
SYSTEMATICS AND EVOLUTION OF THE GENUS *PETREA* (VERBENACEAE)¹

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ABSTRACT

Fourteen of the 35 previously accepted species of *Petrea* L. (Verbenaceae) are accepted in the present revision, three known only as fossils. Morphological, anatomical, and ecological characteristics of the species of *Petrea* are presented, along with descriptions, illustrations, and distribution maps. A cladistic analysis of the tribe Petreeae Briq., using *Citharexylum* L. and *Duranta* L. for outgroup comparison, revealed that *Petrea* is most closely related to *Xolocotzia* Miranda. *Xolocotzia* was then used as an outgroup to polarize the character states within *Petrea*, resulting in a cladogram with a consistency index of 0.74 and a retention index of 0.86, after three rounds of successive weighting.

RESUMEN

El número de aceptadas especies en el género *Petrea* L. (Verbenaceae) fue reducido de 35 a 14; tres son sólo conocidas de fósiles. Características morfológicas, anatómicas, y ecológicas de las especies de *Petrea* son presentadas, junto con descripciones, ilustraciones, y mapas de distribuciones. En el análisis cladístico de la tribu Petreeae Briq., se usó como grupo externo *Citharexylum* L. y *Duranta* L.; este análisis reveló que *Xolocotzia* Miranda es el más cercano evolutivamente al género *Petrea*. *Xolocotzia* fue usado como grupo externo para polarizar el estado de los caracteres dentro de *Petrea*, resultando un cladograma con un índice de consistencia de 0.74 y un índice de retención de 0.86, después de tres corridas de revalorización de los caracteres.

Petrea L. is a poorly known genus of the Verbenaceae. The most recent taxonomic treatment was written by Moldenke (1938). This monograph has long been outdated, making identification of the species difficult. A considerable number of discrepancies have been found between the characters used in the keys and those given in the individual descriptions of the species. Moreover, additional

collections and new species described since 1938 have rendered the keys obsolete.

Moldenke (1938) included 29 species in *Petrea*, and six additional species were described later, one as a preliminary part of the present study (Rueda, 1992). *Petrea*, as interpreted here, contains 14 species, three of which are known only from fossils.

The extant species are exclusively neotropical,

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growing in diverse habitats such as riparian forests and savannas and on soil types such as white sand and limestone. The species range from southern Mexico through Central America and the West Indies to Bolivia, Paraguay, and Brazil, being most diverse and concentrated in northern Brazil and the Guianas. Fossils are known from the former Czechoslovakia, Colorado, and California. One species is widely cultivated in warm and temperate regions of the world.

Petrea possesses three distinctive features: usually asperous leaves, an enlarged persistent calyx that provides wings for wind dispersal or flotation for water dispersal, and a calycinal crest that protects the corolla in prefloration and protects the ovary after the corolla falls. A cladistic assessment of both inter- and intrageneric relationships was made using data on gross morphology, anatomy, and ecology. While many characters in *Petrea* are unique to the genus, and thus useful systematically only within the genus, the polarity of others can be ascertained by using the monotypic Mesoamerican genus *Xolocotzia* as an outgroup. *Petrea*, as a genus, is cladistically defined by the presence of a calycinal crest.

HISTORY OF THE GENUS

The first known reference to a plant belonging to *Petrea* was in 1736 when Philip Miller gave Linnaeus unpublished Houstoun notes entitled *Houstounia Genera Plantarum Americanarum Nova Communicata* (Stafleu & Cowan, 1979), in which was included the name *Petrea*. This name was used by Houstoun to accommodate the single species *P. volubilis* L. He named the genus after Robert James Petre, a famous English collector of living plants (Moldenke, 1938). The name was first published by Linnaeus in his *Genera Plantarum* (1737), and *Petrea volubilis* appeared in his *Species Plantarum* (Linnaeus, 1753). The material of this species came from a cultivated plant in Europe which had been brought from Veracruz, Mexico.

Petrea is a distinctive genus in the Verbenaceae and its delimitation has never been a problem. Indeed, Agardh (1858) placed *Petrea* in its own family, but other authors have uniformly included it in Verbenaceae, although its placement within the family has been debated. Schauer (1847) placed it in his seventh subtribe, the monogeneric Petreae, in the tribe Verbeneae Dumort. Bentham & Hooker (1876) placed it in the tribe Verbeneae along with such diverse genera as *Baillonia* Bocq., *Casselia* Nees & Mart., *Citharexylum* L., *Duranta* L., *Ghania* Schreber, and *Verbena* L. For Briquet (1895) the tribe Petreeae was part of the subfamily Ver-

benoideae and comprised two genera, *Casselia* Nees & Mart. and *Petrea* L. Junnel (1934), in one of the most recent studies of the phylogeny of the family, reverted to Schauer's original system and treated *Petrea* as constituting a separate subtribe in the tribe Verbeneae.

After Linnaeus's (1753) publication of the genus, along with its first species, nothing was published about *Petrea* for more than 60 years. In the nineteenth century, however, new species were described by Humboldt, Bonpland & Kunth (1818) and Schauer (1847). Pittier (1925) described an additional new species. In 1938, Moldenke published the first modern monograph of the genus, including several new species. Unfortunately, his study was based solely on herbarium material, and many of the species he described have proven to be variants due to cultivation or environmental factors.

Since Moldenke's (1938) monograph, taxonomic work on *Petrea* has consisted entirely of local floristic treatments (MacBride, 1960; Gibson, 1970; Moldenke, 1973) and isolated publications of new species, mainly by Moldenke. The last new species published before this study was *P. sulphurea* Jansen-Jacobs, in the treatment of the Verbenaceae of French Guiana by Jansen-Jacobs (1988).

MORPHOLOGY

The species included in *Petrea* share unique characteristics (e.g., calycinal crest, winged calyx), which have made the phylogenetic placement of the genus in the family difficult. In the discussion of morphological characteristics of *Petrea* given below, the degree of variation for each character is presented, as well as an evaluation of the importance of each character in the taxonomy of the genus.

HABIT

All *Petrea* species are woody, ranging from lianas and shrubs to trees. The habit in *Petrea* seems to be very plastic, and individuals of the same species can be a liana, shrub, or tree as in other scandent Verbenaceae. Putz (1982) found that *Aegiphila cephalophora* Standl. grows as a liana in the forest but as a small shrubby tree in the open. The ability of the species of the genus to reproduce vegetatively by sprouting from stumps was confirmed by field observations.

ROOTS

The root system of *Petrea* species consists of a radiating array of shallow white roots, with an

abundance of periderm that falls off easily. Excluding two collections (*Croat 9432* and *Hammel 1868*) from Panama that report *Petrea* as an epiphyte, all the species of *Petrea* have been found to be rooted in the ground. Stems of *Petrea* root easily; stems that are forced to the ground during a treefall root and give rise to new shoots that may later become independent individuals.

STEMS

The stems of *Petrea* species are mostly slender, whitish, grayish, or brownish in color, with conspicuous lenticels, and may be glabrous or asperous. A cross section of the stem of *Petrea* shows four or five thick rays going to each of the furrows, and this can be used to identify the genus vegetatively. However, in many species the stem is cylindrical and the rays are equal in thickness, making it more difficult to distinguish the genus. Stems of the tree species tend to be irregular and oval in shape. In lianas the stem is sometimes four-angled and/or furrowed. According to Carlquist (1988), *Petrea* has only a single cambium, situated in the normal position between the xylem and the phloem; furrowed stems are formed because the cambium is not equally active around the whole periphery of the axis. In its simplest form, the cambium irregularly produces axes that are oval or elliptic instead of circular, e.g., in *Petrea pubescens* Turcz. In more extreme forms, the stem can be strongly furrowed, as sometimes occurs in *Petrea volubilis* L.

PUBESCENCE

Nine distinct hair types (see Table 1) were found in *Petrea* and *Xolocotzia*:

(1) Conic hairs are the most abundant type of hairs on the surfaces of the leaves. These hairs are called silicified conical papillae by Metcalfe & Chalk (1972) and have only been found in *Petrea* and *Xolocotzia*. They are short, broad-based, conical-tipped, unicellular, silicified and make the leaf rough to the touch. These hairs are an outgrowth of the epidermis, where they are found in shallow depressions (Fig. 1A, B).

(2) Bulbous hairs (Moldenke, 1938) are found on upper leaf surfaces and sometimes on bracts

TABLE 1. Types of hairs and plant parts and where they occur in *Petrea* (P) and *Xolocotzia* (X).

Hair type	Peti- ole	Leaf	Bract	Calyx	Co- rolla	Pedi- cel
Bulbous	PX	PX	PX			
Clavate						
glandular	P	P	P	P	P	P
Ciliate	P	P	P			P
Conic		PX				
Falcate	X					
Lageniform				PX		
Ribbon					PX	
Subsessile						
glandular		PX				
Warty					P	

and petioles of *Petrea* and *Xolocotzia*. These hairs are bulbous at the base (Fig. 1C, D). They are rarely found in older leaves, apparently because they break and fall off with age.

(3) Ciliate hairs (sensu Hewson, 1988) are more common than bulbous on the different structures of *Petrea* and *Xolocotzia*. These hairs grow at an angle of 45° with the surface on which they are found.

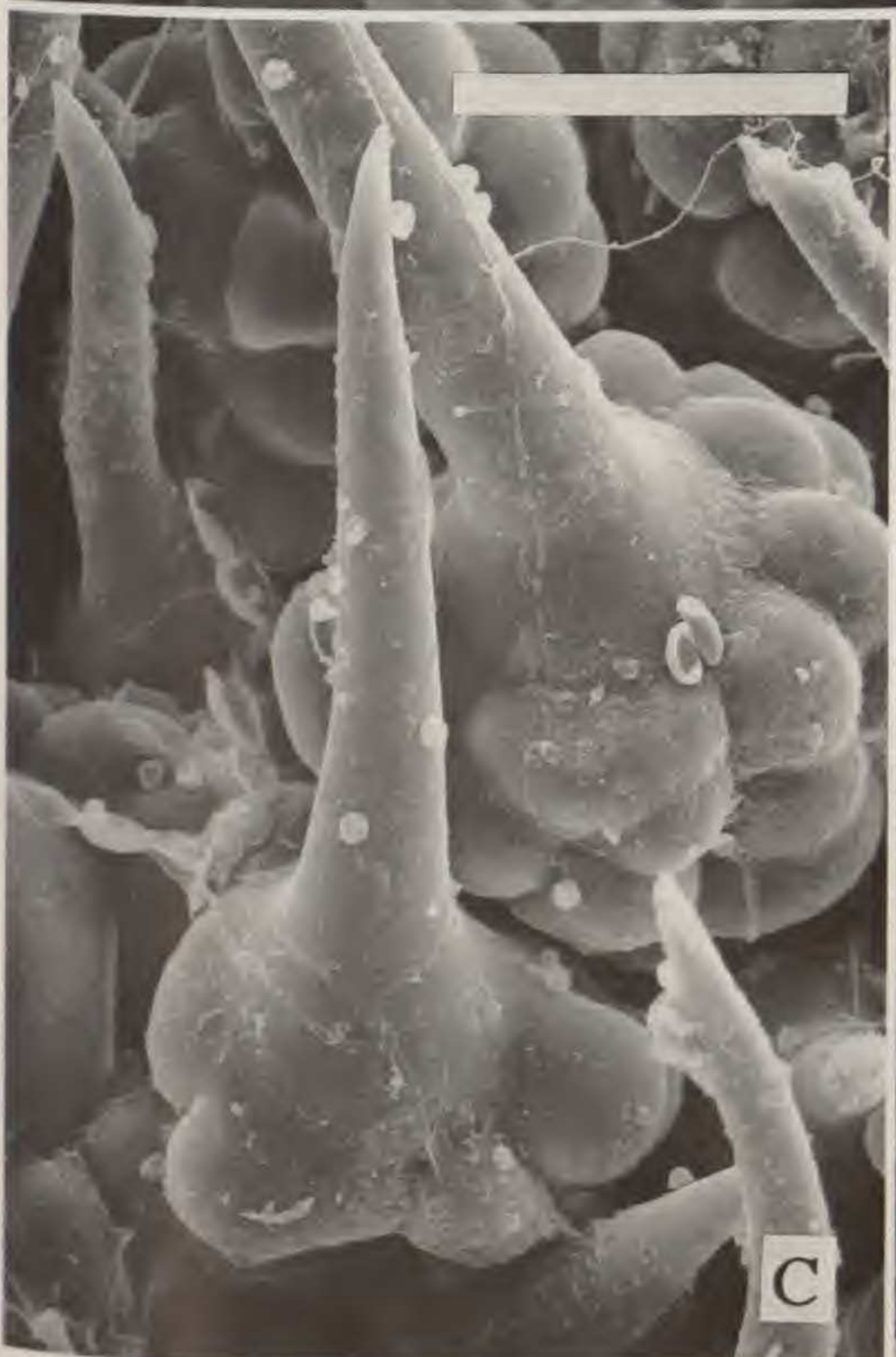
(4) Subsessile glandular hairs (Abu-Asab & Cantino, 1987) are common on lower leaf surfaces and fewer in number on upper surfaces, where they are sunken. While subsessile glandular hairs may appear sessile in surface view, a short, usually discoid stalk cell may be seen in cross section (Abu-Asab & Cantino, 1987). The subsessile glandular hairs can be single-celled as in *P. sulphurea* or multicellular as in *P. pubescens*. Puff (1978) also reported stalked glandular hairs on the leaves of *P. volubilis*, but they were not observed in this study.

(5) Falcate hairs (sensu Payne, 1978) have the tip curved and are only found on petioles of *Xolocotzia*.

(6) Clavate glandular hairs (Abu-Asab & Cantino, 1987) occur on leaves but are more common on calyces and corollas of *Petrea*. Clavate glandular hairs are spherical-headed with a long unicellular stalk. The head is yellowish and consists of several radially arranged secretory cells.

(7) Lageniform hairs (sensu Payne, 1978) are

FIGURE 1. Pubescence in the genera *Petrea* and *Xolocotzia*.—A. *P. bracteata* (Rueda & Ruiz 590), B. *X. asperifolia* (Neill 5477), showing conic hairs found on leaves.—C. *P. blanchetiana* (Martius 1029), D. *X. asperifolia* (Neill 5477), showing bulbous hairs found on leaves, bracts, and petioles of *Petrea* and *Xolocotzia*. (SEM photos; bars in A, B = 50 μm, C, D = 5 μm.)



found on the calyx of *Petrea* and *Xolocotzia*. They are flask-shaped hairs.

(8) Ribbon hairs (sensu Payne, 1978) are found on the calyx and corolla of *Petrea* and *Xolocotzia*. These hairs are shaped like a flowing ribbon.

(9) Warty hairs (sensu Hewson, 1988) are found in the interior of the corolla of *Petrea*. These hairs are covered with wartlike protuberances (Fig. 2A, B). They may help retain pollen close to the stigma.

LEAVES

Leaves are highly variable in size and texture, even within species. They often feel like sandpaper. This roughness is due to the presence of special hairs found on the surface(s) of the leaves (see Pubescence). The underside of the leaves is useful in separating species. Pitted leaves (Fig. 2C) are only present in *P. brevicalyx* Ducke, *P. campinae* Rueda, and *P. macrostachya* Benth., whereas bulate leaves (Fig. 21B) are only present in *P. rugosa* Kunth. All other species have the leaves smooth underneath (Fig. 2D). Leaf texture is useful as a taxonomic character, although it is in some cases difficult to define except on a comparative basis.

Leaves of *Petrea* are uniformly simple and opposite or whorled. Some species are characterized by verticils of three or four leaves. However, other species may have 90% of the leaves decussate and 10% verticillate, while others show the opposite percentage.

Venation patterns are not useful in separating species because all are brochidodromous (Hickey, 1979), with the angle formed by the secondary veins and the midrib and the anastomosing of the veins near the margin similar in all species. The tertiary venation is variable and densely netted. This type of venation is common in other verbena-ceous genera, such as *Aegiphila*, *Citharexylum*, *Cornutia*, and *Duranta*.

Stomatal patterns have proven to be useful taxonomically (Cantino, 1990), and three groups of species may be recognized within *Petrea*. Stomata were observed and photographed with an S-450 scanning electron microscope (SEM). Additional observations were made with the plastic imprint technique of Sinclair & Dunn (1961), and classification of stomata follows Cantino (1990). Three basic types of stomata were found in the genus (see

Table 2). The type of stomata is not helpful at the species level. However, the type of stomata can be useful for making groups. Thus, the anomocytic type (Fig. 3A) is present in species such as *P. brevicalyx* and *P. insignis* Schauer; diallelocytic stomata (Fig. 3B) occur in *P. pubescens*, *P. rugosa*, *P. sulphurea*, and in *X. asperifolia* Miranda (outgroup). The paracytic type (Fig. 3C) is found in *P. blanchetiana* Schauer, *P. maynensis* Huber, and *P. volubilis*.

POLLEN

Pollen of *Petrea* is characteristic of the genus but has little interspecific differentiation. Scanning electron micrographs show that pollen of all species is more or less triangular and tricolpate. The ornamentation of the exine of all species is psilate or smooth without sculpturing (Fig. 3D). The pollen in *Xolocotzia* (outgroup) differs from that of *Petrea* in being more spherical and in having a reticulate exine (Fig. 3E).

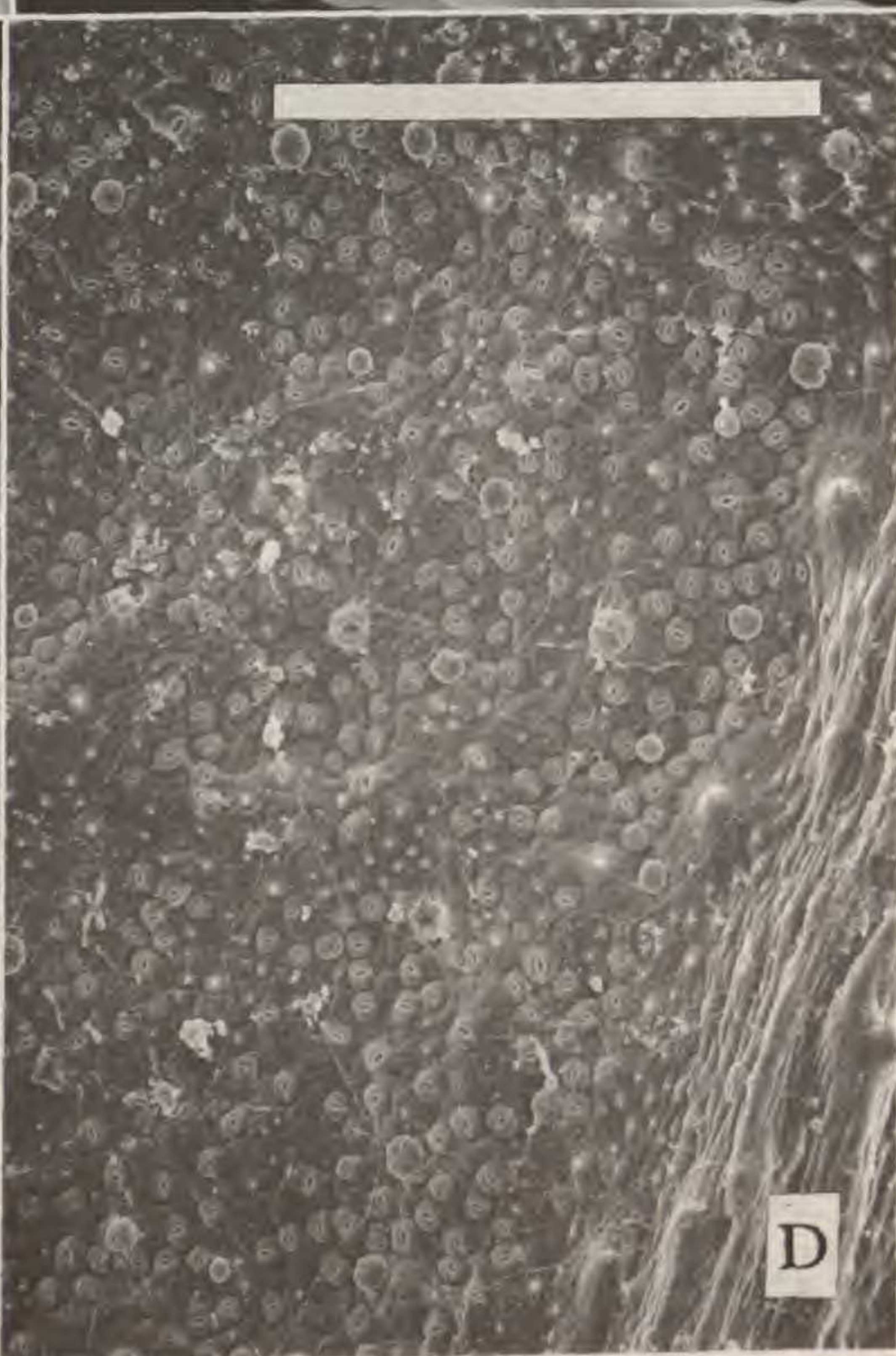
FRUITS AND SEEDS

The fruit of *Petrea* is drupaceous and enclosed by the calyx. The accrescent fruiting calyx, which encloses the fruit, usually has the same color as the flowers, but sometimes becomes green (e.g., *P. volubilis*). The lobes do not change much in shape but become stiffer and harder with maturation, forming a near right angle with the tube. The fruit, once out of the calyx, shows remnants of the style on one end and remnants of the receptacle on the other end. The exocarp is leathery or fleshy; the endocarp is hard and bony, 2-celled, and forms two stones. The stones are not easy to separate, and each has one seed. However, sometimes, as in *P. blanchetiana*, there is only one seed found in the fruit. Seeds are laterally or apically attached, and lack endosperm. None of these characters are helpful in separating species or groups of species.

ANATOMY

Anatomical studies were carried out for the distinct parts of the plants. Fresh samples of primary stem, wood, and leaf were collected in 70% ethanol for anatomical studies. Three samples from different individuals of each species were dehydrated in

FIGURE 2. Pubescence and leaf surface in the genus *Petrea*.—A. *P. volubilis* (Gimate 911), B. *P. macrostachya* (Jansen-Jacobs et al. 341), showing warty hairs present in the interior of the corolla.—C. *P. macrostachya* (Pipoly 7588), showing a pitted leaf surface.—D. *P. maynensis* (White 860), showing a smooth leaf surface. (SEM photos; bars in A = 5 μ m, B = 50 μ m, C, D = 500 μ m.)



a series of increasing concentrations of ethanol, embedded in Paraplast, and sectioned on a rotary microtome set at 10–15 μm . Staining was carried out using Johansen's (1940) Safranin-Fast Green technique. Longitudinal and cross sections of shoot apices were stained using the zinc chloride technique (Sharman, 1943) to better discern meristematically active areas.

For taxa available only from herbarium specimens, material was placed in a vial with deionized water and wetting agent and left in a 60°C oven overnight. The material was then washed and stored in 70% FPA and subsequently prepared as described above. All leaves used for clearing studies were obtained from herbarium specimens. The leaves were placed for one day in water to which Aerosol-OT was added, then transferred to a 5% NaOH solution for one week. The leaves were then rinsed with water and placed in 5.25% NaHCO₃ (commercial laundry bleach) for one hour. After an ethanol dehydration series, staining was carried out using a 0.5% solution of safranin in 95% ethanol (Johansen, 1940). The trichomes were examined and compared for all the species using light and scanning electron microscopes.

Most of the stem samples were collected from herbarium specimens. These were soaked in equal parts of 60% ethanol and glycerin for three months. The samples were frozen using a Super Histo-Freeze, an appropriate method when stem samples are less than one inch in diameter (R. Keating, pers. comm.), and then slides were made in cross, radial, and tangential section using an 860 American Optical sliding microtome set at 15–25 μm . Section stems were then stained by covering the samples with Johansen's safranin for two hours, followed by rinsing in an ethanol series (Johansen, 1940).

PRIMARY STEM ANATOMY

The anatomy of the primary stem was studied in two species of the genus, *Petrea pubescens* (a tree) and *P. maynensis* (a liana). Lianas and trees show exactly the same histological zones. From outside to inside these zones are: epidermis, cortical zone, stelar zone, and the pith. The epidermis is one cell thick and decorated with 2–3 types of hairs. The cortical zone and stelar zone do not show any special features. The pith is composed of parenchyma cells with no observable special features.

LEAF ANATOMY

In the study of leaf histology three samples of each species of *Petrea* were obtained. The numbers

TABLE 2. Types of stomata found in extant *Petrea* and *Xolocotzia*.

Taxon	Stomatal type		
	Ano-mocytic	Dialle-locytic	Para-cytic
<i>Petrea bracteata</i>	X		
<i>P. brevicalyx</i>	X		
<i>P. campinae</i>	X		
<i>P. insignis</i>	X		
<i>P. macrostachya</i>	X		
<i>P. pubescens</i>		X	
<i>P. rugosa</i>		X	
<i>P. sulphurea</i>		X	
<i>Xolocotzia</i>		X	
<i>Petrea blanchetiana</i>			X
<i>P. maynensis</i>			X
<i>P. volubilis</i>			X

of cell rows forming the epidermis and the number of palisade layers were found to be good characters for species grouping (Table 3). *Petrea campinae* has four rows of epidermal cells, *P. brevicalyx*, *P. macrostachya*, and *P. maynensis* have two rows, and all other species have only a single row. The mesophyll of the leaf of *Petrea* has a palisade tissue consisting of one to several layers of cells, confirming the earlier observations of Metcalfe & Chalk (1972). Sclerenchymatous fibers are present in the mesophyll, and crystals of different sizes are found in the parenchymatous tissues. The vascular bundles of the larger and smaller veins are accompanied by sclerenchyma.

The petiole has a median vascular strand consisting of an almost closed cylinder of xylem surrounded by completely closed cylinders of phloem and fibers. The number of petiolar lateral traces varies among species. Thus, *P. insignis* has no lateral traces, *P. blanchetiana*, *P. macrostachya*, and *P. maynensis* have four lateral traces, and all the remaining species have only two lateral traces.

WOOD ANATOMY

The young stems are commonly quadrangular or terete in transverse section, except in *Petrea sulphurea* M. J. Jansen-Jacobs, where they are angular and winged. Mature stems of the species of *Petrea* show growth rings. According to Welle & Détienne (1988), growth rings are formed by the combination of marginal parenchyma and a difference in vessel diameter. The vessels are round to oval in shape, with simple perforations, solitary or in clusters of 2–6, 20–40 per mm², with a diameter that varies from 25 to 250 μm . The rays

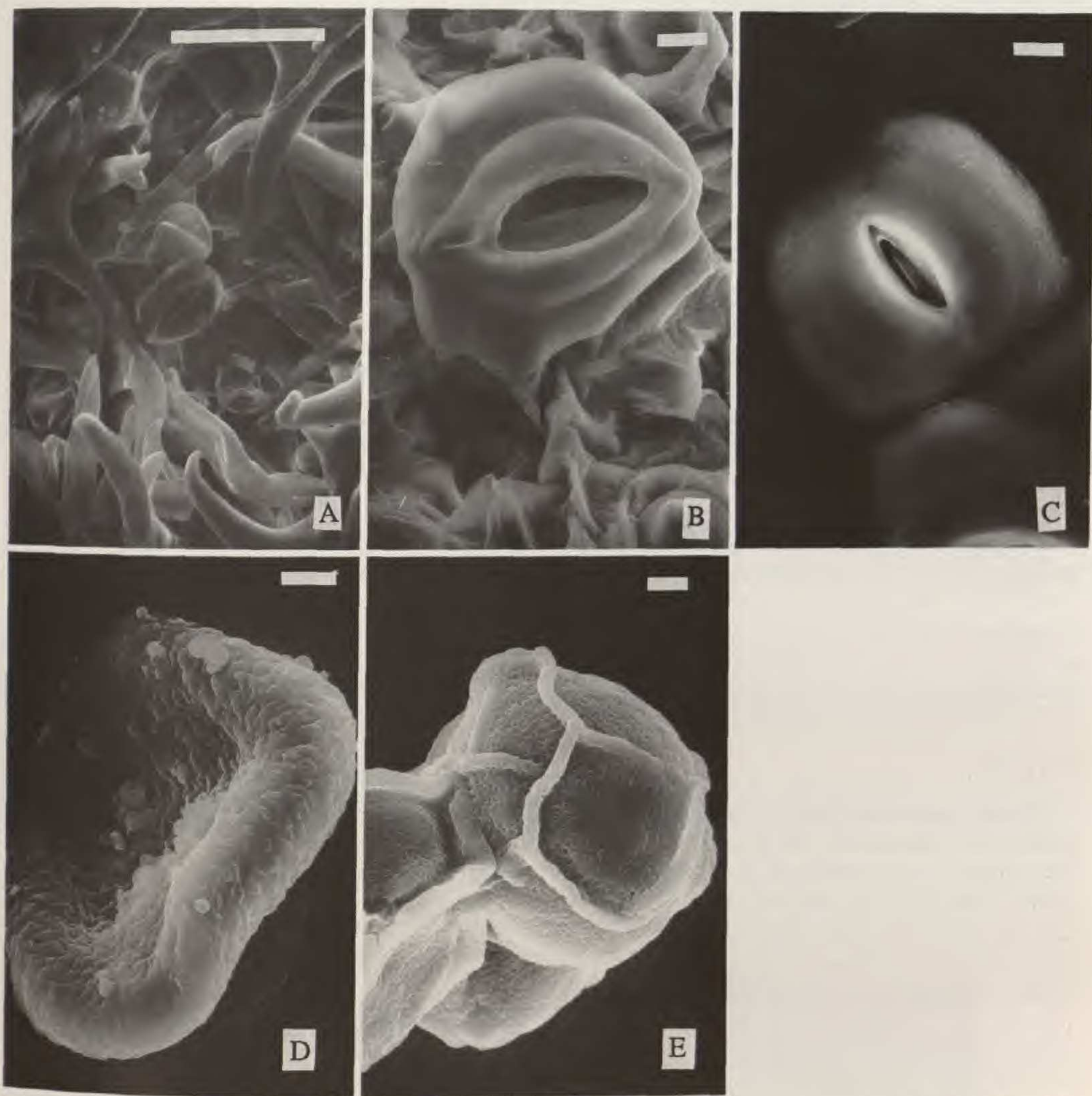


FIGURE 3. Stomata and pollen in the genera *Petrea* and *Xolocotzia*. —A. *P. brevicalyx* (Ducke 22544), showing anomocytic stomata. —B. *X. asperifolia* (Villeda 134), showing diallelocytic stomata. —C. *P. volubilis* (Gentry 7794), showing paracytic stoma. —D. *P. sulphurea* (Billiet & Jadin 1705); this triangular-shaped pollen is characteristic of the species of *Petrea*. —E. *X. asperifolia*, with round pollen grains. (SEM photos; bars in A = 50 μm , B-E = 5 μm .)

are uniseriate, as observed in *P. sulphurea*, or multiseriate (1–12 cells wide), as observed in *P. volubilis*. Record & Hess (1941) described the heartwood of *P. arborea* Kunth, now part of *P. volubilis*, as tasteless, odorless, pale orange-brown, and not too well differentiated from the yellowish or light olive sapwood. They also reported distinct ray flecks on radial surfaces. The wood is moderately hard and heavy, medium textured, with straight to finely undulate grain, and has good working properties and fairly high luster. According to Metcalfe & Chalk (1972, 1979), the cork orig-

inates superficially and is tabular and thickened on the outer tangential walls. The pericycle contains a composite and continuous ring, and its sclerenchyma includes stone cells as well as fibers. Solitary crystals in the pericycle are associated with the sclerenchyma and are sometimes enclosed within the stone cells.

The wood has silica in all the elements. The fibers are typically septate, but nonseptate in *P. bracteata* and *P. macrostachya*. The pits are mostly simple in the radial walls, but have small borders in some specimens of *P. volubilis*.

TABLE 3. Histological features of the leaves of *Petrea* and *Xolocotzia*.

Taxon	Number of cell rows forming the epidermis	Number of palisade layers	Voucher
<i>X. asperifolia</i>	1	1	Neill 5477 (MO)
<i>P. blanchetiana</i>	1	1	Rueda 507 (MO)
<i>P. bracteata</i>	1	2	Rueda 730 (MO)
<i>P. brevicalyx</i>	2	1	Ducke 140 (MO)
<i>P. campinae</i>	4	2-4	Cordeiro et al. 76 (SP)
<i>P. insignis</i>	1	1	Ducke 688 (MO)
<i>P. macrostachya</i>	2	1	Smith 2626 (F)
<i>P. maynensis</i>	2	1	Rueda 1129 (MO)
<i>P. pubescens</i>	1	1	Rueda 1010 (MO)
<i>P. rugosa</i>	1	2	García 6472 (COL)
<i>P. sulphurea</i>	1	1	Billiet & Jadin 1705 (BR)
<i>P. volubilis</i>	1	1	Rueda 431 (MO)

CYTOLOGY

Number and morphology of chromosomes have not proven to be useful in the separation of species. Two species were studied: *Petrea volubilis* from plants cultivated at the Missouri Botanical Garden

that originally came from Central America and Brazil; and *P. blanchetiana* from Peru (Rueda 615). All the observations showed a constant chromosome number of $2n = 34$, which is the same result that Goldblatt (1988) reported for *Petrea volubilis*. The chromosome size is also generally invariable. The length of the chromosomes ranges from 1 to 1.5 μm , and the width is less than 1 μm (Fig. 4).

ECOLOGY

HABITAT AND ENDEMISM

The species of *Petrea* are found in the lowlands of the American tropics. Some species are restricted to very specific soil types resulting in narrow endemism. For example, *P. brevicalyx* and *P. insignis* occur primarily in seasonally inundated forest (igapó) in Brazil. *Petrea campinae* is known only from white sand campinas in Roraima, Brazil. Other species have restricted distribution with no obvious ecological correlations. For example, *Petrea macrostachya* is known only from the Guianas but occurs in a wide range of habitat types, including white sand forest. *Petrea volubilis* can be found in many different environments, but it is more common within 300 m of extant or former rivers and in open areas such as gaps or along trails. In general, the distribution of a species often is very patchy even within its habitat, with scattered



FIGURE 4. *Petrea volubilis* (Rueda & Cuadros 431), showing the chromosomes found in the genus *Petrea*. (Bar = 10 μm .)

clumps of six to ten individuals. *Petrea volubilis* can also be found on cliffs. There the rope stems are typically 1–2 cm in diameter and hang 5–6 m, with the leaves grouped at the end, but the inflorescences are upright.

POLLINATION BIOLOGY

Petrea species seem to have a mass-flowering “big bang” phenology at the beginning of their flowering season, but then continue to flower more evenly producing only a few flowers at a time for two or three months. *Petrea blanchetiana* in full bloom was observed to have up to eight groups of inflorescences in 20 m², each group with 20 inflorescences, 30–40 cm long, with an estimated 25–30 flowers apiece. Thus *P. blanchetiana* in full flower may produce 4000–6000 flowers in 20 m².

The principal visitors to *Petrea* flowers are bees of the tribe Euglossini, although an introduced species of *Apis*, species of *Bombus*, and Heliconiidae butterflies were also observed. Thrips commonly feed on the petals (up to eight counted in a single flower), but they appear to have a negligible role in pollination because they remain in the flowers after the pollen is dry. Euglossine bees are the most commonly observed flower visitors and are, presumably, the most important pollinators of *Petrea*. The most often captured bees in this study were species of *Euglossa*. Individuals of this genus often follow a repeated foraging circuit or “trapline” among successive flowers or clumps of flowers (Janzen, 1971). The sex ratio of these bees at *Petrea* is nearly equal in contrast to the observations of Gentry (1976) in the Bignoniaceae.

The Apinae visitors of *Petrea* were species of *Bombus* and the introduced genus *Apis*. Although *Apis* may now be a significant pollinator of *Petrea*, it is surely not a co-evolved one, since *Apis* has only recently reached the Neotropics.

SEED SET

Fertile fruits appearing swollen or incrassate are easily distinguished from infertile ones, which appear flat. Seed set in *Petrea* is remarkably low, and approximately 80% of flowers abort their ovules. In addition to ovule abortion, predation of fruits limits *Petrea*'s reproductive success. Little predation appears to occur on the plants, but about 40% of the fruits observed found on the ground had been eaten by Curculionidae larvae.

DISTRIBUTION

The 11 extant species of *Petrea* are distributed throughout the Neotropics. They range from south-

ern Mexico (Veracruz) through the West Indies and Central America to Brazil, Paraguay, and Bolivia. The main concentration of species is in northern Amazonia, in Brazil, and the Guianas. *Petrea volubilis* is the “weedy” species of the genus, being found throughout the entire distribution of the genus (Fig. 5). Other wide-ranging species include *P. blanchetiana*, found from Panama, Colombia, and Venezuela south to Peru and southeast to Brazil and the Guianas (Fig. 6); *P. maynensis* occurs from Colombia south to Peru, Brazil, and Bolivia (Fig. 7); *P. pubescens* ranges from Venezuela south to Colombia, Ecuador, and Peru (Fig. 8); *P. bracteata* ranges from the Guianas southwest through Brazil to Amazonian Peru (Fig. 9). *Petrea macrostachya* is endemic to the Guianas (Fig. 10); *P. sulphurea* is known only from French Guiana (Fig. 10); and *P. insignis* is restricted to northern Amazonian Brazil (Fig. 10). *Petrea brevicalyx* and *P. campinae* are endemic to Amazonian Brazil (Fig. 11); *P. rugosa* is endemic to southern Colombia and adjacent Venezuela (Fig. 11). In addition, fossil species are known from the United States and from the former Czechoslovakia (Moldenke, 1938).

USES

The known uses of *Petrea* are limited. In flower or fruit the plants are attractive; they were first grown as an ornamental in 1733 when W. Houstoun brought *Petrea volubilis* into cultivation from Veracruz, Mexico (Aiton, 1812). Most of the species are grown locally; only *P. volubilis* is widespread in cultivation. *Petrea maynensis*, *P. pubescens*, and *P. rugosa* are, at least locally, used in horticulture. *Petrea* plants are easily propagated by cuttings or layering.

Record & Hess (1941) considered the wood of *Petrea* to be poorly resistant to decay and without any commercial value. The wood is very hard to cut when dry and seems to be good as firewood, burning fast, without much smoke (pers. obs.).

There are also scattered reports of the use of *Petrea* as a medicinal plant in the West Indies, Ecuador, and the Guianas. In the West Indies, *P. volubilis* is mixed with *Chiococca alba* (L.) Hitchc., to prepare a tea for use as an abortifacient (Ayensu, 1981). In Ecuador *P. maynensis*, mixed with three other plants, is used as a contraceptive (Wilbert & Neill, 1987). In the Guianas, the ash obtained from the vegetative part of *P. bracteata* is applied to legs to relieve aches and pains (R. DeFilips, pers. comm.).

The pharmacological action of *Petrea* is unknown but Andray et al. (1982) reported phenylpropanoid glycosides in *Petrea* and in more than

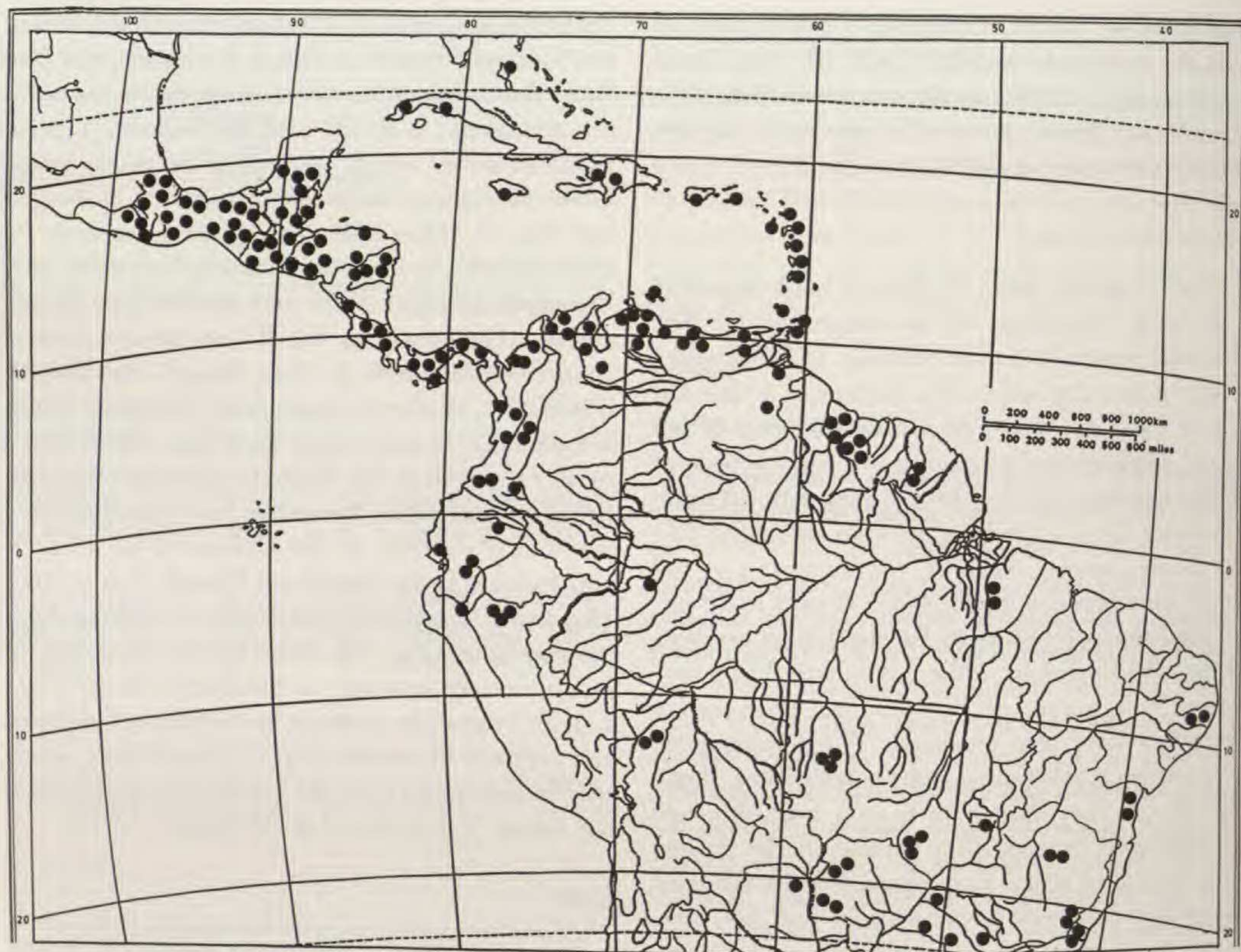


FIGURE 5. Distribution of *Petrea volubilis*.

40 other genera that are used in folk medicine. These compounds have proved to have good antibacterial, antihypertensive, and analgesic properties (Garnier et al., 1989).

Finally, *Petrea rugosa* is used as a melliferous plant for hive honeybees in Medellín, Colombia. Echeverry (1984) also reported that *P. pubescens* and *P. rugosa* are used as melliferous plants in the department of Tolima.

PHYLOGENY

More than 1000 species and about 40 genera of Verbenaceae occur in the New World. *Petrea* has always been considered distinct and separate from other American genera by the calycinal crest present on the calyx and by the asperous leaves. In this treatment, *Petrea* is placed along with *Caselia* Nees & Martius, *Lampaya* F. Philippi, *Recordia* Moldenke, and *Xolocotzia* Miranda in the tribe Petreeae Briq., following Briquet (1895) and Moldenke (1971). Defining characters shared by members of this tribe include fruits with two 1-celled and 1-seeded pyrenes, characters originally used by Briquet (1895) for tribal delimitation.

METHODS

Hypotheses of the phylogenetic relationships of *Petrea* to the other genera in the Petreeae, as well as relationships between the species of *Petrea*, were generated by a cladistic analysis. For the analysis of the tribal as well as species relationships, the distribution of synapomorphies was analyzed using parsimony criterion (minimizing homoplasy; Kaplan, 1984). On the basis of these synapomorphies, taxa were ordered into one or more patterns represented by hierarchical branching patterns. Character polarity for the characters selected was determined by the outgroup comparison method (Maddison et al., 1984). Data were analyzed using Farris's phylogenetic package, Hennig86 (version 1.5; Farris, 1988), applying the implicit enumeration option for calculating trees. In the analysis of *Petrea* characters 2, 4, and 10 were considered unordered. The successive weighting procedure in Hennig86 was also used, which calculates weights from the best fits to the most parsimonious tree, using rescaled consistency (rc), which is the product of the character consistency (c) and the character retention index (r). The product is scaled to lie in the range 0–10. The weighting procedure is re-

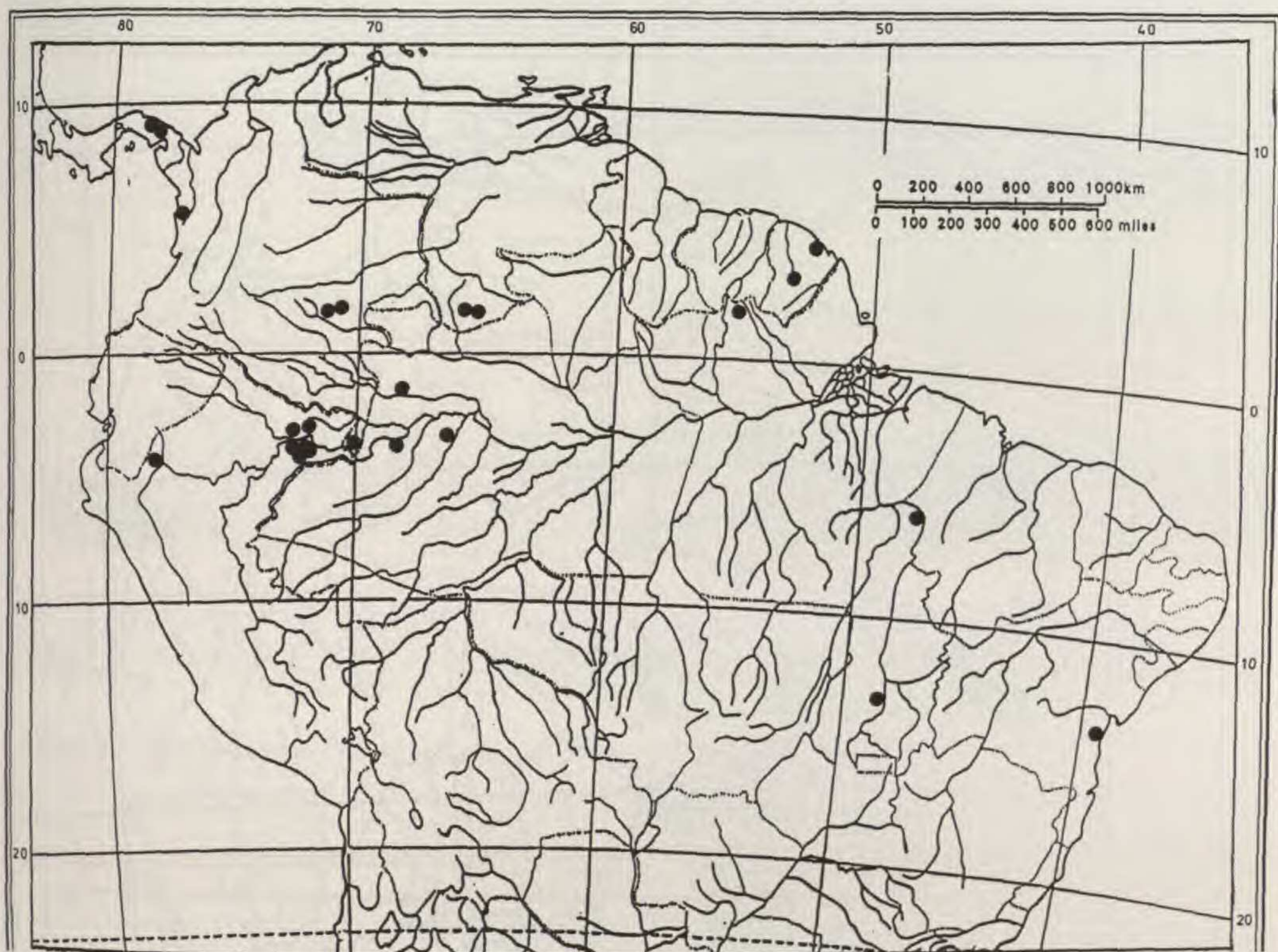


FIGURE 6. Distribution of *Petrea blanchetiana*.

peated on successively produced trees until the trees no longer change (Farris, 1989). The program Clados (version 1.1; Nixon, 1992) was used for examination of character and distributions and production of the figures.

CLADISTIC ANALYSIS OF THE TRIBE PETREEAE

One of the most difficult tasks in attempting a cladistic analysis lies in the choice of appropriate outgroups (Watrous & Wheeler, 1981). However, if outgroups are explicitly designated, the phylogenetic hypothesis can be modified as more data on the relationships of the genera become available. *Citharexylum* and *Duranta* of the tribe Citharexyleae in the subfamily Verbenoideae were chosen for the cladistic analysis of the tribe Petreeae (which is also Verbenoideae). Citharexyleae are clearly delimited in the subfamily by having fruit composed of two or four 2-celled and 2-seeded pyrenes. *Citharexylum* and *Duranta* are well known, making character evaluation less problematic than in some of the other genera of the tribe, where most species and even entire genera are known only from a few collections.

Once the character states were determined and polarized (Table 4), a variety of procedures for hypothesizing relationships were possible. Autapomorphies (characters that occur only in one taxon) were omitted because they are uninformative about taxonomic relationships. However, these autapomorphies were used to define species before running the cladistic analysis. All the characters used were polarized by outgroup comparison with the two members of the Citharexyleae. The only synapomorphy that is shared by the two tribes is the spicate or racemiform, indeterminate, and centripetal inflorescence.

The data matrix for the study of generic relationships is presented in Table 5. A single most parsimonious tree to length 12, consistency index of 0.83, and a retention index of 0.81 was obtained for the subtribe Petreeae. The tree (Fig. 12A) has a basal trichotomy, and *Petrea* and *Xolocotzia* appear as a distinct clade defined by two unique character states, leaves with bulbous-based hairs (Fig. 1C, D) and a lobed calyx. In addition, each genus is defined by its own autapomorphies. *Xolocotzia* is defined by having round reticulated pollen, whereas *Petrea* is defined by having triangular

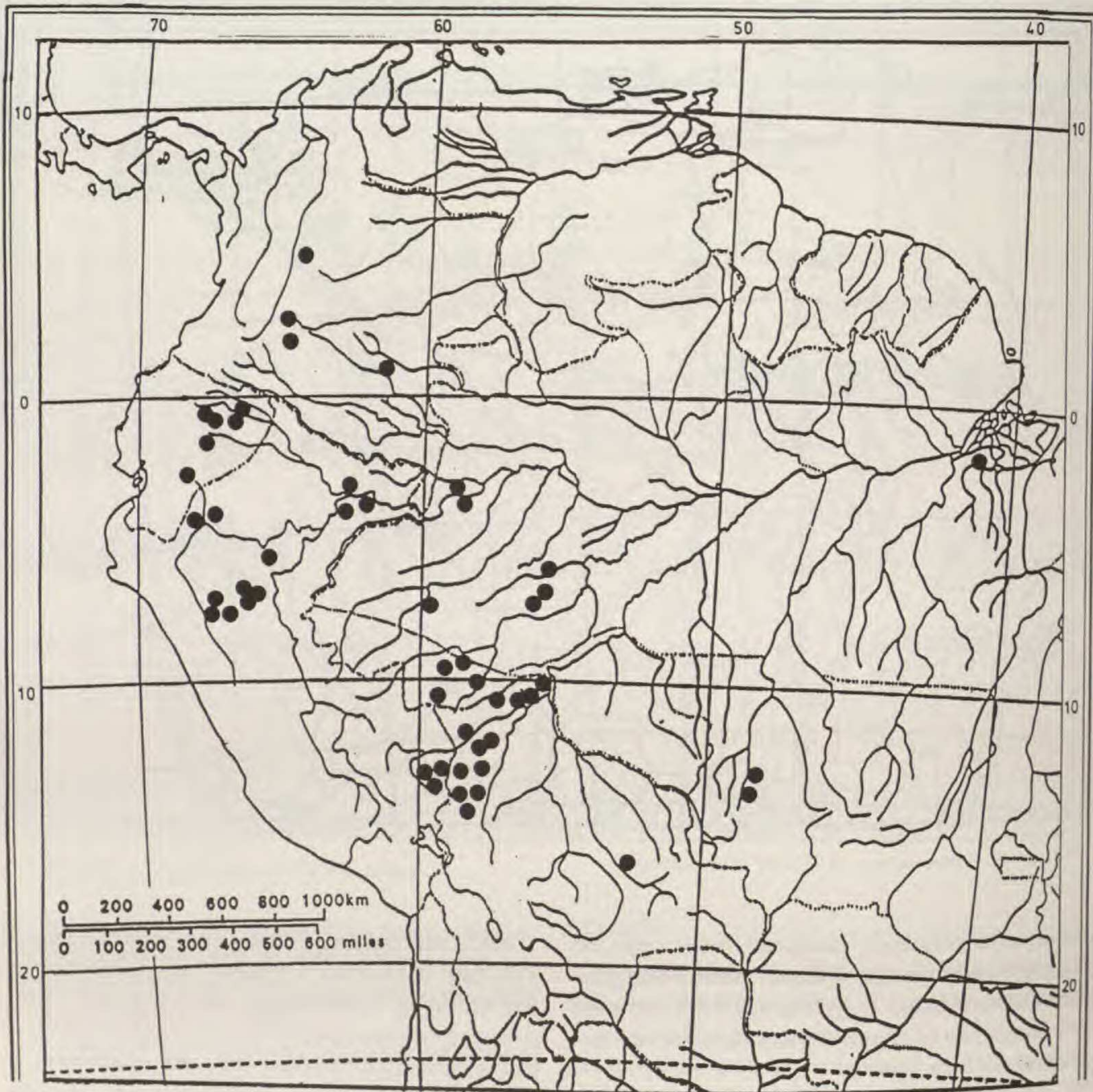


FIGURE 7. Distribution of *Petrea maynensis*.

smooth pollen and a calycinal crest on the calyx. The use of more than one character to infer a common ancestry for this clade does not support the possibility that these relationships are due to homoplasies rather than to homologies.

CLADISTIC ANALYSIS OF THE GENUS *PETREA*

The cladistic analysis conducted to determine hypotheses of relationships among the species of the genus *Petrea* followed the same procedure as that used for the tribe Petreeae. The character states (Tables 6, 7) were polarized using the genus *Xolocotzia* as an outgroup. After three rounds of successive weighting, one fully resolved tree of length 122, consistency index of 0.74, and a re-

tention index of 0.86 was obtained (Fig. 12B). The resulting tree shows that *Petrea* is monophyletic and contains the following eight monophyletic groups: (1) comprises all species but *P. insignis*, which is the only species in the genus without lateral traces; (2) *P. maynensis* and *P. volubilis* both with aborted axillary racemes; (3) *P. pubescens* and *P. rugosa*, the only erect species in the genus; (4) all the remaining species except *P. sulphurea*, the species in this clade with a pair of bracteoles on the pedicel; (5) the remaining species except *P. bracteata*, the species in this clade with more than one layer of palisade tissue; (6) all the remaining species except *P. blanchetiana*, the species in the clade with a mesophyll of more than four layers of palisade; (7) the remaining species except *P.*

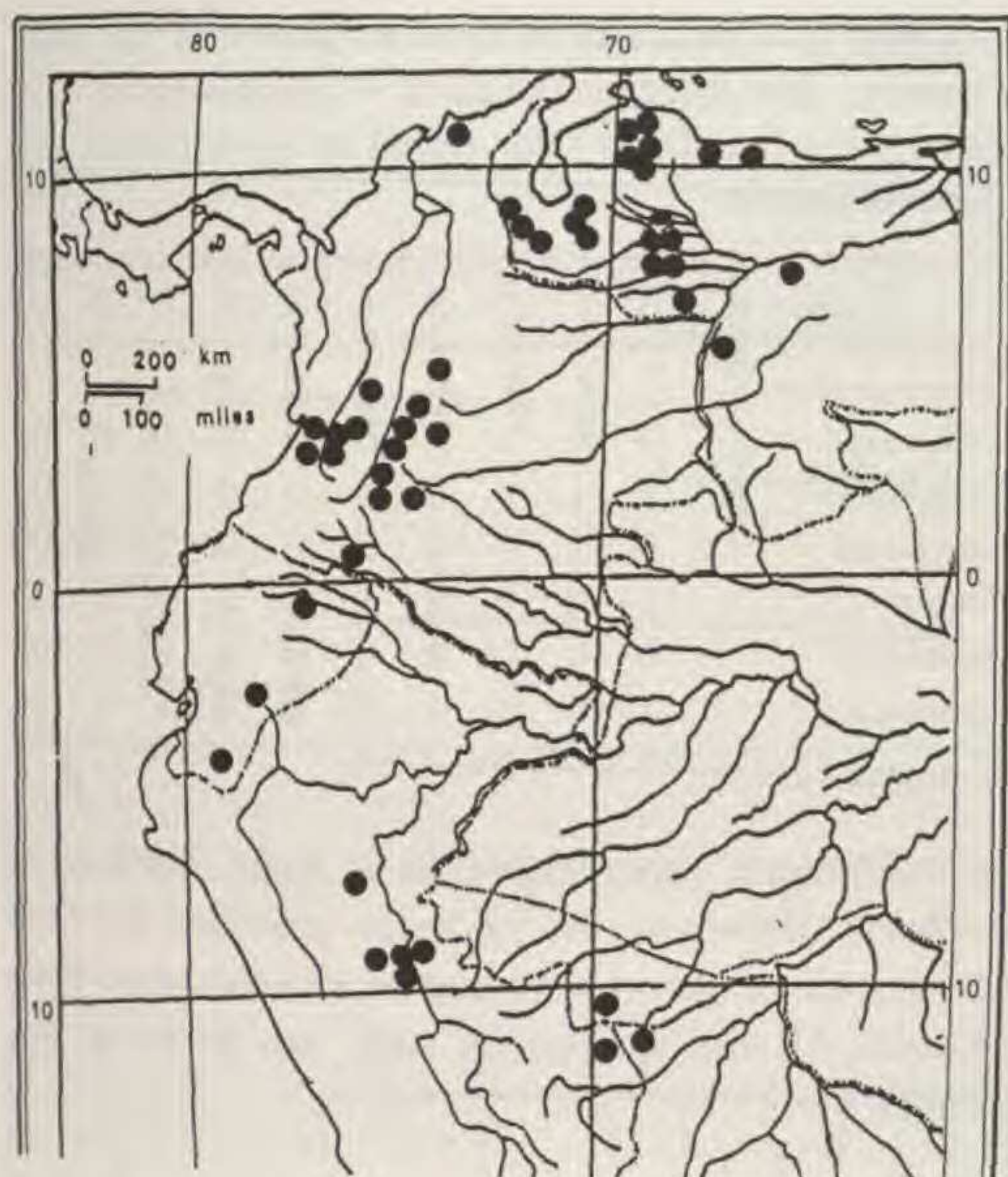


FIGURE 8. Distribution of *Petrea pubescens*.

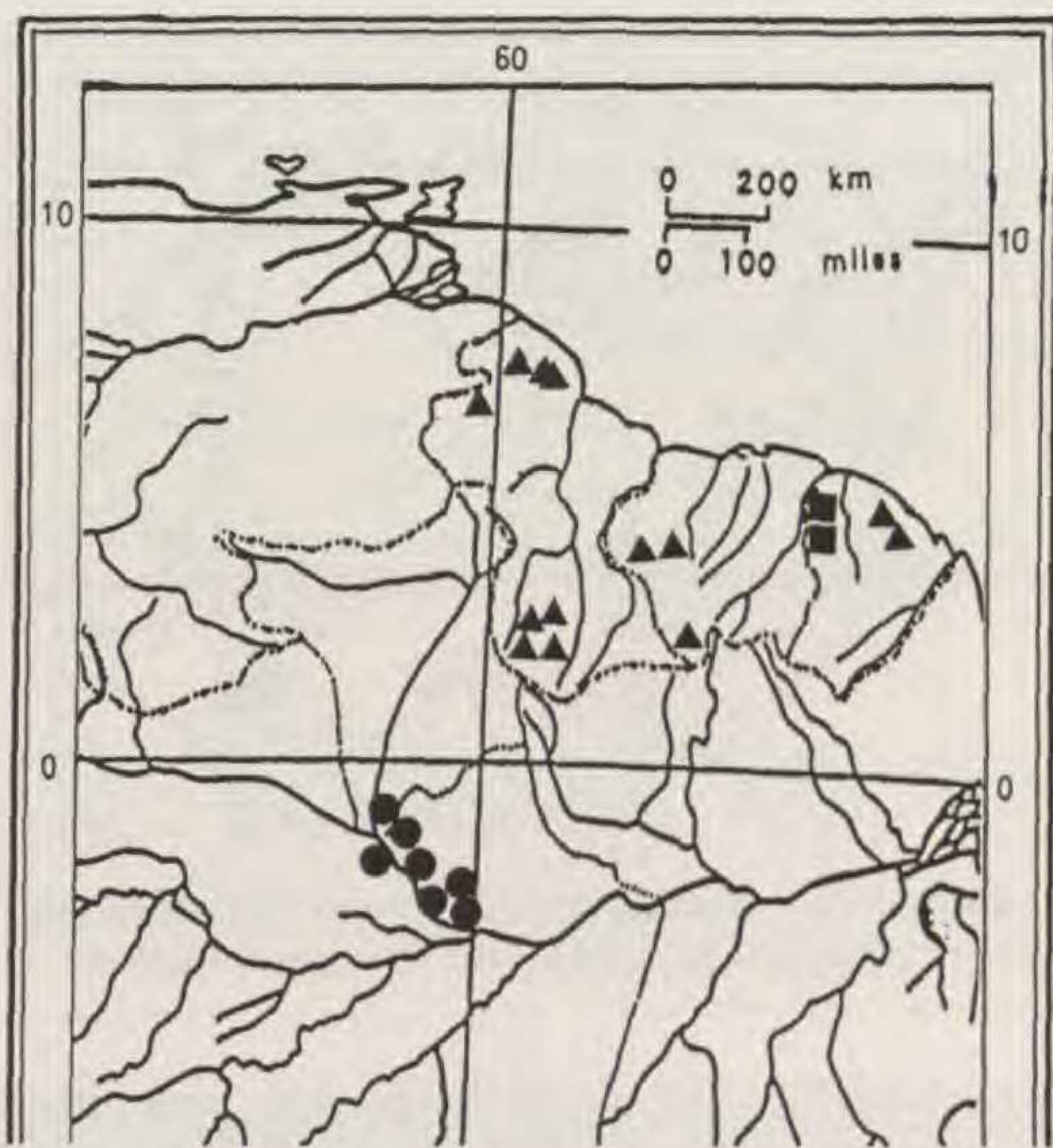


FIGURE 10. Distribution of *P. insignis* (circle), *P. macrostachya* (triangle), and *P. sulphurea* (square).

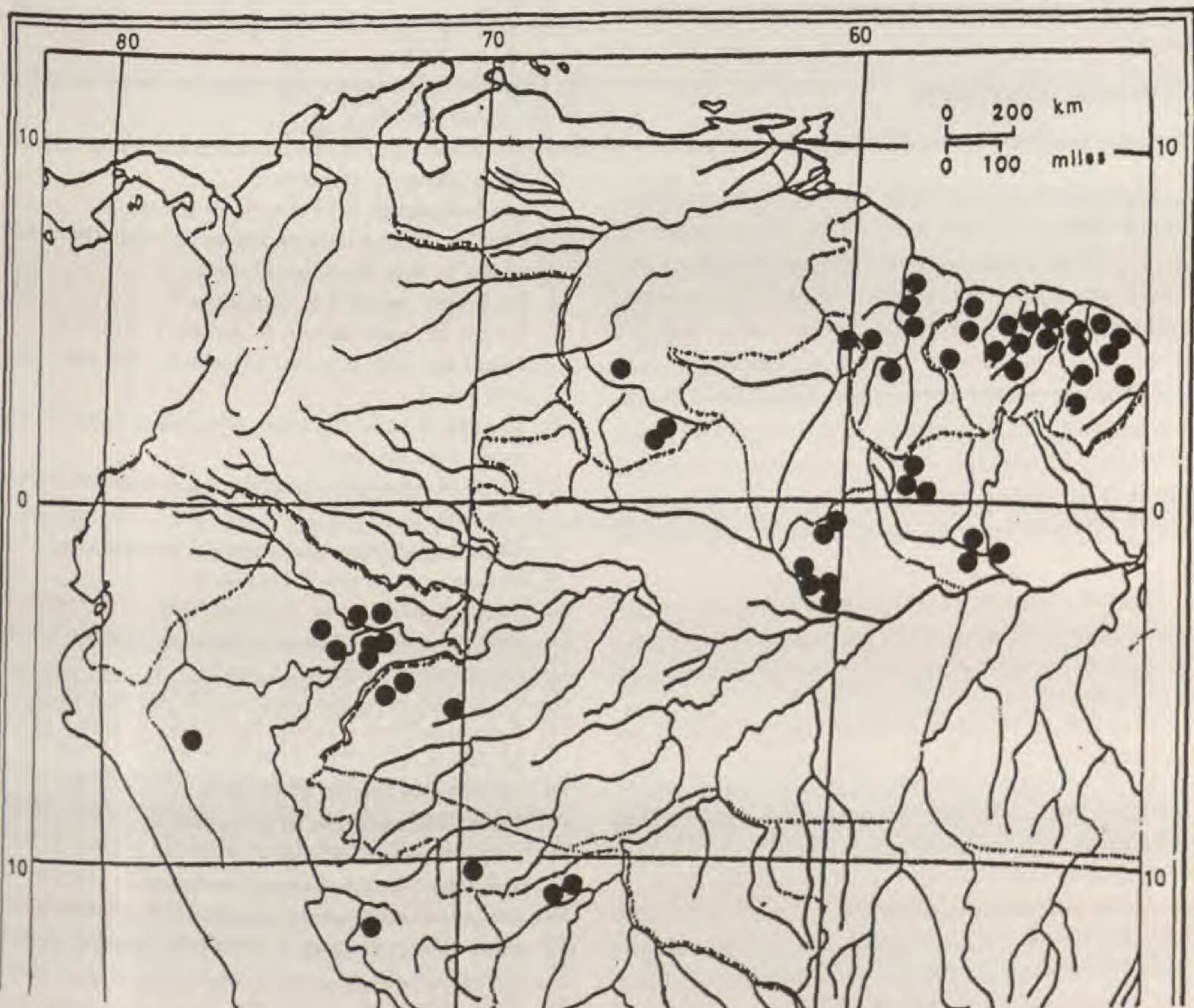


FIGURE 9. Distribution of *Petrea bracteata*.

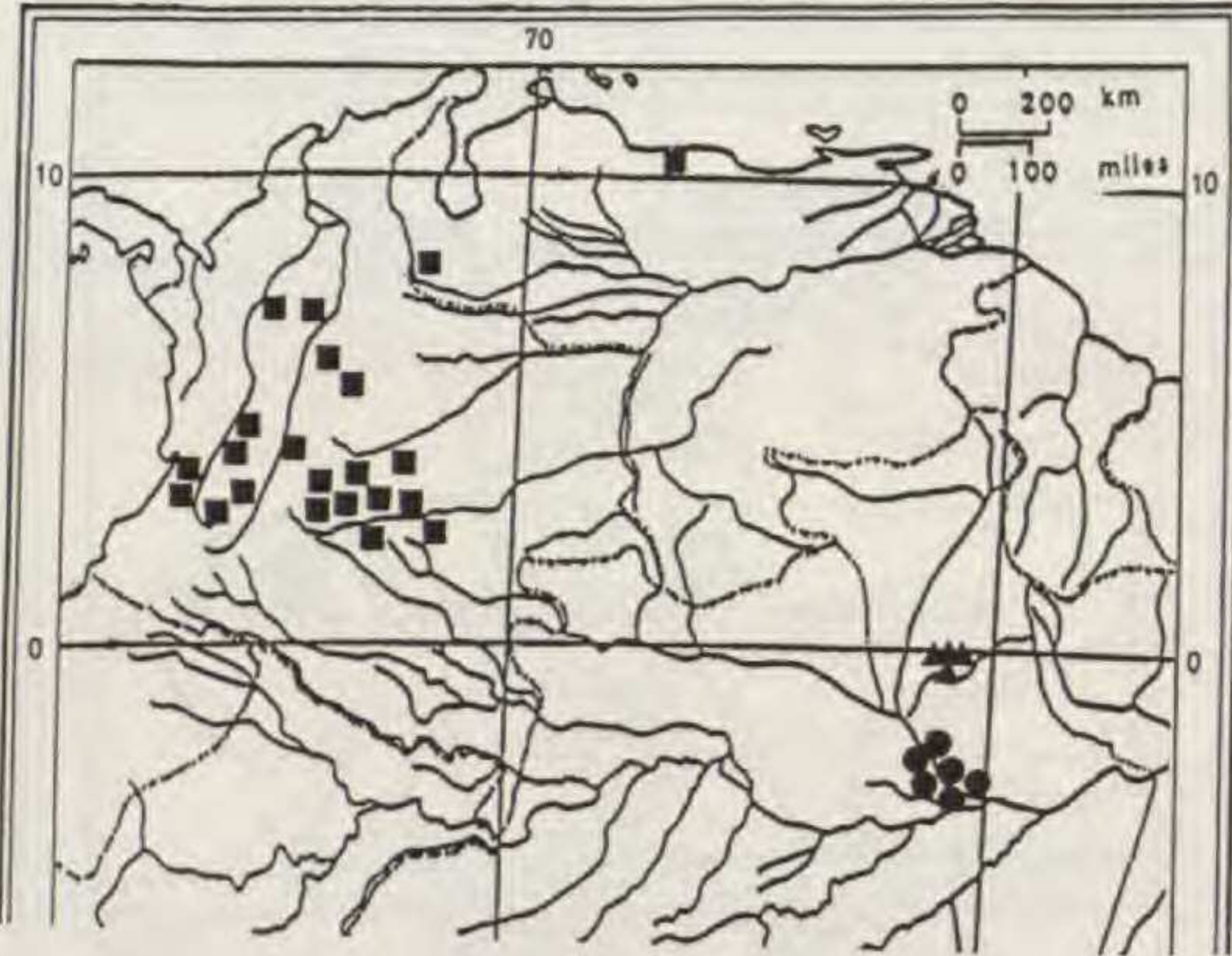


FIGURE 11. Distribution of *Petrea brevicalyx* (circle), *P. campinae* (triangle), and *P. rugosa* (square).

macrostachya, the species in the clade with pitted leaf beneath; (8) a clade formed by *P. brevicalyx* and *P. campinae*. The character shared among the last three species is the pitted leaves; *Petrea brevicalyx*, *P. campinae*, and *P. macrostachya* occur in northern Brazil and the Guianas, where the main concentration of species in the genus is found.

SYSTEMATIC TREATMENT

CRITERIA FOLLOWED IN THE SPECIFIC TREATMENTS

The delimitation of taxa was based on morphological characters that were measured as indicated in the Morphology section. Measurements of the leaves are given for mature leaves on terminal branches. For practical purposes, only discrete characters are included in the key. Moreover, only the characters that differ from those of the genus are given in the description of each species. A list of representative specimens examined is provided for each species. This list reflects as much as possible an overview of the distributional range as well

TABLE 4. Characters and character states for analysis of the tribe Petreeae.

0. Leaves smooth 0, rough-scabrous 1.
1. Leaf-scar swollen and corky 0, neither swollen nor corky 1.
2. Hairs not bulbous-based 0, hairs bulbous-based 1.
3. Calyx mainly dentate or truncate 0, calyx mainly lobed 1.
4. Degree of sepals fused: >0.50, 0; ≤0.50, 1.
5. Torus not swollen 0, swollen 1.
6. Calyx costate 0, not costate 1.
7. With staminode 0, without staminode 1.
8. Anthers sagittate 0, not sagittate 1.
9. Ovary without basal disk 0, with basal disk 1.

TABLE 5. Data matrix for the genera of the tribe Petreeae. The character states 0 = plesiomorphic, 1 = apomorphic. See Table 4 for definition of characters and character states.

Taxon	0	1	2	3	4	5	6	7	8	9
<i>Citharexylum/</i>										
<i>Duranta</i>	0	0	0	0	0	0	0	0	0	0
<i>Casselia</i>	0	1	1	0	0	0	0	1	1	0
<i>Lampaya</i>	0	1	0	0	0	0	0	1	1	0
<i>Petrea</i>	1	0	1	1	1	1	1	0	1	1
<i>Recordia</i>	0	0	0	0	0	0	0	0	0	0
<i>Xolocotzia</i>	1	0	0	1	1	1	1	1	1	1

as collections represented in a large number of herbaria. However, on the maps provided for each species all of the collections examined have been plotted. All the specimens seen are listed in Appendix 1.

Petrea L., Sp. Pl., ed. 1: 626. 1753. TYPE: *P. volubilis* (LINN. 781.1).

Woody vines, shrubs, or trees. Leaves decussate-opposite or whorled, deciduous, often rough-

TABLE 6. Characters and character states for analysis of the genus *Petrea*.

0. Erect plants 0, climbers 1.
1. Longest petiole ≤10 mm 0, >10 mm 1.
2. Petioles without lateral traces 0, with two lateral traces 1, with four lateral traces 2.
3. Leaf apex rounded 0, cuspidate 1.
4. Leaves beneath smooth 0, bullate 1, pitted 2.
5. Epidermis with one row of cells 0, with more than one row 1.
6. Mesophyll with one layer of palisade tissue 0, with more than one layer 1.
7. Head of subsessile glandular hairs with >4 cells 0, <4 cells 1.
8. Clavate glandular hairs absent 0, present 1.
9. Stomata not in pits 0, in pits 1.
10. Stomata diallelocytic 0, anomocytic 1, paracytic 2.
11. Aborted axillary racemes absent 0, present 1.
12. Inflorescence terminal 0, axillary 1.
13. Longest floral pedicel length ≤15 mm 0, >15 mm 1.
14. Pedicel without a pair of bracteoles 0, with a pair of bracteoles 1.
15. Calyx pubescent 0, glabrous 1.
16. Calyx not corrugate 0, corrugate 1.
17. Calyx fusion ≤50% 0, >50% 1.
18. Calyx lobe axils separated 0, united 1.
19. Longest corolla tube ≤15 mm 0, >15 mm 1.
20. Ribbon hairs present in corolla 0, absent 1.
21. Staminode absent 0, present 1.
22. Style pubescent 0, glabrous 1.
23. Stigma subcapitate 0, capitate 1.

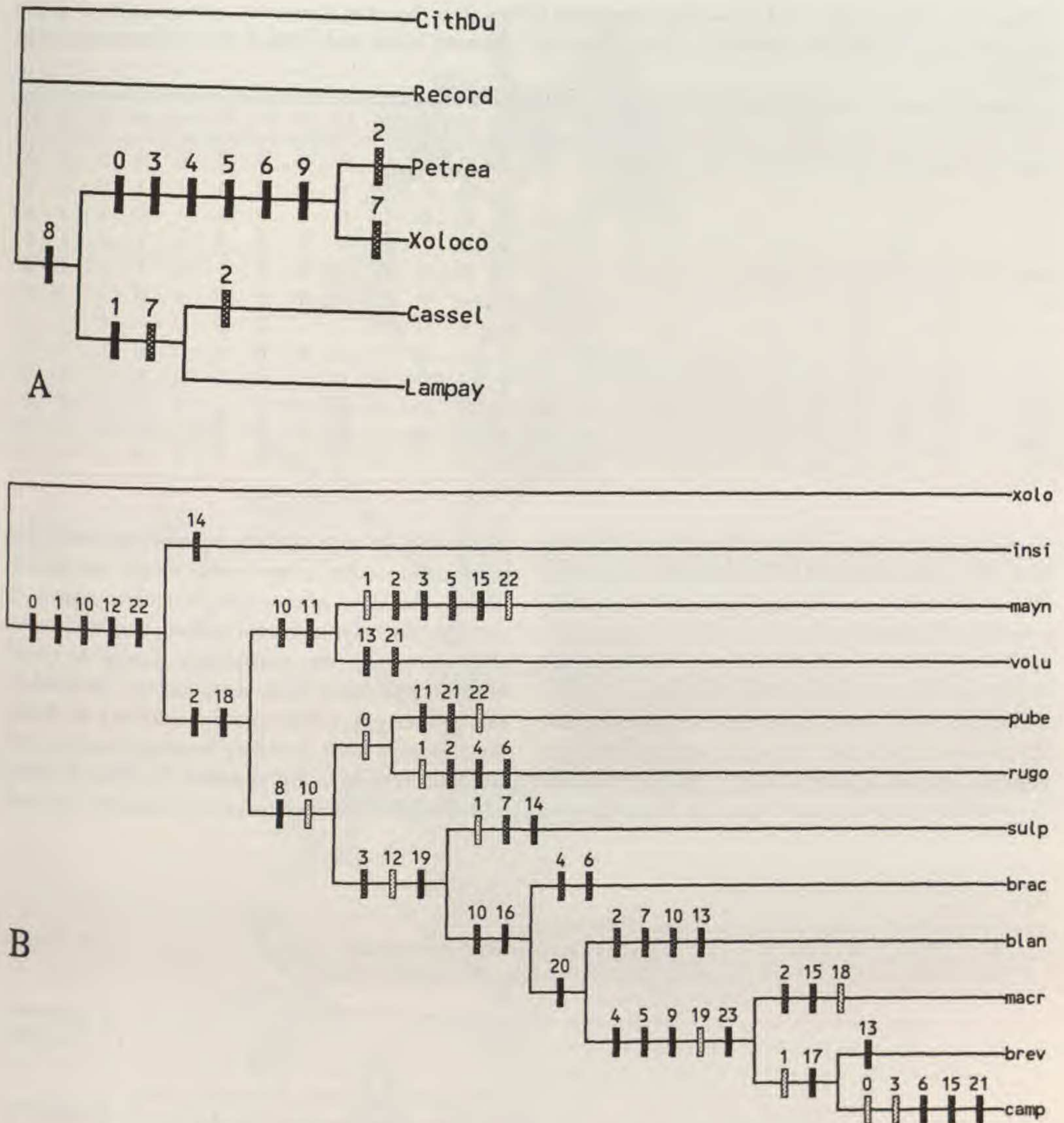


FIGURE 12. —A. Most parsimonious tree for relationships of the tribe *Petreeae*.—B. Most parsimonious tree for relationships of the species of the genus *Petrea*.

ened, brochidodromous. Inflorescence axillary or terminal, racemose, the rachis with several pairs of additional bractlets in the lower portion not subtending any flowers; bracts caducous. Flowers perfect, hypogynous, subtended by one or more bracteoles; torus mostly swollen; calyx gamosepalous, violet, purple, pale green, or white, mostly actinomorphic, the tube cylindric or campanulate, its rim normally 5-lobed, the lobes sometimes unequal, mostly longer than the tube, alternate with the petals; calycinal crest present in the inner part of the lobes, 5-lobed, the lobes alternate with the sepals; corolla gamopetalous, hypocrateriform,

usually darker blue or purple than the calyx, sometimes white or yellow, occasionally with white or yellowish spot in the center, slightly zygomorphic, warty pubescent inside, the tube cylindric, urceolate, or infundibular, the limb rotate, normally 5-lobed, the lobes mostly of 2 sizes, much shorter than the calyx-lobes and alternate with them; stamens 4, didynamous, sometimes homodynamous, inserted near the middle of the corolla-tube, included; the filaments are wiry or stout flattened; anthers oblong or ovate, dorsifixed near the base, 2-celled, opening by longitudinal slits, introrse, the connective enlarged, often surpassing the thecae;

TABLE 7. Data matrix for the species of the genus *Petrea*. The character states 0 = plesiomorphic, 1 & 2 = apomorphic. See Table 6 for definitions of characters and character states and Table 3 for unabbreviated species epithets.

Taxa	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Xolo	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
blan	1	1	2	1	0	0	0	1	1	0	2	0	0	1	0	0	1	0	1	1	1	0	1	0
brac	1	1	1	1	1	0	1	0	1	0	1	0	0	0	0	0	1	0	1	1	0	0	1	0
brev	1	0	1	1	2	1	0	0	1	1	1	0	0	1	0	0	1	1	1	0	1	0	1	1
camp	0	0	1	0	2	1	1	0	1	1	1	0	0	0	0	1	1	1	1	0	1	1	1	1
insi	1	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0
macr	1	1	2	1	2	1	0	0	1	1	1	0	0	0	0	1	1	0	0	0	1	0	1	1
mayn	1	0	2	1	0	1	0	0	0	0	2	1	1	0	0	1	0	0	1	0	0	0	0	0
pube	0	1	1	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0
rugo	0	0	2	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0
sulp	1	0	1	1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0
volu	1	1	1	0	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1	0	0	1	1	0

staminode sometimes present; basal nectariferous disk ca. 1 mm long and 2.5 mm wide; ovary superior, subglobose or oblong, borne on a conspicuous disk, 2-celled, each cell 1-ovulate, compound, but 1-carpellate through the abortion of one carpel; ovules lateral, ascending, hemianatropous, or orthotropous; style included in the corolla-tube, usually shorter than the stamens, single, terminal, filiform; stigma capitate, mostly oblique, bilobed. Fruit within the persistent calyx, the fruiting-calyx

incrassate, its tube slightly accrescent, mostly losing its blue color, very hard, tough and usually ribbed, the lobes accrescent, reticulate-veined, divergent, the calycinal crest callose, curving inwards and converging, thus completely closing the mouth of the calyx-tube; fruit drupaceous, enclosed by the mature calyx, the exocarp leathery or fleshy, the endocarp hard, 2-celled, forming 2 stones, each stone 1-seeded, or by abortion the fruit 1-stoned and 1-seeded; seeds laterally or apically attached.

KEY TO THE LIVING SPECIES OF *PETREA*

- 1a. Inflorescence mainly axillary; leaf apex mostly rounded.
 2a. Pedicels with a pair of leaflike bracteoles; calyx lobe sinuses opened 5. *P. insignis*
 2b. Pedicels without a pair of leaflike bracteoles; calyx lobe sinuses closed.
 3a. Climbing plants; clavate glandular hairs present.
 4a. Leaves ternate; the longest petiole ≤ 10 mm 7. *P. maynensis*
 4b. Leaves opposite; the longest petiole > 10 mm 11. *P. volubilis*
 3b. Erect plants; clavate glandular hairs absent.
 5a. Tree with mature leaves not bullate; with aborted racemes; staminode present 8. *P. pubescens*
 5b. Shrub with mature leaves bullate; without aborted racemes; staminode absent 9. *P. rugosa*
- 1b. Inflorescence mainly terminal; leaf apex mostly cuspidate.
 6a. Calyx lobes of 2 sizes of lobes; corolla yellow; stem winged 10. *P. sulphurea*
 6b. Calyx with equal-sized lobes; corolla blue; stem not winged.
 7a. Mature leaves bullate; mostly with three inflorescences at the tips of branches 2. *P. bracteata*
 7b. Mature leaves smooth or pitted but not bullate; with one inflorescence at the tips of branches.
 8a. Mature leaves smooth, the stomata not in pits; the longest corolla tube > 15 mm long 1. *P. blanchetiana*
 8b. Mature leaves pitted, the stomata in pits; the longest corolla tube ≤ 15 mm long.
 9a. Longest petioles > 10 mm; calyx not corrugate; calyx fusion $\leq 50\%$; calyx lobe sinuses opened 6. *P. macrostachya*
 9b. Longest petioles ≤ 10 mm; calyx corrugate; calyx fusion $> 50\%$; calyx lobe sinuses closed.
 10a. Liana; the longest floral pedicel > 15 mm; calyx pubescent 3. *P. brevicalyx*
 10b. Shrub; the longest floral pedicels ≤ 15 mm; calyx glabrous 4. *P. campinae*.

1. *Petrea blanchetiana* Schauer in DC., Prod. 11: 617-618. 1847. TYPE: Brazil. Bahía: Martius 1029 (lectotype, selected by Rueda

(1993), BR; isoelectotypes, BM, G(2), GH, L, LE, M(2), MO, NY, S; photo of isoelectotype, NY). Figure 13.



FIGURE 13. Habit of *Petrea blanchetiana* Schauer (Nevers 5812).

- Petrea peruviana* Moldenke, Feddes Repert. 43: 206. 1938. TYPE: Peru. Loreto: Mishayacú, near Iquitos, 100 m elev., Dec. 1929 (fl, fr), *Klug 637* (holotype, NY; isotypes, F, US).
- Petrea peruviana* var. *acuminata* Feddes Repert. 43: 208. 1938. TYPE: Peru. Loreto: Iquitos, Jan. 1975, *Melin s.n.* (holotype, S; fragment of holotype, NY; photos of holotype and isotype, NY, TEX, US).
- Petrea morii* Moldenke, Phytologia 45: 469. 1980. TYPE: Panama. San Blas: El Llano Cartí road, 12 Apr. 1925, *Mori & Kallunki 5521* (holotype, US; isotype, MO; fruits of isotype and photo of holotype, TEX).
- Petrea algentryi* Moldenke, Phytologia 54: 67. 1983. TYPE: Colombia. Chocó: Río Tagachi, 12 km W of Río Atrato, 19 June 1982, *Gentry et al. 37075* (lectotype, selected by Rueda (1993), MO; isolecotype, MO).

Liana; the branchlets tetragonal, puberulent. Leaves with petioles 3–15 mm long, puberulent; blades ovate-elliptic, 6–30 cm long, 3–16 cm wide, the apex acute to acuminate, the base acute to subcordate, membranous, smooth to the touch or very slightly roughened, sometimes slightly pubescent on both surfaces, sometimes impressed-punctate on both surfaces. Inflorescences terminal, racemiform, 8–53 cm long, 3–9 cm wide; pedicels 10–31 mm long, often bearing a bracteole. Flowers with the calyx-tube 5–7 mm long, the base 2–3 mm wide, the apex 4–7 mm wide, corrugated, slightly pubescent, 5-lobed, the lobes membranous, obovate, 16–25 mm long, 2–4 mm wide at base, 5–9 mm wide at the widest point, the apex acute, glabrous; calycinal crest with the lobes ca. 1.5 mm long, 2 mm wide at base, the apex blunt, glabrous; corolla fragrant, 13–18 mm long, the base 1.5–2.5 mm wide, ampliate to 7–20(–50) mm across at apex, pubescent, the limb rotate, 5-lobed, the anterior lobe largest, the remaining lobes similar; stamens 4; filaments ca. 2 mm long, sparsely pilose; anthers ca. 1.5 mm long and 0.6 mm wide; ovary oblong, ca. 2 mm long and 1.5 mm wide, glabrous; style 2.5 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 6). This species ranges from Panama to Venezuela, French Guiana, Brazil, and Peru. In Peru it is very common on white sand soils, growing up to 6 m in chamizal forest or up to 20 m on more fertile soil in varillal forest. It is sometimes found in patches; for example, Nevers (sub 3959) reported seven individuals in full bloom growing within 150 m of each other in Panama.

Selected specimens examined. PANAMA. **San Blas:** El Llano–Cartí road, 24.5–25 km from Panamerican hwy., near continental divide, 12 Apr. 1975, *Mori & Kallunki 5521* (MO, TEX, US). COLOMBIA. **Vaupés:** Alto Vaupés, near Miraflores, 300 m, 2, 4, 5 Feb. 1944, *Gutiérrez & Schultes 760* (COL, GH, NY, S). VENEZUELA. **Amazonas:** Río Negro, 1–4 km E of Cerro

Neblina, Camp on Río Mawarinuma, 140 m, 10 Feb. 1984, *Liesner & Funk 15826* (MO). FRENCH GUIANA. **Cayenne:** forest around the runway, 10 m, 10 Apr. 1983, *Kahn & Granville 5400* (BR, CAY(3), U); Creek Mulet Mort, S of Saul, 10 Feb. 1966, *Oldeman 2012* (CAY, TEX). PERU. **Amazonas:** Valle del Río de Santiago, Quebrada Caterpiza, 2–3 km behind Caterpiza community, 200 m, 29 Nov. 1979, *Tunqui 171* (MO, TEX). **Loreto:** Prov. Maynas, Tamshiyacu, 29 Nov. 1980, *Ayala et al. 2894* (F, MO, NY); Alpahuayo, 4 June 1986, *Ayala & Rimachi 4509* (MO); Via Nauta–Iquitos, 28 June 1979, *Díaz & Jaramillo 1243* (MO); Mishana, between Río Nanay and Río Itaya, 130 m, 29 Nov. 1977, *Gentry et al. 20982* (MO); Río Momón behind tourist camp, vicinity of Iquitos, 120 m, 12 May 1978, *Gentry et al. 21721* (F, MO(2), TEX); Iquitos, Mishuyacú, 100 m, Oct.–Nov. 1929, *Klug 170* (F, NY, US); Zungaro Cocha road, near Quebrada Shushuna, 160 m, 4 Feb. 1983, *Rimachi 6539* (BR, NY); Puerto Almendras, 7 July 1992, *Rueda & Ruiz 701* (MO); Fernando Lores, Tamshiyacu, Constancia, 50 m, 9 July 1992, *Rueda & Ruiz 730* (MO). BRAZIL. **Amazonas:** Amapá, Rio Oiapoque, Igarape Nataia 5 Feb. 1950, *Frões 25871* (IAN, NY, S); São Paulo de Olivença, basin of Creek Belém, 26 Oct.–11 Dec. 1936 *Krukoff 9112* (NY). **Bahia:** 1857, *Blanchet s.n.* (BR(2)). **Distrito Federal:** Brasília, *Blanch s.n.* (S); 1842, *Dupre s.n.* (P). **Pará:** 25 Sep. 1928, *Sampaio 5092* (NY, R). **Roraima:** Rio Maturuca, Missao Salesiana, 1 Jan. 1966, *Silva & Brazao 60806* (CAY).

Local names and uses. In Panama, “kwagi tupa”; Peru, “lija sachá,” “lija caspi,” “sanango sachá”; Venezuela, “tostadito.” No use is known.

Petrea blanchetiana resembles *P. bracteata* but has smooth leaves and one inflorescence at the branch tip, as opposed to bullate leaves and mostly three inflorescences in *P. bracteata*. In addition, in the latter species the longest pedicels are less than 15 mm and in *P. blanchetiana* they are much longer than 15 mm. This species has the largest flowers known in the genus, up to 5 cm across when fresh.

2. *Petrea bracteata* Steudel, Flora 26: 764. 1843. TYPE: Suriname. Apr. 1842, *Hostmann & Kappler 39* (lectotype, selected by Rueda (1993), W; isolecotypes, B, BM, C, F, G(2), K, LE, MO, S, U, W(2); fragments of isolecotype, MO, NY; photos of isolecotype, MO, NY, TEX; photos of two isolecotypes overlaid in the same picture, NY). Figure 14.

Petrea martiana Schauer in DC., Prod. 11: 620. 1847. TYPE: Brazil. Pará: San Antonio de Gurupá, 3–16 Sep. 1819, *Martius s.n.* (lectotype, selected by Rueda (1993), M; fragment of lectotype, NY).

Petrea schomburgkiana Schauer in DC., Prod. 11: 619. 1847. TYPE: Guyana. 1840–1844, *Schomburgk 108* (photolectotype, selected by Rueda (1993), MO; duplicate photos, TEX, US).

Petrea martiana var. *glabrescens* Moldenke, Phytologia 32: 458. 1975. TYPE: Brazil. Pará: Curucambam, Obidos, 9 June 1926, *Ducke 14291* (holotype, NY).

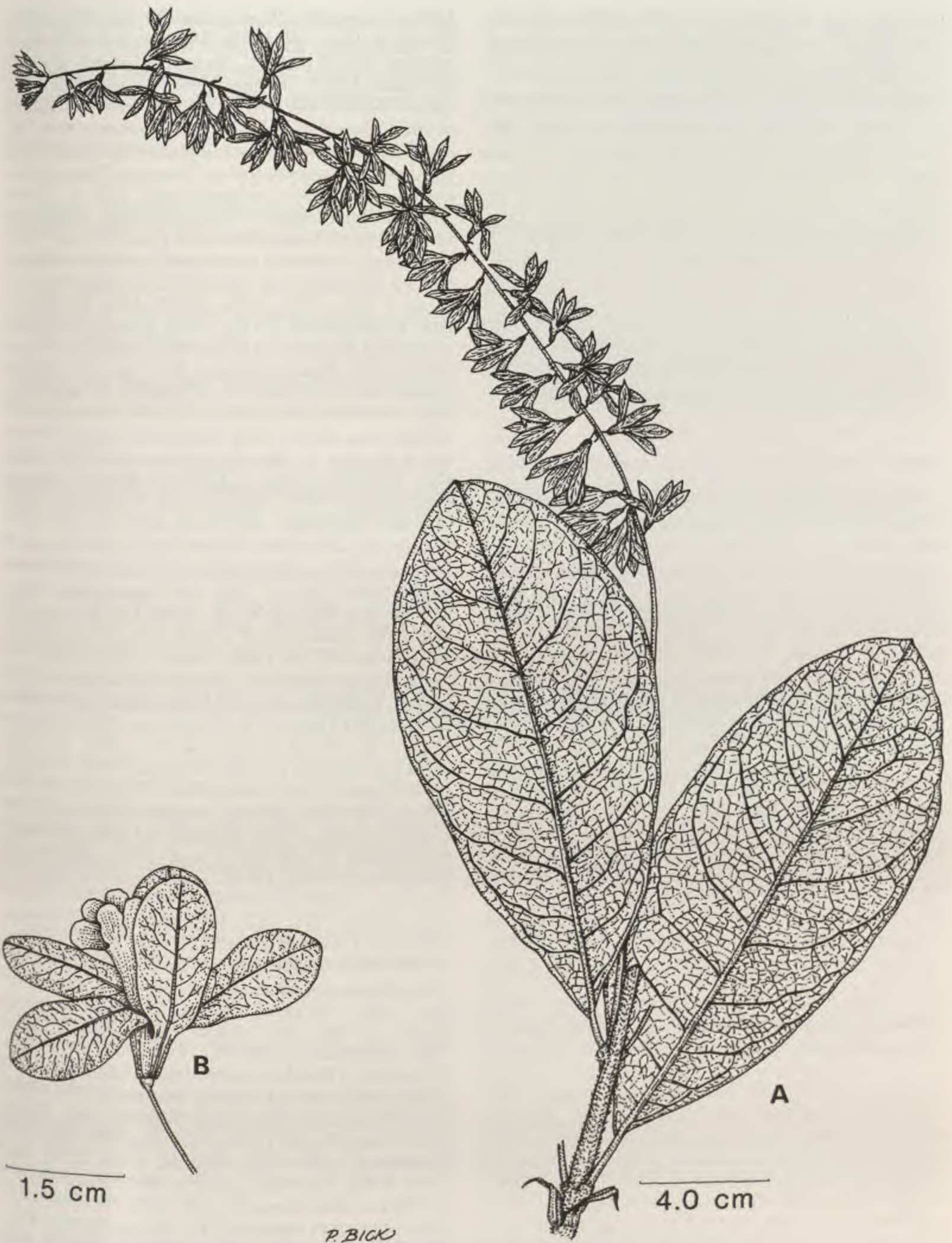


FIGURE 14. *Petrea bracteata* Steudel (Feuillet 739).—A. Habit.—B. Flower.

Liana; the branchlets tetragonal, short-pubescent; often with one or two leaflike bracts below the petioles or on the outer side of the branchlets. Leaves with petioles 5–20 mm long, short-pubescent; blades ovate-elliptic, 3.5–30 cm long, 1.8–13.5 cm wide, the apex obtusely acute or very

short-acuminate, the base acute to broadly rounded, membranous or subcoriaceous, very densely asperous on both surfaces, bullate beneath when mature. Inflorescences mainly terminal, racemiform, 19–50 cm long, 4–9 cm wide; pedicels to 1 cm long; puberulent. Flowers with the calyx-tube

4–5 mm long, the base ca. 3 mm wide, 4–5.5 mm wide at apex, corrugated, short-pubescent, 5-lobed, the lobes membranous, oblong or elliptic, 11.5–17 mm long, the base 2–3 mm wide, the widest point 3–10 mm wide, the apex rounded or acute, glabrous; calycinal crest with the lobes ca. 1.5 mm long, 1 mm wide at the base, the apex blunt, glabrous; corolla with throat white and hairy, 8.5–20 mm long, the base 2–3 mm wide, ampliate to 6.5–9 mm at the apex, pubescent, the limb rotate, 5-lobed, the anterior lobe larger, the remaining lobes similar; stamens 4; filaments ca. 2 mm long, sparsely pilose; anthers ca. 2 mm long; ovary obovate, ca. 2 mm long and wide, glabrous; style ca. 2.5 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 9). This species is found from Venezuela and the Guianas to Brazil and Peru.

Selected specimens examined. VENEZUELA. **Amazonas:** Río Orinoco, between Tama-Tama and Caño Manaviche, 150 m, 19 Apr. 1954, *Level 5* (NY); Río Cunucunuma, 30 km from Playa Alta, 200 m, 28 Dec. 1950, *Maguire et al. 30444* (NY, S, US). GUYANA. Groete Creek, 10 Oct. 1948, *Atkinson 4* (BM, MICH); Essequibo Islands, Bartica, on bank of Essequibo river, 5 Nov. 1948, *Atkinson 17* (BM); Mazaruni-Potaro, junction of Mazaruni and Cuyuni rivers, July 1914, *Graham 254* (NY, US); St. Elie road, 4 Mar. 1978, *Raynal-Roques 20183* (CAY). SURINAME. Brokopondo, along trail from Brownsveg to Mazaroni peak, 300 m, 11 Feb. 1963, *Boer 642* (BR, U); Brokopondo natural reserve, Brownsberg small fall above Mazaroni fall, 15 Mar. 1976, *Tjon-Lim-Sang & Wiel 188* (U); Marowijne, Nassua mountains, Marowijne river, 475 m, 10 Jan. 1955, *Cowan & Lindeman 39221* (B, NY, S, U); Bakhuis-mountains, SW slopes, 818 m, 4 Mar. 1966, *Florschütz & Maas 3145* (U). FRENCH GUIANA. **Cayenne:** road St. Laurent to Paul Isnard, 15 Nov. 1982, *Billiet & Jadin 1697* (BR, CAY, U); Sinnamary River, 25 Feb. 1988, *Billiet & Jadin 4481* (BR, CAY); 20 km of Petit Saut road, 40 m, 26 Feb. 1988, *Billiet & Jadin 4510* (BR, CAY); S of St. Jean du Maroni, 19 Feb. 1956, *Cremers 7673* (CAY); region of Paul Isnard, Mont du Decou Decou, 400 m, 8 Sep. 1983, *Cremers 8175* (CAY, U); Piste de Saint-Elie, 22 Apr. 1984, *Sauvain 119* (CAY(3), U). PERU. **Cerro de Pasco:** Oxapampa, Palcazú Valley, Iscozacín, above PEPP project camp; forestry experimental strip, 6 Apr. 1985, *Salick 7251* (MO). **Loreto:** Maynas, Explornapo Camp, Quebrada Sucusari, N side, tributary of Río Napo, 140 m, 14 June 1986, *Gentry et al. 54345* (MO); road Nauta-Iquitos, 3 km N of Nauta, 140 m, 28 June 1979, *Díaz & Jaramillo 1243* (MO); Mishana, trail from village to Campamento 1, 140 m, 22 July 1980, *Gentry et al. 28928* (TEX); Río Santa María, trail E of Sencoya, 100 m, 9 Feb. 1979, *King 493* (F); Nauta, Quebrada Sapira, near Florida, ca. 8 km above Nauta, 26 May 1979, *McDaniel 22533* (F, BR); Explorama forest in the tourist camp of Explorama, 110 m, 30 June 1992, *Rueda & Ruiz 590* (MO); forest of the Research Institute of Peruvian Amazon, km 21 on road Quistococha-Nauta, 5 July 1992, *Rueda & Ruiz 628* (MO); Tahuampa forest around the town of Manacamiri, 6 July 1992, *Rueda & Ruiz 681* (MO); Fernando

Lores, Tamshiyacu, Constanca, 50 m, 9 July 1992, *Rueda & Ruiz 720* (MO); Requena, 4 km NE of Arboretum Jenaro Herrera, along Río Ucayalí, Quebrada de Colima, 180 m, 13 Nov. 1981, *Spichiger & Encarnación 1039* (G(4), MO, NY); Bora native community of Brillo Nuevo, ca. 150 km of Yaguasyacu river, 106 m, 13 Nov. 1981, *Treacy & Alcorn 519* (F). **San Martín:** Lamas, Convento, trail to Tiyacu and Nuevo Lamas, km 68 of Tarapoto-Yurinawas road, 200 m, 19 Apr. 1986, *Knapp & Mallet 7120* (F). BRAZIL. **Amazonas:** km 148, on Manaus-Caracarái road, 24 Sep. 1973, *Bisby et al. P18063* (NY); Uaupes, San Gabriel de Cachoeira, 19 Feb. 1975, *Cordeiro 220* (IAN); Esperanza, Río Javari, 3 Feb. 1942, *Ducke 872* (F, IAN, MO, R); Manaus, Ducke reserve, 23 Jan. 1963, *Lanna & Castellano 338* (TEX); Río Javari, 8 Aug. 1973, *Lleras et al. P17213* (INPA, NY); Manaus, between Boa Vista road and Itacoatiara road, ca. 60 km N of Manaus, 17 Apr. 1981, *Lowe 4087* (INPA); Río Negro, between Manaus and São Gabriel along BR 307, São Gabriel, near Igarape Freitas and at Equator, 17 July 1979, *Poole 2021* (INPA, MG, NY); Manaus-Igarape, 5 km from Manaus-Caracarái road, 26 Jan. 1971, *Prance et al. 11454* (NY, TEX); Cachoeira Republica, Rio Curuquete, 25 July 1971, *Prance et al. 14620* (F, NY, S, TEX); Río Negro, road from Camanaus to Uaupes airport, 30 Oct. 1971, *Prance 15858* (INPA, NY, S, TEX, US); base of Serra Araca, 0–3 km S of Central Masiff, 3 km E of Río Javari, 8 Feb. 1984, *Prance et al. 28906* (NY); Totobi, basin of Río Demeni, 25 Feb. 1969, *Prance 10236* (F, MG, NY, R, S); Manaus-Caracarái road, km 45, Campina reserve, 11 Dec. 1980, *Renner 57* (INPA, TEX, US); Río Negro São Gabriel, 19 Feb. 1975, *Ribeiro s.n.* (TEX, S); Igarape da Cachoeira Alta do Taruma, 28 Dec. 1961, *Rodrigues & Chagas 4041* (NY). **Mato Grosso Norte:** Jatuarana river, Machado river region, Dec. 1931, *Krukoff 1575* (BM, G, GH, S, U). **Pará:** Oriximina, left margin of Rio Mapuera, 3 Aug. 1985, *Almeida 213* (MG); left margin of Cachoeira Vira-Mundo, 5 Aug. 1985, *Almeida 229* (MG); Río Trombetas km 54, access road from Cachoeira Porteira to Perimetral do Norte, 24 May 1974, *Campbell et al. P22257* (NY, TEX, US); basin of Río Trombetas, 3 km S of Cachoeira Porteira, 8 June 1974, *Campbell et al. P22570* (M, MG, MO, NY); Oriximina, Río Trombetas, left margin across Mineração Santa Patricia, 13 June 1980, *Cid et al. 1481* (INPA); Río Branco de Obidos, 11 Dec. 1913, *Ducke 15127* (BM(2), G); Río Negro, Alto Padauri, 19 Oct. 1947, *Froes 22628* (IAN, NY); Estrada BR-163, near Rio Cuminamirin, 74 km of Oriximina, 60 m 3 Apr. 1980, *Martinelli 6757* (INPA, NY); BR 163, km 1229; Cuiaba-Santarem hwy., 18 Nov. 1977, *Prance et al. P25519* (F, GH, HBG, MG, MO). **Rondônia:** basin of Río Madeira, 8 km NE of Porto Velho, 7 Nov. 1968, *Prance et al. 8256* (F(2), MG, NY, S, TEX); Cuiaba-Santarem, km 1180, 17 Nov. 1977, *Silva et al. 240* (MG, NY, U); Tapajó National Park, Villa Pimental, 25 Nov. 1978, *Silva & Rosario 3939* (MG, NY).

Local names and uses. In Brazil “viuvinha”; Guyana, “sandpaper”; Peru, “ana yo ki,” “hierba aspera”; Suriname, “batjetje.” In Peru its leaves are used to clean out guns; also the leaves are soaked in water until the liquid is black and then applied to snakebites (*Salick 7251*).

The presence of bullate mature leaves (see Fig. 14B) in *P. bracteata* makes this species easy to separate from the closely related species *P. blanchetiana* (see discussion under the latter species).

3. ***Petrea brevicalyx*** Ducke, Bull. Mus. Hist. Nat. Paris, ser. 2, 4: 748–749. 1932. TYPE: Brazil. Amazonas: Manaus, Igarapé da Cachoeira Grande, at the borders of swamps and on river shores, *Ducke s.n.* (lectotype, selected by Rueda (1993), NY; isolectotypes, G, K, RB, S, U, US; photos of isolectotypes, GH(2), NY, TEX). Figure 15.

Liana; the branchlets tetragonal or subterete, with minutely glandular-based hairs. Leaves with petioles 0.5–3 cm long, short-pubescent; blades elliptic or obovate-oblong, 5–16 cm long, 3–9 cm wide, the apex obtuse, the base acute or attenuate, coriaceous, rough to the touch, minutely pubescent above, intricately pitted beneath with abundant short hairs in the pits. Inflorescences mainly terminal, racemiform, 12–55 cm long, 2–3.5 cm wide; pedicels 0.5–2 cm long, minutely pubescent; bracts caducous. Flowers with the calyx-tube 6–10 mm long, corrugated, minutely puberulent, 5-lobed, the lobes membranous, triangular-ovate, 2–3 mm long; calycinal crest with the lobes ca. 1 mm long, the apex truncate; corolla deep violet, glandular short pubescent, 8–15 mm long, one of the lobes slightly longer than the others; stamens 4; the filaments ca. 1.5 mm long, sparsely pilose; anthers oblong; ovary oblong; style ca. 2.5 mm long, glabrous; stigma capitate, bilobed.

Distribution (Fig. 11). This species is only known from Brazil (Amazonas), growing in igapó (black-water inundated forest) on sandy river banks.

Specimens examined. BRAZIL. Amazonas: Manaus, Estrado do Francês Novo, 31 Jan. 1959, *Chagas 39* (MG, UB); Igarapé da Cachoeira Grande, 7 Dec. 1927, *Ducke s.n.* (K, G, NY, S, U, US), 29 Jan. 1936, *Ducke 140* (F, GH, IAN, MO, NY, UC, US), 22 Feb. 1945, *Frões 20501* (IAN, NY, US); ZF3, BR 174, Fazenda Porto Alegre, 20 Mar. 1986, *Garcia 18* (MG), Nov. 1918, *Kuhlmann 2276* (NY, SP); road Manaus to Manacapuru, km 35, 5 Jan. 1967, *Prance et al. 3912* (F, INPA, NY, S); Rio Negro, Dec. 1901, *Ule 5982* (G, NY).

Local names and uses. In Brazil “cipó de fogo,” “viuvinha.” No use is known. It is most closely related to *P. campinae* (see discussion under that species).

4. ***Petrea campinae*** Rueda, Novon 4: 417. 1992. TYPE: Brazil. Roraima: along the road

from Manaus to Caracarái, km 350, left side, 00°06'N, 60°40'W, 12 Feb. 1979 (fl), *Rodríguez et al. 10100* (holotype, MG; isotypes, COL, INPA; drawing of holotype, MO). Figure 16.

Shrub 1.5–5 m tall; the branchlets tetragonal or subterete, minutely pubescent, pith well developed. Leaves with petiole 3–8 mm long; blades elliptic, 5–10 cm long, 1.5–6 cm wide, the apex apiculate or truncate, the base obtuse, coriaceous, asperous, glabrous above, intricately pitted beneath with abundant short hairs in the pits. Inflorescences mainly terminal, racemiform, 10–22 cm long, 2–5 cm wide; bracts setaceous to foliaceous; pedicels 6–10 mm long, pubescent. Flowers with calyx corrugate, glabrous, 5-lobed, unequal, rounded, 4–8 mm long; calycinal crest with the lobes ca. 1.5 mm long; corolla 1.2–1.5 cm long, the limb lobed, 5–8 mm wide, the lobes 5, ovate, 3–6 mm long, unequal; straight or curved, blue, glandular-pubescent; stamens 4, the filaments ca. 1.5 mm long, the anthers oblong, staminode sometimes present; ovary globose, the style 2–3 mm long, glabrous; the stigma capitate.

Distribution (Fig. 11). This species is only known from a few patches of scrub campina forest on white sand, near km 350 on the Manaus–Caracarái road, in Roraima, Brazil.

Specimens examined. BRAZIL. Roraima: along BR 174, between Manaus and Caracarái, 6 km S of equator, in a campina, 00°04'S 60°40'W, 17 June 1985, *Cordeiro et al. 76* (INPA, SP).

Local names and uses. None reported.

Petrea campinae resembles *P. brevicalyx* in having elliptic leaves that are intricately pitted beneath and a calyx with short rounded lobes. It differs in its erect habit and its unequal calyx lobes twice as long as those of the lianaceous *P. brevicalyx*.

5. ***Petrea insignis*** Schauer, in DC., Prod. 11: 620. 1847. TYPE: Brazil. Pará: exact locality unknown, 1–21 Aug. 1819, *Martius s.n.* (holotype, M). Figure 17.

Petrea duckei Moldenke, Phytologia 1: 469–470. 1940. TYPE: Brazil. Amazonas: lower Rio Negro, Paraná de Anavilhana, on inundated shores, 24 July 1929, *Ducke s.n.* (holotype, NY; isotype, RB).

Liana; the branchlets puberulent-asperulous. Leaves with petiole 3.5–12 mm long, with minute dark brown hairs; blades elliptic, 3–18.5 cm long, 1.5–8 cm wide, the apex acute or obtuse, the base



FIGURE 15. Habit of *Petrea brevicalyx* Ducke (Fróes 20501).

acute or rounded, chartaceous; membranous, somewhat asperous, glossy and glandular above, glabrous beneath except on the minutely pubescent veins. Inflorescences axillary, racemiform, 14–37 cm long; bracts elliptic, apiculate, 6–10 mm long, bractlets leaflike, in pairs on the pedicels; pedicels

3–15 mm long, glandular-puberulent. Flowers with calyx-tube 5–10 mm long, 5-lobed, the lobes petaloid, sinuses between petals opened, obovate, 10–13 mm long, 12 mm wide, puberulent; calycinal crest with the lobes ca. 5 mm long; corolla 12–16 mm long, the limb 5-lobed, one of the lobes slightly

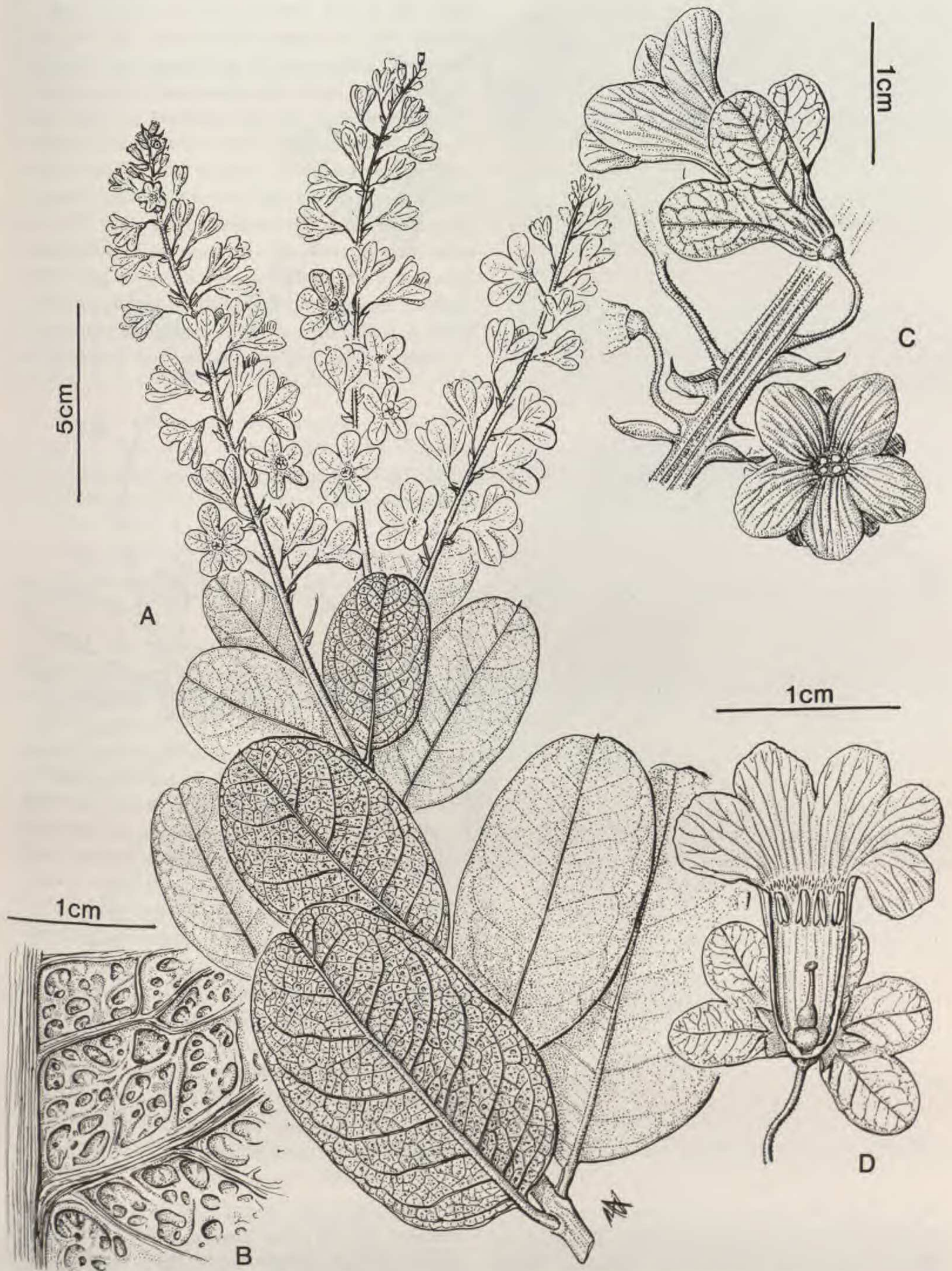


FIGURE 16. *Petrea campinae* Rueda (Rodrigues et al. 10100).—A. Habit.—B. Close up of abaxial leaf surface, showing pits.—C. Flower.—D. Flower, cut longitudinally and laid open.

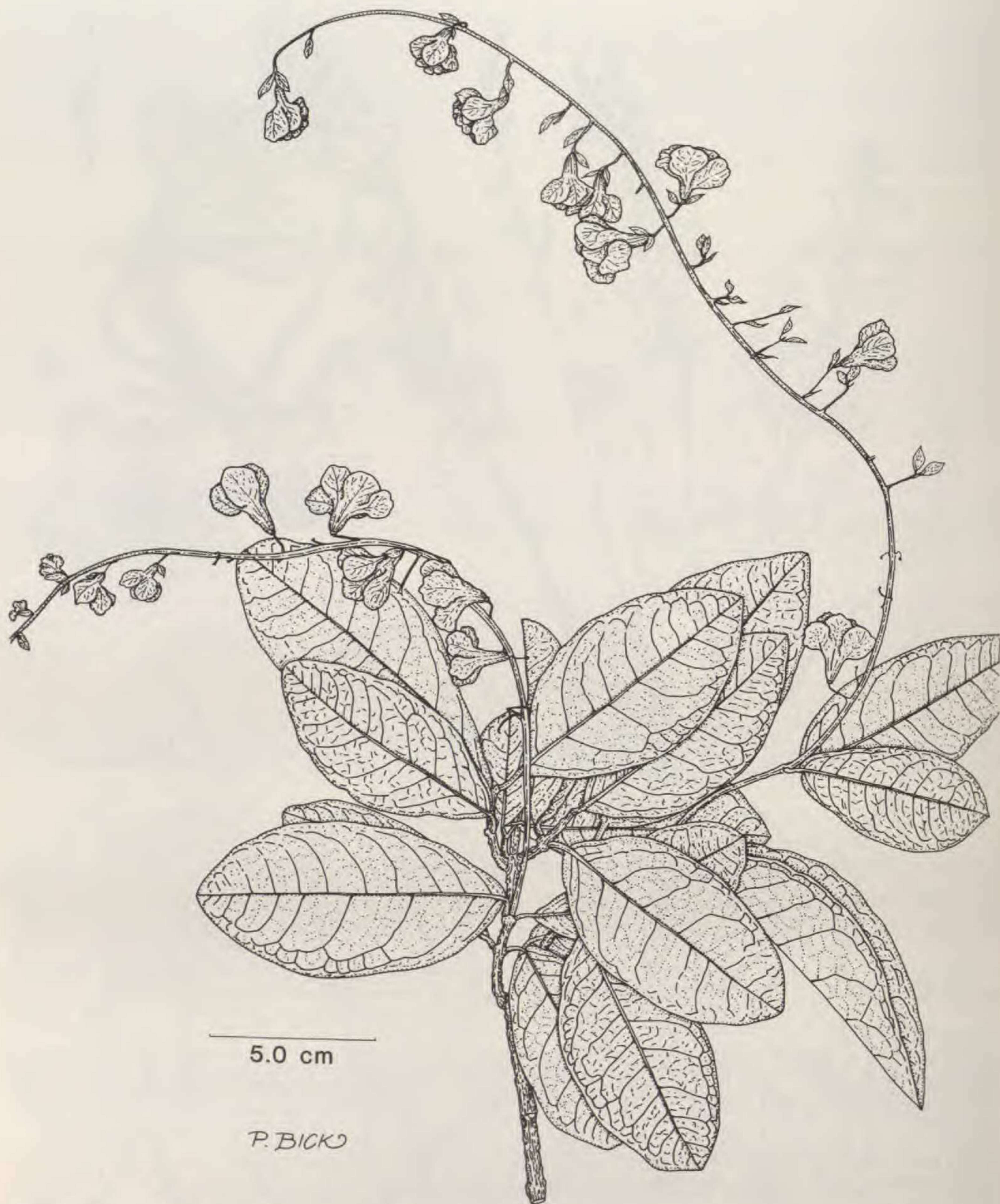


FIGURE 17. Habit of *Petrea insignis* Schauer (Anderson 229).

larger than the others, short-pubescent; stamens 4, filaments ca. 2 mm long, anthers oblong; ovary oblong, the style ca. 3 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 10). This species is endemic to Brazil (Amazonas), growing on white sand river banks, along black-water-flooded rivers.

Selected specimens examined. BRAZIL. Amazonas: Manaus, Francês Novo, 12 Mar. 1956, Chagas

s.n. (TEX); Barcelos, margins of Rio Aracá, 29 July 1985, Cordeiro 307 (SP); Rio Taruma, 14 Aug. 1949, Frôes 25053 (NY(2)); Igarapé Ponta Negra, 22 May 1955, Frôes 29568 (IAN); Rio Negro opposite Manaus, 3-6 km upstream, 8 Apr. 1971, Prance et al. 11768 (NY, TEX, U), 21 June 1882, Schwacke 3638 (G); Rio Negro, river side and small islets of Rio Negro within 100 km upstream from Manaus, 13 Aug. 1987, Tsugaru & Sano B-1001 (NY).

Local names and uses. In Brazil "flor de São Miguel," "viuvinha." No uses have been recorded.

This species is quite distinct and is the sister group to the rest of the genus in the cladistic analysis, thus appearing to be a relict. However, it shares some characters with more advanced species, such as bractlets on the petioles as in *P. sulphurea* and calyx hole sinuses opened as in *P. macrostachya*, but neither of these species has a terminal inflorescence or the leaf apex cuspidate as in *P. insignis*. Whereas the wide geographic distribution of *P. volubilis* has been perceived as supporting its primitive position in the genus, this is not supported by the cladistic analysis. Perhaps this greater distribution of *P. volubilis* is a result of increased dispersability of the lighter calyx.

6. ***Petrea macrostachya*** Benth., *Ann. Nat. Hist.*, ser. 1, 2: 448. 1839. TYPE: Guyana. Along the brook Currapawaak, 1835–1839, *Schomburgk 158* (lectotype, selected by Rueda (1993), K; isoelectotypes, BM, BR, F, G, GH, K(2), LE; fragment of isoelectotype, NY; photos of isoelectotypes, F, MO, TEX). Figure 18.

Liana; the branchlets obtusely tetragonal, minutely pubescent. Leaves with petioles 4–20 mm long, minutely puberulent; blades broadly elliptic or ovate-elliptic, 5–21 cm long, 2.5–15 cm wide, the apex obtuse or acuminate, sometimes apiculate, the base rounded or acute, coriaceous, asperous, glabrous above, intricately pitted beneath with abundant short hairs in the pits, with strongly defined veinlets delimiting the pits. Inflorescences mainly terminal, racemiform, many-flowered, 20–70 cm long; bracts 2–8 mm long; pedicels 4–15 mm long, minutely puberulent. Flowers with the calyx-tube 6–11 mm long, glabrous, 5-lobed, the lobes obovate, 15–35 mm long, 3–10 mm wide, with the sinuses between petals opened; calycinal crest with lobes ca. 1 mm long, the apex obtuse or rounded, glabrous; corolla blue to violet-purple, 8–13 mm long, the lobes 5–12 mm long, one larger than the other 4, the apex rounded, short pubescent; stamens 4; the filaments ca. 2 mm long, the anthers ca. 1 mm long; ovary oblong, 1–2 mm long, glabrous; style ca. 2.5 mm long, glabrous; stigma capitate.

Distribution (Fig. 10). *Petrea macrostachya* is endemic to Guyana, French Guiana, and Suriname, growing in high dense forest, along creeks, savanna edges, in forest of *Eperua* and *Mora* on sand, and in swampy forest. It is common in these habitats, climbing up to 10 m or more in crowns of *Diptotropis* and *Mora* trees, at altitudes up to 800 m.

Selected specimens examined. GUYANA. Mazuruni river, Takutu Creek to Puruni river, 29 Nov. 1944, *Forest Department of Guyana 4854* (NY); Potaro-Siparuni region, approximately 1–3 km SW of Paramakatoi, 650 m, 13 Mar. 1989, *Hahn et al. 5644* (US); Kanuku mountains, along creek, 300 m, 21 Feb. 1985, *Jansen-Jacobs et al. 341* (B, CAY, MO, WIS); upper Demerara region, Mabura hill, 150 m, 16 Sep. 1986, *Pipoly & Boyan 8517* (US); along the brook Currapawaak, 1835–1839, *Schomburgk 158* (BM, BR(2), F, G, GH, K(2), NY); basin of Kuyuwini river (Essequibo tributary), ca. 150 mi. from mouth, 21–26 Nov. 1937, *Smith 2626* (F, G, GH, MAD, U). SURINAME. 9 km N of Lucie river, 12 km W of Oost River, 275 m, 31 July 1963, *Irwin et al. 54511* (F, NY); Sipaliwini savanna area on Brazilian frontier, 3–5 km NW of Meyers farm, at hill foot toward river valley, Feb. 1970, *Oldenburger et al. 1261* (U); Wihelmina mountains, creek valley at the S base of Juliana Top, 5 Aug. 1963, *Schultz 10330* (U, US, WIS). FRENCH GUIANA. Cayenne, E road in the mountains near Neyrat, 4 Feb. 1977, *Cremers 4302* (CAY); on Kourou road near Montsinery road, 18 Apr. 1982, *Fournet 201* (CAY).

Local names and uses. It is called “sandpaper vine” in Guyana. No use is known.

This species is closely related to *P. brevicalyx* and *P. campinae*, which also have pitted leaves. However, *P. macrostachya* is the only species among the three that has the calyx united less than half of the total length and the calyx lobe sinuses opened. This species has the longest rachis in the genus (reportedly to 70 cm, presumably the source of the specific epithet).

7. ***Petrea maynensis*** Huber, *Bol. Mus. Pará.*, 4: 602. 1906. TYPE: Peru. Loreto: Río Ucayalí, between Contamana and Canchahuaya, Nov. 1898, *Huber 1489* (lectotype, selected by Rueda (1993), MG; isoelectotype, RB; fragment of lectotype, F; photo of lectotype, F, NY, TEX). Figure 19.

Petrea longifolia Moldenke, *Feddes Repert.* 43: 197. 1938. TYPE: without locality, date, or collector (holotype, P; isotype, P; fragments of holotype, F, NY; photos of holotype, NY, TEX).

Liana; the branchlets obtusely tetragonal, often striate-costate, short-pubescent. Leaves whorled in 3s or 4s, rarely some decussate-opposite; petioles 5–11 mm long, puberulent; blades elliptic or ovate, 5–32 cm long, 2–9 cm wide, the apex acute or obtuse, the base acute, slightly asperulous on both surfaces. Inflorescences axillary, the racemes 6–50 cm long, 2.5–5 cm wide, with aborted racemes in its axils; pedicels 4–9 mm long. Flowers with the calyx-tube 3–5 mm long, 2–4 mm wide at the base, ca. 5 mm wide at apex, glabrous, 5-lobed, the lobes membranous, oblong, 11–15 mm long,





FIGURE 19. Habit of *Petrea maynensis* Huber (Ferreyra 8100).

FIGURE 18. Habit of *Petrea macrostachya* Benth. (Schulz 10330).

2–4 mm wide, the apex acute, glabrous; calycinal crest with the lobes ca. 2.5 mm long, and ca. 1 mm wide, the apex acute, glabrous; corolla fragrant, with white spots at throat, corolla-tube ca. 8 mm long, the base ca. 2.5 mm wide, to ca. 6 mm at apex, short-pubescent, the limb sometimes with dark blue lines, rotate, 5-parted, the anterior lobe largest, and sometimes white with blue margins, the remaining lobes similar, smaller, and light blue; stamens 4; filaments ca. 1.5 mm long, glabrous; anthers ca. 1 mm long and ca. 0.5 mm wide, the connective ending with an erect apiculation, glabrous; ovary oblong, ca. 1.5 mm long and ca. 1 mm wide, short-pubescent; style ca. 2 mm long, short-pubescent; stigma subcapitate, bilobed.

Distribution (Fig. 7). This species occurs from Colombia through Ecuador, Brazil, Peru, and Bolivia, growing on non-alluvial red clay soil, on river banks, and forested hills in tropical rainforest and in flood plain forest (varzea). It has been reported from altitudes from 100 to 750 m, sometimes occurring in forest characterized by scattered huge emergent trees of *Bertholletia excelsa* Humboldt & Bonpland.

Selected specimens examined. COLOMBIA. **Cundinamarca:** Medina, along left margin of Río Humea, 450 m, 4 Mar. 1987, *Lozano 5426* (COL). **Meta:** La Macarena, S side of Río Guayabero, 14 Mar. 1959, *Barclay 7146* (MO). **Vaupés:** near Miraflores, 300 m, 8, 10, 14 Feb. 1914, *Gutiérrez & Schultes 783* (COL, GH). ECUADOR. **Morona-Santiago:** Gualaquiza, Misión Bomboiza, 750 m, 27 Sep.–4 Oct. 1967, *Sparre 19187* (UEC). **Napo:** Río Napo & Río Huabuno junction, 450 m, 11 June 1985, *Marles EE80* (F, MO); Jatun Sacha reserve, trails 1 and 3, near Río Chinguipino, 380 m, 11 Aug. 1992, *Rueda 1128* (MO); Reserva de Producción Faunística Cuyabeno, 1 km N of Laguna Grande, trail behind the Cuyabeno Station, Apr.–Oct. 1988, *Paz y Miño 81.012* (MO). PERU. **Amazonas:** Río Cenepa, Huampami, ca. 5 km E of Quebrada Chigki Shinuk, 200 m, 11 Aug. 1978, *Ancuash 1388* (F, MO, TEX); Río Santiago, 180 m, 14 Nov. 1979, *Tunqui 53* (MO, TEX(2)). **Huanuco:** near Puente Tulumayo, road Tingo Maria-Pucallpa, 700 m, 2 Oct. 1950, *Ferreyra 8100* (MO, US); Pachitea, Honoria forest in San Marcos, Turnavista, 350 m, 1 Aug. 1968, *Schunke 2131* (F, G, NY, US). **Loreto:** Yurimaguas, road to Tarapoto, 150 m, 15 Sep. 1948, *Ferreyra 4496A* (MO); Fernando Loes, Tamshiyacu, trails between Constancia and Serafin, 50 m, 10 July 1992, *Rueda & Ruiz 808* (MO). **Madre de Dios:** Tambopata, Río Tambopata reserve, at mouth of Río D'Orbingy, 250 m, 2 Mar. 1981, *Gentry & Young 31877* (MO, TEX); Manu National Park, Cocha Cashú uplands, 400 m, 11 Sep. 1986, *Nuñez 6083* (MO). **San Martín:** Tocache Nuevo, SE of Tocache Nuevo airport, 400 m, 19 Jan. 1970, *Schunke 3682* (F, G, NY, US). BRAZIL. **Acre:** Canamari, downstream from Cruziero do Sul, 150 m, 23 Aug. 1986, *Croat 62570* (MO); 12 km from Río

Branco, on Rio Branco-Porto Velho road, 30 Sep. 1980, *Lowrie et al. 291* (GH, MG, MO, NY). **Amazonas:** São Paulo de Olivença, Rio Solimoes, 2 Feb. 1937, *Ducke 35657* (G, NY, P); Rio Jandiatuba, from mouth to 10 km upstream, 26 Feb. 1977, *Mori et al. 9131* (NY, U, US). **Mato Grosso Norte:** near scientific center Aripuana, 5 Sep. 1976, *Andrade 3292* (UEC); 200 km NW of Cuiaba, 200 m, 26 Sep. 1963, *Maguire et al. 56867* (F, NY, TEX, US). **Pará:** Belém, 12 Jan. 1928, *Ducke 22543* (NY). **Rio de Janeiro:** São Paulo de Olivença, Rio Solimoes, 2 Feb. 1937, *Ducke s.n.* (U). **Rondônia:** Guajara-Mirim, Rio Pacaas Novos, 15 Aug. 1976, *Cavalcante 3297* (MG); between Porto Velho and Cuiaba vicinity of Jarú, 16 Aug. 1968, *Forero & Wrigley 7106* (F, INPA, M, MG, L, U). BOLIVIA. **Beni:** Vaca Diez, Riberalta, 28 Sep. 1923, *Kuhlmann 22541* (NY); junction of Río Beni and Madre de Dios, Aug. 1886, *Rusby 932* (BM, CAS, F, G(2), GH, MO); 20.8 km E of Riberalta on road to Guayaramarín, path on right side, 230 m, 25 Sep. 1981, *Solomon 6433* (MO). **La Paz:** Mapiri, July–Aug. 1892, *Bang 1480* (BM, F, G(2), GH(3)); Mapiri, 570 m, Nov. 1907, *Buchtien 1967* (US); Rurrenabaque, 300 m, 6 Oct. 1921, *White 860* (NY). **Pando:** Madre de Dios, along Río Madre de Dios, 19 km by air from Riberalta, 125 m, 18 Aug. 1985, *Nee 31377* (F, MO, NY); Jatata, forest around the camp of the Western Geophysical, 130 m, 26 July 1992, *Rueda 941* (MO). **Santa Cruz:** Sarah Guaytu forest, 27 Sep. 1917, *Steinbach 347* (G, NY(2)); Río Surutic, 400 m, 2 Oct. 1924, *Steinbach 6544* (BM, F, GH).

Local names and uses. In Bolivia, natives decorate their houses with flowers of this species. It is also used as an ornamental in parks and along avenues. It is called “viuvinha” in Brazil and is used as an ornamental. In Ecuador it is called “pilchi huasca” in Quichua and “kalatara” and “bejuco de calabaza” in Spanish; there the stems and leaves combined with *Usnea* and *Tabernaemontana* are used for birth control and sterilization (Wilbert & Neill, 1987). It is called “yahua-piripiri” in Peru and is used for snakebites.

This species is related to *P. volubilis* with which it shares a lianaceous habit with axillary aborted racemes and clavate glandular hairs. *Petrea maynensis* is easily separated by its verticillate leaves; *P. volubilis* is opposite-decussate. In addition, the longest petioles of *P. maynensis* do not reach more than 10 mm as in *P. volubilis*.

8. *Petrea pubescens* Turcz., Bull. Soc. Imp. Nat. Mosc. 36: 211–212. 1863. TYPE: Venezuela. Mérida: near San Cristóbal, 600 m elev., Nov. 1846, *Funck & Schlim 1504* (lectotype, selected by Rueda (1993), BM; isoelectotypes, BR, G(2), P, U, W; photo of isoelectotype, F, MO, NY, TEX). Figure 20.

Petrea glandulosa Pittier, Bol. Cient. Tecn. Mus. Com. Venez. 1: 70. 1925. TYPE: Venezuela. Portuguesa: near Guanare, Mar. 1924, *Peraza 11532* (lecto-



FIGURE 20. Habit of *Petrea pubescens* Turcz. (Neill 10014).

type, selected by Rueda (1993), VEN; isolectotypes, NY, US; photos of lectotype, NY, TEX; photos of isolectotypes, NY, TEX).

Petrea andrei Moldenke, Feddes Rept. 43: 188. 1938.

TYPE: Ecuador. 7 Jan. 1877, *André 4707* (holotype, K; fragment of holotype, NY; photos of holotype, NY, TEX).

Petrea pubescens var. *klugii* Moldenke, Feddes Rept. 43: 172. 1938.

TYPE: Peru. San Martín: Río Hualaya, Chazuta, elev. 260 m, May 1935, *Klug 4155* (holotype, NY; isotypes, BM, F, GH, MO, S, UC, US).

Petrea scaberrima Moldenke, Feddes Rept. 43: 177. 1938.

TYPE: Colombia. Cundinamarca: near Bogotá, 1844–1845, *Purdie s.n.* (holotype, GH; isotype, K; fragment of holotype, NY; photos of holotype, NY, TEX).

Petrea pubescens var. *albicalyx* Moldenke, Phytologia 18: 72. 1969.

TYPE: Venezuela. Táchira: N of San Juan de Colón, on hwy. from La Fría to San Cristóbal, from a cultivated plant, 27 Sep. 1967, *Bunting 2369* (holotype, TEX; isotype, TEX).

Tree up to 20 m tall, bole not straight, often oval in cross section; the branchlets slender, brown or grayish, obtusely tetragonal, densely short pubescent. Leaves decussate-opposite or whorled in 3s or 4s; petioles 1–13 mm long, short-pubescent with fulvous or yellowish hairs like the adjacent twigs; blades elliptic, or ovate-elliptic, 3–18.5 cm long, 1.5–9 cm wide, the apex rounded or obtuse, the base attenuate to subacuminate, membranous, rough to touch, often short pubescent on both surfaces. Inflorescences mainly axillary, racemes mostly clustered near the tips of the branchlet, 5–25 cm long, 2–4 cm wide, with aborted racemes in its axils; pedicels 1–10 mm long, densely pubescent, often bearing bractlets to 12 mm long. Flowers with the calyx-tube white or blue, 3–5 mm long, 2–3 mm wide at base, the apex 3.5–5.5 mm wide, densely pubescent, 5-lobed, the lobes membranous, obovate or elliptic, 11–18 mm long, 2–5 mm at the widest point, acute or blunt at apex, glabrous; calycinal crest with the lobes ca. 1.5 mm long and wide, the apex sharply acute, translucent and ciliate on the margins, pubescent; corolla-tube 6–7 mm long, the base 1.5–3 mm wide, ampliate to 4–5.5 mm at apex, pubescent, the limb sometimes with white-blue dots, rotate, 5-lobed, the anterior lobe largest, the remaining lobes similar, but smaller; stamens 4; filaments 1.5–2 mm long, glabrous; anthers 1–2 mm long, 0.4–1.2 mm wide; staminode sometimes present; ovary globose, 1–1.5 mm long, 1–2 mm wide, glabrous; style ca. 18–25 mm long, pubescent; stigma subcapitate.

Distribution (Fig. 8). This species is found from northern South America south to northern Bolivia, and northwestern Brazil. This species has

been collected at 2200 m elevation, representing the highest altitude for any recorded collection of the genus.

Selected specimens examined. COLOMBIA. **Antioquia:** Medellín, 22 Apr. 1927, *Toro 242* (NY, US). **Cauca:** Río Quilichao, between Santander and San Pedro, 1150 m, 5 Oct. 1954, *Fernandez 2768* (COL); La Paila, 23 Aug. 1853, *Holton 572* (GH). **Cundinamarca:** Fusagasugá, Boquerón de Fusa, 400 m, 20 Aug. 1975, *López-Palacios & Idrobo 3693* (COL, NY, TEX, S); Girardot, between Girardot and Melgar, near El Paso, 420 m, 7 Aug. 1939, *Perez & Cuatrecasas 6577* (COL, NY, US). **Huila:** Neiva, 18 June 1961, *Schwabe s.n.* (B); San Alfonso, Aug. 1934, *Guevara 2E* (US). **Magdalena:** Manaure, Sierra de Santa Marta, 960 m, 25 Aug. 1946, *Foster & Foster 1591* (COL), 1898–1901, *Smith 1521* (BR, BM, F, G(2), GH(3), LE, U, UC). **Meta:** Jan. 1937, *García 5206* (COL, US); La Macarena, at the junction of the rivers Sansa and Guejar, margin of Río Guejar, 490 m, 22 Feb. 1956, *Idrobo 2041* (COL). **Norte de Santander:** Pamplona, 1842–1843, *Linden 1357* (BM(2), G(3), GH, W(2)). **Putumayo:** Umbria, 325 m, Dec. 1930, *Klug 1894* (BM, F, GH(2), MO). **Santander:** between Cucuta and Pamplona, along Río Pamplonita, near La Donduana, 700 m, 25 July 1940, *Cuatrecasas & García 10173* (COL, US). **Tolima:** San Luis, near Corregimiento de Payande, 1300 m, 13 Mar. 1965, *García-Barriga 18167* (COL, GH, US); Lerida, 1300 m, 14 Mar. 1965, *García-Barriga 18182* (COL, GH, NY, US). **Valle de Cauca:** Dagua, drainage of upper Dagua Valley, 14 km above Dagua, on road to Cali, 1500 m, 25 Nov. 1963, *Hutchison & Wright 3271* (BR, F, G(2), GH, LE, M, MO, UC). VENEZUELA. **Amazonas:** Puerto Ayacucho, Atures, on road to El Burro, 6 km N of Puerto Ayacucho, 5 Apr. 1984, *Plowman 13497* (F, MO, NY, U). **Apure:** Rómulo Gallegos, Caño Caribe, ca. 19 airline km SW of Elorza, 90 m, 8 Mar. 1979, *Davidse & González 6214* (MO, SP, TEX). **Aragua:** 12 km S of San Casimiro, 6 June 1967, *Robertson 152* (MO). **Barinas:** Pedraza, Feb. 1953, *Aristeguieta 1602* (NY), Apr. 1959, *Aristeguieta 3864* (NY); 850 m, 4 June 1957, *Bernardi 6350* (G(2)). **Bolívar:** Cedeño, near Caño Villaca, road Caicara to El Burro, 18 Apr. 1984, *Stergios et al. 8570* (MO(2), PORT). **Carabobo:** Hwy. Valencia to Puerto Cabello, 21 Apr. 1976, *Guevara 2288* (BM). **Lara:** Moran, 20 km N of Guárico on road to Villanueva, 1200 m, 5 Mar. 1983, *Aymard et al. 1864; 1865* (PORT), 3–4 km NE of Sicarigua, along Panamerican hwy., 140 m, *Gentry et al. 11010* (MO, US). **Mérida:** 26 June 1956, *Bernardi 3331* (NY); Tovar, road San Francisco–Guaraque, 1600 m, 10 May 1967, *Berti 1722* (BR, U). **Portuguesa:** Guanare, 26 Feb. 1981, *Aymard 99* (NY, PORT); Ospinos, 10 km N of La Estación, 700 m, 25 June 1984, *Aymard 2585* (PORT). **Táchira:** around San Cristóbal, Mar. 1960, *Aristeguieta-Agostini 4113* (AAU, U(2)); road La Fría–San Cristóbal, N of San Juan de Colón road, 27 Sep. 1967, *Bunting 2369* (TEX). **Trujillo:** Carache del Río, between Las Peñas and Las Palmas, 1 Dec. 1979, *Benitez 2659* (F); between Timotes and La Puerta, 1700 m, 20 Mar. 1969, *Oberwinkler 15144* (M). ECUADOR. **Morona-Santiago:** Morona, Cordillera de Cutucu, road Méndez–Morona, 800 m, 4 Feb. 1989, *van der Werff & Palacios 10417* (MO). **Napo:** Orellana, 20 km S of Coca, on Via Auca, toward Río Tiputini, 270 m, 20 Nov.

1991, Neill & Rojas 10014 (MO); 15 km S of Coca, 225 m, 4 Aug. 1992, Rueda et al. 1010 (MO). **Zamora-Chinchipe:** Zamora, E slope of the Cordillera, valley of the rivers Negro and Chupianza, 550 m, 12 Dec. 1944, Camp E-1450 (NY, US). **PERU. Huanuco:** Puerto Inca, Yayapichis, Unidad Modelo de Manejo y Producción Forestal Dantas, 270 m, 1–15 Dec. 1989, Flores & Tello 47 (MO). **Madre de Dios:** Tahuamanu, Iberia, Río Tahuamanu, 330 m, 4 Sep. 1945, Seibert 2164 (MO, US). **San Martín:** Huallaga, Chazuta, Río Huallaga, 260 m, May 1935, Klug 4155 (F, GH, MO, NY, S, UC). **BRAZIL. Acre:** Río Acre, Aug. 1911, Ule 9722 (G(2), NY(2), US). **BOLIVIA. Pando:** 54 km SW of Cobija, 250 m, 24 July 1988, Pennington et al. 35 (LPB).

Local names and uses. It is named “pluma” and “chaparro” in Colombia and “penitente” in Venezuela. It is widely cultivated as an ornamental in Venezuela.

This species is similar to *P. rugosa*, but the latter is primarily a shrub that does not reach more than 5 m, as opposed to *P. pubescens*, a tree reaching up to 20–25 m. The leaves of *P. pubescens* tend to be whorled rather than opposite-decussate as in *P. rugosa*. The mature leaves in the latter species are bullate as opposed to smooth in *P. pubescens*. Flowers with white calyces are known for this species from both wild and cultivated plants.

9. ***Petrea rugosa* Kunth, Nov. Gen. Sp., 2: 282. 1818.** TYPE: Venezuela. Distrito Federal: Caracas, *Humboldt & Bonpland s.n.* (lectotype, selected by Rueda (1993), P-HB; isolectotypes, F, P; photos of lectotype, TEX, US; photos of isolectotypes, F, MO, NY(2), TEX). Figure 21.

Petrea obtusifolia Benth., Pl. Hartw. 1846. TYPE: Colombia. Tolima: 1843, *Hartweg 1359* (lectotype, selected by Rueda (1993), K; isolectotypes, BM, G, K; fragment of isolectotype, NY; photos of lectotype, NY, TEX).

Petrea rugosa var. *casta* Moldenke, Feddes Repert. 43: 48. 1938. TYPE: Panama. Canal Zone: from a cultivated plant, 2 Dec. 1936, *Lindsay 452* (holotype, NY).

Shrub to 3 m tall; the branchlets obtusely tetragonal, pubescent. Leaves with petioles 1–6 mm long, pubescent; blades elliptic to oblong, 3–11 cm long, 2.5–8 cm wide, the apex obtuse, or rounded, the base rounded or obtuse, membranous, rough to the touch on both surfaces, pubescent especially beneath, mature leaves bullate. Inflorescences mainly axillary, abundant, racemes 12–45 cm long, 3–6 cm wide; pedicels 1–10 mm, pubescent. Flowers with the calyx blue or white, calyx-tube ca. 6 mm long, ca. 2 mm wide at base, ca. 4 mm wide at apex, short-pubescent, 5-lobed, obovate, 10–13

mm long, ca. 3 mm wide at base, 5–7 mm wide at the widest point; calycinal crest with the lobes ca. 1.5 mm long, and 2 mm wide at base, acute at apex, puberulent; corolla blue or white, the tube 8–11 mm long, the base ca. 2 mm wide, ampliate, to 4–6 mm at apex, the anterior lobe largest, broadly elliptic, ca. 6 mm long, ca. 7 mm wide, the remaining lobes ca. 5 mm long, ca. 6 mm wide, puberulent; stamens 4; filaments ca. 1.5 mm long, pilose; anthers ca. 1.5 mm long, ca. 0.5 mm wide; ovary ca. 1.2 mm long and wide, glabrous; style ca. 3 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 11). This species occurs in Colombia and Venezuela, growing in mountain savanna with shrubby growth, or on open rocky slopes, at altitudes of up to 1700 m.

Selected specimens examined. COLOMBIA. **Antioquia:** San Jerónimo, 900 m, July 1968, *Barkley 38C494* (TEX); Segovia, 750 m, 18 June 1979, *Rentería et al. 1630* (COL). **Caldas:** La Dorada, 250 m, 18 Dec. 1936, *Haught 2103* (F, GH, NY, S, US(2)); Victoria, Río Guarino, 200 m, 5 June 1970, *Uribe 6442* (COL, NY, US). **Cauca:** Rosas, La Esperanza, 11 Sep. 1975, *López-Palacios & Idrobo 3831* (COL, NY, TEX). **Cundinamarca:** Silvania, S of Silvania on toll road to Fusagasugá, near km 37 turn W and proceed for 1 km on road to Tibacuy, 1400 m, 26 May 1972, *Barclay et al. 3461* (COL); Fusagasugá, Feb. 1860, *Lindig 620* (P). **Huila:** Garzón, Vereda de Las Quebraditas, 900 m, 21–26 Feb. 1947, *Bermudez 34935* (UC); Garzón–Zuloaga road, 1400 m, 29 Sep. 1976, *Echeverry 194* (COL). **Magdalena:** 600 m, Dec., *Lehmann 8645* (GH(3), L, NY(2), US); 400 m, 1851–1857, *Triana s.n.* (US). **Meta:** 6 km SE of Altamira along road to Florencia, mountain savanna with shrubby growth in gullies, 800 m, 9 Jan. 1974, *Davidse et al. 5599* (COL, MO, TEX). **Tolima:** Honda, Aug. 1919, *Ariste-Joseph, Bro s.n.* (US); Mariquita, 6 Jan. 1948, *Schneidern 512* (S); Purificación, valley of the Magdalena river, 1843, *Hartweg 1359* (BM, G, K(2), NY). **Valle de Cauca:** Cali, 1000 m, 15 June 1938, *Duque-Jaramillo 4340-A* (COL); Palmira, 2 May 1935, *Archer 3358* (US). **Valparaiso:** Murillo, 1000 m, 7 Mar. 1938, *Dryander 2303* (BM, US). VENEZUELA. **Táchira:** Capacho, between El Monumento Cristo Rey and La Zona Militar, 1650 m, 12 Aug. 1985, *Bond 5080* (MO). **Distrito Federal:** Caracas, *Humboldt & Bonpland s.n.* (P(2)).

Local names and uses. *Petrea rugosa* is known as “azulino carrasposo,” “azulito,” “chapparito,” “chaparrillo,” “heliotropo blanco,” “mamoncillo,” “pavita,” “pluma del rey,” “pluma de la reina,” “plumilla,” and “sombbrero” in Colombia, where it is used as an ornamental.

It is closely related to *P. pubescens* (see discussion under that species). Occasional plants of this species with white flowers, or at least with white calyces, are known both wild and in cultivation.



FIGURE 21. *Petrea rugosa* Kunth (García 6472).—A. Habit.—B. Close-up of abaxially bullate leaf surface.

10. *Petrea sulphurea* M. J. Jansen-Jacobs, *Flora Guianas* 4: 60–63. 1988. TYPE: French Guiana. Piste de St. Laurent à Paul Isnard, 15 Nov. 1982, *Granville 5341* (holotype, CAY; isotypes, BR, P, U). Figure 22.

Liana; the branchlets tetragonal, winged, often twisted, pubescent, some of the hairs glandular. Leaves with petioles 5–11 mm long; blades elliptic, 3.5–15 cm long, 2.5–7 cm wide, the apex acute and apiculate, the base acute or broadly acute, coriaceous, asperous, glabrous above except on the

primary vein, minutely pubescent and glandular dotted beneath. Inflorescences terminal, racemes 9–16 cm long; bracts narrowly ovate, 5–10 mm long; bractlets one pair on the pedicels, setaceous, 1–2 mm long; pedicels 1–3 mm long. Flowers with the calyx-tube 6–8 mm long, the lobes rounded or apiculate, unequal, 2 lobes narrowly elliptic-oblong, ca. 20 mm, ca. 6 mm wide, acute-obtuse, 3 lobes broadly ovate, ca. 5 mm long, ca. 6 mm wide, acute-acuminate, greenish, short-pubescent; calycinal crest 5-cleft, the lobes ca. 2 mm long, pubescent; corolla yellow, 2–3 cm long, the lobes



FIGURE 22. Habit of *Petrea sulphurea* M. J. Jansen-Jacobs (Granville 5341).

rounded, ca. 0.5 cm long, glandular pubescent; stamens 4; filaments 7–10 mm long, glandular pubescent around the insertion; anthers ca. 2 mm long, glabrous; ovary oblong, ca. 1 mm long, glabrous; style 17–20 mm long, glabrous, stigma subcapitate.

Distribution (Fig. 10). *Petrea sulphurea* is only known from a very narrow area in French Guiana, growing in clearings in primary forest.

Specimens examined. FRENCH GUIANA, km 80 Piste de St. Laurent à Paul Isnard, 15 Nov. 1982, Gran-

ville 5341 (BR, CAY(2), P, U); km 40 Piste de St. Laurent à Paul Isnard, between Citron and Le Guet de la Crique Mousse, 15 Nov. 1982, *Billiet & Jadin 1705* (BR).

Local names and uses. None reported.

This is a distinctive species in the cladistic analysis but close to the clade where *P. bracteata* is found. *Petrea sulphurea* is similar to the latter species in having the longest pedicels in the genus, more than 15 mm long, and petioles with two lateral traces. However, *P. sulphurea* has calyx lobes of two sizes whereas they are equal in *P. bracteata*. It also shares with *P. insignis* a pair of bractlets on the floral pedicels. While both *P. insignis* and *P. bracteata* have blue flowers, *P. sulphurea* is the only species in the genus with yellow flowers.

11. *Petrea volubilis* L., Sp. Pl., ed. 1: 626. 1753. TYPE: Netherlands. Hartecamp, cultivated in George Clifford's garden from material from Veracruz, Mexico, 1735–1737, *Linnaeus s.n.* (holotype, BM, herb. Linnaeus 781.1; photos of holotype, MO, TEX). Figure 23.

Petrea arborea Kunth, Nov. Gen. Sp., 2: 282–283. 1818. TYPE: Venezuela. Aragua: near Cura, near Guacara and Hacienda de Cura, 1800, *Humboldt & Bonpland s.n.* (lectotype, selected by Rueda (1993), P).

Petrea racemosa Nees, Flora 4: 300. 1821. TYPE: Brazil. Bahía: Rio Grande de Belmonte, 23 July–21 Dec. 1816, *Wied-Neuwied s.n.* (lectotype, selected by Rueda (1993), BR; isoelectotype, G; photos of lectotype, MO, NY, TEX).

Petrea mexicana Cham., Linnaea 7: 367. 1832. TYPE: Mexico. Tamaulipas: Tampicos, 1829, *Berlandier 136* (lectotype, selected by Rueda (1993), G; isoelectotype, L; photo of lectotype, TEX).

Petrea subserrata Cham., Linnaea 7: 368. 1832. TYPE: Brazil. *Sellow s.n.* (lectotype, selected by Rueda (1993), K; photo-isoelectotype, US).

Petrea kohautiana C. Presl, Bot. Bemerk. 99. 1844. TYPE: Windward Islands. Martinique, 1819–1821, *Kohaut s.n.* (lectotype, selected Rueda (1993), BR; isoelectotypes, B(2), F, G, L, M; fragment of isoelectotype, NY; photo of isoelectotype, GH).

Petrea ovata M. Martens & Galeotti, Bull. Acad. Roy. Sci. Belgique 11: 329. 1844. TYPE: Mexico. Veracruz: Jalapa, Aug. 1940, *Galeotti 793* (lectotype, selected by Rueda (1993), BR; isoelectotypes, BR, G(2), GH, LE, U, US; fragment of isoelectotypes, NY; photo of lectotype and isoelectotype, TEX).

Petrea aspera Turcz., Bull. Soc. Imp. Nat. Mosc. 36: 211. 1863. TYPE: Venezuela. Carabobo: San Estevan, 300 m elev., Apr. 1845, *Funck & Schlim 507* (lectotype, selected by Rueda (1993), BR; isoelectotypes, BM, G(2), P, W; fragment of isoelectotype, US; photos of isoelectotype, F, MO, NY(2), TEX, U, W).

Petrea vincentina Turcz., Bull. Soc. Imp. Nat. Mosc. 36: 212. 1863. TYPE: Windward Islands. St. Vincent,

Caley s.n. (lectotype, selected by Rueda (1993), G; isoelectotype, G; photo of isoelectotype, NY).

Petrea fragrantissima Rusby, Mem. New York Bot. Gard. 7: 338. 1927. TYPE: Bolivia. La Paz: Rurrenabaque, 300 m elev., Oct. 1921, *Rusby 860a* (holotype, NY; isotype, TEX).

Petrea volubilis var. *albiflora* (Standl.) Moldenke, Revista Sudamer. Bot. 5: 2. 1937. TYPE: Belize. Sitte river, 17 Mar. 1931, *Schipp 727* (holotype, F; isotypes, BM, G, MICH, MO, NY, S; photo of holotype, TEX).

Petrea amazonica Moldenke, Feddes Repert. 43: 173. 1938. TYPE: Brazil. Amazonas: mouth of the Rio Embira, 19 June 1933, *Krukoff 4930* (holotype, NY; isotypes, G, GH, K; photos of isotype, NY, TEX).

Petrea arborea var. *broadwayi* Moldenke, Feddes Repert. 43: 26. 1938. TYPE: Trinidad. St. Ann's, 1908, *Broadway s.n.* (holotype, UC; isotype, MO; photos of holotype, NY, TEX).

Petrea atrocoerulea Moldenke, Feddes Repert. 43: 195. 1938. TYPE: Colombia. Antioquia: Río Porce, 7 May 1980, *Kalbreyer 1634* (lectotype, selected by Rueda (1993), K; fragment-isoelectotype, NY; photo-isoelectotypes, NY, TEX).

Petrea colombiana Moldenke, Feddes Repert. 43: 174. 1938. TYPE: Colombia. Santander Sur: Bucaramanga, from a cultivated plant, 1000 m elev., 8 Feb. 1927, *Killip & Smith 19067* (holotype, GH; isotypes, GH, NY, US; photos of holotype, NY, TEX).

Petrea kohautiana var. *anomala* Moldenke, Feddes Repert. 43: 31. 1938. TYPE: Trinidad. St. Clair, May 1911, *Broadway s.n.* (holotype, NY).

Petrea nitidula Moldenke, Feddes Repert. 43: 168. 1938. TYPE: Brazil. Amazonas: near Panuré, Rio Uaupés, Oct. 1852–Jan. 1853, *Spruce 2926* (holotype, G; isotypes, BM, BR, F, G, GH, LE, NY; photos of holotype, NY, TEX; photos of isotype, F, MO).

Petrea riparia Moldenke, Feddes Repert. 43: 194. 1938. TYPE: Brazil. Pará: São Luis, Rio Tapajos, 6 Dec. 1915, *Ducke 15822* (holotype, G; isotype, BM; fragment of isotype, NY; photos of holotype, NY, TEX).

Petrea rivularis Moldenke, Feddes Repert. 43: 191. 1938. TYPE: Guyana. Waini river, Nov. 1910, *Anderson s.n.* (holotype, K; isotype, K; fragment of holotype, NY; photo of holotype, TEX).

Petrea swalleni Moldenke, Feddes Repert. 43: 192. 1938. TYPE: Brazil. Pará: Boa Vista, Rio Tapajos, 7–13 Jan. 1934, *Swallen 3127* (holotype, US; isotype, NY; photos of holotype, NY, TEX).

Petrea volubilis var. *pubescens* Moldenke, Feddes Repert. 43: 45. 1938. TYPE: Honduras. Comayagua: San Luis, 6 May 1933, *Edwards P601* (holotype, US; isotypes, BR, F; photo of holotype, TEX).

Petrea aspera f. *albiflora* Moldenke, Phytologia 18: 421. 1969. TYPE: Panama. San Blas: 23 Apr. 1933, *Cooper 234* (holotype, NY).

Liana, sometimes shrubby with stem ca. 10 cm DBH; the branchlets obtusely tetragonal, pubescent or glabrous. Leaves decussate-opposite, rarely some whorled; petioles 1–16 mm long, sometimes pubescent; blades elliptic, 3–25 cm long, 1.4–11 cm wide, the apex short-acuminate, the base rounded or acute, entire, sometimes serrate or denticu-

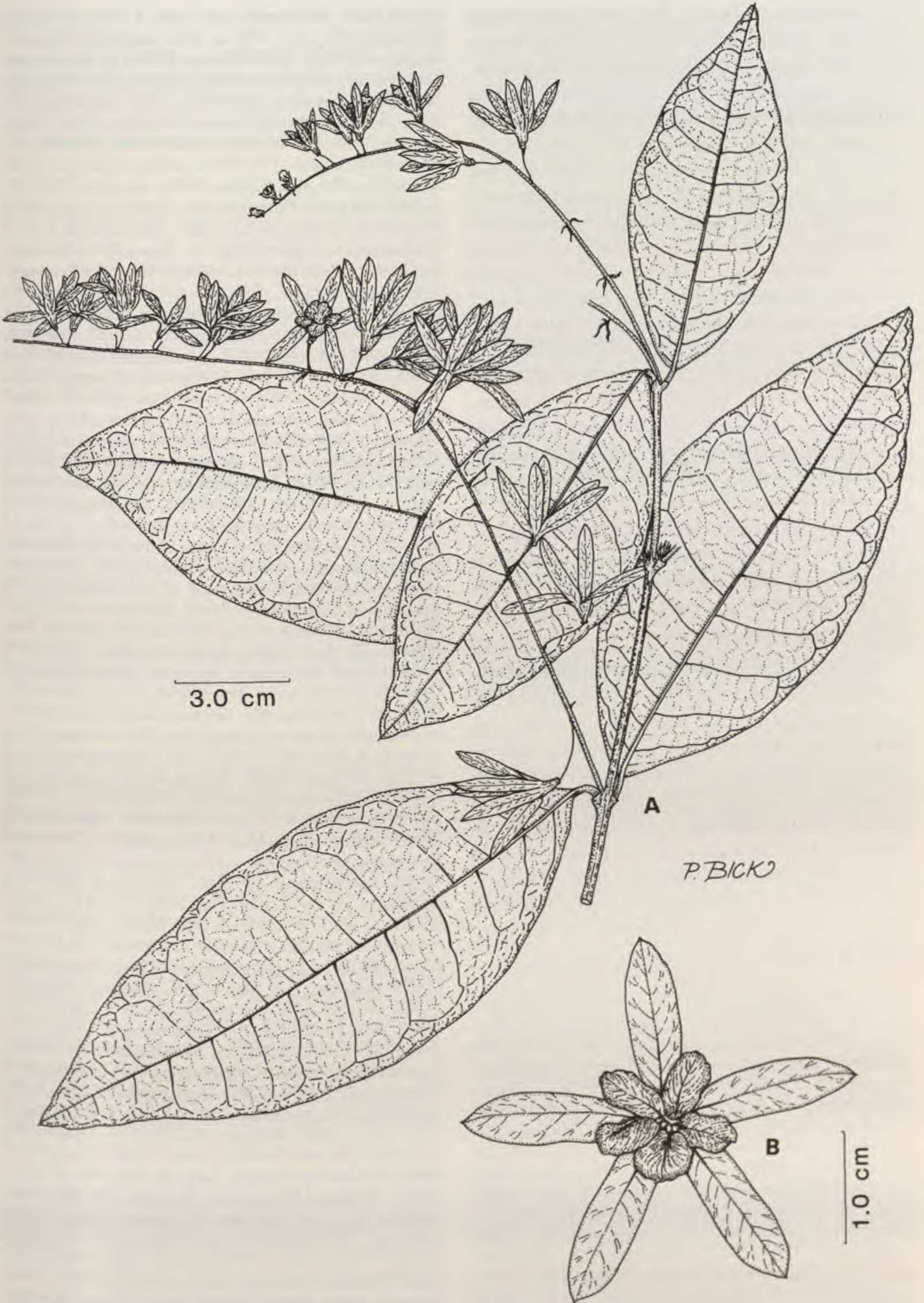


FIGURE 23. *Petrea volubilis* L. (Martínez 11375).—A. Habit.—B. Flower.

late, asperulous, rough to the touch, glabrous or pubescent. Inflorescences axillary, racemiform, 4–58 (> 80 cm in cultivated plants) cm long, 1.5–9.5 cm wide, with aborted racemes in the axils; pedicels 10–35 mm long; a bractlet lanceolate, sometimes borne on the pedicel, 4–7 mm long, 1–2 mm wide. Flowers with the calyx white or blue, calyx-tube 3–7 mm long, 2.5–5 mm wide at base, 2.5–7 mm wide at apex, glabrous or pubescent, 5-lobed, the lobes membranous, oblong, 8–29 mm long, 2–10 mm wide, the apex rounded; calycinal crest with the lobes 1.2–2.5 mm long and 1.5–2 mm wide, ciliate on the margins, the apex acute; corolla blue or white, fragrant, 6–15 mm long, the base 1.5–3 mm wide, conspicuously ampliate to 3–9 mm at apex, pubescent, the limb rotate, 5-parted, the anterior lobe largest, sometimes punctate and with white spots, puberulent, the remaining lobes similar, but smaller; stamens 4, didynamous to homodidynamous; filaments 1.2–2 mm long, glabrous; anthers ca. 1.5 mm long, ca. 0.8 mm wide, pilose; staminode ca. 1 mm long sometimes present; ovary oblong, 1.2–3.5 mm long, 1.5–2.5 mm wide, glabrous; style 2–4 mm long, glabrous; stigma subcapitate.

Distribution (Fig. 5). This is the most widely distributed species in the genus. It ranges from the southern half of Mexico throughout the West Indies to Peru and Paraguay. It grows in seasonal evergreen forest along streams, roadsides, steep limestone walls in dry forest, limestone outcrops, pastures on clay and rocky soil, and on rock. In Mexico it has been reported growing with such genera as *Brosimum*, *Capparis*, *Ceiba*, *Tabebuia*, and *Trichilia* (i.e., sub *Breedlove* 49633), and the flowers are visited by honeybees (sub *Nee & Taylor* 26607).

Selected specimens examined. MEXICO. **Campeche:** Champotón, 20 km N of Ruinas Edzna, 29 Mar. 1982, *Cabrera & Cabrera* 2348 (BM, MEXU). **Oaxaca:** Tuxtepec, Cerro Buenos Aires, W of La Presa Temazcal, 60 m, 6 Mar. 1986, *Cortéz et al.* 197 (MEXU). **Quintana Roo:** km 4 Chetumal–Bacalar road, 4 Mar. 1958, *Schubert & Gómez* 1686 (GH, MEXU). **Tabasco:** Balancán, on road to El Triunfo, 3 Nov. 1976, *Méndez* 441 (MO). **Veracruz:** Actopan, on road to Cerro de la Mesa, 1 km from Mozomboa, 50 m, 16 Apr. 1985, *Acosta & Acosta* 245 (CHAPA). **Yucatan:** Tizimín, Dzonot Ake Community, 24 km of Tizimín, 25 Feb. 1986, *Aguilar et al.* 130 (MEXU). GUATEMALA. **Alta Verapaz:** Río Cahabon, Finca Canihor, 250 m, 5 Apr. 1940, *Stuart* 36 (MICH). **Izabal:** Lake Izabal, 22 May 1966, *Snedaker* D67 (F, GH). **Petén:** Tikal National Park, S of the Hotel Posada La Selva, 18 Mar. 1970, *Tun* 785 (F, S, WIS). **Santa Rosa:** Aguas Calientes, 23 Jan. 1908, *Kellerman* 7738 (F). **Zacapa:** Loma El Picacho, above Santa Rosalia, 1400 m, 15 Jan. 1942, *Steyermark* 42728

(F). BELIZE. **Belize:** Gracie Rock, 1.5–4 mi. S of mi. 22 on western hwy., 100 m, 21 Jan. 1974, *Liesner & Dwyer* 1498 (MO, US). **Orange Walk:** on path between Lago Tan and N of San Antonio Village, July 1973, *Leino* 223 (MO). **Toledo:** trail to Esperanza, beginning 1 mi. N of Columbia forest station, 12 June 1973, *Dwyer* 11132 (MO). HONDURAS. **Atlántida:** La Ceiba, 10 May 1985, *Bados* 174 (MO). **Colón:** road to Castilla, 2.5 mi. E of Trujillo, 22 Apr. 1980, *Saunders* 196 (BM, F, MO, NY). **El Paraíso:** near Danlí, 14 Apr. 1970, *Barkley & Barkley* 40156 (MO, TEX). **Yoro:** 5 km E of Morazán, on road to Yoro, 21 May 1987, *Blackmore & Chorley* 4035 (BM). EL SALVADOR. **San Vicente:** 400 m, 2–11 Mar. 1922, *Standley* 21187 (GH, MO, NY, US). **Santa Ana:** Hacienda San Miguel, near Metapan, Summit of Cerro El Pinal, 1000 m, 22 Feb. 1946, *Carlson* 849 (F). NICARAGUA. **Carazo:** Quebrada La Chota, ca. 7 km NE from Chacocente biological station, 100 m, 19 Mar. 1983, *Grijalva* 2430 (HNMN). **Jinotega:** vicinity of Jinotega, 1070 m, 19 June–9 July 1947, *Standley* 10065 (F). **Zelaya:** Siuna, vicinity of La Luz, 175 m, 14 Mar. 1961, *Bunting & Licht* 649 (NY, F, US). COSTA RICA. **Alajuela:** San Ramón, Los Angeles, 28 Mar. 1931, *Brenes* 13620 (NY). **Guanacaste:** along Panamerican hwy., near Nicaraguan frontier, 100 m, 11 Mar. 1976, *Fallon & Solomon* 2636 (MO). **Heredia:** Sarapiquí, La Selva biological station, the OTS field station on the Río Puerto Viejo, just E of its junction with Río Sarapiquí, 100 m, 12 Jan. 1982, *Oberbauer* 101 (F, U). **Puntarenas:** Monteverde, Valle del Río de San Luis, 900 m, 28 Apr. 1989, *Bello* 827 (MO). PANAMA. **Colón:** Canal Area, Barro Colorado Island, shoreline of Colorado peninsula, 13 May 1968, *Croat* 5538 (MO). **Darién:** Punta Guayobo Grande, along beach and approximately 50 m from water edge, 25 m, 20 Apr. 1980, *Antonio & Hahn* 4247 (MO, TEX). **Panamá:** Serranía de Maje, between Charco Rico and trail along Río Ipeti Grande, confluence with Río Agua Fria, 300 m, 28 Jan. 1984, *Churchill & Nevers* 4436 (MO). **San Blas:** El Llano–Cartí road, 2 Mar. 1986, *Nevers* 7231 (MO). **Veraguas:** San Francisco, Feb. 1924, *Powell s.n.* (US). CUBA. **Cienfuegos:** 10 Mar. 1926, *Jack* 4249 (US). **Santiago:** 18 Apr. 1902, *Hamilton* 127 (NY). JAMAICA. Ca. 2 mi. NW of Mandeville, 600 m, 5 Mar. 1980, *Proctor* 38629 (NY). DOMINICAN REPUBLIC. **Guazumal,** 10 Feb. 1946, *Jimenez* 1028 (US). PUERTO RICO. **Naguabo,** 12 Mar. 1965, *Wagner* 786 (GH). LEEWARD ISLANDS. **Antigua:** Dunning Valley, 5 Sep. 1937, *Box* 1033 (BM, F). **Guadeloupe:** 1944–1946, *Bena* 1227 (P). COLOMBIA. **Amazonas:** Leticia, forest near outskirts of town on Brazilian frontier, 17 Nov. 1974, *Gentry* 12728 (MO, TEX). **Antioquia:** Turbo, Corregimiento de Lomas Aisladas, 50 m, 8 Feb. 1985, *Renteria et al.* 3615 (MO). **Bolívar:** San Juan de Nepomuceno, Loma Los Colorados, 200 m, 2 Sep. 1986, *Cuadros* 3130 (MO). **Chocó:** Los Kativos National Park, NE of Tilupo, 160 m, 6 Mar. 1976, *Forero & León* 120 (MO). **Santander:** Barranca Bermeja, Magdalena valley, between Sogamoso and Colorado rivers, 300 m, 19 Feb. 1935, *Haught* 1568 (US). VENEZUELA. **Amazonas:** Atabapo, Quebrada El Grillo, *Steyermark* 129383 (COL). **Aragua:** Henri Pittier National Park, N from Maracay, 700 m, 9 Feb. 1969, *Oberwinkler* 14704 (M). **Bolívar:** Campamento La Yagua, ca. 24 km NE of Caserio Los Rosos, 16–25 June 1965, *Blanco* 145 (MO). **Miranda:** Distrito Páez, between Río Guapo and drainage of the Río Guapo, 300 m, 1–2 June 1977, *Davidse & González*

13511 (MO, U). **Zulia:** Lagunillas, along Río Grande, 13 km N of Embalse, 600 m, 1–5 Apr. 1982, *Bunting et al.* 11278 (NY, TEX). TRINIDAD. St. Ann's, Hololo mountains road, 24 Apr. 1930, *Broadway* 7568 (BM, F, G(2), E. MO, UCLA). GUYANA. Essequibo, Itanime Falls, Essequibo river, 29 Sep. 1937, *Smith* 2148 (GH, NY). SURINAME. Nickerie, area of Kabalebo dam project, at km 16.5, 7 km E of Ferry over Kabalebo, 20 Nov. 1976, *Heyde & Lindeman* 229 (U). FRENCH GUIANA. St. Laurent, above mouth of Maroni river, island in Moroni river, near Antecum Pata, 140 m, 21 Aug. 1987, *Weitzman* 243 (MO). PERU. **Amazonas:** Bagua, road between Chiviaco and El Muyo, both sides of the road, 500 m, 19 Nov. 1990, *Díaz & Amaro* 4261 (F). **Loreto:** Maynas, Mishana, trail from village to Campamento 1, 140 m, 22 July 1980, *Gentry et al.* 28928 (MO). BRAZIL. **Amazonas:** Vila Bittencourt, left margin of Rio Japura, 14 Nov. 1982, *Amaral et al.* 446 (NY). **Bahia:** Rio Jequitonha, in the road to Itaimbe, 7 Apr. 1971, *Santos* 1580 (TEX). **Minas Gerais:** Carmo do Rio Claro, Fazenda Novo Horizonte, 28 Aug. 1961, *Andrade* 951 (R). **Pará:** Paimeru, Parque Indígena de Tumucumaque, Rio Paru do Oeste, Missão Tiriyo, 16 Feb. 1970, *Cavalcante* 2392 (NY, TEX). **Paraná:** Cerro Azul, Rio Turvo, 5 Oct. 1977, *Hatschach* 40343 (NY). BOLIVIA. **Beni:** Rurrenabaque, 300 m, Oct. 1921, *Rusby* 860A (NY, TEX). PARAGUAY. May, *Hassler* 11234 (G(3), GH). ECUADOR. **Morona-Santiago:** Santiago, Taisha, 500 m, 3 Feb. 1962, *Cazalet & Pennington* 7649 (B, NY, UC, US). **Napo:** Yasuni National Park, Pozo Amo 2, trail to Río Daymi, 230 m, 14 Jan. 1988, *Cerón* 3320 (MO).

Local names and uses. Because of the wide distribution of *Petrea volubilis*, it is known by numerous common names: Brazil, "cipó de São Miguel," "flor de São Jose," "flor de São Miguel," "flor de viuva," "jasmin roxo," "toucado de viuva," "viuvinha"; Colombia, "chaparro"; Costa Rica, "choreque"; Honduras, "chaparro," "flor del diablo," "flor de Jesus," "lengua de vaca," "lija," "manto del nazareno," "raspa guacal," "sombbrero"; El Salvador, "adolfina," "flor de Jesus," "manto de Jesus"; French Guiana, "kaytapa," "mayapi"; Mexico, "aax," "bejuco de lija," "bejuco de soltero," "bejuco lava plato," "bejuco pan tostado," "bejuco tieso," "capitan lila," "espuela de caballero," "piocha vieja," "raspa sombrero," "Santa Rita," "thathup ts'aah," "tochpzimin," "tuchicon," "veracuza," "xob-tzimin," "yoch opp tzi min," "yoxop jimin"; Nicaragua, "machigua"; Panama, "bejuco de ajo," "flor de niño"; United States, "purple wreath," "queen wreath"; Venezuela, "bejuco de mayo," "bejuco de palo," "flor de mayo," "moradito," "nasareno," "sandpaper vine," "Santa Lucia," "serae serae," "tostadito," "tukuinamedu"; West Indies, "fleur de la fete de dieu," "flor de papel," "liane rude," "liane de St. Jean." This species is mostly used as an ornamental; it is cultivated worldwide. In Mexico the leaves are used to feed domestic animals such as horses

and cows, and in Venezuela the wood is used to make toys.

Petrea volubilis is closely related to *P. maynensis* (see discussion under that species). White flowers are known from this species in some cultivated plants. This species is highly variable in leaf and flower size, habit and indument, the reason for the numerous synonyms throughout its range. The continuity of this variation can be clearly seen when the material from the entire distribution is observed.

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LIST OF EXSICCATAE. Numbers in parentheses correspond to species as numbered in the text.

Acevedo, P., 4239 (11); 4840 (2). Acosta, R., 245 (11). Aguilar, J. A., 130 (11). Aguilar, J. I., 1212 (11). Aguilar, M., 362 (11). Alcorn, J. B., 2451A, 2920A, 2013, 3527 (11). Allard, H. A., 13175, 14534 (11). Allen, P. H., 960, 4293, 5733, 6272 (11). Almeda, F., 4077 (11). Almeida, S. S., 213, 229 (2). Alston, A. H., 5976 (11). Alvarado, F., 187 (11). Amaral, I. L., 446 (11). Amaral, J., 3 (11). Ancuash, E., 1388 (7). Anderson, A., 229 (5). Anderson, E., 5232 (11). Anderson, C. W., s.n. (11). Andrade, A. G., 951 (11). Andrade, J. B., 3292 (7). André, E. F., 4707 (8). Antonio, T. M., 4247, 4621 (11). Apollinaire, Bro., s.n. (11). Appun, C., s.n. (9). Araquistain, M., 3786 (11). Archer, W. A., 3358 (9). Argeñal, F. J., 67 (11). Arias, L. M., 86 (11). Aristeguieta, Bro., s.n. (9). Aristeguieta, L., 1602, 3463, 4113, 4674 (8). Arnason, T., 17046 (11). Arnoldo, U., 1052, 1363 (11). Artamanoff, G., 193 (11). Atkinson, D. J., 4, 17 (2). Aviles, S., 14 (11). Ayala, F., 2894, 4509 (1). Aymard, G., 99, 1864, 1865, 2585, 4446, 6569 (8); 336, 998, 2529, 8888, 8889 (11).

Badillo, V. M., 3081, 4793a (11). Bados, D. R., 174 (11). Bailey, L. H., 579, 648 (11). Bamps, P., 5228 (11). Banda, E. A., 3114 (11). Bang, A. M., 1480 (7). Bangham, W. N., 601 (11). Banzon, G. T., 2 (11). Barboza, H., 117 (11). Barclay, A. S., 3461 (9). Barclay, H. G., 7146 (7). Barkley, F. A., 17M174, 40156 (11); 38C494 (9). Barreto, M., 3264, 3267, 3268 (11). Bartlett, H. H., 11494, 12133, 12566, 12559 (11). Basurto, F., s.n. (11). Beard, P., 1071, 1475 (11). Beck, S., 16699 (7). Bello, E., 827 (11). Belshaw, C. M., 3420 (11). Bena, P., 1227 (11). Bendeck, C., 180 (11). Benitez, C. E., 150, 2199 (11); 2659 (8). Benson, C., 234 (11). Bequaert, J., 9 (11). Berendsohn, W., 180 (11). Berg, C. C., P18404 (11). Berlandier, J., 136, 182 (11). Bermudez, L., 34935 (9). Bernardi, A. L., 1224, 3331, 6350 (8). Bernoulli, C., 2234 (11). Berti, M., 1722 (8). Beuther, A., 94 (11). Billiet, F., 1697, 4481, 4510 (2). 1705 (10). Bisby, F., P18063 (2). Black, G. A., 48-2954 (11). Blackmore, S., 4035 (11). Blanchet, J., 90, 112

- (11); *s.n.* (1). Blanco, C., 145, 499 (11). Blum, K. E., 2232 (11). Boer, J. G. W., 642, 960 (2). Boke, N. H., 17 (11). Bond, J., 5080 (9). Boom, B., 1163 (2); 6583 (11). Bos, J. J., 1486 (11). Boucher, D. H., 465 (11). Bourgeau, M., 212 (11). Bourgeau, E., 2125 (11). Box, H. E., 1033 (11). Brade, A. C., 5767, 15946 (11). Brand, J., 1162 (11). Bravo, H., 1321 (11). Breedlove, D. E., 9016, 9925, 10681, 23706, 30532, 33771, 33997, 47329, 49633, 49835, 50472, 50223, 56898 (11). Brenes, A. M., 13620, 14290, 20462, 20468, 21462, *s.n.* (11). Breteler, F., 4572, 5149 (11). Bristan, N., 3342 (11). Britez, R. M., 1027 (11). Britton, N. L., 224, 8161, 2689 (11). Broadway, E. 4769, 5271, 7568, *s.n.* (11). Brown, S., 2154 (11). Bruijn, J. de, 1824 (11). Brumbach, W., 6986, 8325 (11). Buch, W., 1140 (11). Buchtien, O., 1967 (7). Bunting, G. S., 649, 7129, 8808, 9003, 11278 (11); 2369 (8). Burchell, W. J., 7539 (11). Burger, W. C., 5190 (11).
Cabrera, A. L., 31501 (11). Cabrera, E., 678, 1112, 1228, 1327, 1564, 1630, 1908, 2166, 2348, 2594, 4425, 10857 (11). Calderón, S., 115, 268 (11). Calderon, Y., 115 (11). Caley, G., *s.n.* (11). Callejas, R., 5880 (11). Calzada, J. I., 175, 5300, 9604, 9769 (11). Camp, W. H., E1450 (8). Campbell, D., P22257, P22570 (2). Carlson, M. C., 503, 849, 1940 (11). Carocci-Buzi, V. P., 149 (11). Carrasquilla, 257 (11). Caravajal, A., 114 (11). Castellanos, A., 24099 (11). Castillo, G., 2602, 695, 1911 (11). Castro, J. F., 41 (11). Castro, M., 63 (11). Cavalcante, P., 289, 3297 (7); 2392 (11). Cazalet, P. C., 7649 (11). Cerati, T. M., 72 (11). Cerna, S. C., 138 (11). Cerón, E., 1634 (7); 3320 (11). Chacón, L., 125, 126 (11). Chagas, J., 39 (3); 803 (2); *s.n.* (5). Chan, K. Y., 1436 (11). Chaneck, M., 143 (11); Charpin, A., 13351 (8). Chavelas, J., ES-1190, ES-1029, ES-805 (11). Chazaro, M., 71 (11). Chiang, F., 343 (11). Christ, P., 45 (11). Churchill, H. W., 4436 (11). Cid, C. A., 1481, 2132 (2); 6224 (11). Claussen, P., 382, 629, 432, *s.n.* (11). Cogollo, A., 1399 (11). Collins, G. N., 44 (11). Converse, O., 45 (11). Conzatti, C., 2100, 5305 (11). Cook, O. F., 316 (11). Cooper, G. P., 234 (11). Cordeiro, I., 76 (4); 307 (5). Cordeiro, M., 220 (2). Córdoba, J. J., 833 (11). Correa, S., 365 (11). Cortéz, L., 197 (11). Cowan, R. S., 38577 (11); 39221 (2). Cowell, J. F., 374 (11). Cox, D. K., MC850, MC853 (11). Crane, C. J., 64, 156, 271 (11). Cremers, G., 4302 (6); 7184, 7673, 8175 (2). Crisman, G. E., 200 (11). Croat, T., 62570 (7); 16, 661, 4858, 5534, 5538, 5718, 5731, 64100, 8746, 9002, 9432, 12374, 23410, 34412, 34587, 34719, 64778 (11). Croizat, L., *s.n.* (11). Crutchfield, J., 5201 (11). Cruxent, J. M., 289, 290, 291, 292 (11). Cuadros, H., 2151, 3130 (11). Cuatrecasas, J., 6577, 10173 (8). Cuming, H., 48 (11). Cunou, H. M., 203M (11). Custodio, A., 337 (11).
D'Arcy, W. G., 11388 (11). Daniel, Bro., 2665 (9). Daniels, A. G., 947 (2). Darwin, S., 2075 (11). Daubemire, R., 575, 713 (11). Davidse, G., 5599 (9); 16214 (8); 13511, 16604, 16396, 32581 (11). Davis, W., *s.n.* (11). Deam, C. C., 199, 6370 (11). Defferrard, C., 4683 (11). Degener, O., 17851, 18788 (11). Delgado, E., 101, 135 (11). Delgado, G. G., 117 (11). Devia, W., 2305 (8). Díaz, C., 4261 (11); 1243 (2). Dick, C., 78 (2). Dickson, J. D., 1466 (11). Dilmy, A., *s.n.* (11). Djoemadi, N., 94 (11). Dodge, C. W., 6474 (11). Dodson, C. H., 3029 (11). Donselaar, J. van, 2406, 3115, 3217 (2). Dorantes, J., 197, 520 (11). Dorr, L. J., 5040 (8). Drake, E., 1354 (5); 2172, 2536 (1). Dryander, E., 2303 (9). Duce, A., 140 (3); 688 (5); 872, 1133, 1982, 7971, 8079, 15127 (2); 212, 3267, 3914, 9303, 10071, 14294, 15451 (11); 22543, *s.n.* (7). Duenas, C. C., 58 (11). Dupre, M., *s.n.* (1). Duque-Jaramillo, J. M., 2426 (11); 4340-A (9). Dusén, P., 10745, 10216, 15874, *s.n.* (11). Duss, P., 1979, 2390 (11). Dwyer, J. D., 208, 3747, 11132, 12522, 14728A, 12022 (11).
Eastwood, A., *s.n.* (11). Echeverry, R., 194 (9). Edwall, G., 110 (11). Edwards, J. B., P586, P601 (11). Egler, F. E., 4293 (11). Eijnatten, C., 1102 (11). Ekman, E. L., 13050, H9121 (11). Elias, Bro., 357, 1201 (11). Elmore, F. H., L41 (11). Emigdio, L., 1831, 1870 (7). Emmerich, G. M., 255, 746 (11). Emwiogbon, J., 57964 (11). Enriquez, O., 396 (11). Erazo, M., 79 (11). Ernst, W. R., 1075 (11). Espinal, S., 2273 (9). Espinoza, R. 1171 (11).
Fallon, M., 2636 (11). Fairchild, D., *s.n.* (2). Fendler, A., 557, 867 (11). Fernández, A., 2768 (8). Fernández, R., 1594, 1385 (11). Ferreyra, R., 4496A, 8100, 10165 (7). Feuillet, C., 270, 564, 593, 736, 737, 739 (2). Flores, C., 47, 206, 2149, 1678 (8). Flores, A., 1160 (11). Flores, J. S., 9103 (11). Florschütz, J., 169, 1127, 3145 (2). Foldats, E., 130-A (11). Folsom, J. P., 2452, 3435 (11). Forero, E., 120, 1597 (9); 6344, 8381 (11); 7106, 7134 (7). Forest Department of Guyana, 4470, 4471 (2); 4854 (6). Fosberg, F. R., 19234 (9). Foster, M. B., 1591 (8); 780 (11). Fournet, A., 201 (6); 482 (7). Fournier, E., *s.n.* (11). Fox, W., 96 (2). Froehner, C., 288 (7). Fróes, R. L., 20501 (3); 22440, 25053, 29568 (5); 25871, 22628 (2); 21121, 33439 (11). Fromm, E., 1412 (11). Frost, S. W., 196 (11). Fryxell, P. A., 3488 (11). Fuentes, M., 53 (11). Funck, N., 507 (11); 1504 (8).
Galeotti, H., 793, 795 (11). Gandolfi, S., 11606 (2). García, H., 3358, 6472 (9); 5206, 12344 (8). García-Barriga, H., 12344, 13314, 18167, 18182 (8). García, J., 572, 646 (11). García, M. V., 18 (3). Gardner, G., 5127 (11). Garwood, N. C., 721, 2087A (11). Gaudichaud, M., 169 (11). Gaumer, F. G., 379, 23585, 23673, *s.n.* (11). Gentle, P. H., 316, 2366, 4972, 8867 (11). Gentry, A. H., 2164, 3181, 3187, 3228, 3232, 3330, 3331, 3343, 3289, 5582, 7191, 7794, 12728, 18250, 28575, 28928, 32506, 37844, 57138, 59132 (11); 37075, 21721, 22418, 20982 (1); 13325, 54345, (2); 57827, 60154 (7); 9189 (9), 11010, 71866 (8). Gilly, C. L., 57 (11). Gimete, J., 911 (11). Glaziou, A., 2652, 4957, 4967 (11); 14166 (5); 15324 (11); *s.n.* (11). Goldman, E. A., 714, 751, 1868 (11). Gómez, R., 166 (11). Gómez, L. D. 23358 (11). Gonçalves, P., *s.n.* (11). González, A. C., 801, 919 (11). González, L., 561 (11). Gottsberger, G., 16, 906, 16-26970 (11). Graham, E. H., 254 (2). Granville, J., 6485 (2); B4670, B4671, B5007, B5280 (11); 5341 (10). Grayum, M., 8214 (11). Greenman, J. M., 415, 5902 (11). Gregory, D. P., 589 (11). Grenand, P., 570 (11). Grijalva, A., 2329, 2430 (11). Guedes, T. N., 496 (11). Guevara, V., 2E (8). Guevara, L. C., 2288 (8); 4420 (11). Gutiérrez, G., 760, 781 (1); 783 (7). Guzman, J., 28 (11). Guzman, M., 108 (11).
Haenke, T., 1582 (11). Hahn, L., 270 (11). Hahn, W., 5644 (6). Halle, F., 516, 747 (11); 585 (2). Hallier, H., C119, C120 (11). Hamilton, S., 127 (11). Hammel, B., 1868, 12303 (11). Hansen, B., 1759 (11). Harriman, N., 10925 (11). Hartman, R. L., 12233 (11). Hartweg, C. T., 1359 (9). Harvey, D. R., 5278 (11). Hassler, E., 11234 (11). Hatheway, W., 1161 (11). Hatschach, G., 18074, 24863, 32638, 34824, 40343 (11). Haught, O., 2103 (9); 1328, 1568, 4046, 4569, 4791 (11).

- Hawke, W., 83 (11). Hayes, S., 34 (11). Heiner, A., 206 (11). Held, J. J., FC88 (11). Hemmendorff, *s.n.* (11). Herinberger, E. P., 428 (11). Heringer, E., 11553 (11). Hernández, A., 195 (11). Hernández, X., E., 283 (11). Hernández, J., 1134 (11). Hernández, L., 1044 (11). Herrera, A., 67 (11). Herrera, H. 1186 (1). Heyde, E. T., 552, 735 (11). Heyde, N. M., 15, 636 (2); 229 (11). Higgins, J. E., 451 (9). Hinton, G. B., 14135, 34135 (11). Hitchcock, A., 17249 (2). Hodge, W. H., 870, 984, 3016, 3102, 3279, 3651 (11). Hoehne, F. C., 683, 28316, *s.n.* (11). Holt, E. G., 323 (11). Holton, I. F., 572 (8). Hostmann, F. W., 39 (2). Howard, R. A., 10401, 11303, 11757, 18202, 18203, 19236, 19536 (11). Hu, S. Y., 12961 (11). Huber, J., 1489, 3676 (7). Huft, M., 1949 (11). Hugh-Jones, D., 42 (2). Hulk, J. F., 87 (2). Humboldt, F. H., *s.n.* (9); *s.n.* (11). Hummel, D., *s.n.* (11). Hunter, A. A., 658 (11). Hurd, R. P., 72 (11). Hutchison, P. C., 3271 (8).
- Ibarra, J. A., 49 (11). Idrobo, J. M., 2041, 10999 (8); 10985 (9). Irwin, H. S., 47158 (1); 54511 (6).
- Jack, J. G., 4249 (11). Jacquemin, H., 1585, 1761 (11). Jahn, A., 343 (11); 906 (8). Jameson, W., *s.n.* (8). Jansen-Jacobs, M. J., 341, 877 (6). Janzen, D. H., *s.n.* (11). Jenman, G. S., 4905 (6); 3882, 5125, 5454, 5455, 5456 (2). Jeremie, J., 155 (11). Jiménez, J. J., 1028 (11). Johnson, H., 1265 (11). Johnston, J. R., 1149 (11). Jonker-Verhoef, A. M. E., 372, 455, 652 (2). Judd, A. F., *s.n.* (11). Judziewicz, E., 4568 (11). Jurgensen, C., 28 (11).
- Kahn, F., 5400 (1). Kalbreyer, W., 1634 (11). Karwinsky, W. T., 709, *s.n.*, *s.n.* (11). Kellerman, W., 7738, *s.n.* (11). Kelly, G. E., 248 (11). Kelly, I., 900 (11). Kennedy, H., 3110 (11). Kenoyer, L. A., 3566 (11). Killip, E. P., 19067, 37068, 43554, 45530, 19067 (11). King, R. M., 4307 (11). King, S. R., 3, 493 (2). Klug, G., 170 (1). Klug, G., 637 (1); 1894, 4155 (8). Knapp, S. 3916, 3900 (11); 7120 (2). Kohaut, F., *s.n.* (11). Kramer, K. U., 2830 (2). Krukoff, B. A., 1575 (2); 4694, 4930 (11); 9112 (1); 10729, 10735 (7). Kruse, H., 174 (11). Kuhlmann, J. G., 1295, 1296 (11); 2276 (3); 22541 (7). Kuhlmann, M., 3996 (11). Kummrow, R., 1966 (11).
- Lang, H., 87 (2). Lanjouw, J., 852, 1298, 1321, 1971 (2). Lanna, S., 338 (2). Laughlin, R. M., 178 (11). Leblond, M., 270 (11). Ledoux, D. G., 2525 (11). Ledoux, P., 130 (11). Lehmann, F. C., 8234 (8); 8645 (9). Leino, P. W., 223 (11). Leitao, H. F., 18747 (11). Leng, H., B9 (11). León, J., 1746 (11). León, Bro., 17259 (11). Leonard, E. C., 10143 (11). Leonard, J., 7381 (1). Leopold, S. M., 175, 190, 191, 192, 193, 218, 219 (11). Leprieur, M., *s.n.* (11). LeSueur, H., 542 (11). Level, J. S., 5 (2). Levy, P., 1069 (11). Lewis, W. H., 195, 1591, 5317, 5427, 10003, 10335 (11). Lewton, F. L., 322 (11). Liebmann, M. F., 11278, 11286 (11). Liesner, R., 369, 464, 1498, 6015, 11196 (11); 10587, 10703 (8); 15826, 15658 (1). Lindeman, J. C., 4748, 4889 (2); 3155, 6357a (11). Linden, I., 1357 (8). Linden, J., 18 (11). Linder, D. H., 143 (2). Lindsay, W. R., 259 (11); 452 (9). Linnaeus, C., *s.n.* (11). Lleras, E., P17213 (2). Lloyd, F. E., 615 (11). Loefgren, A., 385, *s.n.* (11). López, W., 759 (11). López-Palacios, S., 87, 2549, 2586, 3549, 3589, 3620, 3655, 3928 (11); 2553, 2664, 3238, 3693 (8); 3704, 3703, 3831, 3838, 3867, 4033 (9). Lorzing, J. A., 11844 (11). Lowe, J., 4087 (2). Lowrie, S. R., 291 (7). Lozano, G., 5426 (7). Lundell, C. L., 1204, 3431, 4972, 7413, 7329, 15637, 16842, 16883, 17938 (11). Luschath, B., *s.n.* (11). Lutz, A., 857 (11).
- MacDougall, T., H279, H357, 598S (11). Macedo, A., 6, 1987 (11). Maguire, B., 22885, 24831, 30444, 54229 (2); 39297, 39344, 40506 (11); 46234 (6); 56613, 56867 (7). Manara, B., *s.n.* (11). Marcano-Berti, L., 321-979, 325-979, *s.n.* (11); 148-980, 1722, 22-3-77, 87-980, 982-125, 983-015, *s.n.* (8). Marcovitz, W., *s.n.* (11). Maringoni, A., P16 (11). Marles, R., EE80 (7). Marquand, E., *s.n.* (11). Márquez, W., 28 (11). Martin, P. S., 31, 1242 (11). Martinelli, G., 6757 (2); 9775 (11). Martínez O., E., 23, 85, 149, 251, 11375, 11471, 11514, 11919, 12190, 20121, 3528 (11). Martínez M., F., 10016 (11). Martínez C., G., 702, 1373 (11). Martínez, M. A. 359 (11). Martius, F. P., 118, 1698, 1902, 9021, *s.n.* (11); 1029, *s.n.* (1); *s.n.* (9); *s.n.* (2); *s.n.* (5). Mathias, M. E., 5093 (2); 6088 (7). Mattos, M., 170 (11). Matuda, E., 1478, 17492, 18414, 37474 (11). McDaniel, S., 22533 (2). McVaugh, R., 22468 (11). Meave, J., 1380 (11). Mecca, M., 15088 (11). Medrano, F. G., 12116 (11). Melin, D., *s.n.* (1). Mélinon, M., 165, 334 (11); 86, 87, 110, *s.n.* (2). Mell, C. D., *s.n.* (11). Méndez, A., 4257, 5590, 5644, 5678, 5833, 5884 (11). Méndez, F., 229, 441 (11). Mennega, A. M., 290, 373 (2). Merrill, E. D., 4085 (11). Mexia, I., 6498 (1). Mexia, Y., 1933a (11). Meyer, F. G., 9876, 9947 (11). Miller, J. S., 558 (11); 2312 (7). Mizoguchi, K., 1671, 2273 (11). Moldenke, A. L., 19604, 19605, 19623, 19657, 19800, 19825, 19887, 20600 (11). Moldenke, H. N., 4644, 10409, 21869, 28131, 28344 (11). Molina R., A., 154, 2899, 7593, 20794 (11). Molina, D., 147 (11). Monot, M., 43 (2). Montaldo, P., 4006 (11). Montgomery, G., 183 (11). Moore, H. E., 2536 (11). Moreno, J., 61, 64 (11). Moreno, P. P., 23551 (11). Moretti, C., 313 (2). Mori, S. A., 2930 (11); 5521 (1); 8136, 8160 (2); 9131 (7); 20385 (5). Moritz, J. W. K., 791 (11). Morton, C. V., 5435, 7080, 7837 (11). Morton, J. K., SL623 (11). Mosén, H., 545, 4321 (11). Mutis, J. C., 896, 1055 (8); 899, 914, 447, 448, 4428, 4183 (9).
- Neale, K., 5174 (11). Nee, M., 9380, 11366, 26607, 26048 (11); 31324, 31377 (7). Neill, D., 5516, 7762, 7787 (7); 10014 (8). Nelson, B. W., 520 (7). Nelson, C., 4371, 7381 (11). Nelson, E. W., 411, 2318 (11). Netto, L., 337 (11). Nevers, G., 3959, 5311, 5812 (1); 7231 (11). Neves, A., 9 (11). Newhall, G., 14 (11). Nichols, C. E., 2123 (11). Nuñez, P., 6083, 6183 (7). Nogueira, P. E., 186 (11).
- Oberbauer, S., 15144 (8); 101, 14704, 15144 (11). Oldeman, R. A., 1094, B1313, 1625 (2); 2012 (1); T488, B940, B1098, B1440, 1457, B2436, 2450, 2630, B3129 (11). Oldenburger, F. H., 1261 (6). Oliveira, A. A., 332 (2). Oliveira, E., 2376, 4211 (11). O'Neil, H., 1378, *s.n.* (11). Opler, P. A., 1746 (11). Orcutt, C. R., 3042, 5235 (11). Ordoñez, M. J., 193 (11). Orozco, J. M., 316 (11). Orsted, A. S., 11284 (11). Ortega, F., 1343, 3006 (11); 6763 (8). Ortega, R., 2624 (11). Ortíz, F., 1047, 1089 (11). Otero, J. I., 252 (11). Otto, E., 570 (11).
- Pabst, G., 530 (11). Padilla, S. A., 141 (11). Palmer, E., 279, 317, 395, 1064, 1074 (11). Pancho, J. V., 2959, 3078 (11). Paray, L., 567 (11). Paul, Bro., 281 (11). Paz y Miño, C., 81.012 (7). Peck, M. E., 388 (11). Pelaéz, S., 6 (11). Pelly, R. S., 34 (11). Pennel, F. W., 2737, 3563 (9). Peraza, R., 11532 (8). Pereira, E., 7161 (11). Pérez, E., 37 (7); 3020 (9); 6577 (8). Perrottet, M., *s.n.* (11). Pickel, D. B., 2974, 3112 (11). Pieri, A., *s.n.* (11). Pineda, V., 228 (11). Pipoly, J. J., 7588 (5); 8517 (6). Pires, J. M., 1050 (2); 13884B (5); 1622

- 3622, 56867 (11). Pittier, H., 309, 2275, 6063, 6531, 7786, 7853, 8744, 8774, 8855, 9449, 11749, 11769, 13573, 15306, 15327, 15430, 16655 (11). Plee, A., 753 (11). Plowman, T., 13497 (8); 3165, 13724 (11). Poiteau, M., *s.n.* (11). Ponce, F., 307 (11). Poole, J. M., 2021 (2). Popenoe, W., 1203 (11). Poveda, L. J., 1647 (11). Powell, C. W., *s.n.* (11). Prance, G. T., 15868 (1); 3793, 8256, 10236, 11454, 14620, P25519, P25469, 15858, 28906 (2); 3912 (3); 11768, 15117 (5); 2585, 6224, 6477 (7); 5236, 3302, 14640, P25462, P26490, 59470 (11). Prevost, M. F., 198 (2). Pride, G. H., 297 (11). Pringle, C. G., 5003, 8004, *s.n.* (11). Proctor, G. R., 234, 16185, 17943, 20980, 30113, 38629 (11). Pruski, J., 1738, 2779 (11). Puig, H., 810 (11). Pulle, A., 177 (2); 227 (11). Purdie, W., *s.n.* (8). Purpus, C. A., 306, 3763, 6354, 7549, 12000, 12054, 13677, 14010 (11). Quarles, L. H., 333 (11). Quick, B. E., *s.n.* (11). Raets, G. H., 174 (8). Raizada, M. B., 21593 (11). Ramirez, R., 5 (2). Ramsammy, J., 19 (2). Raynal-Roques, A., 20183 (2). Record, S. J., *s.n.* (11). Regnell, A. F., 216, T385, 5127, *s.n.* (11). Reitz, P. R., 11249, 5903, 6255 (11). Reko, B. P., 6086 (11). Renner, P., 57 (2). Renson, C., 98, 234 (11). Renteria, E., 1630, 3615 (11). Repton, J. E., 7786 (11). Revilla, J., 2115 (1). Revirosa, J., 118 (11). Ribeiro, B. G., *s.n.*, 261 (2). Richard, L. C., *s.n.* (11). Richardson, A., 1230 (11). Ricksecker, J., 329 (1). Rico, L., 798 (11). Riedel, L., 120, 598, 1361 (11). Rimachi, M., 4418, 6539 (1). Rivero, R., 1036 (8). Robertson, K., 152 (8). Robleto, W., 939 (11). Rodrigues, W., 2873 (5); 3131, 4041 (2); 10100 (4). Rodríguez, F. C., 1442 (11). Rodríguez, L., 6232 (11). Rodríguez, R., 139, 366 (11). Romero, H., 76 (11). Romero, R., 3850, 3929 (1). Rose, J. N., 3479 (11). Rueda, R., 431, 433, 434, 435 (11); 507, 615, 698, 701, 706, 730 (1); 577, 578, 579, 590, 628, 681, 707, 709, 715, 716, 717, 720, 730 (2); 1010 (8); 808, 900, 901, 903, 941, 1128, 1129 (7). Ruisch, G. H., 5028 (11). Ruiz, T., 4080 (11). Ruiz-Terán, L., 826, 1504, 1989, 10421 (8); 6169, 9784, 10870 (11). Rusby, H. H., 932, 933 (7); 1132 (9); 860A (11). Russel, A., 217 (11). Rutkis, E., 998 (11). Rzedowski, J., 7346, 30544, 25615 (11). Sabatier, D., 516 (2); 723 (11). Sáenz, V., 65 (11). Saer, J., 393 (8); 831 (11). Sagot, P., 1320 (2). Saint-Hilaire, A., 518, *s.n.* (11). Salas, J. G., 1403 (11). Salazar, F., *s.n.* (11). Saldias, M., 1258 (7). Salick, J., 7251, 7364 (2). Sampaio, A. J., 5092 (1); 5196 (9); 8232, 8408, *s.n.* (11). Samuels, J. A., 469 (2). Sandeman, C., 5783 (7). Sandino, J. C., 4151, 4216, 4309 (11). Santoro, J., 678 (11). Santos, J. L., 690 (4). Santos, T. S., 1580 (11); 2158 (1). Sarukan, J., 2784, 4494 (11). Sastre, C., 1444, 4679 (11). Sauer, J. D., 4335, 4233 (11). Saunders, J. D., 43, 196, *s.n.* (11). Sauvain, M., 141 (11); 579, 119 (2). Schipp, W. A., S-556, 727, 8556 (11). Schmalzel, R. J., 32 (11). Schnee, L., *s.n.* (11). Schneidern, M., 512 (9). Schnell, R., 11334 (2). Schomburgk, R. M., 150 (11); 158 (6); 173, 174 (2). Schrenk, H., *s.n.* (11). Schubert, B., 1686 (11). Schultes, R., 569, 6063 (11); 13591 (7). Schulz, J. P., 10330 (6). Schunke, J., 2131, 3682, 4978, 6832, 7720 (7). Schwabe, W., *s.n.* (8). Schwacke, C., 3638 (5). Scolnik, R., 1176 (7). Sehnem, P. A., 9175 (11). Seibert, R. J., 1880 (1); 2164 (8). Seifritz, W., 123 (11). Seligson, D., 473 (11). Sello, F., 180, 493, 626, 1029, 1833, *s.n.*, *s.n.* (11). Sermeno, A., 107 (11). Severen, A., 19 (11). Shattuck, O., 412 (11). Shepherd, H., *s.n.* (11). Sherman, C., 153 (11). Silva, A., 240 (2); 8869 (11). Silva, F. C., 129 (11). Silva, M. G., 953 (5); 3939 (2). Silva, N. T., 3046 (11), 60806 (1); 446, 4633 (2). Simpson, D. R., 739 (2). Skog, L. E., 1205 (11); 7529 (2). Slane, V., 427, 464 (11). Smith, A. C., 4, 2148, 5785 (11); 2626 (6). Smith, C. L., 1017, *s.n.* (11). Smith, C. E., 4526 (11). Smith, H. H., 2787 (11). Smith, J. D., 1497, 1702 (11). Smith, L. C., 359 (11). Smith, S. F., 506 (7). Snedaker, S., D67 (11). C. Sneidern, K., 5765, 6765 (11). Solomon, J. C., 6433 (7). Songgrijp, M., *s.n.* (2). Soukup, J., 4621 (7); 2903 (11). Sousa, M., 845, 1699 (11). Souviron, M. J., 68 (11). Sparre, B., 19187 (7). Spichiger, R., 1039 (2). Splitgerber, F., 736 (2). Spruce, R., 2172, 2526, 2926, 2971 (11); *s.n.* (5). Stabel, G., 405 (2). Standley, P. C., 2279, 3636, 3829, 5009, 5230, 6740, 10065, 16526, 16650, 18098, 21187, 22755, 25845, 28457, 28458, 40206, 72220, 77082, 88384 (11). Stearn, W. T., C13 (11). Steege, H., 247 (6). Steere, W. C., 1508 (11). Steggerda, M., 27a (11). Stehla, H., 5762 (11). Stehle, H., 217, 5397, 5754, 5762, 6890, 6921 (11). Steinbach, J., 3470, 6546 (7). Stergios, B., 1839, 2265, 3385, 6710, 8570 (8); 5118, 5304 (11). Stern, W. L., 22 (11). Stevens, D. W., 3757, 7419, 8757 (11). Steyermark, J., 39880, 42149, 42728, 55546, 62368, 62801, 98878, 99055, 106909, 106953, 112675, 116348, 116927, 129383 (11); 104926, 106799 (8). Stuart, L. C., 34, 36 (11). Sturrock, B. M., 258 (11). Sucre, D., 1422 (11). Surapat, P., 43 (11). Swallen, J. R., 3127 (11). Swentorzecky, I., *s.n.* (11). Taroda, N., 6621 (11). Teixeira, B., 306 (11). Teixeira, G., 2559 (11). Tellez, O., 1012, 1406, 1955, 2140, 2421, 3639, 6302 (11). Tello, A., 140, 783, 1256, 2799 (8). Tenorio, P., 8555 (11). Tessmann, G., 3960 (7). Thieme, C., 5410 (11). Thomas, W., 3692, 3980 (11). Thompson, C., 156 (11). Tjon-Lim-Sang, R. J. M., 188 (2). Toepffer, A., 576 (11). Tonduz, A., 149, 150, 13843 (11). Toro, R. A., 242 (8). Torres, R., 2309 (11). Treacy, J., 519 (2). Triana, J. J., 254 (8); 2077, 3710, *s.n.*, *s.n.* (9). Troll, C., 279 (11); 2725 (7). Troon, F., 14206 (2). Troupin, G., 16333 (11). Trujillo, B., 6101 (11). Tsugaru, S., B-1001 (5). Tulleken, J., 56 (2). Tun, R., 785, 882 (11). Tunqui, S., 53 (7); 171 (1). Tutin, T. G., 110 (2). Tyson, E. L., 3849, 3892 (11). Ule, E., 158 (11); 5982 (3); 8956 (5); 9722 (8). Uribe, L., 6442 (9). Utley, K., 5947 (11). Valerio, R., J., 1172, 2077, 2213, 2429 (11). Valerio, M., 63, 513 (11). Valiente, A., 102 (11). Valio, I. M., 47 (11). Valverde, F., 77 (11). Valverde, L., 1264 (11). Vásquez, B., 740 (11). Vázquez T., M., 652 (11). Vásquez, R., 2472 (7); 2747 (1); 8557, 10348 (2). Velasquez, N., 10 (11). Vélez, I., 555 (11). Venancio, J., 28, 2245 (11). Ventura, E., 924, 1215 (11). Ventura A. F., 937, 1003, 12619, 3218, 12639, 13853, 15111 (11). Vera, J., 2856 (11). Versteeg, G. M., 122, 593 (2). Viegas, A. P., 6869 (11). Vieira, G., 464 (7). Villanueva, R., 91, 109 (11). Villeda, M. E., 115 (11). Vincelli, P., 363 (11). Vincent, D., *s.n.* (11). Vivaldi, J. L., 72-182 (11). Vogel, P. C., 315, 939, 1182 (1); 298, 299, 1178, 1182, 1532 (11). Voorhies, B., 28-5 (11). Vovides, A., 720 (11). Wachenheim, M., 5, 249 (2). Wagner, M., 586 (11). Wagner, R. J., 786 (11). Walker, E. H., 8074 (11). Walker, R. L., 1229 (11). Warren, L. B., *s.n.* (11). Wasshausen, D., 357 (11). Watdahnahsahp, B., 70 (11). Webster, G. L., 9086 (11). Weitzman, A., 243 (11). Welch, W. H., 9667 (11). Wendt, T., 122 (11). Werff, H. van der, 9823 (1); 10417 (8). Wetmore, R. H., 162

- (11). Wheeler, H. E., *s.n.* (11). White, O. E., 860 (7). Whitefoord, C., 2812, 4262, 5401 (11). Widgren, J. F., 150, 359, *s.n.* (11). Wied-Neuwied, M. A. P., *s.n.* (11). Wiley, J. R., 526 (11). Williams, G. R., 631 (7); G412, 702 (11). Williams, L. O., 647, 11475, 10035, 10061, 10077, 10160, 11943, 14063 (11). Williams, Ll., 690, 8106 (1). Wilson, C. L., 334 (11). Wilson, J. S., 12327 (11). Winkler, H., 611 (11). Winters, H. F., 580 (11). Wonderly, H., 32 (11). Woodworth, R., 385 (11). Woytkowski, F., 5471, 7246, 7640 (7); 5642 (11). Wullschlägel, H., 411, 1537 (2); 428 (11). Wurdack, J. J., 39641, 41293 (11); 43583 (2). Yeshoda, K., 610 (11). Yuncker, T. G., 4705 (9); 4524, 17584 (11). Zanoni, T., 11343, 11346, 16040 (11). Zoraya, B., 7 (11).