *R. cataractae*, *R. francoanum* as it is indicated by the optimal reconstructions at their nodes (Fig. 61).

According to the second DIVA analysis, the ancestor of *R. tepuiense* was widespread in the Southern and Northern

Guayana and the ancestor of R. fuchsioides was widespread in the Southern Guayana and in the Subandean Region. Two vicariant events probably caused these species to evolve in their current areas of distribution.

There are several hypothesis proposed to explain the geographical isolation of populations that caused the diversification of the Neotropical biota (Haffer, 1997). For instance, the successive marine transgressions that created a seaway in the late Miocene, connecting the Atlantic with the proto-Caribbean (~10 my) (Rasanen et al., 1995); and the presence of a Pleistocene sea in the Amazon basin (~5 my) (Haq et al., 1987), among others. These vicariant events would be probably correlated to those postulated in nodes 9 (Fig. 60) or 17 (Fig. 61), because they could divide the Southern Guayana from the Brazilian Shield or from the Subandean Region.

The vicariant events postulated for the division of the two areas of the Guayana Region might be related or not to the climatic-vegetational fluctuations during the tertiary and Quaternary. As original stated, the Refuge hypothesis postulated the existence of forest refugia and non-forest refugia during the peaks of dry and wet climatic periods over the last 60 million years (Haffer, 1982, 1997). However, this hypothesis has been related mainly to the recent Pleistocene climatic changes. Particularly in the Guayana Region, the Pantepui Refuge was postulated by Steyermark (1979, 1982), but paleoecological data did not support its presence, at least during the pleistocene (Rull, 1991).

One important limitation of the DIVA analysis is it assumes that current distributions were the result of vicariant events. The optimal solution in DIVA assigns cost to dispersal and extinction, and no cost for vicariance. Considering that the results may underestimate the number of dispersal, and overestimate the number of vicariance events, the results obtained should be considered as the minimum number of dispersals, and the maximum number of vicariance events (Xiang & Soltis, 2001). If so, the vicariant events postulated for Retiniphyllum could probably correspond to dispersals. Because vicariant events such as those mentioned before (e.g. the seaway) had to affect more than one taxon, it would be expected that additional taxa would show the same pattern. Phylogenies from additional taxa distributed in northern South America are needed, in order to test the vicariant events hypothesized here for Retiniphyllum.

2.3.4.2. Test of Kubitzki's hypothesis

The results presented here support Kubitzki's hypothesis (1989), according to which Retiniphyllum diversified on white-sand areas in the lowlands, and from there radiated into surrounding lowland regions, upland regions, and highlands. The ancestral distributions of almost all the nodes in Fig. 60 and many nodes in Fig. 61, postulate a diversification in the Southern Guayana followed by dispersals to the Northern Guayana Region, the Amazon, and the Brazilian Shield. The vicariant events postulated here also include the Southern Guayana. Recent phylogenetic studies have supported Kubitzki's hypothesis as well. In the Gentianaceae, the most basally positioned evolutionary lineages in Aripuana, Irlbachia, and Potalia are distributed on white-sand areas in the lowlands of the Guayana region (Struwe, 1999). Preliminary results indicate that perhaps the same is true in the tribe Helieae and in the subtribe Potaliinae of the same family (Struwe et al., 2002). Additional examples that show basal lineages distributed on white-sand areas in the lowlands of the Guayana region are Brocchinia in the Bromeliaceae (Givnish et al., 1997), and several genera of the Rapateaceae (Givnish et al., 2000).

2.3.5. Conclusions

The history of diversification of Retiniphyllum started in the Southern Guayana Region, and this region is postulated to be the ancestral distribution for many of the nodes present in the phylogenies used.

The history of the diversification of Retiniphyllum includes more dispersal than vicariance events. Because of the limitations of the method used, phylogenies from additional genera with similar distributions are needed to test the vicariant events postulated here. Until that data becomes available, Retiniphyllum provides new evidence that support Kubitzki's hypothesis (1989), that the lowlands were an important center for diversification of the core elements of the Guyana flora.

Appendix A. Specimens investigated in the palynological survey. All specimens are deposited at NY.

Retiniphyllum cataractae Ducke: Brazil, Amazonas, Curicuriary, Ducke 35067.

Retiniphyllum chloranthum Ducke: Venezuela, Amazonas, Casiquiare, Colella 1895.

Retiniphyllum concolor (Spruce ex Benth.) Muell. Arg.: Colombia, Vaupés, Mitú, Cortés 1646; Cortés 1611; Venezuela, Amazonas, San Carlos de Rio Negro, Clarck 6916.

Retiniphyllum discolor (Spruce ex Benth.) Muell. Arg.: Venezuela, Amazonas, Río Ventuarí, Huber 6119; Venezuela, Amazonas, Río Negro, Spruce 2010.

Retiniphyllum fuchsioides Krause: Perú, Huanuco, Cerros del Sira, Dudley 13175.

Retiniphyllum glabrum Steyerm.: Brazil, Amazonas, Inaporé, Schultes 9100

Retiniphyllum guianense Steyerm.: Guyana, Merumé Mountain Tillet 44824.

Retiniphyllum kuhlmannii Standl.: Brazil, Mato Grosso, Serra dos Parecis, Maguire 56447.

Retiniphyllum laxiflorum (Benth.) N. E. Br.: Venezuela, Amazonas, Cerro Sipapo, Maguire 28707.

Retiniphyllym longiflorum Steyerm.: Brazil, Amazonas, Rio Vaupés, Cavalcante 712.

Retiniphyllum maguirei Standl.: Surinam, Tafelberg, Maguire 24220, Maguire 24787.

Retiniphyllum parvifolium Steyerm.: Brazil, Pará, Serra do Cachimbo, Amaral 1118, Prance 25239.

Retiniphyllum pauciflorum Kunth. ex Krause: Venezuela, Amazonas, San Fernando de Atabapo, Wurdack 42752.

Retiniphyllum pilosum (Spruce ex Benth.) Muell. Arg.: Venezuela, Amazonas, San Carlos de Río Negro, Clark 7170; Venezuela, Amazonas, Maroa, Wurdack 43270.

Retiniphyllum rhabdocalyx Muell. Arg.: Colombia, Vaupés, Mitú, Cortés 1648; Brazil, Amazonas, Manaos, Berg P19524.

Retiniphyllum scabrum Benth.: Venezuela, Amazonas, Cerro Duida, Maguire 29674; Venezuela, Bolivar, Gran Sabana, Steyermark 104202.

Retiniphyllum schomburgkii (Benth.) Muell. Arg.: Venezuela, Amazonas, Cerro Moriche, Maguire 30901

Retiniphyllum secundiflorum Bonpl.: Venezuela, Amazonas, Atabapo, Huber 3701; Venezuela, Amazonas, Casiquiare, Huber 3413; Venezuela, Amazonas, Pimichín, Maguire 35607

Retiniphyllum tepuiense Steyerm.: Venezuela, Amazonas, Cerro de la Neblina, Maguire 37030.

Retiniphyllum truncatum Müll. Arg: Brazil, Amazonas, Rio Negro, Murça-Pires 742.

Appendix B: Aligned trnL-F sequences. Gaps are indicated by -. Informative gaps are coded as 0 and 1.

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                  ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                          10         20         30         40         50         60         70         80         90
Psychotria        AAATAAACTA TTTGACTCCC CAACTATTT- ATTTCT-ATA TCCCTCTTTT TGTTATAGGT -TCAA----- -AATTCCTTA T--CCATTCA
Cinchona          AAAAAGCCTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCTTCTTTT CATTAGCGGT -TCCA----- -AATTCCTTA G--CCATTCA
Gonzalagunia      ---------- -------CCC CGACTATTT- ----ATCCTA TCCTTCTTTT CGTTAGCGGT -TCAA----- -AATTCTTTA T--CTATTCA
Portlandia        -AAAAGCGTA TTTGACTCCC CAACGATTT- ----ATCCTA TCCTTCTTTT CGTTAGCGGT -TCAA----- -AATTCCTTA T--CCATTTG
Rondeletia        AAAAAGCCTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCTTCTTTT CGTTAGCGGT -TCAA----- -AATTCCTGA T--CCATCCA
Aidia             --AAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Aleisanthia       AAAAAGCATA TTTGA-CCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CATTAGCGGT -TAAA----- -AATACCTTA T--TCATTTA
Alibertia         AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Amphidasya        AAAAAGACTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT TGTTAGAGGT -TCAA----- -AATTCCTTA T--CCATTCA
Bertiera          AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATT-A
Borojoa           -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Botryarrhena      AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCT-TT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Calochone         -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Calycophyllum     AAAAAGAATA TTTGACTCCC CAACTATTT- ----AGCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Catunaregam       AAAAAACATA TTGGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TTAA----- -AATACCTTA T--TCATTTA
Ceriscoides       -AAAAATATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Coffea            AAAAAACATA TTTGATCCCC C--------- ---------- -------TTT CGTTAGCG-- ---------- ------CTTA T--TCATTTA
Condaminea        AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Cremaspora        --AAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Deccania          -AAAAACATA TTGGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TTAA----- -AATACCTTA T--TCATTTA
Dialypetalanthus  AAAAAGCATA TTTGACTCCC TAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TTAA----- -AATCCCTTA T--TCATTCA
Didymosalpynx     ---------A TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCAGT -TCAA----- -AATACCTTA T--TCATTTA
Duperrea          AAAAAACATA TTGGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Euclinia          AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Fadogia           AAAAAGCGTA TTTGAACCTC CAACTATTT- ----ATCATA TCCCCCCTTT CATTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Ferdinandusa      AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAAG---- --ATCCCTTA T--TCATTCA
Feretia           AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Fernelia          --------TA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGGGGT -TCAA----- -AATACCTTA T--TCATTTA
Gardenia          AAAAAATATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Genipa            AAAAAATATA TTTGATCCCC CGACGATTT- ----ATCTTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Gleasonia         AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCCTA T--TCATTCA
Heinsia           AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT TGGTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Hippotis          AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Ibetralia         -AAAAGCATA TTTAATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Ixora             --------TA TTTGA-CCCC CAACTATTTT ATTTATCCTA TCCCCCTTTT CATTAGCGGT GTCAA----- -AATACCTTA T--TCATTTA
Kailarsenia       -AAAAATATA TTTGATCCCC CAACTATTT- ----ATCCTA TTCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Keetia            ---AAGCGT- TTTGACCCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CATTAGCAGT -TCAA----- -AATACCTTA T--TCATTTA
Kutchubaea        AAAAAACATA TTTGATCCCC CGACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Leptacina         AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCTCCCTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Limnosipanea      AAAAAGCATA TTTGACTCCC CAACTAGAT- ---TATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCTTA T--TCATTCA
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Macrosphyra                  -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Maguireothamnus              AAAAAGCATA TTTGACTCCC CAACTATAT- ---TATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCTTA T--TCATTCA
Mussaenda                    AAAAAGCGTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT TGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Ottoschmidtia                AAAAAGCCTA TTTGACTCCT CAACTATTT- ----ATCCTA TCCTTCTTTT CGTTATCGGT -TCAA----- -AATTCCTTA T--CCATTCA
Oxyanthus                    AAAAAACATA GTTGATCCCC CAACTATTT- ----ATCCTA TCCC-TTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Pavetta                      AAAAAACATA TTTGATACCC CAACTATTT- ----ATCCTA TCCCCCTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Pentagonia                   AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Platycarpum                  AAAAAGCGTA TTTGACTTCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCTTA T--TCATTCA
Polysphaeria                 AAAAAGCATA TTTGACCCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CATTAGCAGT -TCAA----- -AATACCTTA T--TCATTTA
Posoqueria                   AAAAAGCATA TTTGACTCCC CAACTATTT- ----CTCCTA TCCCTCTTTT CGTTAACGAT -TCAA----- -AATCCCTTA T--TCATTCA
Pouchetia                    AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Pseudomussaenda              AAAAAGCGTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT TGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Psilanthus                   ---------- TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-CTTT CGTTAGCGGT -TCAA----- -AAAACCTTA T--TCATTTA
Psydrax                      AAAAAGCGTA TTTGACCCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CATTAGCAGT -TCAA----- -AATACCTTA T--TCATTTA
Pyrostria                    AAAGAG-GTA TTCATGCCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CTTTT-CATT AGGG-GTTCA AAATACCTTA T--CCATTTA
Randia                       AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCTCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Retiniphyllum_concolor       ---------- ---------- -AACTATTCT ----GTCCTA TCCCTCTTTT CATTAGCGGT -TCAA----- -AATCCCTTA T--TAATTTA
Retiniphyllum rhabdocalyx    ---------- ---------- ---------- -------CTA TCCCTCTTTT CATTAGCGGT -TCAA----- -AATCCCTTA T--TAATTTA
Retiniphyllum schomburgki    AAAAAGCATA TTTGAACCCC CAACTATTT- ----GTCCTA TCCCTCTTTT CATTAGCGGT -TCAA----- -AATCCCTTA T--TAATTTA
Retiniphyllum maguirei       AAAAAGAATA TTTGGACCCC CAACTATTT- ----GTCCTA TCCCTCTTTT CATTAGCGGT -TCAA----- -AATCCCTTA T--TAATTTA
Retiniphyllum_secundiflor    --CAAGC-TA TTTGAC-CCC CGACTATTT- ----GTCCTA TCCCTCTTTT CATTAGCGGT -TCAA----- -AATCCCTTA T--TAATTTA
Rosenbergiodendron           -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Rothmania                    AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA TATTCATTTA
Rutidea                      AAAAAACATA TTTGATCCCC C--------- ---------- ------TT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Schumaniophyton              AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TAATTTA
Scyphiphora                  AAAAAGCAAA TTTGACCCCC CAACTATTT- ----ATCCTA TCCTCCTTTT CGTTAGCGGT -TCAA----- -AATACCTT- ----------
Sherbournia                  -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Simira                       AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Sipanea_acinifolia           --------TA TTTGACTCCC CAACTACTT- ATT-CTTTTT TCTCTCTTTT CGTTAACGGT GTCAA----- -AATCCCTTA T--TCATTCA
Sipanea_biflora              AAAAAGCATA GTTGACTCCC CAACTACTT- ----ATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCTTA T--TCATTCA
Sipanea_wilson-brownei       AAAAAGCATA TTTGACTCCG CAACTACTT- ----ATCCTA TCCCTCTTTT CGTTAACGGT -TCwA----- -AATCCCTTA T--TCATTCA
Sipaneopsis                  AAAAAGTATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Sphinctanthus                -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Stachyarrhena                AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Sukunia                      -AAAAACATA TTGGGTCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTGA
Tamilnadia                   -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Tarenna                      AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCCTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Tocoyena                     -------ATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Tricalysia                   AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCCTT-T CGTTAGCGGT -TCAA----- -AAAACCTTA T--TCATTTA
Vangueria                    ---AAGCATA TTTGACCCTC CAACTATTT- ----ATCCTA TCTCCCTTTT CATTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                           100        110        120        130        140        150        160        170        180
Psychotria         CTTTCTTCTC TTAGAA-TTG AT-CGGTGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA ---------- ----TTTAT-
Cinchona           CTCTATTCTC TTAGAAATCG AT-CTGGGCG GA0---AATG CCTT------ 0------TTT C-TTATCACA AGGC----TT GT--TATAT-
Gonzalagunia       CTCTATTCTC TTAGAAATCG AT-TTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GT--TATAT-
Portlandia         CTCTATTCTC TTAGAAATCG AT-CTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCATA AATC----TT GT--TATAT-
Rondeletia         CTCTATTCTC TTAGAAATAG AT-CTGGTCG TA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GT--TATAT-
Aidia              CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Aleisanthia        CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Alibertia          CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Amphidasya         CTCTATTCTC TTAGAA-TCG AT-CTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA --TC------ ------TAT-
Bertiera           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTAT-T-
Borojoa            CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Botryarrhena       CTCGATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Calochone          CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Calycophyllum      CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Catunaregam        CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Ceriscoides        CTCTATTCTC TTAAAAATCG AT-CTGGACG GA0---AAAG CCCC------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Coffea             CTCTATTCTC TTAG----CG AT-CTGGACG GA0---AAAG CTCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Condaminea         CTCTATTCTC GTAGAAATCA AT-CTGGACA GA0---AATG CTCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Cremaspora         CTCTATTCTC TTAGAAATCA AT-CTGGACA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT CTGTTATTT-
Deccania           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Dialypetalanthus   CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Didymosalpynx      CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Duperrea           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Euclinia           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TG TGGTTATTTT
Fadogia            CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG ACCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Ferdinandusa       CTCTATTCTC G--------G AT-CTGG-CG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Feretia            CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT CTGGTATTT-
Fernelia           CTCTATTCTC TTAGAAATCG AT-CTGGCCA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT CTGTTATTT-
Gardenia           CTCTATTCTC TTAGAAATCA AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Genipa             CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCT------ 0------TTT -TTTATCACA AATC----TT GTGTTATTT-
Gleasonia          CTCTATTCCC TTAGAAATCG AT-CTGGACA GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Heinsia            CTCTATTCTC TTAGAAATAG AT-CTGGACG GA0---AATG CTCT------ 0------TTT C-TTATCACA AGTCAGTCTT GTGTTATGT-
Hippotis           CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Ibetralia          CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCTTTTCCT 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Ixora              TTCTATTCTC TTAGAAAGAG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Kailarsenia        CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG C--T------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Keetia             CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Kutchubaea         CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCC------- 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Leptacina          CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Limnosipanea       CTCCATTCTC TTAGAAATCG AT-CTGGACA GA1AATGATG ACCT------ 0------TTT C-TTATCACT AGTC----TT GTGTTATAT-
Macrosphyra        CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Maguireothamnus    CTCCATTCTC TTAGAAATCG AT-CTGGACA GA0---AGTG ACCT------ 0------TTT C-TTATCCCA AGTC----TT GTGTTATAT-
Mussaenda          CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AATG ATCT------ 0------TTT C-TTATCACA AGTCAGTCTT GTGTTATAT-
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Ottoschmidtia	CTCTATTCTC	TTAGAAATCG	AT-CTGGGCG	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTC------	TTGTTATAT-
Oxyanthus	TTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Pavetta	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Pentagonia	CTCTATTCTC	GTAAAAATCG	AT-CTGGACG	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTC----TT	GTGTTATAT-
Platycarpum	CTCTATTCTC	TTAGAAATCG	AT-CTGGACA	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTC----TT	GTGTTATAT-
Polysphaeria	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	AA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Posoqueria	CTCTATTCTC	TTAGAAATAG	AT-CTGGACA	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTC----TT	GTGTTATAT-
Pouchetia	CTCTATTCTC	TTAGAAATCG	AT-CTGGACA	GA0---AAAG	CCCTTT----	0------TTT	CTTTATCACA	AATC----TT	CTGGTTATTT
Pseudomussaenda	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AATG	ATCT------	0------TTT	C-TTATCATA	AGTCAGTCTT	GT-TTCTAT-
Psilanthus	CTCTATTCTC	TTAGA-----	----TGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Psydrax	CTCTATTCTC	TTAGAAATCG	ATGCTGGACG	AA0---AAAG	CCCT------	0------TTT	CTTTATCACA	AATC----TT	GTGTTATTT-
Pyrostria	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	AA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Randia	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Retiniphyllum concolor	CTCTATTCTC	TTAGAGATCG	AT-CTGGACG	GA0---AAAG	CCAC------	0------TTT	C-TTATCACA	AATG----TT	GTGTTATAT-
Retiniphyllum rhabdocalyx	CTCTATTCTC	TTAGAGATCG	GATCTGGACG	GA0---AA-G	CCAC------	0------TTT	C-TTATCACA	AATG----TT	GTGTTATAT-
Retiniphyllum schomburgkii	CTCTATTCTC	TTAGAGATCG	AT-CTGGACG	GA0---AAAG	CCAC------	0------TTT	C-TTATCACA	AATG----TT	GTGTTATAT-
Retiniphyllum maguirei	CTCTATTCTC	TTAGAGATCG	AT-CTGGACG	GA0---AAAG	CCAC------	0------TTT	C-TTATCACA	AATG----TT	GTGTTATAT-
Retiniphyllum secundiflorum	CTCTATTCTC	TTAGAGATCG	AT-CTGGACG	GA0---AAAG	CCAC------	0------TTT	C-TTATCACA	AATG----TT	GTGTTATAT-
Rosenbergiodendron	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCGCA	AATC----TT	GTGTTATTT-
Rothmania	CTCTATTCTC	TTAGAAATCA	AT-CTGGACG	GA0---AAAG	CCCT------	1TTTCCTTTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Rutidea	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Schumaniophyton	CTCTACTCTC	TTAGAAATCG	AT-CTGCACC	GA0---AAAG	ACCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Scyphiphora	-TCTATTCTC	TTAG----CG	AT-CTGGACG	AA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Sherbournia	TTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Simira	CTCTATTCTC	GTAGAAATCG	AT-CTGGACG	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTC----TT	GTGTTATAT-
Sipanea_acinifolia	CTCTATTCTC	TTAGCAATTG	AT-CTGGACA	GA1AAAAATG	CCCT------	0------TTT	C-TTATCACA	AGTT----TT	GTGTTATAT-
Sipanea_biflora	CTCTATTCTC	TTAGAAATTG	AT-CTGGACA	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTT----TT	GTGTTATAT-
Sipanea_wilson-brownei	CTCTATTCTC	TTAGAAATTG	AT-CTGGACA	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTT----TT	GTGTTATAT-
Sipaneopsis	CTCTATTCTC	TTAGAAATTG	AT-CTGGGCG	GA0---AATG	CCCT------	0------TTT	C-TTATCACA	AGTC----TT	ATGTTATAT-
Sphinctanthus	CTCTATTATC	TTAGAAATTG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Stachyarrhena	CTCGATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	1TTTCCTTTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Sukunia	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Tamilnadia	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTGTTT-
Tarenna	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Tocoyena	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Tricalysia	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	GA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATC----TT	GTGTTATTT-
Vangueria	CTCTATTCTC	TTAGAAATCG	AT-CTGGACG	AA0---AAAG	CCCT------	0------TTT	C-TTATCACA	AATG----TT	GTGTTATTT-

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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                           190        200        210        220        230        240        250        260        270
Psychotria          ATGATATACA ------TACA AATGAAACAT CCTTTAGCAA GAAATA-CCA TT-----TGA AT-----GAT TTACA-ATCT ATATAATT--
Cinchona            ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATA-------
Gonzalagunia        ATGGTATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAAAT--
Portlandia          ATGATATACA -TACAATACA AATGAA-CAT TTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAAAT--
Rondeletia          ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----TAT TTACA-ATCG ATATAAAT--
Aidia               ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Aleisanthia         ATGATAT--- ---------- -------TAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Alibertia           ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACTCA TTTGAATTGA AT-----GGT TTACA-ATCG ATATAACT--
Amphidasya          ATGATATACA ------TACA AATGAA-CAT CTTTGAGGAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCT ATATAATTTA
Bertiera            ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Borojoa             ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACTCA TT-----TGA ATTGAATGGT TTACA-ATCG ATATAACT--
Botryarrhena        ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Calochone           ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT---A-GGT TTACA-ATCG ATATAACT--
Calycophyllum       ATGATATACA ------TACA ACTGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Catunaregam         ATGATATACA ------TATA AATGA----- ------GCAA GAAATAACCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Ceriscoides         ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Coffea              ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Condaminea          ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATTG ATATAACT--
Cremaspora          ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Deccania            ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Dialypetalanthus    ATGATATACA ------TACA ACTGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Didymosalpynx       ATGATA--CA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTCCA-ATCG ATATAACT--
Duperrea            ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Euclinia            ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Fadogia             ATGATATA-- ---------- ----AA-CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-AT-- ----------
Ferdinandusa        ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Feretia             ATGATA--CA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Fernelia            ATGTTTATGA TATACATATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Gardenia            ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Genipa              ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Gleasonia           ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTAGA-ATCG ATATAACT--
Heinsia             ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATAG ATATAACT--
Hippotis            ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Ibetralia           ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Ixora               ATGATAT--- --------TA AA-----CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Kailarsenia         ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Keetia              ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Kutchubaea          ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Leptacina           ATGATATACA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Limnosipanea        ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCGA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Macrosphyra         ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Maguireothamnus     ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAG TAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Mussaenda           ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Ottoschmidtia       ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAAAT--
Oxyanthus           ATGATATACA -TATAAATTA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
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Pavetta                     ATGATA--CA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Pentagonia                  ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Platycarpum                 ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Polysphaeria                ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Posoqueria                  ACGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Pouchetia                   ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA ATG----GGT T-ACA-ATCG ATATAACT--
Pseudomussaenda             ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAATT--
Psilanthus                  ATGATATACA ------TATA AATGAA-CAT CTTTGATCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Psydrax                     ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Pyrostria                   ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Randia                      ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Retiniphyllum_concolor      ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum rhabdocalyx   ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum schomburgki   ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum maguirei      ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum_secundiflor   ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Rosenbergiodendron          ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Rothmania                   ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACAGTCCG ATATACCT--
Rutidea                     ATGATATACA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Schumaniophyton             ATGATATACA ----GTTTTA TATGATA-TA CATATAATGG AGCAGGACCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Scyphiphora                 ATGATATAAA ---------- -------CAT CTTTGAGCAA GAAATTCCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Sherbournia                 ATGATATACA ------TATA AATGA----T AAATGAGCAA GAAATACCCA TT-----TGA AT---A-G-T TTACA-ATCG ATATAACT--
Simira                      ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Sipanea_acinifolia          AGGATATACA ------GAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATCTAACT--
Sipanea_biflora             ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCA ATATAACT--
Sipanea_wilson-brownei      ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Sipaneopsis                 ATCATATACA TAGAAATGAA CATCTT-TAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Sphinctanthus               ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Stachyarrhena               ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Sukunia                     ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tamilnadia                  ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tarenna                     ATGATA--CA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tocoyena                    ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tricalysia                  ATGATATACA -ATACATATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Vangueria                   ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
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                        280        290        300        310        320        330        340        350        360
Psychotria        ---AC-TAAT -ACTGAAA-- CTCCCAAA-G TCCTCTTTTT TAAGATCCAA GTC-AAG-CA A-TTTCAGTA CCTAAAT-AA AACTTGGGAA
Cinchona          -------CAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Gonzalagunia      ---AT-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Portlandia        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTTCAGTA CCTAGAT-AA AACTTTGTAA
Rondeletia        ---AT-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Aidia             ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Aleisanthia       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Alibertia         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AG A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Amphidasya        ATTAC-TCAT -ACTGAAA-- CTTCCAAA-G TCCTCTTTTT T------GAG ATCCAAG-AA A-TTTCAGTA CCTAAAT-AA AACTTTTTAA
Bertiera          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Borojoa           ---AC-TCAT -ATTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Botryarrhena      ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Calochone         ---AC-TTAT TACTGAAA-- CTTACAAA-G TACTATTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Calycophyllum     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATACAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Catunaregam       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGATAAA GACTTTGTAA
Ceriscoides       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Coffea            ---AT-TCAT -ACTGAAA-- CTTACAAA-G TACTCTCTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Condaminea        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Cremaspora        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCTAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTATAA
Deccania          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Dialypetalanthus  ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Didymosalpynx     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Duperrea          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Euclinia          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Fadogia           ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACT------ ---------G ATCCAAG-AA A-TTCGAGTG CCTAGAT-AA AACTTTGTAA
Ferdinandusa      ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Feretia           ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Fernelia          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTC CCTAGAT-AA AACTTTGTAA
Gardenia          ---AC-TCAT -ACTGAAG-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Genipa            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Gleasonia         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Heinsia           ---AC-TCAT -ACTGAAA-- CTTCCAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGGAA
Hippotis          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Ibetralia         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG--A A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Ixora             ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Kailarsenia       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA ACCTTTGTAA
Keetia            ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACTATTTT- ---------- ---------- ---------- TCTAGAT-AA AACTTTGTAA
Kutchubaea        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Leptacina         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG A-CCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Limnosipanea      ---AC-TCAT -ACCGAAA-- CTTACAAA-G GACTCTGGGT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Macrosphyra       ---AC-TTAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Maguireothamnus   ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Mussaenda         ---AC-TCAT -ACTGAAA-- CTTCCAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTAGAA
Ottoschmidtia     ---AT-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
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Oxyanthus                   ---AC-TCAT -ACTGAA--- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Pavetta                     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Pentagonia                  ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Platycarpum                 ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Polysphaeria                ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Posoqueria                  ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Pouchetia                   ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Pseudomussaenda             ---AC-TCAT -ACTGAAA-- CTTCCAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTAGAA
Psilanthus                  ---AT-CCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Psydrax                     ---AC-TCAT -CCTGAAA-- CTTACAAA-G ---------- ---------- ---------- ---------- -CTAGAT-AA AACTTTGTAA
Pyrostria                   ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Randia                      ---AC-TCAT -ACTGAAA-- CTTACAAAAG TATTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Retiniphyllum_concolor      ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum rhabdocalyx   ---ACCTCAT -ACTGAAAAC CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum schomburgki   ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum maguirei      ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum_secundiflor   ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAA-AA ATTTTTATAA
Rosenbergiodendron          ---AT-TCAT -ACTGAAA-- CTTACAAAAG TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Rothmania                   ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Rutidea                     ---AC-TCAT -ACTGAAA-- CTGACAAA-G TACTCTTTTT T------AAG ACCCAAGAAA ATTTCTAGTA CCTAGAT-AA AACTTTGTCA
Schumaniophyton             ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Scyphiphora                 ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Sherbournia                 ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Simira                      ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Sipanea_acinifolia          ---AT-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AATTTTGTAA
Sipanea_biflora             ---AT-TCAT -ACTGAAA-- CTTACAAA-G TATTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AATTTTGTAA
Sipanea_wilson-brownei      ---AT-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AATTTTGTAA
Sipaneopsis                 ---AT-TCAG -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Sphinctanthus               ---AC-TCAT -ACTGAAA-- CTTACAAAAG TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Stachyarrhena               ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AATTTTGTAA
Sukunia                     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AG A-TTCTAGTA CCTAGAT-AA GACTTTGTAA
Tamilnadia                  ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA ACTAGAT-AA AACTTTGTAA
Tarenna                     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Tocoyena                    ---AC-TCAT -ACTGAAA-- CTTACAAAAG TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Tricalysia                  ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG A----AG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Vangueria                   ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACT------ ---------G ATCCAAG-CA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|.
                          370        380        390        400        410        420        430        440
Psychotria          TTCTACTTC- TTCTTTT--- ----AATTGA CACGGCTCCC A-TTTTCGAA TAAAATGA-G GATACT-ATG TTGCG-ACTG GTCGGG
Cinchona            TCCGCTTTCC TTCTTTT--- ----AATTGA CATAGACCTC A-TTTTCTAA GAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Gonzalagunia        TTCGCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Portlandia          TTTGCTTTCC TTCTTTT--- ----AATTGA CATGGATCTC A-TTTTCTAA TAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Rondeletia          TCCGCCTTCC TTCTTCT--- ----AATTGA CATAGACCCC -GTTTTCTAA TAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Aidia               TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CCTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Aleisanthia         TCCCCCTTCC TTCTTTTA-- ----AATTGA CAAAGCCCCA -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGT-ACTG GTCGGG
Alibertia           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Amphidasya          TCCCATTTCC TTCTTTT--- ----AATTGA CATAGACCGC A-TTTTCGAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Bertiera            TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Borojoa             TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Botryarrhena        TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTGCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TAGGG-ACTG GTCGGG
Calochone           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACT- ------
Calycophyllum       TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Catunaregam         TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Ceriscoides         TCCCCTTCCC TTCTTTT--- ----AATTGA CATAGACCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Coffea              TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Condaminea          TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTGTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Cremaspora          TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGGG-CTG GTCGGG
Deccania            TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Dialypetalanthus    TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Didymosalpynx       TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTA GTCGGG
Duperrea            TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Euclinia            TACCCTTTCC T--------- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Fadogia             TCCCCTTTCy TTCTTTT--- ----AATTGA CATAG-CCCA CTTTTTCTCA TAAAATGA-G TCTGGT-ACA TTGGG-CCTG GTCGGG
Ferdinandusa        TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Feretia             TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Fernelia            TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Gardenia            TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Genipa              TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Gleasonia           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGATCCC ATTTT-CT-- ---------- -------ACA TTGGG-ACTG GTCGGG
Heinsia             TCCCCTTCCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Hippotis            TCCACTTTGC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Ibetralia           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Ixora               TCCCCTTTCC TTCTTTT--- ----AATTGA CAAAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGT-ACTG GTCGGG
Kailarsenia         TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Keetia              TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCAC -TTTTTCTCA TAAAATGAGG GATGCT-ACA TTGGG-ACTG GGTGGG
Kutchubaea          TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Leptacina           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAACTCCC ATTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Limnosipanea        TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCT A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTCG--ACTG GTCGGG
Macrosphyra         TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Maguireothamnus     TCCCCTTTCC TTTTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Mussaenda           TTCCTTTCCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Ottoschmidtia       TTCGCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G TATGTT-ACA TTGGG-ACTG GTCGGG
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Oxyanthus                    TCCCCTTTCC TTCTTTTA-- TTTTAATTGA CATAGCCCCC ATTTTTCTCA TAAAATGA-G GATG------ -----GACTG GTCGGG
Pavetta                      TCCCCTTTCC TTCTTTT--- ----AATTGA CATAACTCCC ATTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Pentagonia                   TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Platycarpum                  TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGATCCC A-TTTTCTAA TAAAATGA-G GATACT-ACG TTGGG-ACTG GTCGGG
Polysphaeria                 TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCAC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Posoqueria                   TCTCCTTTCC TTCTTTT--- ----AATTGA CATAGATCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Pouchetia                    TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Pseudomussaenda              TCCCTTTCCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Psilanthus                   TCCCCTTTCC TGTTTTT--- ----AATTGA CATAGCCTCC C-TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Psydrax                      TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCAC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Pyrostria                    TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCAC TTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Randia                       TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Retiniphyllum_concolor       TCCCCTTACC TTCTTTT--- ----AATTGA CATAACCCCC C--TTTGTCA TAAAACGA-G AATGCT-ACA TTGGG-ACTG GGCGGG
Retiniphyllum rhabdocalyx    TCCCCTTACC TTCTTTT--- ----AATTGA CATAACCCCC C--TTTCTCA TAAAATGA-G AATGCT-ACA TTGGG-ACTG GTCGGG
Retiniphyllum schomburgki    TCCCCTTACC TTCTTTT--- ----AATTGA CATAACCCCC C--TTTCTCA TAAAATGA-G AATGCT-ACA TTGGG-ACTG GTCGGG
Retiniphyllum maguirei       TCCCCTTACC TTCTTTT--- ----AATTGA CATAACCCCC C--TTTCTCA TAAAATGA-G AATGCT-ACA TTGGG-ACTG GTCGGG
Retiniphyllum_secundiflor    TCCCCTTACC TTCTTTT--- ----AATTGA CATA-ACCCC C-CTTTCTCA TAAAATGA-G AATGCT-ACA TTGGG-ACTG GTCGGG
Rosenbergiodendron           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATTA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Rothmania                    TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGGGACTG GTCGGG
Rutidea                      TCCCCTTTCC TTCTTTT--- ----AATTGA CATAACTCCC ATTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Schumaniophyton              TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACCG GTCGGG
Scyphiphora                  TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC C-TTTTCTCA TAAAATGA-G GATGCT-GCA TTGGG-ACTG GTCGGG
Sherbournia                  TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCAGG
Simira                       TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Sipanea_acinifolia           TCCCCTTCCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Sipanea_biflora              TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Sipanea_wilson-brownei       TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Sipaneopsis                  TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GAGGCT-ACA TTGGG-ACTG GTCGGG
Sphinctanthus                TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Stachyarrhena                TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTGCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TAGGG-ACTG GTCGGG
Sukunia                      TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Tamilnadia                   TCCCCTTTCC TTCTTTTATC TTTTAATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Tarenna                      TCCCCTTTCC TTCTTTT--- ----AATTGA CATAACTCCC ATTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Tocoyena                     TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATTA-G GATGCT-ACA TTGAG-ACTG GTCGGG
Tricalysia                   TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC C-ATTTCTCA TAAAATGA-G GGATGCTACA TTGGGGACTG G-CGGG
Vangueria                    TCCCTTTTCC TTCTTTT--- ----AATTGA CATAGCCCAC -TTTTTCTCA TAAAATGA-G TATGCT-ACA TTGGGG-CTG GTCGGG
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Appendix c: Aligned rps16 sequences. Gaps are indicated by -. Informative gaps are coded as 0 and 1.

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                  ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                          10         20         30         40         50         60         70         80         90
Psychotria        AAATAAACTA TTTGACTCCC CAACTATTT- ATTTCT-ATA TCCCTCTTTT TGTTATAGGT -TCAA----- -AATTCCTTA T--CCATTCA
Cinchona          AAAAAGCCTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCTTCTTTT CATTAGCGGT -TCCA----- -AATTCCTTA G--CCATTCA
Gonzalagunia      ---------- -------CCC CGACTATTT- ----ATCCTA TCCTTCTTTT CGTTAGCGGT -TCAA----- -AATTCTTTA T--CTATTCA
Portlandia        -AAAAGCGTA TTTGACTCCC CAACGATTT- ----ATCCTA TCCTTCTTTT CGTTAGCGGT -TCAA----- -AATTCCTTA T--CCATTTG
Rondeletia        AAAAAGCCTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCTTCTTTT CGTTAGCGGT -TCAA----- -AATTCCTGA T--CCATCCA
Aidia             --AAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Aleisanthia       AAAAAGCATA TTTGA-CCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CATTAGCGGT -TAAA----- -AATACCTTA T--TCATTTA
Alibertia         AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Amphidasya        AAAAAGACTA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT TGTTAGAGGT -TCAA----- -AATTCCTTA T--CCATTCA
Bertiera          AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATT-A
Borojoa           -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Botryarrhena      AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCT-TT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Calochone         -AAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Calycophyllum     AAAAAGAATA TTTGACTCCC CAACTATTT- ----AGCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Catunaregam       AAAAAACATA TTGGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TTAA----- -AATACCTTA T--TCATTTA
Ceriscoides       -AAAAATATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Coffea            AAAAAACATA TTTGATCCCC C--------- ---------- -------TTT CGTTAGCG-- ---------- ------CTTA T--TCATTTA
Condaminea        AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Cremaspora        --AAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Deccania          -AAAAACATA TTGGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TTAA----- -AATACCTTA T--TCATTTA
Dialypetalanthus  AAAAAGCATA TTTGACTCCC TAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TTAA----- -AATCCCTTA T--TCATTCA
Didymosalpynx     ---------A TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCAGT -TCAA----- -AATACCTTA T--TCATTTA
Duperrea          AAAAAACATA TTGGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Euclinia          AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Fadogia           AAAAAGCGTA TTTGAACCTC CAACTATTT- ----ATCATA TCCCCCCTTT CATTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Ferdinandusa      AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAAG---- --ATCCCTTA T--TCATTCA
Feretia           AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Fernelia          --------TA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGGGGT -TCAA----- -AATACCTTA T--TCATTTA
Gardenia          AAAAAATATA TTTGATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Genipa            AAAAAATATA TTTGATCCCC CGACGATTT- ----ATCTTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Gleasonia         AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCCTA T--TCATTCA
Heinsia           AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT TGGTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Hippotis          AAAAAGCATA TTTGACTCCC CAACTATTT- ----ATCCTA TCCCTCTTTT CGTTAGCGGT -TCAA----- -AATCCCTTA T--TCATTCA
Ibetralia         -AAAAGCATA TTTAATCCCC CAACTATTT- ----ATCCTA TCCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Ixora             --------TA TTTGA-CCCC CAACTATTTT ATTTATCCTA TCCCCCTTTT CATTAGCGGT GTCAA----- -AATACCTTA T--TCATTTA
Kailarsenia       -AAAAATATA TTTGATCCCC CAACTATTT- ----ATCCTA TTCCC-TTTT CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Keetia            ---AAGCGT- TTTGACCCCC CAACTATTT- ----ATCCTA TCCCCCTTTT CATTAGCAGT -TCAA----- -AATACCTTA T--TCATTTA
Kutchubaea        AAAAAACATA TTTGATCCCC CGACTATTT- ----ATCCTA TCCCCTTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Leptacina         AAAAAACATA TTTGATCCCC CAACTATTT- ----ATCCTA TCTCCCTT-T CGTTAGCGGT -TCAA----- -AATACCTTA T--TCATTTA
Limnosipanea      AAAAAGCATA TTTGACTCCC CAACTAGAT- ---TATCCTA TCCCTCTTTT CGTTAACGGT -TCAA----- -AATCCCTTA T--TCATTCA
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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                           100        110        120        130        140        150        160        170        180
Psychotria          CTTTCTTCTC TTAGAA-TTG AT-CGGTGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA ---------- ----TTTAT-
Cinchona            CTCTATTCTC TTAGAAATCG AT-CTGGGCG GA0---AATG CCTT------ 0------TTT C-TTATCACA AGGC----TT GT--TATAT-
Gonzalagunia        CTCTATTCTC TTAGAAATCG AT-TTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GT--TATAT-
Portlandia          CTCTATTCTC TTAGAAATCG AT-CTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCATA AATC----TT GT--TATAT-
Rondeletia          CTCTATTCTC TTAGAAATAG AT-CTGGTCG TA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GT--TATAT-
Aidia               CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Aleisanthia         CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Alibertia           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Amphidasya          CTCTATTCTC TTAGAA-TCG AT-CTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA --TC------ ------TAT-
Bertiera            CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTAT-T-
Borojoa             CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Botryarrhena        CTCGATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Calochone           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Calycophyllum       CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Catunaregam         CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Ceriscoides         CTCTATTCTC TTAAAAATCG AT-CTGGACG GA0---AAAG CCCC------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Coffea              CTCTATTCTC TTAG----CG AT-CTGGACG GA0---AAAG CTCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Condaminea          CTCTATTCTC GTAGAAATCA AT-CTGGACA GA0---AATG CTCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Cremaspora          CTCTATTCTC TTAGAAATCA AT-CTGGACA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT CTGTTATTT-
Deccania            CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Dialypetalanthus    CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Didymosalpynx       CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Duperrea            CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Euclinia            CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TG TGGTTATTTT
Fadogia             CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG ACCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Ferdinandusa        CTCTATTCTC G--------G AT-CTGG-CG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Feretia             CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT CTGGTATTT-
Fernelia            CTCTATTCTC TTAGAAATCG AT-CTGGCCA GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT CTGTTATTT-
Gardenia            CTCTATTCTC TTAGAAATCA AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Genipa              CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCT------ 0------TTT -TTTATCACA AATC----TT GTGTTATTT-
Gleasonia           CTCTATTCCC TTAGAAATCG AT-CTGGACA GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Heinsia             CTCTATTCTC TTAGAAATAG AT-CTGGACG GA0---AATG CTCT------ 0------TTT C-TTATCACA AGTCAGTCTT GTGTTATGT-
Hippotis            CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Ibetralia           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCTTTTCCT 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Ixora               TTCTATTCTC TTAGAAAGAG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Kailarsenia         CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG C--T------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Keetia              CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Kutchubaea          CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCC------- 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Leptacina           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Limnosipanea        CTCCATTCTC TTAGAAATCG AT-CTGGACA GA1AATGATG ACCT------ 0------TTT C-TTATCACT AGTC----TT GTGTTATAT-
Macrosphyra         CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Maguireothamnus     CTCCATTCTC TTAGAAATCG AT-CTGGACA GA0---AGTG ACCT------ 0------TTT C-TTATCCCA AGTC----TT GTGTTATAT-
Mussaenda           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AATG ATCT------ 0------TTT C-TTATCACA AGTCAGTCTT GTGTTATAT-
Ottoschmidtia       CTCTATTCTC TTAGAAATCG AT-CTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC------ TTGTTATAT-
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Oxyanthus                    TTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Pavetta                      CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Pentagonia                   CTCTATTCTC GTAAAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Platycarpum                  CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Polysphaeria                 CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Posoqueria                   CTCTATTCTC TTAGAAATAG AT-CTGGACA GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Pouchetia                    CTCTATTCTC TTAGAAATCG AT-CTGGACA GA0---AAAG CCCTTT---- 0------TTT CTTTATCACA AATC----TT CTGGTTATTT
Pseudomussaenda              CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AATG ATCT------ 0------TTT C-TTATCATA AGTCAGTCTT GT-TTCTAT-
Psilanthus                   CTCTATTCTC TTAGA----- ----TGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Psydrax                      CTCTATTCTC TTAGAAATCG ATGCTGGACG AA0---AAAG CCCT------ 0------TTT CTTTATCACA AATC----TT GTGTTATTT-
Pyrostria                    CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Randia                       CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Retiniphyllum_concolor       CTCTATTCTC TTAGAGATCG AT-CTGGACG GA0---AAAG CCAC------ 0------TTT C-TTATCACA AATG----TT GTGTTATAT-
Retiniphyllum rhabdocalyx    CTCTATTCTC TTAGAGATCG GATCTGGACG GA0---AA-G CCAC------ 0------TTT C-TTATCACA AATG----TT GTGTTATAT-
Retiniphyllum schomburgki    CTCTATTCTC TTAGAGATCG AT-CTGGACG GA0---AAAG CCAC------ 0------TTT C-TTATCACA AATG----TT GTGTTATAT-
Retiniphyllum maguirei       CTCTATTCTC TTAGAGATCG AT-CTGGACG GA0---AAAG CCAC------ 0------TTT C-TTATCACA AATG----TT GTGTTATAT-
Retiniphyllum_secundiflor    CTCTATTCTC TTAGAGATCG AT-CTGGACG GA0---AAAG CCAC------ 0------TTT C-TTATCACA AATG----TT GTGTTATAT-
Rosenbergiodendron           CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCGCA AATC----TT GTGTTATTT-
Rothmania                    CTCTATTCTC TTAGAAATCA AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Rutidea                      CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Schumaniophyton              CTCTACTCTC TTAGAAATCG AT-CTGCACC GA0---AAAG ACCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Scyphiphora                  -TCTATTCTC TTAG----CG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Sherbournia                  TTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Simira                       CTCTATTCTC GTAGAAATCG AT-CTGGACG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT GTGTTATAT-
Sipanea_acinifolia           CTCTATTCTC TTAGCAATTG AT-CTGGACA GA1AAAAATG CCCT------ 0------TTT C-TTATCACA AGTT----TT GTGTTATAT-
Sipanea_biflora              CTCTATTCTC TTAGAAATTG AT-CTGGACA GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTT----TT GTGTTATAT-
Sipanea_wilson-brownei       CTCTATTCTC TTAGAAATTG AT-CTGGACA GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTT----TT GTGTTATAT-
Sipaneopsis                  CTCTATTCTC TTAGAAATTG AT-CTGGGCG GA0---AATG CCCT------ 0------TTT C-TTATCACA AGTC----TT ATGTTATAT-
Sphinctanthus                CTCTATTATC TTAGAAATTG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Stachyarrhena                CTCGATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 1TTTCCTTTT C-TTATCACA AATC----TT GTGTTATTT-
Sukunia                      CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Tamilnadia                   CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTGTTT-
Tarenna                      CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Tocoyena                     CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Tricalysia                   CTCTATTCTC TTAGAAATCG AT-CTGGACG GA0---AAAG CCCT------ 0------TTT C-TTATCACA AATC----TT GTGTTATTT-
Vangueria                    CTCTATTCTC TTAGAAATCG AT-CTGGACG AA0---AAAG CCCT------ 0------TTT C-TTATCACA AATG----TT GTGTTATTT-
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                               190        200        210        220        230        240        250        260        270
Psychotria                ATGATATACA ------TACA AATGAAACAT CCTTTAGCAA GAAATA-CCA TT-----TGA AT-----GAT TTACA-ATCT ATATAATT--
Cinchona                  ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATA-------
Gonzalagunia              ATGGTATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAAAT--
Portlandia                ATGATATACA -TACAATACA AATGAA-CAT TTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAAAT--
Rondeletia                ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----TAT TTACA-ATCG ATATAAAT--
Aidia                     ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Aleisanthia               ATGATAT--- ---------- -------TAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Alibertia                 ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACTCA TTTGAATTGA AT-----GGT TTACA-ATCG ATATAACT--
Amphidasya                ATGATATACA ------TACA AATGAA-CAT CTTTGAGGAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCT ATATAATTTA
Bertiera                  ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Borojoa                   ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACTCA TT-----TGA ATTGAATGGT TTACA-ATCG ATATAACT--
Botryarrhena              ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Calochone                 ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT---A-GGT TTACA-ATCG ATATAACT--
Calycophyllum             ATGATATACA ------TACA ACTGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Catunaregam               ATGATATACA ------TATA AATGA----- ------GCAA GAAATAACCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Ceriscoidea               ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Coffea                    ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Condaminea                ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATTG ATATAACT--
Cremaspora                ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Deccania                  ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Dialypetalanthus          ATGATATACA ------TACA ACTGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Didymosalpynx             ATGATA--CA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTCCA-ATCG ATATAACT--
Duperrea                  ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Euclinia                  ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Fadogia                   ATGATATA-- ---------- ----AA-CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-AT-- ----------
Ferdinandusa              ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Feretia                   ATGATA--CA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Fernelia                  ATGTTTATGA TATACATATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Gardenia                  ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Genipa                    ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Gleasonia                 ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTAGA-ATCG ATATAACT--
Heinsia                   ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATAG ATATAACT--
Hippotis                  ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Ibetralia                 ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Ixora                     ATGATAT--- --------TA AA-----CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Kailarsenia               ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Keetia                    ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Kutchubaea                ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Leptacina                 ATGATATACA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Limnosipanea              ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCGA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Macrosphyra               ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Maguireothamnus           ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAG TAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Mussaenda                 ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Ottoschmidtia             ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAAAT--
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Oxyanthus                    ATGATATACA -TATAAATTA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Pavetta                      ATGATA--CA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Pentagonia                   ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Platycarpum                  ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Polysphaeria                 ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Posoqueria                   ACGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Pouchetia                    ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA ATG----GGT T-ACA-ATCG ATATAACT--
Pseudomussaenda              ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAATT--
Psilanthus                   ATGATATACA ------TATA AATGAA-CAT CTTTGATCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Psydrax                      ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Pyrostria                    ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
Randia                       ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Retiniphyllum_concolor       ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum rhabdocalyx    ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum schomburgki    ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum maguirei       ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Retiniphyllum_secundiflor    ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA CT-----GAT TTACA-ATCG ATATAACT--
Rosenbergiodendron           ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Rothmania                    ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACAGTCCG ATATACCT--
Rutidea                      ATGATATACA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Schumaniophyton              ATGATATACA ----GTTTTA TATGATA-TA CATATAATGG AGCAGGACCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Scyphiphora                  ATGATATAAA ---------- -------CAT CTTTGAGCAA GAAATTCCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Sherbournia                  ATGATATACA ------TATA AATGA----T AAATGAGCAA GAAATACCCA TT-----TGA AT---A-G-T TTACA-ATCG ATATAACT--
Simira                       ATGATATACA ------TACA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Sipanea_acinifolia           AGGATATACA ------GAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATCTAACT--
Sipanea_biflora              ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCA ATATAACT--
Sipanea_wilson-brownei       ATGATATACA ------TAGA AATGAA-CAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Sipaneopsis                  ATCATATACA TAGAAATGAA CATCTT-TAT CTTTGAGCAA GAAATCCCCA TT-----TGA AT-----GAT TTACA-ATCG ATATAACT--
Sphinctanthus                ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Stachyarrhena                ATGATATACA ------TATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Sukunia                      ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tamilnadia                   ATGATATACA ------TATA AATGA----- ------GCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tarenna                      ATGATA--CA ------TAAA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tocoyena                     ATGATATACA ------TATA AATGA----- ------GCAA GAAATATCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Tricalysia                   ATGATATACA -ATACATATA AATGAA-CAT CTTTGAGCAA GAAATACCCA TT-----TGA AT-----GGT TTACA-ATCG ATATAACT--
Vangueria                    ATGATAT--- ---------A AA-----CAT CTTT-----A GAAATCCCCA TT-----TGA AT-----GCT TTACA-ATCG ATATAACT--
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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                           280        290        300        310        320        330        340        350        360
Psychotria          ---AC-TAAT -ACTGAAA-- CTCCCAAA-G TCCTCTTTTT TAAGATCCAA GTC-AAG-CA A-TTTCAGTA CCTAAAT-AA AACTTGGGAA
Cinchona            -------CAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Gonzalagunia        ---AT-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Portlandia          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTTCAGTA CCTAGAT-AA AACTTTGTAA
Rondeletia          ---AT-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Aidia               ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Aleisanthia         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Alibertia           ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AG A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Amphidasya          ATTAC-TCAT -ACTGAAA-- CTTCCAAA-G TCCTCTTTTT T------GAG ATCCAAG-AA A-TTTCAGTA CCTAAAT-AA AACTTTTTAA
Bertiera            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Borojoa             ---AC-TCAT -ATTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Botryarrhena        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Calochone           ---AC-TTAT TACTGAAA-- CTTACAAA-G TACTATTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Calycophyllum       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATACAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Catunaregam         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGATAAA GACTTTGTAA
Ceriscoides         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Coffea              ---AT-TCAT -ACTGAAA-- CTTACAAA-G TACTCTCTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Condaminea          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Cremaspora          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCTAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTATAA
Deccania            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Dialypetalanthus    ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Didymosalpynx       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Duperrea            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Euclinia            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Fadogia             ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACT------ ---------G ATCCAAG-AA A-TTCGAGTG CCTAGAT-AA AACTTTGTAA
Ferdinandusa        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Feretia             ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Fernelia            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTC CCTAGAT-AA AACTTTGTAA
Gardenia            ---AC-TCAT -ACTGAAG-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Genipa              ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Gleasonia           ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Heinsia             ---AC-TCAT -ACTGAAA-- CTTCCAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGGAA
Hippotis            ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Ibetralia           ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG--A A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Ixora               ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Kailarsenia         ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA ACCTTTGTAA
Keetia              ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACTATTTT- ---------- ---------- ---------- TCTAGAT-AA AACTTTGTAA
Kutchubaea          ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Leptacina           ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG A-CCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Limnosipanea        ---AC-TCAT -ACCGAAA-- CTTACAAA-G GACTCTGGGT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Macrosphyra         ---AC-TTAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Maguireothamnus     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Mussaenda           ---AC-TCAT -ACTGAAA-- CTTCCAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTAGAA
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Ottoschmidtia                 ---AT-TCAT -ACTGAAA-- CTTACAAA-G TCCTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Oxyanthus                     ---AC-TCAT -ACTGAA--- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Pavetta                       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Pentagonia                    ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Platycarpum                   ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Polysphaeria                  ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Posoqueria                    ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Pouchetia                     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Pseudomussaenda               ---AC-TCAT -ACTGAAA-- CTTCCAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA AACTTTAGAA
Psilanthus                    ---AT-CCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Psydrax                       ---AC-TCAT -CCTGAAA-- CTTACAAA-G ---------- ---------- ---------- ---------- -CTAGAT-AA AACTTTGTAA
Pyrostria                     ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Randia                        ---AC-TCAT -ACTGAAA-- CTTACAAAAG TATTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Retiniphyllum_concolor        ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum rhabdocalyx     ---ACCTCAT -ACTGAAAAC CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum schomburgki     ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum maguirei        ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAT-AA ATTTTTATAA
Retiniphyllum_secundiflor     ---AC-TCAT -ACTGAAA-- CTTATAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCAGTA CCTAGAA-AA ATTTTTATAA
Rosenbergiodendron            ---AT-TCAT -ACTGAAA-- CTTACAAAAG TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Rothmania                     ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Rutidea                       ---AC-TCAT -ACTGAAA-- CTGACAAA-G TACTCTTTTT T------AAG ACCCAAGAAA ATTTCTAGTA CCTAGAT-AA AACTTTGTCA
Schumaniophyton               ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Scyphiphora                   ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Sherbournia                   ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Simira                        ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCCACTA CCTAGAT-AA AACTTTGTAA
Sipanea_acinifolia            ---AT-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AATTTTGTAA
Sipanea_biflora               ---AT-TCAT -ACTGAAA-- CTTACAAA-G TATTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AATTTTGTAA
Sipanea_wilson-brownei        ---AT-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AATTTTGTAA
Sipaneopsis                   ---AT-TCAG -ACTGAAA-- CTTACAAA-G TACTCTTGGT T------AAG ATCCAAG-AG A-TTCCAGTA CCTAGAT-AA AACTTTGTAA
Sphinctanthus                 ---AC-TCAT -ACTGAAA-- CTTACAAAAG TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Stachyarrhena                 ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT TAAGATTAAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AATTTTGTAA
Sukunia                       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AG A-TTCTAGTA CCTAGAT-AA GACTTTGTAA
Tamilnadia                    ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA ACTAGAT-AA AACTTTGTAA
Tarenna                       ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Tocoyena                      ---AC-TCAT -ACTGAAA-- CTTACAAAAG TACTCTTTTT T------AAG ATCCAAG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Tricalysia                    ---AC-TCAT -ACTGAAA-- CTTACAAA-G TACTCTTTTT T------AAG A----AG-AA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
Vangueria                     ---AC-TCAT -CCTGAAA-- CTTACAAA-G TACT------ ---------G ATCCAAG-CA A-TTCTAGTA CCTAGAT-AA AACTTTGTAA
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                   ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|.
                         370        380        390        400        410        420        430        440
Psychotria         TTCTACTTC- TTCTTTT--- ----AATTGA CACGGCTCCC A-TTTTCGAA TAAAATGA-G GATACT-ATG TTGCG-ACTG GTCGGG
Cinchona           TCCGCTTTCC TTCTTTT--- ----AATTGA CATAGACCTC A-TTTTCTAA GAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Gonzalagunia       TTCGCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Portlandia         TTTGCTTTCC TTCTTTT--- ----AATTGA CATGGATCTC A-TTTTCTAA TAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Rondeletia         TCCGCCTTCC TTCTTCT--- ----AATTGA CATAGACCCC -GTTTTCTAA TAAAATGA-G GATGTT-ACA TTGGG-ACTG GTCGGG
Aidia              TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CCTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Aleisanthia        TCCCCCTTCC TTCTTTTA-- ----AATTGA CAAAGCCCCA -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGT-ACTG GTCGGG
Alibertia          TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Amphidasya         TCCCATTTCC TTCTTTT--- ----AATTGA CATAGACCGC A-TTTTCGAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Bertiera           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Borojoa            TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Botryarrhena       TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTGCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TAGGG-ACTG GTCGGG
Calochone          TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACT- ------
Calycophyllum      TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Catunaregam        TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Ceriscoides        TCCCCTTCCC TTCTTTT--- ----AATTGA CATAGACCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Coffea             TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Condaminea         TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTGTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Cremaspora         TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGGG-CTG GTCGGG
Deccania           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Dialypetalanthus   TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Didymosalpynx      TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTA GTCGGG
Duperrea           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Euclinia           TACCCTTTCC T--------- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Fadogia            TCCCCTTTCy TTCTTTT--- ----AATTGA CATAG-CCCA CTTTTTCTCA TAAAATGA-G TCTGGT-ACA TTGGG-CCTG GTCGGG
Ferdinandusa       TCCACTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Feretia            TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Fernelia           TTCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC --TTTTCTCA TAAAATGA-A GATGCT-ACA TTGGG-ACTG GTCGGG
Gardenia           TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Genipa             TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Gleasonia          TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGATCCC ATTTT-CT-- ---------- -------ACA TTGGG-ACTG GTCGGG
Heinsia            TCCCCTTCCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Hippotis           TCCACTTTGC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Ibetralia          TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Ixora              TCCCCTTTCC TTCTTTT--- ----AATTGA CAAAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGT-ACTG GTCGGG
Kailarsenia        TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Keetia             TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCAC -TTTTTCTCA TAAAATGAGG GATGCT-ACA TTGGG-ACTG GGTGGG
Kutchubaea         TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGTCCCC CTTTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Leptacina          TCCCCTTTCC TTCTTTT--- ----AATTGA CATAACTCCC ATTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Limnosipanea       TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGACCCT A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTCG--ACTG GTCGGG
Macrosphyra        TCCCCTTTCC TTCTTTT--- ----AATTGA CATAGCCCCC -TTTTTCTCA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Maguireothamnus    TCCCCTTTCC TTTTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G GATGCT-ACA TTGGG-ACTG GTCGGG
Mussaenda          TTCCTTTCCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTCA TAAAATGA-G GATGCT-ACG TTGGG-ACTG GTCGGG
Ottoschmidtia      TTCGCTTTCC TTCTTTT--- ----AATTGA CATAGACCCC A-TTTTCTAA TAAAATGA-G TATGTT-ACA TTGGG-ACTG GTCGGG
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Oxyanthus	TCCCCTTTCC	TTCTTTTA--	TTTTAATTGA	CATAGCCCCC	ATTTTTCTCA	TAAAATGA-G	GATG------	-----GACTG	GTCGGG
Pavetta	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAACTCCC	ATTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Pentagonia	TCCACTTTCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTAA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Platycarpum	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGATCCC	A-TTTTCTAA	TAAAATGA-G	GATACT-ACG	TTGGG-ACTG	GTCGGG
Polysphaeria	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCAC	-TTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Posoqueria	TCTCCTTTCC	TTCTTTT---	----AATTGA	CATAGATCCC	A-TTTTCTAA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Pouchetia	TTCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	--TTTTCTCA	TAAAATGA-A	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Pseudomussaenda	TCCCTTTCCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTCA	TAAAATGA-G	GATGCT-ACG	TTGGG-ACTG	GTCGGG
Psilanthus	TCCCCTTTCC	TGTTTTT---	----AATTGA	CATAGCCTCC	C-TTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Psydrax	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCAC	-TTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Pyrostria	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCAC	TTTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Randia	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	-TTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Retiniphyllum_concolor	TCCCCTTACC	TTCTTTT---	----AATTGA	CATAACCCCC	C--TTTGTCA	TAAAACGA-G	AATGCT-ACA	TTGGG-ACTG	GGCGGG
Retiniphyllum rhabdocalyx	TCCCCTTACC	TTCTTTT---	----AATTGA	CATAACCCCC	C--TTTCTCA	TAAAATGA-G	AATGCT-ACA	TTGGG-ACTG	GTCGGG
Retiniphyllum schomburgki	TCCCCTTACC	TTCTTTT---	----AATTGA	CATAACCCCC	C--TTTCTCA	TAAAATGA-G	AATGCT-ACA	TTGGG-ACTG	GTCGGG
Retiniphyllum maguirei	TCCCCTTACC	TTCTTTT---	----AATTGA	CATAACCCCC	C--TTTCTCA	TAAAATGA-G	AATGCT-ACA	TTGGG-ACTG	GTCGGG
Retiniphyllum_secundiflor	TCCCCTTACC	TTCTTTT---	----AATTGA	CATA-ACCCC	C-CTTTCTCA	TAAAATGA-G	AATGCT-ACA	TTGGG-ACTG	GTCGGG
Rosenbergiodendron	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	-TTTTTCTCA	TAAAATTA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Rothmania	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	CTTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGGGACTG	GTCGGG
Rutidea	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAACTCCC	ATTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Schumaniophyton	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	-TTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACCG	GTCGGG
Scyphiphora	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	C-TTTTCTCA	TAAAATGA-G	GATGCT-GCA	TTGGG-ACTG	GTCGGG
Sherbournia	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	CTTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCAGG
Simira	TCCACTTTCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTAA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Sipanea_acinifolia	TCCCCTTCCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTAA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Sipanea_biflora	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTAA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Sipanea_wilson-brownei	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTAA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Sipaneopsis	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGACCCC	A-TTTTCTAA	TAAAATGA-G	GAGGCT-ACA	TTGGG-ACTG	GTCGGG
Sphinctanthus	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	-TTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Stachyarrhena	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGTGCCC	CTTTTTCTCA	TAAAATGA-G	GATGCT-ACG	TAGGG-ACTG	GTCGGG
Sukunia	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	CTTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Tamilnadia	TCCCCTTTCC	TTCTTTTATC	TTTTAATTGA	CATAGCCCCC	CTTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Tarenna	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAACTCCC	ATTTTTCTCA	TAAAATGA-G	GATGCT-ACA	TTGGG-ACTG	GTCGGG
Tocoyena	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	-TTTTTCTCA	TAAAATTA-G	GATGCT-ACA	TTGAG-ACTG	GTCGGG
Tricalysia	TCCCCTTTCC	TTCTTTT---	----AATTGA	CATAGCCCCC	C-ATTTCTCA	TAAAATGA-G	GGATGCTACA	TTGGGGACTG	G-CGGG
Vangueria	TCCCTTTTCC	TTCTTTT---	----AATTGA	CATAGCCCAC	-TTTTTCTCA	TAAAATGA-G	TATGCT-ACA	TTGGGG-CTG	GTCGGG

Appendix D: Aligned ITS sequences. Gaps are indicated by -. Informative gaps are coded as 0 and 1 at the end of the alignment.

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                ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                        10         20         30         40         50         60         70         80         90
Ixora           aaagacagac gaccgcgaac t-cgtg-taa ctgccgggcg tccgggaacg gg-cggggtg acttgaccgt ccctcgctcc ttccctggc-
R._chloranthum  -aa-g-agac gactgtgaac tt-gtgctaa aact-gggcc cttgggttt- ggacggaaa- accttcctgt cttccc---- ---acgggct
R._concolor     gaa-gtagac gactgtgaac tt-gtgctaa aact-gggcc cttgggttt- ggacggaaa- accttcctgt cttccc---- ---acgggct
R._discolor     aaa-gcagac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttcctat tttccc---- ---acgggct
R._laxiflorum   aagagcagac gactgtgaac t-cgtgctaa aattt-ggcc cttgggttt- ggacgggaa- -ccttcctat cttccc---- ---atgggct
R._maguirei     aaga-cagac gactgtgaac ttcgtgctaa aattc-ggcc cttgggttt- ggacgggaa- -cctttctat cttccc---- ---atgggct
R._parvifolium  aaa-g-agac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttcctat cttccc---- ---atgggct
R._pilosum      aaa-g-aaac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttccaat cttccc---- ---atgggct
R._rhabdocalyx  aaa-g-agac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttcctat cttccc---- ---acgggct
R._scabrum      aaa-g-agac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttcctat cttccc---- ----tgggct
R._schomburgkii -aa-g-agac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttcctat cttccc---- ---acgggct
R._secundifloru aaa-tcgtat gactgtgaac tt-gtgttaa aact-gggcc cttgggtttt ggacgggaa- accttcctat cttccc---- ---acgggct
R._truncatum    aaa-g-agac gactgtgaac t-cgtgctaa aattc-ggcc cttgggttt- ggacgggaa- accttcctat cttccc---- ---acgggct
                ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                       100        110        120        130        140        150        160        170        180
Ixora           gct-ccccg- tgcgctcgtc gcacggacga a-caactcaa ccccggcgcg gaaagcgcca aggaaaactt caaaatgatc gctcgctccc
R._chloranthum  gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa tcccggcgtg aaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._concolor     gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa tcccggcgcg aaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._discolor     gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa tcccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._laxiflorum   gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa acccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._maguirei     gcttgttcgc ttcgcctgtc gt-gcggaca atcaactcaa ccccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._parvifolium  gcttgttcgc t-cgcccgtc gt-gcggaca aacaactcaa tcccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._pilosum      gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa tcccggcgcg aaaagcgcca aggaaaact- caacatgatc gctcagcccc
R._rhabdocalyx  gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa tcccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._scabrum      gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa acccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._schomburgkii acttgttcgc t-cgcctgtc gt-gcggaca atcaactcaa tcccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
R._secundifloru gcttg-tctg tacgcccgtc gt-gcggaca accaactcaa tcccggcgcg gaaagcgcca aggaatact- aaaaatgatc gctcagcccc
R._truncatum    gcttgttcgc t-cgcccgtc gt-gcggaca atcaactcaa tcccggcgcg gaaagcgcca aggaaaact- caaaatgatc gctcagcccc
                ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                       190        200        210        220        230        240        250        260        270
Ixora           cctttgaccc cgttcgcggt gcgcaacggg ggatgccgcg gcgtctgtcg taaccaaaac gactctcggc aacggatatc tcggctctcg
R._chloranthum  cggtcgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._concolor     tggtcg-tcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtca taaacttaac gactctcggc aacggatatc tcggctctcg
R._discolor     tggccgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._laxiflorum   tggccgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._maguirei     tggccg-tcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._parvifolium  tggctgctcc cgttcgcggt g-gcggttgg ggatgttgtg gtgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._pilosum      tggccgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._rhabdocalyx  tgaccgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._scabrum      tggccgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._schomburgkii tagccgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._secundifloru tagtcgctcc cgttcgcggt gc-cggttgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
R._truncatum    tggtcgctcc cgttcgcggt gc-cggctgg ggatgttgtg gcgtttgtcg taaacttaac gactctcggc aacggatatc tcggctctcg
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                  ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                         280        290        300        310        320        330        340        350        360
Ixora             catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgcgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._chloranthum    catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._concolor       catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._discolor       catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._laxiflorum     catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._maguirei       catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._parvifolium    catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._pilosum        catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._rhabdocalyx    catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._scabrum        catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._schomburgkii   catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._secundifloru   catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
R._truncatum      catcgatgaa gaacgtagcg aaatgcgata cttggtgtga attgcagaat cccgtgaacc atcgagtctt tgaacgcaag ttgcgcccga
                  ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                         370        380        390        400        410        420        430        440        450
Ixora             agccattagg ccgagggcac gtctgcctgg gcgtcacgca tcgcgtcgcc accccccttc ttgggggg-c ggcggagatt ggcttcccgt
R._chloranthum    agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-tac cttttggggt ggcggaaaat ggcctcccgt
R._concolor       agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-tac ctgtg-gggt ggcggaaaat ggcctcccgt
R._discolor       agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc acaccc-taa ctttg-gtgt ggcggaaaat ggcctcccgt
R._laxiflorum     agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-tac ctttg-gggt ggcggaaaat ggcctcccgt
R._maguirei       agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-acc ctttg-gggt ggcggaaaat ggcctcccgt
R._parvifolium    agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc acaccc-tac cttgg-gggt ggcggaaaat ggcctcccgt
R._pilosum        agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-tac ctttg-gggt ggcggaaatt ggcctcccgt
R._rhabdocalyx    agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc acaccc-tac ctctg--tgt ggcggaaaat ggcctcccgt
R._scabrum        agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-tat ctttg-gggt ggcggaaaat ggcctcccgt
R._schomburgkii   agccattagg ctgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc acaccc-act ctttg-gtgt ggcggaaaat ggcctcccgt
R._secundifloru   agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc accccc-tac ctttg-gggt ggcggaaaat ggcctcccgt
R._truncatum      agccattagg ccgagggcac gtctgcctgg gcgtcacgca ttgtgtcgcc acaccc-tac ctttg-gtgt ggcggaaaat ggcctcccgt
                  ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                         460        470        480        490        500        510        520        530        540
Ixora             gcccctaggc gcggccggcc taaatgcgag tcctcggcga gggacgtcac gactagtggt ggttgaactc ctcaactcga gtccttgttc
R._chloranthum    gtcccgtggc gtggctggcc taaatgtgag tccttggcga gggacgtcac gatcagtggt ggttgaatgt ctcaacttga gtccttgt-c
R._concolor       gtcccgtggc gtggctggcc taaatgtgag tccttggcga gggacgtcac gattagtggt ggttgaatgt ctcaacttga gtccttgt-c
R._discolor       gtcccgtggc gtggctggcc taaatgcgag tccttggcaa gggacgtcac gatcagtggt ggttgaatgt ctcaacttga gtccttgt-c
R._laxiflorum     gtcccgtggc gtggctggcc taaatgtgag tccttggcaa gggacgtcac gatcaatggt ggttgaatgt ctcaactcga gtccttgt-c
R._maguirei       gtcccgtggc gtggctggcc taaatgtgag tccttggcaa gggacgtcac gatcaatggt ggttgaatgt ctcaactcga gtccttgt-c
R._parvifolium    gtcccgtggc gtggctggcc taaatgcgag tccttggcaa gggacgtcac gattagtggt ggttgaatgt ctcaacttga gtccttgt-c
R._pilosum        gtcccgtggc gtggctggcc taaatgtgag tccttggcat gggacgtcac gatcagtggt ggttgaatgt ctcaactcga gtccttgt-c
R._rhabdocalyx    gtcccgtggc gtggctggcc taaatgcgag tccttggcaa gggacgtcac gatcagtggt ggttgaatgt ctcaacttga gtccttgt-c
R._scabrum        gtcccgtggc gtggctggcc taaatgtgag tccttggcaa gggacgtcac gatcagtggt ggttgaatgt ctcaacttga gtccttgt-c
R._schomburgkii   gtcccgtggc gtggctggcc taaatgcgag tccttggcaa gggacgtcac gatcagtggt ggttgaatgt ctcaactcga gtccttgt-c
R._secundifloru   gtcccttggc gcggctggcc taaatgtgag tccttggcga gggacgtcac gattagtggt ggttgaatgt ctcaactcga gtccttgt-c
R._truncatum      gtcccgtggc gtggctggcc taaatgcgag tccttggcaa gggacgtcac gatcagtggt ggttgaatgt ctcaacttga gtccttgt-c
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                    ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....| ....|....|
                            550        560        570        580        590        600        610        620        630
Ixora               gtgacggcga accccgtcgt aaatcgcg-- ctccaacgac cctca????? ?????????? ?????????? ?????????? ?????00100
R._chloranthum      gtgccggcaa tcctcctgcc aattctcggc ctccatcgac cctcat???? ?????????? ?????????? ?????????? ?????11011
R._concolor         gtgccggcaa tcctcctgcc aattctcggc ctccattgac cctcattgcc catgtggcct cgatcgcgac cccaagtcag gcg--10011
R._discolor         gtgtcggcat tcctcctgcc aaatctcggc ctccatcgac cctcattgcc catgtggcct cgatcgcgac cccaggtcag gcggg10100
R._laxiflorum       gtgccggcaa tcctcctgcc aattctcggc ctccaacgac cctcattgcc catgtggcct cgatcgcgac cccaggtcag gcgg-00100
R._maguirei         gtgccggcaa tcctcctgcc aaatctcggc ctccatcgac cctcattgcc catgtggcct cgatcgcgac cccag-tcag gcggg00000
R._parvifolium      gtgtcggcaa tcctcctgcc aaatcttggc ctctattgac cctcattgcc catgtggcct cgatcgcgac cccaggtcag gcggg11100
R._pilosum          gtgccggcaa tcctcctgcc aattcttggc ctccatcgac cctcattgcc catgcggcct cgatcgcgac cccaggtcag gcggg11100
R._rhabdocalyx      gtgtcggcaa tcctcctgcc aaatctcggc ctccatcgac cctcattgcc catgtggcct cgatcgcgac cccaggtcag gcggg11100
R._scabrum          gtgccggcaa tccccctgcc aattcttggc ctccatcgac cctcattgcc catgtggcct cgatcgcgac cccaggtcag gcgg-11100
R._schomburgkii     gtgtcggcaa tcctcctgcc aaatctcggc ctccatcgac cctcattgcc catgtggcct cgatcgcgac cccag-tcag g----11100
R._secundifloru     gtgccggcaa tcctcgttcc aattctcggg ctccatcgac cctcattgcc cgtgcggcct cgatcgcgac cccaggtcag gcggg10011
R._truncatum        gtgtcggcaa tcctcctgcc aaatctcggc ctccatcgac cctcattgcc catgtggcct cgatcgcgac cccaggtcag gcggg11100

                    ....|

Ixora               00000
R._chloranthum      01011
R._concolor         01011
R._discolor         11011
R._laxiflorum       11111
R._maguirei         11101
R._parvifolium      11010
R._pilosum          11011
R._rhabdocalyx      11011
R._scabrum          11011
R._schomburgkii     11011
R._secundifloru     00001
R._truncatum        11011
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