
Cyphomandra (Solanaceae)
Author(s): Lynn Bohs
Source: *Flora Neotropica*, Vol. 63, Cyphomandra (Solanaceae) (Jul. 5, 1994), pp. 1-175
Published by: New York Botanical Garden Press on behalf of Organization for Flora Neotropica
Stable URL: http://www.jstor.org/stable/4393848
Accessed: 02-03-2016 18:53 UTC

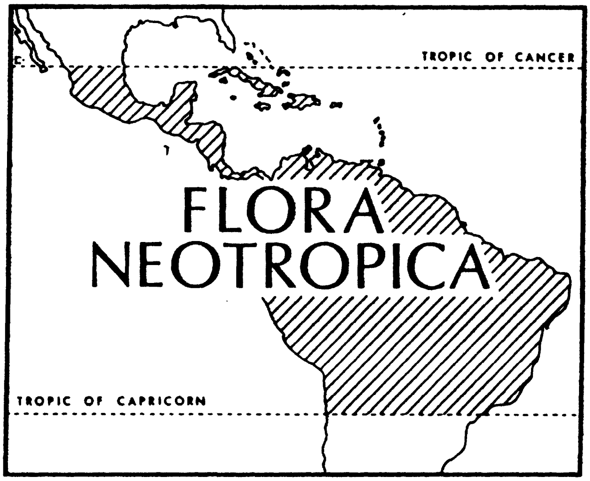
FLORA NEOTROPICA

MONOGRAPH 63

CYPHOMANDRA (SOLANACEAE)

by

Lynn Bohs



Published for

Organization for Flora Neotropica

by

The New York Botanical Garden

New York

Issued 5 July 1994

Published by
The New York Botanical Garden
Bronx, New York 10458

Composition by Carol Johnson

International Standard Serial Number 0071-5794

The paper used in this publication meets the minimum requirements of American National Standard for Information Sciences—Permanence of Paper for Publications and Documents in Libraries and Archives ANSI/NISO (Z39.48–1992.

Printed in the United States on recycled paper

Library of Congress Cataloging in Publication Data

Flora neotropica. — Monograph no. 1 — New York: Published for Organization for Flora Neotropica by the New York Botanical Garden, 1968–
v.: ill.; 26 cm.

Irregular.
Each issue has distinctive title.
Separately cataloged and classified in LC before monograph no. 40.
ISSN 0071-5794 = Flora neotropica.

1. Botany—Latin America—Classification—Collected works. 2. Botany—Tropics— Classification—Collected works. 3. Botany—Classification—Collected works. I. Organization for Flora Neotropica. II. New York Botanical Garden.

QK205.F58 581.98′012—dc19 85-647083
AACR 2 MARC-S

Library of Congress [8508]
ISBN 0-89327-385-6

CYPHOMANDRA (SOLANACEAE)

LYNN BOHS

TABLE OF CONTENTS

ABSTRACT

Bohs, Lynn (Department of Biology, University of Utah, Salt Lake City, UT 84112, U.S.A.) *Cyphomandra* (Solanaceae) Flora Neotropica **63:** 1–176, 1994. The genus *Cyphomandra* (Solanaceae) includes about 35 species of shrubs and small trees native to the Neotropics. *Cyphomandra* ranges from Mexico to northern Argentina and east to southeastern Brazil. Most species are small trees that exploit light gaps in the primary forest. Several species are grown for their edible fruits and one, *Cyphomandra betacea*, the tree tomato or tamarillo, is cultivated worldwide in tropical and subtropical areas. This species is currently known only from cultivation.

This monograph covers aspects of the taxonomic history, morphology, ecology, reproductive biology, infrageneric relationships, biogeography, and uses of *Cyphomandra*. Thirty-two species are recognized in this treatment, and two insufficiently known taxa are discussed. Five informal species groups are described. All issues of nomenclature and typification pertaining to the genus are comprehensively examined. The genus is defined on the basis of the enlarged anther connective. In addition, the unusually large chromosomes of *Cyphomandra* are useful in generic delimitation.

Unusual ecological aspects of *Cyphomandra* include its pollination syndrome and herbivore relationships. Male euglossine bees may be important pollinators of *Cyphomandra* flowers, and the primary attractants may not be pollen, but odor substances secreted by the anther connectives. Specialized herbivores known for *Cyphomandra* are larvae of neotropical butterflies of the nymphalid subfamily Ithomiinae. Further examination of these plant/insect relationships may elucidate the functional significance of the anther connective in pollination and provide insight into the comparative chemistry of *Cyphomandra* alkaloids.

Key words: *Cyphomandra*, *Solanum*, Solanaceae, tree tomato, tamarillo, anther connective, euglossine bees, Ithomiinae.

RESUMEN

El género *Cyphomandra* (Solanaceae) incluye cerca de 35 especies neotropicales de arbustos y árboles pequeños. La distribución de *Cyphomandra* va desde México hasta el norte de Argentina y al este hasta el sureste de Brasil. La mayoría de las especies son árboles pequeños que ocupan los claros del bosque primario. Algunas especies se cultivan por sus frutos comestibles y *Cyphomandra betacea*, el tomate de árbol o tamarillo, se cultiva en las regiones tropicales y subtropicales del mundo. Actualmente esta especie no se conoce en forma salvaje y la información acerca de ella proviene sólo de ejemplares cultivados.

Esta monografía comprende aspectos de la historia taxonómica, morfología, ecología, biología reproductiva, relaciones infragenéricas, biogeografía, y los usos de *Cyphomandra*. Treinta y dos de estas especies están reconocidas formalmente en este trabajo, y además se proporciona información sobre los dos taxa que poco se conocen. Se describen cinco grupos de especies, pero no se establecen categorías infragenéricas formales. Todos los aspectos de nomenclatura y clasificación acerca del género son examinados ampliamente. El género se distingue por el engrosamiento del tejido conectivo de las anteras y sus cromosomas excepcionalmente grandes.

Algunos aspectos ecológicos extraordinarios de *Cyphomandra* son el síndrome de polinización y las relaciones con los herbívoros. Abejas machos euglossines pueden ser polinizadores importantes de las flores de *Cyphomandra*, y la atracción primaria puede no ser el polen, sino substancias odoríferas secretadas por los conectivos de las anteras. Las larvas de mariposas neotropicales de la subfamilia Ithomiinae de las Nymphalidae son herbívoros especializados en *Cyphomandra*. El reconocimiento adicional de estas relaciones entre plantas e insectos puede aclarar el significado funcional del conectivo de la antera en la polinización y dar información sobre la química comparativa de los alcaloides de *Cyphomandra*.

INTRODUCTION

The Solanaceae comprise some 96 genera and about 2300 species. The family is of considerable economic importance as food crops, sources of alkaloids and poisons, ornamentals, weeds, and subjects of scientific research. Although many of the economically important groups or genera have received much attention, much of the family is still poorly known from a systematic point of view. Problems of both generic and specific delimitation exist throughout the family, and no phylogenetic hypotheses exist for most solanaceous groups. Some of the worst problems concern the genus *Solanum*. The latest estimate (D'Arcy, 1991) places the number of species in this genus at around 1000, most of which occur in the New World. Only a handful of infrageneric groups in *Solanum* have been treated taxonomically, and the genus is widely perceived as being a "mess," "morass," or "quagmire."

Cyphomandra is closely allied with *Solanum*. Both genera have anthers that dehisce by apical pores. Although *Cyphomandra* was first described in 1845 on the basis of the enlarged anther connective, its relationship to and delimitation from *Solanum* has been a continual problem.

Cyphomandra, as defined here, may be recognized by the presence of a prominent and abaxially swollen anther connective. Other Solanaceae may have variously thickened anthers, but generally either the thickened region is not swollen abaxially or is not sharply delimited from the thin-walled anther thecae. Clarification of the characters separating *Cyphomandra* from *Solanum* can be found in Bohs (1989a).

In the course of these studies it has become clear that the sister group to *Cyphomandra* is *Solanum* section *Cyphomandropsis*, a relatively unknown group of about 10 to 20 species of South American shrubs. This finding casts doubt on the monophyly of *Solanum* as it is currently defined and raises questions about the monophyly of *Cyphomandra* itself. These questions are not completely answered here. In this treatment, I have attempted to define *Cyphomandra* in the traditional sense, delimit and describe its component species, and point out relationships within the genus and between *Cyphomandra* and other taxa that remain to be examined in the future. Thus, *Solanum*, its relatives, and much of the Solanaceae still remain a taxonomic "morass," but piecemeal these problems are being brought under control.

Resolution of the systematics of *Cyphomandra* is desirable because of the economic importance of this genus. *Cyphomandra betacea*, the tree tomato, is widely grown as a fruit crop in Latin America and is now being commercially cultivated in New Zealand. Several wild species are also grown for their edible fruits. The emergence of *C. betacea* as a commerical fruit crop and the potential uses of other *Cyphomandra* species have underscored the need for accurate species identifications and consideration of the reproductive biology of the group, particularly with regard to the breeding and improvement of the tree tomato.

GENERIC DELIMITATION AND RELATIONSHIPS

Recent treatments divide the Solanaceae into two subfamilies, the Solanoideae and the Cestroideae (D'Arcy, 1979, 1991; Hunziker, 1979a). [A third subfamily, the Nolanoideae, is sometimes also included in the Solanaceae (D'Arcy, 1979, 1991).] *Cyphomandra* belongs to the subfamily Solanoideae, characterized by flattened seeds with curved embryos. Other characters often found in the Solanoideae are actinomorphic corollas, stamens inserted low in the floral tube, berry fruits, and a chromosome base number of 12 (D'Arcy, 1979). Armstrong (1986) describes the vasculature of the Solanoideae as consisting of pedicels with nine to ten discrete xylem strands and a 5-trace, 5-gap pattern of calyx vascularization. All of the characters listed above are manifested in the genus *Cyphomandra*.

In the most recent survey of subfamilial classification of the Solanaceae, D'Arcy (1991) divides the Solanoideae into seven tribes: Datureae, Hyoscyameae, Jaboroseae, Juanulloeae, Lycieae, Nicandreae, Solandreae, and Solaneae. *Cyphomandra* belongs to the tribe Solaneae, characterized by seeds with abundant endosperm; valvate, induplicate, or plicate corolla aestivation; and filaments inserted near the base of the anthers. Wettstein (1891) differs in placing *Cyphomandra* in the subtribe Mandragorinae, members of which supposedly have the filaments attached at the back of the anthers or, if attached at the base, with the anther connective thickened. This grouping is erroneous, and both Hunziker (1979a) and D'Arcy (1991) have assigned all the genera originally in Wettstein's Mandragorinae to other tribes.

Cyphomandra is one of the five genera in the Solanaceae with anthers that dehisce by terminal pores. The others are *Solanum*, *Lycopersicon*, *Lycianthes*, and *Triguera*, all of which are placed in the tribe Solaneae (D'Arcy, 1991). Whether or not terminal anther dehiscence is a synapomorphy that unites these genera is unresolved.

Cyphomandra has been closely allied with *Solanum*, and the taxonomic distinctions between the two genera have been unclear in the past. Much of the problem stems from the large size of *Solanum*, with an estimated 1000 species (D'Arcy, 1991). This genus is very diverse morphologically and poorly understood taxonomically. Recently, the generic boundary between *Cyphomandra* and *Solanum* has been examined in detail (Bohs, 1989a).

Traditionally, *Cyphomandra* has been delimited from *Solanum* on the basis of anther structure. Sendtner (1845) was the first to use the enlarged anther connective in defining *Cyphomandra.* The connective region is thickened and prominent abaxially, and is sharply delimited from the thin-walled anther thecae (Bohs, 1989a). Some species of *Solanum* may have thickened anthers, but the thickened region is not expanded abaxially and is contiguous with the thecal walls (Bohs, 1989a).

Cyphomandra can also be distinguished from *Solanum* on the basis of chromosome size. Evidence to date indicates that *Solanum* and the segregate genus *Lycopersicon* have small chromosomes, generally less than 4 μm long (Bernardello & Anderson, 1990; Roe, 1967). In contrast, all the species of *Cyphomandra* that have been examined cytologically have large chromosomes and large amounts of DNA (Bohs, 1989a; Pringle & Murray, 1991a; see CHROMOSOMES).

Architecture and branching patterns can also be useful in delimiting *Cyphomandra* (see MORPHOLOGY), but intermediates exist and not enough species of *Cyphomandra* and *Solanum* have been examined for these characters to assess their taxonomic value (Bohs, 1989a).

Recent studies (Bohs, unpub. data) indicate that *Cyphomandra* is most closely allied with *Solanum* section *Cyphomandropsis* Bitter (Bitter, 1913a), a group of about 20 species of South American shrubs. Members of this section have thickened anthers, but the type of thickening is more like that of *Solanum* than *Cyphomandra*, for the thickened region extends over the abaxial walls of the anther thecae. This section is intermediate between *Cyphomandra* and *Solanum* in other morphological features. For instance, some species have many-leaved sympodial units on the crown branches like some *Solanum* species, whereas others have the three- to four-leaved sympodial units typical of *Cyphomandra.* Four species of *Solanum* section *Cyphomandropsis* have been examined cytologically, and all have the large chromosomes characteristic of *Cyphomandra* (L. Bohs, unpub. data; E. Moscone, unpub. data). Data from a study of chloroplast DNA restriction sites supports a close relationship between *Cyphomandra* and *Solanum* section *Cyphomandropsis* (Olmstead & Palmer, 1992). Currently no information exists about groups in *Solanum* that might be related to this putative *Cyphomandra*/*Cyphomandropsis* clade.

Unfortunately, virtually nothing is known about *Solanum* section *Cyphomandropsis* from a taxonomic perspective. Seithe (1962), Gilli (1970), Danert (1970), and Morton (1976) include the section in *Solanum*, while D'Arcy (1972) and Child (1984) place it in *Cyphomandra.* Consideration of the species limits and proper rank of section *Cyphomandropsis* is beyond the scope of this monograph, and will be dealt with in a future publication. For now, species of section *Cyphomandropsis* that have been described in *Cyphomandra* are included under DOUBTFUL NAMES.

TAXONOMIC HISTORY

Plants later assigned to the genus *Cyphomandra* were first brought back to European botanists from the extensive New World expeditions undertaken at the end of the 18th century. These species were at first placed in *Solanum.* Aublet in 1775 was the first to describe a species which would later be included in *Cyphomandra, Solanum tegore* from French Guiana. Other species were enumerated in the volumes resulting from expeditions to tropical America by Ruiz and Pavón (1777–1788) and Humboldt and Bonpland (1799–1804). In 1799, Cavanilles described *Solanum betaceum* from a plant in cultivation at the Jardín Botánico Real in Madrid.

In his 1813 thesis, *Histoire des Solanum*, and later in a revision of this work, *Solanorum generumque affinium synopsis* (1816), Michel Félix Dunal attempted to monograph *Solanum* and related genera. In these works he summarized the species previously described by Aublet, Ruiz and Pavón, and Cavanilles. In 1813 he designated an infrageneric group, *Pachyphylla*, composed of four species of *Solanum* (*pendulum, obliquum, viridiflorum*, and *betaceum*) that were later transferred to *Cyphomandra.* Dunal did not clearly specify the rank of this name in his 1813 and 1816 works, but later in 1852 indicates its status as a section. [This is contrary to Knapp (1983), who states that *Pachyphylla* was first accorded sectional rank by D'Arcy (1972). However, Dunal (1852) does not appear to validly make the transfer of section *Pachyphylla* from *Solanum* to *Cyphomandra* (Art. 33.1; Greuter et al., 1988), and thus the combination *Cyphomandra* section *Pachyphylla* dates to D'Arcy (1972).] In his 1816 work Dunal published *Solanum diversifolium*, a name he attributed to Humboldt and Bonpland and one later included in their *Nova Genera et Species Plantarum* (1818). According to Stafleu and Cowan (1979), new taxa in this latter work were drafted by Kunth, although Hawkes and Hjerting (1969) assert that the genus *Solanum* was monographed by Dunal. Martius in 1829 described two new species from has Brazilian trip of 1817–1820 under the genus *Witheringia*; these were later transferred to *Cyphomandra*. Vellozo's *Flora fluminensis* (1829) included four newly described species from coastal Brazil that would eventually become associated with *Cyphomandra*.

Don's (1837) and Walpers' (1844) compendia summarized and organized the species of Solanaceae published up to that time. For the most part, they relied heavily on the species descriptions of previous authors such as Dunal and Martius. In their works, species later placed in *Cyphomandra* were included in *Solanum* and *Witheringia*.

Cyphomandra was first established as a distinct genus by Otto Sendtner in 1845. His name *Cyphomandra*, Greek for "curved" or "swollen anther," is based on the dorsally gibbous anther connective that is joined to the two anther thecae. He used this swollen anther connective as the primary character in the separation of *Cyphomandra* from *Solanum*, and pointed out the unusual leaf arrangement of the flowering branches. Twelve species were included in his treatment, distinguished by the relative lengths of the calyx and corolla, the shapes of the stigma and style, the structures of the inflorescences, and the shapes of the fruits.

At about the same time, John Miers erected his new genus *Pionandra*, encompassing 17 species and 4 doubtful taxa (Miers, 1845). He too emphasized the enlarged anther connective as the major criterion for inclusion within the genus. He grouped the species into two sections, *Ceratostemon* and *Euthystemon*, according to whether the flowers had straight or very curved stamens. Sendtner's publication of *Cyphomandra* preceded the appearance of *Pionandra* by several months, thereby reducing the latter name to synonymy. Miers attempted to resurrect his genus *Pionandra* in his publications of 1854 and 1855 by equating Sendtner's *Cyphomandra* with Miers' section *Ceratostemon* and retaining the species of the section *Euthystemon* in *Pionandra*. Later authors recognized that Miers' two sections do not warrant generic standing and again relegated *Pionandra* to synonymy under *Cyphomandra*.

In his treatment of the Solanaceae for Martius' *Flora Brasiliensis* in 1846, Sendtner described three new species and transferred four others to *Cyphomandra*, bringing the total to 15 Brazilian species. He also doubtfully included three of Miers' *Pionandra* species without transferring the epithets. This beautifully illustrated work is still a useful, though out-of-date, reference on Brazilian Solanaceae.

Walpers in 1847 summarized the taxonomy of the group to date and included 28 species in *Cyphomandra*. He considered 13 of these taxa to be "species dubiae," but nonetheless transferred them to *Cyphomandra*. Ten of these were new combinations. In making the transfers Walpers cited "Sendtner mss.," but the location and contents of these manuscripts are unknown.

The last attempt at a complete monograph of the entire genus was that of Dunal in 1852 for the treatment of the Solanaceae in DeCandolle's *Prodromus*. In this work he included 34 species of *Cyphomandra*, eight of them new. This valuable work did much to consolidate the taxonomy of the genus and remains the most complete summary of the species of *Cyphomandra* throughout its range, but unfortunately it does not include the many species described in the last 130 years.

Except for the publication of a few new species, most notably by Rusby around the turn of the century, no further taxonomic work was undertaken in the genus until Bitter's works on the Solanaceae appeared in the early twentieth century. Bitter's meticulous observations and tireless taxonomic writings were a solid contribution which clarified many of the systematic problems in *Solanum* and related genera. Yet the overall value of his work is diminished by the absence of a consolidated summary and lack of keys to his species and sections. Bitter had planned to write a monograph on *Solanum*, but he died in 1927. Many of Bitter's types were destroyed in the bombing of the Berlin herbarium during World War II, adding to the taxonomic and nomenclatural difficulties of the group.

From Bitter's time on, various authors described new species of *Cyphomandra* or mentioned them in floristic works, but no revisionary or monographic works were prepared. The most important of these floristic treatments are Rusby (1896, 1899, 1907, 1912, 1920) for Bolivia and Colombia; Pittier (1947), Steyermark (1966), and Steyermark and Huber (1978) for Venezuela; Standley (1927, 1928, 1929), Standley and Morton (1938), Standley and Steyermark (1940) and Gentry and Standley (1974) for Central America; Macbride (1962) for Peru; Smith and Downs (1966) for southeastern Brazil; and D'Arcy (1973) for Panama.

Recently Alan Child, working in Yorkshire, England, provided a synopsis of the species of *Cyphomandra* and erected six sections within the genus (Child, 1984). He did not address the species limits and synonymy of the many taxa within *Cyphomandra.*

There is presently an active community of botanists interested in clarifying the taxonomy of the Solanaceae. Work on the sections of *Solanum* and on problematic genera in the Solanaceae is proceeding at a slow but steady rate. It is hoped that the present treatment of the genus *Cyphomandra* will contribute significantly toward the elucidation of taxonomic relationships in this important family.

MORPHOLOGY

Habit, Architecture, and Stems

Most species of *Cyphomandra* are treelets, reaching from 0.5 to over 15 m tall. Some of the smallest representatives, such as *C. benensis*, *C. calycina*, *C. corymbiflora*, *C. heterophylla*, and *C. ovum-fringillae*, rarely exceed 3 m in height. In contrast, *C. hartwegii* and *C. endopogon* may become over 15 m tall. All species are woody at the base, sometimes with a trunk diameter exceeding 10 cm. The brittle wood forms a thin cylinder surrounding the sometimes chambered pith.

Young stems are often succulent, usually green or purplish, and frequently dotted with light-colored idioblasts containing crystal sand. Older stems have smooth, light-colored bark with small lenticels and narrow longitudinal fissures. The bark does not exfoliate. There is apparently little taxonomically useful variation in bark characters.

Most specimens of *Cyphomandra* observed in the field and greenhouse have a distinctive architecture composed of an upright (orthotropic) trunk surmounted by a spreading crown of horizontal (plagiotropic) branches. Both trunk and branches are sympodial, with each module ending in a terminal inflorescence. Each trunk module contains many leaves arranged in 2/5 phyllotaxy. After a terminal inflorescence is produced, usually three plagiotropic shoots grow out from buds located just below the inflorescence. These plagiotropic shoots branch sympodially, producing a spreading crown. The leaf arrangement of the plagiotropic crown branches differs greatly from that of the trunk, and is described below. Eventually the crown branches begin to senesce, and a new trunk module originates from a bud on the old trunk below the branch tier. The characteristic growth form resulting from this sequence of events is diagramatically shown in Bohs (1989a).

The presence of an orthotropic trunk and plagiotropic branches that are both modular in construction corresponds to Prévost's model in the architectural scheme of Hallé et al. (1978). [The assertion that *Cyphomandra* architecture is intermediate between Prévost's and Nozeran's models in Bohs (1989a) is probably incorrect. In Nozeran's model the plagiotropic branches are monopodial and thus not modular, whereas in Prévost's model both trunk and branches are sympodial (Prévost, 1978). The latter situation occurs in *Cyphomandra.*] The following species of *Cyphomandra* are known from field or greenhouse observations or from detailed herbarium information to exhibit Prévost's model: *C. acuminata*, *C. diploconos*, *C. diversifolia*, *C. endopogon*, *C. foetida*, *C. hartwegii*, *C. obliqua*, *C. sibundoyensis*, *C. stellata*, and *C. uniloba*. Several other species (e.g., *C. corymbiflora*, *C. dolichocarpa*, *C. pendula*, *C. pilosa*, *C. tegore*, and *C. tenuisetosa*) produced a single trunk with plagiotropic and sympodial crown branches, but successive trunk modules were not observed. *Cyphomandra betacea* and *C. cajanumensis* differed from most of the other species in that two, rather than three, main plagiotropic crown branches grew out below the terminal trunk inflorescence. The crown branches in these two taxa also have a more upright orientation than in other species observed, although the leaf arrangement on the crown branches differs from that of the trunk. *Cyphomandra betacea* and *C. cajanu-*

mensis thus verge on Leeuwenberg's model, in which all axes are modular but orthotropic and equivalent. Other Solanaceae, such as some species of *Capsicum* and *Solanum*, exhibit Leeuwenberg's model (Hallé et al., 1978). Leeuwenberg's model has a close relationship with Prévost's model, the main difference being the strong differentiation between trunk and crown modules in the latter, as is characteristic of *Cyphomandra*. Ecologically, species with Leeuwenberg's model are often of small stature and occupy secondary habitats, whereas those with Prevost's model are usually taller, more long-lived species of the deep forest (Hallé et al., 1978).

A few species, such as *C. tenuisetosa*, *C. acuminata*, and *C. uniloba*, have slender trunks with scandent branches and have been described as being vines, although it is doubtful that the stems truly twine.

Leaf arrangement and branching pattern on the plagiotropic crown branches are also important in distinguishing *Cyphomandra* from related taxa. Branching patterns in the Solanaceae are often complex and have been used as taxonomic characters to differentiate genera (Child, 1979; Danert, 1958) as well as infrageneric groups in *Solanum* (Danert, 1967). In the crown branches of *Cyphomandra*, generally two replacement shoots grow sylleptically from buds below the terminal inflorescences, so that the inflorescence appears to be located in a branch fork. This is known as dichasial branching. In some cases, the inflorescence may be carried up onto one of the replacement shoots, and may thus appear to be extra-axillary. Later orders of branching may be monochasial, with only a single replacement shoot that originates from the axillary bud just proximal to the inflorescence. The leaves subtending the replacement shoots are usually carried up the elongating axis to a postion nearly opposite the first leaf on the replacement shoot (prophyll) so that the two leaves are paired. However, the paired leaves actually belong to successive sympodial shoot generations and often differ in morphology, with the subtending leaf usually larger than the prophyll. The subtending leaf often has an axillary bud, whereas the prophyll does not. In some species the paired leaves are followed by a solitary leaf. The next two leaves subtend axillary buds that grow out to form replacement shoots. Each shoot module is thus composed of 3- to 4- (rarely 5-)leaved sympodia. A diagrammatic representation of this leaf arrangement is given in Bohs (1989a).

Cyphomandra betacea and *C. diploconos* deviate somewhat from the typical branching pattern seen in other species of the genus. In *C. betacea*, there is a varying degree of fusion of the inflorescence and subtending leaves to the elongating replacement shoot. Inflorescences often appear to be extra-axillary, and leaf arrangements can vary from solitary to paired to pseudo-whorls of three leaves. Supernumerary buds frequently develop in leaf or inflorescence axils and further complicate the picture. In *C. diploconos*, all leaves on the shoot are in anisophyllous pairs. Both leaves of the first pair on the replacement shoots lack evident buds. The next leaf pair has a single bud in the angle formed by the two petioles. I interpret this pair to represent a subtending leaf and a precociously expanded prophyll of its axillary shoot. Sympodial units in this species thus appear to be four-leaved. *Cyphomandra corymbiflora* can have five-leaved sympodia due to the production of two intervening leaves between those subtending replacement shoots.

Few other Solanaceae are known at present to have a shoot structure composed of three- to four-leaved sympodial units and inflorescences situated in branch forks. This branching pattern, thought to be unique to *Cyphomandra* (Bohs, 1986), was used by Child (1979) to distinguish the genus from other Solanaceae. However, at least one species outside *Cyphomandra*, *Solanum allophyllum*, has a similar branching pattern (Bohs, 1989a). Furthermore, some members of *Solanum* section *Cyphomandropsis* may have branching patterns similar to those seen in *Cyphomandra*. This section has not been examined taxonomically, and its generic position and relationships to *Solanum* and *Cyphomandra* remain to be worked out. Therefore, although the branching pattern described above is indicative of *Cyphomandra*, it is apparently not unique to it.

Cyphomandra stems have bicollateral bundles with a well-defined region of internal phloem, as is characteristic of the Solanaceae. Nodal anatomy was examined in crown branches of *C. betacea*, *C. corymbiflora*, *C. diploconos*, *C. diversifolia*, and *C. uniloba*. All had unilacunar nodes with three leaf traces.

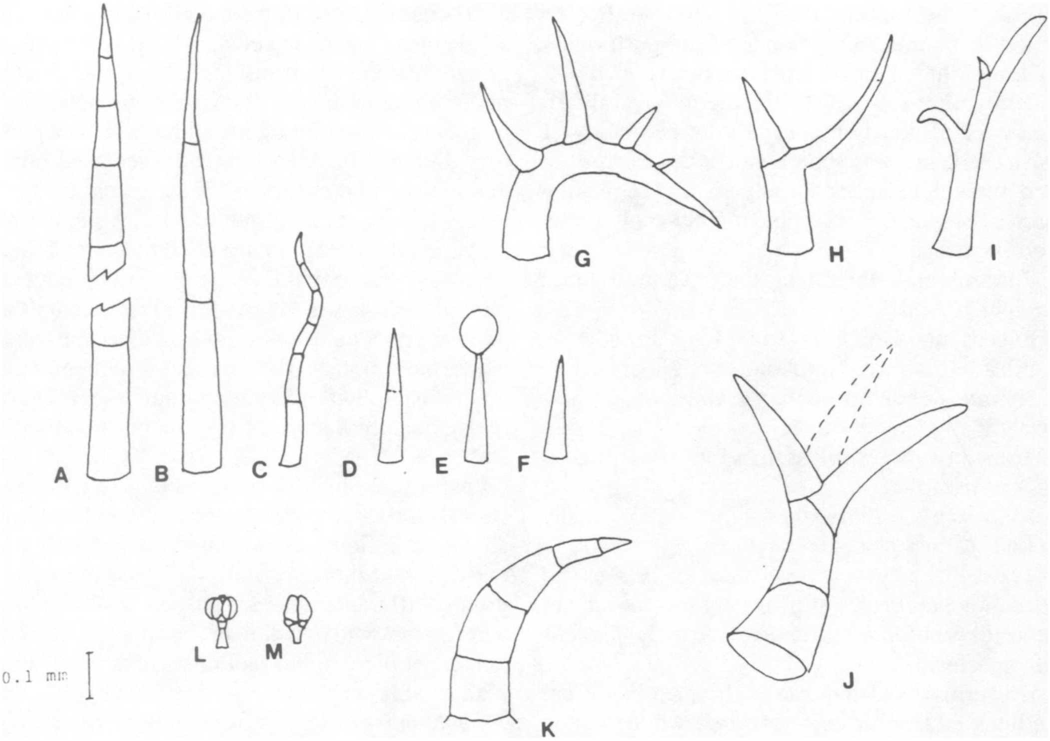


FIG. 1. Hair types in *Cyphomandra.* A–D, F, K. Finger hairs; E. Gland-tipped finger hair; G–J. Branchlet hairs; L–M. Multicellular glands. **A.** *C. pilosa*, leaf blade; **B.** *C. hartwegii*–leaf blade; **C.** *C. hartwegii* subspecies *ramosa*, corolla margin; **D–F.** *C. betacea*, leaf blade; **G–I.** *C. betacea*, leaf margin; **J.** *C. pendula*, corolla lobe; **K.** *C. uniloba*, leaf margin; **L.** *C. diploconos*, petiole; **M.** *C. betacea*, leaf blade.

Trichomes

The indumentum of *Cyphomandra* is composed of four types of trichomes, following the scheme of Seithe (1979): (1) finger hairs, (2) gland-tipped finger hairs, (3) multicellular glands, and (4) branchlet hairs (Fig. 1). Finger hairs, or uniseriate, multicellular, unbranched trichomes, are the most commmon and may vary in length from under 0.2 mm to several millimeters in length. Gland-tipped finger hairs are less frequent. They also vary in length; longer gland-tipped finger hairs are especially typical of *C. foetida.* Short-stalked, multicellular glands are common on the vegetative parts and impart a strong smell to the plants. These glands are also known as square or quadrat glands because of their 4-celled secretory heads. Seithe (1962) and Edmonds (1982) have noted that similar multicellular glands are abundant in *Solanum.* Because these glands are uniformly present in most *Cyphomandra* species, they are of little use as a taxonomic character. Branchlet hairs, which are forked or dendritically divided, may occur occasionally on the leaf margins or more frequently on the corolla lobes. Small branchlet hairs are also found on the style of *C. corymbiflora.* Stellate trichomes and prickles are absent.

Many species have multicellular eglandular hairs whose cell walls are verrucose, or covered with small bumps. This feature is evident with light microscopy and is even visible with a dissecting microscope. Edmonds (1982) has described this verrucose surface morphology in epidermal hairs of *Solanum* section *Solanum*, and it is also seen in the illustrations of *Cyphomandra* *betacea* trichomes in Mahlberg (1985). Whether or not this character is species-specific, or whether it varies in relation to age or position on an individual plant has not been determined.

Terms that are used to convey the overall appearance of the trichomes are defined below. I have used the terms puberulent, pubescent, pilose and hirsute to apply chiefly to the vegetative parts. Tomentose and ciliate mainly apply to the corolla margins.

Puberulent—Hairs less than 0.5 mm long, straight.

Pubescent—Hairs 0.5–1 mm long, straight.

Pilose—Hairs 1–3 mm long, straight or curled.

Hirsute—Hairs more than 3 mm long, usually straight.

Tomentose—Hairs less than 1 mm long, curled (often forked).

Ciliate—Hairs more than 1 mm long, usually curled.

Though the type of indumentum is a useful taxonomic character, it is usually too variable to be employed alone in distinguishing *Cyphomandra* species.

Epidermal sand-punctae are frequently present and have the appearance of small white dots on the surface of the stems. Often they occur on other parts of the plant, such as the leaves, inflorescence axes, and flowers. They are most noticeable in taxa with rather membranaceous leaves, such as *C. fragilis*.

Leaves

The leaves of *Cyphomandra* are petiolate and exstipulate, with brochidodromous venation and entire to undulate margins. The leaves can vary in size from the small crown leaves of *C. ovum-fringillae* and *C. benensis*, reaching a length of only 1.5 to about 9 cm, to the trunk leaves of *C. betacea*, *C. cajanumensis*, *C. dolichocarpa*, *C. endopogon*, *C. hartwegii*, and *C. sycocarpa*, which can be over 40 cm long. The leaf blade ranges from simple and entire to pinnately lobed or compound. The species with at least some compound or lobed leaves are *C. diploconos*, *C. diversifolia*, *C. endopogon*, *C. fragilis*, *C. hartwegii*, *C. heterophylla*, *C. oblongifolia*, *C. ovum-fringillae*, *C. pendula*, *C. pinetorum*, *C. sciadostylis*, *C. sycocarpa*, *C. tegore*, and *C. tenuisetosa*. Not only does leaf size and morphology vary between species, but striking differences also occur between trunk and crown regions of a single plant, and even between leaves on a single crown branch. The trunk leaves may be similar or dissimilar in shape to those of the branches, but in general they are larger and have longer petioles. In many taxa the branch leaves are simple and entire, whereas those of the trunk are pinnately lobed or compound. In species such as *C. hartwegii* and *C. diploconos* that can have lobed trunk leaves, the first five to ten leaves produced on the seedling are unlobed. If all leaves on the plant are divided (as in *C. diversifolia*), the trunk leaves have more leaflets or lobes. Frequently the most distal leaflets of compound leaves are basiscopically decurrent (expanded toward the leaf base.)

Leaf morphology on a single branch can vary significantly. As already noted, the leaf pair above the inflorescence consists of leaves from two different shoot generations. These leaves are usually different in size and shape, the subtending leaf larger, with shallower basal lobes and a longer petiole. The next solitary leaf is often large with an oblique base.

Cyphomandra leaves frequently have cordate bases. Occasionally the basal lobes may be very long and overlap one another, but not with enough consistency to be taxonomically useful. A few species have cuneate, truncate, or decurrent leaf bases. The base of the blade is often oblique. In the species descriptions, leaf blades are described as unlobed or pinnately lobed. This refers to the shape of the whole blade, not the base.

The terms for shape, apex, and base of the leaf are those of Hickey (1979). Leaf blade measurements are taken from the insertion of the blade at the petiole to the apex, and width is measured at the widest point. If the base is cordate, the basal lobes are measured from the lowest point to the insertion of the blade on the midrib. The length of the petiole is measured from the leaf axil to the blade insertion.

The petioles are often terete in the living state but appear to be adaxially channelled when dried. The petiole vestiture is generally similar to that of the stem.

Given the variability in leaf form which may occur on a single plant, it should be used with caution as a taxonomic character.

Inflorescences

The inflorescence of *Cyphomandra* is a scorpioid cyme, with the flowers arranged in a double series along the axis. The position of the inflorescence is morphologically terminal in all species. Due to the growth of one or more renewal shoots from axillary buds below the inflorescence, it may appear to be axillary or, on older branches, in the axil of a branch fork. Occasionally it is "carried up" on the renewal shoot for a centimeter or two and appears extra-axillary. The peduncle and pedicels are usually pendulous.

Some species have predominantly simple, others mostly branched inflorescences. This character should be used with caution. Much variation in the degree of inflorescence branching can occur within a single plant.

I have divided the inflorescence into three regions: the peduncle, rachis, and pedicels. The peduncle is defined as the length of the inflorescence axis from the stem to the first pedicel; the rachis is the axis bearing the pedicels. In the case of a branched inflorescence, the rachis length is measured to the first branching point on the peduncle. In all species of *Cyphomandra* the pedicels are articulated at or above the base and leave prominent scars or short pegs on the rachis. The length of these pegs and the spacing between the pedicels are useful taxonomic characters. The peduncle, rachis, and pedicels are often thick and elongated in fruit. All inflorescence measurements are taken from flowering material unless noted otherwise. The number of flowers per inflorescence can be determined by counting the number of pedicel remnants or scars.

The inflorescence is ebracteate in all species except *C. hartwegii* and *C. endopogon*, in which leaf-like bracts may occur. The pubescence of the inflorescence axis is similar to that of the stem except it is usually sparser and has more abundant gland-tipped hairs.

Flowers

All species have perfect, actinomorphic, pentamerous flowers. The flowers are sympetalous and synsepalous. The calyx is usually small, but the lobes may approach the size of the corolla lobes in *C. calycina* and *C. diversifolia.* The calyx may be membranaceous or fleshy in texture; it is usually densely glandular adaxially. In fruit, the calyx is persistent and slightly enlarged. Most species have five calyx lobes, but occasionally the calyx margin can rupture irregularly. The lobes are usually more or less triangular and have acute, obtuse, or apiculate apices. In general, the length of the calyx is more useful than the shape of the lobes in distinguishing species.

The corolla varies widely among species and provides several useful taxonomic characters. Corolla shapes fall into three main categories: urceolate (divided much less than halfway to base; e.g., *C. diversifolia*), campanulate (divided about halfway to 2/3 to base; e.g., *C. pilosa*, *C. oblongifolia*), or stellate (divided nearly to base, with tube only about 2–3 mm long; e.g., *C. hartwegii*). A diagrammatic representation of these corolla shapes is given in Fig. 2. The corolla lobes reflex to expose the anthers and style. In species such as *C. betacea* and *C. hartwegii*, the corolla lobes loosely close again as the flower ages. The corolla is usually green, white, or purple; exceptions are *C. betacea* and *C. acuminata*, which have pinkish or reddish flowers. The corolla is often more darkly pigmented on the adaxial surface and on the midveins of the lobes. A few species, such as *C. diploconos* and *C. corymbiflora*, have corollas that fade from purple to yellow or white as they age.

All species have five stamens of equal length inserted in the corolla base, sometimes on a ring of tissue surrounding the ovary. Stamen morphology provides one of the most useful characters in delimiting species. The anthers dehisce by terminal pores that do not open into longitudinal slits. The anther connective is dorsally elaborated and is composed of much thicker tissue than the anther thecae. Both connective and thecae are noticably papillose. Unlike most species of *Solanum*, the anthers and connective are not necessarily yellow, but can be purple, reddish, green, or white. The anther thecae and connective region far exceed the very short (ca. 1 mm) glabrous filaments. Except for the *C. obliqua* group, most species have tapered anthers. The connective may be expanded adaxially and abaxially in some species.

The bilocular ovary in all species is superior and conical; placentation is axile and there are numerous (usually several hundred) ovules. The style is straight and cylindrical or dilated upward

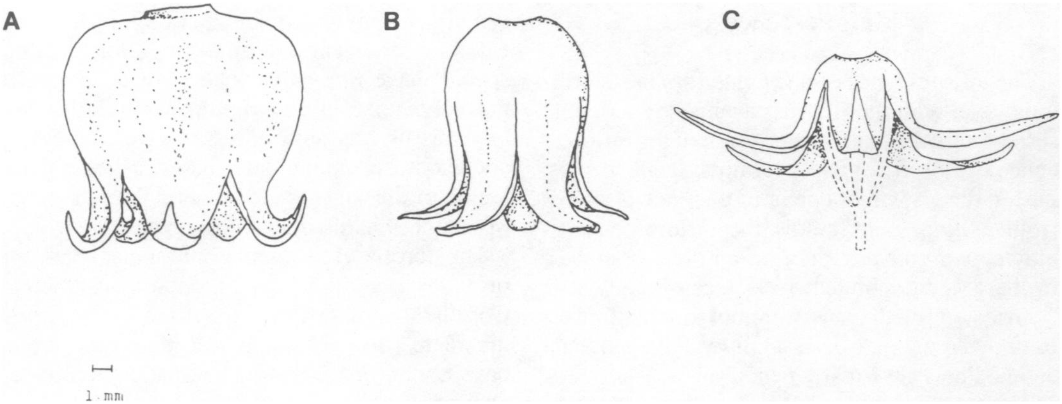


FIG. 2. Corolla types in *Cyphomandra.* **A.** Urceolate (*C. diversifolia*). **B.** Campanulate (*C. pilosa*). **C.** Stellate (*C. hartwegii*).

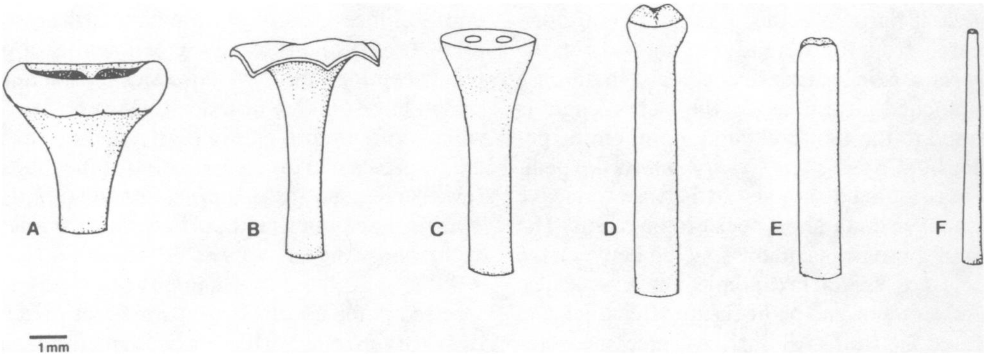


FIG. 3. Stigmas and styles of *Cyphomandra.* Styles end at abscission zone at apex of ovary. **A.** *C. diploconos.* **B.** *C. obliqua.* **C.** *C. uniloba.* **D.** *C. diversifolia.* **E.** *C. betacea.* **F.** *C. hartwegii* subspecies *ramosa.*

into an expanded stigma. An abscission zone forms at the apex of the ovary. Stigma morphology varies considerably and is taxonomically significant. The stigma is always more or less bilobed, reflecting the 2-carpellate nature of the gynoecium, but the stigmatic surface ranges from very small (e.g., *C. hartwegii*) to very expanded and biglandular (e.g., *C. diploconos*, *C. obliqua*). Figure 3 compares stigmas of six different taxa and shows a range of style and stigma shapes, from obconical (*C. diploconos*) to peltiform (*C. obliqua* and *C. uniloba*) to capitate (*C. diversifolia*) and truncate (*C. betacea* and *C. hartwegii* subspecies *ramosa*). The nature of the prominent glands present on the stigmas of taxa such as *C. obliqua* and *C. uniloba* has not been investigated.

Fruits

The fruits of *Cyphomandra* are pendent, fleshy berries. The numerous seeds are borne on intruded placentae, and the watery or juicy fruit pulp can be yellow, orange, cream, or nearly transparent. Some species have very large fruits with a mild sweet flavor (e.g., *C. betacea*, *C. hartwegii*, *C. sibundoyensis*); others are small and acidulous. Fruits are most commonly yellow to orange when ripe, often with darker longitudinal stripes. *Cyphomandra betacea* sometimes has dark red to purple fruits. Fruits vary in shape from obovate and obtuse in *C. sycocarpa* to ellipsoidal, elongated, and pointed in *C. dolichocarpa*. Minute glandular hairs or longer glandular or eglandular hairs cover the fruit surface in some taxa. The presence of trichomes on the fruits is often a specific character, but some fruits that are pubescent when young become glabrescent with age.

Stone cell aggregates are present in the majority of taxa. These sclerotic bodies lie beneath the exocarp in the midline and apical regions of the fruit. They stain deeply using phloroglucinol-HCl, indicating lignification. An analysis of the stone cell aggregates extracted from *C. betacea* indicated that they are composed of large amounts of sodium and calcium, probably as silicates, borates, aluminates, aluminum-magnesium-oxygen complexes, or magnesium oxides. Small amounts of tin, copper, chromium, iron, and phosphorus were also found (analysis performed by State of Florida Department of Agriculture; information provided by G. Pringle). Morton (1982) mentions these concretions in the fruits of *C. betacea*, calling them "abnormalities," but in fact they regularly occur in this and other species. Their true taxonomic significance remains to be investigated; Bitter (1914) considered them to be important characters that delimit generic groups in the Solanaceae, while Morton (1944) considered them to be insignificant. The size, shape, and presence or absence of stone cell aggregates may be species-specific. They sometimes reach several centimeters in length, and the surface ranges from smooth to warty. Often smaller stone cell aggregates are found in the distal region of the fruit.

Seeds

Cyphomandra seeds are flattened and reniform in outline, and tan or yellowish to dark brown. In some species, the flattened margin forms a narrow wing encircling the seed. Seed size may be a useful character, and it varies considerably among species, from less than 3 mm (e.g., *C. corymbiflora*, *C. diploconos*, *C. divaricata*) to nearly 1 cm in length (e.g., *C. acuminata*, *C. hartwegii*, *C. sibundoyensis*) (Fig. 4). Large seeds are characteristically but not exclusively found in the *C. hartwegii* species group.

Although the seeds appear to be glabrous in some species, in general the surface is covered with hair-like projections (Fig. 5). These apparent hairs are actually thickenings in the anticlinal walls of the testa epidermis. The outer periclinal wall is very fragile and easily rubbed off, leaving the projecting thickenings. Such thickenings have been observed in many other members of the Solanaceae (Edmonds, 1983; Souèges, 1907). In *Cyphomandra*, the length of these projections can be taxonomically useful. For instance, *C. acuminata* seeds are covered with conspicuous hair-like projections which often reach 1 or 2 mm in length. In the species descriptions, seed surfaces are described as being pubescent, puberulent, etc. It should be kept in mind, however, that the seed surface projections are remnants of wall thickenings rather than true hairs, which are made up of entire cells. The function of these projections is unknown, but possibly they trap water and serve to hydrate the seeds. *Cyphomandra* seeds within the fruits are typically surrounded by a mucilaginous layer that is composed in part of these water-holding projections.

As in other genera of the tribe Solaneae (Hunziker, 1979a, 1979b), *Cyphomandra* seeds have curved embryos with incumbent cotyledons and abundant endosperm.

Pollen

Twenty-eight species of *Cyphomandra* were examined for pollen size (Table I) and fifteen species were examined with the scanning electron microscope (SEM) to observe surface features (Table II). Pollen size measurements were made with a light microscope from fresh samples gathered from greenhouse plants or from dried herbarium specimens. The grains were shaken into a mixture of aniline blue-lactophenol (Hauser & Morrison, 1964) and allowed to stand for 24 hours before measurement. The polar and equatorial diameters were measured on 30 grains per sample using 400 × camera lucida projection onto a digitizer. Diameters were measured on stained grains only, and the distance was measured between the innermost layers of the pollen grain wall. For SEM studies, dried pollen from herbarium specimens was mounted on a stub with double-stick tape, coated with gold-palladium, and examined.

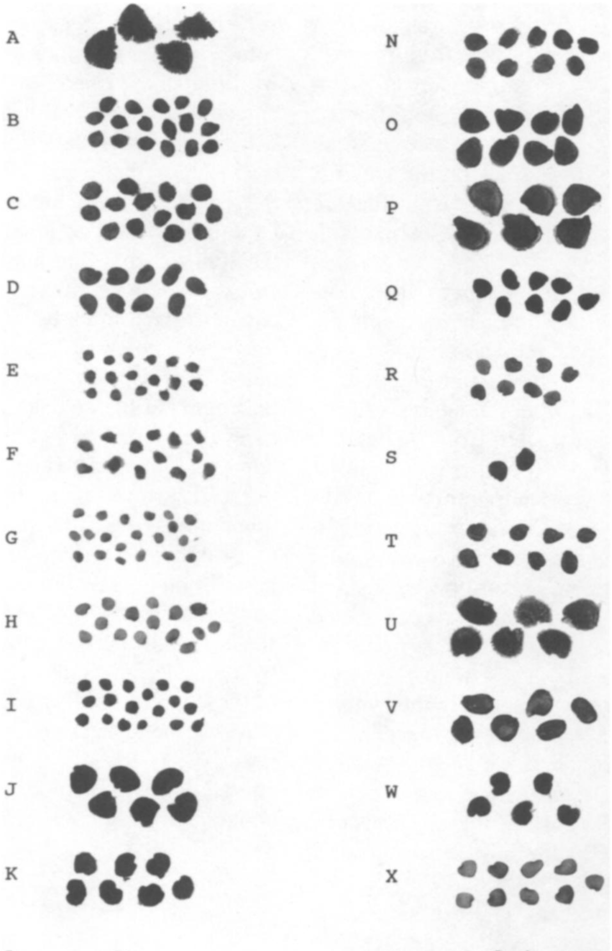


FIG. 4. Seeds of *Cyphomandra.* Scale bar = 1 cm. **A.** *C. acuminata* (*Solomon & Escobar 12458*). **B.** *C. betacea* (*Bohs 1599*). **C.** *C. betacea* (*Bohs 2192*). **D.** *C. cajanumensis* (seeds ex G. Pringle, New Zealand). **E.** *C. calycina* (*Soares s.n.*). **F.** *C. corymbiflora* (*Bohs 2343*). **G.** *C. diploconos* (*Bohs 2335*). **H.** *C. divaricata* (*Soares s.n.*). **I.** *C. diversifolia* subspecies *diversifolia* (*Benitez de Rojas 2744*). **J.** *C. diversifolia* subspecies *chlorantha* (*Bunting & Drummond 6287*). **K.** *C. dolichocarpa* (*Bohs & McPherson 2312*). **L.** *C. endopogon* subspecies *endopogon* (*Williams 8241*). **M.** *C. endopogon* subspecies *guianensis* (*Granville 2220*). **N.** *C. foetida* (*de Albuquerque et al. 1384*). **O.** *C. hartwegii* subspecies *hartwegii* (*Rury 580*). **P.** *C. hartwegii* subspecies *ramosa* (*Buch s.n.*). **Q.** *C. hypomalaca* (*Madison et al. 4972*). **R.** *C. obliqua* (*Plowman & Schunke 11550*). **S.** *C. oblongifolia* (*Maas 416*). **T.** *C. rojasiana* (*Steyermark 33743*). **U.** *C. sibundoyensis* (*Bohs & Juajibioy 2222*). **V.** *C. stellata* (*Rimachi 2923*). **W.** *C. sycocarpa* (*Hage & dos Santos 1490*). **X.** *C. tegore* (*Boerboom (LBB)12032*). **Y.** *C. tobagensis* (*Steyermark & Nilsson 183*). **Z.** *C. uniloba* (*Sperling & King 5500*).

Most of the pollen grains observed were tricolporate (Fig. 6), with a few tetracolporate grains in some samples. The colpi are not fused at the poles, and the endoaperture (os) is laterally elongated (lalongate). In equatorial view the grains are spheroidal to prolate-spheroidal; in

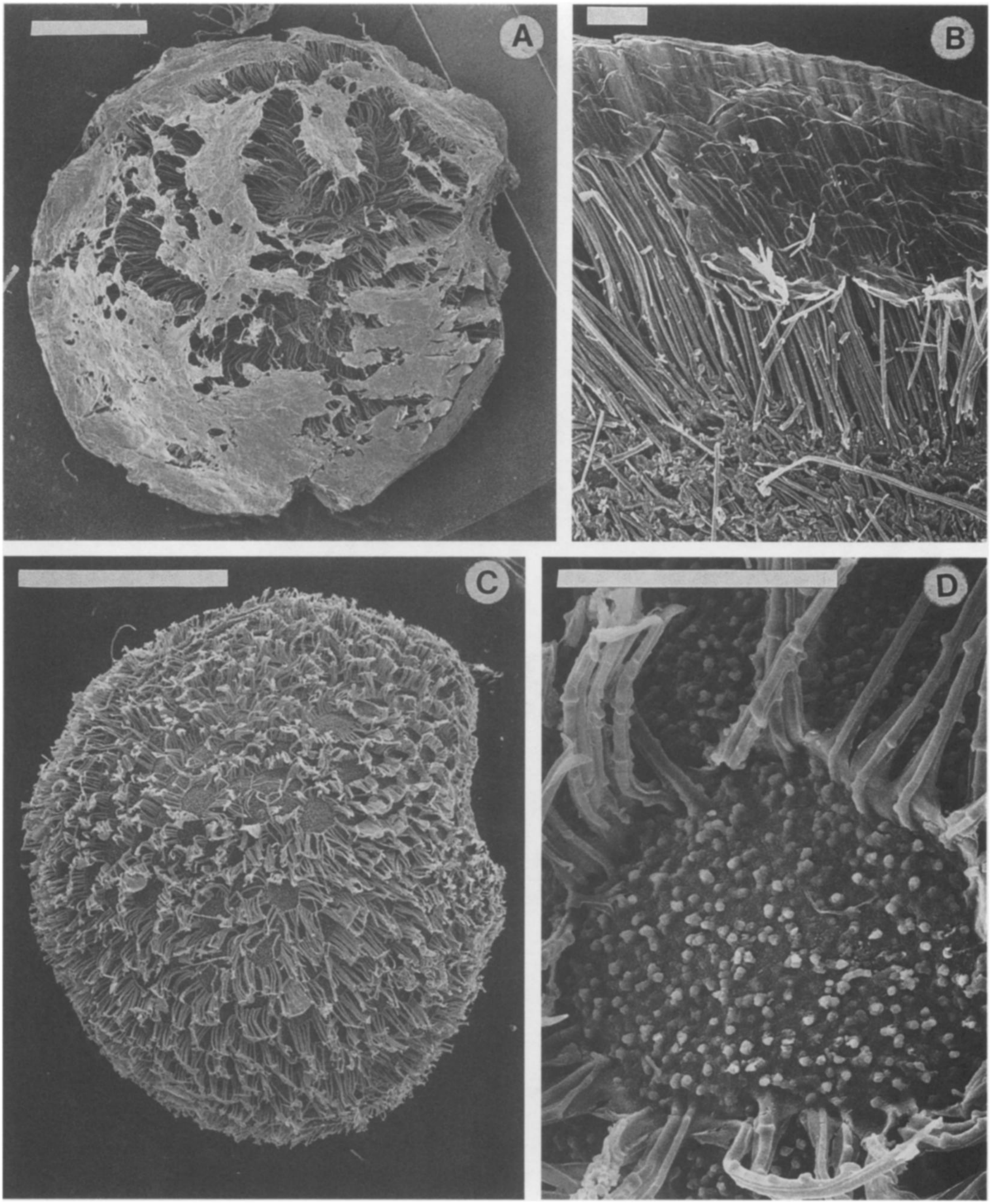


FIG. 5. Seeds of *Cyphomandra* observed with the SEM. A, C. Scale bar = 1 mm. B, D. Scale bar = 100 µm. A–B. *C. betacea*. Outer periclinal walls of testa epidermis are visible. **A.** Whole seed washed in alcohol. **B.** Seed surface. **C–D.** *C. diploconos*. Outer periclinal walls have been washed away. **C.** Whole seed washed in alcohol. **D.** Surface view of epidermal cell of C.

Table I

Pollen size measurements of *Cyphomandra* species. The symbol V: indicates that fresh pollen from greenhouse plants was used; herbarium voucher from same greenhouse plant (Bohs collections) or from seed parent (other collections) cited for the sample. Otherwise, pollen was removed from the dried herbarium specimen cited. Values are means of 30 grains. Standard deviations in parentheses.

Taxon	Polar diameter (µm)	Equatorial diameter (µm)
C. acuminata		
Bang 2281 (NY)	30.24(3.02)	25.53(2.55)
C. benensis		
Rusby 840 (NY)	21.76(1.31)	20.90(1.87)
C. betacea		
V: Nee 30359 (UT)	20.16(1.00)	19.64(1.23)
Killip 39617 (US)	22.16(1.27)	19.83(1.33)
C. cajanumensis		
Cuatrecasas 23917 (F)	21.88(1.42)	20.64(1.39)
C. calycina		
Soares s.n. (UT)	23.88(1.19)	19.69(1.59)
C. corymbiflora		
subspecies *corymbiflora*		
V: Bohs 2343 (GH)	18.79(0.98)	17.20(1.09)
Hatschbach 14964 (NY)	19.86(0.74)	16.84(0.90)
subspecies *mortoniana*		
Smith et al. 7639 (US)	20.02(0.98)	18.22(0.98)
C. diploconos		
V: Bohs 2335 (GH)	22.67(1.70)	21.77(1.43)
Hatschbach 13204 (NY)	24.68(1.08)	20.19(1.27)
C. divaricata		
Hatschbach 23266 (NY)	22.73(0.93)	18.95(1.02)
C. diversifolia		
subspecies *diversifolia*		
V: Bohs 2341 (GH)	28.23(1.51)	27.43(1.73)
Steyermark 91497 (US)	27.08(1.17)	24.27(1.25)
subspecies *chlorantha*		
Steyermark 55774 (F)	23.32(1.51)	21.69(1.22)
C. dolichocarpa		
Hammel 2364 (NY)	23.01(1.24)	19.82(1.40)
C. endopogon		
subspecies *endopogon*		
Schunke 14033 (MO)	24.35(1.47)	24.25(1.24)
C. foetida		
Schunke 4325 (F)	16.87(0.79)	15.72(1.10)
C. fragilis		
Palacios 2233 (UT)	18.38(0.85)	15.45(0.80)

Table I *(continued)*

Taxon	Polar diameter (µm)	Equatorial diameter (µm)
C. hartwegii		
subspecies *hartwegii*		
Beaman et al. 5855 (F)	21.66(1.32)	19.60(1.41)
subspecies *ramosa*		
V: Bohs 1644 (GH)	19.28(1.11)	18.41(1.59)
C. heterophylla		
Gehrt 4661 (US)	23.39(1.62)	21.33(1.50)
C. obliqua		
Plowman & Schunke 11550 (GH)	22.50(1.10)	20.38(1.24)
C. oblongifolia		
Maas 416 (WIS)	21.42(1.27)	19.53(1.64)
C. pendula		
Nelson 822 (F)	22.31(1.11)	20.79(1.33)
C. pilosa		
Cerón & Cerón 4654 (UT)	21.49(1.04)	18.57(0.99)
C. pinetorum		
Kummrow & Soares 3118 (UT)	19.92(0.87)	17.76(1.18)
C. premnifolia		
Sucre 6405 (UT)	24.93(1.15)	20.76(1.48)
C. sciadostylis		
Kummrow & Soares 3117 (UT)	26.58(1.11)	24.86(1.18)
C. stellata		
Palacios 2851 (UT)	24.81(1.69)	20.95(1.70)
C. sycocarpa		
Sucre 6200 (UT)	24.33(1.29)	22.72(1.75)
Mori et al. 10758 (US)	26.75(2.44)	23.87(2.24)
C. tegore		
Cowan 38154 (US)	22.25(1.47)	19.50(1.38)
C. tenuisetosa		
Wasshausen & Encarnación 528 (US)	23.53(1.25)	19.71(1.63)
C. tobagensis		
Steyermark 95044 (US)	26.90(1.43)	22.61(1.26)
C. uniloba		
V: Bohs 2284 (GH)	25.52(1.59)	25.43(1.51)
Nee et al. 35368 (NY)	21.80(1.30)	19.27(1.51)

Table II

Exine sculpturing of *Cyphomandra* species examined with SEM.
Herbarium vouchers given after species name

C. acuminata Bohs 2338 (GH)	granulate
C. betacea Bohs & Juajibioy 1599 (GH)	psilate-subgranulate
C. cajanumensis Hutchison & von Bismarck 6528 (MO)	granulate
C. corymbiflora subspecies *corymbiflora* Hatschbach 14964 (NY)	granulate
subspecies *mortoniana* Smith et al. 7639 (US)	psilate-subgranulate
C. diploconos Hatschbach 13204 (NY)	granulate
C. divaricata Hatschbach 23266 (NY)	granulate
C. diversifolia Bohs 2341 (GH)	psilate-subgranulate
C. endopogon subspecies *endopogon* Schunke 14033 (GH)	granulate-punctulate
C. foetida Schunke 4235 (F)	granulate
C. hartwegii subspecies *hartwegii* Happel & Neill 01 (ECON)	granulate-punctulate
subspecies *ramosa* Bohs 1643 (GH)	granulate-punctulate
C. obliqua Plowman & Schunke 11550 (GH)	granulate-punctulate
C. pendula Schunke 14031 (GH)	psilate
C. pilosa Bohs & Schunke 2169 (GH)	psilate
C. sibundoyensis Bohs & Juajibioy 2222 (GH)	granulate
C. uniloba Sperling & King 5500 (GH)	granulate

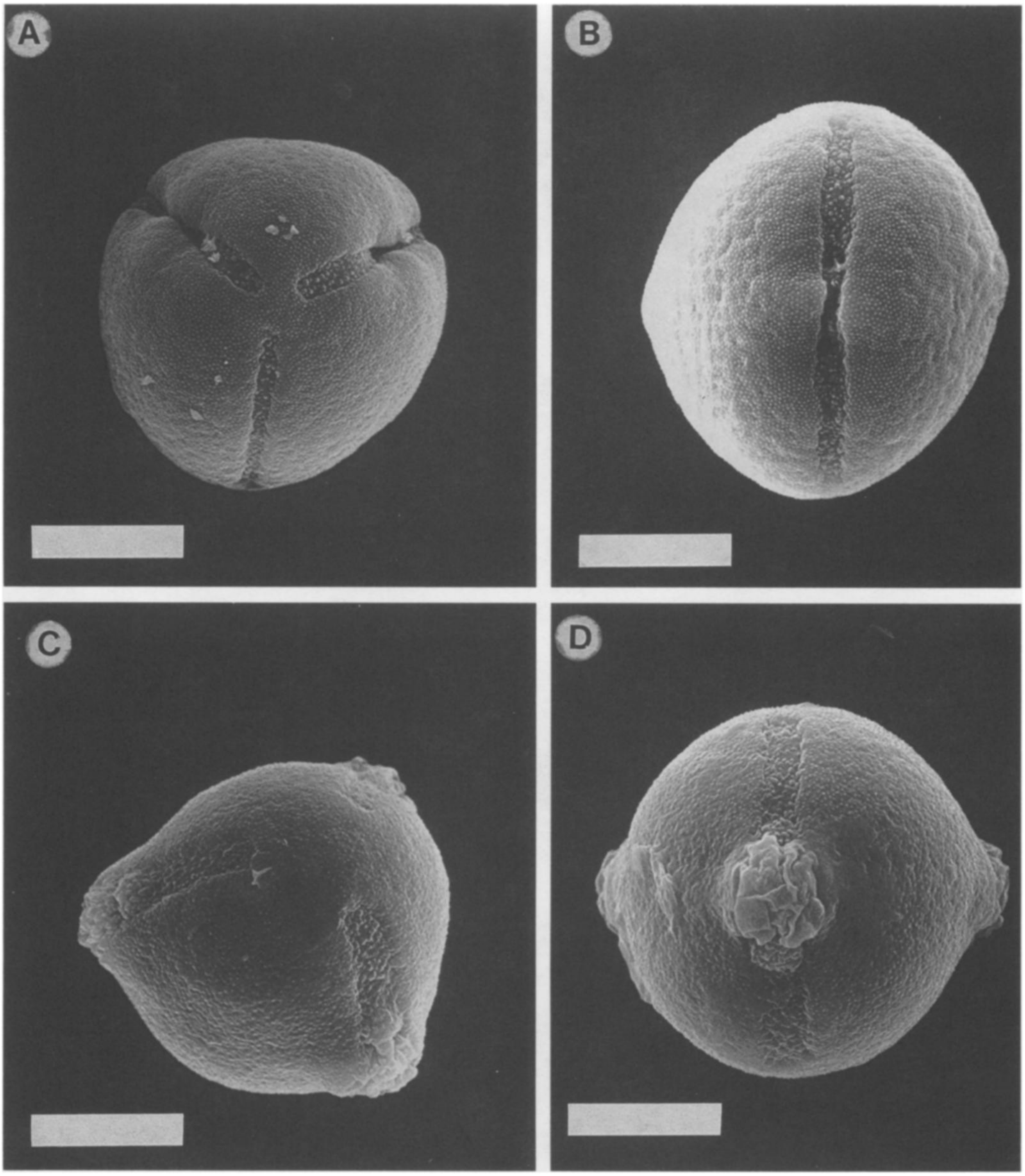


FIG. 6. Pollen grains of *Cyphomandra* observed with the SEM. Scale bars = 10 μm. **A–B.** *C. uniloba.* **C–D.** *C. diversifolia.* A, C. Polar view. B, D. Equatorial view.

polar view the apertures protrude somewhat so the grains are semiangular in outline. Among the species examined the grains vary in diameter from about 15 to 30 μm (Table I) and thus fall into the small to medium size categories of Erdtman (1952, 1969).

Surface features of the exine were not obvious under the light microscope, but under the SEM most species were ornamented with small bumps or granules less than 1 μm in diameter (Fig. 7; Table II). Somewhat larger and more widely spaced granules also occur on the colpal mem-

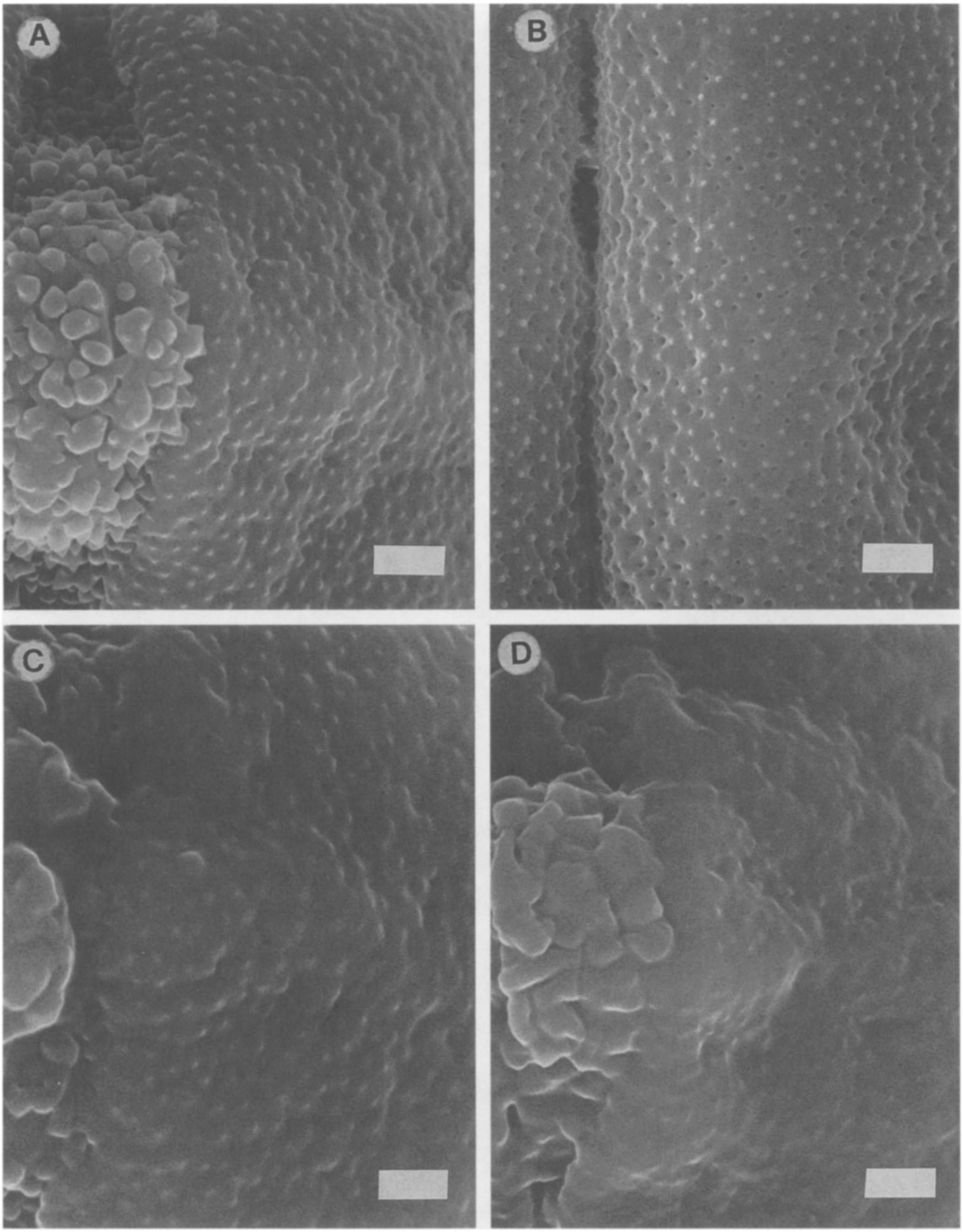


FIG. 7. Surface features of *Cyphomandra* pollen observed with the SEM. Scale bars = 1 µm. **A.** *C. diploconos*. **B.** *C. hartwegii* subspecies *ramosa*. **C.** *C. betacea*. **D.** *C. pendula*.

branes. In some species, the surface is covered with both granules and minute pits (Fig. 7B). Two species examined lack obvious granules and have nearly smooth (psilate) exines (Fig. 7D).

Pollen grains in *Cyphomandra* are rather homogeneous and resemble those of other genera in the tribe Solaneae. The size of the grains falls within that reported for species of the tribe Solaneae (Basak, 1967) and subtribe Solaninae (Murry & Eshbaugh, 1971). Pollen grains of *C. hartwegii* from Panama examined by Roubik and Moreno (1991) were much larger than those measured in this study (36–39 um vs. 19–22 um). Considerable variability in pollen size may exist among populations of this widespread species. It should also be noted that pollen was acetolysed in the above studies, whereas it was not acetolysed in the present study. Acetolysis often causes swelling of grains. However, pollen size may be affected by many factors, including method of preservation, type of chemical treatment, and choice of mounting medium (Reitsma, 1969). SEM studies have revealed finely granular exine sculpturing in *Solanum* sections *Basarthrum* (Anderson & Gensel, 1976), *Solanum* (Edmonds, 1984), *Geminata* (Knapp, 1986a), and *Allophyllum* (Bohs, 1989a). Studies with the light microscope usually describe the exine as being psilate to reticulate in the tribe Solaneae (Basak, 1967) and subtribe Solaninae (Murry & Eshbaugh, 1971). Although Murry and Eshbaugh (1971) could distinguish species and genera of the subtribe Solaninae on the basis of qualitative and quantitative characters, the present study is not detailed enough to arrive at this degree of resolution. In general it appears that pollen characters are of limited value in distinguishing *Cyphomandra* from other genera of the Solaneae and Solaninae. Surface features of the grains are very similar to those reported for *Solanum*. Symon (1979) has postulated that small grains with little surface ornamentation may aid in expulsion of pollen from anther pores.

Within *Cyphomandra*, relative size of the grains may be consistent among species and may thus be a useful taxonomic character, as Anderson and Gensel (1976) found within *Solanum* section *Basarthrum*, but such a conclusion cannot be drawn from the present analysis. More detailed studies on additional representatives may show that pollen size is useful in distinguishing species or species groups within *Cyphomandra*.

CHROMOSOMES

Ten species of *Cyphomandra* have been examined cytologically. All are diploids with $n = 12$ chromosomes (Table III), with the exception of spontaneous triploids and tetraploids of *C. betacea* found at low frequencies in commercial tree tomato orchards in New Zealand (Pringle, 1991; Pringle & Murray, 1991a). A chromosome number of $n = 12$ is commonly found in *Solanum* and predominates in the subfamily Solanoideae.

Karyotypes for eight species are found in Pringle (1991) and Pringle and Murray (1991a). Pringle (1991) notes that the chromosomes of *Cyphomandra* are morphologically homogeneous. All species investigated have predominantly metacentric and submetacentric chromosomes, with at least one pair of acrocentrics. Most species have two pairs of satellited chromosomes. *Cyphomandra corymbiflora* and *C. diploconos* share a subterminal secondary constriction on one of the satellited pairs that is lacking in the other species studied. Using C-banding, Pringle (1991) was able to distinguish homologues with more certainty. C-banding patterns showed some consistent differences at the generic level. *Cyphomandra* had mostly terminal C-bands, while the single member of *Solanum* section *Cyphomandropsis* investigated had large interstitial C-bands. Both *Cyphomandra* and *Cyphomandropsis* differed from other genera of Solanaceae such as *Solanum*, *Petunia*, and *Nicotiana* in lacking centromeric C-bands. Pringle (1991) and Pringle and Murray (1991a) found that chromosome morphology and C-banding patterns were not correlated with subgeneric species groupings based on morphological characters.

An unusual feature of *Cyphomandra* chromosomes is their large size. In those species that have been examined, the length of individual chromosomes ranges from about 3 to 14 µm, with an average length of about 8 µm (Bohs, 1989a; Pringle & Murray, 1991a; Fig. 8). In contrast, species of *Solanum* and *Lycopersicon* have chromosomes less than 4 µm in length (Bernardello & Anderson, 1990; Roe, 1967). Pringle and Murray (1991a) measured nuclear DNA amounts of

Table III
Chromosome numbers in *Cyphomandra.*

Species	Number	Reference or voucher
C. acuminata	$2n = 24$	Bohs, 1989b
C. betacea	$2n = 24$	Bohs, 1989b; van der Mey et al., 1969; Pringle and Murray, 1991a; Roe, 1967; Vignoli, 1945; Whitaker, 1933
C. cajanumensis	$2n = 24$	Bohs, 1989b; Pringle and Murray, 1991a
C. corymbiflora		
subsp. *corymbiflora*	$2n = 24$	Bohs, 1989b; Pringle and Murray, 1991a
C. diploconos	$n = 12$	Bohs, 1989b
	$2n = 24$	Pringle and Murray, 1991a
C. diversifolia		
subsp. *diversifolia*	$n = 12$	Bohs, 1989b
	$2n = 24$	Pringle and Murray, 1991a
C. hartwegii	$2n = 24$	Pringle and Murray, 1991a
subsp. *hartwegii*	$2n = 24$	Bohs, unpublished (voucher: *McPherson 13469*)
subsp. *ramosa*	$2n = 24$	Bohs, 1989b
C. obliqua	$2n = 24$	Pringle and Murray, 1991a
C. sibundoyensis	$2n = 24$	Bohs, unpublished (voucher: *Bohs and Juajibioy 2222*); Pringle and Murray, 1991a
C. uniloba	$2n = 24$	Bohs, 1989b; Pringle and Murray, 1991a

nine species of *Cyphomandra* using flow cytometry, and found the results were concordant with chromosome size. DNA amounts ranged from 13.5 (in *C. corymbiflora*) to 49.6 (in *C. hartwegii*) picograms per 2C nucleus, making them the largest yet reported in the Solanaceae. Although nuclear DNA amounts were significantly correlated with mitotic metaphase chromosome size, there was no obvious relationship between genome size and pollen volume, guard cell chloroplast number, or mean seed weight. Likewise, differences in genome size among species did not follow any discernable phylogenetic pattern. It is likely that large chromosome sizes and large DNA amounts distinguish *Cyphomandra* from *Solanum*, *Lycopersicon*, and perhaps other solanaceous genera, but more species need to be examined.

REPRODUCTIVE BIOLOGY

Breeding systems have been determined for ten species of *Cyphomandra* (Bohs, 1989a, 1991; Pringle & Murray, 1991c; Table IV). Of these, eight are self-incompatible (SI), and only two, *C. betacea* and *C. cajanumensis*, are self-compatible (SC). Evidence such as arrest of incompatible pollen tubes in the style, binucleate pollen grains, homomorphic flowers, wet stigmatic surfaces, and the widespread occurrence of gametophytic self-incompatibility in other Solanaceae argues for the operation of a gametophytic system of SI in *Cyphomandra* as well (Bohs, 1991; Brewbaker, 1957; de Nettancourt, 1977; Pandey, 1960; Pringle & Murray, 1991c).

Rao and Rauoof (1970) in India and Pringle (1991) and Pringle and Murray (1991c) in New

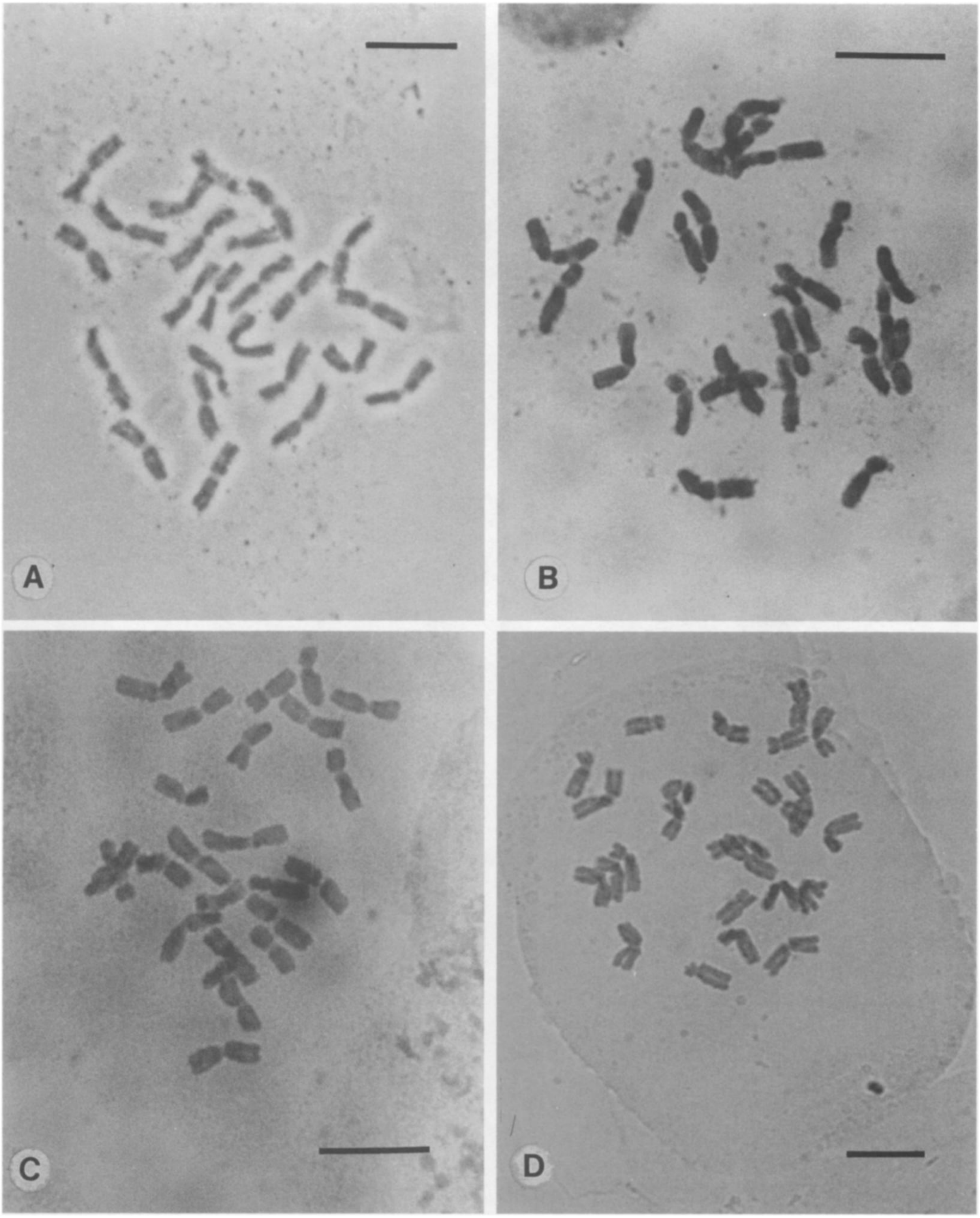


FIG. 8. Mitotic chromosomes from root tip preparations of *Cyphomandra*. Scale bars = 10 µm. **A.** *C. hartwegii* subspecies *hartwegii*. **B.** *C. diversifolia* subspecies *diversifolia*. **C.** *C. corymbiflora*. **D.** *C. corymbiflora* × *diploconos* hybrid.

Zealand examined some aspects of the reproductive biology of *C. betacea*. Rao and Rauoof observed that flower anthesis occurred from 8 A.M. to 2 P.M. with a peak between 9 and 10 A.M. Anther dehiscence occurred throughout the day. Although they describe the flowers as being prot-

Table IV

Distribution of self-incompatibility (SI) and self-compatibility (SC) in *Cyphomandra.*

Taxon		Reference
C. acuminata	SI	Bohs, 1989a
C. betacea	SC	Bohs, 1989a; Pringle and Murray, 1991c
C. cajanumensis	SC	Pringle and Murray, 1991c
C. calycina	SI	Soares et al., 1989
C. corymbiflora		
subsp. *corymbiflora*	SI	Bohs, 1989a; Pringle and Murray, 1991c
C. diploconos	SI	Bohs, 1989a; Pringle and Murray, 1991c
C. diversifolia		
subsp. *diversifolia*	SI	Bohs, 1989a; Pringle and Murray, 1991c
C. hartwegii		
subsp. *hartwegii*	SI	Pringle and Murray, 1991c; Bohs, unpublished (voucher: *Bohs 2437*)
subsp. *ramosa*	SI	Bohs, 1989a; Pringle and Murray, 1991c
C. obliqua	SI	Pringle and Murray, 1991c
C. uniloba	SI	Bohs, 1989a; Pringle and Murray, 1991c

androus, Lewis (1985) reports that the stigma of *C. betacea* is receptive from three days before to three days after anthesis. Unpollinated flowers abscise 3 to 4 days after anthesis. They determined the average number of pollen grains per anther to be 793,000. Pringle and Murray (1991c) counted 467 (± 46) and 323 (± 37) ovules per flower in two lines of *C. betacea.* The resultant pollen/ovule (P/O) ratio is approximately 8500 to 12,300. These values exceed Cruden's (1977) estimate of the minimum mean P/O ratio of obligately xenogamous plants (P/O = 5859.2 ± 936.5) even though *C. betacea* is one of the few species in the genus that is SC. Rao and Rauoof (1970) found that *C. betacea* pollen germinates best *in vitro* using a solution of 10 per cent sucrose and 0.7 per cent agar, and that the grains germinate within a half hour of sowing. Pollen longevity, as determined by *in vitro* germination, dropped steadily after collection to 13.6 per cent after 11 days and 0 per cent after 17 days when kept at temperatures of 15 ± 3° C (Rao & Rauoof, 1970). Pringle and Murray (1991c) measured pollen longevity by staining with fluorescein diacetate and obtained comparable results: viability dropped to around 10 per cent after 8 days at room temperature, but 60 to 70 per cent of the grains remained viable after 20 days when stored at 4° C. Both authors as well as Bohs (1991) observed that fertilization in *C. betacea* occurred within 48 hours after pollination.

Interspecific crossing patterns of nine species of *Cyphomandra* were reported by Bohs (1991), Pringle (1991), and Pringle and Murray (1991b). Pollen tubes reached the ovary and ovules in nearly all interspecific pollinations. However, less than five per cent of the crosses produced F_1 hybrid plants, indicating that post-zygotic barriers to hybridization were well-developed in the species tested (Bohs, 1991). Abortion of hybrid seeds was a common type of crossing barrier seen in *Cyphomandra*; such barriers are also common in interspecific crosses in *Solanum* (Whalen, 1984). Pringle (1991) and Pringle and Murray (1991b) obtained viable F_1 hybrid seed from only one crossing combination, *C. corymbiflora* × *diploconos.* Bohs (1991) produced F_1 hybrid plants from the following interspecific combinations (female parent listed first): *C. acuminata* × *betacea*, *C. betacea* × *acuminata*, *C. corymbiflora* × *diploconos*, *C. hartwegii* subspecies *ramosa* × *diploconos*, and *C. uniloba* × *betacea.* Morphological characteristics, breeding systems, pollen viability, and meiotic chromosome behavior were investigated in hybrid plants from three crossing combinations (*C. betacea* × *acuminata*, *C. uniloba* × *betacea*, and *C. corymbiflora* × *diploconos*). All hybrids were morphologically intermediate between the parent species. Both hybrid combinations with a *C. betacea* parent produced self-compatible F_1

plants, whereas the *C. corymbiflora* × *diploconos* hybrids were self-incompatible. Pollen stainability of all three hybrid combinations was reduced as compared with the parent species, and all three hybrid combinations showed some meiotic abnormalities, including unpaired univalents, fragments, and chains. The *C. corymbiflora* × *diploconos* hybrid consistently had ten bivalents and one chain quadrivalent at meiotic metaphase I, a configuration diagnostic for a translocation heterozygote. It appears that structural differences in the chromosomes are responsible at least in part for the sterility of the F_1 hybrids. F_2 and backcross progeny have been obtained in most combinations.

These studies confirm the findings of Whalen (1984) for *Solanum*: most species are isolated by post-zygotic reproductive barriers, acting largely by abortion of hybrid seed. The success of interspecific crosses among *C. acuminata*, *betacea*, and *uniloba* is congruent with morphological similarity and perhaps with phylogenetic relatedness (see SPECIES GROUPS). The case with the morphologically dissimilar species *C. corymbiflora* and *diploconos* is less clear. The ability of *C. acuminata* and *uniloba* to form fertile hybrids with *C. betacea* may have significance in breeding programs aimed at the improvement of the tree tomato. Embryo rescue has not yet been tried in *Cyphomandra*, but should be investigated as a means of producing hybrid plants in cases where lack of endosperm development is responsible for crossing failure.

SPECIES GROUPS AND CHARACTER EVOLUTION

Miers (1845, 1854, 1855) and Child (1984) are the only previous workers to propose formal infrageneric categories in *Cyphomandra*. Miers, in his classification schemes of 1854 and 1855, divided the approximately 40 then-described species into two sections, based mainly on the morphology of the stamens and gynoecium. Miers included these species in the genus *Pionandra*, but Sendtner's slightly earlier name of *Cyphomandra* took priority. Miers' section *Ceratostemon* included 21 species with very curved and thick stamens connivent at the apices. The style was more or less obconical and the stigma greatly expanded. He later elevated this section to the generic level as *Cyphomandra* (Miers, 1855).

Miers' *Pionandra* section *Euthystemon* included 16 species with more erect anthers and slender styles with small clavate or truncate stigmas. This section was later elevated to generic status as *Pionandra* (Miers, 1855) upon removal of section *Ceratostemon* to *Cyphomandra*. Miers' genera *Cyphomandra* and *Pionandra* have been combined and considered as a single genus by all subsequent workers.

Child (1984) enlarged upon Miers' section *Euthystemon*, included 44 described species, and changed its name to section *Cyphomandra* in accordance with Article 22 of the *International Code of Botanical Nomenclature* (Greuter et al., 1988) because this section includes the type species of the genus (*C. betacea*). According to him, these species all had erect anthers and mostly cylindrical styles. The stigma could be only slightly to very broadly expanded. Child (1984) maintained Miers' section *Ceratostemon*, but limited it to six species with geniculate stamens and obconical styles. He also included four other sections in *Cyphomandra*, sections *Allophylla*, *Rhynchantherum*, *Cornigera*, and *Cyphomandropsis*. These four sections are presently placed in *Solanum* and are excluded from *Cyphomandra* in the present treatment.

There are serious problems with the infrageneric groups of Miers and Child. In the first place, neither worker critically examined species limits, with the result that their classifications are replete with synonyms. In some instances, names that I treat as synonyms of the same species are placed by them in different sections. In the second place, the two sections of Miers and Child are insufficient to describe the patterns of morphological variation in the genus. At least four, and perhaps five, groups are needed. These are described below and summarized in Table V.

It has been extremely difficult to define clear-cut infrageneric groups in *Cyphomandra*. Issues of character evolution such as homology, polymorphism, variation, and convergence are still poorly resolved. In the following section the species groups I recognize are briefly described and some speculation is made regarding phylogenetic relationships. The monophyly of each of the proposed groups has not been tested using a rigorous

Table V

Species groups in *Cyphomandra*

I. C. obliqua group: acuminata, betacea, heterophylla, obliqua, rojasiana, sycocarpa, uniloba

II. C. calycina group: calycina, diploconos, premnifolia, sciadostylis

III. C. pendula group: benensis, diversifolia, pendula, tenuisetosa

IV. C. hartwegii group: cajanumensis, dolichocarpa, endopogon, foetida, fragilis, hartwegii, oblongifolia, sibundoyensis, stellata, tegore, tobagensis

V. C. corymbiflora group: corymbiflora, hypomalaca, pinetorum

phylogenetic analysis, in part because of uncertainty regarding the choice of outgroups of *Cyphomandra*. One probable sister group of the genus has been identified, *Solanum* section *Cyphomandropsis*, but it remains to be characterized taxonomically at even the most rudimentary level. Hypotheses about character polarity have been made on the basis of preliminary outgroup comparison with *Solanum* section *Cyphomandropsis*, but admittedly the character state distributions in this latter group are imperfectly known. Other outgroups have been used for comparison where mentioned. The species groups are not given formal taxonomic recognition but are presented as a hypothetical infrageneric structure to be corroborated and refined as more information becomes available. Three species (*C. divaricata*, *C. ovum-fringillae*, and *C. pilosa*) are very distinctive morphologically, but I have been unable to place them unambiguously in any of the species groups.

I. *C. obliqua* group (7 species). The *C. obliqua* group is characterized by the following character states: (1) corollas coriaceous, green to purplish or occasionally white or pinkish; (2) anthers short and broad; (3) anther connectives not prolonged abaxially much beyond the bases of the anther thecae, ca. (3)4–6 mm long and 1–2 mm wide, more or less oblong in outline and often nearly covering the entire abaxial surface of the anthers; (4) styles thick, usually much expanded distally, with the stigmas 1–3 mm in diameter, often with two apical glands; (5) leaves often coriaceous, mostly simple and unlobed but pinnately lobed or compound in *C. heterophylla* and *C. sycocarpa*. Stone cell aggregates in the fruits are present or absent. Often the inflorescences are contracted, with nearly contiguous pedicels.

Cyphomandra heterophylla and *C. sycocarpa* of southeastern Brazil are unusual in occupying seaside habitats where their fleshy stems and leaves may allow them to tolerate saline conditions, as is the case in a number of other succulent halophytic species (Waisel, 1972). Although these species can be distinguished by consistent morphological differences, further study may reveal that they are variants of a single taxon. Both have a unique anther structure in which the connective is prolonged distally beyond the apices of the anther thecae. This character state can also be seen to a lesser degree in the Andean *C. uniloba*, in which the connective is extended slightly beyond the apices of the thecae. This is best seen in fresh material; in dried specimens the prolonged connective region appears to be folded down on the adaxial side between the thecae to form a hardened flap.

Cyphomandra uniloba, *C. betacea*, and *C. acuminata* are apparently closely related. *Cyphomandra uniloba* and *C. acuminata* are extremely similar morphologically and can scarcely be distinguished on herbarium sheets unless mature seeds are present. The two species are sympatric in Bolivia, but *C. acuminata* is found at higher elevations than *C. uniloba*. The two species failed to produce hybrids in greenhouse crosses, indicating isolation by internal barriers.

The origin and natural range of *C. betacea* are still unclear, but it is evident that this species is related to *C. uniloba* and *C. acuminata*. Vegetatively it is very similar to *C. uniloba*, but the cylindrical, unexpanded stigmas and styles and pinkish corollas more closely resemble those of *C. acuminata*. *Cyphomandra betacea* hybridizes with both *C. acuminata* and *C. uniloba* in greenhouse crosses (see REPRODUCTIVE BIOLOGY and Bohs, 1991).

Within this group of three species *C. uniloba* manifests the characters of green corollas, subpeltiform stigmas, small seeds, and broad, deeply cordate leaves. *Cyphomandra acuminata* has reddish or pinkish corollas, truncate to subcapitate stigmas, and very large seeds. In addition, *C. acuminata* has unusually long, narrow, and nearly glabrous leaves with truncate to very shallowly cordate bases. *Cyphomandra betacea* combines character states of the two species with its pinkish corollas, truncate stigmas, small seeds, and broad, deeply cordate leaves. *Cyphomandra betacea* also has the derived state of self-compatibility, which may be related to its cultivated status.

Cyphomandra obliqua is found in the western Amazon and has the following suite of characters: contracted inflorescences with nearly contiguous pedicels; broadly expanded, biglandular stigmas; and anther thecae apically longer than the connectives and abaxially bent over them. It most closely resembles *C. rojasiana* of southern Mexico, Guatemala, and Belize. Either the ancestor of both taxa previously occupied a much wider range and became extinct in the intervening region, or long-distance dispersal occurred followed by diversification into the two species seen today. The reduced inflorescences and pubescent fruits of *C. rojasiana* are probably autapomorphies.

The relationships of the *C. obliqua* group to other species groups in *Cyphomandra* are unclear.

II. *C. calycina* group (4 species). The four species included here form the core of section *Ceratostemon* of Miers and Child. All four are found in southeastern Brazil and adjacent areas of Argentina and Paraguay. The species in this group have (1) inflorescences usually unbranched with broadly spaced pedicels, (2) corollas coriaceous or fleshy, campanulate, usually purplish at anthesis but turning greenish yellow with age, (3) stamens short and broad, geniculate at the base, (4) anther connective broad at the base and abruptly narrowed distally so that it does not entirely cover the abaxial side of the thecae, (5) styles distally expanded and stigmas large, with two apical glands, and (6) pubescent fruits. Two species pairs can be distinguished: *C. calycina* and *C. premnifolia*, and *C. diploconos* and *C. sciadostylis*. The first pair have styles relatively longer, narrower, and less expanded distally than the latter two species. Within the first pair, *C. calycina* is distinguished by its large calyces and long, ellipsoid-fusiform fruits. The densely puberulent style of *C. sciadostylis* is apparently an autapomorphy, for it occurs in no other species of *Cyphomandra* or *Solanum* section *Cyphomandropsis*. *Cyphomandra calycina* and *C. premnifolia* are sympatric in parts of their ranges, but may be separated by altitudinal differences or by other unknown isolating mechanisms. The ranges of *C. diploconos* and *C. sciadostylis* are also more or less sympatric, but the former species has a more coastal distribution. Other isolating mechanisms between the two species remain to be investigated.

The *C. calycina* group probably has strongest ties to the *C. pendula* group. Most striking is the similarity of *C. calycina* to *C. diversifolia* in calyx and fruit characters. Geniculate stamens and purplish corollas also link the members of this group to *C. diversifolia*. A tendency to produce pinnately lobed or compound leaves may be further evidence for a close relationship with the *C. pendula* group, although the presence of pinnately lobed or compound leaves may be a plesiomorphic character state that occurs widely in many *Solanum* groups. The expanded styles and stigmas of the *C. calycina* group resemble those of the *C. obliqua* group. Whether this represents convergence in gynoecial structure between the two groups or whether it should be regarded as a synapomorphy linking the two is unclear.

III. *C. pendula* group (3–4 species). This group includes *C. diversifolia* of Central America and northwestern South America and *C. pendula* and *C. benensis* from western South America. The species of this group have (1) simple to pinnately compound leaves, (2) usually unbranched to forked inflorescences, (3) purplish, urceolate or campanulate (occasionally stellate) corollas, (4) broad anther connectives that often nearly cover the entire abaxial side of the anther thecae, and (5) cylindrical styles with capitate stigmas.

Cyphomandra diversifolia is the only species in the genus with an urceolate corolla. Large calyces and fusiform fruits are other presumably derived features of this species; these characters are also found in *C. calycina* of southeastern Brazil. The densely tomentose vestiture of the abaxial corolla surface is a synapomorphy uniting *C. pendula* and *C. benensis*. *Cyphomandra pendula* has campanulate corollas, anthers without an adaxial extension of the connective, and glabrous fruits, whereas *C. benensis* has stellate corollas, anthers with the connective expanded adaxially, and pubescent fruits. The latter two character states are probably derived. Stellate corollas occur widely in *Cyphomandra* and in *Solanum* section *Cyphomandropsis*; thus, the stellate corolla of *C. benensis* may be a plesiomorphic feature or an autapomorphy derived by convergence.

Cyphomandra tenuisetosa is perhaps associated with the *C. pendula* group. It also has purplish campanulate corollas, usually unbranched inflorescences, large abaxially swollen connectives, and cylindrical styles with capitate stigmas. The trunk leaves are often pinnately lobed, but usually only three lobes are present, giving the leaves a hastate outline. *Cyphomandra tenuisetosa* has a relatively large calyx similar to that of *C. pendula*. Unlike *C. pendula* and *C. benensis*, the abaxial corolla surface of *C. tenuisetosa* is glabrous. *Cyphomandra tenuisetosa* occurs in western South America, with its range more or less coincident with that of *C. pendula*.

The affinities of the *C. pendula* group probably lie with the *C. calycina* group.

IV. *C. hartwegii* group (10–11 species). This is the largest and most widespread species group in *Cyphomandra*. The group is characterized by (1) simple to pinnately lobed leaves, (2) often very elongated inflorescences, (3) purplish or green, usually stellate corollas, (4) long narrow anthers, (5) long cylindrical styles with usually truncate to capitate stigmas, and (6) fruits with large flattened seeds and prominent stone cell aggregates. Probable plesiomorphic character states seen in the *C. hartwegii* group include unbranched inflorescences, stellate corollas with tomentose margins, triangular and acute corolla lobes, narrow cylindrical styles, truncate stigmas, and glabrous, obtuse fruits. Possible apomorphic character states of this group include branched inflorescences, campanulate corollas, ciliate corolla margins, oblong and obtuse corolla lobes, distally dilated styles, large expanded stigmas, and pubescent, acute fruits. According to these criteria, *C. hartwegii* subspecies *hartwegii* is probably basal in the group, while *C. endopogon* subspecies *guianensis* exhibits the greatest number of presumably derived characters, including oblong, obtuse corolla lobes with ciliate margins, distally dilated styles with large, expanded stigmas, and puberulent fruits. The evolutionary polarity of cordate vs. the truncate to subcordate leaf bases seen in species such as *C. tobagensis*, *C. stellata*, and *C. dolichocarpa* remains to be determined. Two closely related species pairs may turn out to be variants of the same species. These are *C. dolichocarpa* and *C. tobagensis*, distinguished mainly by the puberulent fruits of the latter species, and *C. tegore* and *C. foetida*, the latter distinguished by its pointed fruits.

Cyphomandra fragilis exhibits all the presumbly plesiomorphic character states given above for the *C. hartwegii* group except for its ciliate rather than tomentose corolla margins. In addition, this species has two striking autapomorphies. These include small, membranaceous leaves with abundant and conspicuous sand-punctae and shallowly cordate and often slightly decurrent bases, and anther tips united into a ring around the style. Pinnnately compound leaves may occasionally occur in this species, but are not well represented in the herbarium material available.

Cyphomandra cajanumensis has been difficult to characterize taxonomically with the material available. Many of the character states evaluated for the *C. hartwegii* group are variable within *C. cajanumensis*. The flowers, fruits, and large simple leaves of *C. cajanumensis* resemble those of *C. sibundoyensis*. The rather broad anther connectives that do not extend below the anther thecae are anomalous in the *C. hartwegii* group, and the conspicuously thickened fruiting pedicels are similar to those of *C. pendula* in the *C. pendula* group.

Species of the *C. hartwegii* group occur in Central America and Andean and Amazonian South America. Several species extend into the Guianas and eastern Brazil around the Amazon delta, but most inhabit the eastern Andes as far south as Bolivia. *Cyphomandra oblongifolia* is primarily Amazonian in distribution, and its range reaches the Planalto de Mato Grosso in south-central Brazil.

V. *C. corymbiflora* group (2–3 species). *Cyphomandra corymbiflora* and *C. pinetorum*, both of southeastern Brazil, constitute a separate species group. *Cyphomandra hypomalaca* of western Ecuador is tentatively included. This species group is less well defined than the others and shares many characteristics with *Solanum* section *Cyphomandropsis*. The members of this group generally have (1) abundant vegetative pubescence, (2) leaves with cordate bases (unlobed in *C. corymbiflora* and *C. hypomalaca* but occasionally with pinnately 2–3-lobed trunk leaves in *C. pinetorum*), (3) unbranched to highly branched inflorescences, (4) white, pink, or purple stellate corollas, (5) narrow cylindrical styles with small truncate stigmas, and (6) densely pubescent ovaries and fruits. *Cyphomandra corymbiflora* and *C. pinetorum* have chartaceous corollas and are so similar to each other morphologically that a close relationship between them is almost certain. Both *C. pinetorum* and *C. hypomalaca* have an anther structure similar to *Solanum* section *Cyphomandropsis*, with the connective region broad and not extending beyond the proximal edges of the thecae. *Cyphomandra corymbiflora*, on the other hand, has anther connectives prolonged below the bases of the anther thecae and abruptly narrowed distally like those of the *C. calycina* group. *Cyphomandra hypomalaca* has small globose fruits with large prismatic rather than flattened seeds; both characters are seen in some species of *Solanum* section *Cyphomandropsis*. The position of the three species in the *C. corymbiflora* group is unclear, and their relationships need evaluation.

The following species have not been associated with any species group. Further study may reveal their affinities.

1. *C. pilosa*. This recently described species occurs on the eastern Andean slopes. Its shallowly cordate leaves, coriaceous campanulate corollas, short anthers with broad connectives, somewhat dilated styles, and densely pubescent fruits with small seeds cannot be reconciled at present with any of the existing species groups.

2. *C. divaricata*. This species is widespread in southeastern Brazil, where it is often found in *Araucaria* groves. Its geniculate stamens with the connectives abruptly narrowed above the base, campanulate corollas, and small seeds suggest affinity with the *C. calycina* group. However, its long narrow anthers, cylindrical styles with small stigmas, and glabrous fruits are anomalous in that group, and suggest affinity with the *C. hartwegii* complex.

3. *C. ovum-fringillae*. This species has been collected only twice, from northeastern Brazil. Its flowers and fruits are still not well characterized. It appears that the leaves are often compound and the corollas densely pubescent abaxially, which suggests an alliance with the *C. pendula* group.

ECOLOGY

Habitats

With few exceptions, cyphomandras are small trees of the humid tropical forest. At least in western South America, they are most often found in light gaps in primary forest. Frequently they are also found in secondary vegetation and in disturbed areas such as pastures, clearings, roadsides, and forest margins. Usually *Cyphomandra* plants are rather rare in a given area, with few trees growing in each light gap but with individual species occupying extensive ranges. They do not occur in dense monospecific stands and do not show the weedy tendencies of many other solanaceous species such as those of *Solanum* section *Solanum* and *Solanum* subgenus *Leptostemonum*. In habitat preferences, they resemble many members of *Solanum* section *Geminata*, which are also primary forest trees adapted to light gaps (Knapp, 1986a).

The rapid growth of most cyphomandras allows them to quickly exploit light gaps that occur in the canopy. Their peculiar architecture composed of successive spreading crowns may also be an adaptation to light gaps. According to Hallé et al. (1978), Prévost's model is known mainly from forest trees exhibiting a K strategy where long-term survival of individual trees is more important than biotope saturation. The life span of individual *Cyphomandra* trees has not been determined, and it is not known how well various species are able to tolerate shading and thus persist as a gap fills in.

Species of *Cyphomandra* are found at elevations between 0 and 3000 m, with most occurring below 2000 m. About a third of the species are found only at elevations below 1000 m. The altitudinal preferences of *C. ovum-fringillae* are unknown, and those of *C. heterophylla* not known with certainty.

In Central America and in Andean and Amazonian South America, most cyphomandras are found in areas of high rainfall corresponding to the tropical moist, wet, or pluvial (rain) forest life zones of Gentry (1978) modified from Holdridge et al. (1971). In these environments, rainfall ranges from around 2000 to over 5000 mm per year. Many species grow in areas where precipitation averages over 2500 mm per year and no pronounced dry season exists. A few species (e.g., *C. obliqua*, *C. oblongifolia*, *C. endopogon*, *C. stellata*) have been found in seasonally flooded Amazonian *varzea*, but these and other lowland species occur most frequently on nonflooded *terra firme*. In western South America, only *C. hypomalaca* occupies an unusual habitat, being found in the Jauneche forest of western Ecuador. This formation is in the tropical moist forest life zone, has a pronounced dry season, and is characterized by semi-deciduous forests. The possible adaptation of *C. hypomalaca* to drier conditions than other *Cyphomandra* species is interesting in light of its postulated relationship with *Solanum* section *Cyphomandropsis*.

In eastern Brazil, most *Cyphomandra* species inhabit the Atlantic coastal rain forest and/or are associated with groves of the Paraná pine, *Araucaria angustifolia* (Bertol.) Kuntze. *Cyphomandra corymbiflora* and *C. sciadostylis* extend westward into the Argentinian provinces of Misiones and Corrientes. This area belongs to the phytogeographic region designated as the Provincia Paranaense by Cabrera (1976). With the exceptions mentioned below, the eastern Brazilian species, like their Andean and Amazonian counterparts, inhabit warm and very humid areas generally without a pronounced dry season. My limited field studies of these species suggest that they also pursue the light gap strategy described above. There are several notable exceptions to the humid forest preferences of the eastern Brazilian species. *Cyphomandra sycocarpa* and *C. heterophylla* are apparently restricted to restinga vegetation along the seashore. These two species are morphologically specialized within the genus, so they probably represent a derived element that has become adapted to beach habitats. Another exception to the humid forest habitat apparently occurs with *C. ovum-fringillae*. Only two collections of this species are known, one from coastal Pernambuco, possibly from restinga vegetation, and the other from the semiarid caatinga formation of northeastern Brazil in Bahia.

Pollination

The few published reports of insect visitors to *Cyphomandra* suggest male euglossine bees as important pollinators. In Costa Rica and Panama, *C. hartwegii* was visited by male *Eulaema bombiformis* and *Eulaema meriana* (Dressler, 1979; Sazima & Vogel, 1989; Williams, 1982; *Dressler 3070*; S. Mori, pers. comm.). Williams (1982) reports that the flowers exude an odor of benzyl acetate, a compound known to attract male euglossines (Williams & Dodson, 1972). Males of *Euplusia violacea* were collected from *C. sciadostylis* in southeastern Brazil (Sazima & Vogel, 1989), and males of *Euglossa* (*Euglossella*) *mandibularis* visited *C. calycina* in Minas Gerais, Brazil (Soares et al., 1989; *Vieira 256*). The males of *E. mandibularis* were strongly attracted to flowers of *C. calycina*, even before anthesis, but the chemical nature of the attractant is still unknown. The bees were observed brushing the anther connectives with their forelegs in order to collect odor substances. In the process, pollen was deposited on the bee's mesosternum. Soares et al. (1989) consider it likely that the male bees effect pollination of *C. calycina* in the process of scent gathering. Soares et al. (1989) also reported that bees of the genera *Augochlora* (Halictidae) and *Paratetrapedia* (Anthophoridae) collected pollen from *C. calycina* by buzzing the anthers, although these were much less common than *E. mandibularis* males. Bumblebees (*Bombus* sp.) and honeybees (*Apis mellifera*) are common visitors to *C. betacea* flowers in New Zealand tree tomato orchards (Pringle & Murray, 1991c).

The suggestion that male euglossine bees are the chief pollinators of *Cyphomandra* is intriguing. Until now, pollen was the only known reward offered by *Cyphomandra*. The poricidally dehiscent anthers of this genus are similar to those of *Solanum*, in which buzz pollination has

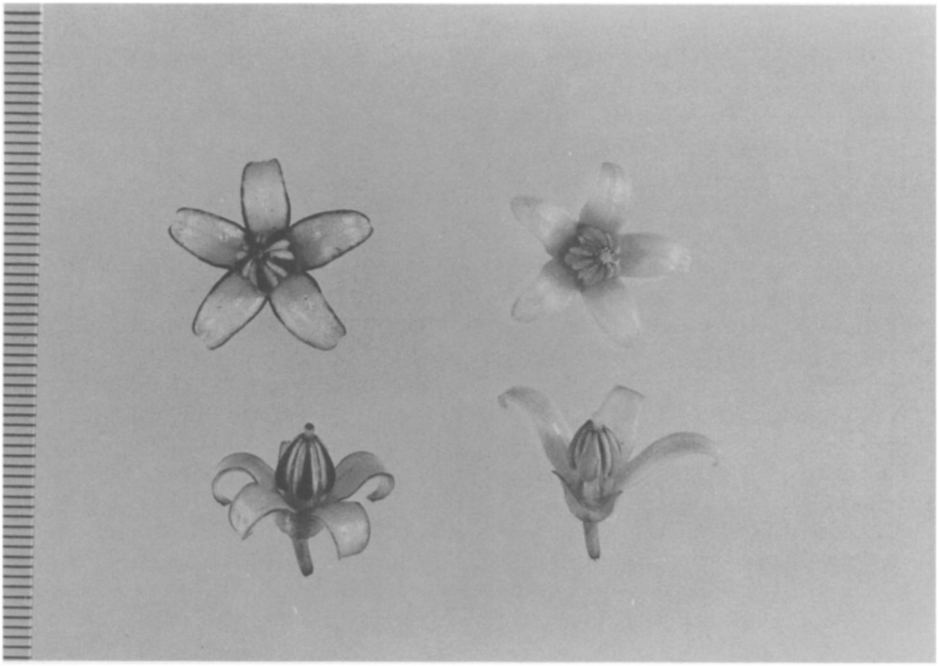


FIG. 9. Flowers of *C. betacea* before (right) and after (left) staining in 1:10,000 aqueous neutral red. Scale in millimeters.

been well documented (e.g., Buchmann, 1983; Haber, 1983; Knapp, 1986a, 1986b; Michener, 1962). Buzz pollination was presumed to operate also in *Cyphomandra*. Female euglossines buzz flowers to collect pollen (Buchmann, 1983; Dressler, 1982; Williams, 1982). Males do not gather pollen, but collect nectar from many sources and volatile fragrance compounds from various flowers, particularly from orchids (Dressler, 1968; Williams, 1982). The male bees scrape flower surfaces with their forelegs to gather odor substances, eventually depositing them in fragrance-storage organs on their hind legs (Dressler, 1968, 1982; Williams, 1978). The fate of these odor substances is unknown, but Williams (1982) believes that they are modified by the bees into substances that attract mates.

The behavior of *E. mandibularis* males on *C. calycina* indicates that buzz pollination may be relatively unimportant in *Cyphomandra*, and that this genus may be among the few dicotyledons known to exhibit the "male euglossine syndrome" (Williams, 1978, 1982). The role of the anther connective in pollinator attraction has not been elucidated, but the studies of Soares et al. (1989) suggest that it secretes volatile chemical attractants gathered by the bees. The morphology of the anther connective is consistent with that of an osmophore, or fragrance-secreting glandular area (Vogel, 1990; see MORPHOLOGY). The anther connective stains densely when fresh flowers are placed in the vital stain neutral red, a further indication of its secretory nature (Stern et al., 1986; Vogel, 1990; Fig. 9). Secretion of non-volatile floral oils which are gathered by insects has also been documented in the Solanaceae (in *Nierembergia*; Cocucci, 1991; Simpson & Neff, 1981) but has not been reported in *Cyphomandra*.

The possibility that odor-collecting male euglossine bees are major pollen vectors of *Cyphomandra* has interesting implications for speciation in the genus. Most cyphomandras have the characteristics described by Janzen (1971) typical of euglossine pollination: they are large, woody species that occur as widely scattered individuals, and each plant bears only a few flowers at any one time, although a plant may bloom for many months. Many species have greenish corollas and most have inflorescences that hang below the foliage, so it is doubtful that they are readily visible in the dense understory vegetation. Furthermore, most species of *Cyphomandra* are self-incompatible (Bohs, 1991; see REPRODUCTIVE BIOLOGY). Plants such as these depend upon bees that do not require strong visual cues to locate flowers and that fly long distances between plant patches. Such behavior has been observed in Neotropical euglossines, which apparently forage over long distances and exhibit great constancy in their flower visits, a procedure known as "trap-lining." Male and female euglossines can fly long distances (Ackerman et al., 1982; Dressler, 1982; Janzen, 1971; Williams & Dodson, 1972) and thus may be important in moving pollen among widely separated individuals.

The relationship between odor substances produced by the flowers and various species of male euglossines could indicate that there is a greater degree of pollinator specificity in cyphomandras with the male euglossine syndrome than in buzz pollinated plants. Buzz-pollinating bees are often polylectic, foraging for pollen among many different species (Buchmann, 1983). On the other hand, variations in the component odor substances often result in highly specific plant/pollinator relationships in species that attract male euglossines (Dressler, 1968, 1982; Williams & Dodson, 1972). If such pollinator specificity exists in *Cyphomandra*, it may be important as an interspecific isolating mechanism, particularly in sympatric species with few internal barriers to hybridization (Dressler, 1968). Floral morphology may not be as important as variation in scent components in attracting or excluding specific pollinators.

Dispersal

Nothing is known about fruit or seed dispersal in *Cyphomandra*. Most species produce pendent, fleshy, yellow, orange, or greenish fruits. About half the species have trichomes on the fruit surface, ranging from minute puberulence which easily rubs off at maturity (e.g., *C. diploconos*) to dense long hairs that would seem to deter frugivores (e.g., *C. pinetorum*). Among the smallest fruits in the genus are those of *C. ovum-fringillae* and *C. hypomalaca*, which are about 1–1.5 cm in diameter. The largest fruits are about 10 cm long, as in *C. betacea*, *C. cajanumensis*, *C. dolichocarpa*, *C. hartwegii*, *C. sibundoyensis*, and *C. tenuisetosa*. Nearly all species have abundant, juicy, sweetish fruit pulp; an exception is *C. hypomalaca*, which has only a thin mesocarp around the seeds. When ripe, *Cyphomandra* fruits detach at the base of the pedicel, with the fruit and pedicel falling as a unit. At least in the greenhouse, the fruits of some species remain on the plant for many months before ripening and falling to the ground. Because of their pendent orientation, their yellow, orange, or green color, and abundant fruit pulp, the fruits are probably mammal-dispersed. Cyphomandras exhibit some of the characteristics associated with dispersal by bats (chiropterochory): large dull-colored fruits that dangle at the ends of pendulous inflorescences, and the branches themselves borne in tiers so that the fruits hang beneath the foliage (van der Pijl, 1982). Bats eat fruits of *Solanum* in Costa Rica (Dinerstein, 1986; Heithaus et al., 1975; Knapp, 1986a, 1986b); in general, however, these fruits are much smaller than those of *Cyphomandra*, although many are pendent and similarly colored. Primates or other arboreal mammals may also eat *Cyphomandra* fruits, and ground-dwelling animals may disperse fallen fruits. Birds have been observed eating solanaceous fruits in Costa Rica (Knapp, 1986a; Murray, 1987; Wheelwright et al., 1984), but the dull colors, large size, and pendent orientation of *Cyphomandra* fruits makes bird dispersal unlikely. Studies on fruit and seed dispersal in *Cyphomandra* are badly needed, and tropical biologists are urged to report any instances of *Cyphomandra* frugivory.

Herbivory

The Solanaceae are renowned for their quantity and variety of secondary compounds (Brown, 1987a; Levin, 1976). In general solanaceous plants are well defended from insect attack, and presumably these substances deter herbivores from eating the foliage. However, in some cases herbivores may use secondary compounds to locate specific food sources and many can detoxify or sequester otherwise harmful substances for use in their own defenses against predators (Levin, 1976).

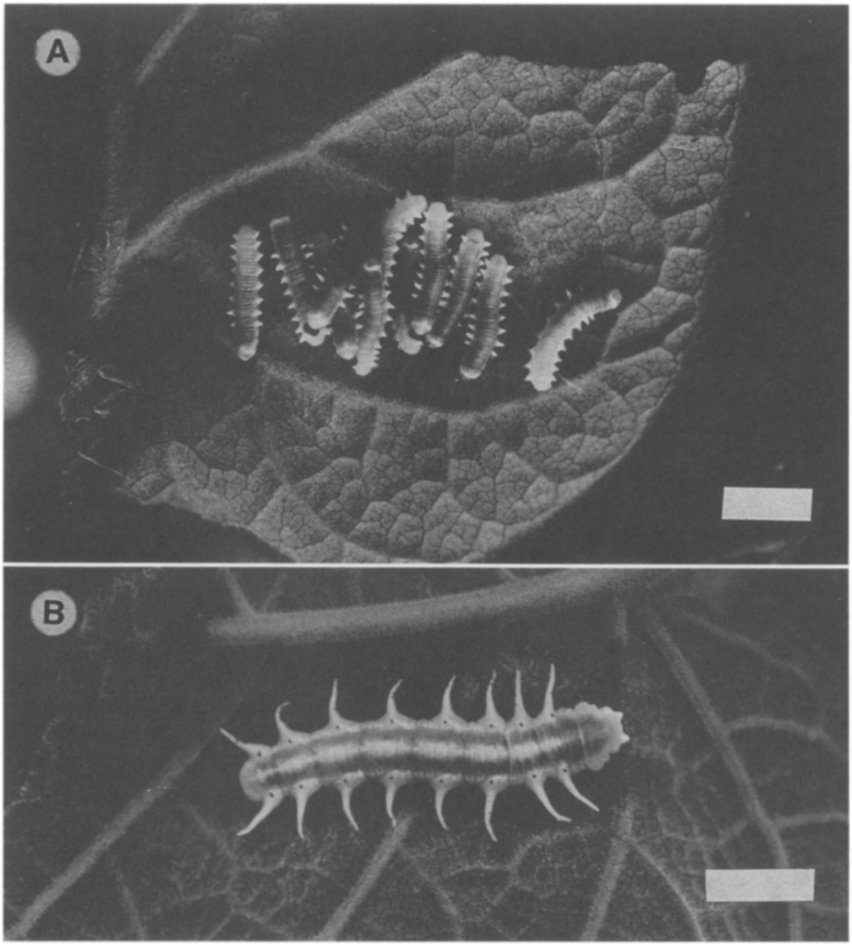


FIG. 10. A, B. Larvae of *Mechanitis lysimnia* on *Cyphomandra corymbiflora* in Paraná, Brazil. Scale bars = 5 mm. Larvae identified by Dr. K. S. Brown, Jr.

The chemical constituents of *Cyphomandra* are not well known. Various alkaloids and other secondary metabolites have been isolated from *Cyphomandra* species (e.g., Bohs, 1989c; Brown, 1987a; Tétényi, 1987). The abundant glandular hairs on the vegetative parts of most species may act as feeding deterrents to insects, either due to toxic substances in the trichome exudates (as in *Lycopersicon hirsutum* f. *glabrum*; Williams et al., 1980) or to the mechanical trapping of small insects in the sticky fluid (as in some wild potato species; Gibson, 1971; Harborne, 1986). The foliage of most *Cyphomandra* species is very malodorous.

Because of the abundance of secondary compounds found in the plants, few insect herbivores are known to feed on Solanaceae (Brown, 1987a; Hsiao, 1986). The only insect herbivores known from *Cyphomandra* are larvae of neotropical butterflies of the nymphalid subfamily Ithomiinae (Fig. 10). Cyphomandras are the larval host plants of two species of *Mechanitis*, one species of *Pteronymia*, one species of *Thyridia*, and possibly one species of *Placidula* (DeVries, 1985; Drummond & Brown, 1987; Table VI). *Cyphomandra* is also the probable host plant of one species of *Paititia* (Drummond & Brown, 1987). Drummond (1986) notes that all known larval

Table VI
Records of ithomiine larvae feeding on species of *Cyphomandra*.
Plant names have been corrected to agree with current usage. AR—Argentina,
BR—Brazil, CR—Costa Rica, EC—Ecuador, VE—Venezuela

Butterfly	Host plant and country	Reference
Mechanitis lysimnia	*C. betacea* (AR, BR)	Drummond and Brown, 1987
	C. diploconos (BR)	Drummond and Brown, 1987
	C. sciadostylis (BR)	Drummond and Brown, 1987
	C. divaricata (BR)	Vasconcellos-Neto, 1991
	C. corymbiflora (BR)	Bohs, unpub. data
Mechanitis polymnia	*C. hartwegii* (EC)	Drummond and Brown, 1987
	C. diploconos (BR)	Drummond and Brown, 1987
	C. sciadostylis (BR)	Drummond and Brown, 1987
Placidula euryanassa	*C. betacea* (?) (BR)	Drummond and Brown, 1987
Pteronymia lonera[a]	*C. hartwegii* (CR)	DeVries, 1985
Thyridia psidii	*C. betacea* (CR, VE, BR)	Drummond and Brown, 1987
	C. hartwegii (CR, EC)	Drummond and Brown, 1987; Haber, 1978[b]
	C. diversifolia (VE)	Drummond and Brown, 1987
	C. divaricata (BR)	Drummond and Brown, 1987
	C. diploconos (BR)	Drummond and Brown, 1987
	C. sciadostylis (BR)	Drummond and Brown, 1987

[a] As "new genus *lonera* (Butler & Druce)" in Drummond and Brown (1987).
[b] As *Xanthocleis aedesia* in Haber (1978).

food plants of the genus *Thyridia* belong to *Cyphomandra*, but Knapp (*Knapp & Mallet 6642*, NY, US; pers. comm.) observed *Thyridia* ovipositing on *Solanum morellifolium* in *Solanum* section *Allophyllum* (Bohs, 1990). Whether *Thyridia* larvae successfully use *S. morellifolium* as a larval host plant is unclear.

Vasconcellos-Neto (1991) hypothesizes that marked differences in juvenile and adult leaf shape in *Cyphomandra* may deter insects from ovipositing on the foliage by interfering with their ability to locate the host plants. A similar defensive function has been proposed by Gilbert (1975) for divergent leaf shapes among species of *Passiflora* that are eaten by larvae of *Heliconius* butterflies.

Ithomiine adults are aposematic and apparently distasteful to predators (Brown, 1987a; Drummond, 1986). Despite the number of secondary substances present in most Solanaceae, it appears that adult Ithomiinae do not use solanaceous compounds as defenses against predators. Rather, the adult butterflies feed mainly on plant juices and nectar from species of Boraginaceae and Asteraceae which are high in dehydropyrrolizidine alkaloids. These substances are sequestered in the adults and contribute to their unpalatability (Brown, 1987a).

Although ithomiine butterfly larvae attack many solanaceous plants, the relationship between butterfly species and their larval host plants is often quite specific (Brown, 1987a;

Drummond, 1986). However, the food plant preferences for a particular ithomiine species do not indicate that a coevolutionary relationship exists between the butterflies and their food plants. *Mechanitis polymnia* and *M. lysimnia* oviposit on *Cyphomandra* as well as on *Lycopersicon* and members of *Solanum* subgenera *Brevantherum*, *Leptostemonum*, and *Solanum* (Drummond & Brown, 1987). A report of *Placidula euryanassa* feeding on *Cyphomandra*, *Datura*, and *Brugmansia* is interesting, but the *Cyphomandra* record is questionable (Drummond & Brown, 1987). The proposed phylogenetic sequence of Ithomiinae does not match that of Solanaceae genera, calling into question the hypothesis of coevolution between the butterflies and their larval food hosts (Brown, 1987a; Drummond, 1986). Rather, coevolution seems more likely between the Ithomiinae and their pyrrolizidine alkaloid sources in the Asteraceae (Brown, 1987a). The specificity between solanaceous species and their associated ithomiine herbivores may be indicative of chemical differences in the larval host plants, but few conclusions can be drawn given the scarcity of data on chemical composition of solanaceous species and the incompleteness of larval feeding records. Such insect-plant interactions should be more intensively studied, and may throw considerable light on comparative chemistry and perhaps on intergeneric relationships in the Solanaceae.

FOSSIL AND ARCHAEOLOGICAL RECORD

No fossils of *Cyphomandra* have been reported. Muller (1970) cites macrofossil remains of *Solanum* from the Eocene, but I could find no further information about them. D'Arcy (1991) cites a report of *Solanum* pollen from Quaternary deposits in the Colombian Andes, but otherwise I have found no records of Solanaceae pollen in the paleobotanical literature. *Cyphomandra* pollen is very similar to that of *Solanum*, so even if a pollen record existed for these taxa, it could be impossible to identify to genus.

Despite the possible use of *C. betacea* fruits by pre-Columbian peoples of South America, no remains of *Cyphomandra* have been reported from any of the Peruvian coastal sites that have yielded well-preserved plant material. Safford (1917) identifies *C. betacea* as one of the species represented on pre-Columbian pottery from coastal Peru, but the similarity of *C. betacea* fruits to those of other solanaceous species cultivated in this area casts doubt on this interpretation (Bohs, 1989c).

DISTRIBUTION AND BIOGEOGRAPHY

All species of *Cyphomandra* are native to tropical America between latitudes of approximately 20° N and 30° S (Fig. 11; Table VII). In addition, *C. betacea* is cultivated in many subtropical areas throughout the world. The postulated history of dispersal of *C. betacea* is discussed in Bohs (1989c).

The restriction of *Cyphomandra* to tropical America, particularly to South America, argues for a relatively recent origin of the genus and/or a relatively low vagility (dispersibility). The related genus *Solanum* is represented on all continents except Antarctica; whether its distribution predates the breakup of the Gondwana continent in the late Mesozoic and Tertiary or is the result of more recent long-distance dispersal is unknown (D'Arcy, 1991; Hawkes & Smith, 1965). [See Olmstead and Palmer (1992) for evidence supporting the latter view.]

Cyphomandras are most abundant in mesic forest areas of Central America and western South America, with another center of species diversity in southeastern Brazil. No *Cyphomandra* species is native to the West Indies. The genus is absent from arid areas along the coast of Peru and Chile, from temperate regions below 30° S latitude, and from unforested areas such as the llanos of Colombia and Venezuela. With the exception of *C. tobagensis*, cyphomandras have not been collected from the Guayana highlands or from the Rio Negro drainage. Likewise, only one species, *C. oblongifolia*, is found on the Planalto de Mato Grosso in Brazil. *Cyphomandra ovum-fringillae* is the only species known to grow in the caatinga formation of northeastern Brazil. Adaptation of this species to the semiarid caatingas is unusual for *Cyphomandra*, but perhaps *C. ovum-fringillae* actually grows in the brejos, or forest islands, that occur in the midst of this formation

FIG. 11. Distribution of *Cyphomandra.* This map a composite of all the species maps included in the systematic treatment.

on the summits of southeast-facing slopes and condense water vapor from the prevailing winds because of their altitude and aspect (Andrade-Lima, 1982). Further collecting in these and other areas could greatly change the picture of distributional patterns in *Cyphomandra.*

The natural range of *C. betacea* is unclear. On the map of Fig. 11 all the known localities of *C. betacea* in the Neotropics are included, and cultivated individuals probably account for many of the outlying points. For instance, the five northernmost points in Mexico, the five points below 30° S latitude in Argentina and Chile, and the collections from the Galapagos and Caribbean (with the exception of Tobago) represent collections of *C. betacea.* These may be from cultivated or naturalized plants. Resolution of the natural range and center of origin of *C. betacea* will aid in the solution of many biological problems associated with this species, and is a high priority before habitat destruction eliminates wild populations that may still exist.

Only four species of *Cyphomandra* are found in Central America. Two, *C. rojasiana* and *C. dolichocarpa*, are narrowly endemic, whereas *C. hartwegii* and *C. diversifolia* have wider ranges that extend into northern South America. All of the Central American species are related to taxa

Table VII

Distribution of *Cyphomandra* species by country. Asterisks indicate species endemic to the country listed. The cultivated species *C. betacea* is excluded.

MEXICO: hartwegii, rojasiana

GUATEMALA: rojasiana

BELIZE: rojasiana

HONDURAS: hartwegii

NICARAGUA: hartwegii

COSTA RICA: diversifolia, dolichocarpa, hartwegii

PANAMA: diversifolia, dolichocarpa, hartwegii

COLOMBIA: cajanumensis, diversifolia, endopogon, fragilis, hartwegii, hypomalaca, obliqua, pilosa, sibundoyensis*, stellata

VENEZUELA: diversifolia, hartwegii, tobagensis

TRINIDAD & TOBAGO: tobagensis

GUYANA: tobagensis

SURINAME: hartwegii, oblongifolia, tegore

FRENCH GUIANA: endopogon, hartwegii, tegore

ECUADOR: cajanumensis, endopogon, foetida, fragilis, hartwegii, hypomalaca, pendula, pilosa, stellata

PERU: cajanumensis, endopogon, foetida, fragilis, hartwegii, obliqua, oblongifolia, pendula, pilosa, stellata, tenuisetosa

BRAZIL: calycina*, corymbiflora, diploconos*, divaricata*, endopogon, foetida, fragilis, hartwegii, heterophylla*, obliqua, oblongifolia, ovum-fringillae*, pendula, pinetorum*, premnifolia*, sciadostylis, sycocarpa*, tegore, tenuisetosa

BOLIVIA: acuminata*, benensis*, hartwegii, oblongifolia, pendula, uniloba*

PARAGUAY: sciadostylis

ARGENTINA: corymbiflora, sciadostylis

from western South America. *Cyphomandra* evidently moved into Central America from a South American center. Direct migration via local dispersal would have been possible only after the land connection had been established between South America and Central America by the uplift of Panama in the late Pliocene about 5.7 million years ago (Raven & Axelrod, 1974). Long-distance dispersal was also possible, and may have occurred in the case of *C. rojasiana* from southern Mexico, which is disjunct from its nearest relatives in Peru and Bolivia. Long-distance dispersal is less likely than direct migration in the cases of *C. hartwegii* and *C. diversifolia.* Earlier migration via the West Indies seems unlikely because of the absence of wild cyphomandras on any of the present islands.

The distribution of *Cyphomandra* species by country is given in Table VII. Brazil contains the most species (19) and has eight endemics, all in the eastern coastal region. The other Brazilian taxa mostly represent widely distributed species of the western Amazon and eastern Andean slope. With the exception of the cultivated *C.*

betacea, there are no species in common between western South America and eastern Brazil. The range of *C. oblongifolia* extends from the western Amazon to the Planalto de Mato Grosso; it does not enter the Atlantic rain forest or *Araucaria* forests of southeastern Brazil. With the exception of *C. sycocarpa* and *C. heterophylla*, which may have Andean affinities, the eastern Brazilian species are apparently more closely related to each other than to species from other areas. These two centers of differentiation probably reflect pre-Quaternary patterns of isolation (Simpson & Haffer, 1978).

Data derived from palynological and geomorphological studies in the neotropics, particularly in South America, have indicated that the Pleistocene was characterized by fluctuating climatic regimes, resulting in alternating dry and humid conditions. These climatic changes altered vegetational patterns in the Andean highlands and influenced the distribution of lowland humid forest, which had formerly been thought to have been unaffected by Pleistocene glacial and interglacial regimes apparent in higher latitudes. During dry periods the lowland forests may have been restricted to small discontinuous pockets, or refugia. The isolation of forest populations in refugia permitted differentiation to occur before the forests expanded during the next moist period. It is thought that these periods of isolation and subsequent forest expansion contributed to the extremely high levels of taxonomic diversity characteristic of the neotropical lowland forest. When species and subspecies distributions for diverse groups such as plants, butterflies, birds, and reptiles are examined, areas of high diversity and endemism are strikingly coincident. This has led to the postulation of refuge areas such as those of Haffer (1969, 1987b) for birds, Prance (1973, 1982, 1987) for plants, and Brown (1982, 1987b) for butterflies. Haffer (1969), working with birds, found evidence of secondary contact zones that were located between the postulated refuge areas, providing further support for the model. A summary of the refugium hypothesis and a synthesis of endemism patterns of neotropical plants, butterflies, and birds combined with refuges proposed from paleoecological data can be found in Whitmore and Prance (1987).

Several criticisms have been leveled at the refugium theory. One competing hypothesis is that centers of endemism are correlated not with past, but with present climatic, edaphic, and ecological factors. Many of the refugia occur in areas of high rainfall or high habitat diversity, and these factors could be responsible for high rates of speciation or species survival. Little is known of the causes, mechanisms, or rates of evolutionary divergence and speciation in neotropical forest taxa, so the biological events that have resulted in the species distribution patterns seen today are largely a matter of speculation. If mechanisms other than allopatric speciation are involved in differentiation, forest fragmentation is diminished as a probable cause of species diversity.

Furthermore, present biogeographic patterns may primarily reflect pre-Pleistocene events. Because the refugium theory is chiefly aimed at explaining differentiation at the population, subspecific, or specific level and is concerned with relatively recent events, its applications to evolutionary patterns of higher level taxa may be limited.

Despite these uncertainties, I will point out patterns in the distribution of *Cyphomandra* species and examine their correspondence with centers of endemism and species diversity described for other neotropical taxa. More detailed hypotheses of speciation patterns and processes must await further knowledge of phylogenetic relationships within the genus. Nonetheless, identification of areas of high species richness may be important in establishing criteria for conservation programs aimed at preserving tropical forest diversity.

A few examples of similar range disjunctions occur within species of *Cyphomandra*. For instance, *C. endopogon* is primarily a species of the western Amazon, but disjunct, subspecifically differentiated populations occur in French Guiana and eastern Brazil near the mouth of the Amazon, separated by at least 1500 km. *Cyphomandra hartwegii* shows a similar disjunction between western South America and Suriname, and populations also occur along the coast of Venezuela. Similarly, *C. oblongifolia* is typically a species of the central Amazon, and disjunct populations occur in Suriname, French Guiana, and near the mouth of the Amazon. However, *C. hartwegii* and *C. oblongifolia* are often difficult to distinguish from each other, so there is some doubt of the correct identification of the disjunct specimens.

The same pattern of disjunction between Amazonia and the Guianas has been described for *Mouriri oligantha* Pilg. (Melastomataceae) by Prance (1982). Possible explanations for these disjunctions are (1) long distance dispersal, (2) fragmentation of a formerly more continuous range by changes in the forest cover, and (3) undercollecting in the intervening area creating an apparent disjunction. The third explanation is unlikely. Long-distance dispersal is possible, but is argued against by the size of the diaspores, the widespread self-incompatibility in the genus, and the probable dependency on specialized pollinators; should a long distance dispersal event happen, the resultant plants may not be able to reproduce. More information about the reproductive and population biology of *Cyphomandra* species and populations needs to be amassed, however, before this explanation can be ruled out. The hypothesis that forest fragmentation produced relict populations from a formerly wider distribution is the most attractive.

A further example of disjunction occurs in *C. obliqua* and *C. rojasiana.* The two are closely related, but their ranges are separated by nearly 2800 km. *Cyphomandra obliqua* is distributed along the western Amazon and its tributaries, while *C. rojasiana* is endemic to Guatemala, Belize, and southern Mexico. Either long distance dispersal or range fragmentation of a more widespread ancestral species could account for the wide disjunction between these two similar species. The ranges of both *C. obliqua* and *C. rojasiana* roughly correspond to proposed forest refugia; *C. obliqua* occurs in the East Peru/Acre refuge of Prance (1982, 1987) and the Huallaga-Pachitea and Chanchamayo refuges of Brown (1982), and the distribution of *C. rojasiana* is coincident with the Soconusco refuge of Toledo (1982) and the Pacifico refuge of Brown (1982). However, long-distance dispersal from South to Central America is perhaps the more likely explanation for the disjunct distibution of *C. rojasiana.* The absence of any *C. obliqua* relative from large intervening areas of Central and northern South America supports this view (but see unnamed taxon 2). Similar patterns of disjunction also occur in the *Solanum nitidum* group of *Solanum* section *Holophylla* (Knapp, 1989). Knapp (1989) considered long distance dispersal from South America the likely source of the Central American disjunct, but the coincidence of the two patterns may argue for a vicariance explanation via forest fragmentation.

Centers of species diversity in *Cyphomandra* can also be compared with those noted for other neotropical taxa. The numbers of *Cyphomandra* species in tropical America are given in Fig. 12. *Cyphomandra betacea* is not included because of the uncertainty about its natural range. Seven areas in South America contain at least five species; these are denoted by letters A–G on Fig. 12, and the species found in each of these areas are listed in Table VIII. Area A includes nine species with one endemic (*C. sibundoyensis*). Area B contains ten species, none endemic. Areas A and B have eight species in common, so there is a strong floristic affinity between them. Parts of both of these areas have been noted as regions of high species endemism and have been designated as refuges by Prance (1982, 1987), Brown (1982, 1987b), and Haffer (1987b). Area A has been called the Napo refuge by all three authors. Area B is called the East Peru-Acre refuge by Prance (1982, 1987) and corresponds to the Huallaga-Pachitea and Chanchamayo refuges of Brown (1982). Both also occur in centers of high rainfall; an estimated 3000–4000 mm of rain falls each year in area A, while area B receives about 1500–4000 mm per year (Brown, 1982; Haffer, 1987a). Area C contains five species, none endemic. It has strong affinities with area B, for all five of its species are also found there. Four of the five species of area C extend their ranges eastward into the Amazon basin. This area has been included as a part of the Napo refuge by Prance (1982, 1987) and described as the Loreto refuge by Brown (1987b). It can for all practical purposes be considered an Amazonian extension of area B. Area D contains eight species, none endemic. It shares seven species with area B, and thus is closely allied with it floristically. This area has not been previously noted as a refuge for plants by Prance (1982, 1987), but it roughly conforms to the Inambari refuge of Brown (1982, 1987b) and Haffer (1987b). Area E contains five species with one endemic (*C. acuminata*). It shares three species with area D and two species with area B. One of the latter two species is the widespread *C. hartwegii* that is found also in areas A, B, and D. Thus the affinities of area E most strongly lie with area D. Area E corresponds

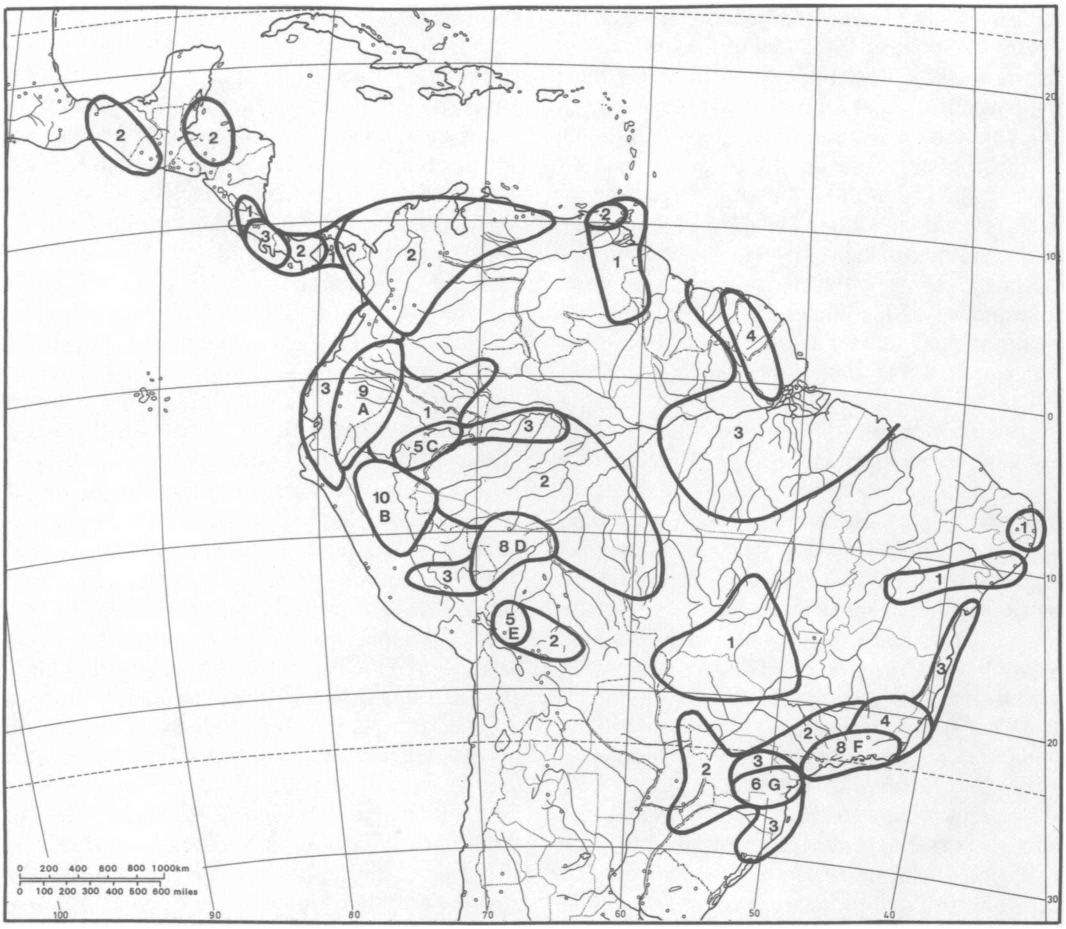


FIG. 12. Taxonomic diversity map of *Cyphomandra*. Numbers represent species within black lines. Letters A through G correspond to areas in Table VIII. See discussion in text.

to the Beni refuge of Prance (1982, 1987) and the Yungas refuge of Brown (1982). It is unique in that it occurs at a higher altitude than most of the other proposed refugia and is not characterized by particularly high rainfall, but is nevertheless a center of endemism for many different taxa (Prance, 1987).

Southeastern Brazil contains two important centers of species diversity for *Cyphomandra*. The first, designated as area F, contains eight species, none completely endemic to the area. The other, area G, contains six species, none endemic, and shares five species with area F. The only species from area G not also found in area F is *C. corymbiflora*, characteristic of the more southern and western *Araucaria* forests. Area F corresponds to the Rio Espirito Santo refuge of Prance (1982, 1987), the Itabapoana part of the Rio de Janeiro refuge of Brown (1982), and the Serra do Mar refuge of Haffer (1987b). Area G was not specified as a refuge for plants by Prance (1982, 1987) or birds (Haffer, 1987b), but was considered as the Paranaguá part of the Rio de Janeiro refuge by Brown (1982). Rainfall is high in these two areas relative to the surrounding cerrado further inland. Area F receives about 1500–2000 mm of rainfall per year, while area G receives about 1000–2500 mm per year (Brown, 1982).

Table VIII

Cyphomandra species occurring in each of the areas A through G of Fig. 12.

Area A: endopogon, foetida, fragilis, hartwegii, obliqua, pendula, pilosa, sibundoyensis, stellata

Area B: endopogon, foetida, fragilis, hartwegii, obliqua, oblongifolia, pendula, pilosa, stellata, tenuisetosa

Area C: endopogon, obliqua, oblongifolia, pilosa, stellata

Area D: benensis, foetida, fragilis, hartwegii, obliqua, oblongifolia, pendula, tenuisetosa

Area E: acuminata, benensis, hartwegii, pendula, uniloba

Area F: calycina, diploconos, divaricata, heterophylla, pinetorum, premnifolia, sciadostylis, sycocarpa

Area G: corymbiflora, diploconos, divaricata, pinetorum, premnifolia, sciadostylis

Cyphomandra species are also concentrated to a lesser extent in other proposed refuge areas, such as the Bahia refuge (3 species, no endemics), the East Guiana refuge of Prance (1982, 1987) and Oyapock of Brown (1982, 1987b) (4 species, with one endemic subspecies of *C. endopogon*), the Paria refuge of Prance (1982) and the Sucre/Trinidad refuge of Brown (1982, 1987b) (2 species, no endemics), and the Chiriquí refuge of Brown (1982, 1987b) (3 species, 1 endemic).

In most cases, areas of high species diversity in *Cyphomandra* correspond with the refuges proposed by other authors. In most instances, areas of high species diversity are correlated with areas of high rainfall, the notable exception being area E. Although the areas noted in Fig. 12 represent areas of species richness, nothing is known about how these patterns originated. Definitive conclusions about the factors responsible for the present distribution patterns in *Cyphomandra* must await further understanding of the phylogenetic relationships of this group and the causes, mechanisms, and rates of specific and infraspecific differentiation.

USES

Uses of *Cyphomandra* fall into three categories: (1) fruits of many species are edible, (2) various parts of the plants are used medicinally, and (3) a few species are used as dyes. General uses of *Cyphomandra* are summarized here. Further information is given under the individual species treatments and in Bohs (1989c).

Among the taxa with edible fruits, *Cyphomandra betacea*, the tree tomato, is the only species that is cultivated commercially. Although it is apparently known only as a domesticate, Bohs (1989c) reports that wild populations of *C. betacea* may exist in southern Bolivia and northwestern Argentina. It is commonly known in Latin America under the name "tomate de árbol," and has recently been imported into the United States from New Zealand under the name "tamarillo." The fruits are eaten raw or made into various types of juices or cooked dishes. The plants are frequently grown in dooryard gardens in tropical America, and are cultivated worldwide in subtropical and warm temperate areas. For a detailed view of cultural requirements and probable migration routes, see Bohs (1989c).

Other species such as *Cyphomandra hartwegii*, *C. uniloba*, *C. sibundoyensis*, and *C. cajanumensis* may be promising fruit crops in their own right (National Research Council, 1989) or may be useful in breeding programs aimed at the improvement of *C. betacea* (Bohs, 1991).

Various species of *Cyphomandra* are used medicinally by native peoples in Latin America, presumably because of the alkaloid content of the plants. Most frequently the leaves or stems are applied as a poultice to the affected part or prepared in a hot or cold infusion that is taken internally. Species most commonly employed medicinally include *C. obliqua*, *C. endopogon*, *C. pilosa*, *C. hartwegii*, and *C. stellata*. Details can be found under the individual species treatments.

Cyphomandra betacea is the only species that has been examined chemically. This species contains both tropane and steroidal alkaloids as well as non-tropane bases (Evans, 1979; Evans et al., 1972; Evans & Somanabandhu, 1980; Schreiber, 1979). The tropane alkaloids and non-tropane bases were isolated from fresh and dried roots, whereas the material used for isolation of steroidal alkaloids was not specified. Because most often the aerial parts of the plants are used medicinally, it would be worthwhile to survey leaves and stems of wild *Cyphomandra* species for physiologically active compounds.

The juices of the fruits or leaves of *Cyphomandra hartwegii* and *C. pilosa* serve as black or white dyes for clay pots made by natives of northeastern Ecuador and adjacent Colombia (Bohs, 1989c).

SYSTEMATIC TREATMENT

Cyphomandra Martius ex Sendtner, Flora **28:** 162. 1845 (March); Sendtner *in* Martius, Fl. Bras. **10:** 113. 1846; Dunal *in* DC. Prodr. **13(1):** 387. 1852. Lectotype species. *Cyphomandra betacea* (Cavanilles) Sendtner, designated by Benitez de Rojas, Rev. Fac. Agron. (Maracay) **7(3):** 75. 1974. From Greek κυφος= hump and ανηρ or ανδρος = man, referring to the thickened anther connective.

Solanum b. *Pachyphylla* Dunal, Histoire des Solanum, pp. 122, 168. 1813 (grad. ambig.). Lectotype species. *Solanum betaceum* Cav., designated by D'Arcy, Ann. Missouri Bot. Gard. **59:** 272. 1972. From Greek παχυς = thick, and φυλλον = leaf.

Cyathostyles Schott ex Meisner, Pl. Vasc. Gen. **2:** 184. 1840, nomen nudum, pro syn. *Witheringia* L'Heritier. Placed here as a synonym according to the material annotated by Schott. From Greek κυαθος = cup and στυλος = style, apparently referring to the expanded styles of some species.

Pionandra Miers, London J. Bot. **4:** 353. 1845 (July); Miers, Ill. S. Amer. pl. 1: 34. 1850; Miers, Ann. Mag. Nat. Hist., ser. 2, **15:** 198. 1855; Miers, Ill. S. Amer. pl. 2: 141. 1857. Lectotype species. *Pionandra floribunda* Miers, designated by D'Arcy, Solanaceae Newsletter **2(4):** 18. 1986. From Greek πιων= fat and ανηρ or ανδρος = man, referring to the thickened anther connective.

Pionandra section *Ceratostemon* Miers, London J. Bot. **4:** 354. 1845. Lectotype species. *Pionandra floribunda* Miers, designated by Child, Feddes Repert. **95:** 291. 1984. From Greek κερας= horn and στημων = stamen.

Pionandra section *Euthystemon* Miers, London J. Bot. **4:** 360. 1845. Lectotype species. *Pionandra hartwegii* Miers, here designated. From Greek ενθις = straight and στημων = stamen.

Pallavicinia De Notaris, Flora **30:** 567. 1847. Type species. *Pallavicinia fragrans* (Hooker) De Notaris. Named for the Marquis Ignatz Pallavicino, who grew this species in his garden.

Solanum section *Pachyphylla* (Dunal) Dunal *in* DC. Prodr., **13(1):** 387. 1852. Lectotype species. *Solanum betaceum* Cav., designated by D'Arcy, Ann. Missouri Bot. Gard. **59:** 272. 1972.

Cyphomandra section *Pachyphylla* (Dunal) D'Arcy, Ann. Missouri Bot. Gard. **59:** 277. 1972. Lectotype species. *Cyphomandra betacea* (Cav.) Sendtn.

Cyphomandra section *Ceratostemon* (Miers) Child, Feddes Repert. **95:** 290. 1984. Lectotype species. *Cyphomandra floribunda* (Miers) Dunal, designated by Child, Feddes Repert. **95:** 291. 1984.

Generic Description

Unarmed *trees* or *shrubs*, rarely herbs. *Architecture* usually conforming to Prévost's model. *Bark* light-colored and usually smooth. *Stems* with wood in a cylinder surrounding a large central spongy or chambered pith; vascular bundles bicollateral. *Indumentum* of uniseriate, multicellular, glandular and eglandular, simple or rarely dendritically branched hairs; stellate hairs absent. *Trunk leaves* alternate with 2/5 phyllotaxis, petiolate, simple or imparipinnate, unlobed or pinnately lobed, often with cordate bases. *Crown leaves* 3–4 per sympodial unit, similar or dissimilar to those of the main stem, the two leaves above the inflorescence often paired. *Venation* brochidodromous; veins usually spreading at base, ascending at apex and curved toward margin. *Inflorescence* a scorpioid cyme, terminal but often appearing axillary or extra-axillary, unbranched or branched, usually ebracteate, usually pendent; pedicels secund, usually pendent, articulated at or near the base, leaving pedicellar remnants or prominent scars on the rachis. *Flowers* perfect, actinomorphic, 5-merous. *Calyx* synsepalous, cyathiform, persistent and scarcely enlarged in fruit. *Corolla* sympetalous, hypogynous, white, pink, purple, green, or brownish, stellate, campanulate, or occasionally urceolate; aestivation valvate or induplicate. *Stamens* equal; filaments glabrous, short, inserted in the corolla tube near its base; anthers basifixed, the thecae minutely papillose, often tapered toward apex, dehiscent by apical pores; anther connective papillose, expanded abaxially and often also adaxially; pollen tricolporate. *Ovary* superior, bilocular; placentation axile on fleshy intrusions; style articulated at base, glabrous or occasionally pubescent; stigma more or less bilobed, sometimes broadly expanded at apex, often with two apical glands. *Fruit* a berry, usually pendent, usually yellowish when ripe, often with darker longitudinal stripes; mesocarp frequently with stone cell aggregates. *Seeds* numerous, flattened, reniform, often appearing pubescent; embryo strongly curved; endosperm abundant. *Germination* epigeal. $n = 12$.

About 35 species, all native to the New World from Mexico to South America (Fig. 11). *Cyphomandra betacea* (q.v.) has been distributed worldwide by humans.

Species Concept

This treatment is based mainly on the study of herbarium specimens, augmented where possible by observations of living plants in the field and greenhouse. The taxa recognized are for the most part delimited by use of the morphological or taxonomic species concept in which assemblages of population samples (sets of specimens) are separated from each other by morphological discontinuities (Davis & Heywood, 1963). In most cases these discontinuities exist in many characters. Furthermore, these morphological entities often have unique geographical, elevational, and/or ecological preferences. Where character differences exist among populations but no consistent patterns of variation are observed, I recognize a single polymorphic species (as in *C. hartwegii*). Subspecies are the only infraspecific taxa recognized, and are delimited on the basis of consistent yet relatively minor morphological differences, such as density of pubescence or corolla size. In most cases the subspecies have distinct geographic ranges.

New species have not been described on the basis of incomplete herbarium samples. Two potential new species are noted in this treatment, but not enough information is available to give them species status. These taxa are described briefly at the end of the species treatments.

Typification

Retroactive application of the rules for botanical nomenclature and typification often causes problems. To minimize these difficulties, I have strictly followed the ICBN (Greuter et al., 1988) guidelines in interpreting type material. A specimen is only regarded as the holotype if it was definitely indicated as such by the original author of the taxon. If a single specimen was not designated as the holotype, I have chosen a lectotype from among the extant duplicates of the type collection number (isotypes) or from the syntypes mentioned by the original author. In each instance, I have tried to take into account all indications of which specimens the author actually examined in formulating his protologue. Specific notes on lectotypification can be found following their respective species in the taxonomic section.

Many type specimens of Solanaceae formerly housed at the Berlin herbarium (B) were destroyed during World War II. Where appropriate, lectotypes have been chosen from among the extant isotypes. No isotypes have been found for *C. dolichocarpa* and *C. tenuisetosa*, but photos of the original B specimens taken before the war allow positive identification to species. Neotypes have been chosen for these two species.

Notes on the Systematic Treatment

Species are listed alphabetically by specific epithet. The dichotomous key is artificial and is not intended to reflect evolutionary relationships.

Measurements were made from dried herbarium specimens, material preserved in fluid (FAA or ethanol), and dried flowers rehydrated in boiling water. The majority of collections examined were dried herbarium specimens. Colors given are based on personal field observations and herbarium label data.

All specimens cited in the treatment have been seen by the author except where noted as "n.v." All specimens have been cited in the treatment with the exception of *C. hartwegii*, where a list of representative specimens is given. These were chosen on the basis of geographic representation and wide distribution in many herbaria. Only the New World collections are cited for *C. betacea*, although a list is given of the other countries where this species has been found. Complete specimen lists for these two species are available from the author. All specimens seen in this study are included in the List of Exsiccatae.

Distribution maps were prepared from Flora Neotropica Base Map No. 1, © University of Utrecht. All dots represent specimens I have seen.

DICHOTOMOUS KEY TO THE SPECIES OF CYPHOMANDRA

1\. Corolla lobes densely tomentose abaxially with hairs almost completely obscuring the corolla tissue.
2\. Corolla stellate, the tube 2–3 mm long; anther connective 3–4 mm long, visible adaxially; crown leaves usually simple; fruits pubescent . . . . 2. *C. benensis*.
2\. Corolla campanulate, the tube 5–8 mm long; anther connective 4–6 mm long, not visible adaxially; crown leaves usually pinnately compound; fruits glabrous . . . . 20. *C. pendula*.
1\. Corolla lobes glabrous or pubescent abaxially with hairs not completely obscuring the corolla tissue.
3\. Corolla urceolate, divided less than half its length . . . . 9. *C. diversifolia*.
3\. Corolla campanulate to stellate, divided more than half its length.
4\. Style strongly dilated distally into a stigma greater than 2 mm in diameter; if less than 2 mm in diameter, then stigma more than twice the diameter of the base of the style.
5\. Connective prolonged distally beyond apices of anther thecae; succulent plants of coastal Brazil.
6\. Leaves and stems glabrous; leaf blades simple, lobed or unlobed . . . 28. *C. sycocarpa*.
6\. Leaves and stems puberulent; leaf blades simple or pinnately compound . . . . .15. *C. heterophylla*.
5\. Connective ending at or below apices of anther thecae, not prolonged distally beyond anther thecae; plants of various regions.
7\. Anthers 8–10 mm long X 1–2 mm wide; style 9–12 mm long; corolla margins conspicuously ciliate with hairs 1–2 mm long. . . . . 11. *C. endopogon*.
7\. Anthers 3–5 mm long X 1.5–3 mm wide; style 2–6 mm long; corolla margins tomentose with hairs less than 1 mm long.
8\. Anther connective abruptly narrowed distally, not completely covering anthers abaxially; plants of southeastern Brazil.
9\. Calyx radius 7–14 mm, the calyx at least half as long as the corolla . . . . 5. *C. calycina*.
9\. Calyx radius 3–7 mm, the calyx less than half as long as the corolla.
10\. Style densely puberulent . . . . 25. *C. sciadostylis*.
10\. Style glabrous or sparsely and minutely puberulent.
11\. Style broadly obconical, 2–4.5 mm in diameter . . 7. *C. diploconos*.
11\. Style narrowly obconical to broadly clavate, 1–2 mm in diameter . . . . 23. *C. premnifolia*.
8\. Anther connective gradually narrowed distally, almost completely covering anthers abaxially; plants of Central America and western South America.
12\. Leaves glabrous abaxially or nearly so; pedicels 2–6 mm apart, leaving remnants 1–3 mm long on the inflorescence axis . . . . 32. *C. uniloba*.
12\. Leaves moderately to densely puberulent abaxially; pedicels 1–3 mm apart, leaving remnants less than 1 mm long on the inflorescence axis.
13\. Inflorescence 5–10-flowered, 2.5–3.5 cm long; fruits puberulent; plants of Mexico, Guatemala, and Belize . . . . 24. *C. rojasiana*.
13\. Inflorescence 30–50-flowered, 3–16 cm long; fruits usually glabrous; plants of South America . . . . 17. *C. obliqua*.
4\. Style not strongly dilated distally, the stigma usually less than 2 mm in diam. and less than twice the diam. of the style base.
14\. Ovaries and fruits puberulent, pubescent, or pilose, at least when young.
15\. Corolla margins ciliate with hairs 1–2 mm long; anther thecae usually more than four times longer than wide.

16. Vegetative parts densely pubescent-pilose; long hairs abundant and up to 4 mm long . . . 12. *C. foetida.*
16. Vegetative parts glabrous to densely puberulent; long hairs sparse if present and less than 2 mm long . . .
   17. Style dilated distally; inflorescences usually much branched . . 27. *C. stellata.*
   17. Style not dilated distally; inflorescences unbranched.
      18. Corolla green; fruits obtuse at apex; trunk leaves sometimes pinnately lobed; crown leaves often cordate at base . . . 29. *C. tegore.*
      18. Corolla usually purple; fruits acute at apex; trunk leaves unlobed; crown leaves usually cuneate at base . . . 31. *C. tobagensis.*

15. Corolla margins tomentose with hairs usually less than 1 mm long; anther thecae less than 3.5 times longer than wide.
   19. Fruits puberulent with hairs less than 0.5 mm long.
      20. Fruits globose, 1–1.5 cm in diameter; pericarp thin and closely investing the seeds; pedicel remnants 2–6 mm long . . . 16. *C. hypomalaca.*
      20. Fruits ellipsoidal, more than 1.5 cm in diameter; pericarp abundant and juicy; pedicel remnants 0–2 mm long . . . 4. *C. cajanumensis.*
   19. Fruits pubescent to pilose with at least some hairs 1 mm or more long.
      21. Crown leaves cuneate or truncate to very shallowly cordate at base; pedicel remnants less than 1 mm long; plants of western South America . . . 21. *C. pilosa.*
      21. Crown leaves cordate at base; pedicel remnants 1–2 mm long; plants of southeastern Brazil.
         22. Inflorescences usually unbranched, 5–15(–20)-flowered; crown leaves shallowly cordate with basal sinuses up to 2 cm deep; anther thecae (5-)6–7 mm long; anther connective gradually narrowed distally . . . 22. *C. pinetorum.*
         22. Inflorescences usually branched, 15–40+-flowered; crown leaves cordate, at least some with basal sinuses more than 2 cm deep; anther thecae 3–6 mm long; anther connective strongly and abruptly narrowed distally . . . 6. *C. corymbiflora.*

14. Ovaries and fruits glabrous.
   23. Crown leaves (at least some) cordate at base with basal sinuses more than 1 cm deep.
      24. Corolla campanulate, the tube more than 4 mm long.
         25. Vegetative parts abundantly pilose with long (1–3 mm) hairs; style 6–10 mm long . . . 30. *C. tenuisetosa.*
         25. Vegetative parts glabrate, long hairs sparse if present; style 4–5 mm long . . . 18. *C. oblongifolia.*
      24. Corolla stellate, the tube less than 4 mm long.
         26. Corolla lobes puberulent adaxially.
            27. Trunk leaves often pinnately lobed; anther connective longer than thecae at base; plants widespread . . . 14. *C. hartwegii.*
            27. Trunk leaves unlobed; anther connective equal to or slightly longer than thecae at base; plants endemic to southern Colombia . . . 26. *C. sibundoyensis.*
         26. Corolla lobes glabrous adaxially.
            28. Corolla pink, whitish, or reddish; corolla tube 2–4 mm long.
               29. Vegetative parts densely puberulent; crown leaves cordate at base with basal sinuses 1.5 cm or more deep; seeds pubescent with hairs less than 1 mm long . . . 3. *C. betacea.*
               29. Vegetative parts nearly glabrous; crown leaves truncate to subcordate at base with basal sinuses up to 1.5 cm deep; seeds pilose with hairs 1–2 mm long . . . 1. *C. acuminata.*
            28. Corolla greenish or purplish, rarely whitish; corolla tube less than 2 mm long.
               30. Anther thecae 2–4 mm wide; anther connective equal to or slightly longer than thecae at base . . . 4. *C. cajanumensis.*
               30. Anther thecae 1–2 mm wide; anther connective 0.5–1 mm longer than thecae at base.
                  31. Crown leaves (at least some of them) cordate with basal sinuses more than 1.5 cm deep; style usually more than 5 mm long . . . 14. *C. hartwegii.*

32. Crown leaves truncate to subcordate with basal sinuses less than 1.5 cm deep; style less than 5 mm long 18. *C. oblongifolia.*
23. Crown leaves cuneate, truncate, decurrent, or shallowly cordate with basal sinuses less than 1 cm deep.
    33. Apices of anther thecae connate into a ring; crown leaves often decurrent at base . . . . 13. *C. fragilis.*
    33. Apices of anther thecae free, not connate; crown leaves cuneate, truncate, or shallowly cordate at base.
        34. Corolla tube 1–2 mm long; anther thecae 2–4 mm wide . . .4. *C. cajanumensis.*
        34. Corolla tube more than 2 mm long; anther thecae up to 2 mm wide.
            35. Corolla lobes glabrous abaxially.
                36. Crown leaves 10 cm or more wide, cuneate at base; fruits ellipsoid-fusiform, acute at apex; plants of Central America . . . . 10. *C. dolichocarpa.*
                36. Crown leaves less than 10 cm wide, truncate to subcordate at base; fruits globose, ovoid, or ellipsoidal, obtuse at apex; plants of South America . . . . .1. *C. acuminata.*
            35. Corolla lobes puberulent to pilose abaxially.
                37. Anther thecae 3–4 mm long; style ca. 5 mm long; inflorescence shorter than 5 cm . . . . 19. *C. ovum-fringillae.*
                37. Anther thecae 7 mm long or longer; style 6 mm long or longer; inflorescence longer than 5 cm . . . . 8. *C. divaricata.*

Synoptic List of Cyphomandra Characters

This character synopsis is included as an added convenience in identifying *Cyphomandra* specimens. Often either flowers or fruits are lacking in herbarium material, making use of the dichotomous key difficult.

The following is a list of distinctive (usually derived) character states with the species possessing them denoted by numbers corresponding to those in the taxonomic treatment. Numbers in parentheses indicate that the character state is uncommon in that species. Inclusion of a species within a category does not eliminate it from inclusion in another contrasting category; for example, a species varying in fruit pubescence may be listed under "fruits pubescent" and under "fruits glabrous." In many cases, diagnostic character states are listed but the alternatives are not; for instance, "style densely puberulent" is a characteristic of 25, *C. sciadostylis*, but no alternative "style glabrous" is given.

Plants found in seaside habitats of southeastern Brazil: 15, 28

Vegetative parts nearly glabrous: 1, 4, 7, (8), 9, 10, 11, 13, 14, 18, 26, (27), 28, (31), 32

Vegetative parts conspicuously and abundantly pilose with hairs more than 1 mm long: 4, 5, 6, (7), 8, 12, (14), 19, 20, 21, 22, 23, 25, (29), 30

Leaves pinnately compound: 9, 13, 15, 19, 20, 25

Leaves pinnately lobed: 7, 11, 14, 18, 22, 25, 28, 29, 30

At least some of the crown leaves deeply cordate at base with basal sinuses more than 1.5 cm deep: 3, 4, 5, 6, (7), 11, (12), 14, 16, 17, (22), 23, 24, 25, 26, 27, (29), 30, 32

Inflorescences branched, with three or more rachises: (1), 3, 4, 6, (9), 14, 16, 26, 27, (30), (32)

Calyx radius more than 6 mm long, the calyx measuring at least half the length of the corolla: 5, 9, (20)

Corolla pinkish or reddish: 1, 3, (6)

Corolla urceolate, divided up to half its length: 9, (20)

Corolla campanulate: 5, 7, 8, (9), 10, 15, 18, 19, 20, 21, 23, 25, 28, 30

Corolla stellate: 1, 2, 3, 4, 6, (8), 11, 12, 13, 14, 15, 16, 17, (18), 22, (23), 24, 26, 27, 28, 29, 31, 32

Corolla lobes densely tomentose abaxially with hairs almost completely obscuring the corolla tissue: 2, (9), 20

Corolla glabrous abaxially and adaxially: 1, 3, 4, 7, 9, 10, 14, (17), 18, (23), 24, (25), 29

Corolla margins ciliate with hairs 1 mm long or more: (4), (5), 8, 10, 11, 12, 13, (22), 27, 29, 31

Anther tips united into a ring: 13

Connective distally prolonged beyond apices of anther thecae: 15, 28, (32)

Style strongly dilated distally into a broad stigma 2 mm or more in diam.: 5, 7, 11, 15, 17, 23, 24, 25, 28, (30), 32

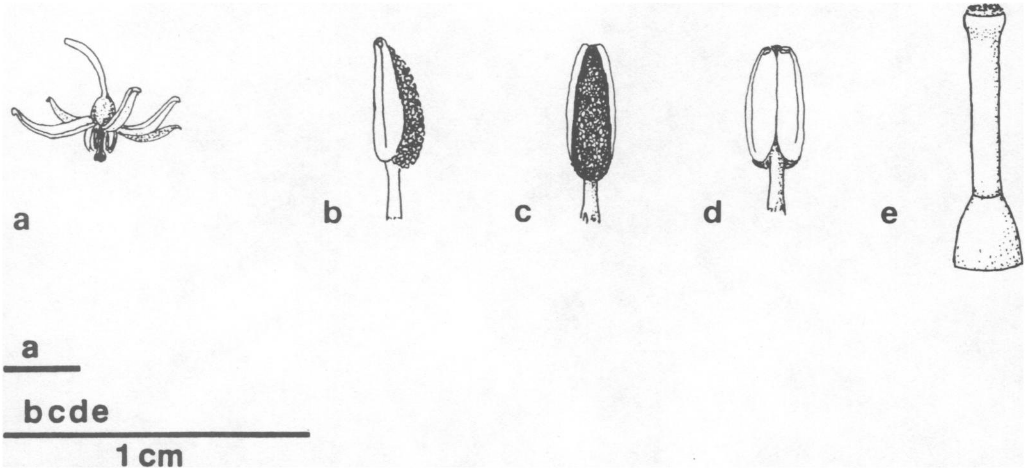


FIG. 13. *Cyphomandra acuminata.* **a.** Flower. **b–d.** Stamens (b, side view. c, abaxial view. d, adaxial view.) **e.** Gynoecium. All based on greenhouse material of *Bohs 2338.*

Style densely puberulent: 25
Fruits puberulent, pubescent, or pilose: 2, 4, 5, 6, 7, (8), 11, 12, 16, (17), 21, 22, 23, 24, 25, 27, 29, 31
Fruits glabrous: 1, 3, 4, 8, 9, 10, 11, 13, 14, 15?, 17, 18, 19, 20, 26, 28, 30, 31, 32
Fruits red or purple when ripe: 3
Fruits more than twice as long as wide and pointed at apex: 4, 5, 9, 10, 12, 22, 23, 25, 31
Fruits less than 3 cm long at maturity: 2, 6, (7), (9), 16, 19, (20), (21), (22), 23, 25, 28, 29
Seeds densely pilose with hairs 1–2 mm long: 1

1. Cyphomandra acuminata Rusby, Bull. Torrey Bot. Club **26:** 196. 1899. Type. Bolivia. La Paz: Yungas, elev. 6000 ft, 1885, *Rusby 2600* (lectotype, NY, here designated; isolectotype, NY). Figs. 13, 14.

Small *tree* 2–5 m tall. *Branches* glabrate. *Leaf blades* simple, unlobed, subcoriaceous, acuminate at apex, glabrous adaxially except for sparse glandular puberulence along veins, glabrous abaxially; petioles glabrescent or occasionally with a few eglandular hairs 2–3 mm long. *Trunk leaves* simple, unlobed, the blade ovate, 17–24 cm long, 8–13 cm wide, length:width ratio (1.5–) 2–2.5:1, the base truncate to cordate with basal lobes up to 2.5 cm long; petioles 6–13 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade ovate, 6–23 cm long, 3–9 cm wide, length:width ratio (1.5–)2–3(–5):1, the base truncate to subcordate with basal lobes less than 1 cm long; petioles 1.5–8 cm long. *Inflorescence* unbranched or forked (rarely further branched), 15–50-flowered, 4–22 cm long; peduncle 1–6 cm long; rachis 3–20 cm long; pedicels 10–15 mm long, in fruit 30–50 mm long, 2–5(–20) mm apart, articulated above the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachis, and pedicels glabrous. *Flower buds* ellipsoidal, obtuse to acute at apex. *Calyx* fleshy, glabrous to sparsely glandular-puberulent, the radius 4 mm, the lobes 1–2 mm long, 2–3 mm wide, deltate, apiculate. *Corolla* purple or reddish, subcoriaceous or fleshy, stellate, the radius ca. 10–15 mm, the tube 3–4 mm long, the lobes narrowly triangular, 8–14 mm long, 2–5 mm wide, glabrous abaxially and adaxially, the margin tomentose, the apex acute. *Anther thecae* pinkish or purplish, oblong, 3.5–4 mm long, 2 mm wide, the pores directed distally and laterally; connective purple or reddish brown, oblong, 4–6 mm long, 1.5–2 mm wide, abaxially slightly shorter than thecae at apex, slightly exceeding them at base, adaxially present or absent. *Ovary* glabrous; style glabrous, cylindrical, somewhat dilated apically, 5–7 mm long, 0.6–1.5 mm in diam., about equalling the stamens or exserted up to 2 mm beyond them; stigma truncate or subcapitate, 1–2 mm in diam. *Fruit* globose to ellipsoidal, obtuse or acute at apex, 2.5–4 cm long, 2–3 cm in diam., glabrous, yellow or orange when mature; mesocarp with stone cell aggregates;

FIG. 14. *Cyphomandra acuminata.* **A.** Flower. **B.** Fruits. Scale bars = 1 cm. From greenhouse material of *Bohs 2338.*

seeds 5–9 mm long, 4–7 mm wide, densely dark brown-pilose with hairs ca. 1–2 mm long.

Distribution (Fig. 15) and phenology. Cloud forest, 1500–2400 m elevation, western Bolivia in Department of La Paz and perhaps also southern Peru. Flowering specimens have been collected in May. Fruiting specimens have been collected in January, May, August, and October.

Additional specimens examined. BOLIVIA. La Paz: Prov. Murillo, Valle de Zongo, above Jarca at border of Rio Chuchulluni, 31 May 1980 (fl, fr), *Beck 3605* (ECON); Prov. Nor Yungas, S of Caranavi, ascending path to Illimani, 1500 m, 16 Jan 1984 (fr), *Beck 8782* (GH); grown in greenhouse at the University of Vermont as *Bohs 2338* (GH, VT) from seed of *Solomon & Escobar 12458*, collected in Prov. Nor Yungas, 8.7 km below Chuspipata on road to Yolosa, 2100 m, 5 Oct 1984; Prov. Nor Yungas, 8.7 km below Chuspipata on road to Yolosa, 16° 16'S, 67° 47'W, 2100 m, 23 Jan 1983 (fr), *Solomon 9313* (MO); Prov. Sud Yungas, Santa Barbara, 5000 ft, 30 Aug 1902 (fr), *R. S. Williams 1556* (BM, NY, US). Without other locality: *Bang 2281* (E, F, G, GH, MO, NY, US, WIS).

Cyphomandra acuminata appears to be most closely related to *C. betacea* and *C. uniloba*. Its pinkish, stellate corollas are similar to those of *C. betacea*, but it differs from the latter species by its nearly glabrous leaves and stems and very large seeds. Hybrids have been produced in the greenhouse between these two species (Bohs, 1991). *Cyphomandra acuminata* may be one of the closest wild relatives of *C. betacea*.

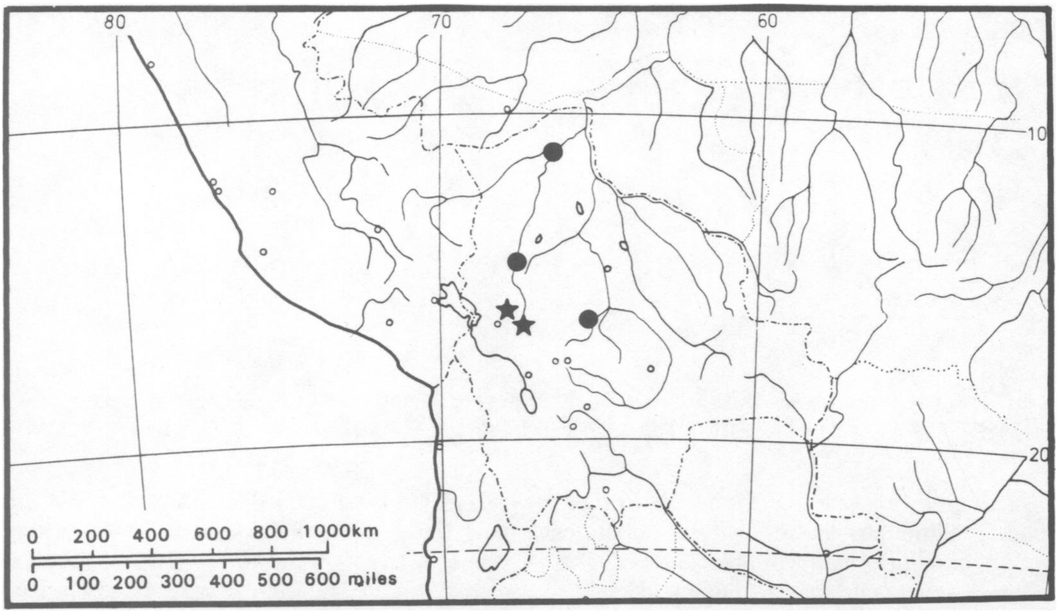


FIG. 15. Distribution of *C. acuminata* (stars) and *C. benensis* (dots).

Cyphomandra acuminata is often almost indistinguishable from *C. uniloba* on herbarium sheets. Both species occur in nearly the same areas of upland Bolivia. *Cyphomandra acuminata* is found above 1500 meters, whereas *C. uniloba* grows at lower elevations. Both species have ovate leaves with cordate bases and sparse, inconspicuous pubescence. However, the leaves of *C. uniloba* are consistently broader and have deeper basal lobes than those of *C. acuminata*. *Cyphomandra uniloba* generally retains some puberulence on the abaxial leaf surfaces and adaxial corolla surfaces, whereas *C. acuminata* is nearly glabrous at maturity. Living specimens of *C. acuminata* have darker and glossier leaves than *C. uniloba*. Fresh flowers of *C. acuminata* have purplish or reddish corollas, in contrast with the green, yellow green, or whitish corollas of *C. uniloba*. The connective and anther thecae have a reddish or purplish cast in *C. acuminata*, unlike the yellowish connective of *C. uniloba*. The stigma of *C. acuminata*, although slightly dilated at the apex of the style, is not as broad as that of *C. uniloba* and lacks the two conspicuous apical glands present in the latter species.

Cyphomandra acuminata can be distinguished from all other species in the genus by its unusually large and conspicuously pubescent seeds. Other species with large seeds such as *C. hartwegii*, *C. endopogon*, and *C. sibundoyensis* have whitish seed hairs generally less than 1 mm long.

The collection of *Plowman and Davis 4929* (F, GH) from Prov. Paucartambo, Dept. Cuzco, Peru may belong to *C. acuminata*. The fruits and seeds agree with those of *C. acuminata*, but the leaves have truncate or cuneate rather than cordate bases. Only fruits are present on this collection, and a decision to include it in *C. acuminata* or segregate it as a different taxon must await additional collections.

One of the two sheets of *Rusby 2600* at NY annotated by Rusby has been chosen as the lectotype. Unfortunately, neither sheet has fruits or flowers, though *Bang 2281*, cited by Rusby as a paratype, has both.

2. **Cyphomandra benensis** Britton, *in* Rusby, Bull. Torrey Bot. Club **26:** 196. 1899. Type. Bolivia. Junction of Rivers Beni and Madre de Dios, Aug 1886 (fl), *Rusby 840* (erroneously cited in the protologue as *Rusby 1840*) (lectotype, NY, here designated; isolectotypes, BM, E, G, GH, MO, NY, P, US, W, WIS).

Fig. 16.

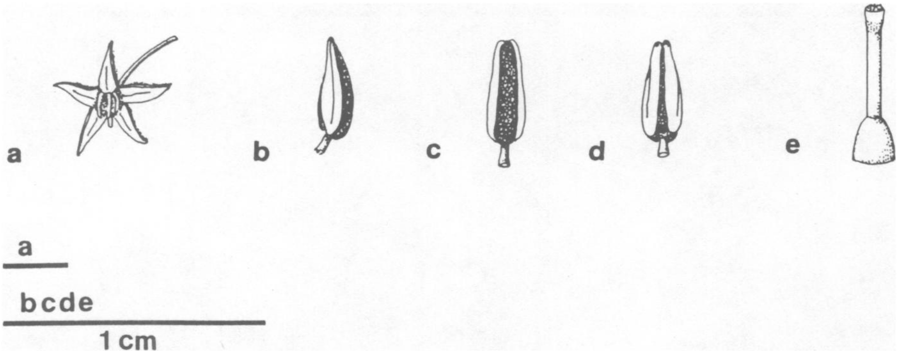


FIG. 16. *Cyphomandra benensis*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a–d based on *Rusby 840* (MO). e, based on *Cárdenas 5268* (L).

Small *tree* or *shrub* ca. 1 m tall. *Branches* densely glandular- and eglandular-puberulent (-pubescent). *Leaf blades* simple, unlobed, chartaceous, acute-acuminate at apex, sparsely to moderately puberulent-pubescent adaxially, moderately to densely puberulent abaxially; petioles densely puberulent. *Trunk leaves* not seen. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade ovate to elliptic, 2–9 cm long, 1–5 cm wide, length:width ratio 2:1, the base truncate to subcordate with basal lobes up to 0.5 cm long; petioles 0.5–2 cm long. *Inflorescence* unbranched, 20–30-flowered, 3–7 cm long; peduncle 0.5–1 cm long; rachis 3–6 cm long; pedicels 10–12 mm long, 10–15 mm long in fruit, 1–3 mm apart, articulated above the base, leaving pedicellar remnants 1 mm long. Peduncle, rachis, and pedicels densely glandular- and eglandular-puberulent. *Flower buds* ovoid, acute at apex. *Calyx* chartaceous, densely puberulent-pubescent, the radius 3–4 mm, the lobes 2–3 mm long, 1.5–2 mm wide, deltate, acute, apiculate. *Corolla* white, greenish, or violet, subcoriaceous, stellate, the radius ca. 10 mm, the tube 2–3 mm long, the lobes triangular, 5–8 mm long, 2–3 mm wide, densely tomentose abaxially, glabrous adaxially, the margin tomentose, the apex acute to acuminate. *Anther thecae* ovate, the color unknown, 3–4 mm long, 1.5 mm wide, the pores introrse and directed laterally; connective oblong, the color unknown, 3–4 long, 1 mm wide, abaxially about equal to thecae at apex, exceeding them by ca. 0.5 mm at base, adaxially present as a narrow swelling extending the entire length of the thecae. *Ovary* glabrous or finely puberulent; style cylindrical, glabrous, slightly dilated distally, 3–4 mm long, 0.5–1 mm in diam., exserted 1 mm beyond stamens; stigma truncate to capitate, 1 mm in diam. *Fruit* ovoid, acute at apex, 1–2.5 cm long, 0.7–2 cm in diam., densely glandular- and eglandular-pubescent, the color when ripe unknown; mesocarp with stone cell aggregates; seeds unknown.

Distribution (Fig. 15) and phenology. Restricted to valleys of Río Beni and Río Chapare in Bolivia, 300–700 m elevation. Flowering specimens have been collected in August, September, and February. Fruiting specimens have been collected in September and February.

Additional specimens examined. BOLIVIA. Beni: Vic. of Reyes, Rurrenabaque on the Río Beni, Oct-Dec 1930 (fl), *Fleischmann 140* (S); Rurrenabaque, 1000 ft, 6 Sep 1921 (fl, fr), *Rusby 800* (F, GH, K, NY, US). Cochabamba: Todos Santos, 700 m, Feb 1954 (fl, fr), *Cardenas 5268* (L).

This poorly known species is very similar to *C. pendula* but differs in its diminutive appearance, very short peduncles, stellate corollas, and pubescent fruits. The anther connective is prominent on the adaxial side of the anthers in *C. benensis*, but not in *C. pendula*. The range of *C. benensis* is sympatric with that of *C. pendula* in Bolivia.

Britton did not designate a holotype, so the lectotype has been chosen from among the elements he annotated.

3. **Cyphomandra betacea** (Cavanilles) Sendtner, Flora **28:** 172. Tab. 6, fig. 1–6. 1845; Anon., Bull. Misc. Inform. 2. 1887; J. D. Hook., Bot. Mag., ser. 3, **60**, Tab. 7682. 1899. Figs. 17, 18, 19.

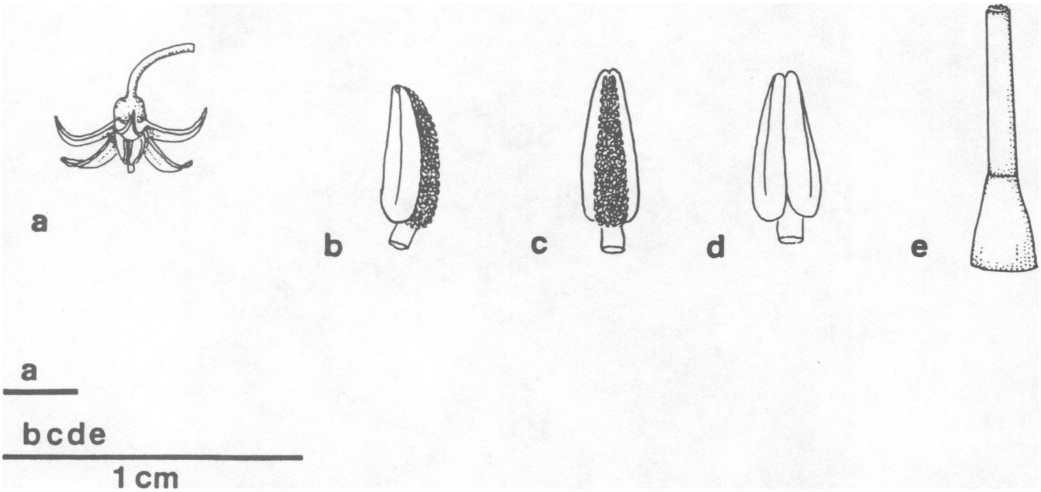


FIG. 17. *Cyphomandra betacea.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on greenhouse material of *Bohs 2274.*

Solanum betaceum Cavanilles, Anales Hist. Nat. **1:** 44. 1799; Cavanilles, Icones **6:** 15. Tab. 524. 1800. Type. Spain, cultivated in Madrid, 1798–1799, *Cavanilles s.n.* (lectotype, MA 308535, here designated; isolectotype, F [fragment]; possible isolectotypes, C ["Cavanilles misit e Madrid"], C ["h. Madrid 1801"], G ["Cavan. misit"]; photos of C specimen [F neg. 22930 F, GH, WIS]).

Solanum crassifolium Ortega, Nov. Pl. Descr. Dec. **9:** 117. 1800, non *Solanum crassifolium* Lam. (1794), nec Salisb. (1796). Type. Spain, cultivated in Madrid (No types extant?).

Pionandra betacea (Cavanilles) Miers, London J. Bot. **4:** 358. 1845.

Cyphomandra procera Wawra, Oesterreichische Bot. Zeitschr. **7:** 221. 1863. Type. Austria, cultivated in hort. Schönbrunn (type, W?).

Solanum insigne R. Lowe, Man. Fl. Madeira, **2(1):** 84. 1868; Lowe, J. Roy. Hort. Soc. N. S. **1(4):** 178. 1867. Type. Madeira, cultivated at Caminho do Torriao, Funchal, May 1871 (st), *Lowe s.n.* (lectotype, BM, here designated).

Cyphomandra crassifolia (Ortega) Kuntze, Revisio Gen. Plant. **3(2):** 220. 1898.

Cyphomandra crassifolia (Ortega) Macbride, Publ. Field Columbian Mus. Nat. Hist., Bot. Ser. **8:** 112. 1930.

Small *tree* 2–7 m tall. *Branches* densely puberulent. *Leaf blades* simple, unlobed, chartaceous, acuminate at apex, moderately puberulent adaxially, more densely so on veins, densely puberulent abaxially; petioles densely puberulent. *Trunk leaves* simple, unlobed, the blade ovate, 25–40 cm long, 20–35 cm wide, length:width ratio ca. 1–1.5:1, the base cordate to auriculate with basal lobes 3–6 cm long; petioles 15–25 cm long. *Crown leaves* (3-)4 per sympodial unit, simple, unlobed, the blade ovate, 7–20 cm long, 6–15 cm wide, length:width ratio ca. 1.5:1, the base cordate to auriculate with basal lobes 1.5–3 cm long; petioles 3–10 cm long. *Inflorescence* (unbranched or) branched, 10–50-flowered, 2.5–15 cm long; peduncle 1.5–9 cm long; rachises 2–8 cm long; pedicels 10–20 mm long, 15–50 mm long in fruit, 3–10 mm apart, articulated above the base, leaving pedicellar remnants 1–3 mm long; peduncle, rachises, and pedicels moderately to densely puberulent. *Flower buds* ellipsoidal to ovoid, obtuse to acuminate at apex. *Calyx* fleshy, sparsely to densely puberulent, the radius 3–5 mm, the lobes 1–2 mm long, 2–3 mm wide, obtuse to truncate, apiculate. *Corolla* pinkish white, subcoriaceous to fleshy, stellate, the radius 10–15 mm, the tube 2–3 mm long, the lobes narrowly triangular, 7–12 mm long, 2.5–4 mm wide, glabrous abaxially and adaxially, the margin tomentose, the apex acute. *Anther thecae* pale yellow, lanceolate, 5–6 mm long, 2–2.5 mm wide, the pores directed adaxially and distally; connective bright lemon-yellow, narrowly triangular, 4.5–5 mm long, 1–2 mm wide, abaxially slightly shorter than thecae at apex, equal to or

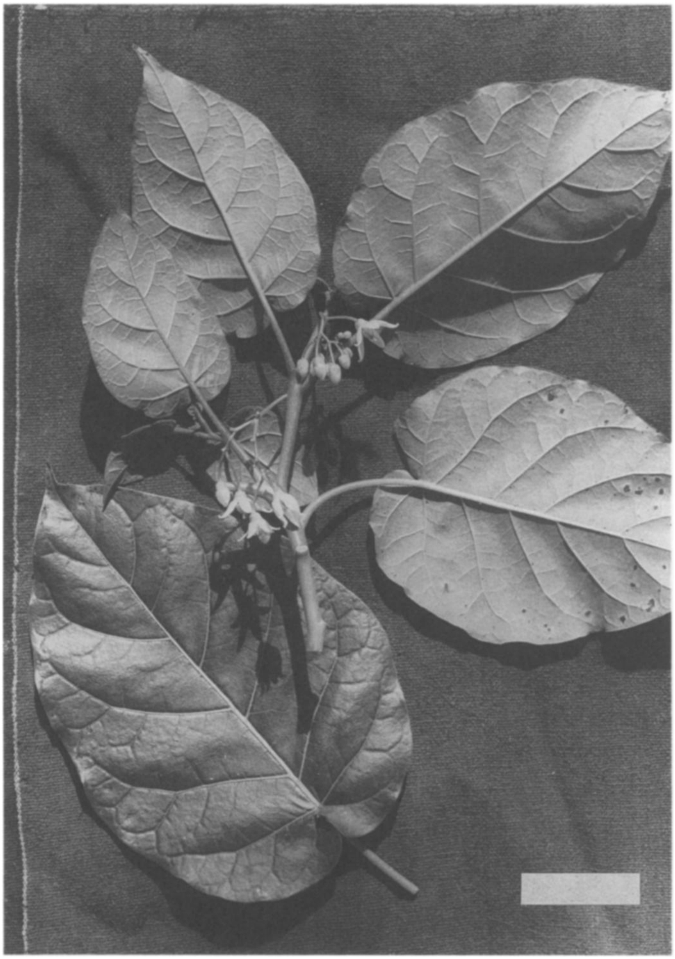


FIG. 18. *Cyphomandra betacea*. Scale bar = 5 cm. Photo from greenhouse material of *Bohs 2274*.

slightly shorter than them at base, adaxially absent. *Ovary* glabrous; style glabrous, cylindrical, not dilated distally, 5–6 mm long, 0.5–1 mm in diam., exserted 1–2.5 mm beyond stamens; stigma truncate, 0.5–1 mm in diam. *Fruit* ellipsoidal or ovoid, obtuse or acute at apex, 4–10 cm long, 3–5 cm in diam., glabrous, yellow to orange, red, or purple, often with darker longitudinal stripes; mesocarp with stone cell aggregates; seeds 3–4 mm long, 3.5–4 mm wide, densely pubescent.

Distribution (Fig. 20) and phenology. Cultivated throughout the Andes in subtropical climates, 1000–3000 m in elevation; probably introduced into Mexico, Central America, and the West Indies; in cultivation in Spain, Portugal, France, the United Kingdom, the Netherlands, Italy, the Canary Islands, Ghana, Ethiopia, Zaire, Uganda, Tanzania, Zimbabwe, South Africa, India, Ceylon, Bhutan, Sumatra, Java, New Guinea, New Caledonia, New Zealand, Australia, and the United States. Flowering and fruiting throughout the year.

Additional specimens examined. (New World citations only, excluding the United States.) **MEXICO.** CHIAPAS: Mun. Tenejapa, 6000 ft, 11 Aug 1965 (fl, fr), *Breedlove 11695* (LL, US); Fraylesca, near Siltepec, 1600 m, 6 Mar 1945 (fl, fr), *Matuda 5195* (F, LL); Mt. Ovando, Escuintla, 14 Nov 1945 (fl, fr), *Matuda 16215* (US); same locality, 5 May 1948 (fl), *Matuda 17746* (F). GUANAJUATO: without locality, May 1897 (fl), *Dugès*

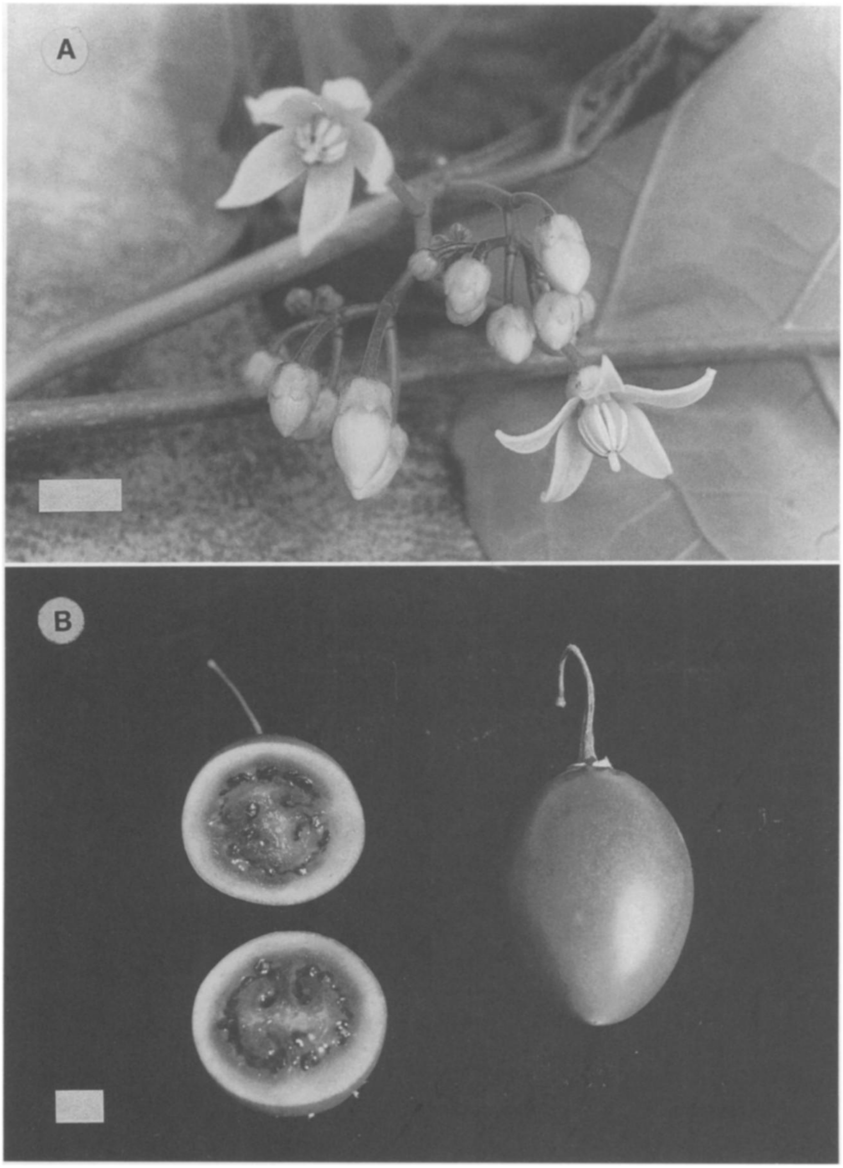


FIG. 19. *Cyphomandra betacea.* **A.** Inflorescence. From greenhouse material of *Bohs 2274.* **B.** Fruits. Fruits imported from New Zealand; purchased in grocery store, Burlington, VT. Scale bars = 1 cm.

393A (GH). **Jalisco:** Guadalajara, Sep 1886 (fl, fr), *Palmer 636* (GH). **Veracruz:** Pedregal Esquilon, near Jilotepec, 10 km N of Xalapa, cultivated, 1300 m, 31 Dec 1981 (fr), *Bohs et al. 1687* (GH); Xalapa, Cerro de Macuiltépetl, in city of Xalapa, 9 Jun 1976 (fl, fr), *Calzada 2411* (F, LL, NY); Coatepec, Congregación La Pitaya, 19° 30'N, 96° 56'W, 1250 m, 16 Nov 1977 (fr), *Castillo et al. 216* (F); near bridge over Río Jamapa on Hwy 125 from Coscomatepec to Huatusco ca. 4 mi NE of Coscomatepec, 300 m, 23 Aug 1977 (fr), *Croat 43967* (MO); Jilotepec, road Xalapa-Naolinco, 1400 m, 2 Mar 1976 (fr), *Hernández et al. 49* (F, K, MO); 6 km ENE of Naolinco on the road to Misantla (Hwy 136), 19° 40'N, 96° 50'W, 1750 m, 5 Jan 1982 (st), *Judziewicz 3127* (WIS); Campo Experimental Centro de Ensenanza e Investigación Fruticola "Las Trancas", 3.5 km SE of Xalapa on road to

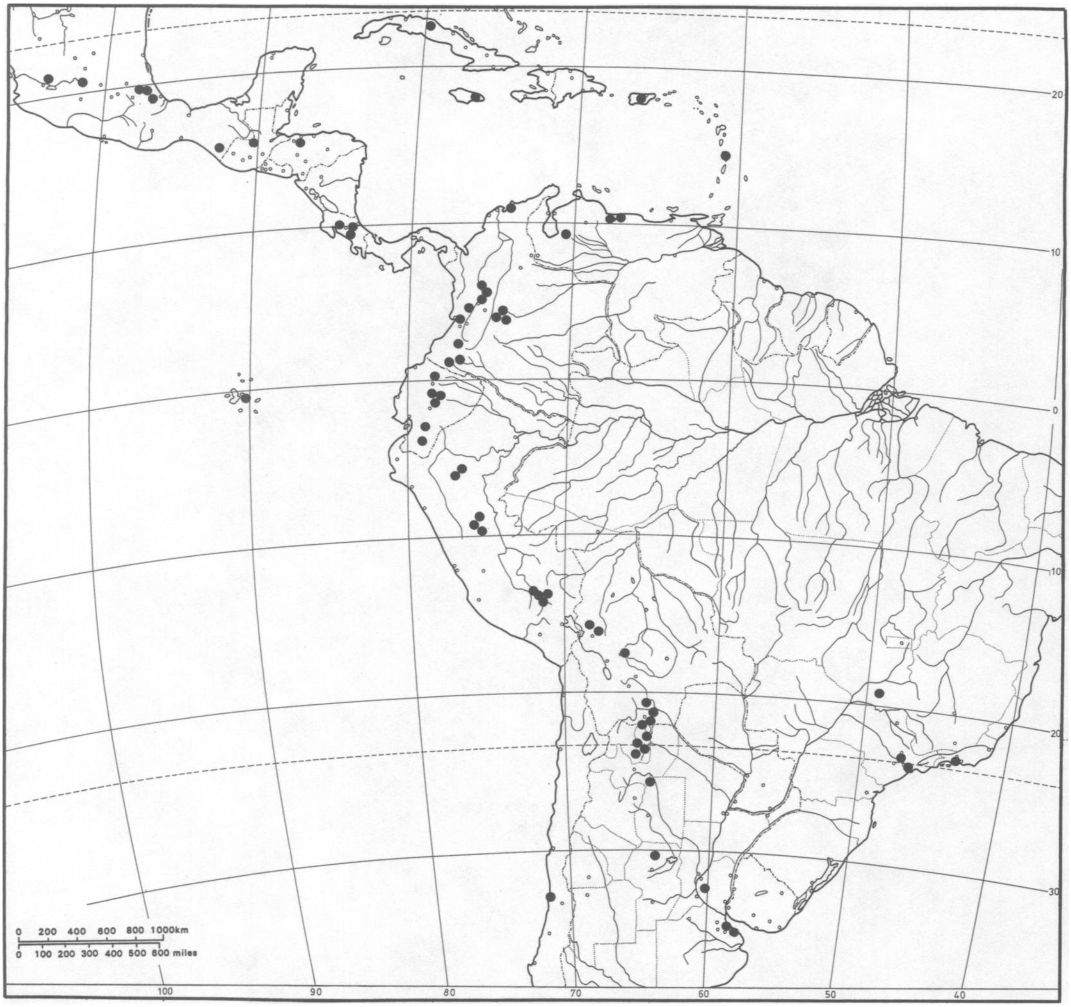


FIG. 20. Distribution of *C. betacea* in the Neotropics.

Veracruz, semicultivated in coffee plantations, 1200 m, 14 Dec 1977 (fl, fr), *León Arteta s.n.* (F); vic. "La Calavera," 10 km N of Altotonga, on road to Tlapacoyan, possibly planted, 19° 51'N, 97° 13'W, 1350 m, 28 Jun 1980 (fr), *Nee & Hansen 18648* (BH, F); Jardín Botánico Fco. Javier Clavijero, 2 km S of Xalapa along old road to Coatepec, probably persisiting from cultivation or naturalized, 19° 30'N, 96° 56'W, 1300 m, 20 Nov 1981 (fl, fr), *Nee 23344* (BH, F, LL, MA, WIS); El Esquilón, Jilotepec, 1260 m, 8 Jul 1976 (fl, fr), *Zola 469* (F).

GUATEMALA. Alta Verapaz: between San Pedro Carchá and Sanoyoú, 1300 m, 11 May 1963 (fl), *Molina 12046* (F, NY, US); vic. of Cobán, cultivated, ca. 1300 m, 23 Mar–19 Apr 1941 (fr), *Standley 90903* (F).

HONDURAS. Morazán: Zamorano, 800 m, Feb 1945 (fl), *Valerio 2270* (F); vicinity of El Zamorano, cultivated, 780–900 m, 17 Feb–8 Mar 1947 (fr), *Standley 3884* (F).

COSTA RICA. Cartago: Turrialba, cultivated, 620 m, 2 Feb 1952 (fl, fr), *Carpenter 488* (US); Instituto Interamericano de Ciencias Agrícolas, 600 m, 24 Feb 1958 (fl), *Córdoba 385* (MO); same locality, 18 Nov 1950 (st), *León 2855* (CR); Las Cóncavas, cultivated, 1400 m, 27 Feb 1924 (fl, fr), *Standley 35995* (US). **Puntarenas:** 2 km SE of Monteverde on Pacific watershed, cultivated field, 10° 18'N, 84° 48'W, 1500–1550 m, 18–21 Mar 1973 (fl), *Gentry & Burger 2741* (F). **San José:** road from San Antonio-Escazú to Pico Blanco, 31 Aug 1983 (fr), *Gómez 20734* (GH); San José, Mar 1936 (fl, fr), *Umaña 15* (F);

Cordillera de Talamanca, ca. 25 km N of San Isidro de El General along PanAm Hwy., 3200 m, 29 Jan 1965 (fr), *L. O. Williams et al. 28621* (F). **Without Province:** San Ramón de Tres Ríos, cultivated, 1500 m, Feb 1972 (st), *Gómez s.n.* (CR).

CUBA. Prov. Santa Clara: cultivated in Harvard Botanic Garden, 19 Apr 1929 (fl), *Jack 7291* (NY, US); without locality, 1860–1864, *Wright s.n.* (GH, GOET).

WINDWARD ISLANDS. Martinique: Camp Balata and on Morne-Rouge, cultivated, Aug 1900 (fl), *Duss 4429* (NY).

JAMAICA. Cinchona, 5000 ft, 18 Feb 1900 (fl), *Clute 220* (B, K, E, MO, US); Mandeville, June 1904 (fl), *Collins 102* (US); Port Royal Hills and Blue Mountain districts, above 2500 ft, no date, *Harris 484* (K); Gordon Town, Govt. Cinchona Plantation, *Hart s.n.* (NY, US); in Beaham's, Montague, Apr 1903 (fl), *Prior s.n.* (K).

PUERTO RICO. Barros, 25 Apr 1928 (fl), *Barrus 74* (BH); near Barranquitas, 26 Apr 1926 (fl, fr), *Gleason & Cook Y3* (NY); Adjuntas, cultivated, 29 Mar 1886 (fl, fr), *Sintenis 4058* (G, GH, GOET, HBG, LD, M, NY, S, US).

COLOMBIA. Antioquia: Medellín, cultivated, 1500 m, 8 Oct 1930 (fl, fr), *Archer & Mesa 838* (US); Río Negro, La Granja, vic. Medellín, cultivated, 1650 m, 16 Feb 1946 (fr), *Hodge 6713* (ECON, F, NY). **Boyacá:** Duitama, 2500 m, 18 Mar 1976 (fl, fr), *Quiñones & Barrero s.n.* (COL). **Caldas:** vic. Manizales, cultivated, 2150–2250 m, no date, *Duque Jaramillo 2672-A* (NY). **Cauca:** near San Alfonso, 2000 m, 8 Sep 1944 (fl), *Core 1184* (US); without locality, 800–2000 m, *Lehmann 6433* (K); near El Tambo, cultivated, 1700 m, 19 Oct 1939 (fl), *von Sneidern 2612* (S). **Cundinamarca:** Bogotá, cultivated, D.E., Jul 1980 (fl, fr), *Cadena & Peña s.n.* (COL); Mun. Arbelaez, Vereda Santa Barbara, sector La Hoya, km 2 on road to La Hoya, cultivated, 1700 m, 28 May 1980 (fl), *Devia & Moreno 70* (COL); Cachipay, railroad line to Giradot, 1700 m, Nov 1943 (fl), *García-Barriga 10896* (COL); Fusagasugá, Vereda Bóchicha, Finca Cafetera "Lolandia," 1780–1900 m, 12 Jul 1981 (fl, fr), *García-Barriga 21286* (COL); same locality, 1700–1800 m, 25 Apr 1982 (fl), *García-Barriga 21339* (COL); Bogotá, cultivated, 13 Feb 1854 (fl), *Holton s.n.* (K, NY). **Magdalena:** vic. San Andrés, cultivated, 1300 m, 17 Jan 1959 (fr), *Romero-Castañeda 6948* (COL); San Andrés, Mun. de Ciénaga, 1300–1500 m, 22 May 1961 (fl, fr), *Romero-Castañeda 9007* (COL). **Nariño:** region of Pedregal, highway between Pasto and Túquerres, S of Yacuanquer, 2 Jun 1946 (fl), *Schultes & Villarreal 7862* (ECON, F, US). **Norte de Santander:** Ocaña, cultivated, 4000–5500 ft, 3 Jan 1879 (fl), *Kalbreyer 1019* (K). **Putumayo:** Valle de Sibundoy, cultivated, 6 Aug 1981 (fl, fr), *Bohs 1599* (GH); 3 km S of Sibundoy, cultivated, ca. 2200 m, 14 Apr 1963 (fl, fr), *Bristol 777* (ECON); vic. Sibundoy, 2250 m, 18 Feb 1942 (fr), *Schultes 3258* (GH). **Valle:** valley of Río Cali, left slope of Río Pichindé, El Cairo, 2100–2180 m, 6 Aug 1946 (fl), *Cuatrecasas 21969* (F, US); Mun. Tuluá, Corregimiento de Barragán, finca La Florida, 2900 m, 18 Sep 1984 (fl, fr), *Devia 641* (MO); Pichindé, cultivated, 1500 m, no date, *Duque Jaramillo 1707* (F). **Without Department:** without locality, cultivated, *Goudot 101* (K).

VENEZUELA. Distrito Federal: vic. Caracas, cultivated, Oct 1916, *Rose 21634* (fruit), *21797* (ECON, US). **Mérida:** La Mueuy, 17 May 1953 (fl), *Bernardi 548* (NY); Quebrada de la Virgen, between Tabay and Cacute, 1600 m, 3 Apr 1967 (fl, fr), *Skog 1262* (US). **Miranda:** El Cedral de las Ajuntas, near Los Teques, 1000–1800 m, 26–28 Apr 1913 (fl), *Pittier 6097* (US). **Without State:** Punta de lanza, Apr 1939 (fl), *Lasser 52* (F); La Trinidad, El Avila, 19 May 1938 (fl), *Ll. Williams 10105* (F).

ECUADOR. Azuay: Chullabamba, 10 km N of Cuenca in the Cuenca Valley near the river, estate of Marcelo Jaramillo, cultivated, 2350 m, 10 Oct 1981 (fr), *Dodson & Dodson 11794* (MO). **Galapagos Islands:** Isla Santa Cruz (Indefatigable Island), 1 km above Bella Vista, toward Mt. Crocker, cultivated in orchard at Horneman's Ranch, 425 m, 19 Feb 1967 (fr), *Wiggins & Porter 681* (GH, US). **Loja:** cultivated at Renaldo Espinosa Gardens, University of Loja, 2300 m, 23 Jul 1977 (fl), *Hart 956* (A, US); in gardens around Loja, *Lehmann 7818* (F, K). **Pichincha:** Nanegalito, 78° 41'W, 0° 8'N, ca. 1400 m, 8 Nov 1981 (st), *Filskov et al. 37010* (AAU). **Tungurahua:** vic. Ambato and Huachi, cultivated, 2650–2700 m, 29 Oct 1944 (fl, fr), *Acosta Solís 8856* (F); Ambato, cultivated, 2600 m, 15 Dec 1944 (fl), *Acosta Solís 9482* (F); Baños, cultivated just S of town, 9 Aug 1983 (fl, fr), *Bohs 2192* (GH, QCA); vic. Ambato, 24–26 Aug 1918 (fr), *Rose s.n.* (US); village of Pillaro (13 km from the Pan American Hwy.), cultivated, 78° 33'W, 1° 10'S, 2900 m, 24 Oct 1981 (fl), *Sperling 5298* (GH).

PERU. Amazonas: Prov. Chachapoyas, Ubilón, between Chachapoyas and Leimebamba, km 57, 1900–2000 m, 12 Apr 1950 (fl), *Ferreyra 7109* (MO, US, USM, WIS); Suyobamba, 3 km NE of Pedro Ruíz Gallo, semicultivated, 77° 58'W, 5° 55'S, 1400 m, 6 Feb 1988 (fl, fr), *A. Gentry et al. 61315* (NY); Bongara, ca. 7 km above Pedro Ruíz on road to Pomacochas, 5° 58'S, 77° 57'W, ca. 1500 m, 3 Jul 1984 (fl), *Knapp & Mallet 6560* (BH, MO, US); same locality, 5° 55'S, 77° 53'W, 1500–1600 m, 3 Jun 1986 (fr), *Knapp & Alcorn 7558* (NY). **Cuzco:** Ollantaytambo, 3000 m, 16 May 1915 (st), *Cook & Gilbert 770* (NY, US); Torontoy, Urubamba Valley, 2400 m, 5 Jun 1915 (st), *Cook & Gilbert 1101* (US); Prov. Urubamba, Machu Picchu, cultivated, 2400 m, 18 Nov 1947 (fl, fr), *Ferreyra 2708* (US, USM); Prov. La Convención, 2 km from Quillabamba, 1080 m, 12 Jul 1963 (st), *Gade s.n.* (WIS); Paucartambo Valley, 3000 m, Jul 1930 (fl, fr), *Herrera 2984* (A, US); Ruinas Machu Picchu, 80 km WNW of Cuzco, base of Huayna Picchu, cultivated, ca. 2500 m, 3 Jan 1983 (fl), *Iltis et al. 1068* (F, WIS); Prov. La Convención, Quillabamba, Mandor, 12° 53'30"S, 72° 44'W, 1200 m, 16 Oct 1987 (fl), *Núñez et al. 8257* (NY); near La Máquina (Machu Picchu station), 2050 m, 25 Sep 1936 (fl), *West 8044* (GH, MO). **Huánuco:** Tingo María, 3 Aug 1964 (fr), *Dwyer 6257* (MO); Huacachi, station near Muña, cultivated, ca. 6500 ft, 20 May–1 Jun 1923 (fl), *Macbride 3875* (F, G, US); Puente Durand, N of Huánuco, Valley of Rio Chinchao, 1300 m, 4 Nov 1938 (fl, fr), *Stork & Horton 9595* (F). **Pasco:** Oxapampa, 10° 35'S, 75° 35'W, 1850 m, 10 Mar 1984 (fr), *Knapp et al. 6314* (BH, US).

BRAZIL. Minas Gerais: Mun. Tupaciguara, 5 Sep 1976 (fl, fr), *Andrade 3357* (US). **Rio de Janeiro:** Petrópolis, in Cachambú, Aug–Sep 1876 (fl), *Glaziou*

7789 (G, P, K). **São Paulo:** Campinas, Oct 1939 (fl), *Gomara 5130* (SP); São Paulo, cultivated, 4 Feb 1918 (fl, fr), *Hoehne s.n.* (SP, US); Ypiranga, cultivated, Oct 1908 (fl), *Luederwaldt s.n.* (SP).

BOLIVIA. Cochabamba: Cochabamba, purchased in market, 2550 m, 14 Nov 1984 (fr), *Nee 30359* (NY); Prov. Chapare, Incachaca, 2300 m, 17 Feb 1929 (fl), *J. Steinbach 9166* (BM, GH, NY, S). **La Paz:** Sirupaya, 2100 m, Nov 1906 (fl), *Buchtien 340* (US); Coroico, grounds of hotel, 21 May 1980 (fl), *D'Arcy & Bejarano 13870* (MO); Prov. Nor Yungas, Sirupaya, cultivated, 3000 m, 15 Apr 1939 (fl, fr), *Eyerdam 25355* (F, K); Sorata, cultivated, Nov 1919 (fl), *Gunther 5851* (US); Prov. Larecaja, village of Sorata, cultivated, 68° 40'W, 15° 45'S, 2750 m, 8 Dec 1981 (fl), *Sperling & King 5406* (GH); same locality, cultivated in garden of Residencial Sorata, 8 Dec 1981 (fl), *Sperling & King 5415* (GH); Coroico, cultivated, 1851, *Weddell s.n.* (P). **Tarija:** Prov. O'Connor, Entre Ríos 8 km toward Villamontes, 1180 m, 23 Oct 1983 (fl), *Beck & Liberman 9675* (GH); 3 km S of Entre Ríos, 21° 33'S, 64° 12'W, 29 Apr 1983 (fl, fr), *Krapovickas & Schinini 38854* (C, CTES, WIS); Cuesta de San Simón, 21° 25'S, 64° 05'W, 30 Apr 1983 (fl, fr), *Krapovickas & Schinini 39059* (CTES); Prov. Arce, vic. comunidad Sidras, 22° 14'S, 64° 32'W, 900 m, 6 May 1983 (fr), *Solomon 10538* (MO); Prov. O'Connor, 15.8 km E of Narvaez on road to Entre Ríos (12.5 km W of Entre Ríos), 21° 28'S, 64° 12'W, 900 m, 4 Oct 1983 (fl), *Solomon 11050* (GH); Prov. Arce, vic. Sidras (5.5 km N of Emborozú), 22° 12'S, 64° 32'W, 950 m, 9–11 Oct 1983 (fl), *Solomon 11097* (GH); Valley of the Río Chillaguatas, below Rancho Nogalar on trail between Sidaras and Tariquia, 22° 05'S, 64° 25'W, 1100 m, 14–16 Oct 1983 (fl), *Solomon 11227* (GH). **Without Department:** Calopampa, 11 Jul 1894 (fl), *Bang 2337* (E, G, M, NY, W, Z) (a mixed collection; the other element is *C. uniloba* Rusby); *Bang s.n.* (NY).

CHILE. Valparaiso, cultivated, 1829, *Bertero 1325* (G, GH, MO, P).

ARGENTINA. Buenos Aires: La Plata, cultivated, 10 Nov 1940 (fl, fr), *Rodrigo 2750* (LP); Buenos Aires, cultivated, ?1867, *Tweedie s.n.* (K). **Córdoba:** Huerta Grande, 19 Dec 1899 (fl, fr), *Stuckert 6785* (G). **Entre Ríos:** Diamante, cultivated, 20 Dec 1963 (fl), *Gamerro 1337* (LP). **Jujuy:** Dept. Ledesma, road to Valle Grande, 18 Oct 1964 (fl), *Cabrera & Fabris 16014* (SI); Dept. Valle Grande, Abra de Cañas to Valle Grande, between Río Jordán and San Francisco, 14 Sep 1976 (fl), *Cabrera et al. 27868* (SI); Dept. Ledesma, Abra de Cañas, road to Valle Grande, 21 Oct 1979 (fl), *Cabrera et al. 30923* (SI); Dept. Valle Grande, Mesada de las Colmenas, S of Río Jordán, 17 Dec 1962 (fl, fr), *Fabris 3411* (CTES); Dept. Capital, road to Tilquiza, 25 Nov 1975 (fl), *Kiesling et al. 1155* (SI). **Salta:** Urundel, 25 Oct 1948 (fl), *Fries s.n.* (S); Quebrada del Diablo, NW of Urundel, 300–400 m, 25 Oct 1948 (fl), *Killip 39617* (US); Dept. Orán, El Candado Grande, finca of Espuchi, 24 km from P. Río Bermejo, 22 Oct 1968 (fr), *Legname & Cuezzo 5872C* (GH, TEX); Dept. Santa Victoria, 5 km before Sonda al Lipeo, 1500 m, 2 Nov 1971 (fl, fr), *Marmol et al. 8856C* (GH); same locality, before Lipeo, 1700 m, 16 Sep 1972 (fl), *Marmol et al. 9242* (CTES); Dept. Orán, Quebrada del Diablo, 1948, *Sparre s.n.* (C). **Santiago del Estero:** Dept. C. Pellegrini, Estancia El Remate, 500 m, 21 Feb 1928 (fl, fr), *Venturi 5954* (A, US). **Tucumán:** Quebrada de Las Pavas, 24 Mar 1953 (fr), *Schulz 8421* (CTES); same locality, cultivated, Dec 1972 (fl), *Schulz 18402* (CTES). **Without Province:** San Andres near Orán, 17–24 Sep 1873 (fl), *Lorentz & Hieronymus 251* (G, GOET, NY).

Local names and uses. *Cyphomandra betacea* is most commonly called "tomate de árbol" (Spanish), "tomate de árvore" (Portuguese), and "tree tomato" (English). In New Zealand, the fruits are known as "tamarillos." For a more complete list of vernacular names of this species, see Bohs (1989c).

The fruits are very popular in Latin America, where they are eaten raw and cooked in various dishes. The leaves are used medicinally as a poultice against sore throat in Ecuador (*Filskov et al. 37010*). For a more information on the uses of this species, see Bohs (1989c).

Cyphomandra betacea can be distinguished from all other members of the genus by its white or pinkish, subcoriaceous corollas, its cylindrical styles and unexpanded stigmas, and its large, orange or reddish fruits. It is most closely related to *C. acuminata* and *C. uniloba* and can form hybrids with both of these species in greenhouse crosses (Bohs, 1991). It differs from both by having chartaceous leaf blades with deep basal lobes, abundant puberulence, and reddish fruits. *Cyphomandra betacea* superficially resembles *C. hypomalaca*; both have similar leaves, inflorescences, and gynoecia. However, *C. hypomalaca* most likely belongs to the *Cyphomandropsis* alliance and therefore is not a close relative of *C. betacea*. *Cyphomandra hypomalaca* has denser and longer indumentum and small, globose, pubescent fruits.

The tree tomato is grown worldwide in subtropical areas for its edible fruits, but the natural range and place of origin of this species are still unknown. Herbarium specimens exist from nearly all countries in the Western Hemisphere, but many of these collections are from cultivated plants, and herbarium records do not reveal reliably whether a collection is wild, cultivated, or naturalized. Indeed, *C. betacea* has often been described as being known only from cultivation. According to several recent reports (Bohs, 1989c; Brücher, 1968, 1977; J. Solomon, pers. comm.; E. Zardini, pers. comm.), wild populations of *C. betacea* can be found in southern

Bolivia and adjacent areas of northwestern Argentina in the floristic province known as "bosque Tucumano-Boliviana" (Cabrera, 1976).

Herbarium specimens from these areas show no morphological differences from those of other regions of Latin America and the Old World. Field studies may distinguish wild from cultivated populations with characters not preserved in herbarium material, e.g., fruit characters or differences in breeding systems. The apparent close relationship of *C. betacea* with *C. acuminata* and *C. uniloba*, both from Bolivia, is additional evidence for a Bolivian origin of *C. betacea.*

The fruits of *C. betacea* are becoming an important item in international commerce, thanks to the commercial cultivation and horticultural improvement undertaken in New Zealand. The recent development of *C. betacea* as a specialty fruit crop has given new importance to the search for wild populations and place of origin. Germplasm collection from wild populations should be a high priority.

Considerable confusion has existed with regard to the correct name of the cultivated tree tomato. Cavanilles was the first to describe this taxon, as *Solanum betaceum*, from a specimen growing at the Real Jardín Botánico in Madrid. His first description appears in 1799 in Volume 1 of the *Anales de Historia Natural*; a later description and plate were published in 1801 in Cavanilles' *Icones.* In 1800 Ortega described *Solanum crassifolium* from a cultivated specimen in Madrid. This name is synonymous with Cavanilles' species, and is a later homonym of *Solanum crassifolium* Lam. (1794) and *Solanum crassifolium* Salisb. (1796).

Difficulties arose when later authors transferred the species to *Cyphomandra.* Sendtner (1845) properly used the name *Cyphomandra betacea*, but Kuntze, ignoring Cavanilles' name, erected the combination *Cyphomandra crassifolia* (Ort.) Kuntze in 1898. Adding to the confusion, Macbride in 1930, stating that the tree tomato "has never been christened properly," made the combination *C. crassifolia* (Ort.) Macbride. His citation incorrectly lists the date of Ortega's ninth decade as 1797 and omits Cavanilles' earliest publication of the name *S. betaceum* in the *Anales de Historia Natural.* Sandwith (1938) clarified this situation, concluding that the rightful name of the tree tomato is indeed *C. betacea* (Cav.) Sendtn. Macbride, however, persisted in the use of the name *C. crassifolia* (Ort.) Kuntze in his *Flora of Peru* (Macbride, 1962) and confusion has prevailed. The name *C. crassifolia* should be retired once and for all, and the tree tomato must be called *C. betacea* (Cav.) Sendtner.

The sheet annotated as *Solanum betaceum* by Cavanilles at MA has been designated as the lectotype of this name; this sheet also includes Cavanilles' notes and drawings he used when formulating his description. Several other specimens at C and G were apparently sent by Cavanilles from Madrid and may be isolectotypes.

No type specimens have yet been located for *Solanum crassifolium* Ortega. This taxon, like *S. betaceum* Cav., was described from a plant cultivated at Madrid. Perhaps no type specimens were ever preserved.

Lowe first mentioned *Solanum insigne* in 1867 from a plant cultivated on the island of Madeira. However, Lowe used this name provisionally in 1867, and thus it was not validly published (Art. 34 of ICBN; Greuter et al., 1988) until 1868 when he provided a description and Latin diagnosis. Lowe did not cite a type specimen, but a specimen at BM marked "*Solanum insigne* Lowe" collected on Madeira in 1871 has been designated as the lectotype.

I have not been able to positively locate the type of *C. procera* Wawra. There is a specimen at W collected by Drs. Wawra and Maly with the annotation "*Cyphomandra betacea* Sendt., Schönbr." This collection belongs to *C. betacea* and has a sinuate and lobed leaf as noted in Wawra's protologue, probably as the result of a viral infection. However, nowhere does this or any other sheet examined have the annotation *C. procera.* Regardless of the location of the type, Wawra's description fits *C. betacea* in all particulars and his *C. procera* is here regarded as a synonym.

4. Cyphomandra cajanumensis (HBK) Walpers, Repert. Bot. Syst. **6:** 579. 1847; Dunal *in* DC. Prodr. **13(1):** 401. 1852. Figs. 21, 22.

Solanum cajanumense Humboldt, Bonpland, & Kunth, Nov. Gen. Sp. **3:** 37 (47 in other copies). 1818. Type. Ecuador. In sylvis Cajanumae et Urutusingae, prope Loxa Nova-Granatensium, 6240 ft, *Humboldt & Bonp-*

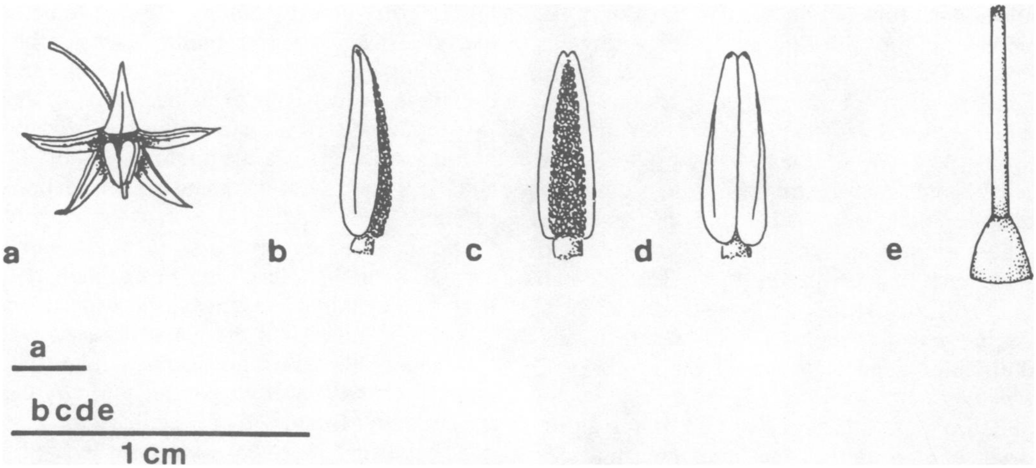


FIG. 21. *Cyphomandra cajanumensis.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Vivar s.n.* (GH).

land 3410 (lectotype, P-HBK, here designated [F neg. 39020 US, WIS]; isolectotype, P).

Pionandra cajanumensis (HBK) Miers, London J. Bot. **4:** 363. 1845.

Cyphomandra casana Child, Feddes Repert. **97:** 143. 1986. Type. Originally from Ecuador, near Loja, estancia of Mrs. J. H. Hoffmann, ca. 3000 m, 1978; grown at Whangarei, Northland, New Zealand, 1982, *Endt s.n.* (holotype, K, n.v.).

Small *tree* 1–5 m tall. *Branches* glabrous to densely puberulent and often also pilose with curled hairs 2–3 mm long. *Leaf blades* simple, unlobed, subcoriaceous, acute to acuminate at apex, glabrous to densely puberulent or moderately pilose adaxially and adaxially, especially on veins, sometimes densely tomentose to villous adaxially and abaxially; petioles glabrous to densely puberulent or pilose with curled eglandular hairs ca. 2 mm long. *Trunk leaves* simple, unlobed, the blade ovate to elliptic, 26–40 cm long, 18–40 cm wide, length:width ratio ca. 1–1.5:1, the base truncate to cordate with basal lobes 0–10 cm long; petioles 10–27 cm long. *Crown leaves* 3 per sympodial unit, simple, unlobed, the blade ovate to elliptic, 5–25 cm long, 3.5–18 cm wide, length:width ratio ca. 1–2:1, the base truncate to cordate with basal lobes 0–2 cm long; petioles 2.5–11 cm long. *Inflorescence* simple or branched, 10–30-flowered, 3–15 cm long; peduncle 2.5–6 cm long; rachises 1–12 cm long; pedicels 10–20 mm long, 20–50 mm long and very corky and woody in fruit, 1–10 mm apart, articulated at or near the base, leaving nearly sessile scars or pedicellar remnants 1–2 mm long; peduncle, rachises, and pedicels glabrous to densely puberulent or pilose with eglandular hairs 2–3 mm long. *Flower buds* ovoid, acute at apex. *Calyx* fleshy, glabrate to sparsely pilose, the radius 3–5 mm, the lobes 1–3 mm long, 2.5–3 mm wide, deltate to oblong, obtuse, apiculate. *Corolla* purple to greenish or whitish, subcoriaceous, stellate, the radius 8–19 mm, the tube 1–2 mm long, the lobes narrowly triangular, ca. 7–17 mm long, 3–5 mm wide, glabrous to sparsely pubescent or tomentose abaxially, especially toward apices, glabrous adaxially, the margin tomentose (rarely ciliate), the apex acute-acuminate. *Anther thecae* violet, lanceolate, 5–8 mm long, 2–4 mm wide at base, the pores directed adaxially and distally; connective yellow, orange, or brownish, lanceolate, 5–8 mm long, 1–4 mm wide, abaxially slightly shorter than thecae at apex, about equal to or slightly exceeding them at base, adaxially present as a small swelling at base or absent. *Ovary* glabrous or glandular-puberulent; style glabrous or sparsely puberulent, cylindrical, not dilated apically, 6–10 mm long, 0.5–1 mm in diam., exserted 1–2 mm beyond stamens; stigma truncate, 0.5–1 mm in diam. *Fruits* ellipsoidal, acute or

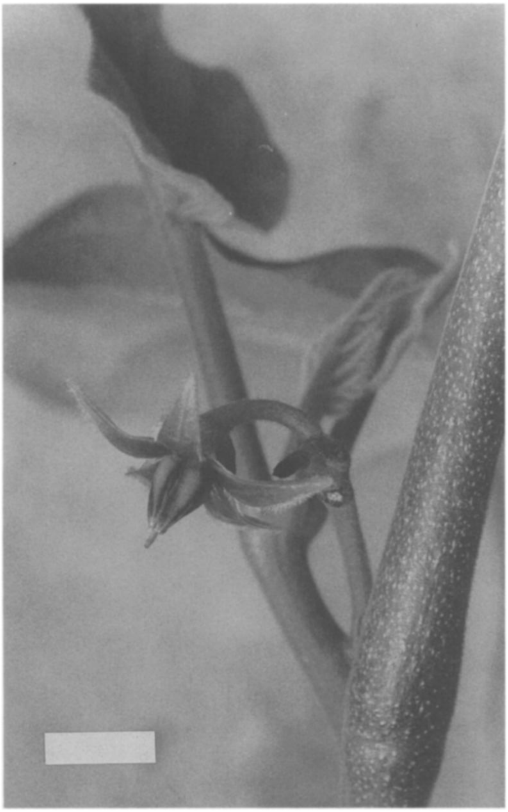


FIG. 22. *Cyphomandra cajanumensis*. Scale bar = 1 cm. Photo from greenhouse material; seeds originally sent from New Zealand by G. Pringle.

obtuse at apex, 4.5–10 cm long, 2.5–4.5 cm in diam., glabrous to moderately puberulent, especially when young, yellow when mature, darker stripes present when immature; mesocarp with or without stone cell aggregates; seeds 4–5 mm long, 3–3.5 mm wide, reticulate and moderately to densely white-puberulent.

Distribution (Fig. 23) and phenology. Andes of Colombia, Ecuador, and northern Peru, especially on western slope, 1500–3000 m. Flowering mainly January through September; fruiting mainly July through November.

Additional specimens examined. COLOMBIA. TOLIMA: Río Tetuán and Cucuana, Magdalena Valley, Mar 1844 (fl, fr), *Goudot s.n.* (K, P). VALLE: Valley of Río Dagua, ravine of Río San Juan, above Queremal, Las Colonias, 1950–2050 m, 20 Mar 1947 (fl, fr), *Cuatrecasas 23917* (F, US).

ECUADOR. CARCHI: Road Tulcán-Tufiño-Maldonado, sector La Pradera, 2360–2640 m, 11 Oct 1986 (fr), *Zak 1388* (NY). COTOPAXI: Pilaló, km 80 Quevedo to Latacunga, 2500 m, 3 Nov 1984 (fr), *Dodson & Dodson 15395* (NY); Pilaló, 2500–3000 m, 1–3 May 1959 (fl), *Harling 4899* (S). LOJA: El Coposo, 2400 m, 26 Jul 1983 (fl, fr), *Vivar s.n.* (GH). PICHINCHA: along road from Quito to Santo Domingo de Los Colorados, ca. 6000 ft, 15 Jan. 1945 (fl), *Camp E–1733* (NY); Volcán Atacazo, (fl), *Sodiro s.n.* (P); Corazón, Aug 1873 (fl), *Sodiro s.n.* (P).

PERU. CAJAMARCA: Prov. Hualgayoc, Hacienda Taulis, vic. Casa Hacienda, 2300 m, 5 Sep 1964 (fl, fr), *Hutchison & Bismarck 6528* (F, MO, NY, US).

Local names and uses. Ecuador: Tomate silvestre (*Vivar s.n.*). New Zealand: Casana (Child, 1986). The fruits are edible, large, and have a sweet taste. This species is now being cultivated in New Zealand as a possible fruit crop (Bohs, 1989c; Child, 1986; G. Pringle, pers. comm.).

Cyphomandra cajanumensis is a problematic species. It is variable in leaf shape, pubescence, and flower and fruit morphology. In general, it can be distinguished from other species of *Cyphomandra* by having succulent stems and large, coriaceous leaves; subcoriaceous, stellate, and usually glabrate corollas; rather broad anther connectives which barely exceed the thecae at the bases; cylindrical styles and truncate stigmas; and usually pointed fruits with thick woody inflorescence axes. Most collections attributable to *C. cajanumensis* have glandular-puberulent ovaries and young fruits; the hairs apparently break off as the fruits mature. The collections of *Hutchison & Bismarck 6528* have fruits that are more noticeably puberulent than other collections; they may also preserve their pubescence at maturity. Stone cell aggregates can be present or absent in the fruits of this species.

Leaf shape and vegetative pubescence vary within *C. cajanumensis*. The type and other specimens collected around Loja, Ecuador as well as *Hutchison & Bismarck 6528* from Cajamarca, Peru, have ovate leaves with deeply cordate bases. The more northerly collections tend toward ovate to elliptic leaves with truncate or shallowly cordate bases (an exception is *Goudot s.n.* from Colombia, which has deeply cordate leaf bases). Many representatives of *C. cajanumensis* have abundant pubescence on the foliage and axes, in the form of long eglandular hairs or in a few cases very dense tomentum on

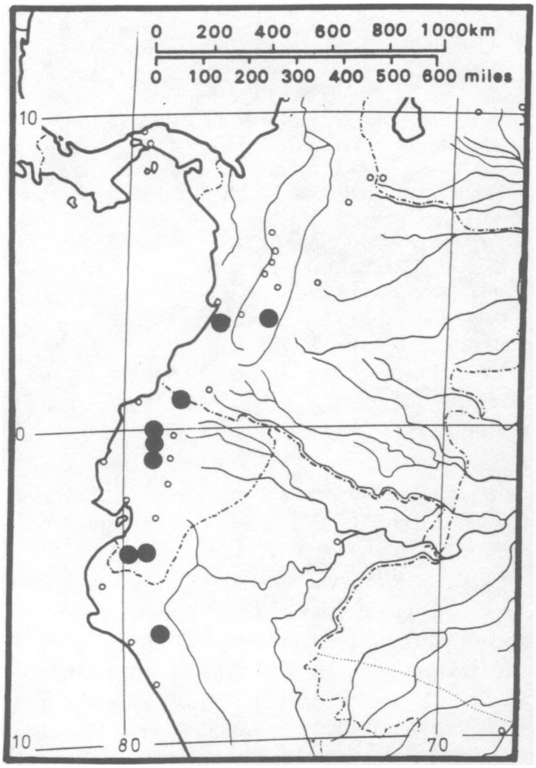


FIG. 23. Distribution of *C. cajanumensis.*

the undersurface of the leaves. Collections from central Ecuador are nearly glabrous on the leaves and axes.

In *C. cajanumensis* the pedicels and inflorescence axes thicken conspicuously in fruit. Several collections of *C. pendula* also have thickened and woody fruiting pedicels. The relationship between these two species is unclear. The two species can be distinguished by the dense tomentum on the abaxial surface of the corolla lobes and the glabrous, obtuse fruits of *C. pendula* and the nearly glabrous corolla lobes and frequently puberulent, acute fruits of *C. cajanumensis. Cyphomandra pendula* is most common at elevations of 200–3000 m on the eastern slope of the Andes, whereas *C. cajanumensis* occurs at 1500–3000 m, primarily on the western Andean slope.

Another problematic association of *C. cajanumensis* is with *C. viridiflora*, originally described by Ruiz and Pavón from Peru. Their protologue mentions that *C. viridiflora* is allied to *C. pendula*, although the plate shows *C. viridiflora* to have pubescent fruits, whereas those of *C. pendula* are glabrous. Unfortunately, the plate and protologue are apparently all that remain for the interpretation of the concept of *C. viridiflora*, for a search of the herbarium at MA turned up no specimens. Without a type specimen it is not possible to pin down the identity of *C. viridiflora*, but it may conform to the concept of *C. cajanumensis*. The collection locality of the *C. viridiflora* type is unknown.

Two sheets of *Humboldt & Bonpland 3410* exist at P. The specimen in the HBK herbarium has been designated as the lectotype. Child (1986) designated the New Zealand-grown specimen of *C. casana* at K as a lectotype when rightly it is the holotype of this name.

Cyphomandra cajanumensis is now being cultivated and tried as a fruit crop in New Zealand. The fresh fruits are said to be sweet, and Child (1986) describes their flavor as a mixture of peach and cape gooseberry. The preference of this species for high altitudes may mean that it is suitable for cultivation in temperate climates, and the lack of stone cell aggregates in the fruits of some accessions will facilitate their processing.

5. Cyphomandra calycina Sendtner, Flora **28:** 167. Tab. 1, fig. 1–7. 1845 (March). Type. Brazil. *Sellow 112* (lectotype, P, here designated; isolectotypes, B (destroyed) [F neg. 2925 F, G, GH, NY, WIS], F (fragment)). Chosen from syntypes *Martius* herb. fl. Bras. *1260, Raben 843, Schott s.n.* (*5449*?), and *Sellow 112.* Fig. 24.

Pionandra gardneri Miers, London J. Bot. **4:** 358. 1845 (July). Type. Brazil. Minas Gerais: São Caetano, Oct 1840 (fl), *Gardner 5041* (lectotype, BM, here designated; isolectotype, K).

Cyphomandra calycina var. *rufescens* Dunal, DC. Prodr. **13(1):** 388. 1852. Type. Brazil. Rio de Janeiro, *Sellow 130* (holotype, BM).

Shrub or small *tree* 1.2–4 m tall. *Branches* densely puberulent and often also sparsely to moderately pubescent-pilose with eglandular hairs 1–2(–3) mm long. *Leaf blades* simple, unlobed, chartaceous to subcoriaceous, acuminate at apex, adaxially sparsely to densely puberulent and often also pilose with eglandular hairs ca. 1–2 mm long, densely puberulent-pubescent abaxially; petioles densely puberulent and sparsely to moderately pilose. *Trunk leaves* simple, unlobed,

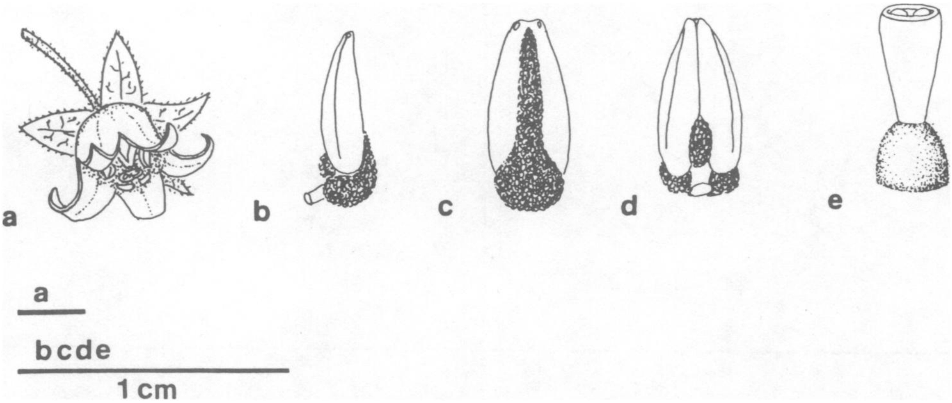


FIG. 24. *Cyphomandra calycina.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Löfgren 3482* (US).

the blade ovate, 13–28 cm long, 7.5–16 cm wide, length:width ratio ca. 1.5–2:1, the base cordate with basal lobes 0.5–2(–3) cm long; petioles 5–9 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade ovate, (2–)3–20 cm long, 2–12 cm wide, length:width ratio ca. 1–2(–2.5):1, the base (truncate to) cordate with basal lobes (0–)0.3–2(–3) cm long; petioles 1–7 cm long. *Inflorescence* unbranched, rarely forked, 15–35(–65)-flowered, 4–30 cm long; peduncle 1–6 cm long; rachis 3–26 cm long; pedicels 10–20 mm long, 20–40 mm long in fruit, (2–)3–10(–14) mm apart, articulated above the base, leaving pedicellar remnants (1–)2–4(–6) mm long; peduncle, rachis, and pedicels densely puberulent and often sparsely to moderately pubescent-pilose. *Flower buds* ovoid, often almost globose, obtuse at apex. *Calyx* chartaceous, moderately to densely puberulent and pubescent-pilose, the radius 7–14 mm, the lobes 5–10 mm long, 3–6 mm wide, broadly ovate, acute. *Corolla* purple, turning pale greenish yellow with age, fleshy, campanulate, the radius 12–20 mm, the tube 4–7(–9) mm long, the lobes triangular, 8–15 mm long, 4–7 mm wide, moderately to densely glandular-puberulent and eglandular pubescent-pilose abaxially, especially toward apex, adaxially glabrous at base, minutely papillose or tomentose at apices, the margin tomentose, the apex acute. *Anther thecae* violet, lanceolate, 4–5 mm long, 2–2.5 mm wide, the pores directed abaxially and laterally; connective broad at base, abruptly narrowed distally, the color unknown, 5(–6) mm long, 1–2.5 mm wide, abaxially slightly shorter than the thecae at apex, exceeding them by ca. 1 mm at base, adaxially present as a small swelling near base. *Ovary* glabrous or puberulent; style obconical, glabrous or puberulent, 4–6 mm long, (0.5–)1 mm in diam. at base, widening distally to (1.5–)2–2.5 mm, about equalling or slightly longer than stamens; stigma bilobed, concave in center, 1.5–2.5 mm in diam. *Fruit* ellipsoid-fusiform, acute at apex, 4–6.3 cm long, 1–1.7 cm in diam., densely puberulent-pubescent, color when ripe unknown; presence of stone cell aggregates in fruits unknown, but possibly absent; seeds unknown.

Distribution (Fig. 25A) and phenology. Coastal rain forest of southeastern Brazil in states of Minas Gerais, Rio de Janeiro, and São Paulo at elevations between about 800 and 1800 meters. Flowering specimens have been collected in May, August, and October through December, with a peak of flowering in October through December. Fruiting specimens have been collected in April and December.

Additional specimens examined. BRAZIL. MINAS GERAIS: Ouro Preto, 28 May 1923 (fl), *Godoy s.n.* (SP); Serra da Mantiqueira, *Martius herb. fl. Bras. 1260* (BR, W); Itambé do Villa do Principe, *Pohl 3456* (W); Viçosa, mata do Centro de Pequisa das Florestas Naturais do UFV, 8 Dec 1987 (fl), *Soares s.n.* (UT, Z); Araponga, Parque Estadual de Serra do Brigadeiro, plant cultivated at apiary, Universidad Federal de Viçosa, 20 Nov 1989 (fl), *Soares*

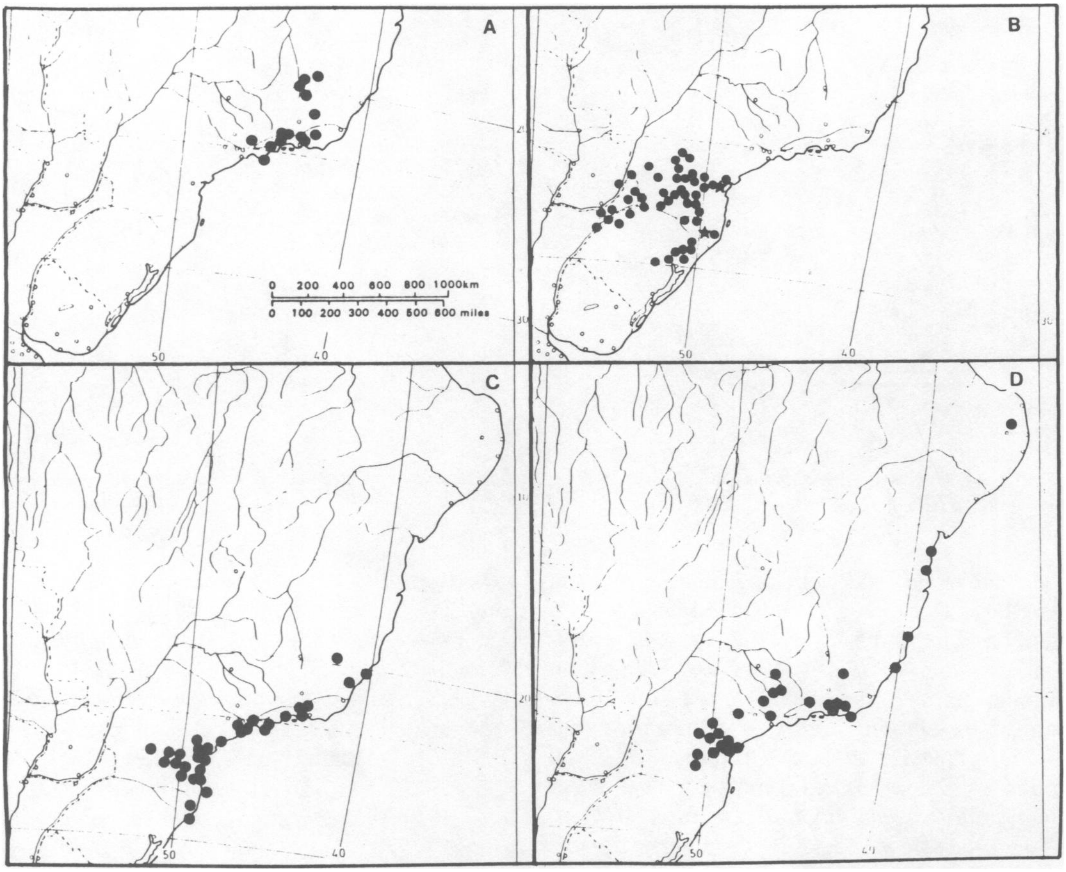


FIG. 25. Distributions of **A.** *C. calycina.* **B.** *C. corymbiflora* (dots, subspecies *corymbiflora*; stars, subspecies *mortoniana*). **C.** *C. diploconos.* **D.** *C. divaricata.*

s.n. (UT); Viçosa, 7 Dec 1985 (fl, fr), *Vieira 256* (GH); Lagoa Santa, *Warming 1019* (C). Rio de Janeiro: Petrópolis, 6 Aug 1868 (fl), *Glaziou 3079* (BR, C, P); Petrópolis, Nova Friburgo, 6 Aug 1880 (fl), *Glaziou 12096* (C, G, K, P); Nova Friburgo, 17 Nov 1890 (fl), *Glaziou 18404* (B, C, K, P); Itatiaia, Maromba, 16 Oct 1922 (fl), *Kuhlmann s.n.* (RB); Mun. de Paraty, road Paraty to Cunha, summit of IBDF area, 15 Dec 1988 (fl), *Nadruz et al. 469* (UT); Nova Friburgo, Macaé de Cima, Sítio Sophronites, 28 Dec 1989 (fl), *Nadruz et al. 563* (UT); near Rio de Janeiro, *Schott s.n.* (W); road between Monte Serrat and Ponte Maromba, Mt. Itatiaya Estacão Biologica, 22° 28'S, 44° 38'W, 800–1000 m, 9 Dec 1928 (fl), *L. Smith 1438* (GH); Serra da Itatiaia, 1300 m, 26 Dec 1895 (fl), *Ule 3745* (HBG); Serra dos Orgãos, 1100 m, 31 Dec 1896 (fl), *Ule 4315* (HBG); Itatiaya-Gebiet, Regenwald am Wege Maromba-Nacieras, ca. 1100–1800 m, 18 Oct 1927 (fl), *Zerny s.n.* (W). **São Paulo:** Campo da Bocaina, Nov 1879 (fl), *Glaziou 11387* (C, G, K, P); Pindamonhangaba, Eugenio Lefevre, ca. 1100 m, 11 Nov 1953 (fl), *Kuhlmann 2928* (SP); Fazenda San Miguel, S.J. dos Barreiros, 28 Apr 1894 (fr), *Löfgren & Edwall 2478* (SP); S. Francisco dos Campos, 20 Dec 1896 (fl), *Löfgren 3482* (SP, US); Alto da Serra, Parque Cajurú, Nov 1909 (fl), *Luederwaldt s.n.* (SP, US); Mun. de Bananal, Estrada de Acesso a Reserva Florestal, 23 Oct 1979 (fl), *Mantovani 145* (SP); Ilha de São Sebastião, 27 Dec 1971 (fl), *Mattos & Mattos 15759* (SP); Cunha, 3 Oct 1940 (fl), *Viegas & Kiehl s.n.* (SP). **Without State:** Canta Gallo, 1859, *Peckolt 90* (BR); *Raben 843* (BR, C); Serra Estrella, *Riedel s.n.* (NY, US); *Schott 5449* (W); *Sellow s.n.* (K).

Cyphomandra calycina is distinguished from all other species in the genus by its exclusively simple leaves, very large calyces, short broad stamens, expanded styles and stigmas, and elongated puberulent fruits. Its fleshy campanulate corolla, broad, short, curved stamens with the connective abruptly narrowed above the base, expanded style and stigma, and puberulent fruits

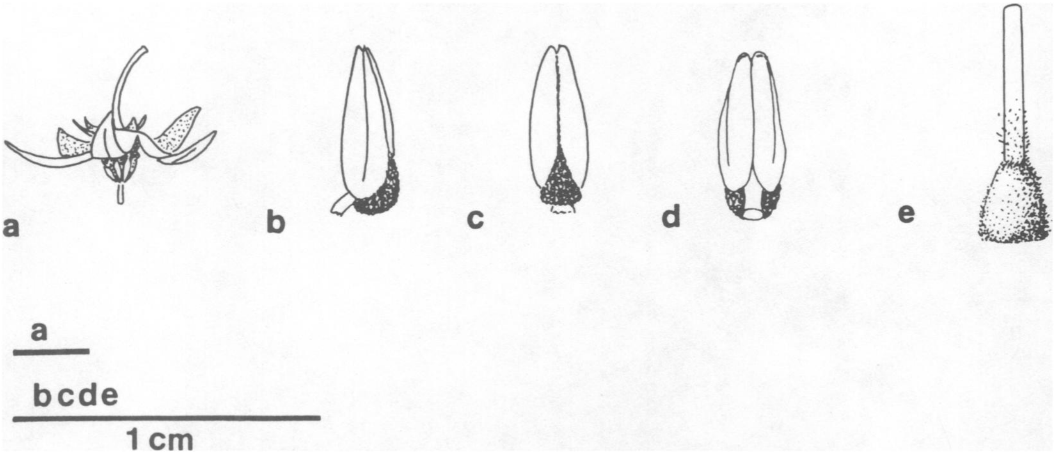


FIG. 26. *Cyphomandra corymbiflora*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on greenhouse material of *Bohs 2343*.

indicate a relationship with *C. diploconos*, *C. sciadostylis*, and *C. premnifolia*, all from southeastern Brazil. The style of *C. calycina* is not nearly as broadly and abruptly expanded as in *C. diploconos* and *C. sciadostylis*. This species differs from *C. premnifolia* by having a larger calyx, broader and shorter style, and an adaxially swollen anther connective. The very large calyx and elongated fruits of *C. calycina* resemble those of the Venezuelan *C. diversifolia* subspecies *diversifolia*, but a close relationship between the two taxa is uncertain.

Sendtner listed four syntypes without collection numbers in his protologue of *C. calycina*. Using Sendtner's annotations as a guide, I believe these correspond to *Martius 1260*, *Raben 843*, *Schott 5449*, and *Sellow 112*. Assuming that Sendtner saw all the sheets bearing annotations in his handwriting, I have chosen the Sellow specimen at P as the lectotype because this material is in the best condition. Another Sellow collection of this species at K bears no number, so I have not considered it an isolectotype.

I have inferred that the sheet labeled *Sellow 130* at BM is the holotype for *C. calycina* variety *rufescens* even though no locality, date, or collection number are given in Dunal's protologue. The sheet bears an annotation of "*Solanum latiflorum*" in Dunal's handwriting, a name that he mentions as a synonym in his protologue.

Miers did not specify a single specimen as the holotype of his *Pionandra gardneri*, so I have chosen the sheet at BM annotated as this species as the lectotype.

6. Cyphomandra corymbiflora Sendtner, Flora **28:** 174. Tab. 8, fig. 1–4. 1845.
Figs. 26, 27, 28.

Shrub or small *tree* 0.5–3 m tall. *Branches* densely puberulent and also often sparsely to densely pubescent-pilose with eglandular hairs 1–4 mm long. *Leaf blades* simple, unlobed, chartaceous to subcoriaceous, (acute-)acuminate at apex, glabrous to densely puberulent, pubescent, or pilose adaxially and abaxially, more densely so on veins; petioles moderately to densely puberulent and also often sparsely to densely pilose. *Trunk leaves* simple, unlobed, the blade ovate to elliptic-ovate, (10–)15–32 cm long, 9–25 cm wide, length:width ratio ca. 1–1.5:1, the base cordate with basal lobes 1–6.5 cm long; petioles 5–18 cm long. *Crown leaves* 4–5 per sympodial unit, simple, unlobed, the blade ovate to elliptic-ovate, 4–22 cm long, 3.5–16 cm wide, length:width ratio ca. 1–2:1, the base cordate with basal lobes 0.5–4(–6) cm long; petioles 2–12 cm long. *Inflorescence* unbranched or branched, ca. 15–40(–60)-flowered, (2-)6–20 cm long; peduncle 1.5–13 cm long; rachises (1-)4.5–14 cm

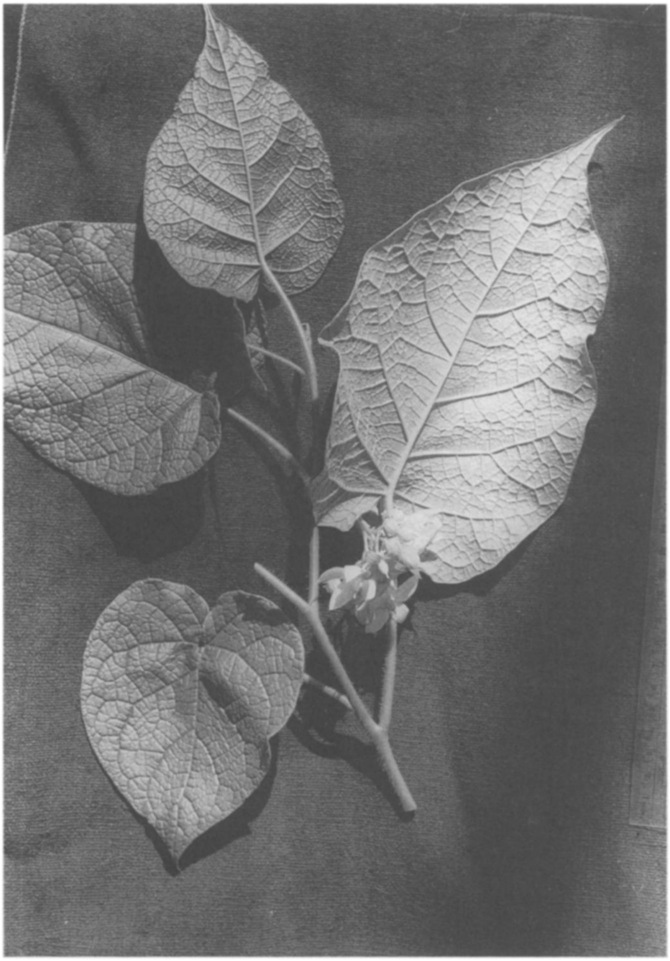


FIG. 27. *Cyphomandra corymbiflora*. From greenhouse material of *Bohs 2343*.

long; pedicels (5–)10–25 mm long, 15–30 mm long in fruit, (1–)3–10(–17) mm apart, articulated above the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachises, and pedicels moderately to densely puberulent and also often sparsely to densely pilose. *Flower buds* ellipsoidal to globose, obtuse at apex. *Calyx* chartaceous, moderately to densely puberulent-pubescent, the radius 3–11 mm, the lobes 2–10 mm long, 1–6 mm wide, ovate, lanceolate, or elliptic, acute. *Corolla* pink, white, or purple, fading to lavender or white with age, chartaceous to membranaceous, stellate, the radius 5–25 mm, the tube 1–7 mm long, the lobes ovate, elliptic, or triangular, 4–25 mm long, (1–)2.5–14 mm wide, sparsely to densely puberulent-pubescent abaxially, glabrous adaxially, the margin tomentose, the apex acute. *Anther thecae* yellow, ovate to elliptic, 3–6 mm long, 1.5–2 mm wide, the pores directed distally; connective yellow-orange, narrowly triangular and strongly tapered distally, 3–6(–7) mm long, 0.75–1(–2) mm wide at base, abaxially slightly shorter than or equal to thecae at apex, nearly equal to or exceeding them by 0.5–1 mm at base, adaxially not present. *Ovary* glabrate to densely pubescent; style cylindrical, usually sparsely pubescent, not dilated or slightly dilated distally, (3–)4–6 mm long, 0.25–1 mm in diam.,

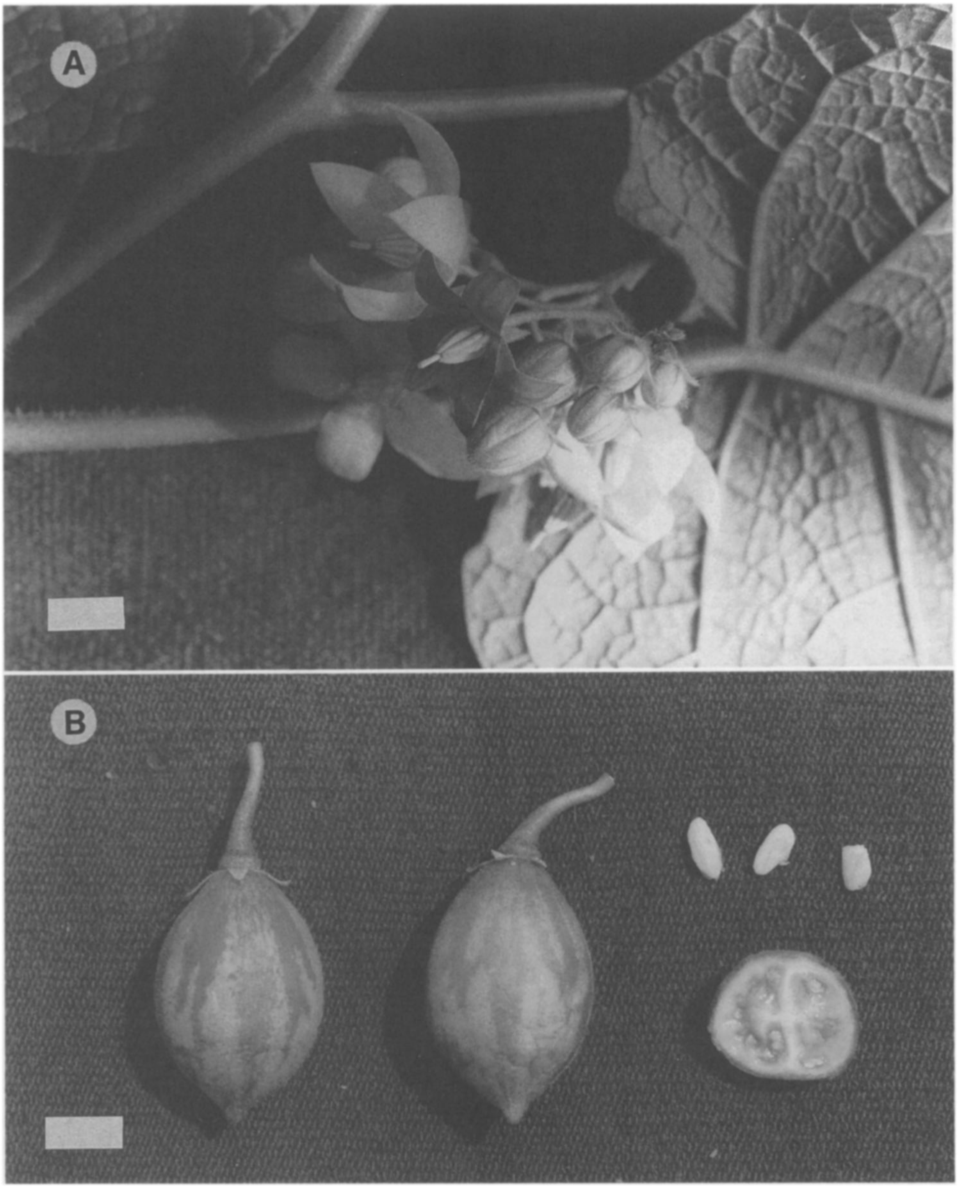


FIG. 28. *Cyphomandra corymbiflora*. **A.** Flowers. **B.** Fruits and stone cell aggregates. Scale bars = 1 cm. From greenhouse material of *Bohs 2343*.

exserted 1–2 mm beyond stamens; stigma truncate to clavate, 0.25–1 mm in diam. *Fruit* ellipsoidal to globose, acute or obtuse at apex, 1–3 cm long, 0.8–2 cm in diam., densely pubescent to pilose, greenish to yellow-green or yellowish with darker longitudinal stripes; mesocarp with stone cell aggregates; seeds 2.5–3.5 mm long, 2–2.5 mm wide, densely puberulent.

Distribution (Fig. 25B). Understory of *Araucaria* stands, cloud forest, and disturbed areas such as clearings, fields, and stream margins, 200–2000 m in elevation, southeastern Brazil in the states of Paraná, Rio Grande do Sul, and Santa Catarina and adjacent provinces of Argentina.

This species is widespread in the humid forests of southeastern Brazil and adjacent Argentina and is a characteristic element in the understory of *Araucaria* stands. It can be distinguished from the other species in the genus by its large, deeply cordate leaves, abundant pubescence, branched inflorescences, white or purple stellate corollas somewhat pubescent abaxially and glabrous adaxially, relatively short and broad anthers, cylindrical styles, and densely pubescent fruits. It most closely resembles *C. pinetorum*, also of southern Brazil. Both species have abundant pubescence on the stems and leaves, purple stellate corollas, and pubescent fruits. *Cyphomandra corymbiflora* can be distinguished from *C. pinetorum* by its strongly tapered anther connective.

Cyphomandra corymbiflora is probably related to *C. pinetorum* on one hand (and thence perhaps with *Cyphomandropsis*) and with the *C. diploconos* group on the other. Although *C. corymbiflora* bears little morphological similarity to *C. diploconos* and its allies, the anther connective is abruptly tapered distally as in the members of that group. *Cyphomandra corymbiflora* can form hybrids with *C. diploconos* in the greenhouse (Bohs, 1991), but whether such hybrids are found under natural conditions is unknown.

The following key distinguishes two subspecies of *C. corymbiflora*. Peduncle length and corolla size together reliably separate the subspecies, but future studies may show that subspecies *mortoniana* is simply a local large-flowered variant of *C. corymbiflora* that does not merit taxonomic recognition. Subspecies *corymbiflora* occurs in *Araucaria* forest, and subspecies *mortoniana* occurs in cloud forest at higher elevations.

KEY TO THE SUBSPECIES OF *CYPHOMANDRA CORYMBIFLORA*

1. Peduncle shorter than 7 cm and corolla radius less than 15 mm with lobes less than 11 mm long (if corollas large, then peduncles short) . . . . a. subsp. *corymbiflora*.
1. Peduncle 7 cm or longer and corolla radius 15 mm or more, the lobes 15 mm or longer . b. subsp. *mortoniana*.

a. *Cyphomandra corymbiflora* Sendtner subspecies *corymbiflora*

Cyphomandra corymbiflora Sendtner, Flora **28:** 174. Tab. 8, fig. 1–4. 1845; Smith & Downs, Fl. Illustr. Catar. pp. 199–201. Fig. 27a, a–d. 1966. Type. Southern Brazil, *Sellow s.n.* (lectotype, P, here designated; isolectotypes, B (destroyed) [F neg. 2927 F, G, GH, NY, US, WIS], F (fragment), K, W).

Cyphomandra macrophylla Smith & Downs, Phytologia **10:** 434. Plate 7, fig. 1–6. 1964; Smith & Downs, Fl. Illustr. Catar. pp. 190–193. Fig. 25, a–f. 1966. Type. Brazil. Santa Catarina: Lauro Müller-Urussanga, Pinhal da Companhia, elev. 300 m, 23 Aug 1958 (fl), *Reitz & Klein 7044* (holotype, US 2323376; isotype, HBR, n.v.)

Cyphomandra kleinii Smith & Downs, Phytologia **10:** 435. Plate 9, fig. 2–6. 1964; Smith & Downs, Fl. Illustr. Catar. pp. 201–203. Fig. 27, b–f. 1966. Type. Brazil. Santa Catarina: Curitibanos, Ponte Alta do Sul, capoeira, elev. 900 m, 19 Apr 1962 (fl), *Reitz & Klein 12576* (holotype, US 2423783; isotype, HBR, n.v.)

Leaf blades glabrous to densely puberulent, pubescent, or pilose adaxially, moderately to densely pubescent on veins, glabrous to densely puberulent-pubescent(-pilose) abaxially, more densely so on veins. *Crown leaves* with blade ovate, 4–19 cm long, 4–16 cm wide, length:width ratio ca. 1–2:1, the base cordate with basal lobes 0.5–4(–6) cm long. *Inflorescence* unbranched or branched, 15–40(–60)-flowered, (2–)6–16 cm long; peduncle 1.5–5(–6.5) cm long; pedicels (5–)10–15(–20) mm long, 15–25 mm long in fruit. *Calyx* radius 3–5(–11) mm, the lobes 2–4(–10) mm long, 1–2 mm wide, narrowly elliptic to lanceolate. *Corolla* radius (5–)7–15(–17) mm, the tube 1–3 mm long, the lobes (4–)5–13(–15) mm long, (1–)2.5–7 mm wide. *Fruit* ellipsoidal to globose, acute or obtuse at apex, 1–3 cm long, 1–2 cm in diam.; seeds 2.5–3.5 mm long, 2–2.5 mm wide, densely puberulent.

Distribution (Fig. 25B) and phenology. In understory of *Araucaria* stands and in disturbed areas, 200–1300 m in elevation, southeastern Brazil in the states of Paraná, Rio Grande do Sul, and Santa Catarina and adjacent areas in Argentina. Flowering specimens have been collected in all months of the year except May, with a peak of flowering in September through December.

Fruiting specimens have been collected in January, March, July, August, and October through December.

Additional specimens examined. BRAZIL. PARANÁ: Bariguí, Curitiba, Oct 1955 (fl), *Braga & Moreira 221* (US); Mun. Curitiba, Recanto das Araucarias, 8 Dec 1987 (fl), *Cordeiro & Silva 474* (UT); São José dos Pinhais, Colonia Muricy, Nov 1966 (fl, fr), *Dombrowski & Kuniyoshi 1910* (US); Bariguí, 10 Oct 1972 (fl), *Dombrowski 4922* (CTES); Marechal Mallet, 1 Jan 1904 (fl, fr), *Dusén 3057* (NY, S, US, WU); Calmão, 13 Mar 1910 (fl, fr), *Dusén 9312* (F, GH, NY, S); Mun. São Mateus do Sul, Rio Potinga, 16 Dec 1956 (fl, fr), *Hatschbach 3485* (MBM); Mun. Contenda, Turvo, 30 Sep 1957 (fl), *Hatschbach 4132* (MBM); Mun. Foz do Iguaçu, Parque Nacional, Estrada do Poço Preto, 15 Oct 1952 (fl), *Hatschbach 9363* (MBM, US); Mun. Fenix, Irapoã, margin of Rio Ivai, 4 Jun 1963 (fl), *Hatschbach 10097* (MBM, US); Catanduba-Camargópolis, 7 Nov 1963 (fl, fr), *Hatschbach & Pereira 10383* (MBM, US); Guarapuava, Aguas Santa Clara, 17 Nov 1963 (fl, fr), *Hatschbach & Pereira 10572* (MBM, US); Mun. Ortigueira, Bairro dos Pretos, 17 Oct 1965 (fl), *Hatschbach 13037* (MBM, P); Mun. Bituruna, Rio Jangada, 17 Oct 1966 (fl), *Hatschbach 14964* (F, M, NY, US); Gal. Carneiro, 13 Dec 1966 (fl), *Hatschbach 15393* (MBM, NY, P, US, UT); Mun. Ponta Grossa, Passo do Pupo, 11 Oct 1967 (fl), *Hatschbach 17440* (F, MBM); Mun. Imbituva, Guaramiranga, 20 Sep 1968 (fl), *Hatschbach & Guimarães 19741* (F); Mun. Laranjeiras do Sul, Campo Novo, 21 Sep 1968 (fl), *Hatschbach 19786* (MBM, UT); Mun. Guarapuava, Guara, 5 Dec 1968 (fl), *Hatschbach & Guimarães 20488* (C, MO); Mun. Guarapuava, Rod. BR–277, Rio das Mortes, 5 Dec 1968 (fl, fr), *Hatschbach & Guimarães 20496* (MBM, UT); Mun. Lapa, Rio Passa-Dois, 1 Oct 1969 (fl), *Hatschbach 22306* (MBM, NY, Z); Mun. Ipiranga, Coatis, 8 Oct 1969 (fl, fr), *Hatschbach 22369* (MBM); Clevelandia, 26 Oct 1969 (fl), *Hatschbach 22693* (MBM), same locality and date (fl), *Hatschbach 22700* (MBM, NY, Z); Mun. Candido de Abreu, Tres Bicos, 9 Jul 1970 (fl), *Hatschbach 24443* (MBM); Mun. Ortigueira, Rio do Barreiro, 20 Oct 1970 (fl), *Hatschbach 24958* (MBM); Mun. Pitanga, Rio Bonito, 25 Feb 1971, *Hatschbach 26504* (MBM); Manuel Ribas, 18 Oct 1973 (fl), *Hatschbach 32843* (BH, C, M, MO); Mun. Piraquara, Col. Santa Maria, 26 Nov 1974 (fl), *Hatschbach 35537* (AAU, Z); Mun. Laranjeiras do Sul, Faxinal Grande, 24 Oct 1975 (fl), *Hatschbach 37342* (C, MBM, Z); Mun. Cascavel, Autodromo de Cascavel, 25 Oct 1975 (fl), *Hatschbach 37351* (M, MO); Mun. Pinhão, Faxinal do Céu, 9 Jan 1980 (fl), *Hatschbach 42696* (MBM); Palmas, 10–15 km W, 12 Dec 1980 (fl, fr), *Hatschbach 43442* (MBM, UT); Mun. Pien, Poço Frio, 6 Oct 1987 (fl), *Hatschbach & Silva 51485* (UT, Z); Mun. Antonio Olinto, Rod. PR–281, km 6, 14 Nov 1988 (fl), *Hatschbach & Cordeiro 52673* (UT, Z); Mun. Curitiba, Parque Barigui, 19 Nov 1973 (fl), *Kummrow 136* (MBM); Mun. Curitiba, Capanema, 14 Aug 1978 (fl), *Kummrow 1262* (MBM, Z); Mun. Curitiba, Parque Iguaçu, 13 Sep 1982 (fl), *Kummrow 1990* (MBM); Mun. Curitiba, Parque Barigui, 14 Dec 1987 (fr), *Kummrow & Soares 2945* (UT); Mun. Curitiba, Parque Iguaçu, 8 Oct 1988 (fl), *Kummrow & Soares 3082* (UT), *3083* (UT); Contenda, 25° 40'S, 49° 35'W, 900 m, 7 Nov 1977 (fl, fr), *Landrum 2444* (MBM); outskirts of Curitiba, ca. 950 m, 25 Sep 1966 (fl), *Lindeman & Haas 2517* (MBM, NY, U); Mun. Curitiba, Parque Mun. do Iguaçu, 16 Oct 1979 (fl), *Oliveira 105* (MBM); same locality, 22 Aug 1984 (fl), *Oliveira 813* (UT); Parque Nacional do Iguaçu, 9 Feb 1960 (fl), *Pereira 5514* (US); Ipiranga, 5 Dec 1934 (fl, fr), *Reiss 47A* (WIS); Mun. Curitiba, Cidade Industrial, 18 Nov 1987 (fl, fr), *J. M. Silva & Ribas 409* (UT); Curitiba, Parque Iguaçu, 16 Dec 1987 (fl, fr), *Soares s.n.* (VIC. 10285) (GH); Campina do Siqueira, Curitiba, 2 Nov 1966 (fl, fr), *Stellfeld 1627* (B, NY, P, US). **RIO GRANDE DO SUL:** Reserva do Turvo, Tenente Portela, 10–15 Dec 1973 (fr), *Baptista et al. 27625* (CTES); Xingú near Palmeira, 200 m, 1–2 Nov 1905 (fl), *Bornmüller 620* (A, GH); road Loreto-Forqueta, 26 Aug 1984 (fl), *Guerra et al. 275* (US); Cabeceira do Rio das Antas, 4 Dec 1971 (fl), *Lindeman et al. 9436* (CTES); near Jaquirana, 1150 m, 9 Nov 1961 (fl), *Pabst 6687 = Pereira 6861* (US); Picada para o Porto Garcia Tte. Portela, 6 Jul 1975 (fl), *Porto 1523* (CTES); São Francisco de Paula, Vila Oliva, 6 Jan 1946 (fr), *Rambo 31117* (B); Pr. Montenegro, Maratá and Linha Bonita, 26 Aug 1949 (fl), *Rambo 43076* (B, US); Kappesberg, near Caxias, 11 Sep 1949 (fl), *Rambo 43388* (MO); Passo da Guarda, p. Bom Jesus, 14 Jan 1952 (fl, fr), *Rambo 51898* (US); Cerro Largo, p. S. Luiz, 20 Nov 1952 (fl, fr), *Rambo 53204* (B); Faz. Englert, p. S. Fr. de Paula, 1 Jan 1954 (fr), *Rambo 54611* (B); São Salvador, Montenegro, 600 m, 30 Sep 1946 (fl), *Sehnem 2156* (B, US); Salvador do Sul, p. Montenegro, 600 m, 12 Sep 1971 (fl), *Sehnem 12422* (US); Aratinga, São Francisco de Paula, Oct 1984 (fl), *Sobral 3228* (TEX); Cerro Comprido, Faxinal do Soturno, 29° 32'S, 53° 34'W, Nov 1988 (fl, fr), *Sobral 5954* (NY). **SANTA CATARINA:** Campos Novos, 1000 m, 29 Oct 1963 (fl), *Klein 4207* (US); Caxambu, Campos Novos, 700 m, 29 Oct 1963 (fl, fr), *Klein 4223* (NY, US); Passo do Socorro, Lajes, 700 m, 31 Oct 1963 (fl), *Klein 4371* (NY, US); Liso, Guaraciaba, 600 m, 1 Sep 1964 (fl), *Klein 5733* (US); Mun. Urubici, Ayo. Cambuí, 4 km NE of Vacas Gordas, 25 Dec 1982 (fl), *Krapovickas & Schinini 38319* (CTES, G, WIS); Mun. Curitibanos, km 262 on BR 116, ca. 900 m, 23 Nov 1977 (fl, fr), *Landrum 2711* (MBM); Mun. Lajes, Painel, ca. 1000 m, 15 Dec 1967 (fl, fr), *Lourteig 2222* (C, P, S, US); Porto União, km 18 of Estrada Porto União-Matos Costa, 6 Nov 1964 (fl), *Mattos 12327* (SP); Serra do Espigão, 30 km from Santa Cecilia, BR–2, 1300 m, 20 Oct 1961 (fl), *Pabst 6073 = Pereira 6246* (US); Novo Horizonte, Lauro Müller, 400 m, 24 Oct 1958 (fl), *Reitz & Klein 7517* (US); Rio dos Patos, Lebon Regis, 900 m, 23 Apr 1962 (fl), *Reitz & Klein 12873* (US); Picadas, km 181 da ERF, Papanduva, 750 m, 25 Oct 1962 (fl), *Reitz & Klein 13533* (B, NY, US); Rio dos Poços, Canoinhas, 750 m, 26 Oct 1962 (fl), *Reitz & Klein 13593* (US); Curitibanos, 900 m, 30 Oct 1962 (fl), *Reitz & Klein 13912* (US); Morro do Pinheiro Seco, Lajes, 950 m, 18 Dec 1962 (fl, fr), *Reitz & Klein 14101* (B, NY, US); Santa Cecilia, 1000 m, 18 Dec 1962 (fl), *Reitz & Klein 14138* (US); Mun. Caçador, 20 km NE of Caçador, 950–1100 m, 22 Dec 1956 (fl), *Smith & Reitz 9044* (TEX, US); Mun. Caçador, 9 km

W of Caçador, 900–1000 m, 6 Feb 1957 (fl), *Smith & Klein 10897* (NY, US); Mun. Xanxerê, 13 km S of Abelardo Luz, 500–600 m, 19 Feb 1957 (fl), *Smith & Klein 11513* (US); Mun. Chapecó, Cordillera, ca. 27° 6'S, 52° 36'W, 400 m, 14 Oct 1964 (fl, fr), *Smith & Reitz 12504* (NY, S, US); Mun. Mondaí, Catre, ca. 27° 8'S, 53° 30'W, 235–300 m, 16 Oct 1964 (fl), *Smith & Reitz 12611* (GH, MO, P, US, WIS).

ARGENTINA. Corrientes: Dept. Santo Tomé, Ruta 40, 6 km SW de Colonia Garabí, Ayo. Ciriaco, 19 Jul 1982 (fl, fr), *Tressens et al. 2085* (CTES). **Misiones:** 5 km from Bernardo de Irigoyen, 25 Nov 1978 (fl, fr), *Bernardi 18825* (MO, NY); Dept. San Pedro, Sierra Imán, 19 Sep 1945 (fl), *Bertoni 1962* (W); Dept. San Pedro, Arroyo Liso, 19 Sep 1945 (fl), *Bertoni 2087* (B); Dept. San Javier, Barra Bonita (Alto Uruguay), 5 Oct 1946 (fl), *Bertoni 2787* (W); Dept. Montecarlo, Reserva, km 56, Ruta 16, Oct 1977 (fl, fr), *Cabrera et al. 28885* (NY, SI); Posadas, Bonpland, 5 Jan 1907 (fl), *Ekman 844* (G, LD, S, US); Bernardo de Irigoyen, 5 Nov 1958 (fl, fr), *Gamerro & Toursakisian 102* (SI); Dept. San Pedro, San Pedro, 30 Sep 1973 (fl), *González 29* (CTES); San Antonio, landing strip, 18 Aug 1969 (fl), *Klein & Eskuche 9059* (Z); Dept. Leandro N. Alem, 12 km E of Leandro N. Alem, Lote 106, 18 Aug 1972 (fl, fr), *Maruñak 378* (CTES, LP, MO, WIS, Z); Dept. San Pedro, "El Soberbio", 500 m, 18 Jul 1957 (fl, fr), *Montes 27479* (NY); San Pedro, 30 Oct 1958 (fr), *Torres 8* (LP); Bernardo de Irigoyen, 5 Nov 1958 (fl, fr), *Torres 95* (LP).

Local names and uses. Brazil: Baga de veado, baga de veado gigante (both from Smith & Downs, 1966). Argentina: Tomate de monte (*Gamerro & Toursakisian 102*). Fruits that matured in the University of Vermont greenhouses had a pleasant taste but were difficult to eat because of their pubescent skin and abundant seeds. This species has potential as an ornamental.

Great morphological variability is present within this taxon, particularly in pubescence, calyx size and shape, corolla size, and fruit shape. Specimens vary from being nearly glabrous to densely pubescent or pilose. All intermediate states of pubescence can be found on herbarium material, so it is impossible to distinguish distinct taxonomic entities based on pubescence characters, as Smith and Downs (1966) attempted to do. The calyx lobes vary from broad to long and narrow, and the corolla diameters range from about 10 mm (in the type of *C. macrophylla*) to around 30 mm. Again, intermediate sizes and shapes are present.

The element segregated by Smith and Downs as *C. macrophylla* is somewhat distinct in having very small flowers, generally large leaves, and elongated, acute fruits. Unfortunately, the only fruits available are very young, and fruits are lacking on most other specimens that have very small corollas. Large leaves are not unique to *C. macrophylla*, and occur in many collections of *C. corymbiflora*. Therefore, *C. macrophylla* is not maintained.

Sendtner did not designate a holotype for *C. corymbiflora*, and the only information given in his protologue is "Brasilia australiore legit Sellovius." Annotations in Sendtner's handwriting appear on Sellow specimens at P, K, and W; none of these has a collection number. Another annotated specimen was present at B with the Sellow number 45, but it has been destroyed. Without collection localities or numbers it is not possible to determine if these specimens are in fact duplicates, but they probably are, in spite of the lack of the number 45 on the specimens at P, K, and W. The P specimen has a label saying "donné por le Mus. de Berlin, 1899," so it is probably a duplicate of the B specimen. I have chosen this P sheet as the lectotype. Whether the K and W sheets should be considered isolectotypes is an open question.

b. *Cyphomandra corymbiflora* Sendtner subspecies *mortoniana* (Smith & Downs) Bohs, comb. et stat. nov.

Cyphomandra mortoniana Smith & Downs, Phytologia **12:** 250. 1965; Smith & Downs, Phytologia **10:** 434, Plate 8, fig. 1–6. 1964; Smith & Downs, Fl. Illustr. Catar., p. 193, Fig. 26, a–f. 1966. Type. Brazil. Santa Catarina: São Joaquim, near Mantiqueira (27 km E of São Joaquim), elev. 1100–1200 m, 16 Jan 1957 (fl), *Smith & Reitz 10219* (holotype, US 2423789; isotypes, GH, HBR, n.v., R, n.v.).

Cyphomandra patrum Smith & Downs, Phytologia **12:** 251. 1965; Smith & Downs, Phytologia 10: 435, Plate 9, fig. 1. 1964; Smith & Downs, Fl. Illustr. Catar. p. 196, Fig. 27a. 1966. Type. Brazil. Santa Catarina: Bom Retiro, Campo dos Padres, elev. 2000 m, 15 Dec 1948 (fl, fr), *Reitz 2364a* (holotype, US 1954522; isotypes, HBR, n.v., L, US).

Leaf blades sparsely to densely puberulent-pubescent adaxially, more so on veins, densely pubescent to pilose abaxially. *Crown leaves* with blade ovate to elliptic-ovate, 6–22 cm long, 3.5–15 cm wide, length:width ratio 1.5–2:1, the base cordate with basal lobes 1–2.5 cm long. *Inflorescence* branched, 30–40-flowered, ca. 20 cm long; peduncle 7–13 cm long; pedicels 15–25 mm long, 20–30 mm long in fruit. *Calyx* radius (4–) 7–10 mm, the lobes (3-)5–8 mm long, 2–6 mm wide, ovate to lanceolate. *Corolla* radius ca. 15–25 mm, the tube (4–)5–7 mm long, the lobes 11–25 mm long, 7–14 mm wide. *Fruit* ellipsoidal, acute at apex, ca. 2 cm long, 1 cm in diam.; seeds unknown.

Distribution (Fig. 25B) and phenology. Restricted to two localities in southeastern Brazil, one in Paraná southeast of Curitiba and the other in the southeastern Serra do Mar region in Santa Catarina around São Joaquim, 950–2000 m in elevation, in clearings, thickets, and waste places in dwarf forest in the mountains. Flowering specimens have been collected in January and October through December. Fruiting specimens have been collected in December.

Additional specimens examined. BRAZIL. PARANÁ: Mun. São José dos Pinhaes, Vossoroca, 6 Nov 1949 (fl), *Hatschbach 1593* (MBM, US); Mun. Tijucas do Sul, Tabatinga, 1 Dec 1964 (fl), *Hatschbach 11922* (MBM, US). **SANTA CATARINA:** Mun. São Joaquim, Serra do Oratório, 14 Dec 1967 (fl), *Lourteig 2129* (P, US); Fazenda da Laranja, Bom Jardim, São Joaquim, 1400 m, 13 Dec 1958 (fl), *Reitz & Klein 4084* (US); Bom Retiro, 950 m, 25 Oct 1957 (fl), *Reitz & Klein 5455* (US); Curral Falso, Bom Jardim, São Joaquim, 1400 m, 10 Dec 1958 (fl), *Reitz & Klein 7744* (US); Mun. Bom Retiro, Campo dos Padres, 1400–1650 m, 16 Nov 1956 (fl), *Smith et al. 7639* (S, US).

Local names and uses. Brazil: Azeitona (*Reitz 2364a*), azeitona braba, baga de veado (both from Smith & Downs, 1966). Fruits edible according to *Reitz 2364a*. This subspecies, along with subspecies *corymbiflora*, may have value as an ornamental due to its short stature and showy flowers.

This subspecies is separated from subspecies *corymbiflora* by its larger corollas and longer peduncles. Those specimens with a corolla radius greater than 15 mm, corolla lobes longer than 11 mm, and a peduncle equal to or greater than 7 cm long probably belong to subspecies *mortoniana*. Collections of subspecies *mortoniana* also have elongated acute fruits.

Cyphomandra patrum was segregated from *C. mortoniana* by Smith and Downs (1964) because of its longer and denser indumentum. However, indumentum varies considerably within subspecies *mortoniana* and in *C. corymbiflora* as a whole and is not sufficiently distinctive in *C. patrum* to justify its recognition as a distinct species.

The two collections of subspecies *mortoniana* from Paraná, *Hatschbach 1593* and *11922*, differ from the other representatives of this taxon in having smaller calyces and pubescent anthers. Although the anther pubescence is unique in the genus and the collections are geographically separated from the rest of the subspecies, they are probably best regarded as aberrant variants of subspecies *mortoniana*.

Smith and Downs first provided descriptions and Latin diagnoses of *C. mortoniana* and *C. patrum* in *Phytologia*, Volume 10 (1964), but failed to designate a type collection for *C. mortoniana* and cited the wrong collection number for the type of *C. patrum*. The valid publication of these names must therefore date from Smith (1965) in which these errors were corrected.

7. Cyphomandra diploconos (Martius) Sendtner, Flora 28: 169, Tab. 3, fig. 1–6. 1845.

Figs. 29, 30.

Witheringia diploconos Martius, Nov. Gen. Sp. Pl. **3:** 76. Tab. 229. 1829. Type. Brazil. Rio de Janeiro (Sebastianópolis): "In via ad Tijuca et prope Fazenda dos Negros," Nov or Dec, *Martius 245* (490 on small tag attached to twig) (lectotype, M, here designated [F neg. 6516 F, NY, US, WIS]).

Solanum fragrans Hooker, Bot. Mag. **65** (vol. 12 of new ser.), Plate 3684. 1839. Type. Cultivated in Glasgow Botanic Garden, sent by Tweedie from southern Brazil. No specimen is extant, so Hooker's Plate 3684 (Fig. 31) is here designated as the lectotype.

Pionandra floribunda Miers, London J. Bot. **4:** 354. 1845. Type. Brazil. Rio de Janeiro: Organ Mountains, Dec 1837–Jan 1838 (fl), *Miers s.n.* (lectotype, BM, here designated; isolectotypes, A, K, NY, P, US).

Pionandra diploconos (Martius) Miers, London J. Bot. **4:** 357. 1845.

Pionandra fragrans (Hooker) Miers, London J. Bot. **4:** 357. 1845.

Cyphomandra fragrans (Hooker) Sendtner, *in* Martius Fl. Bras. **10:** 116. 1846.

Pallavicinia fragrans (Hooker) DeNotaris, Flora **30:** 568. 1847.

Cyphomandra floribunda (Miers) Dunal *in* DC. Prodr. **13(1):** 390. 1852.

Cyphomandra diploconos var. *brevifolia* Dunal *in* DC. Prodr. **13(1):** 390. 1852. Type. Cultivated in Jardin Botanique, Geneva, 1834, *Dunal s.n.* (lectotype, G DC, here designated [US neg. 8497 F, GH, LL, NY, US]).

Cyphomandra piperoides Dunal, DC. Prodr. **13(1):** 390. 1852, pro syn.

Small *tree* 1–4 m tall. *Branches* glabrous to moderately or rarely densely puberulent to pi-

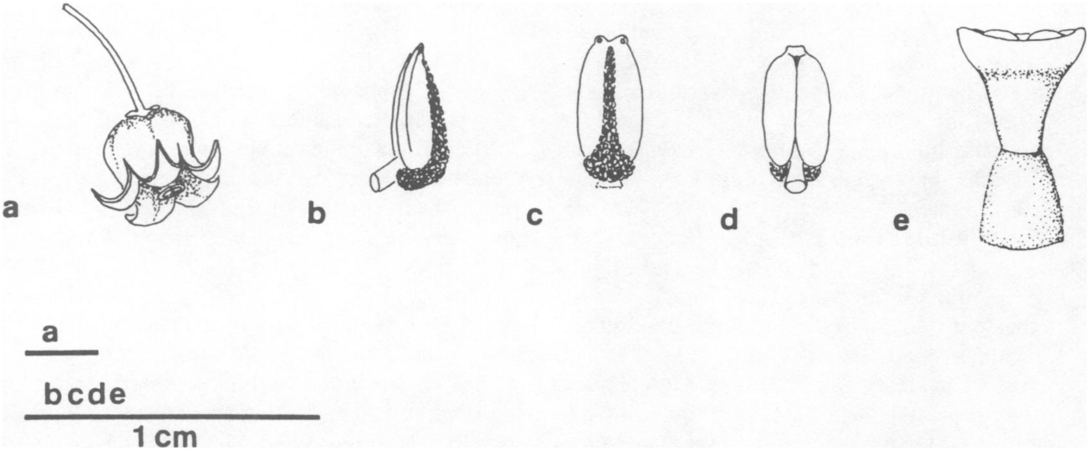


FIG. 29. *Cyphomandra diploconos*. **a.** Flower. **b-d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on greenhouse material of *Bohs 2335*.

lose. *Leaf blades* simple, unlobed or lobed, subcoriaceous, acuminate at apex, glabrous adaxially except for puberulence along midrib and main veins, glabrous to densely puberulent abaxially, pubescent to pilose on both surfaces in a few collections; petioles glabrous to densely puberulent, occasionally pilose, especially in adaxial channel. *Trunk leaves* simple, unlobed or pinnately 3–5-lobed; if unlobed, the blade elliptic to elliptic-ovate, (6-)10–21 cm long, 4–11 cm wide, length:width ratio (1.5–)2–2.5:1, the base cordate to cuneate or truncate with basal lobes up to 1 cm long; if lobed, the blade 12–20 cm long, 9–18 cm wide, divided 1/2–3/4 to midrib, the sinuses rounded, acute, the base truncate to cordate with basal lobes less than 1 cm long; petioles 3.5–14 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade elliptic to ovate, 2.5–15 cm long, 2–8 cm wide, length:width ratio 1.5–2.5(–3):1, the base cuneate to rounded or cordate with basal lobes up to 1 cm long; petioles 1–5 cm long. *Inflorescence* unbranched or rarely forked, 10–20-flowered, 3–15 cm long; peduncle 1–5 cm long; rachis 2–11 cm long; pedicels (10–) 15–25 mm long, 20–30 mm long in fruit, 2–5(–10) mm apart, articulated above the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachis, and pedicels glabrous to sparsely or rarely densely puberulent. *Flower buds* ovoid to oblong, obtuse or apiculate at apex. *Calyx* somewhat fleshy, glabrous to moderately puberulent, the radius 3–6 mm, the lobes 2–3.5 mm long, 2–3 mm wide, deltate, acute to acuminate. *Corolla* purple or greenish-white fading to yellow-green, coriaceous, campanulate, the radius 8–17 mm, the tube 2.5–6 mm long, the lobes triangular, 5–13 mm long, 2–4 mm wide, glabrous to sparsely glandular-puberulent abaxially, minutely papillose adaxially, the margin minutely tomentose, the apex acute to acuminate. *Anther thecae* white or purplish, oblong, 3–5 mm long, 2–3 mm wide, the pores directed abaxially and laterally; connective purple or cream fading to yellowish brown, 4–6 mm long, 1.5–2 mm wide at base, abruptly narrowed distally, abaxially slightly shorter than thecae at apex, exceeding them at base by 0.5–1 mm, adaxially absent. *Ovary* glabrous to minutely puberulent; style obconical, glabrous to sparsely puberulent, strongly dilated distally, 2–4 mm long, 0.5–1.5 mm in diam. at base, 2–4.5 mm in diam. at apex, slightly exserted beyond stamens; stigma concave with two apical glands, 2–4.5 mm in diam. *Fruit* ellipsoidal, obtuse at apex, 2–6 cm long, 2–3 cm in diam., densely puberulent when young, glabrescent when older, yellow to orange when mature; mesocarp without stone cell aggregates; seeds 2–3 mm long, 2–3 mm wide, minutely puberulent.

Distribution (Fig. 25C) and phenology. Clearings and edges of forest in Atlantic coastal rain forest and *Araucaria* stands of southeastern Brazil in the states of Paraná, São Paulo, Minas Gerais, Rio de Janeiro, Santa Catarina, and Rio

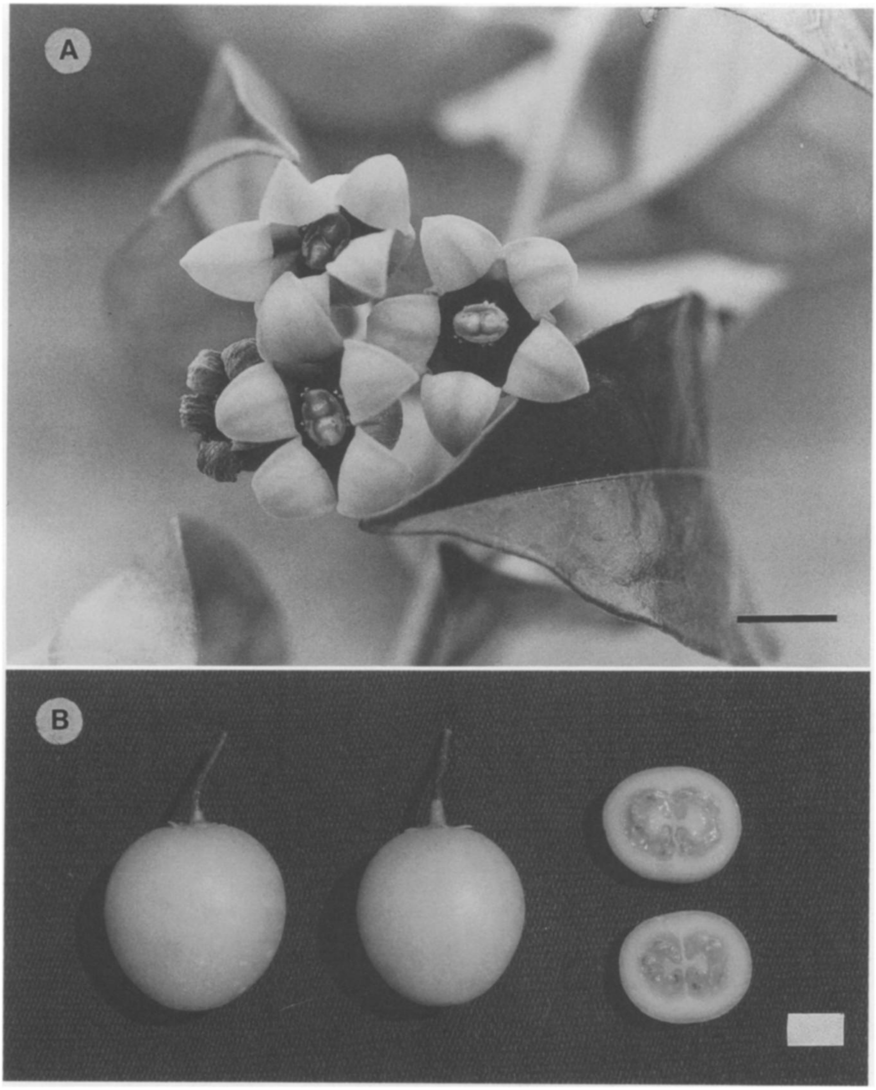


FIG. 30. *Cyphomandra diploconos*. **A.** Flowers. **B.** Fruits. Scale bars = 1 cm. From greenhouse material of *Bohs 2335*.

Grande do Sul at elevations of 50–1000 m. Flowering specimens have been collected in January, February, April, June, and August through December with a peak of flowering in October through January. Fruiting specimens have been collected in January through April, July, November, and December.

Additional specimens examined. BRAZIL. ESPÍRITO SANTO: Mun. de Serra, near Vitória, Estacão Biológica de Mestre Álvaro, 21 Nov 1982 (fl), *Pirani et al. 181* (SP). **MINAS GERAIS:** without locality, *Saint-Hilaire C1 15* (P); Caratinga, Estacão Biológica de Caratinga, 19° 40'S, 41° 50'W, 13 Nov 1983 (fl), *Strier 1296* (NY). **PARANÁ:** Bairro São Nicolau, Curitiba, 18 Nov 1966 (fl), *Caprioglioni 1657* (NY, US); between Curitiba and Joinville, banks of Rio do Santa near bridge of Highway 101 at km 70, 600 m, 5 Jan 1974 (fl), *Conrad & Dietrich 2057* (GH, MO); Capão Grande, 27 Nov 1908 (fl), *Dusén 7284* (GH, NY, S); inter Roca Nova et Banhado, 30 Dec 1908 (fl),

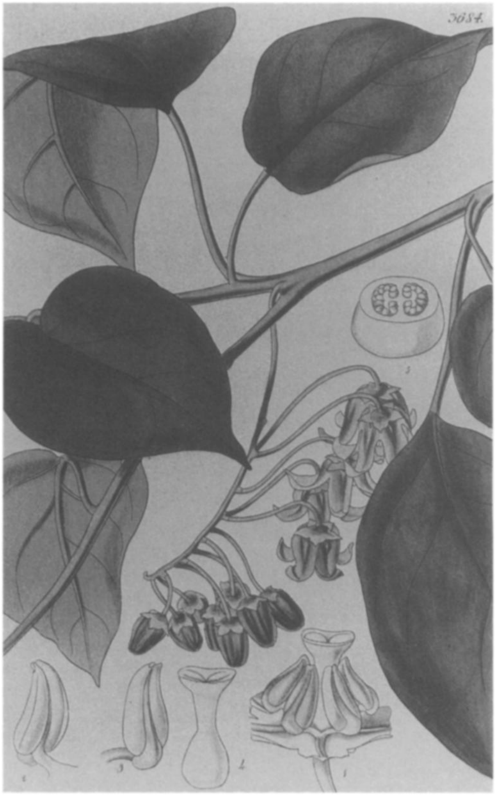


FIG. 31. Illustration of *Solanum fragrans* Hooker, Tab. 3684 from Curtis' Botanical Magazine, chosen as the lectotype of this name.

Dusén 7422 (S); Capão Grande, 4 Feb 1909 (fl), *Dusén 7630* (GH, NY, S); Tres Barras, 21 Jan 1916 (fl, fr), *Dusén 17510* (GH, S); margin of road to Dorizon (Mallet), 12 Mar 1929 (st), *Gurgel 14608* (RB); Cerro Azul, 3 Oct 1949 (fl), *Hatschbach 1514* (MBM, US); Mun. Guaratuba, Pedra Branca de Araraquara, 50–150 m, 13 Dec 1962 (fl), *Hatschbach 9678* (US); Mun. Piraquara, Novo Tirol, 950 m, 27 Nov 1964 (fl), *Hatschbach 11897* (MBM); Mun. Antonina, Rio Cotia, 30 Nov 1965 (fl), *Hatschbach 13204* (F, MA, NY, US, WIS); Mun. Morretes, Rod. BR 277, Estr. Arraial, 17 Jan 1969 (fl), *Hatschbach & Fontella 20821* (C, MO, NY); Mun. San Mateus do Sul, Vargem Grande, 780 m, 16 Dec 1969 (fl), *Hatschbach 23265* (MBM, NY); Mun. Campina Grande do Sul, Figueira, Rio Capivari, 19 Dec 1972 (fl), *Hatschbach 31001* (BH, NY); Mun. Guaratuba, Usina de Guaricana, 30 Dec 1981 (fl), *Kummrow 1647* (MA, MBM); Curitiba, Parque Iguaçu, 21 Nov 1988 (fl), *Kummrow & Soares 3095* (GH, UT); Mun. Morretes, Via Graciosa, Grota Funda, ca. 25° 20'S, 48° 50'W, ca. 600 m, 13 Dec 1977 (fl), *Landrum 2865* (CTES, NY); Mun. Pinhão, Capão Cachambu, 18 Mar 1967 (fr), *Lindeman & Haas 4970* (MBM); Curitiba, Parque Iguaçu, 16 Dec 1987 (fl), *Soares s.n.* (VIC 10284)(GH). **Rio de Janeiro:** Itabapoana, Oct 1909 (fl), *Atamparo 1021* (US); Corcovado Range, ca. 23° S, 300–700 m, 29 Jan 1924 (fr), *Bailey & Bailey 711* (BH); Faz. São José de Cassorotiba, Inoham (E. F. Maricá), Oct 1939 (fl), *Figureido s.n.* (RB); Rio de Janeiro, *Gaudichaud 514* (BR, F, G, P, W [F neg. 2933 F, G, GH, NY, WIS][F neg. 6859 F, GH, NY, WIS]); Petrópolis, 30 Aug 1868 (fl), *Glaziou 3080* (BR, C, K, P); Corcovado, 4 Sep 1886 (fl), *Glaziou 16293* (C, K, P); Sumaré, 2 Nov 1938 (fl), *Markgraf 3122* (RB); border of Mun. Rio Clara-Mangaratiba, near Rio Pires, ca. 400 m, 17 Mar 1978 (fr), *Martinelli 4070* (RB); Sebastianópolis, *Martius 492* (M); Serra dos Orgãos, *Martius 493* (M); Corcovado, Oct 1835 (st), *Riedel s.n.* (NY); Serra dos Orgãos, 1833, *Vauthier 242* (F, G, GH, P). **Rio Grande do Sul:** Estrada Itapeva, Faxinal Torres, 4 Dec 1976 (fl), *Baptista et al. 34090* (CTES). **Santa Catarina:** ca. 8 km SW of Fuck along highway BR–116 to Lajes, 1000 m, 10 Mar 1976 (fr), *Davidse et al. 11077* (AAU, MO, NY); Horto Florestal, I.N.P., Ibirama, 200 m, 27 Nov 1953 (fl), *Gevieski 50* (L, NY, US); Mata do Hoffmann, Brusque, 50 m, 22 Jan 1952 (fr), *Klein 255* (NY, US); Barra Grande, Canoinhas, 750 m, 11 Dec 1962 (fl), *Klein 3754* (US); Ilha de Santa Catarina, Morro do Rio Vermelho, 200 m, 19 Dec 1968 (fl), *Klein & Bresolin 8064* (US); Ibirama, Horto Florestal I.N.P., 300 m, 25 Nov 1957 (fl, fr), *Reitz & Klein 5692* (B, BR, G, L, M, NY, US, Z); Serra do Matador, Rio do Sul, 550 m, 25 Nov 1958 (fl), *Reitz & Klein 7636* (M, US, Z); Novo Horizonte, Lauro Müller, 400 m, 16 Dec 1958 (fl), *Reitz & Klein 8038* (B, G, L, NY, US); Serra do Espigão, Papanduva, 1000 m, 20 Apr 1962 (fr), *Reitz & Klein 12700* (G, US); Mun. Pôrto União, 21 km S of Pôrto União, 750 m, 5 Feb 1957 (fr), *Smith & Klein 10824* (NY, US); Joenvile, Vila Nova, 13 Dec 1988 (fl), *Soares s.n.* (VIC 10627)(GH). **São Paulo:** São Paulo, Reserva do Parque Estadual das Fontes do Ipiranga, 17 Dec 1980 (fl, fr), *Barros 596* (F, SP); Morro das Pedras, Iguape, Apr 1916 (fl), *Brade 8002* (SP, US); São Paulo, grounds of the Instituto Botânico, 860 m, 21 Feb 1976 (fr), *Davidse 10418* (GH); Cachoeira, San Sebastião, 26 Mar 1892 (st), *Edwall 1729* (SP); São Paulo, Jabaquara, 10 Feb 1936 (fl), *Emelen 5* (SP); Mun. de Caraguatatuba, Serra de Caraguatatuba, 7 km from border of Mun. de Paraibuna and 13 km from Rio Santo Antonio, 8 Nov 1961 (fl), *Fontella & Moura 110* (MO, SP, US, W); Santos, Jan 1905 (fl, fr), *Gaczo s.n.* (HBG); Serra da Cantareira, 10 Nov 1932 (fl), *Gonçalves s.n.* (SP, US); Cantareira, 15 Nov 1919 (fl), *Hoehne 3480* (SP, US); Alto da Serra, Estrada do Vergueiro, 23 Dec 1920 (fl), *Hoehne 4702* (US); Ibití, Estacão Experimental, 26 July 1946 (fr), *Kuhlmann 1384* (SP); between Mauá and Ribeirão Pires (railway São Paulo-Santos), 8 Mar 1954 (fr), *Kuhlmann 3025* (SP); Mun. Jundiaí, Serra do Japi, 7 Nov 1981 (fl), *Leitão et al. 13119* (E, NY), *13135* (E, NY); Morro do Itaipú, Praia Grande, 8 Nov 1898 (fl), *Löfgren 4088* (SP, US); São Paulo, Parque Estadual das Fontes do Ipiranga, 29 Oct 1980 (fl), *Lyra 67* (SP); Moji das Cruzes, Serra da Garganta, 27 Apr 1966 (fr), *Mattos 13589* (SP); Santos, below Monte Serrate, 25 Nov 1874 (fl), *Mosén 2907* (S); Chacara Morrinhos, 22 Dec 1938 (fr), *Pickel 4319* (SP); Reserva do Instituto de Botânica de São Paulo, 16 Nov 1980 (fl), *Rosa & Pires 3770* (NY, SP); São Paulo, Jardim Botânico, Parque do Estado, 11 Nov 1970 (fl), *Sendulsky 1167* (SP); São Paulo, Reserva Biológica do Parque Estadual das Fontes de Ipiranga, 28 Nov 1979 (fl), *Silvestre 215* (SP); same locality, 30 June 1980 (fl), *Silvia et al. 101* (SP); Parque do Estado, 15 Dec 1943 (fl), *Toledo & Kuhlmann s.n.* (SP). **From Cultivation:** Ceylon, Hakgala Gardens, 28 Jan 1926 (st), *Fairchild & Dorsett 325* (US); Kew, 1936, *Jones s.n.* (BH); Hort. Bot. Dahlem, 26 May 1922 (fl), *Schlechter s.n.* (B).

Local names and uses. Brazil: Baga de bugre (*Klein 255*), baga de veado (*Klein & Bresolin 8064*; *Kummrow 3095*; *Reitz & Klein 12700*); tomate silvestre (Corrêa, 1975). Fruits reported to be edible when ripe and are being tried in New Zealand under the name "guava tamarillo" (L. Meadows, pers. comm.).

Cyphomandra diploconos can be distinguished from other cyphomandras of southeastern Brazil by its very broadly expanded and nearly glabrous stigma and style, usually glabrous foliage, and globose fruits without stone cell aggregates. Its fleshy, campanulate corolla, broad and curved stamens with the connective abruptly narrowed above the base, expanded style and stigma, and puberulent fruits indicate a close relationship with the Brazilian *C. sciadostylis*, *C. calycina*, and *C. premnifolia.*

Cyphomandra diploconos most closely resembles *C. sciadostylis.* Both species have paired crown leaves, broadly expanded stigmas and styles, and frequently some pinnately lobed leaves, especially on the trunk. *Cyphomandra diploconos* differs from *C. sciadostylis* in that the vegetative parts are nearly always glabrous to minutely puberulent, whereas those of *C. sciadostylis* are densely puberulent and often also pilose with long eglandular hairs. Although both species occasionally produce lobed trunk leaves, those of *C. diploconos* are usually three- to five-lobed, whereas those of *C. sciadostylis* may be pinnately compound with up to nine leaflets. *Cyphomandra diploconos* differs further from *C. sciadostylis* by having a glabrous style. In addition, the fruits of *C. diploconos* are obtuse at the apex, lack stone cell aggregates, and are covered with short glandular hairs that break off with age. The fruits of *C. sciadostylis* are acute at the apex, have obvious stone cell aggregates, and are densely pubescent with longer glandular and eglandular hairs. *Cyphomandra diploconos* is characteristic of the Atlantic coastal rain forest; *C. sciadostylis* occupies a more inland range that extends westward to Argentina and Paraguay.

Many collections of *C. diploconos* have a dense but fine covering of hairs on the abaxial surfaces of the leaves and sometimes also on the stems, inflorescence axes, and abaxial corolla surfaces. Some of these collections also have more acuminate corolla lobes than the glabrate specimens of *C. diploconos*, with the result that the buds appear apiculate when dried. The puberulent collections frequently have the connective prolonged abaxially below the bases of the thecae by about 1 mm, whereas the connective in the glabrate form usually equals the bases of the anther thecae. The collections with fine puberulence beneath the leaves and with apiculate buds have been treated as a distinct species, *C. floribunda* (Miers) Dunal, but these characteristics are variable and intergrade too much to justify taxonomic distinction.

Normally the corolla is a very deep purple upon anthesis, but fades to yellowish green after a few days. One plant that I cultivated in the greenhouse, however, had white or cream-colored corollas that faded to greenish. Except for this difference in corolla color, this plant resembled the others in all particulars.

Three collections from northern Rio de Janeiro, eastern Minas Gerais, and Espírito Santo (*Atamparo 1021*, *Pirani et al. 181*, and *Streier 1296*) have longer (1–2 mm) and denser pubescence than is typical of the other collections of *C. diploconos.* No fruits are present on any of the specimens. These densely pubescent collections may represent an infraspecific variant of *C. diploconos*, but a taxonomic decision is deferred until better material becomes available.

Martius did not clearly specify a type for his *Witheringia diploconos.* No collection number or herbarium location is given, and the protologue gives the type locality as "inter sepes et in sylvis caeduis ad Tijuca et alibi prope Sebastianopolin, nec non in tractu montium, Serra do Mar dicto, Augusto ad Novembrem florebat." Three specimens collected by Martius and annotated as *Witheringia diploconos* Mart. exist at M. The locality information from the labels is as follows: (1) "in via ad Tijuca et prope Fazenda dos Negros, Prov. Sebastianopolis, Dec," (2) "in sepibus ad Sebastianopolis, Prov. Rio de Janeiro, Aug," and (3) "in sepibus M. Serra dos Orgãos, Prov. Rio de Janeiro, Nov." Sheet 1 has a long descriptive note, apparently in Martius' handwriting, giving the collection date as November and the collection number as 245. Sheet 2 has a descriptive note in Sendtner's hand. All three sheets have small tags attached to the twigs with the numbers 490, 492, and 493, respectively. Martius apparently examined all three of these specimens and probably based his description in the protologue on all of them. None of them precisely resembles the illustration of Tab. 229 in Martius (1829), but 2 comes the closest. In the absence of other information and considering the fact that none of the information of the above sheets conflicts with the protologue, I consider the three sheets as syntypes, and have chosen Martius 245 (1 above) as the lectotype.

Cyphomandra diploconos has long been known under the name of *Cyphomandra fragrans* (Hook.) Sendtn., and it is unfortunate that the latter name must be relegated to synonymy. Hooker's epithet has probably been favored because of the excellent colored illustration that accompanied his description of *Solanum fragrans* Hook. in Curtis' *Botanical Magazine* (Hooker, 1839; Fig. 31). No type specimen for this name is known to exist, so the published illustration is here designated as the lectotype.

Dunal described his *C. diploconos* var. *brevifolia* from a living specimen cultivated at the botanic garden in Geneva. A collection at herb. DC taken from this garden and annotated by Dunal is chosen as the lectotype.

The specimen annotated by Miers at BM has been chosen as the lectotype of *Pionandra floribunda* Miers. This sheet is a mixed collection; four leaves apparently belong to *Weir* (Miers?) *467*, collected at Corvo, São Paulo. Although the specimens at A, K, NY, P, and US have very scanty locality data and, with the exception of 4537 on the K specimen, have no collection numbers, it is reasonable to consider them as isolectotypes. All are Miers' collections from Rio de Janeiro annotated as *Cyphomandra floribunda.*

This species has been frequently grown as an ornamental due to its small size and attractive flowers and foliage, and is now being tried as a fruit crop in New Zealand. The thick, leathery mesocarp and glandular puberulence of the berry will probably be obstacles to its acceptance as a fruit crop.

8. **Cyphomandra divaricata** (Martius) Sendtner, Flora **28:** 174. Tab. 9, fig. 1–6. 1845.

Fig. 32.

Witheringia divaricata Martius, Nov. Gen. Sp. Pl. **3:** 75. Tab. 228. 1829. Type. Brazil. São Paulo: Serra do Mar, descent from Mineiro to Lorena in valley of Rio Paraiba, ca. 1200 ft elev., flowering in Dec, *Martius 496* (lectotype, M, here designated).

Cyphomandra divaricata var. *herbacea* Sendtner, Flora **28:** 175. 1845. Type. Southern Brazil, *Sellow 252* (lectotype, P, here designated; isolectotype, B, destroyed [F neg. 2929 F, G, GH, NY, US, WIS]).

Pionandra divaricata (Martius) Miers, London J. Bot. **4:** 361. 1845.

Pionandra capsicoides Miers, London J. Bot. **4:** 360. 1845; Miers, Ill. S. Amer. pl. 1: 41. Tab. 9, figs. 1–7. 1850. Type. Brazil. Rio de Janeiro: Cabo Frio, 1827, *Martius s.n.* (lectotype, BM, here designated; isolectotype, K).

Pionandra ciliata Miers, London J. Bot. **4:** 356. 1845; Type. Brazil. Rio de Janeiro: Serra dos Orgãos, Jan 1838 (fr), *Miers s.n.* (lectotype, BM, here designated).

Cyphomandra divaricata var. *flexipes* Sendtner in Martius, Fl. Bras. **10:** 119. 1846. Type. Brazil. *Schott 5450* (lectotype, W, here designated; isolectotypes, F, W).

Cyphomandra capsicoides (Miers) Walpers, Repert. Bot. Syst. **6:** 579. 1847.

Cyphomandra ciliata (Miers) Walpers, Repert. Bot. Syst. **6:** 578. 1847.

Cyphomandra oxyphylla Dunal *in* DC. Prodr. **13(1):** 396. 1852. Type. Brazil. Bahia, 1830, *Blanchet 124* (holotype, G [herb. DC.]).

Cyphomandra laxiflora Dunal in DC. Prodr. **13(1):** 397. 1852. Type. Brazil, 1815, *Sellow 158* (holotype, BM).

Pionandra oxyphylla (Dunal) Miers, Ann. Mag. Nat. Hist. **15,** ser. 2: 198. 1855.

Pionandra laxiflora (Dunal) Miers, Ann. Mag. Nat. Hist. **15,** ser. 2: 198. 1855.

Small *tree* 1–6 m tall. *Branches* glabrous to densely pubescent-pilose with curled eglandular hairs ca. 1–2 mm long. *Leaf blades* simple, unlobed, chartaceous to membranaceous, acuminate at apex, sparsely to moderately pubescent-pilose adaxially, glabrous to densely pubescent-pilose abaxially; petioles glabrous to densely pubescent-pilose. *Trunk leaves* not represented. *Crown leaves* 4 per sympodial unit, the blade elliptic to ovate, 3–18 cm long, 1.5–7 cm wide, length:width ratio 1.5–3(–4):1, the base cuneate, truncate, or rounded, without basal lobes; petioles 0.5–2 cm long. *Inflorescence* simple, 4–20(–30)-flowered, 5–30 cm long; peduncle 2–6.5 cm long; rachis 3–27 cm long; pedicels (10–)15–25 mm long, 20–35 mm long in fruit,

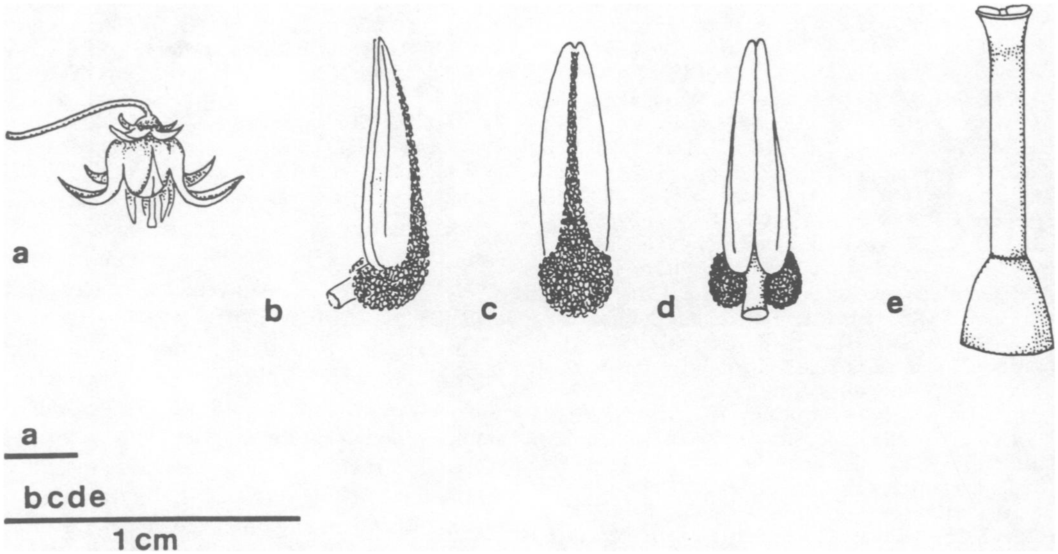


FIG. 32. *Cyphomandra divaricata.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Hatschbach 15323* (L).

(1–)4–15(–30) mm apart, articulated near the base, leaving pedicellar remnants up to 1(–2) mm long; peduncle, rachis, and pedicels glabrous to densely pubescent-pilose. *Flower buds* ovoid, acute or obtuse at apex. *Calyx* chartaceous, moderately pubescent-pilose, the radius 3–7 mm, the lobes (1.5)3–6 mm long, 1.5–2 m wide, triangular, acute, often dentate at base. *Corolla* white, green, or purplish, chartaceous to membranaceous, (stellate-)campanulate, the radius 10–22 mm, the tube 3–4 mm long, the lobes narrowly triangular, 7–19 mm long, 3–5 mm wide, sparsely to densely pubescent-pilose abaxially, glabrous to sparsely pubescent adaxially, the margin tomentose to ciliate with hairs up to 1 mm long, the apex acute. *Anther thecae* yellow, white, or purplish, lanceolate, 7–8 mm long, 1.5–2 mm wide, the pores directed abaxially; connective purple, broad at base, abruptly constricted 1–2 mm above base, 8–9 mm long, 2–3 mm wide at base, abaxially slightly shorter than thecae at apex, exceeding them at base by 1 mm, adaxially absent. *Ovary* glabrous; style glabrous, cylindrical, not to slightly dilated distally, 6–9 mm long, 0.5–1 mm in diam., about equal to or exserted ca. 1–2 mm beyond stamens; stigma truncate, 0.5–1.5 mm in diam. *Fruit* ellipsoidal, obtuse at apex, 2.5–4.5 cm long, 1–3 cm in diam., glabrous (occasionally minutely puberulent), the color when ripe unknown; mesocarp with smooth oval stone cell aggregates ca. 3–5 mm long and 3 mm in diam.; seeds ca. 2–4 mm long, 1–3 mm wide, reticulate.

Distribution (Fig. 25D) and phenology. Primary or secondary forest, often in *Araucaria* groves, coastal rain forest region of southeastern Brazil in the states of Bahia, Espírito Santo, Minas Gerais, Paraiba, Paraná, Rio de Janeiro, Santa Catarina, and São Paulo at elevations of 50–800 m. Flowering specimens have been collected in January, February, May, and September through December, with a peak of flowering from October through January. Fruiting specimens have been collected in January, February, May, and December.

Additional specimens examined. BRAZIL. Bahia: without locality, 1832–1834, *Blanchet s.n.* (BM, F, G); near Ilhéus, *Martius 626* (BM, BR, G [US neg. 8498 F, GH, LL], L, M, MO, P, W); Mun. Itacaré, ramal da torre da Embratel com entrada no km 15 da Rod. Ubaitaba/Itacaré (BR 654), 8 Feb 1979 (fr), *Mori et al. 11513* (RB); Mun. Itacaré, ca. 25 km SE de Ubaitaba, ca. 200–300 m, 21 Oct 1979 (fl), *Mori & Benton 12862* (RB); Mun. Itacaré, acesso a torre da Embratel, 24 Sep 1977 (fl), *Santos 3129 & Mattos 101* (NY, US); Mun. Ilhéus, estrada que liga Olivença a Vila Brasil, 16 Feb 1982 (fr), *Silva et al. 1531* (RB). **Espírito Santo:** 35 km N of Conceição da Barra, 13 Nov 1968 (fl), *Almeida & Santos 233* (F, US); Mun. de Serra, near Vitória, Estacão Biológica Mestre

Álvaro, 21 Nov 1982 (fl), *Pirani et al. 185* (SP). **Minas Gerais:** Viçosa, 3 Feb 1934 (fl), *Kuhlmann 1769* (RB); Caldas, Nov 1854 (fl), *Lindberg 171* (BR); Villa Ricca, *Martius s.n.* (BM); road to Cajurý, Fazenda F. Lopez, 700 m, 17 Nov 1930 (fl), *Mexia 5310* (A, BH, BM, G, GB, GH, MO, NY, S, TEX, U, US, WIS, Z); Dist. Rio Branco, Fazenda Bom Jardim, Pedera, 720 m, 2 Jan 1931 (fr), *Mexia 5474a* (F, GH, US); Caldas, Jan-Feb 1873 (fl), *Mosén 661* (P, S); Caldas, 1860–1861, *Regnell II 218 1/8* (BR, LD, S, US); Viçosa, road to Cajuri, Sitio Canelas, 7 Nov 1989 (fl), *Soares s.n.* (VIC 11218)(UT). **Paraiba:** Areia, Escola de Agronomia do Nordeste, 4 Jun 1953 (st), *Moraes 735* (RB). **Paraná:** Bom Retiro, Curitiba, Nov 1966 (fl), *Dombrowski 2175 & Kuniyoshi 1900* (US); Capão da Imbuia, Curitiba, Oct 1967 (fl), *Dombrowski 2630* (US); Ponta Grossa, 9 Dec 1903 (fl), *Dusén 2485* (BM, GH, S, WU); without locality, 1903, *Dusén 3011* (S, US); Roca Nova-Banhado, 30 Dec 1908 (fl), *Dusén 7421* (GH, NY, S); Capão Grande, 4 Feb 1909 (fr), *Dusén 7526* (S); Ipiranga, 16 Jan 1914 (fl), *Dusén 14400* (F, GH, NY, S); Jaguariaíva, 26 Nov 1914 (fl), *Dusén 15949* (F, GH, NY, P, S); Tres Barras, 21 Jan 1916 (fl), *Dusén 17509* (F, GH, NY, S); Mun. Piraquara, Borda do Campo, 17 Dec 1950 (fl), *Hatschbach 2049* (MBM, US); Mun. Morretes, Picada Eng. Lange-Marumbi, 1 Dec 1966 (fl), *Hatschbach 15323* (F, L, NY, US); Mun. Campina Grande do Sul, Sitio do Belizario, 14 Nov 1967 (fl), *Hatschbach 17820* (F, MBM, Z); Mun. Ponta Grossa, Passo do Pupo, 4 Dec 1967 (fl, fr), *Hatschbach 17980* (C, F, L, MO); Mun. Morretes, Col. Floresta, 100 m, 5 Nov 1968 (fl), *Hatschbach 20195* (MBM); same locality, 50–100 m, 24 Jan 1969 (fl), *Hatschbach & Koczicki 20903* (C, CTES); Mun. S. Mateus do Sul, Vargem Grande, 780 m, 16 Dec 1969 (fl, fr), *Hatschbach 23266* (BH, C, LP, LL, MBM, MO, NY, SP); Mun. Piraquara, Nova Tirol, 29 Oct 1977 (fl), *Hatschbach 40426* (UT); Bocaiuva do Sul, 5 Dec 1978 (fl), *Hatschbach 41913* (MBM, UT); Mun. Antonina, Rio do Nunes, 14 Nov 1980 (fl), *Hatschbach 43280* (MBM, UT, Z); Curitiba, Parque Iguaçu, 23 Nov 1988 (fl), *Kummrow 3102* (GH, UT); Mun. Piraquara, ca. 10 km E of Curitiba, 25° 30'S, 49° 10'W, 1 Dec 1981 (fl), *Landrum 3914* (F); Mun. Lapa, Gruta do Monge, 1 Dec 1982 (fl), *Oliveira 704* (MBM); Mun. Curitiba, Recanto das Araucarias, 16 May 1989 (fl), *Ribas & Cordeiro 99* (UT); Colonia São Nicolau, Curitiba, 20 Dec 1966 (fl), *Stellfeld 1667* (NY, US). **Rio de Janeiro:** Tinguá, 1 Oct 1946 (fl), *Brade 18611* (GH); Mun. Terezópolis, Campo Limpo, 28 May 1977 (fl, fr), *Carvalho 509* (B, F, G, NY, RB, WIS, Z); Serra do Coello, near Rezenda, 21 Nov 1876 (fl), *Glaziou 8870* (C, P); Nova Friburgo, 17 Nov 1890 (fl), *Glaziou 18403* (BR, C, G, P); Mundo Novo, Botafogo, 17 Dec 1920 (fl), *Kuhlmann s.n.* (RB); Mun. Terezópolis, Parque Nacional da Serra dos Orgãos, Subsede do Parque, 300–400 m, 21 Oct 1977 (fl), *Maas & Martinelli 3398* (F, K, U); Organ Mountains, *Miers 4531* (K); Quitandinha, Petrópolis, 1948, *Octavio 68* (SP); Vale do Bomsucesso, Petrópolis, ca. 700 m, 6 Dec 1968 (fr), *Sucre 4206 = Braga 1162* (GH). **Santa Catarina:** Barra Grande, Canoinhas, 750 m, 11 Dec 1962 (fl), *Klein 3746* (B, L, NY, US). **São Paulo:** Morro dos Pedras, Oct 1917 (st), *Brade 8000* (US); São Paulo, native to Jardim Botânico, 23 Nov 1932 (fl), *Handro s.n.* (SP, US); Campinas, *Heiner s.n.* (S); Aracá, Caixa d'agua, 21 Dec 1918 (fl, fr), *Hoehne s.n.* (SP 2645) (SP, US); Itapetininga, near Hôrto Florestal, 13 Nov 1967 (fl), *Mattos & Mattos 15123* (SP); Serra da Caracol, 5 Jan 1876 (fl), *Mosén 4302* (S); Campinas, *Campos Novaes 6153* (SP, US); Campinas, 22 Dec 1931 (fl, fr), *Silva s.n.* (SP 28627) (SP); between Rio Grande and Alto da Serra, ca. 800 m, 1902, *Wacket s.n.* (WU).

Local names and uses. Brazil: Baga de veado (Smith & Downs, 1966), tomate arboreo (*Moraes 735*), unha de veado (Corrêa, 1975). Reputedly ornamental (*Mexia 5310*).

This species is unique among the Brazilian representatives of *Cyphomandra* in having truncate to cuneate leaf bases, long, slender, curved stamens, and cylindrical styles with small stigmas. The structure of the androecium resembles that of the *C. calycina* group, but the anthers are much longer than any other species in the group, and the membranaceous corolla, slender stigma and style, and glabrous fruits are out of place in that alliance. The long narrow anthers, cylindrical styles, and glabrous fruits of *C. divaricata* point toward a resemblance to Andean species such as *C. tenuisetosa*, *C. pendula*, and *C. hartwegii*, but *C. divaricata* differs from each in many characters. The affinities of *C. divaricata* remain unknown.

Several characters exhibit variation throughout the geographical range of *C. divaricata.* Collections from the northern part of the range, in Bahia, Espírito Santo, and Minas Gerais, are often nearly glabrous. Pubescence tends to increase southward. There is also some variation in the size of the calyx. Most collections have large calyces with a radius of 5–7 mm and narrow lobes about 3–4 mm long and 1.5–2 mm wide. A few specimens, especially from the area around Rio de Janeiro, have calyx radii measuring about 3 mm, with shorter and relatively broader lobes about 1.5–2 mm long and 1.5–2 mm wide. These latter collections, which include the types of *C. divaricata* var. *herbacea*, *C. capsicoides*, *C. ciliata*, *C. oxyphylla*, and *C. laxiflora*, also have relatively broad leaf blades and may have minutely puberulent fruits. Further studies are needed to determine if this variation is significant enough to be recognized taxonomically.

Martius (1829) did not designate a single specimen as a type of his *Witheringia divaricata.* I have chosen as lectotype a specimen at M that roughly matches his Figure 228 and that bears the locality data cited in his protologue. The label and protologue give no collection number, but a small tag attached to the twig bears the number 496. Two other sheets at M have the label data "Martius, Iter brasiliense, St. Pauli," and the small tags attached to the twigs bear the numbers 497 and 498. Although it is possible that all three collections are duplicates, I do not consider them isolectotypes because of the differences in the small numbered tags.

Sendtner's type information for *C. divaricata* var. *herbacea* is given simply as "legit in Brasilia australiore Sellow" (Sendtner, 1845). The specimen and photographs I have seen that are annotated as this variety bear the number *Sellow 252*. The only known extant specimen of *Sellow 252* (at P) has been chosen as the lectotype.

Similarly, Sendtner (1846) did not give any further information for his type of *C. divaricata* var. *flexipes* other than "Schott." Without number or locality data it is difficult to be sure of the type, but a sheet of *Schott 5450* at W is annotated as this variety and is here designated as the lectotype.

Miers, in 1845, described *Pionandra capsicoides* and later illustrated it in his volume of 1850 (Fig. 33). In the protologue, he refers to *Solanum capsicoides* Mart., a species originally described in Martius' *Herbarium Florae Brasiliensis* in 1838. Examination of Martius' protologue for *Solanum capsicoides* indicates that this species has stellate hairs and thus probably belongs to *Solanum* subgenus *Leptostemonum*. In addition, Martius states that the specimen was collected in woods on the mountain of Corcovado near the city of Rio de Janeiro and that it bore only fruits and no flowers.

Miers' account of *Pionandra capsicoides* describes the flowers in detail and mentions that it was found at Cabo Frio in the state of Rio de Janeiro and at Villa Rica in Minas Gerais. Evidently he is basing his taxon *Pionandra capsicoides* on Martius' specimens at BM and possibly at K, which were collected at these localities and bear an unpublished herbarium name in the genus *Witheringia*. Thus, Miers apparently did not see the type specimen of Martius' *Solanum capsicoides*, and *Solanum capsicoides* Mart., a true *Solanum*, has nothing to do with Miers' species. The name is here accordingly referred to as *Pionandra capsicoides* Miers rather than *Pionandra capsicoides* (Mart.) Miers.

Furthermore, the BM sheet is a mixture of two collections of this species, one from Cabo Frio, the other from Villa Rica. As this sheet is labeled "Herb. John Miers" and both specimens are mentioned in Miers' protologue, I consider them to be syntypes and have chosen the lectotype as Martius, Cabo Frio, BM with the isolectotype at K.

The sole existing Miers specimen labeled as *C. ciliata* (*"Cerastemon* (sic) *ciliatum*" on the sheet) known to me has been chosen as the lectotype of this name. The specimen bears only fruits, in accordance with Miers' protologue.

Dunal (1852) cites the type of *C. laxiflora* as "Brazil, Sellow, in h. Banks." The only sheet at BM labeled with this epithet is *Sellow 158*, which I take to be the holotype. The specimen has only flowers, in accordance with Dunal's description. The sheet is labeled "*Solanum laxiflorum*," and *Solanum laxiflorum* Dunal is cited by Dunal (1852) as a synonym of *Cyphomandra laxiflora* Dunal. *Solanum laxiflorum* Dunal is not validly published according to Art. 34 of the *International Code of Botanical Nomenclature* (Greuter et al., 1988), although *Cyphomandra laxiflora* Dunal is. *Solanum laxiflorum* Dunal is furthermore a homonym of *Solanum laxiflorum* Sendtner. Sendtner's species has no relationship with Dunal's *C. laxiflora*.

9. **Cyphomandra diversifolia** (Dunal) Bitter, Repert. Spec. Nov. Regni Veg. **17:** 354. 1921.

Figs. 34, 35, 36.

Small *tree* or *shrub* 1–5 m tall. *Branches* glabrous to densely puberulent(-pubescent), sometimes also sparsely pilose. *Leaf blades* simple or pinnately compound, membranaceous to chartaceous, acuminate at apex, glabrous to densely pubescent-pilose adaxially, glabrous to densely puberulent-pubescent abaxially; petioles glabrous to densely puberulent-pilose. *Trunk leaves* simple to 11-pinnate; if simple, the blade elliptic, 11–16 cm long, 5.5–12 cm wide, length:width ratio ca. 2:1, the base truncate to cordate with basal lobes up to 1 cm long; if compound, the blade 15–30 cm long, 12–27 cm wide, the terminal leaflet elliptic to obovate, 11–22 cm long, 2–9

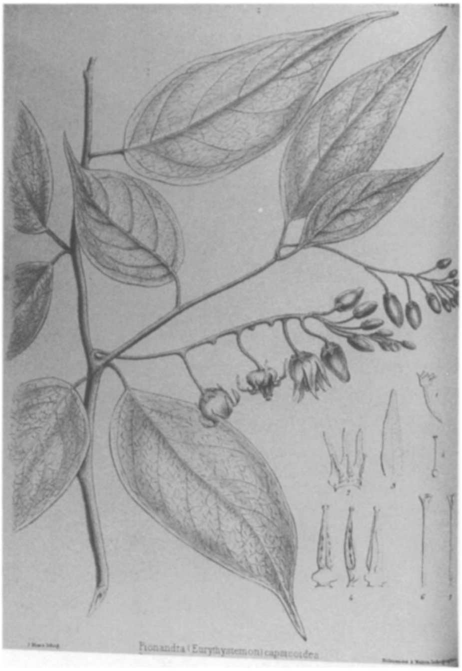


FIG. 33. Illustration of *Pionandra capsicoides* (=*Cyphomandra divaricata*) from Miers (1850).

cm wide, the base cuneate, the petiolule 6–25 mm long, the lateral leaflets 3–18 cm long, 1.5–7 cm wide, the petiolules 0–10 mm long; petioles 2–11.5 cm long. *Crown leaves* 4 per sympodial unit, simple or 3–7-pinnate; if simple, the blade elliptic, 5–20 cm long, 2–12 cm wide, length:width ratio 1.5–3:1, the base cuneate to truncate or shallowly cordate with basal lobes less than 0.5 cm long; if compound, the blade 6–25 cm long, 7–25 cm wide, the terminal leaflet elliptic to obovate, 5–18 cm long, 1.5–8.5 cm wide, the base cuneate, the petiolule 3–30 mm long, the lateral leaflets spreading or ascending, 1.5–13 cm long; petioles 0.5–6 cm long. *Inflorescence* unbranched or branched, 6–40-flowered, 3–30 cm long; peduncle 1–23 cm long; rachises 1–14 cm long; pedicels 8–35 mm long, 15–35 mm long in fruit, 1–13 mm apart, articulated near the base, leaving pedicellar remnants less than 1 mm long; peduncle, rachises, and pedicels glabrous to densely puberulent and sometimes also sparsely pilose. *Flower buds* globose, obtuse at apex. *Calyx* chartaceous to fleshy, glabrous to moderately pubescent, the radius 2–11 mm, the lobes 1–9 mm long, 1.4–4 mm wide, triangular to deltate, acute or obtuse. *Corolla* purple, greenish, or white, somewhat fleshy, urceolate (to campanulate), the radius 8–16 mm, the tube 4–8 mm long, the lobes deltate, 3–7(–10) mm long, 3–7 mm wide, glabrous to densely papillose, puberulent, or tomentose abaxially and adaxially, the margin tomentose, the apex acute. *Anther thecae* white or purple, elliptic-ovate to oblong, 3–5 mm long, 2 mm wide, the pores directed abaxially and laterally; connective yellow or purple, ovate to oblong, 3.5–6 mm long, 1.5–3 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 0.5–1 mm, adaxially not present. *Ovary* glabrous; style glabrous, cylindrical, slightly dilated distally, 5–7.5 mm long, 0.5–1 mm in diam., exserted 1–3 mm beyond stamens; stigma truncate to capitate, 1–1.5 mm in diam. *Fruit* ellipsoidal, globose to fusiform, acute or obtuse at apex, (1–)2–8.5 cm long, 1–3 cm in diam., glabrous, yellow or orange when ripe, often with darker longitudinal stripes; mesocarp without stone cell aggregates; seeds 2.5–6 mm long, 2–5 mm wide, reticulate to minutely puberulent.

Distribution (Fig. 37). Light gaps and disturbed areas in cloud forest in Costa Rica, Panama, Colombia, and Venezuela at elevations of 500–3000 m in South America, 20–400 m in Central America.

This distinctive species can be recognized by its urceolate corollas, usually pinnately compound leaves, and short, curved stamens with broad connectives. It most closely resembles *C. pendula* of Peru and Bolivia, but differs in its lack of dense tomentum on the abaxial corolla surface.

My concept of *C. diversifolia* encompasses a great deal of variation in pubescence and in leaf, calyx, fruit and seed morphology. Nevertheless, most specimens of *C. diversifolia* are readily recognizable as such. At least two morphological and geographical entities can be discerned within the species, and are treated as subspecies. I have avoided recognizing these entities as species in part because they are distinguished by fruit characters, which are often lacking in herbarium material. Other than differences in calyx morphology, which exhibits considerable local variation (see below and Fig. 37), the two subspecies are very similar in vegetative and floral characters.

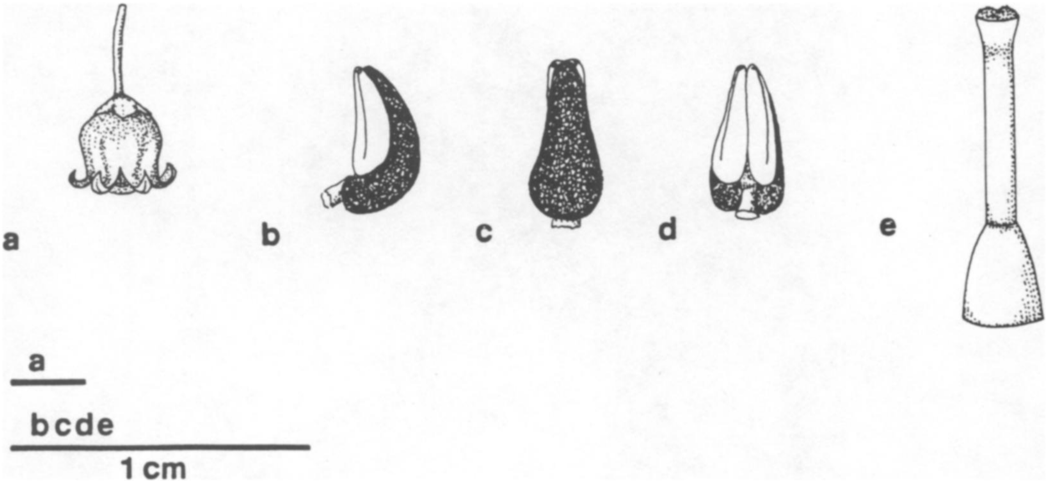


FIG. 34. *Cyphomandra diversifolia.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on greenhouse material of *Benitez de Rojas 2744.*

KEY TO THE SUBSPECIES OF *CYPHOMANDRA DIVERSIFOLIA*

1a.	Fruits elongated, acute at apex; seeds 2–3 mm in diam.	a. subsp. *diversifolia.*
1b.	Fruits ellipsoidal or globose, obtuse at apex; seeds 4–5 mm in diam.	b. subsp. *chlorantha.*

a. *Cyphomandra diversifolia* (Dunal) Bitter subspecies *diversifolia*

Solanum diversifolium Dunal, Solan. Syn. 8. 1816; H.B.K., Nov. Gen. Sp. **3:** 17 or 22. 1818. Type. Venezuela. Near Caracas, alt. 2700 ft, flowering in Mar, *Humboldt & Bonpland s.n.* (holotype, P-HBK) [F neg. 39019 US, WIS]).

Solanum heterophyllum Willdenow ex Roemer et Schultes, Syst. Veg. **4:** 664. 1819, nomen, pro. syn. *S. caracasanum* Roemer et Schultes (1819), non *Solanum heterophyllum* Lamarck (1794).

Solanum caracasanum Roemer et Schultes, Syst. Veg. **4:** 664. 1819. Type. Venezuela. Near Caracas, *Bredemeyer s.n.* (holotype, B (herb. Willd.) n.v. [F neg. 2926 F, G, GH, NY, US, WIS]; isotypes, W).

Cyphomandra caracasana (Roemer et Schultes) Sendtner, Flora **28:** 168. Tab. II, fig. 1–3. 1845.

Cyphomandra glabra Pittier, Cat. Fl. Venez. **2:** 353. 1947, nom. illeg. (sine diag. Lat.).

Cyphomandra campanulata Moritz ex Steyermark et Huber, Flora del Avila, p. 823. 1978, pro syn.

Inflorescences unbranched or forked, the axes glabrous to densely puberulent-pubescent. *Calyx* chartaceous or fleshy, glabrous to moderately pubescent, the radius 3–11 mm, the lobes 1–9 mm long, 1.5–4 mm wide, deltate to triangular, acute or obtuse at apex. *Fruits* ellipsoidal, elongated, acute at apex, 5–8.5 cm long, 1.5–2 cm in diam. *Seeds* 2.5–3 mm long, 2.5–3 mm wide.

Distribution (Fig. 37) and phenology. Disturbed areas and light gaps in cloud forest, 500–1900 m, coastal Venezuela. Flowering specimens have been collected in all months of the year except January, August, September, and December. Fruiting specimens have been collected in May, July, and August.

Additional specimens examined. VENEZUELA. Aragua: Parque Nacional Henri Pittier, near road to Choroni, Distrito Girardot, 900 m, 29 May 1980 (fl), *Benitez de Rojas 2744* (ECON, GH), seeds grown at Harvard University, Cambridge, Mass. as *Bohs 2341* (F, GH, QCNE, VT); along ascent from Maracay to summit of Alto Choroni, Feb 1973 (fl), *Croat 21452* (MO); trail El Limón-Col. Tovar, 1900 m, May 1934 (fl, fr), *Pittier 13520* (F, MO, US); Parque Nacional Henri Pittier, headwaters of the Río Grande del Medio, vic. Quebrada Río Hondo, between Tremaría and La Regresiva del Diablo in the Fila Alta de Choroni, 1000 m, 30 Apr 1972 (fr), *Steyermark & Carreño Espinoza 105837* (MO, U, US). Distrito Federal: near Ávila, between Los Flores and Papelón, Mar 1937 (fl), *Delgado 7* (F, US); near Colonia Tovar, 1854–1855 (fl, fr), *Fendler 1009* (GH, GOET, MO); a few miles SW of Colonia Tovar, 4000 ft., 18 May 1855 (fr), *Fendler 1015* (GH); Caracas, Jul 1842 (fl, fr), *Linden 7* (G, P); El ávila, Quebrada Paraíso, 1600 m, 7

FIG. 35. *Cyphomandra diversifolia*. Scale bar = 10 cm. From greenhouse material of *Benitez de Rojas 2744*.

Aug 1976 (fr), *Manara s.n.* (MO, NY); Colonia Tovar, Feb 1865 (fl), *Moritz 1702* (B (destroyed) [F neg. 2928 F, G, GH, NY, US, WIS], BM); Parque Nacional El Ávila, between Pico El Ávila and the city of Caracas, just below "Papelón," ca. 1600 m, 20 Jul 1979 (fl), *Nee & Whalen 16798* (BH, F, WIS); middle to upper Catuche wood, above Caracas, 1200–1400 m, 13 May 1917 (fl), *Pittier 7161* (GH, US); 5.5 mi. below junction of Junquito-Colonia Tovar road and road to Hacienda El Limón, 1750 m, 7 Jun 1963 (fl), *Steyermark 91497* (F, NY, US); along old road between "Portachuelo" and "Peñita" (Petaquire) and Carayaca, between Colonia Tovar-Junquito road and Hacienda El Limón, 6–8 mi. below junction of Junquito-Colonia Tovar road, 1300–1500 m, 12 Oct 1965 (fl), *Steyermark 94400* (US); cloud forest of Los Venados, Apr 1943 (fl), *Tamayo 2553* (US). **Miranda:** Los Guayabitos, above Baruta, Nov 1965 (fl), *Aristeguieta 5934* (NY); Siquire Valley, Guinand Estate (Cárdenas), 500–1000 m, 19–24 Mar 1913 (fl), *Pittier 5988* (MO, US). **Sucre:** Peninsula de Paria, Cumbre La Estrella, W of Manacal, N of El Paujil, 10° 40'N, 62° 41'W, 800–850 m, 17 Oct 1984 (fl), *Knapp & Mallet 6769* (BH, US); Dist. Cagigal, Peninsula de Paria, below trail between El Paujil and El Brasil, 10° 39–40'N, 62° 43'W, 850–890 m, 21 Feb 1980 (fl, fr), *Steyermark et al. 121496* (NY).

The elongated fruits and relatively small seeds of subspecies *diversifolia* distinguish it from subspecies *chlorantha*. Subspecies *diversifolia* is restricted to the mountains of coastal Venezuela and is geographically separated from subspecies *chlorantha* by the Yaracuy depression in north-central Venezuela that runs between the Cordillera Mérida and the Cordillera de la Costa.

Considerable local geographic variation occurs

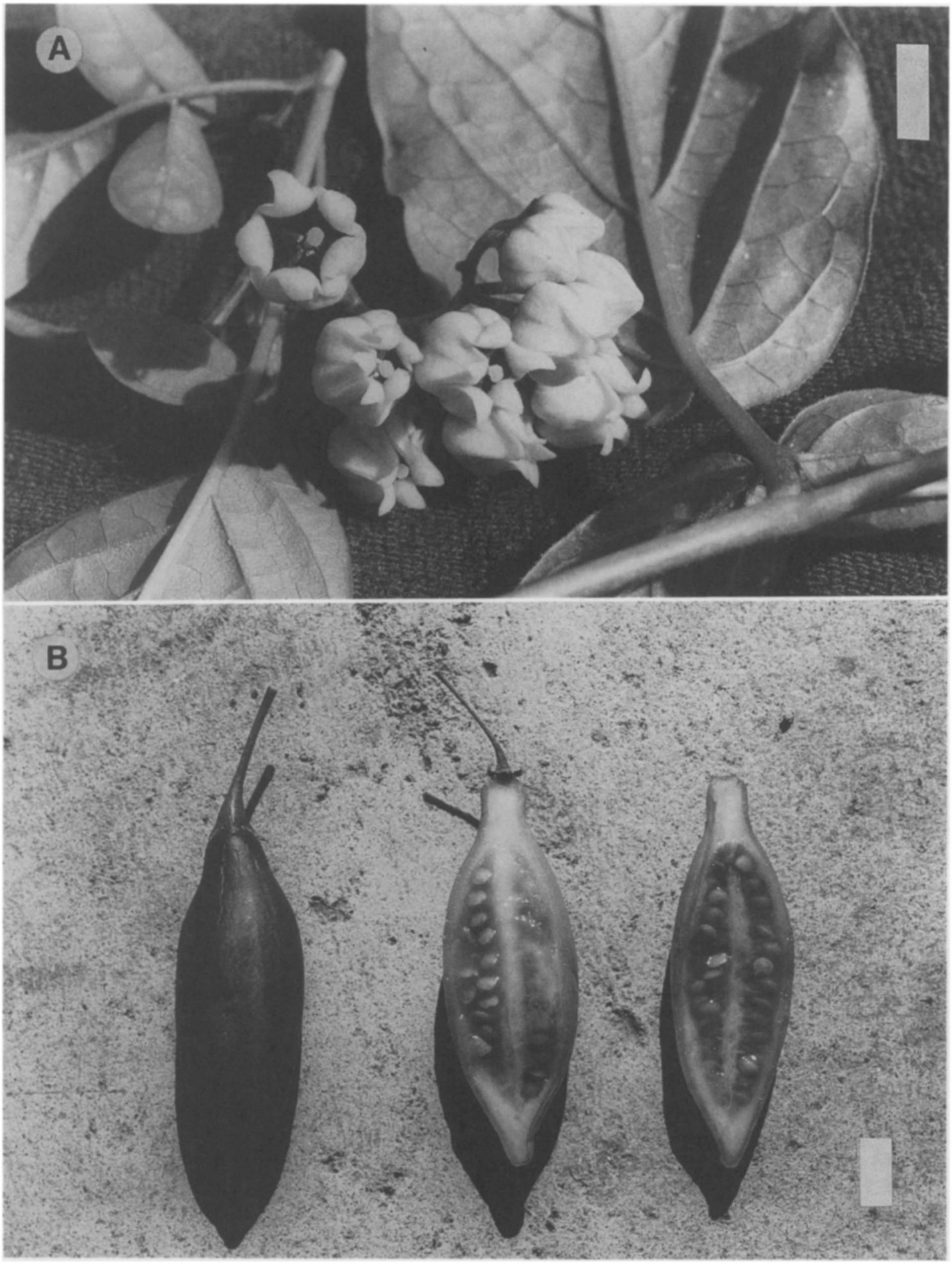


FIG. 36. *Cyphomandra diversifolia*. **A.** Flowers. **B.** Fruits. Scale bars = 1 cm. From greenhouse material of *Benitez de Rojas 2744*.

within subspecies *diversifolia*, perhaps corresponding to isolated populations occupying different peaks of the highly dissected Coastal Cordillera. Steyermark (1979) divided the Coastal Cordillera into several refuges and dispersal centers, emphasizing the distinctness of

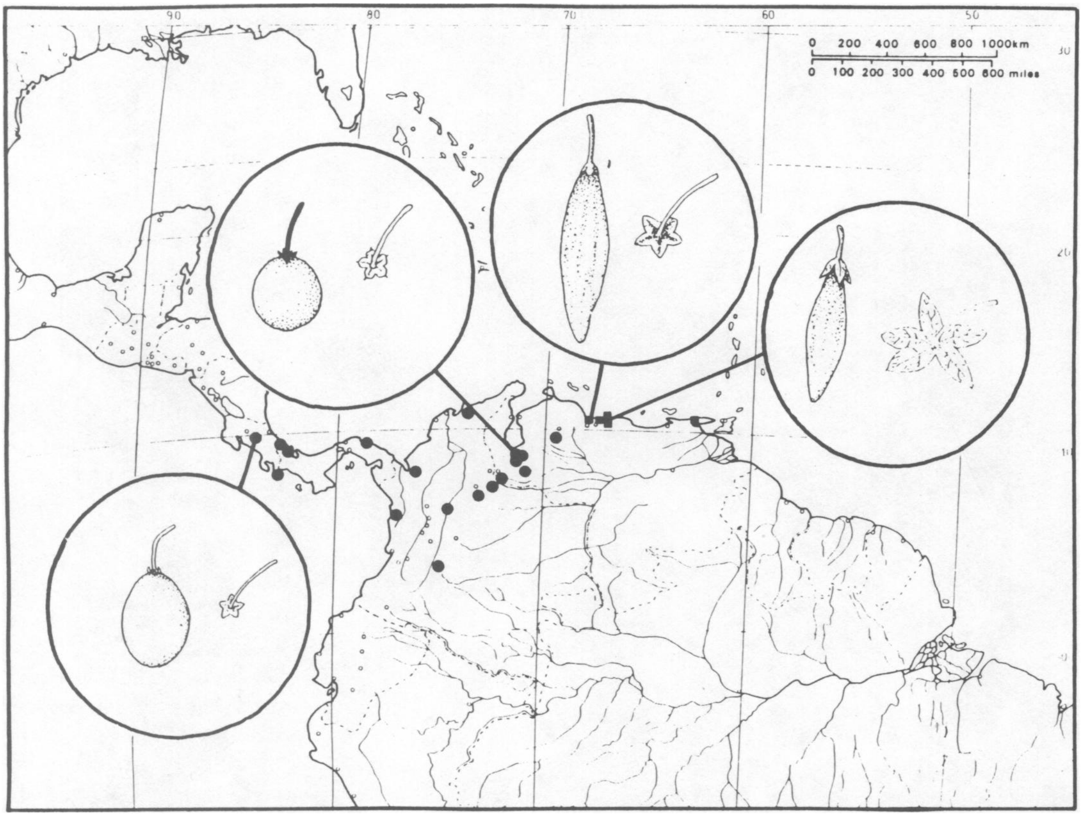


FIG. 37. Distribution of *Cyphomandra diversifolia* subspecies *diversifolia* (squares) and subspecies *chlorantha* (dots). Drawings of fruit and calyx morphology taken from (left to right): *Poveda 1207* (MO); *Bunting & Drummond 6287* (MO); greenhouse material of *Benitez de Rojas 2744*; *Manara s.n.* (MO) (fruit), *Delgado 7* (US) (calyx).

floristic elements in isolated portions of this range. Specimens from Miranda, Distrito Federal, and Aragua near Colonia Tovar have very large calyces (radius 6–11 mm, lobes 4–9 mm long, 3–4 mm wide). Collections from Colonia Tovar are nearly glabrous and were formerly segregated as a separate species, *Cyphomandra glabra* Pittier (Pittier, 1947). These collections are probably better viewed as local variants of subspecies *diversifolia*. Pittier's name is illegitimate because he provided no Latin diagnosis.

Specimens collected in Aragua near Choroni or in the Parque Nacional Henri Pittier differ from the other representatives of subspecies *diversifolia* in their small calyces (radius 3–4 mm, lobes 1–3 mm long, 1.5–2.5 m wide). Collections from the Peninsula of Paría in Estado Sucre may also have small calyces, but my material is not sufficient to evaluate this character critically.

The fruits, though acidulous, are pleasant-tasting and perhaps merit investigation as a fruit crop.

b. *Cyphomandra diversifolia* (Dunal) Bitter subspecies *chlorantha* (Rusby) Bohs, comb. et stat. nov.

Cyphomandra chlorantha Rusby, Descr. S. Amer. Pl. 116. 1920. Type. Colombia. Santa Marta, Valparaiso, rare in damp clearings, flowers January to April, 4500 ft, 26 Jan–25 Feb 1899 (fl, fr), *H. H. Smith 1180*, as '*C. viridiflora* Rusby' (lectotype, NY, here designated; isolectotypes, A, F, G, GH, K, L, LL, MO, NY, P, S, U, US, W, WIS).

Cyphomandra caudata Standley, Publ. Field Columbian Mus., Bot. Ser. **4:** 258. 1929; Standl. *in* Cooper, Trop. Woods **16:** 25. 1928, nom. nudum. Type. Panama. Bocas del Toro: region of Almirante, Daytonia Farm, Jan–Mar 1928 (fl, fr), *Cooper 398* (holotype, F 579172 [F neg. 49358 F, MO, WIS]; isotypes, F, K, NY, US).

Cyphomandra meridensis Pittier *ex* Steyermark & Rojas, Pittieria **7:** 19. 1978; Pittier, Cat. Fl. Venez. **2:** 354. 1947, nom. illeg. Type. Venezuela. Mérida: cloud forest on slopes adjacent to falls of Río La González, below the calcareous outcrops near the road N from La Mesa, E of Jají and SE of La Carbonera, 1900–2100 m, 31 Aug 1966 (fl, fr), *Steyermark & Rabe 97055* (holotype, VEN, n.v.; isotype, US 2583680).

Inflorescences unbranched to branched, the axes glabrous to densely puberulent and often also sparsely pilose. *Calyx* chartaceous, glabrous, the radius 2–8 mm, the lobes 1–6 mm long, 1.5–3 mm wide, deltate to narrowly triangular, acute to apiculate at apex. *Fruits* ellipsoidal or globose, obtuse at apex, (1–)2–3(–5?) cm long, (1–)2–3 cm in diam. *Seeds* 4–6 mm long, 4–5 mm wide.

Distribution (Fig. 37) and phenology. Cloud forest, (90–)600–3000 m in elevation (20–400 m in Costa Rica and Panama), Costa Rica, Panama, Venezuela, and Colombia. Flowering specimens have been collected in January through April, July, September, and November. Fruiting specimens have been collected in January, March, April, May, August, September, November, and December.

Additional specimens examined. COSTA RICA. Alajuela: Buena Vista de Zarcero, 15 Nov 1975 (fr), *Poveda 1207* (F, MO). **Limón:** 1–3 km N of Bribri, Río Sixaola drainage, 9° 38'N, 82° 50'W, 20–200 m, 9–10 Sep 1978 (fl, fr), *Burger & Antonio 11005* (CR, F).

PANAMA. Chiriquí: Burica Peninsula, 8 mi W of Puerto Armuelles, 200 m, 2 Mar 1973 (fl), *Liesner 349* (C, F, L, LL, MO, NY, US). **San Blas:** Kuna reserve Nusagandi on El Llano-Carti road, near summit of road on Caribbean slope, 300–400 m, 24 Feb 1987 (fl), *Bohs & Sperry 2330* (F, GH, PMA, SCZ).

COLOMBIA. Antioquia: Urabá, near Mutatá, 90 m, Jan 1950 (fl), *Uribe 2043* (US). **Chocó:** Carretera Panamericana, before Río Pató, ca. 5° 35'N, 76° 57'W, 22 Apr 1979 (fl), *Forero et al. 5569* (MO, NY). **Huila:** ridge between Quebrada Ariari and Quebrada San Blas, 15 km ENE of Colombia, 3° 26'N, 74° 42'W, 1850 m, 29 Dec 1942 (fr), *Fosberg 19641* (NY, US). **Norte de Santander:** region of Sarare, valley of Río Margua between Campohermoso and Río Negro, 1200–1500 m, 8 Nov 1941 (fl), *Cuatrecasas 12896* (COL, F, US); Río Margua valley, left bank, El Ceibal, 1100 m, 23 Nov 1941 (fr), *Cuatrecasas 13421* (F, US). **Santander:** SE of Puerto Berrio, 100 m, 9 Jul 1939 (fl), *Haught 2859* (COL, NY, US); between Pescador and Piedecuesta, 1005 m, 15 Jun 1962 (fl), *Saravia et al. 880* (COL).

VENEZUELA. Barinas: Mun. Pedraza, Alto de Aguada, 1200–1300 m, 13 Dec 1954 (fl), *Bernardi 1778* (NY). **Lara:** Dist. Jiménez, Parque Nacional Yacambú, cloud forest on hillsides facing SE toward Quebrada Negra, vic. El Blanquito, 19 km SSE of Sanare, 1450 m, 6 Aug 1970 (fr), *Steyermark et al. 103452* (B, US). **Mérida:** cloud forest between Quebrada de la Mucuy and El "Volcan", 2200–2300 m, 15 Jan 1953 (fr), *Bernardi 282* (NY); Dist. Campo Elías, road Mérida-La Azulita, near La Carbonera, km 12 W of Mérida, 2250–2300 m, 10 May 1978 (fr), *Bunting & Drummond 6287* (MO); between Los Corales and Las Cuadras, 1490–3210 m, 25 Mar 1944 (fl), *Steyermark 55774* (F); between La Azulita and La Trampa, on road toward Lagunillas, 1280–2225 m, 27 Apr 1944 (fr), *Steyermark 56159* (F); slopes of Río Capaz, above La Azulita, 2100–2400 m, 1 Sep 1966 (fl), *Steyermark & Rabe 97114* (NY, US). **Táchira:** La Buenaña, 6–12 km. W of Quebrada Colorado, ca. 35 km. SSE of San Cristobal, 7° 28'N, 72° 9'W, 600–1200 m, 20–21 Mar 1981 (fl, fr), *Liesner & González 10877* (GH, MO).

Local names. Panama: Wild cucumber (*Cooper 398*). Venezuela: Ajito de monte (*Bernardi 1778*), forote (*Steyermark 55744*).

This subspecies is distinct in having elliptic or nearly globose fruits with obtuse apices, and large seeds ca. 4–5 mm in diameter. Although some variation occurs in calyx size and shape, no representatives of subspecies *chlorantha* have calyx lobes more than 6 mm long.

The Central American collections differ from those of western Venezuela in having the crown leaves more often pinnately compound, the indumentum sparsely to densely pilose with eglandular curled hairs up to 2 mm long, and the inflorescence frequently trifid with a long peduncle up to about 20 cm in length. The Central American collections also have a more lowland range (up to 400 m elevation). More extensive field work in this area may clarify the relationship between the Central and South American collections.

10. Cyphomandra dolichocarpa Bitter, Repert. Spec. Nov. Regni Veg. **17:** 327. 1921. Type. Costa Rica. La Hondura, on slope facing toward the Pacific Ocean, 900 m, *Wercklé s.n.* (holotype, B, destroyed [F neg. 2930 F, G, GH, NY, US, WIS]). Neotype. Panama. Chiriquí: N of San Felix at Chiriquí-Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, lower montane rain forest, 5000–5500 ft, 5 May 1975 (fl), *Mori & Kallunki 5905* (MO; duplicates, C, GH). Figs. 38, 39.

Small *tree* 2.5–5 m tall. *Branches* glabrous to moderately glandular- and eglandular-puberulent, becoming glabrescent. *Leaf blades* simple, unlobed, subcoriaceous, acute to short-acumi-

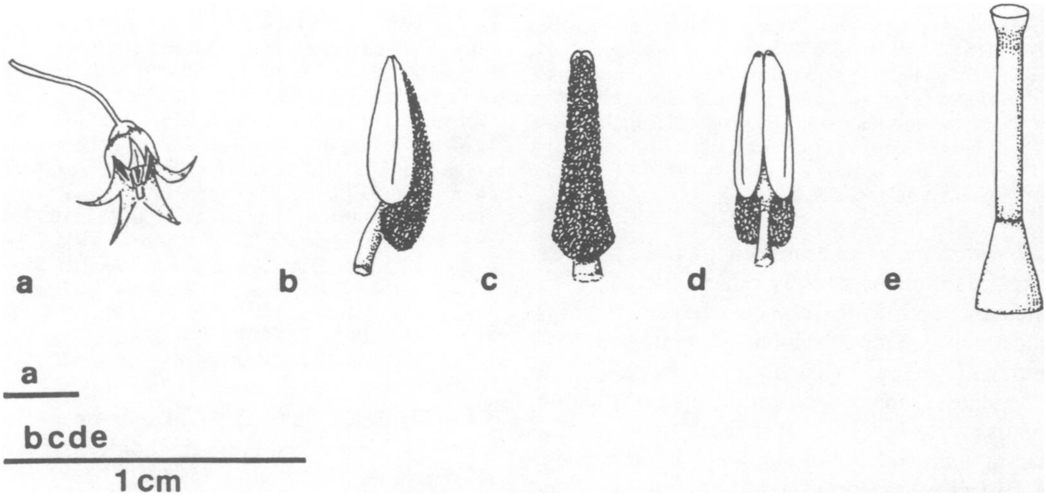


FIG. 38. *Cyphomandra dolichocarpa.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Bohs & McPherson 2312.*

nate at apex, glabrous or glandular-puberulent and sparsely eglandular-pubescent adaxially, more so on veins, glabrous or moderately glandular- and eglandular-puberulent abaxially; petioles glabrous or moderately to densely puberulent. *Trunk leaves* simple, unlobed, the blade elliptic, ca. 40 cm long, 20–22 cm wide, length:width ratio ca. 2:1, the base cuneate, often oblique, without basal lobes; petioles 6–8 cm long. *Crown leaves* 3 per sympodial unit, simple, unlobed, the blade elliptic, 13–30 cm long, 10–20 cm wide, length:width ratio 1.5(–2):1, the base cuneate to truncate, sometimes oblique, without basal lobes; petioles 3–12 cm long. *Inflorescence* unbranched or rarely forked, 15–50-flowered, 3–14 cm long; peduncle 2–4 cm long; rachis 1–10 cm long; pedicels 15–35 mm long, 40–50 mm long in fruit, 1–3 mm apart, articulated near the base, leaving pedicellar remnants ca. 1 mm long; peduncle, rachis, and pedicels glabrous or moderately glandular- and eglandular-puberulent. *Flower buds* narrowly ovoid, acute to acuminate at apex. *Calyx* fleshy, sparsely puberulent, the radius 3–4 mm, the lobes 1.5–2 mm long, 2 mm wide, obtuse, apiculate. *Corolla* white or greenish white, chartaceous to subcoriaceous, stellate-campanulate, the radius ca. 15 mm, the tube 2–4 mm long, the lobes narrowly triangular, 9–11 mm long, 3–4 mm wide, glabrous abaxially and adaxially, the margin tomentose to ciliate, the apex acute. *Anther thecae* white or purplish, lanceolate, ca. 5 mm long, 1.5–2 mm wide, the pores introrse and directed distally; connective tan or cream with purple margins, lanceolate, 6–7 mm long, 1–2 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 1 mm, adaxially absent. *Ovary* glabrous; style cylindrical, glabrous, not dilated distally, 6–8 mm long, 0.3–1 mm in diam., exserted 2 mm beyond stamens; stigma clavate or truncate, 0.3–1 mm in diam. *Fruit* ellipsoidal or fusiform, acuminate at apex, glabrous, 5–9 cm long, 2–3 cm in diam., the color when ripe unknown, but probably yellow; mesocarp without stone cell aggregates; seeds unknown.

Distribution (Fig. 40) and phenology. Montane rain forest or cloud forest, 900–1800 m, Costa Rica and Panama. Flowering specimens have been collected in February, March, April, May and August. Fruiting specimens have been collected in February, April, and August.

Additional specimens examined. **PANAMA. CHIRIQUÍ:** Vic. Fortuna Dam, 1400 m, 7 Feb 1987 (fl, fr), *Bohs & McPherson 2312* (F, GH, PMA); Cerro Colorado, 50 km N of San Felix on the continental divide, 1200–1500 m, 17 Aug 1975 (fl, fr), *Mori & Dressler 7788* (GH, MO). **COCLÉ:** near sawmill above El Copé, ca. 3000 ft, 4 Apr 1978 (fl, fr), *Hammel 2364* (MO, NY); NE slopes of Cerro Caracoral, N rim of El Valle, 900–1100 m, 12 Mar 1981 (fl), *Sytsma 3763* (MO).

FIG. 39. *Cyphomandra dolichocarpa.* Scale bar = 1 cm. Photo taken near Fortuna Dam, Prov. Chiriquí, Panama (*Bohs & McPherson 2312*).

Attempts should be made to find new localities for this rare species from Central America. All extant collections are from Panama and date from after 1975. *Cyphomandra dolichocarpa* is thus not covered in the treatment of the Solanaceae for the *Flora of Panama* (D'Arcy, 1973). The species can be identified from Bitter's detailed Latin description and from photographs of the holotype (destroyed in Berlin during World War II) showing the distinctive elongated fruits and elliptic leaves with cuneate bases. No isotypes have been located, so a neotype has been chosen. The Panamanian collections agree with Bitter's protologue except for the glabrate rather than pubescent leaves and stem, and the different structure of the gynoecium. Bitter describes the style as being obviously thickened into the subpeltate stigma nearly 1.5 mm in diameter. The Panamanian collections show no trace of this thickened style and have very small stigmas. In spite of these discrepancies, I strongly suspect that the Panamanian collections conform to Bitter's *C. dolichocarpa*, so they have been included here under that name.

From the scanty material available, it appears that *C. dolichocarpa* is related to the *C. hartwegii* group. The narrow, tapered anthers and truncate stigma of *C. dolichocarpa* are characteristic of the *C. hartwegii* complex. *Cyphomandra dolichocarpa* is most similar to *C. tobagensis*, which also has elliptic leaves with cuneate bases and pointed fruits. However, the leaves of *C. dolichocarpa* are larger than those of *C. tobagensis* and the fruits of *C. dolichocarpa* are glabrous rather than puberulent.

11. **Cyphomandra endopogon** Bitter, Bot. Jahrb. Syst. **54**, Beibl. 119: 16. 1916. Fig. 41.

Small *tree* 2–15 m tall. *Branches* glabrous to densely puberulent. *Leaf blades* simple, lobed or unlobed, subcoriaceous, acute to short-acuminate at apex, glabrous to sparsely and finely puberulent adaxially except for denser puberulence on main veins, glabrous to densely puberulent abaxially; petioles glabrous to densely puberulent, occasionally sparsely pilose with eglandular hairs 1–2 mm long. *Trunk leaves* simple, unlobed or pinnately (2–)3–5-lobed; if unlobed, the blade elliptic-ovate, 22–35 cm long, 12–21 cm wide, length:width ratio 1.5–2:1, the base cuneate, without basal lobes; if lobed, the blade 20–40 cm long, 20–25 cm wide, divided about halfway to midrib, the sinuses rounded, obtuse, the base cuneate to shallowly cordate with basal lobes up to 2 cm long; petioles 10–20 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade elliptic to ovate, 4–25 cm long, 4–15 cm wide, length:width ratio 1–2:1, the base cuneate to truncate or deeply cordate, often oblique, with basal lobes up to 5 cm long; petioles 1–5 cm long. *Inflorescence* usually unbranched or forked, rarely further branched, 20–40(–100)-flowered, 10–50 cm long; peduncle 4–10 cm long; rachises 3–40 cm long; pedicels 20–35 mm long, 25–35 mm long in fruit, (1–)4–10 mm apart, articulated near the base, leaving pedicellar remnants up to 1 mm long; peduncle, rachises, and pedicels glabrous to densely puberulent, often also sparsely to moderately eglandular-pilose with hairs 1–2 mm long. *Flower buds* narrowly oblong, obtuse at apex. *Calyx* fleshy, glabrous to densely puber-

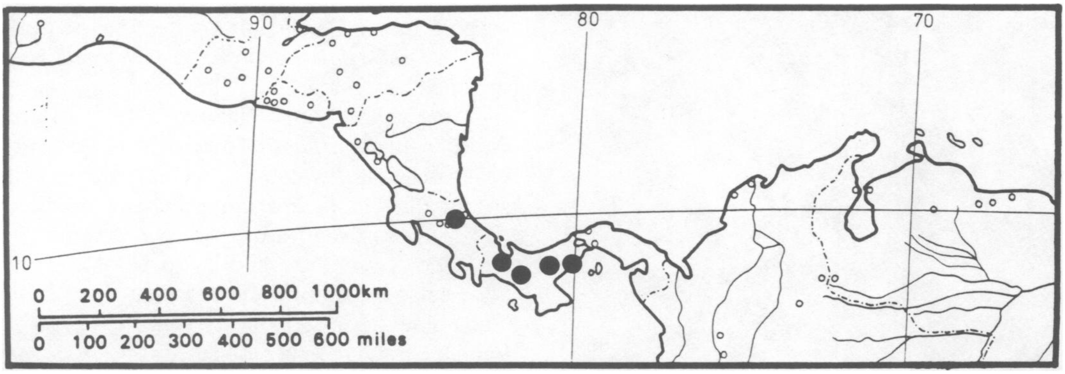


FIG. 40. Distribution of *C. dolichocarpa.*

ulent, sometimes pilose at margin, the radius 3–5 mm, the lobes 1–2 mm long, 2–3 mm wide, truncate, apiculate. *Corolla* purple or whitish fading to green, fleshy or subcoriaceous, stellate, the radius 16–25 mm, the tube 1–2 mm long, the lobes narrowly oblong, 15–22 mm long, 2–3 mm wide, glabrous to moderately puberulent abaxially, sparsely villous adaxially, the margin densely ciliate with hairs 1–2 mm long, the apex obtuse. *Anther thecae* yellow or purplish, narrowly oblong to triangular, 8–10 mm long, 1–2 mm wide, the pores directed adaxially and distally; connective purple, narrowly oblong, 8–10 mm long, 1–2 mm wide, abaxially slightly shorter than thecae at apex, equal to or slightly exceeding them at base, adaxially present as a narrow swelling especially prominent toward base. *Ovary* glabrous to densely puberulent; style cylindrical, glabrous or occasionally sparsely puberulent, strongly dilated distally, 9–12 mm long, 0.5–1 mm in diam., exserted 2–3 mm beyond stamens; stigma umbrella-shaped, concave with two apical protuberances, 2–3 mm in diam. *Fruits* ellipsoidal or globose, obtuse at apex, 4–5 cm long, 3–5 cm in diam., glabrous to moderately puberulent, especially when young, the color when ripe unknown, but probably yellow or whitish; mesocarp with stone cell aggregates; seeds 5–6 mm long, 4–5 mm wide, rugose to sparsely puberulent, especially at margin.

Distribution (Fig. 42). Disturbed areas in tropical rain forest, 100–1000 m in elevation, western Amazon basin in Colombia, Ecuador, Peru, and Brazil with a disjunct element in eastern Brazil and French Guiana.

Cyphomandra endopogon is one of the most distinctive species in the genus, and can be recognized by its obtuse flower buds, long narrow corolla lobes bordered by conspicuous hairs, long narrow anthers, and long slender style strongly dilated at the summit into a broad stigma. The inflorescences are often spectacularly long, and sometimes bear small leaflike bracts near the base.

Cyphomandra endopogon closely resembles *C. stellata.* However, *C. endopogon* has unbranched or forked inflorescences, obtuse flower buds, very long corolla lobes and anthers, and a very broad stigma, unlike *C. stellata.* Both *C. endopogon* subspecies *guianensis* and *C. stellata* have puberulent fruits. *Cyphomandra endopogon* and *C. stellata* have sympatric distributions in the western part of the Amazon basin, and they are so similar that *C. stellata* was previously considered a variety of *C. endopogon* (Bohs, 1986).

Two subspecies are recognized within *C. endopogon* based on their differences in pubescence and disjunct distributions.

KEY TO THE SUBSPECIES OF *CYPHOMANDRA ENDOPOGON*

1. Branches, petioles, inflorescence axes, and abaxial leaf surfaces glabrous to sparsely and minutely puberulent; fruits glabrous; western Amazon . . . . a. subsp. *endopogon.*

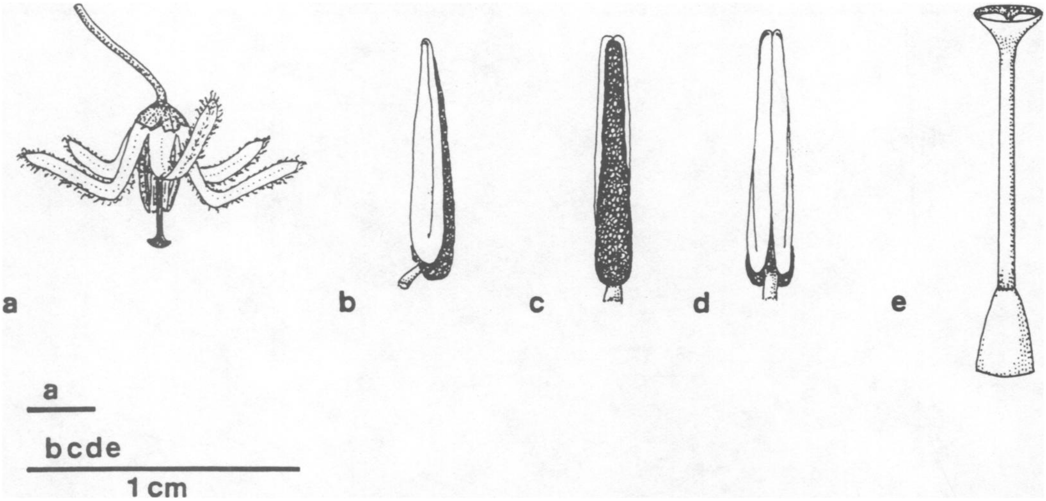


FIG. 41. *Cyphomandra endopogon.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Asplund 12136* (S); b–e, based on *Asplund 9432* (S).

1. Branches, petioles, inflorescence axes, and abaxial leaf surfaces densely puberulent; fruits puberulent, at least when young; French Guiana and eastern Brazil . . . . b. subsp. *guianensis.*

a. *Cyphomandra endopogon* subspecies *endopogon*

Cyphomandra endopogon Bitter, Bot. Jahrb. Syst. **54**, Beibl. **119:** 16. 1916. Type. Peru. Huánuco: Prov. Huánuco, Tal des Mayro, eines Nebenflusses des Palcazú, etwa 10° S, 400 m, "bäumchen, 6 m hoch, im immergrünen Gebusch, bestehend aus Sträuchern und Bäumen, blühend im Juli," *Weberbauer 6757* (lectotype, B, here designated; isolectotypes, B (destroyed) [F neg. 2932 F, G, GH, NY], F [F neg. 57900], GH, US).

Branches glabrous to sparsely and minutely puberulent. *Leaf blades* glabrous to very sparsely puberulent adaxially, glabrous to minutely puberulent abaxially. *Petioles* and *inflorescence axes* glabrous to sparsely and minutely puberulent, also occasionally sparsely pilose with eglandular hairs about 1–2 mm long. *Calyx* glabrous to sparsely puberulent. *Corolla* lobes glabrous to very sparsely puberulent abaxially. *Ovary*, *style*, and *fruits* glabrous.

Distribution (Fig. 42) and phenology. Disturbed areas in tropical rain forest at 100–1000 m in elevation, east of the Andean cordillera in southern Colombia, eastern Ecuador, northeastern Peru, and western Brazil. Flowering specimens have been collected in all months of the year except January and December. A flowering peak occurs in July through October. Fruiting specimens have been collected throughout the year except for June and December, but mostly in July through November.

Additional specimens examined. COLOMBIA. Amazonas: Río Loretoyacu, near Puerto Nariño, vic. Laguna Dolfus, 19 Aug 1964 (fl), *Fernández-Pérez 6863* (ECON, NY). Putumayo: Río Putumayo, Puerto Ospina and vicinity, 0° 10'N, 75° 50'W, 23–26 Mar 1953 (fl), *Schultes & Cabrera 18979* (GH, U, US).

ECUADOR. Morona-Santiago: near Méndez, uplands along Río Upano just N of junction with Río Chupiantza, 1750–2500 ft, 14 Nov 1944 (fl), *Camp E-984* (NY, S); at Río Paute between Méndez and Paute, 78° 19'W, 2° 44'S, ca. 600 m, 11 Jun 1979 (fl), *Lojtnant & Molau 14548* (AAU, GB). Napo: Tena, 18 Oct 1939 (fl, fr), *Asplund 9432* (S); Limoncocha on Río Napo, 300 m, 23 Oct 1974 (fl, fr), *Drummond 7348* (MO); Río Aguarico, N bank of river at San Pablo de las Secoyas, 76° 24'W, 0° 17'S, 230 m, 21 Feb 1980 (fl, fr), *Holm-Nielsen et al. 21721* (AAU); Ciudadela San José, vic. Tena, 1 Apr 1969 (fl), *Lugo 964* (GB, MO); Río Napo, at mouth of Río Huambuno, 3 km downstream from Campana Cocha, 0° 55'S, 77° 25'W, 350 m, 29 Jun 1987 (fl, fr), *Neill et al. 7758* (GH); Jatun Sacha Biological Station, Río Napo, 8 km E of Misahualli, 1° 1'S, 77° 36'W, 450 m, 26 Jul 1987 (fr), *Neill et al. 7793* (GH). Pastaza: Comuna Shuar Amuntay (Kapawi), 2° 31'S, 76° 48'W, 250–300 m, 15 Jul 1988 (fl), *Cerón et al. 4322* (UT); Río Villano ca. 5 km

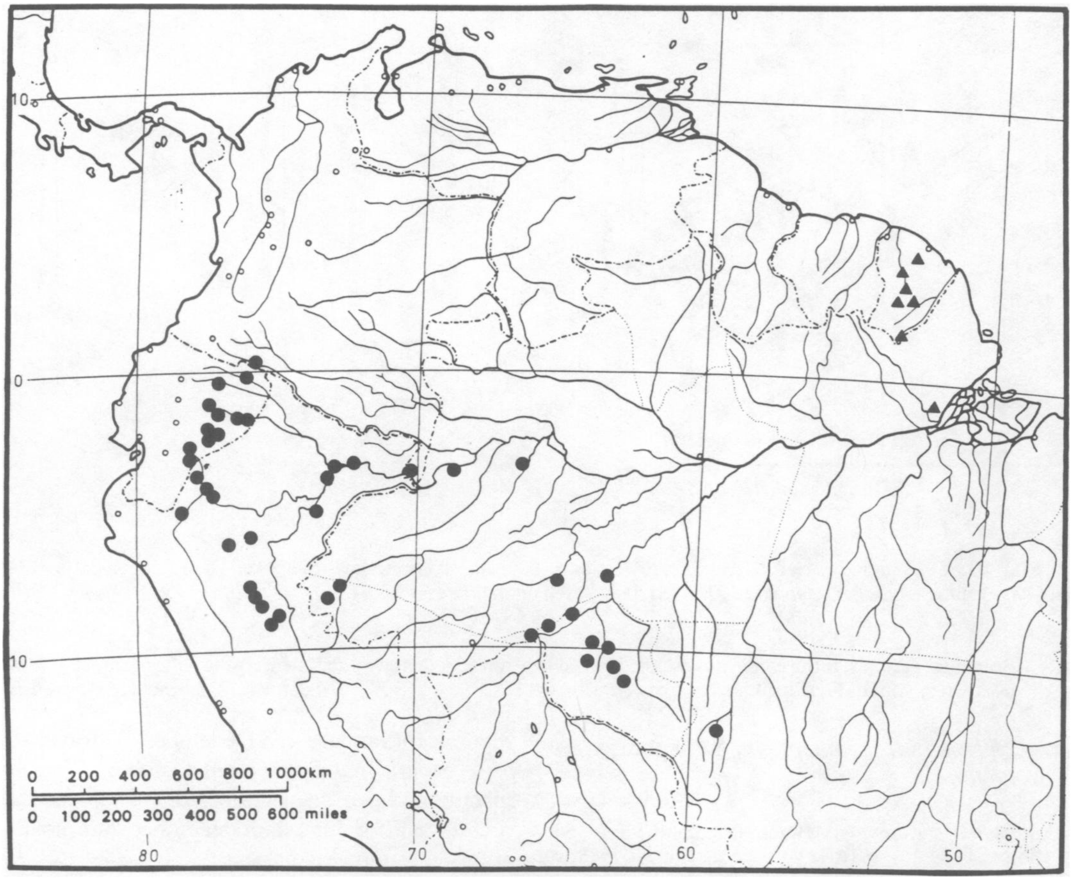


FIG. 42. Distribution of *C. endopogon* subspecies *endopogon* (dots) and subspecies *guianensis* (triangles).

above the confluence with Río Curaray, ca. 200 m, 24 Mar 1980 (fl), *Harling & Andersson 17743* (GB); Kapawí (Amuntai), Río Pastaza, 76° 48'W, 2° 31'S, 235 m, 14–20 Jul 1988 (fl), *Lewis et al. 13686* (UT); same locality, 25–29 Jul 1989 (fl), *Lewis et al. 14008* (Lewis, pers. coll.); Shiguacoche, ca. 5 km E of Puerto Sarayacu, 1 Oct 1974 (fl), *Lugo 3832* (GB, MO); Puerto Sarayacu, 3 Oct 1974 (fl), *Lugo 3878* (GB, MO); Río Zupayacu, ca. 7 km S of Puerto Sarayacu, 11 Oct 1974 (fr), *Lugo 4049* (GB); El Porvenir, 5 km N of Puyo-Pungo, 17 Sep 1976 (fl), *Lugo 4886* (GB); vic. El Porvenir, ca. 5 km W of Puyopungo, 20 Sep 1976 (fl), *Lugo 4938* (GB); Pacayacu on the Río Bobonaza, ca. 16 km NW of Sarayacu, 10 Aug 1979 (fl), *Lugo 5207* (GB); Río Bobonaza ca. 8 km NW of Sarayacu, 12 Aug 1979 (fl), *Lugo 5306* (GB); Sarayaquillo, ca. 5 km N of Sarayacu, 16 Aug 1979 (fl), *Lugo 5498* (GB).

PERU. Amazonas: Río Cenepa, vic. Huampami, ca. 5 km E of Chávez Valdívia, Quebrada Apigkan entsa, 78° 30'W, 4° 30'S, 200–250 m, 8 Mar 1978 (fl), *Ancuash 1273* (MO); same locality, Quebrada Kachaig, 15 Aug 1978 (fl), *Ancuash 1512* (MO); Río Santiago, 1 km behind La Poza, 180 m, 9 Aug 1979 (fl), *Asunción Leveau 27* (MO); 400 m behind La Poza, 180 m, 23 Aug 1979 (fl), *Asunción Leveau 278* (MO); Prov. Bagua, along roadside from Chiriaco to Puente Venezuela (3.9 km NE Chiriaco), 600–800 ft, 31 Oct 1978 (fr), *Barbour 4366* (MO, USM); 3 km from mouth of Quebrada Huampami, 950 ft, 15 Sep 1972 (fl), *Berlin 44* (MO); Río Cenepa, 10 km S of Huampami, 990 ft, 20 Sep 1972 (fr), *Berlin 120* (MO); Río Cenepa, La Banda, Huampami, 860 ft, 15 Oct 1972 (fl), *Berlin 284* (C, MO); Huampami, 600–800 ft, 3 Aug 1974 (fl), *Berlin 1974* (MO); 5 km N of Huampami, 800 ft, 25 Aug 1975 (fl), *Berlin 2009* (MO); 3 km from La Poza, E bank of the Santiago River, Mobil Oil Company trail, 6 Aug 1979 (fl), *Berlin 3513* (MO); 400 m behind La Poza, W side of Río Santiago, 180 m, 23 Aug 1979 (fl, fr), *Dominguez Peña 150* (MO); same locality, 23 Aug 1979 (fl, fr), *Huashikat 154* (MO); Quebrada Huampami, 600 m, 17 Jul 1974 (fr), *Kayap 1185* (GH); Huampami, 800–850 ft., 2 Aug 1974 (fl), *Kayap 1434* (GH); Quebrada Sasa, 600 m, 25 Aug 1975 (fl), *Kayap 2029* (MO); Río Cenepa, vic. Huampami, ca. 5 km E of Chávez Valdívia, ca. 78° 30'W, 4° 30'S, 200–250 m, 12 Aug 1978 (fl), *Kujikat 252* (MO); Huambisa, 1 km behind La Poza, 180 m, 13 Nov 1979 (fr), *Tunqui 49* (MO); Río Santiago valley, Quebrada Caterpisa, 77° 40'W, 3° 50'S, 200 m, 17 Nov 1979 (fr), *Tunqui 96* (MO); Prov. Bagua, along Quebrada Miraná (above km 277 of Marañon road), valley of Río Marañon above Cascadas de Mayasi, 450–500 m, 8 Sep 1962 (fl), *Wurdack 1888* (G, GH, NY, P, S, US, USM); along Río Marañon 2–10 km above mouth of Río Santiago, 250–275 m, 14–15 Oct 1962 (fl, fr), *Wurdack 2244* (F, NY, US). **HUÁNUCO:** Prov. Huánuco, Tingo María, 10 Jul 1940 (fl), *Asplund 12136* (S); vic. Tingo María, km 127, 600–700 m, 13 Aug 1946 (fl), *Ferreyra 959* (US, USM, WIS); Prov. Leoncio Prado, Dist. Rupa Rupa, W of Tingo María, hill in front of the airport, 700–800 m, 3 Aug 1978 (fl), *Schunke 10433* (MO). **LORETO:** Quebrada Shanuce above Yurimaguas, 11 Jul 1972 (fl), *Croat 18023* (CTES, F, MO, NY); 7 km SW of Iquitos, 31 Jul 1972 (fl), *Croat 18620* (BR, C, CR, F, GH, K, L, LL, MO, NY); Río Napo near Casería Canton, 15 Sep 1972 (fl), *Croat 20249* (BR, C, F, GH, K, L, LL, MO, NY, WIS); Prov. Requena, in front of Cedro Isla, below Jenaro Herrera, right shore of Río Ucayali, 21 Aug 1982 (fl), *Encarnación 26446* (MO, NY, US); Yanomono, Explorama Tourist Camp, Río Amazonas above mouth of Río Napo, 3° 22'S, 72° 50'W, 120 m, 22 Mar 1982 (fr), *A. Gentry et al. 36593* (MO); Yurimaguas, lower Río Huallaga, ca. 135 m, 22 Aug–9 Sep 1929 (fl), *Killip & Smith 28182* (F, NY, US); Mishuyacu, near Iquitos, 100 m, Feb 1932 (fl), *Klug 2560* (A, F, NY, S, U, US); Puranchim, Río Sinchiyacu, 2° 50'S, 76° 55'W, 200 m, 21–27 Nov 1986 (fl), *Lewis et al. 12148* (Lewis, pers. coll.); PetroPeru Estación Río Morona, 4° 20'S, 77° 20'W, 160 m, 30 Nov 1986 (fr), *Lewis et al. 12281* (Lewis, pers. coll.); Iquitos, Río Itaya, San Antonio, 30 Jul 1966 (fl), *Martin 1187* (COL, F); between Quistococha and Santo Tomas, 14 km N of Iquitos, 600 m, 18 Aug 1981 (fl), *Moore et al. 121* (F); Prov. Maynas, Quisto Cocha, 120 m, 25 Jun 1981 (st), *Ruiz Macedo 36* (GH); basin of Río Ucayali 10 km from mouth, 1923 (fl), *Tessmann 3056* (G, S); basin of Río Maranon from Iquitos upstream to the mouth of the Río Santiago near Pongo de Manseriche, Puerto Limón, ca. 77° 30'W, 1924 (fl), *Tessmann 3869* (G, NY); Prov. Maynas, Indiana, path to Mazan, NE of Iquitos, 3° 30'S, 72° 58'W, ca. 115 m, 31 Jan 1981 (fr), *Vásquez et al. 1292* (MO); Maynas, Explorama Lodge, near confluence of Napo and Amazon rivers, 3° 25'S, 72° 48'W, ca. 30 m, 28 Aug 1978 (fl), *Webster 23338* (MO, TEX, US); San Juan, Iquitos, 12 Oct 1929 (fl), *Ll. Williams 3716* (F); Iquitos, 9 Apr 1930 (fr), *Ll. Williams 8241* (F). **SAN MARTÍN:** El Recreo "La Charapita" ca. 3 km S of Tocache Nuevo on road to Tingo María, 400–700 m, 25 Apr 1983 (st), *Bohs & Schunke 2160* (GH, USM); Pueblo Mantención, property of Hernán Ortiz, ca. 10 km S of Tocache Nuevo, 500–600 m, 26 Apr 1983 (st), *Bohs & Schunke 2162* (F, GH, MO, USM), *2166* (GH, USM); along road between Moyobamba and Chachapoyas, near km marker 404, 5° 46'S, 77° 28'W, 1150 m, 12 Apr 1984 (fr), *Croat 58189* (GH); Prov. Coronel Portillo, Divisoria, between Tingo María and Pucallpa, 1500–1600 m, 13 Aug 1946 (fl), *Ferreyra 982* (NY, US, USM, WIS); Prov. Mariscal Cáceres, vic. Huicte, near Uchiza, 400–500 m, 6 Aug 1948 (fl), *Ferreyra 4407* (US, USM, WIS); Prov. Mariscal Cáceres, Dist. Tocache Nuevo, road to village of Almendras, 400 m, 10 Aug 1969 (fl), *Schunke 3323* (F, G, MO, NY, US); mouth of Río Mishollo, left bank of Río Huallaga, 350–380 m, 24 Jul 1973 (fl, fr), *Schunke 6387* (C, MO); Canutillo, NW of the carretera marginal, 28 km from Tocache, 525 m, 6 Jul 1974 (fl), *Schunke 7169* (GH, NY); Quebrada de Mantención, near land of Sr. Hernán Ortíz Gonzáles, 500–600 m, 29 Aug 1983 (fl), *Schunke 14030* (COL, G, GH, NY, US, USM); same locality and date (fl, fr), *Schunke 14033* (F, GH, K, MO, USM).

BRAZIL. ACRE: Cruzeiro do Sul, Estrada Alemanha, 8 May 1971 (fl), *Maas et al. P12812* (C, F, G, K, M, NY, P, S, U, US, WIS); same locality, 27 May 1971 (fr), *Maas et al. P13318* (F, K, M, NY, P, S, U, US, WIS). **AMAZONAS:** Mun. Humayta, near Tres Casas, 14 Sep–11 Oct 1934 (fr), *Krukoff 6345* (A, B, BM, BR, F, G, K, MO, NY, S, U, US); Mun. São Paulo de Olivença, near Palmares, 11 Sep–26 Oct 1936 (fl), *Krukoff 8081* (A, BM, F, K, MO, NY, S, U); Rio Purus, Lago Preto, 2 km N of Lábrea, 26 Jun 1971 (fl), *Prance et al. 13740* (F, GH, K, M, NY, P, S, U, US, WIS); Rio Juruá, Juruá Miry, Jul 1901 (fl), *Ule 5689* (G, HBG, K, L). **MATO GROSSO:** picadão leading to Rio Juruena from mining trail of same name, 12 Jun 1977 (fl), *Rosa & Santos 2109* (MO, NY, RB). **RONDÔNIA:** Rondônia São Lourenço cassiterite mine ca. 20 km NW of Rio Madeira, across from Mutumparaná, 15 Jul 1979 (fl, fr), *Calderon et al. 2849* (G, NY, US); Mun. de Costa Marques, Chapada dos Parecis, Dist. de Alta Floresta, highway P–56, km 27, 11° 12'S, 62° 63'W, 14 Jun 1984 (fl), *Cid et al. 4505* (NY); Mun. de Jaru, BR 364, road Cuiabá-Porto Velho, km 428, 10° 11'S, 62° 63'W, 3 Jul 1984 (fl), *Cid et al. 5004* (NY); ca. 2 km N of BR 364, ca. 10 km SE of Ariquemes, 30 May 1984 (fl), *Frame et al. 216* (GH); along Porto Velho-Cuiaba highway between Nova Vida and Rondônia, 24 Sep 1963 (fr), *Maguire et al. 56771* (NY); Rio Jamari, Cachoeira de Sta. Cruz, 28 Jun 1965 (fl), *Pires & Martin 9946* (NY, RB, US); road to cassiterite mines in Serra dos Tres Irmãos, N bank of Rio Madeira, 8 km above Mutumparaná, 6 Jul 1968 (fl), *Prance et al. 5620* (F, NY, S, US, WIS); Porto Velho to Cuiabá highway, vic. Santa Barbara, 15 km E of km 117, 14 Aug 1968 (fl, fr), *Prance & Ramos 6922* (F, K, M, NY, P, S, U, US, WIS); vic. São Lorenço mines, 65° 6'W, 9° 33'S, 28 Nov 1968 (fr), *Prance et al. 8963* (F, GH, M, NY, P, S, U, US, WIS); Mineração Taboca, near Campo de Pouso of Mineração, 63° 20'W, 10° 15'S, 10 Oct 1979 (fr), *Vieira et al. 360* (MO); Mineração Campo Novo (ca. 100 km SW of Ariquemes), 10° 34'S, 63° 37'W, 15 Oct 1979 (fr), *Zarucchi et al. 2705* (GH, MO); same locality and date (fl), *Zarucchi et al. 2706* (GH, MO).

Local names and uses. Ecuador: Ora panga (Quichua) (*Neill et al. 7758*). Peru: Asna panga (*Ll. Williams 8241*), chiwingue iji (Achuar Jivaro) (*Lewis et al. 12148*), chuposacha del monte (*Schunke 6387*), chupo sacha macho (*Schunke 14030, 14033*), chupo sacha masha (*Schunke 3323, 7169*), gallinazo panga (*Ruiz Macedo 36*), gallinazo pango (Mestizo Quichua/Spanish) (*Lewis et al. 12281*), mehegkash (*Kayap 1185, 1434, 2029*), mehénkas (*Berlin 1974*), mejegkush (*Ancuash 1273*), mejéngkash (*Berlin 2009*), siuca sacha (*Croat 18023*, *Martin 1187*), tákup (Huambisa)(*Berlin 3513*, *Dominguez Peña 150*, *Tunqui 49*, *96*).

In Amazonian Peru near Iquitos, the fruit and leaves are mixed with warm or cold water and used to wash skin for "siso," a skin disease (*Martin 1187*). Natives of Amazonian Peru also crush the leaves in cold water to make an infusion. This is then used in a bath to treat bad luck ("saladera") (*Lewis et al. 12281*). The fruits are said to be eaten by natives in Dept. Amazonas, Peru (*Berlin 1974*, *2009*). The lowland Quichua of Ecuador use this species to treat heart attacks and strokes (*Neill et al. 7758*). The Achuar Jivaro of lowland Ecuador scrape the bark into cold water and massage the limbs with the infusion to relieve swellings and prevent infection (*Lewis et al. 12148*).

This subspecies differs from subspecies *guianensis* in its western Amazonian distribution and in being nearly glabrous. Its often pinnately lobed trunk leaves, elongated inflorescences with short pedicellar remnants, long, narrow anthers, and obtuse, glabrous fruits resemble those of *C. hartwegii*. *Cyphomandra endopogon* subspecies *endopogon* can easily be distinguished from *C. hartwegii* by floral characters, but it is often very difficult to distinguish fruiting specimens of the two taxa from lowland Ecuador and Peru.

Although many specimens of this subspecies are almost completely glabrous, some collections, especially those from eastern Ecuador, are sparsely and minutely puberulent on the axes and abaxial leaf surfaces. These hairs are only visible under strong magnification and do not approach the density and conspicuousness of the puberulence seen in subspecies *guianensis*.

Two sheets of the type collection from Berlin have apparently been destroyed, but an extant specimen at B bearing Bitter's annotation label has been chosen as the lectotype.

b. *Cyphomandra endopogon* Bitter subspecies *guianensis* Bohs, subsp. nov. Type. French Guiana. Saul, Monts La Fumée, 3° 37'N, 53° 12'W, 200–400 m elev., 16 Aug 1982 (fl), *Mori & Boom 14709* (holotype, F).

Ab *Cyphomandrae endopogon* subspecie *endopogon* pubescentia densa caulium foliorum inflorescentiarum florum fructuumque differt.

Branches densely puberulent. *Leaf blades* glabrous to very sparsely puberulent adaxially except for dense puberulence on main veins, densely puberulent abaxially. *Petioles* and *inflorescence axes* densely puberulent, also occasionally sparsely pilose with eglandular hairs about 1–2 mm long. *Calyx* densely puberulent, also occasionally sparsely pilose at margin. *Corolla* lobes sparsely to moderately puberulent abaxially. *Ovary* glabrate to densely puberulent. *Style* glabrous or occasionally sparsely puberulent. *Fruits* moderately puberulent.

Distribution (Fig. 42) and phenology. Disturbed areas in tropical rain forest, 200–400 m in elevation, French Guiana and adjacent areas of eastern Brazil. Flowering specimens have been collected in June through October. Fruiting specimens have been collected in March, October, and November.

Additional specimens examined. FRENCH GUIANA. Route N2, road to Cacao, 11 Nov 1981 (fr), *Billiet & Jadin 1343* (BR); Saul, 18 Oct 1986 (fl), *Foresta 669* (NY, U); road from Emérillons, 3 km from Dégrad Claude, 24 Mar 1974 (fr), *Granville 2220* (GH); upper Mana, Saut Gros Tigre, 16 Aug 1981 (fl), *Granville 4901* (BR); upper Mana, Degrad Blanc, 20 Aug 1981 (fl), *Granville 4941* (BR); Trois Sauts, Abatis Peku (Pakusili), 6 Mar 1975 (fr), *Grenand 808* (P); Monts La Fumée, Saul, 3° 37'N, 53° 12'W, 200–400 m, 2 Oct 1982 (fr), *Mori et al. 15028* (F); Fleuve Oyapock, mouth of Notaye creek, 10 Jul 1969 (fl), *Oldeman T.358* (NY); Trois Sauts, upper Oyapock, 9 Sep 1973 (fl), *Oldeman T.982* (MO, NY); upper Approuague ca. 4 km S of the path from Parépou creek, 10 Oct 1968 (fl), *Oldeman B.1906* (MO); Saul, 12 Aug 1984 (fl), *Prévost 1600* (NY).

BRAZIL. **Amapá:** Agua Branca, km 12, 23 Jul 1969 (fl), *Silva 2450* (F). **Pará:** Rio Jarí, Monte Dourado, Planalto B, between Pilo and Repartimento, 28 Oct 1968 (fl), *Silva 1327* (NY, U); Jarí, road between Bandeira and Pilo, km 38, 26 Jun 1969 (fl), *Silva 2246* (F).

Local names. French Guiana: Uluwukasi (Wayapi) (*Grenand 808*).

This subspecies resembles subspecies *endopogon* in all aspects of floral and vegetative morphology except for the dense puberulence of the branches, abaxial leaf surfaces, inflorescence axes, corolla lobes, and fruits. Subspecies *guianensis* is separated from subspecies *endopogon* by a disjunction of nearly 1500 km.

12. Cyphomandra foetida Bohs, Syst. Bot. **13:** 268. 1988. Type. Peru. Huánuco: Prov.

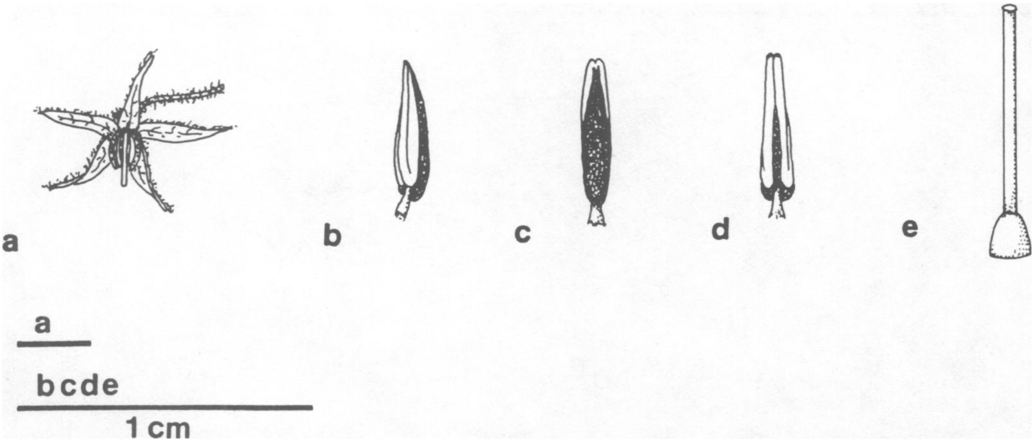


FIG. 43. *Cyphomandra foetida.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Schunke 1159* (MO).

Pachitea, Dist. Honoria, Bosque Nacional de Iparia, along the Río Pachitea near the encampment of Miel de Abeja (1 km above the town of Tournevista or about 20 km above the confluence with the Río Ucayali), 300–400 m, 18 Oct 1966 (fl), *Schunke 1159* (holotype, MO; isotypes, F, G, NY, US). Fig. 43.

Small *tree* 1–7 m tall. *Branches* moderately to densely glandular- and eglandular-pubescent and moderately pilose to hirsute with shining hairs up to 4 mm long. *Leaf blades* simple, unlobed, chartaceous, acuminate at apex, moderately to densely pilose to villous adaxially with white curled hairs, some gland-tipped, more dense on veins, more densely glandular- and eglandular-pubescent to pilose abaxially; petioles densely pubescent-pilose. *Trunk leaves* simple, unlobed, the blade ovate-elliptic, 20–23 cm long, 12–15 cm wide, length:width ratio ca. 1.5:1, the base cordate with basal lobes 0.5–1.5 cm long; petioles 8–12 cm long. *Crown leaves* 3–4 per sympodial unit, simple, unlobed, ovate to elliptic-ovate, 4–22 cm long, 3–15 cm wide, length:width ratio 1–2:1, the base truncate to cordate, sometimes oblique, with basal lobes 0.3–2 cm long; petioles 1.5–9(–14) cm long. *Inflorescence* unbranched or forked, (15-)20–50-flowered, 3–7(–13) cm long; peduncle 0.5–2 cm long; rachises 2–6(–11) cm long; pedicels 10–20 mm long, 25–40 mm long in fruit, 0.5–4 mm apart, articulated at or near the base, leaving pedicellar remnants up to 1(–2) mm long; peduncle, rachises, and pedicels pubescent-pilose. *Flower buds* ovoid, acute-acuminate at apex. *Calyx* chartaceous, densely pilose and glandular, the radius 2–3 mm, the lobes 1.5–2 mm long, 1.5–2.5 mm wide, deltate, acuminate. *Corolla* green to yellowish green, chartaceous to membranaceous, stellate, the radius 8–12(–15) mm, the tube 1–2(–4) mm long, the lobes narrowly triangular, 7–10(–14) mm long, 2–3(–4) mm wide, moderately glandular-tomentose and eglandular-villous abaxially, glabrate to sparsely pubescent adaxially especially on midrib and toward apex, the margin ciliate, the apex acute-acuminate. *Anther thecae* lanceolate, white or yellow, 4–5(–7) mm long, 1–1.5 mm wide, the pores directed adaxially and distally; connective narrowly triangular, the color unknown, 4.5–5 (–8) mm long, 0.5–1 mm wide, abaxially equal to or slightly shorter than thecae at apex, exceeding them at base by 0.5–1 mm, adaxially usually present at base as a linear-triangular swelling ca. 1.5–3 mm long and 0.5 mm wide. *Ovary* glabrous to densely glandular-puberulent; style cylindrical, glabrous, not dilated distally, 5–8 mm long, 0.3–0.5 mm in diam., exserted 2–4 mm beyond stamens; stigma truncate to capitate, 0.3–0.5(–1) mm in diam. *Fruit* ellipsoidal or fusiform, acute at apex, 2.5–7.5 cm long, 1–3 cm in diam., densely glandular- and eglandular-pilose, green when immature with green or greyish longitudinal stripes, the color when ripe unknown; meso-

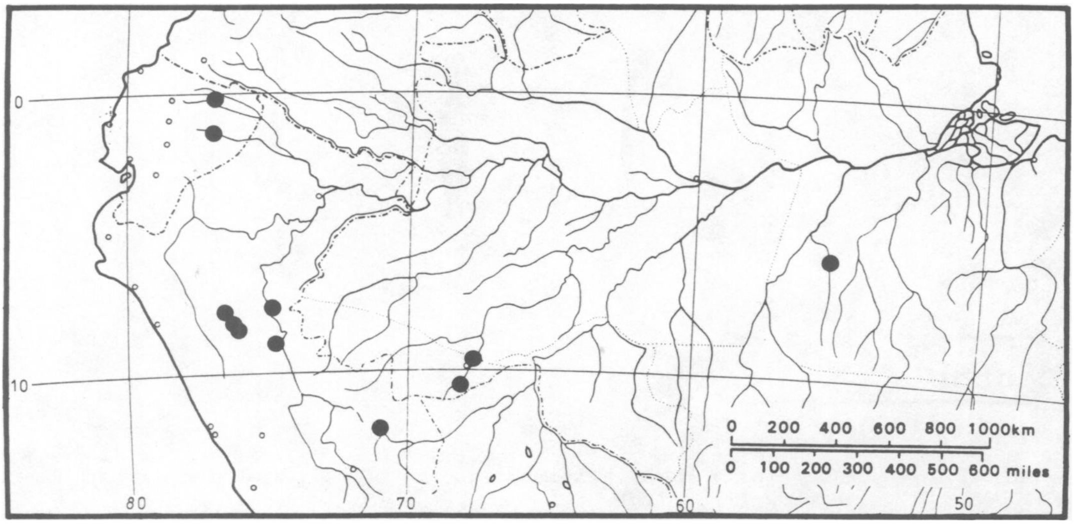


FIG. 44. Distribution of *C. foetida.*

carp with smooth round or oval stone cell aggregates; seeds 4–5 mm long, 3–3.5 mm wide, glabrate and white-puberulent submarginally.

Distribution (Fig. 44) and phenology. Open or disturbed places in rain forest on terra firme, 200–700 m in elevation, eastern slope of Andes in Ecuador and Peru and lowlands of Amazonian Brazil. Flowering specimens have been collected in July and September through November. Fruiting specimens have been collected in February, August, October, and November.

Additional specimens examined. ECUADOR. Napo: Shushufindi (Nueva Loja), road Coca-Lago Agrio, ca. 50 km NE of Coca, ca. 400 m, 16 Feb 1974 (fl), *Harling & Andersson 11995* (GB, MO). **Pastaza:** Curaray (Jesús Pitishka), near the posto militar, ca. 200 m, 18 Mar 1980 (fl), *Harling & Andersson 17377* (GB, MO).

PERU. Loreto: Prov. Ucayali, Contamana, road to Oriente, 180–200 m, 28 Jul 1970 (fl), *McDaniel et al. 2568* (US). **Madre de Dios:** Parque Nacional Manú, Zona Reservada, Río Manú, Cocha Juarez, 12° 5'S, 71° 4'W, 350 m, 28 Sep 1989 (fl), *Foster & Vivar 13272* (F, UT). **San Martín:** Prov. Mariscal Caceres, Dist. Tocache Nuevo, Pueblo Mantención, property of Hernán Ortíz, about 10 km S of Tocache Nuevo, 400–700 m, 26 Apr 1983 (st), *Bohs & Schunke 2164* (GH, USM); Dist. Tocache Nuevo, Fundo Porvenir, 3 Sep 1970 (fl), *Schunke 4325* (COL, F, G, GH, MO, NY, US); Dist. Tocache Nuevo, Cañutillo, 28 km from Tocache, 525 m, 6 Jul 1974 (fl), *Schunke 7175* (GH); Dist. Uchiza, Caserío Nueva Unión below Puerto Huicte, 450–500 m, 1 Aug 1974 (fr), *Schunke 7957* (GH, TEX); Dist. Tocache Nuevo, Quebrada de Mantención, near property of Sr. Hernán Ortíz Gonzáles, 500–600 m, 29 Aug 1983 (fr), *Schunke 14032* (F, GH, MO, USM).

BRAZIL. Acre: Rio Branco-Porto Velho Highway, km 22, 14 Feb 1979 (fr), *de Albuquerque et al. 1384* (MO); road from Rio Branco to Porto Acre, km 39, 13 Oct 1980 (fl, fr), *Cid 2894* (F, GH, RB); 50 km from Rio Branco on Rio Branco-Brasileia road, 2 Oct 1980 (fl), *Lowrie et al. 347* (F, RB). **Pará:** BR 163, km 1131, Cuiabá-Santarém highway, vic. Igarapé Natal, 14 Nov 1977 (fl, fr), *Prance et al. P25404* (MO, RB).

Local names and uses. Peru: Asnapanga (*Schunke 4235*), millua chuposacha (*Schunke 7957*), pepinillo chuposacha (*Schunke 14032*), siuca sacha (*McDaniel et al. 2568*).

Cyphomandra foetida is very similar to *C. tegore.* Both species have simple, cordate crown leaves, unbranched inflorescences with closely spaced pedicels leaving prominent pedicellar remnants, greenish stellate corollas, slender anthers about 5–6 mm long with the connective prolonged below the bases of the thecae, and slender cylindrical styles with small truncate stigmas. Both species are also abundantly pubescent on the axes, leaves, and fruits, but *C. tegore* lacks the long shining hairs present on the axes and leaves of *C. foetida.* The two species may also be distinguished by differences in pubescence of the corolla lobes and by the shape of the fruits: those of *C. foetida* are acute at the apex, whereas those of *C. tegore* are obtuse. *Cyphomandra tegore* may be further distinguished by its pinnately

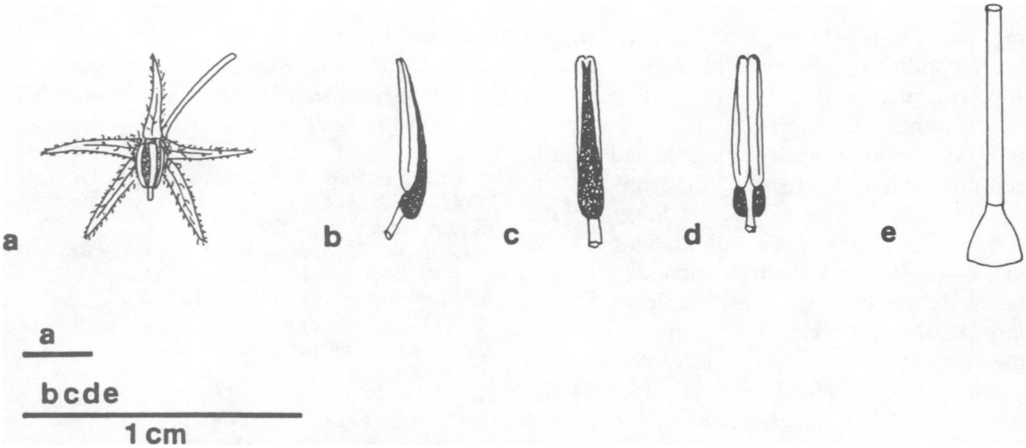


FIG. 45. *Cyphomandra fragilis*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Killip & Smith 26829* (US); b–e, based on *Knapp & Mallet 6293* (US).

lobed trunk leaves, which are thus far unknown in *C. foetida*; however, only one specimen of *C. tegore* has lobed leaves, and it is not known how variable this character state might be within the species. The two species are also separated geographically, with *C. foetida* being found in the western Amazon and *C. tegore* around the mouth of the Amazon in eastern Brazil. This distinction is blurred, however, by the collection of *Prance et al. 25404* from Pará, Brazil, which has the long, shining hairs and acute fruits characteristic of *C. foetida* but falls within the geographical range of *C. tegore*. Additional collections of these two species may further confound their morphological and geographical distinctions and may support consideration of both as a single species.

Two Ecuadorian collections included here as *C. foetida* exhibit a few anomalous morphological features. They conform to *C. foetida* in their axes and leaves clothed with long, shining hairs and simple cordiform leaves. However, they differ from the rest of the material in that the pedicels are articulated at the base and leave almost no pedicellar remnants on the rachis. The flowers are also larger in these collections, with corolla lobes up to 12–14 mm long and anthers up to about 8 mm long. The corolla lobes and vegetative parts are also not as copiously glandular-pubescent as other collections of *C. foetida*. The stigma is relatively broad, with a diameter of about 1 mm. Fruits are not present on either Ecuadorian collection. This element may represent a distinct species, but is included here within *C. foetida* until it is better collected and characterized.

13. Cyphomandra fragilis Bohs, Revista Acad. Colomb. Ci. Exact. **16:** 70. 1988, nom. nov. Fig. 45.

Solanum oxyphyllum C. Morton, Contr. U.S. Natl. Herb. **29:** 49. 1944. Type. Colombia. Putumayo: Umbría, 0° 54'N, 76° 10'W, 325 m, 13 Nov 1930 (fl), *Klug 1776* (holotype, US 1518016; isotypes, A, BM, F, GH, MO, NY).

Small *tree* 2–6 m tall. *Branches* glabrous and abundantly sand-punctate. *Leaf blades* simple or pinnately compound, membranaceous to chartaceous, acuminate at apex, glabrous adaxially and abaxially except for some very short glandular and eglandular hairs scattered on adaxial surface of blade and on veins, abundantly sand-punctate; petioles glabrous except for a puberulent line of hairs in adaxial channel. *Trunk leaves* simple or 2–7-pinnate; if simple, the blade elliptic, 9–20 cm long, 4.5–8 cm wide, length:width ratio ca. 2:1, the base shallowly cordate to truncate or cuneate, often oblique, slightly decurrent into petiole, with basal lobes less than 0.5 cm long; if compound (two leaves represented), the blade 18–32 cm long, ca. 11–25 cm wide, the terminal leaflet elliptic, 16–19 cm long, 5.5–8 cm wide, the base subcordate to truncate and decurrent, the petiolule 20 mm long, the lateral leaflets 7.5–17 cm long, 3.5–6 cm wide, the petiolules 4–10 mm long; petioles 1.5–17 cm long. *Crown leaves* 4 per sympodial unit, simple or 2–3-pinnate; if simple, the blade elliptic, 3.5–19 cm long, 2–8 cm wide, length:width ratio 1–2(–3):1, the base shallowly cordate to truncate or cuneate and slightly decurrent with basal lobes less than 0.5 cm long; if compound, the blade 7–13 cm long, 3–9 cm wide, the terminal leaflet elliptic, 4.5–11 cm long, 2–4.5 cm wide, the base rounded, the petiolule 3–12 mm long, the lateral leaflets 1.5–5 cm long, 0.8–1.5 cm wide, the petiolules 1–6 mm long; petioles 1–3 cm long. *Inflorescence* unbranched, 15–35(–50)-flowered, 3–14 cm long; peduncle 1–3 cm long; rachis 2–11 cm long; pedicels 10–25 mm long, very slender, 20–30 mm long in fruit, 1–5 mm apart, articulated at or near the base, leaving pedicellar remnants up to 0.5 mm long; peduncle, rachis, and pedicels glabrous or sparsely glandular-puberulent. *Flower buds* lanceolate, acute at apex. *Calyx* membranaceous, glabrate, veiny and sand-punctate, the radius 2–3 mm, the lobes 1–1.5 mm long, 1–1.5 mm wide, oblong to deltate, truncate, acute or apiculate at apex. *Corolla* yellow-green, sometimes lilac-tinged, membranaceous, stellate, the radius 10–20 mm, the tube 1–2 mm long, the lobes narrowly triangular, 10–20 mm long, 1.5–2 mm wide, glandular-puberulent abaxially, glabrate to white-puberulent adaxially toward apex, the margin ciliate, the apex acute. *Anther thecae* yellow or white, narrowly oblong, 4–5 mm long, 0.5–1 mm wide, the apices connate into a ring around the style, the pores directed distally and somewhat adaxially; connective whitish or purplish?, narrowly oblong, 5–6 mm long, 0.3–0.5 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 1 mm, adaxially absent. *Ovary* glabrous, often sand-punctate; style cylindrical, glabrous, not dilated distally, 6–9 mm long, 0.2–0.5 mm in diam., exserted 1–3 mm beyond stamens; stigma truncate, 0.3–0.5 mm in diam. *Fruit* pyriform, obovate, or globose, obtuse at apex, 3–5 cm long, 3–5 cm in diam., glabrous, yellow-green with white blotches or longitudinal stripes, probably yellow when ripe; presence of stone cell aggregates in mesocarp unknown; seeds 5–6 mm long, 3–5 mm wide, glabrous to sparsely puberulent.

Distribution (Fig. 46A) and phenology. Tropical moist to wet forest, 200–1600 m, eastern slope of Andes in Colombia, Ecuador, Peru, and western Brazil. Flowering specimens have been collected in all months of the year except April. Fruiting specimens have been collected in March through June and August through November.

Additional specimens examined. COLOMBIA. NARIÑO: Río Rumiyaco, 800 m, 9 Aug 1964 (fl, fr), *Soejarto et al. 1285* (COL, GH, U, US).

ECUADOR. MORONA-SANTIAGO: along Río Metzera Grande on Hacienda Sangay near Palora, ca. 950 m, 1° 40'S, 77° 58'W, 15 Feb 1984 (fl), *Knapp & Mallet 6293* (BH, G, US); Macuma, 23 Dec 1976 (fl), *McElroy 171* (BH). NAPO: Estacion Biológica Jatun Sacha, 8 km E of Misahualli, 1° 4'S, 77° 36'W, 250–300 m, 24 Aug 1988 (fr), *Cerón & Cerón 4671* (UT); same locality, 23–24 May 1989 (fl, fr), *Cerón 6702* (UT); 1.1 km E of Río Conejo on road to Lago Agrio, ca. 340 m, 31 Mar 1972 (fl), *Dwyer & MacBryde 9770* (MO, NY, US); 3 km E of Caserío de Humaní, 0° 43'S, 77° 36'W, 1200 m, 17 Sep 1988 (fr, fl), *Hurtado & Alvarado 341, 343* (UT); San José de Payamino, 40 km W of Coca, 0° 30'S, 77° 20'W, 300–600 m, 26 Nov 1983 (st), *Irvine 354* (F); Coca (Puerto San Francisco de Orellana), 17 Jan 1973 (fl), *Lugo 2829* (GB, MO); Río Payamino, tributary of the Río Napo, vic. Payamino-Capihaura, 19 Jan 1973 (fl), *Lugo 2865* (GB, MO); Añangu, Parque Nacional Yasuní, area of the SEF project, 76° 23'W, 0° 31–32'S, 260–350 m, 30 May–21 Jun 1982 (fl), *Ollgaard et al. 39210* (AAU); road Hollín-Loreto, between Río Guamani and Río Pucuno, km 40, 1200 m, 12 Dec 1987 (fl), *Palacios 2205, 2233* (UT); carretera Hollín-Loreto-Coca, Buena Vista, 0° 40'S, 77° 30'W, 700–750 m, 8 Dec 1987 (fl), *Zak & Jaramillo 3117* (NY).

PERU. HUÁNUCO: Prov. Huánuco, Tingo María, 13 Aug 1940 (fl), *Asplund 13019* (S); Pachitea, Codo de Pozuzo, 75° 25'W, 9° 40'S, 450 m, 18 Oct 1982 (fl, fr), *Foster 9267* (MO); Puerto Lira, along Río Pachitea, 300 m, 23 Jul 1929 (fl), *Killip & Smith 26829* (F, NY, US). LORETO: Prov. Alto Amazonas, Puranchim, Río Sinchiyacu, 2° 50'S, 76° 55'W, 200 m, 30 Mar–1 Apr 1987 (fr), *Lewis et al. 13326* (Lewis, pers. coll.). MADRE DE DIOS: Prov. Tambopata, ca. 30 air km or 70–80 river km SSW of Puerto Maldonado at effluence Río La Torre (Río D'Orbigny)/Río Tambopata (SE bank), Tambopata Nature Reserve, 12° 49'S, 69° 17'W, ca. 260 m, 16 Apr 1980 (fr), *Barbour 4785* (MO); Tambopata Reserve, Río Tambopata at mouth of Río D'Orbigny, 12° 50'S, 69° 17'W, 250 m, 28 Feb 1981 (fl), *A. Gentry & Young 31787* (MO); same locality, 6 Mar 1981 (fl, fr), *A. Gentry & Young 32035* (MO, USM). SAN MARTÍN: Zepelacio, near Moyobamba, 1100–1600 m, Mar 1934 (fl), *Klug 3600* (F, MO, NY, S, US); Prov. Mariscal Cáceres, Dist. Tocache Nuevo, road to old village of Tocache, 17 Jan 1970 (fl), *Schunke 3723* (F, NY, US); Tocache Nuevo, road to Pushurumbo, 5–6 km de Palo Blanco, 500–600 m, 20 Nov 1972 (fl, fr), *Schunke 5568* (F, MO, TEX); Dist. Tocache Nuevo, mouth of Río Mishollo (right margin of Río Huallaga), 350–380 m, 25 Jul 1973 (fl), *Schunke 6402* (C, MO); Puerto Pizana (right margin of Río Huallaga), 350 m, 12 Jun 1974 (fr), *Schunke 6933* (GH).

BRAZIL. ACRE: Serra da Moa, near school, 1 May 1971 (fl), *Maas et al. P12713* (F, K, M, NY, US, WIS).

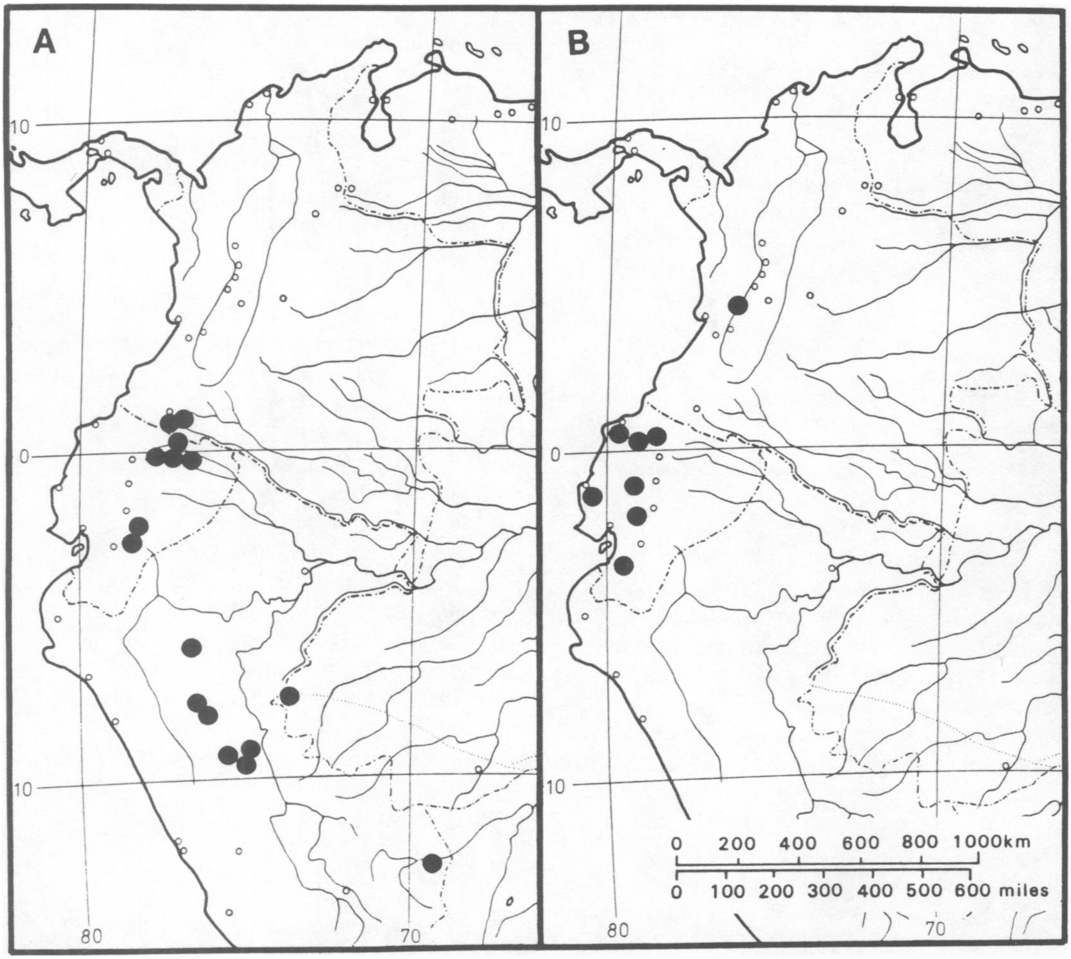


FIG. 46. Distribution of **A.** *C. fragilis*, **B.** *C. hypomalaca.*

Local names and uses. Peru: Overo chuposacha (*Schunke 6933*). The Achuar Jivaro of Amazonian Peru squeeze the juice from 100 grams of bark into 25 ml water. After boiling, the solution is drunk to relieve stomach ache (*Lewis et al. 13326*).

Cyphomandra fragilis is unique in the genus in having the tips of the anthers united into a ring. The membranaceous elliptic leaves with subcordate to decurrent bases are also distinctive. The leaves and fruits of this species resemble those of *C. diversifolia* subspecies *chlorantha*, but the flowers are very different. Those of *C. diversifolia* subspecies *chlorantha* have purplish urceolate corollas, short thick anthers with very swollen connectives, and relatively broad styles and stigmas, whereas the flowers of *C. fragilis* resemble those of *C. foetida* and other members of the *C. hartwegii* group in their greenish stellate corollas, long slender anthers, and narrow styles and stigmas. Like *C. diversifolia* subspecies *chlorantha*, *C. fragilis* may also have some pinnately compound leaves, but these are not well-represented on herbarium specimens.

Although first described as a member of *Solanum* section *Geminata*, this species clearly belongs to *Cyphomandra*. A new name has been chosen because *C. oxyphylla* has already been ap-

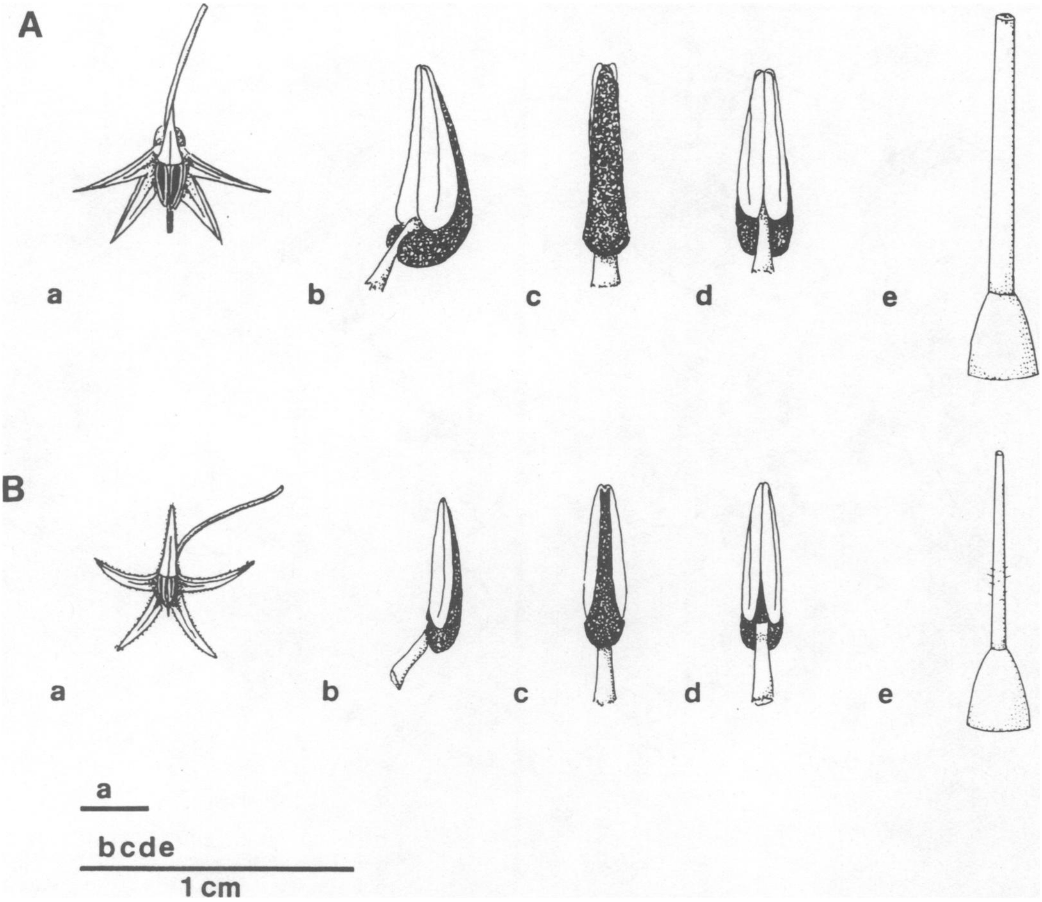


FIG. 47. *Cyphomandra hartwegii.* **A.** subspecies *hartwegii.* **B.** subspecies *ramosa.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. A, based on *Bohs & McPherson 2318*; B, based on greenhouse material of *Bohs 1644*.

plied to a Brazilian species [*C. oxyphylla* Dunal, a synonym of *C. divaricata* (Mart.) Sendtn.].

14. Cyphomandra hartwegii (Miers) Walpers, Repert. Bot. Syst. **6:** 579. 1847. Figs. 47, 48.

Small *tree* 2–12 m tall. *Branches* glabrous to densely puberulent or pubescent, sometimes also sparsely to moderately pilose. *Leaf blades* simple, lobed or unlobed, subcoriaceous, (acute-) acuminate at apex, glabrous to moderately pubescent-pilose adaxially, especially on veins, glabrous to densely pubescent-pilose abaxially; petioles glabrous to densely puberulent, pubescent, or pilose. *Trunk leaves* simple, unlobed or pinnately (2–)5–9(–11)-lobed; if unlobed, the blade ovate or elliptic-ovate, 20–35 cm long, 11–23 cm wide, length:width ratio ca. 1.5–2:1, the base nearly truncate to cordate with basal lobes 0.5–3 cm long; if lobed, the blade 23–50 cm long, 20–40 cm wide, divided 1/2–4/5 to midrib, the sinuses rounded, acute, the base cordate with basal lobes 0.5–3 cm long; petioles 6–30 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed or 2–5(–7)lobed; if unlobed, the blade ovate to elliptic, (3–)5–25(–28) cm long, (3-)5–20 cm wide, length:width ratio 1–2:1, the base truncate to cordate, often oblique, with basal lobes 0.5–3(–4) cm long; if lobed, the blade 10–22 cm long, 10–30 cm wide, divided 2/3–4/5 to midrib, the sinuses rounded, acute, the base truncate to cordate with basal lobes 0.5–3

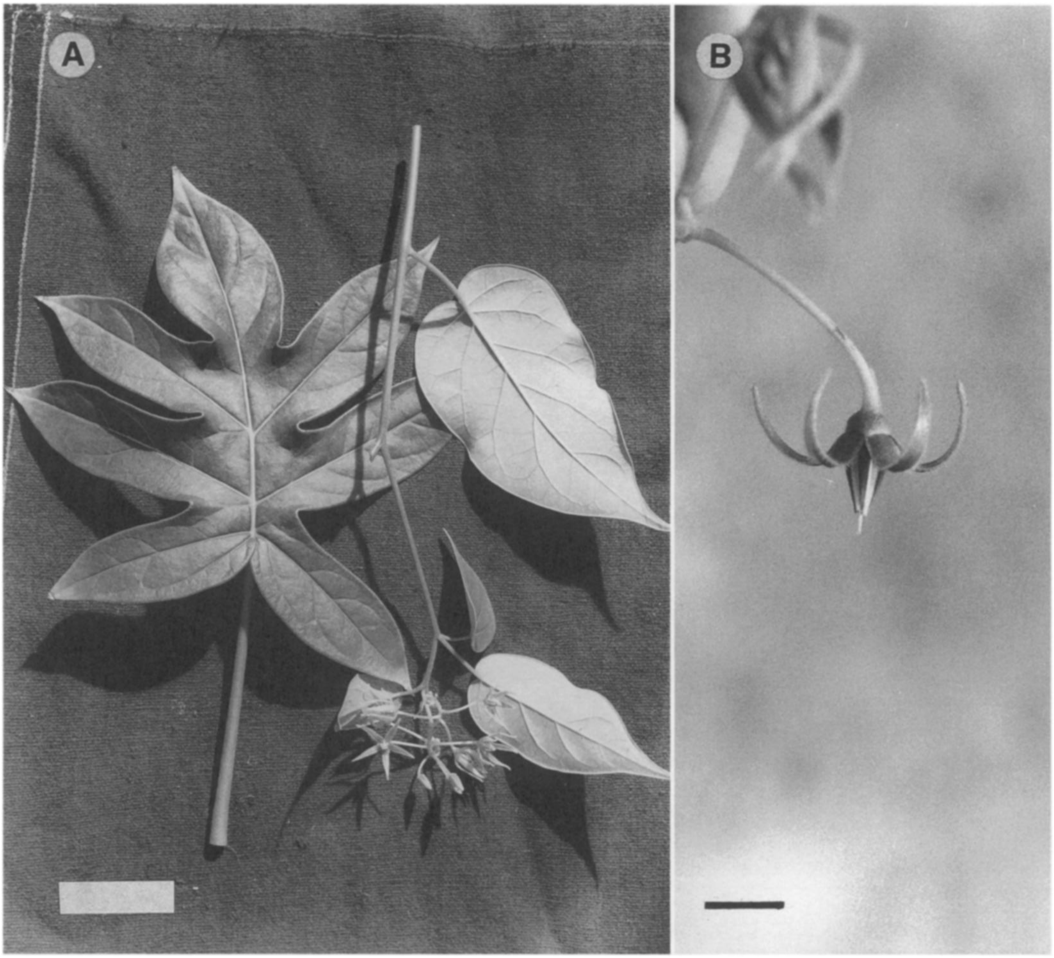


FIG. 48. *Cyphomandra hartwegii* subspecies *ramosa*. **A.** Trunk leaf and crown branch with inflorescence. Scale bar = 5 cm. **B.** Flower. Scale bar = 5 mm. From greenhouse material of *Bohs 1644*.

cm long; petioles 1–10 cm long. *Inflorescence* unbranched or branched, 25–100+ -flowered, 5–60 cm long; peduncle 2–9 cm long; rachises 3–50 cm long; pedicels 15–35 mm long, 25–50 mm long in fruit, 1–6 mm apart, articulated at or near the base, leaving pedicellar remnants up to 1 mm long; peduncle, rachises, and pedicels glabrate to densely pubescent, sometimes also sparsely pilose. *Flower buds* lanceolate, acute at apex. *Calyx* fleshy, glabrous to densely pubescent, the radius 2–5(–8) mm, the lobes 1–2(–6) mm long, 2–3 mm wide, obtuse to truncate, apiculate. *Corolla* usually green, sometimes white or violet, subcoriaceous to fleshy, stellate, the radius 10–25 mm, the tube 1–2 mm long, the lobes narrowly triangular, 10–23 mm long, 2–3 mm wide, glabrous to densely puberulent-pubescent abaxially, glabrous to puberulent adaxially, especially toward apices, the margin tomentose, the apex acute. *Anther thecae* yellow or white, narrowly triangular, (3.5–)5–9 mm long, 1–2 mm wide, the pores directed distally; connective gray, yellow, blue, or purple, narrowly triangular, (3.5–)5–9 mm long, 1–2 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 0.5–1 mm, adaxially present or absent. *Ovary* glabrous; style cylindrical, glabrous or sparsely pubescent, not to slightly dilated dis-

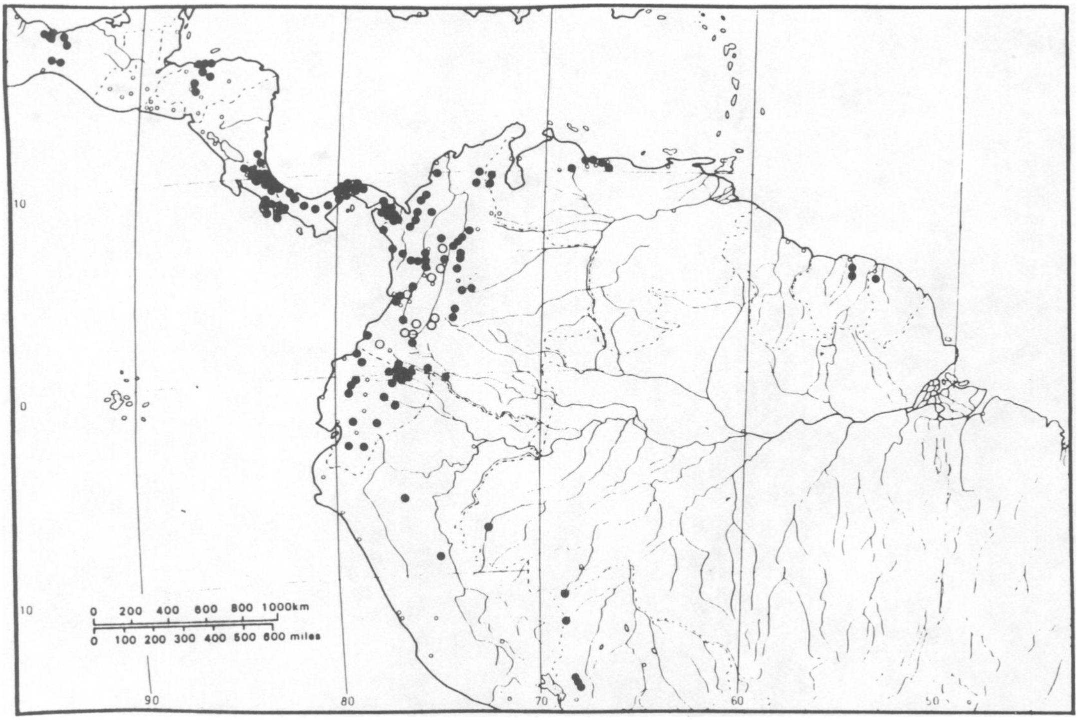


FIG. 49. Distribution of *C. hartwegii* subspecies *hartwegii* (dots) and subspecies *ramosa* (open circles).

tally, (4–)6–10 mm long, 0.2–1 mm in diam., exserted 1–3 mm beyond stamens; stigma truncate to capitate, 0.2–1 mm in diam. *Fruit* ellipsoidal, ovoid, or globose, obtuse at apex, 3–9 cm long, 3–6 cm in diam., glabrous, yellow or orange when mature, often with darker longitudinal stripes; mesocarp with large stone cell aggregates; seeds 4–9 mm long, 3.5–7 mm wide, rugose, sparsely to moderately pubescent.

Distribution (Fig. 49). Disturbed areas, clearings, or tree falls in tropical wet forest, rain forest, or cloud forest, 0–2500 m in elevation, Mexico, Central America, and northwestern South America. In South America, *C. hartwegii* is found both east and west of the Andean cordillera.

Cyphomandra hartwegii is a wide-ranging and variable taxon, but it can be distinguished from the other species of *Cyphomandra* by the following combination of characters: trunk leaves often pinnately lobed, and crown leaves unlobed, ovate, with cordate bases; inflorescences often elongated with pedicels articulating near the bases; greenish, stellate corollas with acute, narrow lobes; narrow, tapered anthers and connectives, with the connective extending below the bases of the thecae; styles not to slightly dilated distally; glabrous fruits with obtuse apices and large stone cell aggregates; and large, flattened, scarcely pubescent seeds. In floral features and seed morphology, *C. hartwegii* most closely resembles *C. endopogon*, *C. oblongifolia*, *C. sibundoyensis*, *C. stellata*, *C. tegore*, and *C. tobagensis*. The glabrous fruits of *C. hartwegii* distinguish it from *C. stellata*, *C. tegore*, and *C. tobagensis*. *Cyphomandra sibundoyensis* has purple rather than green corollas and lacks pinnately lobed trunk leaves. (Although the trunk leaves are not necessarily lobed in *C. hartwegii*, at least a few lobed leaves occur on almost all individuals.) *Cyphomandra hartwegii*, *C. endopogon*, and *C. oblongifolia* all have some lobed trunk leaves and glabrous fruits. However, *C. endopogon* has oblong, obtuse corolla lobes with ciliate margins and styles that are distally dilated, whereas the corolla lobes of *C. hartwegii* are narrowly triangular and acute with tomentose margins, and the styles are not dilated. *Cyphomandra oblongifolia* differs from *C. hartwegii* in its oblong leaves with truncate (rather than cordate) bases and its campanulate (rather than stellate) corollas. These three taxa are distinct throughout most of their range; however, intermediate forms between *C. hartwegii* and *C. endopogon* occur on the eastern slopes of the Andes (recognized as *C. stellata*) and intermediates between *C. hartwegii* and *C. oblongifolia* are found in Suriname. A closer examination of these taxa may show these zones of morphological overlap to be the result of hybridization. Alternatively, the three species may belong to a single, extremely variable taxon. Because of the marked floral differences between them, I have chosen to recognize these three taxa as distinct, albeit closely related, entities.

Two subspecies are recognized within *C. hartwegii*, and may be distinguished in the following key.

KEY TO THE SUBSPECIES OF *CYPHOMANDRA HARTWEGII*

1. Leaves, stems, and inflorescence axes glabrous to puberulent with hairs 0.5 mm long or less (rarely longer); inflorescence simple or branched (if much branched, then plants nearly glabrous) . . . a. subspecies *hartwegii*.

1. Leaves, stems, and inflorescence axes densely pubescent with hairs 1 mm long or more; inflorescence usually highly branched . . . . b. subspecies *ramosa*.

a. *Cyphomandra hartwegii* (Miers) Walpers subspecies *hartwegii*

Pionandra hartwegii Miers, London J. Bot. **4:** 363. 1845. Type. Colombia. Cundinamarca: near Guaduas, Hacienda de Palmar, 1843 (fl), *Hartweg 1297* (holotype, K; isotypes, BM, G [F neg. 23051 F, GH], K, LD).

Cyphomandra splendens Dunal, DC. Prodr. **13(1):** 395. 1852; Macbride, Field Mus. Nat. Hist., Bot. Ser. **13(5B):** 16. 1962. Type. Peru? *Pavon s.n.* (holotype, G [F neg. 8561 F, GH, NY, US, WIS]; isotypes, F (fragment), MA).

Cyphomandra heterophylla J. D. Smith, Bot. Gaz. (Crawfordsville) **27:** 436. 1899, non *Cyphomandra heterophylla* Taubert (1893). Type. Costa Rica. Santa Clara, La Emilia, 250 m, Apr 1896 (fl), *Donnell Smith 6670* (lectotype, US 1335001, here designated; isolectotypes, BM, G, GH, K, M, NY, US). Chosen from syntypes *Cooper 10215*, *Donnell Smith 6670*, *Pittier 9059*, *Pittier 10294*, *Tonduz 6603*, *Tonduz 11496*.

Cyphomandra costaricensis J. D. Smith, Enum. Pl. Guatem. **6:** 84. 1903, nom. nov. for *C. heterophylla* J. D. Smith.

Cyphomandra artocarpophylla Hubert Winkler, Repert. Spec. Nov. Regni Veg. **7:** 246. 1909, 'artocarpophyllos.' Type. Bolivia. La Paz: Charopampa bei Mapiri, lichte Waldstellen, 570 m, Nov 1907 (fl), *Buchtien 1444* (lectotype, M, here designated [F neg. 6519 F, NY, US, WIS]; isolectotype, US 1176791).

Cyphomandra holtonii Hochreutiner, Bull. New York Bot. Gard. **6:** 285. 1910. Type. New Grenada (Colombia). Barcinal, 24 Nov 1853 (fl), *Holton 555* (lectotype, NY, here designated; isolectotypes, G [F neg. 23052 F, GH, WIS], K).

Cyphomandra dendroidea Pittier, Contr. U.S. Natl. Herb. **13:** 116, Fig. 22. 1910. Type. Colombia. Valle: Dagua Valley, margin of the forest at Córdoba, in the rain belt of the Pacific coast, ca. 60 m, 7 Dec 1905 (fl), *Pittier 512* (lectotype, US 530694, here designated; isolectotype, US 1059964).

Cyphomandra naranjilla Pittier, Contr. U.S. Natl. Herb. **13:** 117, Pl. 17 and Fig. 23. 1910; Romero-Castañeda, Frutas Silvestres de Colombia **1:** 276, Fig. 83. 1961. Type. Colombia. Valle: cultivated in the garden at La Manuelita near Palmira, also growing wild in the mountains above Palmira, 1200–1800 m, 2 Jan 1906 (fl), *Pittier 914* (holotype, US 531106; isotype, US 1059967).

Cyphomandra dolichorhachis Bitter, Repert. Spec. Nov. Regni Veg. **17:** 350. 1921. Type. Colombia. Cauca: in dichten Wäldern an den Westgehängen der West Anden von Popayán, "bis 4 m hohe, weichholzige Bäumchen mit flachen, öfter tafelförmigen, ziemlich dichten Kronen; Blätter krautig-ledern, matt-meergrün, Blüten bräunlich-hellgrün, Fruchte enteneigross," 1500–1800 m, *Lehmann 6988* (holotype, B, destroyed [F neg. 2931 F, G, GH, NY, US, WIS]; isotypes, F [F neg. 57901], K).

Cyphomandra mollicella Standley, Publ. Field Columbian Mus., Bot. Ser. **4:** 322. 1929. Type. Honduras. Atlántida: near Tela, sea level, 18 Jan 1928 (fl), *Standley 54720* (holotype, F 583731 [F neg. 49359 F, WIS]; isotypes, A, US 1408431).

Stems, *petioles*, and inflorescence *axes* glabrous to densely puberulent, rarely pubescent, sometimes also sparsely to moderately pilose. *Leaf blades* glabrous to sparsely pilose and sparsely to moderately glandular-puberulent adaxially, especially on veins, glabrous to densely puberulent abaxially. *Inflorescence* unbranched or branched, 25–100+ -flowered. *Calyx* glabrous to puberulent or pubescent, the radius 2–5(–8) mm, the lobes 1–2(–6) mm long. *Corolla* radius 10–25 mm, the lobes 10–23 mm long, glabrous to puberulent abaxially, glabrous to tomentose adaxially, especially toward apices. *Anther thecae* (3.5–)5–9 mm long, 1–2 mm wide; connective (3.5–)5–9 mm long, 1–1.5 mm wide, adaxially present or absent. *Style* (4–)6–10 mm long, 0.3–1 mm in diam., not or slightly dilated distally; stigma truncate to capitate, 0.3–1 mm in diam. *Fruit* ellipsoidal, ovoid, or globose, 3–5 (–7) cm long, 3–4(–6) cm in diam. *Seeds* 4–7 mm long, 3.5–5 mm wide.

Distribution (Fig. 49). Disturbed areas or clearings in tropical wet forest, rain forest, or cloud forest, 0–2000(–2500) m, southern Mexico, Guatemala, and Nicaragua south to Panama and northwestern South America in Colombia, Venezuela, Suriname, Ecuador, Peru, Brazil, and Bolivia. Flowering and fruiting throughout the year.

Representative specimens examined. MEXICO. Oaxaca: Chimalapa, Mun. Santa María Chimalapa, 16° 55'N, 94° 40'30"W, 300 m, 2 Jul 1984 (fl, fr), *Hernández 177* (NY); Chimalapa, Mun. San Miguel Chimalapa, Arroyo El Salto, ca 2 km al NW de la Coralilla (Díaz Ordáz), 16° 43'N, 94° 11'W, 1300 m, 5 Oct 1984 (fr), *Maya 644* (NY). **Veracruz:** Bastonal, ca. 10 km E de Lago Catemaco, 900 m, 22 May 1972 (fl), *Beaman & Alvarez 5855* (F, U); km 3, carretera Cedillo-Río Alegre, Hidalgotitlán, 17° 15'N, 94° 38'W, 120 m, 12 Aug 1974 (fr), *Dorantes 3474* (F); Estación de Biológica Tropical, San Andres Tuxtla, 180 m, 20 May 1970 (fl, fr), *Martínez 3001* (F, K, MO, NY); 7.2 km E of Tebanca, 2.6 km W of Bastonal lumber camp, 910 m, 15 Jan 1981 (fr), *Nee & Schatz 19929* (F, WIS); Mun. Minatitlán, terracería La Laguna-Uxpanapa, 30 km al E del Campamento La Laguna, 17° 14'15"N, 94° 17'00"W, 190 m, 24 Sep 1980 (fr), *Wendt et al. 2692* (LL, MO, NY).

HONDURAS. Atlántida: Mountain Nombre de Dios between Saladito and San Francisco, 200 m, 26 Apr 1967 (fl), *Molina 20844* (F, US); Lancetilla Valley, near Tela, 20–600 m, 6 Dec 1927–20 Mar 1928 (fl), *Standley 56833* (A, F, US); near Puente Alto stop on S.F. Co. R.R., E of Ceiba, 10 Jul 1938 (fr), *Yuncker et al. 8528* (BM, F, G, GH, K, MO, NY, S, TEX, US). **Comayagua:** near El Achote, hills above the plains of Siguatepeque, 1350 m, 30 Jul 1936 (st), *Yuncker et al. 6231* (F, G, GH, K, MO, S, U). **Cortes:** Aldea La Pita, 5 km SW of Puerto Cortés, 50 m, 26–30 Nov 1975 (fl, fr), *Nelson et al. 3097* (MO); near Agua Azul, Lake Yojoa, 650 m, 14 Apr 1951 (fl), *Williams & Molina 17900* (F, GH, US). **Yoro:** montañas al SE del Valle Lean, 15 km de Placencia, 800 m, 25 May 1978 (fl), *Hazlett & Coe 2745* (F).

NICARAGUA. Zelaya: Caño Costa Riquita, ca. 1.8 km SW of Colonia Naciones Unidas, ca. 11° 43'N, 84° 18'W, 150–180 m, 6–7 Nov 1977 (fr), *W.D. Stevens 4938* (BM). **Without Department:** no locality, 1869, *Seemann 83* (BM); Chontales, 16 Jan 1868 (fl), *Tate 248* (K); no locality, *Tate 254* (K).

COSTA RICA. Alajuela: Near Quebrada Guillermina, N side of Volcán Arenal, 10° 29'N, 84° 42'W, 500 m, 21 Apr 1973 (fr), *Lent et al. 3419* (F, MO, U); Santa María National Park, 10° 37'N, 85° 17'W, 600 m, 7 Feb 1978 (fr), *Liesner 5094* (CR, MO); same date (fl), *5128* (CR, MO); near Río San Rafael, 2 km W of La Marina, Llanura de San Carlos, 550 m, 21 Feb 1966 (fl), *Molina et al. 17720* (BM, F, WIS). **Cartago:** 24 km NE of Turrialba on hwy to Limón, 9° 58'N, 83° 34'W, 450–525 m, 10 May 1983 (fl), *Liesner et al. 15388* (MO); Turrialba, 500 m, 15 Sep 1894 (fl), *Pittier 9059* (US); Tuis, Nov 1897 (fl, fr), *Tonduz 11496* (BR, US); Las Vueltas, Tucurrique, 635 m, Nov 1898 (fl), *Tonduz 12747* (F, G, K, W). **Guanacaste:** E slopes of Volcán Miravalles (Cerro la Giganta) above the town of Río Naranjo, 10° 42'N, 85° 07'W, 800 m, 8 Apr 1973 (fl, fr), *J. Gentry & Burger 2890* (BM, F, MO, NY); vic. Tilarán, 500–650 m, 10–31 Jan 1926 (fl), *Standley & Valerio 44953* (US); slopes of Volcán Orosí ca. 15 km SE of La Cruz, 200–450 m, 19 Jan 1968 (fr), *Wilbur & Stone 9804* (F, MO). **Heredia:** La Selva Biological Reserve, near Puerto Viejo de Sarapiquí, 10° 24'26"N, 84° 0'2"W, 200 m, 18 Aug 1981 (fl, fr), *Happel & Neill 01* (ECON); Finca San Bosco, al otro lado del Rio Sarapiquí, al SE de Puerto Viejo, 120 m, 22 Sep 1966 (fl, fr), *Jiménez 4153* (CR, F, GH); Istarú Farm, Tirimbina, Sarapiquí, 220 m, 17 Jan 1970 (fr), *Lent 1873* (F, MO, U); vic. Colonia Virgen del Socorro, 2–5 km E of Cariblanco, 900 m, 10 Aug 1975 (fl, fr), *Utley 2837* (F, MO, U). **Limón:** near Río Catarata between Bribri and the Caribbean Coastal Plain, 9° 37'N, 82° 49'W, 50–100 m, 10 Feb 1977 (fl), *J. Gentry 3730* (F); Waldeck près Madre de Dios, 50 m, Oct 1896 (fl, fr), *Pittier 10294* (US); Río Toro Amarillo (Finca Vieja), cantón de Pococí, ca. 200 m, 30 Aug 1936 (fr), *Solís 428* (CR, F, MO); Finca Montecristo, on the Río Reventazón below Cairo, ca. 25 m, 18–19 Feb 1926 (fl, fr), *Standley & Valerio 48439, 48463, 48475* (all US); Zent, 31 m, Jul 1901 (fl), *Tonduz 14733* (G). **Puntarenas:** Golfito Dulce area, vic. Esquinas Experiment Station, sea level, 8 Apr 1949 (fl, fr), *P.H. Allen 5241* (F, GH, MO, US); N and W of the airfield, ca. 5 km W of Rincón de Osa, 8° 42'N, 83° 31'W, 50–200 m, 24–30 Mar 1973 (fl, fr), *J. Gentry & Burger 2766* (F, MO, NY, S, U), *2767* (MO), *2840* (AAU, F, MO, S), *2851* (F); Playa Blanca Road near Rincón de Osa, near sea level, 16 Feb 1974 (fl, fr), *Liesner 2189* (C, LD, LL, MO, US); Corcovado National Park, near new airfield at Pavo, 8° 30'N, 83° 37'W, 5 m, 7 Jul 1977 (fl, fr), *Liesner 3036* (CR, MO); Buenos Aires, 300 m, Jan 1892 (fl), *Tonduz 6603* (BR, US). **San José:** vic. El General, 1010 m, Jan 1936 (fl), *Skutch 2533* (A, GH, K, MO, NY, S, US); same locality, 700 m, Jan 1939 (fl), *Skutch 3957* (A, K, MO, NY, S, US); "El Rodeo," Villa Colón, 840 m, 7 Oct 1934 (fr), *Valerio 949* (CR, F).

PANAMA. Bocas del Toro: N of Fortuna Dam, Pacific slope, ca. 2 mi off highway between Mali and Rembala, 8° 55'N, 82° 10'W, 250–300 m, 10 Feb 1987 (fl), *Bohs & McPherson 2318* (F, GH, PMS, SCZ); Almirante, just N of Dos Milla, 20 Aug 1964 (fl), *McDaniel 5122* (MO); vic. Chiriquí Lagoon, 8 Oct 1940 (fl), *von Wedel 1080* (GH, MO, US). **Canal Zone:** Barro Colorado Island, 22 Jun 1931 (fl), *Bailey & Bailey 302* (BH, F, GH); B.C.I., N edge of lab clearing, 23 Mar 1970 (fl, fr), *Croat 9016* (F, MO, NY); B.C.I., rear of laboratories, 200 m, 23 Nov 1948 (fl, fr), *Killip 39968* (K, MO, US); along Río Mendosa, 0.5 km upstream from Pipeline Road bridge, 8 km NW of Gamboa, 100 m, 26 Oct 1973 (fl), *Nee 7596*

(G, LL, MO). **Chiriquí:** Progreso, Jul-Aug 1927 (fl), *Cooper & Slater 181* (NY, US); 8 mi W of Puerto Armuelles, vic. San Bartolo Limite, 19 Feb 1973 (fl, fr), *Croat 22024* (MO); 17 mi from Paso Canoas, near Quebrada de "Vuelta," 25 Feb 1973 (fl), *Liesner 226* (L, MO). **Coclé:** Slopes of Cerro Pilón near El Valle, 700–900 m, 10 Jun 1967 (fl), *Duke 12167(5)* (F, MO, NY); 46 km N of Penonome on road to Coclesito, 100 ft, 22 Feb 1978 (fl), *Hammel 1708* (MO). **Colón:** Santa Rita Ridge, 28 Jul 1972 (fl), *D'Arcy & D'Arcy 6156* (C, F, G, GH, K, L, M, NY, US, WIS); along Portobelo-Nombre de Dios road, 10 km W of Nombre de Dios, 9° 39'N, 79° 32'W, 0–20 m, 24 Jun 1982 (fl), *Knapp & Mallet 5684* (GH); 10 mi SW of Portobelo, 2–4 mi from coast, 10–200 m, 24 Mar 1973 (fl), *Liesner 1063* (AAU, BR, C, CR, CTES, F, GH, K, L, LL, MO, NY, P, US, WIS, Z); upper Río Piedras headwaters, ca. 11 km SW of Cerro Braja, 9° 25'N, 79° 35'W, 600–700 m, 30 Apr 1981 (fl, fr), *Sytsma et al. 4175* (MO). **Darién:** Vic. Pinogana, ca. 20 m, 6 Oct 1938 (fl), *P.H. Allen 919* (F, GH, MO, NY, US); 2–3 mi SE of El Real, 18 Jun 1962 (fl), *Duke 4847* (BM, GH, MO, US); Río Pirre, Apr 1966 (st), *Duke & Bristan 8283* (MO); near Santa Fe, 18–19 Jun 1967 (fl), *Duke 12896(3)* (MO, US, WIS); between Paya and Palo de las Letras, 30 Aug 1967 (st), *Duke & Kirkbride 14026* (MO); vic. Campamento Buena Vista, Río Chucunaque above confluence with Río Tuquesa, 4 July 1959 (fl), *Stern et al. 817* (G, GH, MO, US); Río Cocalita, 11 Feb 1982 (fl), *Whiteford & Eddy 152* (BM). **Panamá:** Cerro Jefe, 8 Apr 1970 (fl), *D'Arcy et al. 3958* (C, M, MO, NY); region of Cerro Jefe, 15 Oct 1967 (fl), *Dressler 3070* (F, GH, MO); Campo Tres, 3 mi NE of Altos de Pacora, 500–800 m 10 Mar 1973 (fl), *Liesner 510* (C, F, MO, NY, US); El Llano-Carti road, 9.6 km from Panamerican Hwy., 410 m, 12 Sep 1974 (fl), *Mori & Kallunki 1826* (MO, NY); Cerro Jefe, 1.5 mi down right turnoff 6.7 mi past Goofy Lake, 700 m, 27 Dec 1980 (fl), *Sytsma et al. 2876* (CTES, MO, NY). **San Blas:** along road between Mandinga and Cangandi, 25 Oct 1967 (fl, fr), *Duke 14739(2)* (US). **Veraguas:** ca. 4 km past Escuela Agrícola near Santa Fe, ca. 800 m, 21 Dec 1974 (fr), *Nee et ai. 13994* (GH, MO, WIS).

COLOMBIA. Antioquia: Near Villa Arteaga, 150 m, 5 Feb 1948 (fl), *Agudelo & Klevers 78* (US); Titiribí, 1700 m, 31 Aug 1930 (fr), *Archer 590* (US); cerca de Villa Arteaga, ca. 150 m, 10 Oct 1947 (fl, fr), *Gutiérrez & Barkley 17C119* (COL, F, MO, TEX); near Chigorodo, 40 km S of Turbo, 50 m, 22 May 1945 (fl), *Haught 4701* (COL, NY, S, US); Segovia, vereda La Rubiela, Río Matuna, desemboca al Río Bagre, 750 m, 19 Jul 1979 (fr), *Rentería et al. 1691* (MO); San Agustín, 900 m, 5 Jan 1949 (fl), *Uribe 1897* (COL, US). **Bolívar:** Mun. de Carmen de Bolívar, corregimiento de Caracoli Grande, 600 m, 25 Mar 1983 (fr), *Cuadros 1507* (MO). **Boyacá:** region of Mt. Chapon, 100 km NW of Bogotá, 3700 ft, 25 May 1932 (fl), *Lawrance 118* (A, F, G, K, MA, MO, NY, S, US). **Caldas:** Belalcazar, 1000–1800 m, no date (fl), *Lehmann 7564* (K); "Buenos Aires," N of Supia, 2000–2200 m, 18–19 Sep 1922 (fl), *Pennell 10720* (GH, NY). **Caquetá:** Morelia, 150 m, 22 Nov 1941 (fl), von Sneidern A1353 (LL, S). **Cesar:** Rincón Hondo, 23 Aug 1924 (fl), *C. Allen 488* (MO); 5 km S of Codazzi, 100 m, 29 Oct 1943 (fl), *Haught 3786* (COL, F, NY, US). **Chocó:** between La Oveja and Quibdó, 1–2 Apr 1931 (fl), *Archer 1759* (US); Parque Nacional Los Catios, alrededores del Campamento de Tilupo, 250 m, 31 May 1976 (fl), *Forero et al. 1711* (CTES, MO, NY); Mun. San José del Palmar, hoya Río Torito (afluente del Río Hábita), Finca "Los Guaduales," 730–830 m, 4 Mar 1980 (fl, fr), *Forero 6647* (MO); Serranía del Darién, W of Unguía, near Panamá border, 550–1000 m, 25 Jul 1976 (fl), *A. Gentry et al. 17027* (COL, MO); along Río Pavarandó across from Pavarandó Grande, W of Mutatá, 150 m, 8 Oct 1977 (fl), *A. Gentry & León 20213* (AAU, COL, MO); Jequedó, 42 km W of Las Animas, ca. 250 m, 11 Jan 1979 (fl), *A. Gentry & Rentería 24003* (COL, GH, MO); Bahía Solano, ca. 100 m, 7 Feb 1947 (fl), *Haught 5542* (COL, US). **Córdoba:** Frasquillo, 90–120 m, 5–6 Mar 1918 (fr), *Pennell 4593* (US); Tierra Alta, *Pennell 4645* (NY); Palotal, 4 Jul 1948 (fl), *Romero Castañeda 1142* (F); Quimarí, 500 m, 20 Apr 1949 (fl), *von Sneidern 5763* (F, S, WIS). **Cundinamarca:** El Peñon, 1050–1420 m, 1–3 Aug 1947 (fr), *García-Barriga 12464* (COL, US). **Meta:** carretera a Villavicencio, entre Puente Quetame y Buena Vista, 1000–1400 m, 25 Jan 1968 (fl), *García-Barriga et al. 18935* (COL, ECON, LD); Río Negrito, 70 km E of Villavicencio, 22 Dec 1938 (fl), *Haught 2482* (COL, F, K, NY, US). **Nariño:** Mun. Tumaco, Salisbí, orillas del Río Chaquí, 10 Jul 1951 (fl, fr), *Romero Castañeda 2690* (COL). **Putumayo:** Río Putumayo, P. Ospina-Leguisamo, at El Remanso, 18 May 1963 (fl, fr), *Bristol 1014* (ECON); Río Caqueta, Floresta, downriver from Puerto Limón, 300–350 m, 20 Dec 1968 (fl), *Plowman 2180* (COL, F, GH, S, US); Río San Miguel ó Sucumbios, Conejo y los alrededores, 300 m, 25 Apr 1942 (fl), *Schultes 3652* (COL, ECON, US). **Risaralda:** Santa Cecilia, Pueblo Rico, Tatamá, 800 m, 26 Nov 1945 (fl), *von Sneidern 5014* (F, S, US). **Santander:** Alto de Vélez, Jan 1938 (fl), *Bro. Daniel 3868* (COL, GH, US); vic. Puerto Berrio, S of Carare, 100–700 m, 28 Mar 1935 (fl), *Haught 1617* (COL, GH, US); vic. Barranca Bermeja, on Viscaina Creek ca. 29 km S of El Centro, ca. 100 m, 9 Nov 1936 (fl), *Haught 2063* (COL, F, GH, M, NY, S, US); 15 leagues SE of Barranca Bermeja, 3 km from left bank of Río Opón, ca. 200 m, 10 Oct 1954 (fl), *Romero Castañeda 5022* (COL, F, MO, NY, US). **Tolima:** Chaparral, 4 Sep 1990 (fr), *Debouck et al. DGD2948*, seeds grown in University of Utah greenhouse as *Bohs 2442* (UT). **Valle:** Río Anchicayá, entre Pavas y Miramar, 350–450 m, 15–16 Apr 1943 (fl), *Cuatrecasas 14382* (F, US).

VENEZUELA. Aragua: Dist. Girardot, Parque Nacional Henri Pittier, regresiva hacia Ocumare de La Costa, 21 Jun 1973 (fl), *Benitez de Rojas 1576* (BM, GH); prope coloniam Tovar, 1856–7 (fl), *Fendler 2097* (GH, K, MO); subida al cerro de La Mesa (Pico Guacamayo), 1600 m, Jul 1947 (st), *Pittier 15512* (US). **Carabobo:** Borburata, Jan 1961 (fl), *Aristeguieta & Tamayo 4457* (F, MO, NY). **Miranda:** Guatopo, 400–600 m, 16 Nov 1956 (fr), *Bernardi 5702* (G, NY); near Guayabitos, S of Baruta, 12 Jun 1960 (fr), *Steyermark 86291* (NY, US). **Yaracuy:** cabeceras de la Quebrada Amparo, 7–9 km N de Salom, 1220–1250 m, 30 Nov 1974 (fl), *Steyermark & Carreño Espinoza 111200* (NY, US). **Zulia:** San Carlos del Zulia, ca. 105 km WNW of Santa Barbara, ca. 75 m, 7 Nov 1967 (fr), *de Bruijn 1439* (MO, S, U, US); Cerro Sasa, W de la

Misión de Los Angeles de Tokuku (Tocucu), al SW de Machiques, 375–700 m, 30 Aug 1967 (fl, fr), *Steyermark 99899* (MO, NY, U, US); Perijá, 1917 (fl), *Tejera 45* (US).

SURINAME. Mapane Creek area near camp 8, Jun 1963 (fl), *Boerboom 9605* (U); Jodensavanne-Mapane kreek area (Suriname R.), 12 Dec 1954 (fl), *Lindemann 6812* (U); Brownsberg, 400–450 m, 11 Nov 1974 (fl), *Maas et al. 2359* (U).

FRENCH GUIANA. Region of Paul Isnard, environs of Citron toward Mont Décou Décou, 8 Sept 1983 (fl), *Cremers 8165* (BR).

ECUADOR. Bolívar: Limón, 880–1100 m, 14 Oct 1943 (fr), *Acosta Solís 6361* (F). **Esmeraldas:** Río San Miguel, upstream from Pueblo Cayapas, 78° 54'W, 0° 45'N, 200 m, 31 Aug 1980 (fl), *Holm-Nielsen et al. 25336* (AAU); La Chiquita Forest Research Station S of San Lorenzo, 50 m, 1 Mar 1973 (fl, fr), *Humbles 6221* (GH, MO). **Guayas:** junction of the provinces Guayas, Cañar, Chimborazo, and Bolívar, near village of Bucay, 1000–1250 ft, 8–15 Jun 1945 (fl, fr), *Camp 3675* (AAU, K, NY, S, US); NE of Quillallpa, 150 m, Oct 1952 (fl), *Fagerlind & Wibom 686* (S). **Imbabura:** entre El Pajón y Cachaco, 600 m, 2 Jun 1949 (fl), *Acosta Solís 12715* (F). **Morona-Santiago:** Macuma, path to Tunanza, 18 Dec 1976 (fr), *McElroy 93* (BH). **Napo:** Puerto Misahualli, 11 Aug 1983 (fl), *Bohs 2210* (F, GH, QCA), *2211* (GH, MO, QCNE); Descanzo, 76° 46'W, 0° 27'S, 200 m, 1 Mar 1980 (fr), *Brandbyge & Asanza 30136* (AAU); San Pablo de las Secoyas, 76° 21'W, 0° 15'S, 300 m, 11 Aug 1981 (fl), *Brandbyge et al. 33465* (AAU); Cantón Archidona, road Hollín-Loreto, km 50, Comunidad Guagua Sumaco, S slopes of Volcán Sumaco, 0° 38'S, 77° 27'W, 1000 m, 29 Apr–2 May 1989 (fl), *Cerón & Hurtado 6667* (UT); Río Cuyabeno N of Río Aguas Negras, 75° 57'W, 0° 11'S, 220 m, 16 Feb 1980 (fl), *Holm-Nielsen et al. 21195* (AAU); Canton Archidona, road Hollín-Loreto, km 50, Comuna Huahua Sumaco, S slopes of Volcán Sumaco, 0° 43'S, 77° 34'W, 1000 m, 1–4 May 1989 (fl), *Hurtado et al. 2092* (UT); ca. 38 km S of Coca, 10 Jan 1973 (fl), *Lugo 2603* (GB, MO); Armenia Vieja ca. 12 km SW of Coca, 12 Jan 1973 (fl), *Lugo 2709* (GB, MO); Lago Agrio, 4 Feb 1973 (fl), *Lugo 3114* (GB, MO); Santa Cecilia, 340 m, 28 Mar 1972 (fr), *MacBryde & Dwyer 1298* (US); Limoncocha, 240 m, Jun 1978 (fr), *Madison et al. 5481* (AAU, F, NY); near Tena, 400 m, 2–11 Apr 1935 (fr), *Mexia 7161* (F, US); Dureno, Río Aguarico, 1 Aug 1974 (fl), *Plowman et al. 4065* (GH, MO); Shushufundi, 244 m, 9 Jan 1975 (st), *Vickers 98* (F); 3 Mar 1975 (fl, fr), *196* (F). **El Oro:** Buenaventura, 10.6 mi E de Saracay hacia Piñas, 700 m, 23 Nov–15 Dec 1978 (st), *Escobar 965* (TEX). **Pastaza:** Curaray, 76° 52'W, 1° 25'S, 240 m, 22 Mar 1980 (fr), *Holm-Nielsen et al. 22475* (AAU). **Pichincha:** Km 170–175, road Santo Domingo-Quinindé, 300 m, 12 Sep 1949 (fl), *Acosta Solís 13971* (F); 20 km W of Santo Domingo de los Colorados, 1000 ft, 16 Oct 1961 (fl), *Cazalet & Pennington 5026* (B, K, US); Centinela, 12 km E of Patricia Pilar, 600 m, 23 Aug 1978 (fl), *Dodson et al. 7223* (F, MO); along Río Toachi near Santo Domingo, 700 m, 4 Aug 1962 (fl), *Játiva & Epling 364* (MO, S, U, UC, US); km 23 on the Santo Domingo-Puerto Limón road, 79° 22'W, 0° 21'S, 100 m, 9 Jun 1982 (fr), *Kvist 40191* (MA, NY); Santo Domingo de Colorado, 12 km W to Rancho Grande, 5 Apr 1943 (fl), *Little 6173* (F, K, NY, UC, US); Rio Palenque Centro Cientifico, 2 km S of Patricia Pilar on road from Santo Domingo to Quevedo, 0° 30'S, 79° 20'W, 19 Aug 1984 (fr), *Rury 580* (F, GH, MO, QCA). **Los Rios:** Río Palenque Field Station halfway between Santo Domingo de los Colorados and Quevedo, ca. 200 m, 12 Feb 1974 (fl), *A. Gentry 9867* (F, MO, US). **Zamora-Chinchipe:** Jambo, along path to Zamora, 24 Jul 1959 (fl), *Harling 6072* (S). **Without Province:** Chimborazo, Río Chasnan, no date (fl), *Spruce 6198* (BM, W).

PERU. Huánuco: Bosque Nacional de Iparia, cerca del campamento Miel de Abeja, 300–400 m, 14 Mar 1967 (fl), *Schunke 1769* (F, US). **Junín:** Prov. Chanchamayo, Pichanaki, 700 m, 11 Mar 1986 (fl, fr), *van der Werff et al. 8623* (MO, TEX). **San Martín:** Prov. Rioja, Pedro Ruíz-Moyobamba road, km 390, Venceremos, 77° 45'W, 5° 50'S, 1750 m, 26 Jul 1983 (fr), *D. N. Smith 4353* (MO).

BRAZIL. Acre: Estrada Alemanha, Cruzeiro do Sul, 13 Apr 1971 (fl, fr), *Prance et al. 11822* (F, K, M, NY, S, U, US, WIS).

BOLIVIA. La Paz: Mapiri region, San Miguel, 800 m, 17 Dec 1926 (fl), *Buchtien 1276* (US); San Carlos bei Sarampioni, 600 m, 31 Dec 1926 (fl), *Buchtien 1278* (US); Prov. Iturralde, Esperanza, bank of Río Madre de Dios 20 km (by air) ENE of Puerto Heath, 12° 25'S, 68° 29'W, 140 m, 25 Aug 1985 (st), *Nee 31543* (NY). **Pando:** Cobija, Río Acre, Feb 1912 (st), *Ule 9754* (G).

Local names and uses. Honduras: Fruta de agua (*Nelson et al. 3097*). Costa Rica: Pepinillo (Pittier, 1908), sandillo (*Wilbur & Stone 9804*), zopilote (*Allen 5241*). Panamá: Contra gallinazo (*Duke 8283*), monka prieto (*Cooper & Slater 181*). Colombia: Naranjilla (Pittier, 1910), regalgar (*García-Barriga 12464*), reventadera (*Romero Castañeda 5022*), tomate de indio (*Agudelo & Klevers 78*), tomate del monte (*Pennell 10720*), tonga (*Archer 1759*), tsutsucuru (Kamsá) (*Bristol 1014*), venenillo (*Romero Castañeda 2690*). Suriname: dwergtafrabon (*Boerboom 9605*), tigriston (*Boerboom 9605*). Ecuador: Kó pi (Secoya) (*Vickers 98*, *196*), irayuyu (Quichua)(*Hurtado et al. 2092*), irayuyo, irayo panga (Quichua)(*Cerón & Hurtado 6667*), maluside (*Kvist 40191*), tomate de montaña (*Dodson et al. 7223*), tomate de monte (*Cazalet & Pennington 5026*), tomate silvestre (*Acosta Solís 13971*).

Cyphomandra hartwegii is sporadically cultivated in Central and South America for its edible fruits. They are eaten raw, sweetened and made into preserves or juices, or candied in syrup. A report that the fruits are red and toxic when ripe (*Cazalet & Pennington 5026*) is probably erroneous. In Chiriquí, Panamá, the leaves are mashed in water to treat cuts and sores (*Cooper & Slater

181). The Chocó Indians of eastern Panamá use the crushed leaves to treat sores and swellings around the mouth (*Duke 8283*). Bruised leaves of this species are applied to inflamed wounds by the Colorado Indians of Ecuador (*Kvist 40191*). The cooked leaves are drunk for heart attacks and headaches by the Quichuas of eastern Ecuador (*Cerón & Hurtado 6667*). An infusion of the leaves is used in Costa Rica to cure erysipelas (Pittier, 1908). In Putumayo, Colombia, the bark of the lower stems is used as a vermifugal tea (*Schultes 3652*). The leaves are used to dye pots black by the Kofáns of southern Colombia (*Schultes 3652*; Schultes & Raffauf, 1990). The juice of the fruits and leaves is used to paint designs on pottery by the Sionas, Secoyas, and Quichas in northeastern Ecuador (*Vickers 98, 196*; *Cerón & Hurtado 6667*).

Cyphomandra hartwegii subspecies *hartwegii* is widely distributed in Central America and northwestern South America, generally occurring at lower elevations than subspecies *ramosa*. As is often the case in wide-ranging species, it is quite variable morphologically. Previous authors described many taxa on the basis of a few collections which I regard as synonyms of *C. hartwegii*. These entities failed to show consistent and significant variation when a large number of specimens was examined from Central and South America. A few notable trends in the variation within subspecies *hartwegii* are noted below, but none seem to merit taxonomic recognition.

Little morphological variation occurs in subspecies *hartwegii* throughout its range in Mexico and Central America. Most collections from this area have densely puberulent axes and abaxial leaf surfaces, usually simple and elongated inflorescences, large corollas with puberulent lobes, long, narrow anthers, and small globose fruits. An exception is an anomalous population from Veracruz, Mexico around Lake Catemaco. These specimens have nearly glabrous leaves, frequently bifid or branched inflorescences covered with minute stalked glands, small corollas with glabrate lobes, and short anthers only 3.5–5 mm long. Great variation exists in pubescence, inflorescence branching, and corolla and fruit size in collections from Panama south to Colombia and Ecuador. Specimens from these areas are often nearly glabrous except for some sparse, long eglandular hairs on the vegetative parts and have branched inflorescences and large ellipsoidal fruits. The type collection of *C. dolichorhachis* from Colombia and some specimens from western Ecuador have very large flowers (35–40 mm in diameter), large calyces with a radius of 5–8 mm that are unevenly split into lobes, and slightly expanded stigmas. Despite these anomalous features, the variation among specimens from these areas is so inconsistent that they cannot be recognized as a cohesive taxonomic unit.

The large number of synonyms of *C. hartwegii* subspecies *hartwegii* has given rise to a few nomenclatural points that deserve further discussion.

In 1899, John Donnell Smith published the name and description for *C. heterophylla* from Central America, now regarded as a synonym of *C. hartwegii*. He cited six collections from Costa Rica but designated none as the type collection. His name proved to be a later homonym of *C. heterophylla* Taubert from southeastern Brazil. In 1903, Smith changed the name of his species to *C. costaricensis*, citing his specimen *6670* and referring to his earlier description. The lectotype of this name is here designated as *Donnell Smith 6670* (US), chosen from among the specimens mentioned in his protologue.

Lectotypes were also chosen for *C. artocarpophylla*, *C. holtonii*, and *C. dendroidea* because the location of the holotype was not specifically indicated. In all cases, the lectotype was chosen from among specimens definitely consulted by the author of the name.

Much confusion has arisen over the identity of *C. splendens* Dunal. Dunal's description is based on the specimen from Geneva in which the vegetative axes and inflorescence are separated. This sheet is labeled "*Solanum cordatum*, Peruvia, herb. Pavon." Three isotypes also exist at MA, one of which is labeled "*Solanum cordatum* sp. nov." *Solanum cordatum* Dunal is an unpublished herbarium name. As no specific locality information is given, uncertainty exists as to the provenance of this collection. The inflorescence of the G specimen is nearly glabrous and highly branched. The flowers conform to the concept of *C. hartwegii*, as does Dunal's description.

Adding to the confusion is another sheet at G also marked "*Solanum cordatum* Pav." as well as "*C. splendens* Dun.," apparently by Dunal himself. This collection (*Poeppig 1845*) belongs to

C. obliqua rather than to *C. hartwegii*. Macbride (1962) later equates *C. splendens* and *C. coriacea*, the latter a synonym of *C. obliqua*, an error that has been followed by later authors. In accordance with Dunal's original description and type, *C. splendens* is undoubtedly to be included within *C. hartwegii* and has no affinity with *C. obliqua*.

The name *C. crassifolia* has been erroneously applied to *C. hartwegii* by many authors. *Cyphomandra crassifolia* is an illegitimate name originally used for *C. betacea*; its nomenclatural status is discussed under the latter species.

b. *Cyphomandra hartwegii* (Miers) Walpers subspecies *ramosa* Bohs, Revista Acad. Colomb. Ci. Exact. **16:** 73. 1988. Type. Colombia. Huila: Fundación Merenberg, ca. 1300 m, 18 Aug 1981 (fl, fr), *Bohs 1644* (holotype, COL; isotypes, CAUP, GH).

Cyphomandra kalbreyeri Bitter, Repert. Spec. Nov. Regni Veg. **17:** 347. 1921. Type. Colombia. Antioquia: Amalfi, Quartier Vivera, 1860 m, 10 May 1880 (fl), *Kalbreyer 1662* (holotype, B, destroyed [F neg. 2935 F, G, GH, NY, WIS]; isotype, K).

Stems, *petioles*, and inflorescence *axes* densely pubescent, often also sparsely pilose. *Leaf blades* sparsely to moderately pubescent-pilose abaxially, especially on veins. *Inflorescence* usually highly branched, often 100+ -flowered. *Calyx* moderately to densely pubescent, the radius 3–4 mm, the lobes 1–2 mm long. *Corolla* radius 10–15 mm, the lobes 10–15 mm long, moderately to densely puberulent-pubescent abaxially, nearly glabrous adaxially. *Anther thecae* 4–6 mm long, 1(–2) mm wide; connective 5–6 mm long, 1 mm wide, adaxially present. *Style* 5–7 mm long, 0.2–0.5 mm in diam., not dilated distally; stigma truncate, 0.2–0.5 mm in diam. *Fruit* ellipsoidal or ovoid, 5–9 cm long, 3.5–6 cm in diam. *Seeds* 7–9 mm long, 6–7 mm wide.

Distribution (Fig. 49) and phenology. Tropical wet forest and cloud forest, 1000–2500 m in elevation, valleys of the Magdalena, Cauca, and Patía Rivers, Colombia. Flowering specimens have been collected in February, May, July, August, and December. Fruiting specimens have been collected in February, June, July, and August.

Additional specimens examined. COLOMBIA. HUILA: Fundación Merenberg, near Santa Leticia, ca. 1300 m, 18 Aug 1981 (fl) *Bohs 1643* (GH), *1645* (CAUP, COL, GH); carretera entre Popayán and La Plata, 2000–2300 m, 17 Jul 1979 (fl), *Cabrera et al. 5023* (MO); Mun. de La Plata, vereda Agua Bonita, Finca Merenberg, 1200–1300 m, 12 Jul 1975 (fr), *Díaz et al. 484* (COL); ridge between Quebrada La Candela and Rio Naranjo, 18 km SW of San Agustín, 1° 43'N, 76° 18'W, ca. 1900 m, 12 Feb 1943 (fl, fr), *Fosberg 20136* (NY, US); hoya del Magdalena, San Agustín, km 7 carretera a Santa Rosa, "Mesitas," 1860 m, 28 Aug 1958 (fr), *Idrobo et al. 2901* (COL, NY, P); Baraya to Hacienda Pensilvanica, 15 km E along trail, 7300 ft, 22 Jun 1944 (fr), *Little 8108* (COL, NY, US); Mun. La Plata, Vereda Agua Bonita, Finca Merenberg, 2300 m, 31 Dec 1977 (fl), *Polania 48* (COL); E of Neiva, 1300–1800 m, 1–8 Aug 1917 (fl), *Rusby & Pennell 1003* (NY). NARIÑO: Prov. Tuquerres, vía de Barbacoas, May 1853 (fl), *Triana s.n.* (COL). TOLIMA: Cajamarca a 15 km hacia Ibagué, 1700 m, 11 May 1983 (fl), *López 83-0621* (COL); Prov. de Mariquita, La Palmilla, 2200 m, 1851–1857, *Triana s.n.* (BM, G, P). VALLE: cerca de la Represa del Calima, 1700 m, 12 Aug 1966 (fl), *Espinal 1959* (MO). WITHOUT LOCALITY: *Mutis 1973, 1985, 3566* (US).

Local names and uses. Colombia: Tomate de árbol silvestre (*Polania 48*), tomate de monte (*Little 8108*), tomate macho (*Fosberg 20136*). The fruits of this subspecies are among the largest in *C. hartwegii*, and are used to make a juice when sweetened with sugar (Bohs, 1989c; G. Buch, pers. comm.). Paradoxically, the fruits are also reported to kill beetles (*Kalbreyer 1662*).

Cyphomandra hartwegii subspecies *ramosa* may be distinguished from subspecies *hartwegii* by its abundant long pubescence and highly branched inflorescences. The flowers of subspecies *ramosa* are somewhat smaller than is typical in subspecies *hartwegii*, and the fruits and seeds of subspecies *ramosa* are larger than those of subspecies *hartwegii*. This taxon is recognized at the subspecific level because of its distinctive morphology and its geographical circumscription in the Magdalena and Cauca valleys of Colombia. The morphological similarities that exist between the two taxa do not justify the recognition of subspecies *ramosa* as a distinct species. There is some evidence for the presence of internal crossing barriers betweeen this subspecies and subspecies *hartwegii* (Bohs, 1988b), but the pattern is inconsistent. Hybrid plants have resulted from crosses between the two subspecies using other combinations and accessions. Furthermore, crosses between different accessions of subspecies *hartwegii* sometimes fail to pro-

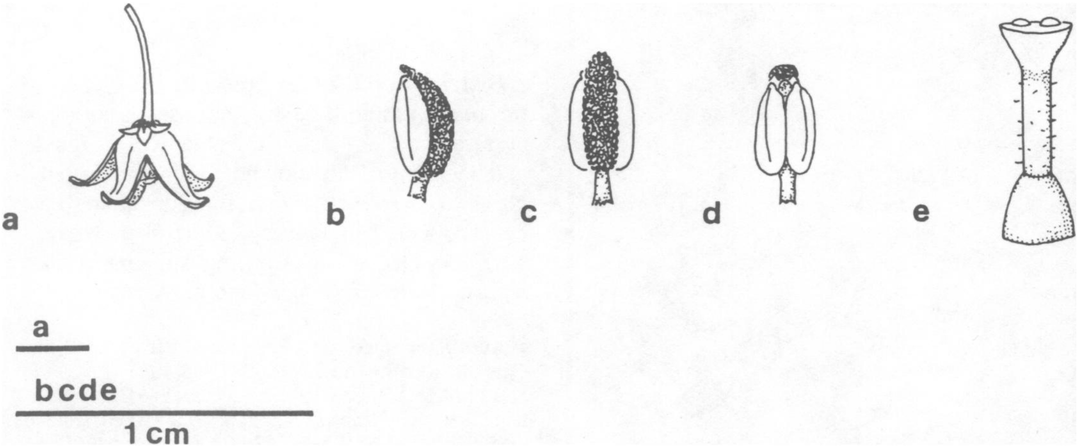


FIG. 50. *Cyphomandra heterophylla*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Glaziou 12097* (C).

duce fruits in spite of successful pollen tube growth into the ovary (Bohs, unpub. data).

The taxonomic status of *C. kalbreyeri*, included here as a synonym, is somewhat doubtful. Minor differences exist in pubescence and and anther shape between the single available specimen of *C. kalbreyeri* and the other collections of subspecies *ramosa* (Bohs, 1988b). Bitter's original description of *C. kalbreyeri* is not sufficient to evaluate conclusively whether *C. kalbreyeri* and subspecies *ramosa* represent the same taxon. Because of the equivocal status of *C. kalbreyeri*, a new name, type, and diagnosis have been chosen for this subspecies (Bohs, 1988b).

15. Cyphomandra heterophylla Taubert, Bot. Jahrb. Syst. **15,** Beibl. **38:** 16. 1893. Type. Brazil. Rio de Janeiro: cultivated at Engenho Velho and São Cristovão, 12 Sep 1880 (fl), *Glaziou 12097* (lectotype, C, here designated [F neg. 22931 F, GH, WIS]; isolectotypes, B, BR, G, K, P). Fig. 50.

Shrub or possibly small *tree* ca. 2 m tall. *Branches* succulent, moderately to densely puberulent. *Leaf blades* simple or pinnately compound, somewhat succulent, acute to acuminate at apex, moderately to densely puberulent adaxially and abaxially; petioles moderately to densely puberulent. *Trunk leaves* 5–11-pinnate, the blade ca. 20 cm long, ca. 13–18 cm wide, the terminal leaflet elliptic, 9.5–12 cm long, 3.5–5.5 cm wide, the base cuneate to shallowly cordate, the petiolule 8–11 mm long, the lateral leaflets 3–11 cm long, 1.5–3.5 cm wide, the petiolules 2–5 mm long; petiole 4–5 cm long. *Crown leaves* 3 per sympodial unit, simple or 3–9-pinnate; if simple, the blade elliptic-ovate, 3–9 cm long, 2–6 cm wide, the length:width ratio 1–1.5:1, the base shallowly cordate with basal lobes ca. 0.5(–1) cm long; if compound, the blade 6–17 cm long, 6.5–14 cm wide, the terminal leaflet ovate or elliptic, 4.5–11 cm long, 1.5–7 cm wide, the base cuneate to truncate or shallowly cordate, the petiolule 5–15 mm long, the lateral leaflets (1–)2.5–8 cm long, 0.5–3.5 cm wide, the petiolules 1–5 mm long; petioles 1–6 cm long. *Inflorescence* unbranched or forked, 10–30-flowered, 2–6 cm long; peduncle 1–4 cm long; rachis 1–4 cm long; pedicels 10–15(–30) mm long, ca. 20(–45) mm long in fruit, 0–5 mm apart, articulated at the base, leaving prominent scars on the rachis; peduncle, rachises, and pedicels sparsely to moderately puberulent. *Flower buds* globose, obtuse at apex. *Calyx* fleshy, glabrate to sparsely puberulent, the radius 3–5(–11) mm, the lobes 1.5–2.5 (–7) mm long, 2–2.5(–4) mm wide, deltate, obtuse. *Corolla* purple, coriaceous to fleshy, campanulate to stellate, the radius ca. 10–20 mm, the tube 3–5 mm long, the lobes narrowly triangular, 8–15 mm long, 3–5 mm wide, glabrous to moderately puberulent abaxially, especially toward

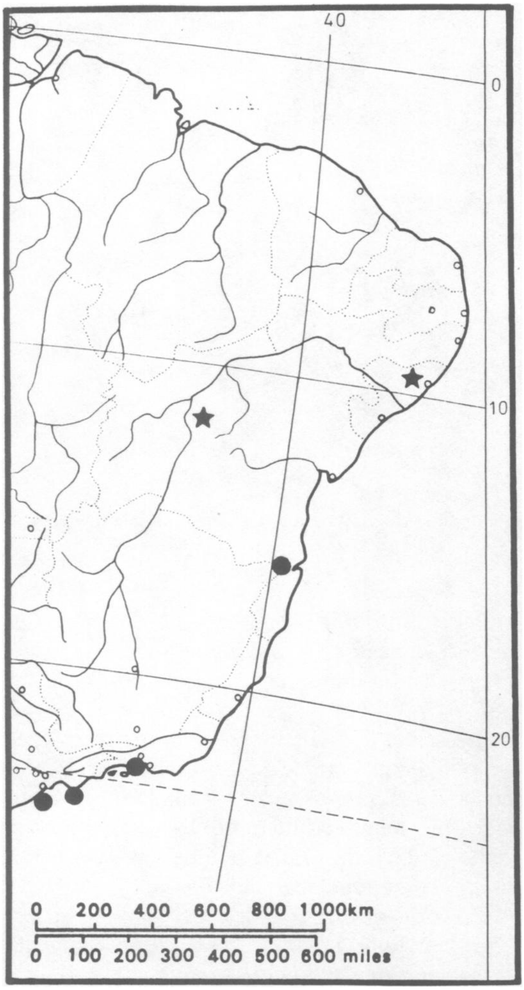


FIG. 51. Distribution of *C. heterophylla* (dots) and *C. ovum-fringillae* (stars).

apices, densely papillose adaxially, the margin minutely tomentose, the apex acute. *Anther thecae* oblong, the color unknown, 3–4 mm long, 2 mm wide, the pores directed distally and laterally; connective oblong, the color unknown, 4–5 mm long, 1.5 mm wide, abaxially exceeding thecae at apex by ca. 0.5 mm, equal to them at base, adaxially absent. *Ovary* glabrous; style glabrous to sparsely puberulent, cylindrical, strongly dilated apically, 4–5 mm long, 1 mm in diam., exserted slightly (ca. 1 mm) beyond stamens; stigma expanded, truncate, bilobed with two apical glands, 2–3 mm in diam. Mature *fruits* not seen, but possibly glabrous, obtuse, and more or less globose from immature ones seen; seeds unknown.

Distribution (Fig. 51) and phenology. Atlantic coastal rain forest along the seashore in southeastern Brazil, in states of Bahia, Rio de Janeiro and São Paulo. Elevation not given, but probably close to sea level. Flowering specimens have been collected in January, September, November, and December. Fruiting specimens have been collected in January and November.

Additional specimens examined. BRAZIL. Bahia: Camacã, road to Rio Branco, 27 Jan 1971 (fl, fr), *dos Santos 1432* (RB, US). **Rio de Janeiro:** São Cristovão, 27 Sep 1880 (fl), *Glaziou s.n.* (P). **São Paulo:** Ilha da Queimada Grande, 3 Nov 1920 (fl, fr), *Gehrt 4661.* (SP, US); Ilha de São Sebastião, 27 Dec 1971 (fl), *Mattos & Mattos 15716* (SP).

Cyphomandra heterophylla is closely allied to *C. sycocarpa*, both occupying seaside habitats of southeastern Brazil. Both species have succulent leaves, stems, and flowers, and both have the anther connective abaxially extended beyond the apices of the thecae. *Cyphomandra heterophylla* differs from *C. sycocarpa* in having puberulent leaves and stems, and pinnately compound rather than pinnately lobed leaves.

There is little information about the range or habitat preferences of *C. heterophylla*; it is presently known only from five collections. Efforts should be made to locate other stations for this species, and field observations are needed to clarify the relationship of *C. heterophylla* to the nearly sympatric and morphologically very similar *C. sycocarpa.*

The pinnately compound leaves and seaside habitat of *C. heterophylla* are reminiscent of *C. cornigera* Dunal, but *C. heterophylla* differs in its floral structure and lack of dendritic pubescence. *Cyphomandra cornigera* belongs to section *Cyphomandropsis* and has no obvious relationship to *C. heterophylla.*

The specimen of *Glaziou 12097* at Copenhagen (C) bears an annotation by Taubert and has been chosen as the lectotype. According to the label data, this collection was made from plants growing in cultivation, but locality data on other gatherings of this species indicates that it is native to the seacoast region very near Glaziou's collecting locality. Taubert's *C. heterophylla* predates the same name proposed by Donnell Smith for a different species of *Cyphomandra*; this latter

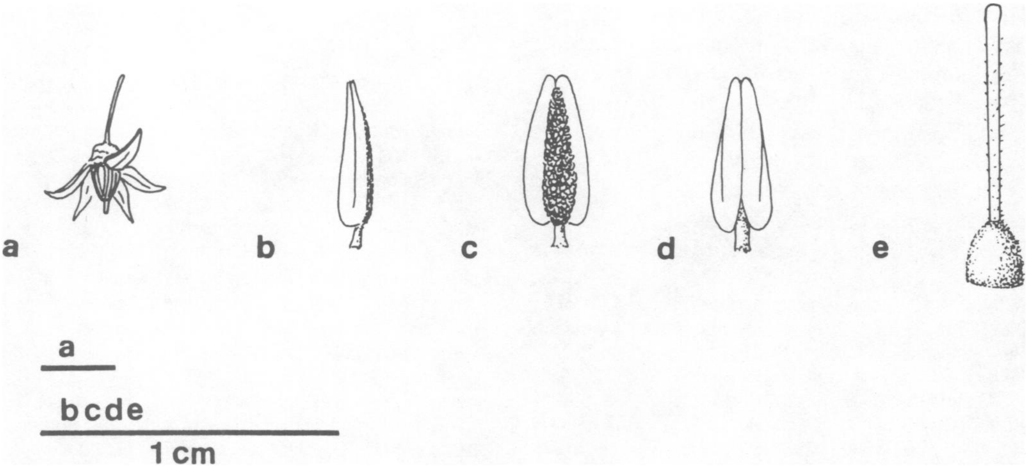


FIG. 52. *Cyphomandra hypomalaca.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, c, based on *Sparre 19484* (S); b, d, based on *Sodiro s.n.* (P); e, based on *Sparre 17919* (S).

name is now considered to be a synonym of *C. hartwegii.*

16. Cyphomandra hypomalaca Bitter, Repert. Spec. Nov. Regni Veg. **17:** 346. 1921. Type. Ecuador. Gualea, subtropical woods, May 1886 (fl, fr), *Sodiro 114/60* (holotype, B, destroyed [F neg. 2934 F, G, GH]; isotypes, P). Fig. 52.

Cyphomandra betacea var. *velutina* Dunal, DC. Prodr. **13(1):** 394. 1852. Type. Peru. *Pavon s.n.* (holotype, G, 2 sheets).

Shrub or small *tree* 2.5–4 m tall. *Branches* moderately to densely glandular- and eglandular-puberulent. *Leaf blades* simple, unlobed, chartaceous or rather succulent, acute at apex, sparsely to moderately puberulent-pubescent adaxially, more so on veins, densely white-pubescent abaxially; petioles moderately to densely puberulent. *Trunk leaves* simple, unlobed, the blade ovate, 22–33 cm long, 15–25 cm wide, length:width ratio 1.5:1, the base cordate, often oblique, with basal lobes 1.5–5 cm long; petioles 10–16 cm long. *Crown leaves* 3 per sympodial unit, simple, unlobed, the blade ovate, 6–30 cm long, 4–20 cm wide, length:width ratio 1–2:1, the base cordate (rarely truncate), with basal lobes (0–)1–4 cm long; petioles 1.5–10 cm long. *Inflorescence* branched, 20–90-flowered, 5–20 cm long; peduncle 2–8 cm long; rachises 2–12 cm long; pedicels 10–20 mm long, 20–30 mm long in fruit, (2–)4–9 mm apart, articulated above the base, leaving pedicellar remnants 2–4(–6 in fruit) mm long; peduncle, rachises, and pedicels moderately puberulent. *Flower buds* ovoid, obtuse at apex. *Calyx* fleshy, moderately pubescent, the radius 2–3 mm, the lobes 1 mm long, 2 mm wide, obtuse to truncate, apiculate. *Corolla* purple, subcoriaceous to fleshy, stellate, the radius 10–15 mm, the tube 1 mm long, the lobes narrowly triangular, 8–13 mm long, 1.5–3 mm wide, sparsely tomentose abaxially toward apex, glabrous adaxially, the margin tomentose, the apex acute. *Anther thecae* yellow or purplish, lanceolate, sagittate at base, 4–5 mm long, 1.5–2 mm wide, the pores directed distally; connective with color unknown, narrowly triangular, 3.5–4.5 mm long, 1 mm wide, abaxially slightly shorter than thecae at apex, equal to or shorter than thecae at base, adaxially absent. *Ovary* densely puberulent; style cylindrical, sparsely puberulent, not dilated distally, 7–9 mm long, 0.3 mm in diam., exserted 1–3 mm beyond stamens; stigma truncate to capitate, 0.3–0.5 mm in diam. *Fruit* globose, obtuse at apex, 1–1.5 cm long, 1–1.2 cm in diam., densely puberulent-pubescent, the color when ripe unknown; mesocarp very thin and closely investing the seeds, without stone cell aggregates; seeds 4–5 mm long, 3–4 mm wide, rugose.

Distribution (Fig. 46B) and phenology. Ravines and forest pockets among dry savanna or scrub, Jauneche forest (tropical moist forest) in western Ecuador, 20–1300 m in elevation, Colombia and western Ecuador. Flowering specimens have been collected in January, April, May, June, August, September, and November. Fruiting specimens have been collected in January, May, June, August, September, October, and December.

Additional specimens examined. COLOMBIA. **VALLE:** Mun. Zarzal, Careterra Panamericana between La Paila and Zarzal, Hacienda El Medio, ca. 975 m, 6 Dec 1986 (fr), *Silverstone-Sopkin et al. 2606* (NY).

ECUADOR. CHIMBORAZO: Valle Pallatanga, Sep 1891 (fl, fr), *Sodiro s.n.* (P). **ESMERALDAS:** Hacienda Timbre, ca. 25 km S of Esmeraldas, 8 Apr 1967 (fl), *Sparre 15248* (S). **IMBABURA:** Collapi, 840 m, 4 Jun 1949 (fr), *Acosta Solís 12847* (F); Tercer Paso, on the San Lorenzo R.R., 1100 m, 7 Jun 1978 (fl, fr), *Madison et al. 4972* (AAU, F). **MANABI:** Cerro Montecristo, S. Manta, 200–300 m, 11 Nov 1966 (fl), *Sparre 19484* (S); El Recreo, 30'S, 22 Aug 1893 (fl, fr), *Eggers 15069* (C, F, GH, M, S, US). **EL ORO:** Ravine above Piñas on W slope of Andes, 3° 9'S, 79° 8'W, 3500 ft, 8 Dec 1965 (st), *Knight 673* (WIS). **PICHINCHA:** Cantón Quito, Reserva Maquipucuna, trail from Hacienda El Carmen to Hacienda Esparragos, ca. 5 km airline SE of Nanegal, 0° 7.5'N, 78° 38'W, ca. 1300 m, 18 Sep 1989 (fl, fr), *Webster & Hebert 27710* (TEX). **LOS RÍOS:** Jauneche forest, Canton Vinces, between Mocachi and Palenque on Estero Peñafiel, 70 m, 3 Aug 1978 (fl, fr), *Dodson & Valverde 6952* (MO); same locality, 3 Oct 1979 (fr), *Dodson et al. 8731* (MO); same locality, 30 Jan 1981 (fl, fr), *A. Gentry 30988* (MO); Hacienda Clementina, between Babahoyo and Montalve, ca. 20 m, 5 Aug 1967 (fl, fr), *Sparre 17919* (S).

Cyphomandra hypomalaca is rather anomalous in the genus, and is here only tentatively considered a *Cyphomandra*. The structure of the calyx, stamens, and fruits suggests an affinity with section *Cyphomandropsis*, as does its apparent preference for drier sites. It is included here because the anther connective is quite obvious in most specimens as is typical of *Cyphomandra*.

This species most closely resembles *C. betacea* in its large puberulent leaves with deeply cordate bases and branched inflorescences with prominent pedicellar remnants. These similarities are probably only superficial, however, and do not imply any close relationship with *C. betacea*.

This species was identified as *Cyphomandra* cf. *crassifolia* in La Flora de Jauneche by Dodson et al. (1985).

17. Cyphomandra obliqua (Ruiz & Pavón) Sendtner, Flora 28: 172. 1845. Fig. 53.

Solanum obliquum Ruiz & Pavón, Fl. Peruv. **2:** 35. Pl. 165, fig. a. 1799. Type. Peru. Chinchao, floret Augusto et Septembri, *Ruiz & Pavón s.n.* (lectotype, MA, here designated [F neg. 12993 F, GH, US, WIS]; isolectotypes, F, MA).

Pionandra obliqua (Ruiz & Pavón) Miers, London J. Bot. **4:** 359. 1845.

Cyphomandra brachypodia Sendtner, Flora **28:** 171. Pl. 5, fig. 1–3. 1845. Type. Brazil. Amazonas: Tefé ("in sylvis ad Ega"), flowering in Dec, *Martius 2917* (lectotype M, here designated [F neg. 6518 F, NY, US, WIS]).

Pionandra coriacea Miers, London J. Bot. **4:** 363. 1845. Type. Peru. Casapi, 1835, *Mathews 1971* (holotype, K; isotype, K).

Cyphomandra coriacea (Miers) Walpers, Repert. Bot. Syst. **6:** 579. 1847.

Cyphomandra ulei Bitter, Repert. Spec. Nov. Regni Veg. **17:** 349. 1921. Type. Brazil. Rio Acre, San Francisco, Apr 1911 (fl), *Ule 9755* (lectotype, K, here designated; isolectotype, G).

Shrub or small *tree* 1–10 m tall. *Branches* moderately to densely puberulent, occasionally also sparsely pilose with eglandular hairs 1–2 mm long. *Leaf blades* simple, unlobed, subcoriaceous, acute to acuminate at apex, glabrescent to moderately puberulent(-pilose) adaxially, more so on veins, densely puberulent(-pilose) abaxially; petioles densely puberulent and occasionally also sparsely pilose. *Trunk leaves* simple, unlobed, the blade ovate, 18–25 cm long, 16–25 cm wide, length:width ratio 1–1.5:1, the base deeply cordate, often oblique, with basal lobes 4–5 cm long; petioles 9–13 cm long. *Crown leaves* (3–)4 per sympodial unit, simple, unlobed, the blade (elliptic to) ovate, (3–)5–20 cm long, (2–)4–17 cm wide, length:width ratio 1–1.5(–2):1, the base cordate, often very oblique, with basal lobes (0.5–)1–4 cm long; petioles 0.5–9 cm long. *Inflorescence* unbranched, (10–)30–50-flowered, (1.5–)3–16 cm long; peduncle 0.5–3 cm long; rachis 0.5–14 cm long; pedicels 15–25 mm long, 25–30(–50) mm long in fruit, ca. 1(–4) mm apart, articulated at the base and leaving conspicuous scars on the rachis or occasionally leaving pedicellar remnants up to 1 mm long; peduncle, rachis, and pedicels densely puberulent(-pilose). *Flower buds* globose, ellipsoidal, or ovoid, acute or obtuse at apex. *Calyx* subcoriaceous, puberulent to pubescent, the radius 2–5 mm, the lobes (0.5–)2–2.5 mm long, (1–)2.5–3 mm wide, deltate, apiculate. *Corolla* green with yellow-brown or purplish tinge adaxially, sometimes violet or brownish-purple, coriaceous (rarely charta-

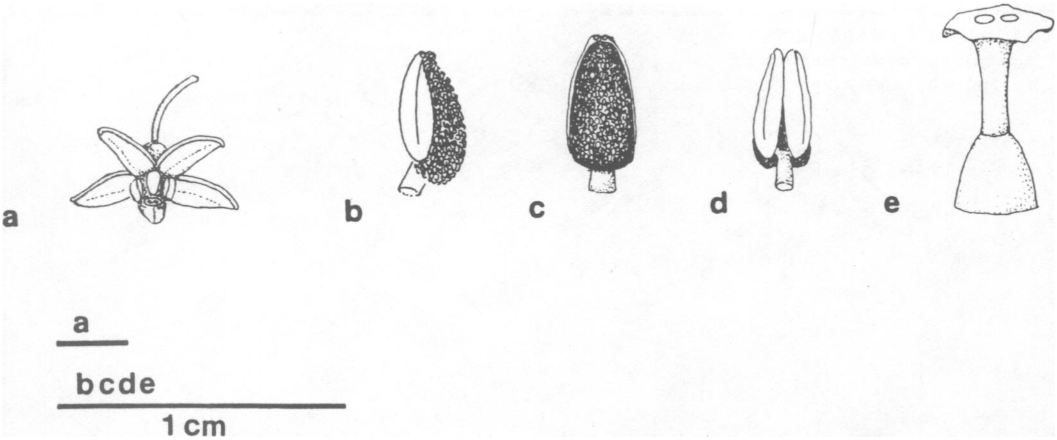


FIG. 53. *Cyphomandra obliqua.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on greenhouse material of *Plowman & Schunke 11550.*

ceous), stellate, the radius 10–20 mm, the tube 2–3 mm long, the lobes narrowly triangular, 7–15 mm long, 2–4 mm wide, glabrous to moderately puberulent abaxially and adaxially, the margin tomentose to ciliate, the apex acute, slightly cucullate. *Anther thecae* white or yellowish, ellipsoidal to oblong, 4–5 mm long, 1.5–2 mm wide, the pores directed abaxially and laterally, occasionally directed distally; connective creamy-white, oblong, 4(–5) mm long, 1–2 mm wide, abaxially slightly shorter than thecae at apex, equal to or slightly exceeding them at base, adaxially absent or produced as a swelling ca. 2 mm long and 0.5–1 mm wide. *Ovary* glabrous; style umbrella-shaped, glabrous, strongly dilated distally, 4–5 mm long, 0.5–1 mm in diam. at base, ca. 2 mm in diam. at apex, equal to or slightly shorter than the stamens; stigma truncate, biglandular, ca. 2 mm in diam. *Fruit* globose or ellipsoidal, obtuse or acute at apex, (2.5–)4–4.5 (–7) cm long, (1.5–)2.5–3.5 cm in diam., glabrous to moderately puberulent, green spotted with white when immature, yellow to orange when mature; mesocarp with very small stone cell aggregates; seeds 3.5–5 mm long, 3–4 mm wide, glabrous to densely pubescent.

Distribution (Fig. 54) and phenology. Clearings and open places in tropical rain forest, 100–1000(–1850) m in elevation, Amazon Valley west to river valleys of eastern Andean slopes in Colombia, Peru, and Brazil. Flowering and fruiting throughout the year.

Additional specimens examined. COLOMBIA. AMAZONAS: E bank of Amazon ca. 1 mi. N of Leticia, 28 Jan 1969 (fl), *Croat 7628* (F, MO, NY); Río Atacuari, 100 m, 10 Oct 1961 (fl), *Idrobo 4725* (COL); Río Amazonas, about 2 km downriver from Puerto Nariño, 28 Jan–7 Feb 1969 (fl, fr), *Plowman et al. 2332* (BR, COL, ECON, F, GH, L, M, MO, NY, P, RB, S); La Victoria on the Amazon River, 21 Aug 1929 (fl, fr), *Ll. Williams 2615* (F); same locality, 27 Aug 1929 (fr), *Ll. Williams 2827* (F, US); Leticia, 4 Sep 1929 (fl, fr), *Ll. Williams 3021* (F).

PERU. HUÁNUCO: Tingo María Botanical Garden, ca. 600 m, 31 May 1977 (fl, fr), *Hart 568* (A); Dist. Churubamba, trail Puente Durand to Exito, 1625 m, 26 Sep 1936 (fl, fr), *Mexia 8235* (B, BH, BM, F, GH, K, MO, NY, S, U, US); Jardín Botánico de Tingo María, 670 m, 8 Dec 1981 (fl, fr), *Plowman & Ramírez 11211* (F); Prov. Leoncio Prado, Dist. Hermilio Valdizán, La Divisoria, 21.8 km E of Puente Pumahuasi (Río Tulumayo) on road from Tingo María to Pucallpa, ca. 9° 5'S, 75° 52'W, 1550 m, 27 Dec 1981 (fr), *Plowman & Schunke 11724* (F, GH, MO); Agua Blanca (carretera Monzón), 22 Apr 1962 (fr), *Schunke 5866* (F, US); Cucharas to Tingo María, 500 m, 2 Jun 1958 (fl), *Woytkowski 5017* (F, MO, P, S); Prov. Huánuco, km 474 on Lima-Tingo Maria road, Huánuco, 1650 m, 2 June 1981 (fr), *Young & Sullivan 634* (NY). LORETO: Iquitos, towards Nanay, 29 Oct 1940 (fl), *Asplund 14135* (S); same locality, 18 Nov 1940 (fl), *Asplund 14568* (S); San Antonio, Río Samiria, 23 Aug 1983 (fl, fr), *Ayala & Arévalo 4230* (F); Quebrada Shanuce above Yurimaguas, 11 Jul 1972 (fl), *Croat 18045* (MO, USM); landing at Mazan from Río Amazonas to Río Napo, 21 Aug 1972 (fl, fr), *Croat 19407* (C, F, MO, NY); Indiana, road to Napo, Rio Amazonas, 24 Oct 1927 (fl), *Ducke RB(22588)* (RB); Tiruntán, Río Ucayali, 7° 53'S, 74° 56'W, ca. 150 m, 5 Nov 1947 (fl), *Fosberg 28993* (WIS); Prov. Maynas, trail from Indiana on Río Amazonas to Río Napo, ca. 200 m, 24 May 1978 (fr), *A. Gentry et al. 22200* (MO); same locality, ca. 130 m, 4 Mar 1979 (fl, fr), *A. Gentry et al. 25388* (MO); Prov. Maynas, Explorama Inn,

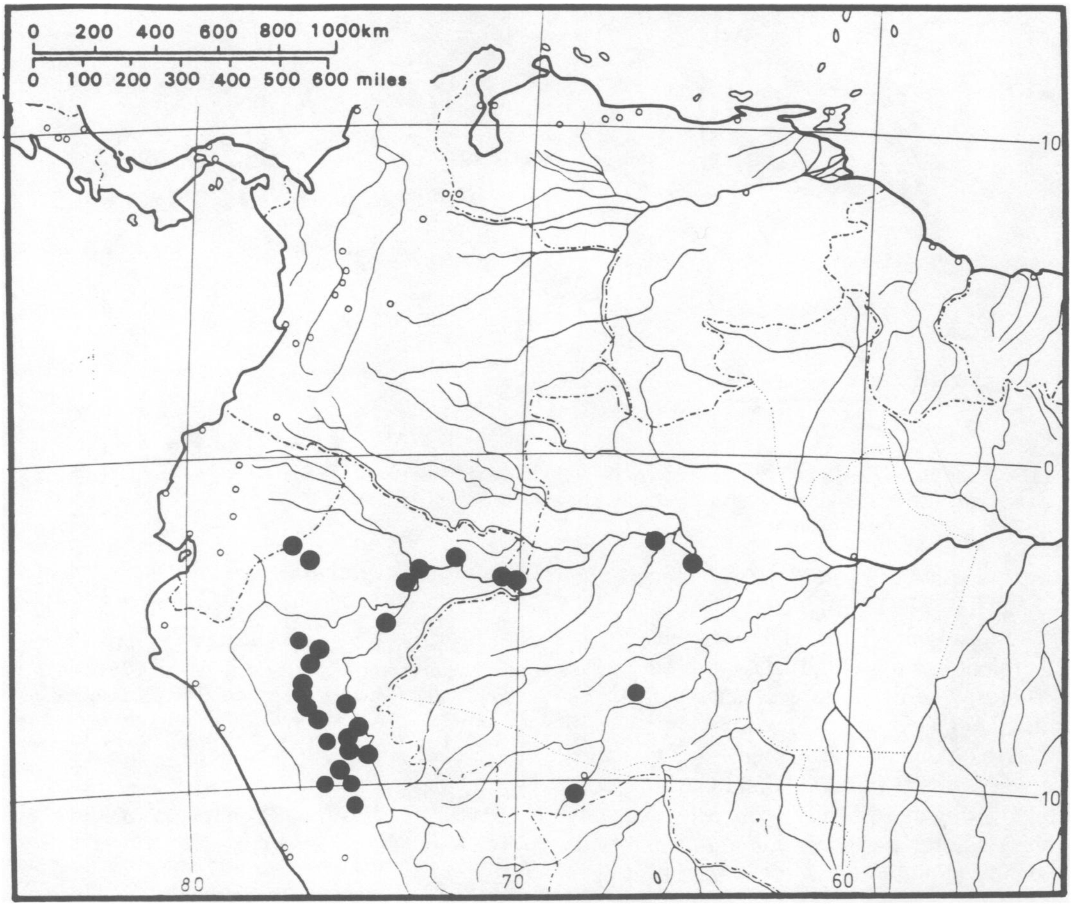


FIG. 54. Distribution of *C. obliqua.*

ca. 2 km W of Indiana on Río Amazonas, 3° 30'S, 73° 2'W, 130 m, 15 Feb 1987 (fr), *A. Gentry et al. 55935* (NY); Contamana, 150 m, 29 Jul 1929 (fl), *Killip & Smith 26872* (F, NY, US); Prov. Alto Amazonas, Huagramona, Río Pastaza, 3° 10'S, 76° 25'W, 185 m, 5 Jul 1986 (fl), *Lewis et al. 11660* (Lewis, pers. coll.); Puranchim, Río Sinchiyacu, 2° 50'S, 76° 55'W, 200 m, 21–27 Nov 1986 (fr), *Lewis et al. 12176* (UT); same locality, 30 Mar–1 Apr 1987 (fl, fr), *Lewis et al. 13236* (Lewis pers. coll.); Prov. Maynas, Dist. Mazan, Baradero de Mazan near Río Amazonas, 15 Aug 1973 (fl), *McDaniel & Rimachi 17800* (NY); Prov. Maynas, Río Ampiyacu, Pebas and vic., 3° 10'S, 71° 49'W, 31 Mar 1977 (fl), *Plowman et al. 6524* (F, GH); Prov. Requena, Cocha Supai, above Jenaro Herrera, right shore of Río Ucayali, 23 Nov 1981 (fl, fr), *Spichiger & Encarnación 1158* (G, MO, NY); middle Ucayali, Contamana, Oct 1923 (fl, fr), *Tessmann 3515* (NY); Prov. Maynas, shore of Sungaro Cocha, 6 Feb 1967 (fl), *Torres 282* (ECON); lower Río Nanay, 23 May 1929 (fl, fr), *Ll. Williams 391* (F); lower Río Huallaga, Fortaleza Yurimaguas, 155–210 m, 28 Oct 1929 (fl, fr), *Ll. Williams 4198* (F). **Pasco:** Oxapampa, ca. 2 km E of village, 10° 35'S, 75° 35'W, 1850 m, 10 Mar 1984 (fl, fr), *Knapp et al. 6315* (BH, G, GH, MO, NY, US); Prov. Oxapampa, 5 km SE of Oxapampa, 75° 23'W, 10° 36'S, 1850 m, 13–16 Dec 1982 (fl, fr), *D. Smith 2959* (NY); Prov. Oxapampa, Palcazu valley, Río San José in the Río Chuchurras drainage, 75° 20'W, 10° 9'S, 400–500 m, 14 May 1983 (fr), *D. Smith 4023* (NY). **San Martín:** Prov. Mariscal Caceres, Dist. Tocache, El Recreo "La Charapita," ca. 3 km S of Tocache Nuevo on road to Tingo María, 25 Apr 1983 (fl, fr), *Bohs & Schunke 2159* (COL, F, G, GH, K, MO, P, S, US, USM); Prov. Huallaga, between Juanjui and Tingo de Saposoa, 200–300 m, 5 Sep 1948 (fl, fr), *Ferreyra 4789* (USM, WIS); Juan Jui, upper Río Huallaga, 400–800 m, Dec 1935 (fl), *Klug 4192* (A, BM, F, K, MO, NY, S, U, US, USM); Pachiza, Rio Huayabamba, 1 Aug 1959 (fl, fr), *Mathias & Taylor 3979* (F); Roque, 7 Oct 1925 (fl), *Melin 329* (S); Prov. Mariscal Caceres, Dist. Tocache Nuevo, found growing wild in Tocache, transplanted and cultivated in garden of José Schunke, 450 m, 1 Jul 1978 (fl, fr), *Plowman & Schunke 7513* (F, U); Dist. Tocache Nuevo, hills behind Recreo "La Charapita," ca. 3 km SE of Tocache Nuevo on road to Tingo María, 8° 12'S, 76° 28'W, 530 m, 20 Dec 1981 (fl), *Plowman & Schunke 11550* (BH, F, GH, MO, NY); Puerto Pizana (right bank of Río Huallaga), 15 Jan 1971 (fl), *Schunke 4651* (F, G, GH, K, NY, P, US); Prov. Lamas, Alonso de Alvarado, Cerro Blanco (carretera a Moyobamba), 900–1000 m, 14 May 1973 (fl), *Schunke 6286* (TEX); Río de la Plata, NE of Tocache, 400 m, 2 May 1975 (fl), *Schunke 8339* (GH); near Tarapoto, 1855–6, *Spruce 4229* (BM, BR, E, G, GH, K, NY, W), *4941* (B, BR, NY, W); Rumizapa, near Tarapoto, 360–900 m, 27 Dec 1929 (fr), *Ll. Williams 6762* (F). UCAYALI: Bosque Nacional de Iparía, along Río Pachitea, campamento Iparía, 300–400 m, 26 Apr 1967 (fl, fr), *Schunke 1883* (F, NY, US); Arboretum of Bosque von Humboldt Experimental Station, km 86 on Pucallpa-Tingo María road, 75° 5'W, 8° 45'S, ca. 330 m, 4 Apr 1982 (fl), *D. Smith et al. 1186* (MO); Prov. Coronel Portillo, Cordillera Azul, km 43 on Tingo Maria-Pucallpa road, ca. 1500 m, 5 Jun 1981 (fr), *Young & Sullivan 741* (MO).

BRAZIL. ACRE: Rio Branco, road to Xapuri, km 40, 5 Jun 1980 (fr), *Coelho et al. 1688* (ECON); Iquiry, 28 Oct 1923 (fl), *Kuhlmann 747* (GH, RB). AMAZONAS: Fonte Bôa, Bara, 4 Apr 1945 (fl, fr), *Lemos Fróes 20644* (K, NY, US); Fonte Bôa, Rio Solimes, Jun 1945 (fl, fr), *Lemos Fróes 21072* (NY, US); Rio Solimes, behind Fonte Bôa, 22 Aug 1973 (fl, fr), *Lleras et al. P17459* (K, MO, NY, S, U, US, WIS); basin of Rio Purus, Rio Cunhuá at Canacã, 6° 34'S, 66° 27'W, 27 Nov 1971 (fl), *Prance et al. 16402* (NY, WIS).

Local names and uses. Peru: Asna panga (*McDaniel & Rimachi 17800*), chupa sacha (*Woytkowski 5017*), chupo sacha (*Bohs & Schunke 2159*; *Mathias & Taylor 3979*; *Schunke 1883*, *4651*, *5866*, *6286*, *8339*), gallinazo panga (*Williams 2615*, *6762*), sihuca sacha (*Torres 282*), sapohuasca (Quichua)(*Lewis et al. 11660*), tomato del campo (*Mexia 8235*), yapu iji (Achual Jívaro)(*Lewis et al. 12176*, *13236*). Brazil: Jurubeba (*Lemos Froes 20644*), tsetsepere (Deni)(*Prance et al. 16402*).

Although *Plowman & Ramírez* (*11211*) and *Mexia* (*8235*) report that the fruits are edible, others say that they are poisonous (*Fosberg 28993*). The juice of the leaves and stems used as an analgesic and sedative for intestinal fever, headaches, rheumatism, kidney ailments, hangovers, muscle aches, and pains of the lower back and stomach (*Bohs & Schunke 2159*; *Mathias & Taylor 3979*; *Plowman & Schunke 7513*; *Plowman & Ramírez 11211*; *Schunke 5866*, *6286*, *8339*; *Woytkowski 5017*). *Plowman & Schunke 7513* gives a more detailed account of the medicinal preparation of this species: The leaf is rasped in cold water, lemon juice is added, and the infusion is taken in the morning before breakfast for three days. *Schunke 5866* reports that an infusion is given in an enema to combat the grippe. Data from *Lewis et al. 11660* indicates that the Quichuas of Loreto, Peru, drink an infusion of the crushed leaves to cure malaria. The Achuar Jívaro of Amazonian Peru scrape the bark into a cold infusion that is used to massage swollen body parts (*Lewis et al. 12176*). A poultice of the leaves is also used to massage the skin around a snake bite (*Lewis et al. 13236*). In Amazonian Brazil, the leaves are heated in water and used to bathe babies, both to keep them healthy and to cure fever (*Prance et al. 16402*).

This species shows the features typical of the *C. obliqua* group: very broad stigmas with two apical glands, short anthers with the connective not much prolonged below the bases of the thecae, and stellate, coriaceous corollas with relatively broad and spreading lobes. The deeply cordate leaves with oblique bases, inflorescences with very short and nearly contiguous pedicel scars, and abundant fine puberulence distinguish this species from *C. uniloba*. It can be distinguished from *C. rojasiana* by its glabrous fruits, longer inflorescences, and South American distribution.

Two sheets of *S. obliquum* collected by Ruiz and Pavón are at MA, and one of them is designated as the lectotype of this name. This sheet was the basis of the illustration accompanying Ruiz and Pavón's (1799) description of the species.

No collection number or herbarium location was given by Sendtner for the type of *C. brachypodia*. The only specimen located with the appropriate annotations and locality information is *Martius 2917* at M, which is chosen here as the lectotype.

Likewise, Bitter gave no herbarium location for *Ule 9755*, the type of his *C. ulei*. Two sheets of this collection have been located, at K and G, but neither shows any evidence that they were examined by Bitter. Although other sheets may eventually turn up in a search of European herbaria, in the absence of other candidates I have selected the specimen at K as the lectotype.

Several collections differ from typical *C. obliqua*, and may either represent regional or elevational variants of *C. obliqua* or may comprise a distinct species. These anomalous collections

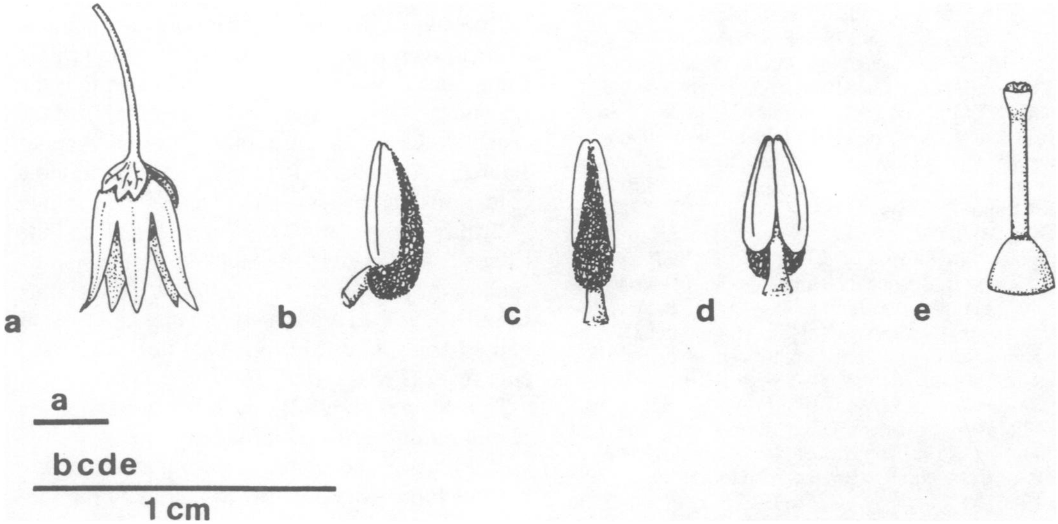


FIG. 55. *Cyphomandra oblongifolia* (campanulate form). **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Maas 416*.

include *Knapp et al. 6315*, *Mathews 1971*, *Mexia 8235*, *Plowman & Schunke 11724*, *Schunke 5866*, *D. Smith 2959*, and *Young & Sullivan 634* and *741*. These collections differ in having abundant long hairs on the foliage and axes, pointed and often pubescent fruits, and purplish, nearly glabrous corollas. The filaments of are quite long for a *Cyphomandra* and may be a distinctive feature. These anomalous collections are found at higher elevations (above 1500 m) than typical *C. obliqua*.

18. Cyphomandra oblongifolia Bohs, Syst. Bot. **13:** 271. 1988. Type. Brazil. Rondônia: Rondônia, secondary vegetation, 20 Aug 1971 (fl, fr), *Maas 416* (holotype, NY; isotypes, F, K, MO, P, U, WIS). Fig. 55.

Small *tree* 2–8 m tall. *Branches* glabrous or glandular-puberulent, sometimes sparsely eglandular pilose with hairs 1–3 mm long. *Leaf blades* simple, lobed or unlobed, subcoriaceous, acute to acuminate at apex, glabrous or occasionally sparsely pilose adaxially, glandular-puberulent on veins, glabrous abaxially; petioles glabrous or sparsely pilose. *Trunk leaves* simple, unlobed or pinnately 3–7-lobed; if unlobed, the blade elliptic or oblong, 15–25 cm long, 8–10 cm wide, length:width ratio 2–2.5:1, the base truncate to shallowly cordate with basal lobes up to 1 cm long; if lobed, the blade 14–20 cm long, 12–22 cm wide, divided 1/2 to 4/5 to midrib, the sinuses acute, rounded, the base truncate, without basal lobes; petioles 3–8 cm long. *Crown leaves* 4 per sympodial unit, unlobed or pinnately 2–3-lobed; if unlobed, the blade elliptic-oblong or ovate, 4–20 cm long, 2.5–8 cm wide, length:width ratio 1.5–2.5:1, the base rounded to truncate or cordate with basal lobes up to 1.5 cm long; if lobed, the blade 12–16 cm long, 5.5–13 cm wide, divided 1/2 to 3/4 to midrib, the sinuses acute, the base rounded to truncate, without basal lobes; petioles 1–5 cm long. *Inflorescence* unbranched or rarely forked, 15–35-flowered, 3–10 cm long; peduncle 1–4 cm long; rachis 2–7 cm long; pedicels 10–25 mm long, 20–30 mm long in fruit, 1–5 mm apart, articulated near the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachis, and pedicels glabrous or glandular-puberulent, occasionally sparsely pilose. *Flower buds* ovoid, acute at apex. *Calyx* somewhat fleshy, punctate and glandular-puberulent or glabrate, the radius 3–6 mm, the lobes (0.5–) 2–3 mm long, (1)2–2.5 mm wide, rounded to truncate, apiculate, often unequal. *Corolla* white, green, yellow green, or purplish, subcoriaceous

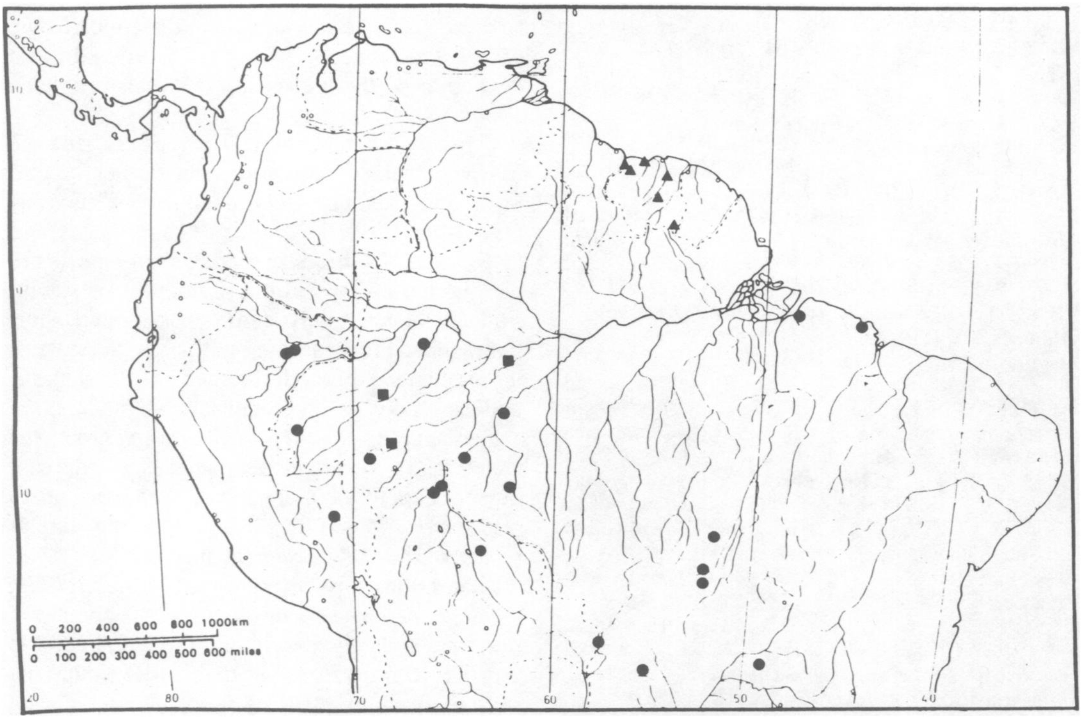


FIG. 56. Distribution of *C. oblongifolia*. Campanulate form (dots). Stellate form (triangles). Small-flowered form (squares).

to fleshy, campanulate (to stellate), the radius (8–)15–20 mm, the tube (1–)3–6 mm long, the lobes narrowly triangular, (5–)10–17 mm long, 2–4 mm wide, glabrous abaxially and adaxially, the margin tomentose, the apex acute. *Anther thecae* yellow or white, lanceolate, 3.5–5 mm long, 1–1.5 mm wide, the pores directed distally; connective purple, narrowly triangular, 3.5–5 mm long, 1 mm wide, abaxially slightly shorter than thecae at apex, exceeding them by 0.5–1 mm at base, adaxially absent. *Ovary* glabrous; style glabrous, cylindrical, not to slightly dilated distally, 4–5 mm long, 0.3–0.5 mm in diam., exserted (0–)1–3 mm beyond stamens; stigma truncate, 0.3–0.5(–1) mm in diam. *Fruit* ellipsoidal to globose, obtuse at apex, 3–5 cm long, 2–5 cm in diam., glabrous, the color when ripe unknown; mesocarp with stone cell aggregates; seeds 4–7 mm long, 3–5 mm wide, glabrous and rugose or pubescent submarginally.

Distribution (Fig. 56) and phenology. Clearings or along streams in tropical rain forest, on varzea or terra firme, 0–350 m in elevation, tributaries of Amazon in Peru, Bolivia, and Brazil; also in Suriname. Flowering specimens have been collected in January and April through November, with a flowering peak in August through November. Fruiting specimens have been collected in all months of the year except April and July.

Additional specimens examined. Campanulate form: **PERU. Loreto:** Prov. Maynas, Padre Isla, Río Amazonas, in front of Iquitos, 120 m, 27 Feb 1978 (fr), *Díaz & Jaramillo 1* (MO); Requena, Jenaro Herrera, 4° 55'S, 73° 40'W, 125 m, 20 Oct 1988 (fl), *Freitas 122* (UT); Moena Caño between Iquitos and Río Itaya, 7 Jan 1976 (fl, fr), *A. Gentry et al. 15689* (GH, NY); Prov. Requena, Río Ucayali, Supay Forest Reserve, Jenaro Herrera, 73° 45'W, 4° 55'S, 20 Feb 1987 (fr), *A. Gentry et al. 56222* (NY). **Madre de Dios:** Parque Nacional de Manu, near Cocha Cashu station on an old ox-bow lake of the Río Manu, 11 Aug 1973 (fl), *Foster 2535* (MO); same locality, between Panagua and Tayakome, 17–24 Aug 1974 (fl), *Foster et al. 3455* (USM); vic. Cocha Cashu Station, 28 Oct 1976 (fr), *Foster & Terborgh 5167* (USM); Parque Nacional Manu, Cocha Cashu Station, Río Manu, 350 m, 30 Sep 1980 (fl), *Foster 5428* (F, MO).

BRAZIL. Acre: Near mouth of Rio Macauhan (tributary of Rio Yaco), Foz do Macauhan, 9° 20'S, 69° W, 12

Aug 1933 (st), *Krukoff 5461* (K, NY); 2–4 km W of Cruzeiro do Sul, 24 Oct 1966 (fr), *Prance et al. 2761* (F, K, NY, S, U, US, WIS); 2–5 km W of Cruzeiro do Sul, 3 Nov 1966 (fr), *Prance et al. 2984* (F, K, NY, S, U, US, WIS). **AMAZONAS:** Mun. Humayta, near Tres Casas, 14 Sep–11 Oct 1934 (fl), *Krukoff 6319* (A, B, BM, BR, F, G, K, MO, NY, S, U, US); Juruá, Marary, Sep 1900 (fl), *Ule 5204* (G, HBG, K, L). **MARANHÃO:** Turiacu, Astonas, 6 Dec 1978 (fr), *Rosa & Vilar 2876* (NY); Km 180 da BR 316, 113 km de acasso, 12 Dec 1978 (st), *Rosa & Vilar 2932* (NY). **MATO GROSSO:** ca. 2.5 km N of Xavantina, 14° 38'S, 52° 14'W, 13 Sep 1967 (fl, fr), *Argent et al. 6378* (E, K, NY, U); Luciara, Santa Terezinha, 15 Dec 1969 (fr), *Mattos 15502* (SP), *15598-b* (SP); vic. Chavantina, margin of Rio Mortes, 25 Sep 1964 (fl), *Prance et al. 59094* (C, F, G, K, MO, NY, S, U, US, WIS); Vale de Sonhos, ca. 80 km S of Xavantina (14° 44'S, 52° 20'W) on the Xavantina-Aragareas road, 5 Sep 1967 (fr), *Ratter et al. 626* (NY); 8 km NE of the Base Camp (12° 54'S, 51° 52'W, ca. 270 km N of Xavantina), 25 Jun 1968 (fr), *Ratter et al. 1977* (E, K, NY, U); Rio Amolar, near source of Rio Paraguay, May 1927 (fl), *D. Smith 183* (K). **MATO GROSSO DO SUL:** Mun. Camapuã, fazenda Pontal (Lagoão) M.S., 4 Nov 1979 (fr), *Silva 116* (US). **MINAS GERAIS:** Mun. Ituiutaba, Fundas, 4 Jul 1948 (fl, fr), *Macedo 1129* (SP, US). **PARÁ:** Belém, new road from Pinheiro near Tapanam, 27 May 1926 (fl), *Ducke RB(22586)* (GH, RB). **RONDÔNIA:** Island in Rio Madeira opposite Jaciparaná, 27 Jun 1968 (fl), *Prance et al. 5277* (F, MO, NY, S, U, US, WIS).

BOLIVIA. BENI: Prov. Vaca Diez, vic. Chácabo village Alto Ivon, 11° 45'S, 66° 02'W, ca. 200 m, 1 Dec 1983 (fr), *Boom 4054* (GH); same locality, 7 Apr 1984 (fl), *Boom 4978* (GH); Río Beni, Cachuela Esperanza, Oct 1924 (fl), *Meyer 237* (U). **SANTA CRUZ:** Prov. Ñuflo de Chavez, Perseverancia, 62° 37'W, 14° 38'S, 200 m, 13 May 1991 (fl), *Mostacedo & Foster 50* (F, UT); Prov. Guarayos, 4 km N of Perseverancia, 14° 41'S, 62° 48'W, 275 m, 9 Sep 1990 (fl), *Nee 38685* (TEX). **WITHOUT DEPARTMENT:** Serrania Ricardo Franco, km 31, 4 Sep 1951 (fl), *Schmidt 18* (M).

Stellate form: **SURINAME.** Nickerie River, forest on levee 1 km W of post Utrecht at mouth of Cupido River, 14 May 1949, (fr) *Lanjouw & Lindemann 3239* (U); W of Coppename mouth, concession Haenen, 1 Mar 1954 (fr), *Lindemann 5535* (U); region Tumuc-Humac (frontier Brazil-French Guiana-Suriname), mouth of Ouarémapan creek, 200 m, 22 Jul 1972 (st), *Sastre 1430* (MO); Lower Suriname River, Plant. Guineesche Vriendschap, 23 Aug 1913 (fl), *Soeprato 301* (U); Cupido rits, dist. Nickerie, 15 Nov 1975 (fl), *Teunissen* (LBB) *15327* (U); Nanni kreek nabij Tomofo kreek, dist. Nickerie, 11 Nov 1975 (st), *Teunissen* (LBB) *15465* (U); near Abontjoeman, Sara creek, Suriname River, May 1910 (fl), *Coll. indigen 267* (U).

Small-flowered form: **BRAZIL. AMAZONAS:** behind Santa Maria, W. bank of Rio Acre opposite Boca do Acre, 17 Sep 1966 (fl), *Prance et al. 2352* (F, K, NY, S, U, US, WIS); Rio Purus between Aiapuá and Moibanda, 22 Nov 1971 (fl), *Prance et al. 16289* (F, K, NY, S, U, US, WIS); Bom Fin, Rio Juruá, Oct 1900 (fl), *Ule 5205* (G, HBG, K, L).

Local names and uses. Peru: Gallinazo panga (*Freitas 122*). Bolivia: shía (Chácabo)(*Boom 4054*). The Chácabo Indians of Bolivia drink a decoction of the leaves to cure liver problems (*Boom 4054*).

Cyphomandra oblongifolia resembles *C. hartwegii* and *C. endopogon* in its nearly glabrous and often pinnately lobed leaves, glabrous obtuse fruits with large stone cell aggregates, and large seeds. It differs from these two species in having oblong or elliptic-oblong leaves with truncate or shallowly cordate bases and short unbranched inflorescences with obvious pedicellar remnants. Although the shape of the stamens and especially the gynoecium of *C. oblongifolia* suggest an affinity with the *C. hartwegii* group, the anthers and styles are shorter than is usually the case in the group; furthermore, the campanulate corolla of *C. oblongifolia* differs from the stellate corollas typical of the *C. hartwegii* alliance.

Most collections referable to *C. oblongifolia* have campanulate corollas with tubes about 3–6 mm long and calyces with a radius of about 3–6 mm. Collections from Suriname differ in having stellate corollas with tubes only 2–3 mm long and very small calyces with a radius of 2–4 mm. These collections with stellate corollas look very similar to *C. hartwegii* except for their oblong leaves, and has been suggested that the Suriname populations may be the result of hybridization between *C. oblongifolia* and *C. hartwegii* (Bohs, 1988a). Only three herbarium sheets with flowers are available from this area, and all have a high percentage of good stainable pollen (>90%). Further biosystematic studies of these two species are needed to shed light on their relationships.

Several collections from Amazonian Brazil differ from both the campanulate and stellate forms of *C. oblongifolia* in having very small flowers with corolla lobes only 5–6 mm long and calyces with a radius of only about 1–2 mm. Except for the small flowers, they resemble the other collections of *C. oblongifolia.*

19. Cyphomandra ovum-fringillae Dunal in DC. Prodr. **13(1):** 394. 1852. Type. Brazil: Bahia, Rio São Francisco, Serra Acuruá (Assuruá), 1838–1839, *Blanchet 2857* (lectotype, G-DC), here designated [F neg. 6857 F, GH, NY, US, WIS]; isolectotypes, B (destroyed)[F neg. 2938 F, GH, NY, US], BM, F (fragment), G, K, MO, P, W). Fig. 57.

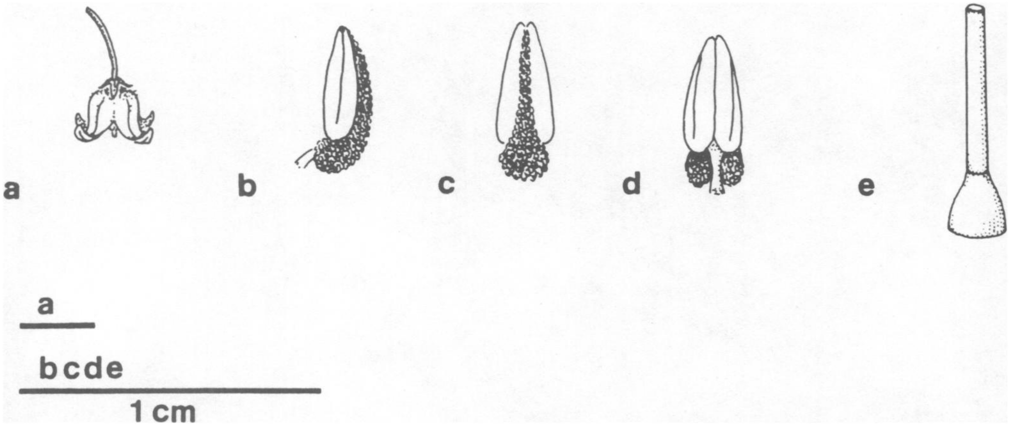


FIG. 57. *Cyphomandra ovum-fringillae.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Blanchet 2857.*

Herb or *shrub* 1–2 m tall. *Branches* slender, densely puberulent and also sparsely to moderately pilose with hairs ca. 1–3 mm long. *Leaf blades* simple to ternately compound, subcoriaceous, acute at apex, moderately to densely puberulent adaxially and abaxially; petioles densely puberulent and also sparsely to moderately pilose with hairs 1–3 mm long. *Trunk leaves* ternately compound, the blade 3.5–7 cm long, ca. 1.5–2.5 cm wide, the terminal leaflet elliptic, 3.5–7 cm long, 1.5–2 cm wide, the base truncate, sessile, the lateral leaflets 1–3 cm long, 0.4–2 cm wide, sessile; petioles 1.5–2 cm long. *Crown leaves* 4 per sympodial unit, the blade simple, ovate-elliptic, sinuate at margin, 1.5–6 cm long, 0.5–3 cm wide, length:width ratio 1.5–2(3):1, the base truncate to cuneate or subcordate with basal lobes less than 0.5 cm long; petioles 0.2–2 cm long. *Inflorescence* unbranched, 6–15-flowered, 2.5–5.5 cm long; peduncle (0.3-)1–2.5 cm long; rachis 1.5–4.5 cm long; pedicels 3–10 mm long, 10–12 mm long in fruit, 1–5 mm apart, articulated near the base, leaving pedicellar remnants up to 1 mm long; peduncle, rachis, and pedicels densely puberulent. *Flower buds* ellipsoidal, obtuse at apex. *Calyx* chartaceous, densely puberulent, the radius 3–4 mm, the lobes 2–3 mm long, 1–1.5 mm wide, deltate to narrowly triangular, acute. *Corolla* violet, somewhat fleshy, campanulate, the radius ca. 11 mm, the tube 4 mm long, the lobes triangular, ca. 7 mm long, 3 mm wide, moderately to densely puberulent abaxially, adaxially puberulent toward apex, glabrous toward base, the margin tomentose, the apex acute. *Anther thecae* yellow (fide Dunal), elliptic-ovate, 3–4 mm long, 1.5 mm wide, the pores directed distally; connective reddish (fide Dunal), lanceolate, 4–5 mm long, 1 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by ca. 1 mm, adaxially absent. *Ovary* glabrous; style cylindrical, glabrous, not dilated distally, ca. 5 mm long, 1 mm in diam., exserted beyond stamens; stigma truncate, 1 mm in diam. *Fruit* ellipsoidal to globose, obtuse at apex, ca. 1 cm long, 1 cm in diam., glabrous, the color when ripe unknown; mesocarp with stone cell aggregates; seeds unknown.

Distribution (Fig. 51) and phenology. Known only from two collections from Bahia and Pernambuco, Brazil; elevation unknown. *Pickel 3200* collected from caatinga. The single dated specimen examined was flowering in January.

Additional specimens examined. BRAZIL. PERNAMBUCO: Russinha, 27 Jan 1933 (fl), *Pickel 3200* (US).

This species is known only from two collections from eastern Brazil. It is a diminutive species, probably a small shrub under 2 m tall with leaves apparently less than 7 cm long. The lower leaves are ternately compound, and the entire plant is covered with a dense pubescence. In many respects it resembles *Cyphomandra*

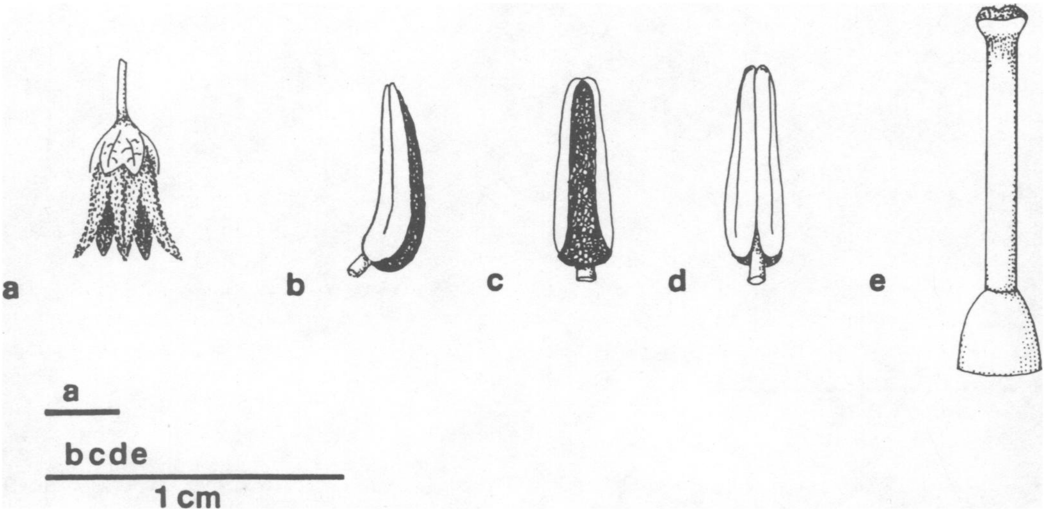


FIG. 58. *Cyphomandra pendula*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Nelson 822*.

cornigera in section *Cyphomandropsis*, but *C. ovum-fringillae* has an indumentum composed exclusively of unbranched hairs, whereas that of *C. cornigera* is made up of dendritically branched trichomes. *Cyphomandra ovum-fringillae* may have affinities with *C. pendula* and *C. benensis* because of its compound leaves, densely pubescent foliage, and pubescent corolla.

It is difficult to ascertain the precise structure of the flowers and mature fruits from the scanty material available. Efforts should be made to collect additional representatives of this species. Only then can a critical assessment be made of the characters of *C. ovum-fringillae* and its placement in relation to other species in the genus.

Dunal (1852) cites the specimens of *Blanchet 2857* in the DeCandolle, Moricand, and Boissier herbaria (all at G) as the types of *C. ovum-fringillae*. The specimens from the DeCandolle and Moricand herbaria are annotated by Dunal, and the specimen in the DeCandolle herbarium has been chosen as the lectotype. Dunal's protologue gives the collection locality as "Serra Acuma," but the correct locality is probably Serra Acuruá (also spelled Assuruá) in the state of Bahia, Brazil. The discrepancy is perhaps due to the illegible handwriting on the specimens.

Sendtner (1846) cited *Blanchet 2857*, the type of *C. ovum-fringillae*, as belonging to his species *C. velloziana*, a nom. nov. for *Solanum elegans* Vellozo, but the characters of Blanchet's herbarium specimens do not resemble those of Vellozo's illustration. For additional notes on *C. velloziana*, see DOUBTFUL NAMES.

20. Cyphomandra pendula (Ruiz & Pavón) Sendtner, Flora 28: 173. Tab. 7, fig. 1–3. 1845. Fig. 58.

Solanum pendulum Ruiz & Pavón, Fl. Peruv. **2:** 39. Pl. 174, fig. a. 1799, non *Solanum pendulum* Steudel (1821), nec *Solanum pendulum* Dunal (1852). Type. Peru. In Panatahuarum Provinciae nemoribus, praesertim in Muña umbrosis locis, floret a Majo ad Augustum, *Ruiz & Pavón s.n.* (lectotype, MA, here designated [F, photo]; isolectotypes, B (destroyed) [F neg. 2936 F, G, GH, NY, US, WIS], F, MA [GH, photos]).

Pionandra pendula (Ruiz & Pavón) Miers, London J. Bot. **4:** 359. 1845.

Cyphomandra arborea Hubert Winkler, Repert. Spec. Nov. Regni Veg. **7:** 246. 1909. Type. Bolivia. Charopampa bei Mapiri, 570 m, Nov 1907 (fl), *Buchtien 1423* (lectotype, US 1176792, here designated; isolectotype, NY). Another sheet probably existed at B but has since been destroyed.

Cyphomandra subcordata Rusby, Bull. New York Bot. Gard. **8:** 119. 1912. Type. Bolivia. San Buena Ventura, 1400 ft, 30 Nov 1901 (fl, fr), *R. S. Williams 606* (lectotype, NY, here designated; isolectotypes, BM, K, NY, US).

Shrub or small *tree* 1–10 m tall. *Branches* moderately to densely pubescent-pilose with hairs up to 2 mm long, often also sparsely pilose-hirsute with hairs up to 4 mm long. *Leaf blades* simple or pinnately compound, chartaceous, acuminate at apex, sparsely to moderately pubescent-pilose adaxially with hairs ca. 1–2 mm long, more densely pubescent abaxially; petioles densely pubescent-pilose. *Trunk leaves* (3–)5–9-pinnate, the blade 30–40 cm long, 25–30 cm wide, the terminal leaflet elliptic, 15–25 cm long, 5–13 cm wide, the base cuneate and often oblique, the petiolule 5–20 mm long, the lateral leaflets 9–22 cm long, 3.5–9 cm wide, the petiolules 0–10 mm long, the upper lateral leaflets often basiscopically decurrent; petioles 6–20 cm long. *Crown leaves* 4 per sympodial unit, simple to (2–)3–5(–6)-pinnate; if simple, the blade ovate, 5–20 cm long, 3–11 cm wide, length:width ratio 1.5–2:1, the base truncate to cordate with basal lobes up to ca. 1 cm long; if compound, the blade 7–25 cm long, 5–20 cm wide, the terminal leaflet ovate to elliptic-obovate, 8–23 cm long, 3–10(–15) cm wide, the base cuneate to truncate, often oblique, the petiolule 3–10 mm long, the lateral leaflets 4–16 cm long, 1.5–5 cm wide, the petiolules 0–5 mm long, the upper lateral leaflets often basiscopically decurrent; petioles 2–8 cm long. *Inflorescence* unbranched or forked, 25–50-flowered, 6–22(–50) cm long; peduncle 3–13 cm long; rachises 2.5–12(–40) cm long; pedicels 10–20 mm long, 20–30 mm long and thickened in fruit, 2–10 mm apart, articulated above the base, leaving pedicellar remnants 1–3 mm long; peduncle, rachises, and pedicels sparsely to densely puberulent-pubescent. *Flower buds* globose, obtuse at apex. *Calyx* chartaceous, moderately puberulent-pubescent, the radius 4–8 mm, the lobes 1–5 mm long, 3–4 mm wide, triangular to ovate, often unequal, acute, obtuse, or apiculate. *Corolla* purple, pink, or white, coriaceous, (urceolate-)campanulate, the radius 10–16 mm, the tube 5–8 mm long, the lobes triangular, 5–10 mm long, 3–5 mm wide, densely tomentose abaxially, glabrous or sparsely pubescent adaxially on prominent midnerve and toward apices, the margin tomentose, the apex acute. *Anther thecae* yellow or violet, narrowly ovate, 4–6 mm long, 1.5–2 mm wide, the pores directed distally and laterally; connective narrowly triangular, the color unknown, 4–6 mm long, 0.5–1 mm wide, abaxially slightly shorter than thecae at apex, about equal or slightly exceeding them at base, adaxially absent. *Ovary* glabrous; style glabrous, cylindrical, slightly dilated distally, 6–9 mm long, 1–1.5 mm in diam., exserted 1.5–4 mm beyond stamens; stigma truncate or capitate, 1–2 mm in diam. *Fruits* ellipsoidal, acute or obtuse at apex, 2–4(–6?) cm long, 1.5–3 cm in diam., glabrous, yellow (fide Ruiz & Pavón); mesocarp with or perhaps without stone cell aggregates; seeds 4–5 mm long, 3 mm wide, rugose-reticulate.

Distribution (Fig. 59A) and phenology. Understories and openings of tropical rain forests, 200–2850 m, eastern slope of the Andes in Ecuador, the valleys of the rivers Huallaga and Ucayali in Peru, the Rio Beni in Bolivia, and adjacent Amazonian Brazil. Flowering specimens have been collected in all months of the year except January, March, and April. Fruiting specimens have been collected in June, October, November, and December.

Additional specimens examined. ECUADOR. Napo: 3.6 km N of Santa Rosa, 1800 m, 25 Oct 1971 (fl, fr), *MacBryde 842* (MO).

PERU. Amazonas: Prov. Bongará, Yambrasbamba-Pomacocha trail between Yambrasbamba and Yanayacu, 1900–2200 m, 24 Jun 1962 (fl, fr), *Wurdack 1023* (NY, US). **Cajamarca:** Prov. Cutervo, San Andrés de Cutervo, camino entre Saucedal y Pajonal, 2300 m, 4 Aug 1988 (fl), *Díaz & Osores 2980* (TEX). **Huánuco:** Prov. Huánuco, Carpish, slope towards Huánuco, 2850 m, 14 Aug 1940 (fl), *Asplund 13049* (S); Huacachi, estación near Muña, ca. 6500 ft, 20 May–1 Jun 1923 (fl), *Macbride 4141* (F, US); Prov. Huánuco, Dist. Churubamba, trail Puente Durand to Éxito, Mt. Santo Toribio, 1625 m, 26 Sep 1936 (fl), *Mexia 8245* (BH, BM, GH, NY, S, US); Prov. Leoncio Prado, Tingo María, Jardín Botánico de Tingo María, 670 m, 7 Dec 1981 (fl, fr), grown from seed collected at La Florida, Río Huallaga, *Plowman & Ramírez 11191* (GH); Huallaga, Muña, 1909–1914 (fl, fr), *Weberbauer 6720* (F, GH, US). **Loreto:** Prov. Coronel Portillo, Dist. Iparia, Bosque Nacional de Iparia, 1 km below Iparia, NW of Río Ucayali (ca. 80 km above confluence with Río Pachitea), 250 m, 2 Sep 1968 (fl), *Schunke 2751* (F, NY); lower Río Huallaga, Fortaleza Yurimaguas, 155–210 m, 29 Oct 1929 (fl), *L. Williams 4281* (F); lower Río Huallaga, Fortaleza Yurimaguas, 155–210 m, 29 Oct 1929 (fl), *L. Williams 4298* (F). **Madre de Dios:** Prov. Manu, Cerro de Pantiacolla, Río Palotoa 10–15 km NNW of Shintuya, 71° 18'W, 12° 35'S, 500–650 m, 8 Dec 1985 (fl), *Foster et al. 10630* (F, NY). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache, Pueblo Mantención, property of Hernán Ortiz, ca. 10 km S of Tocache Nuevo, 400–700 m, 26 Apr 1983 (st), *Bohs & Schunke 2165* (GH, LPB, MO, USM), *2167* (F, GH, USM); Prov. Mariscal Cáceres, near Juanjuí, 200–300 m, 20 Aug 1948 (fl), *Ferreyra 4523* (US); Dist. Tocache Nuevo, quebrada de Cachiyacu de Lopuna (road to Progreso), 500–850 m, 22 Jul 1974 (fl), *Schunke 7658* (C, MO); same location, 500–850 m, 22 Jul 1974 (fl),

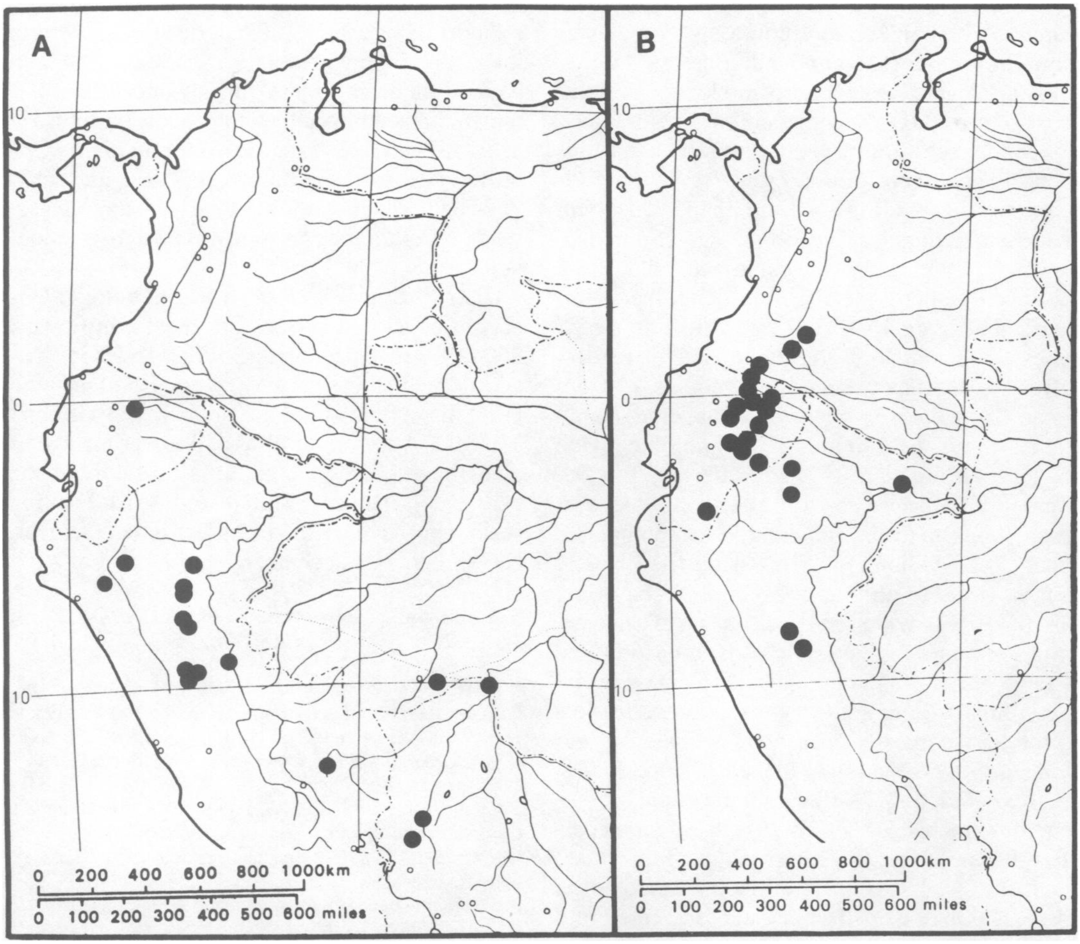


FIG. 59. Distributions of **A.** *C. pendula.* **B.** *C. pilosa.*

Schunke 7662 (MO, US); Dist. Tocache Nuevo, quebrada de Challuayacu, 480–500 m, 4 Feb 1979 (fl), *Schunke 10782* (MO); Dist. Tocache Nuevo, quebrada de Mantención, near property of Sr. Hernán Ortiz Gonzáles, 500–600 m, 29 Aug 1983 (fl), *Schunke 14031* (COL, G, GH, NY, USM); Majo to Saposoa, 500 m, 7 Oct 1959 (fl), *Woytkowski 5494* (F, MO).

BRAZIL. Acre: 30 km from Rio Branco on Rio Branco-Porto Velho road, 6 Oct 1980 (fl), *Lowrie et al. 424* (F, RB); road Rio Branco-Quixadá, km 8, Colonia Cinco Mil (Seita do Cipó), ca. 10 S, 67° 50' W, 26 Oct 1980 (fl, fr), *Nelson 822* (F). **Rondônia:** Falls of Madeira, Oct 1886 (fl), *Rusby 805* (GH, NY, US, WIS).

Local names and uses. Peru: Gallinaso sacha (*Schunke 2751*), monte papaya (Ruiz & Pavón, 1799), papaya del monte (*Mexia 8245*). Despite the local name "wild papaya," the fruits are said to be inedible (*Mexia 8245*) and the whole plant is reputed to be poisonous (*Woytkowski 5494*).

This species may be readily recognized by its densely tomentose, campanulate-urceolate corolla and by its usually pinnately divided leaves. Frequently the most distal pair of leaflets is basiscopically decurrent along the rachis for 1 cm or more. Specimens with ternate and simple leaves also occur.

This species closely resembles *C. diversifolia.* Both have pinnately compound leaves and similar anthers and gynoecia, although the flower parts of *C. pendula* are larger than those of *C. diversifolia.*

Cyphomandra pendula is also quite similar to *C. benensis*, and the ranges of the two species

FIG. 60. Illustration of *Solanum pendulum* from Plate 174 of Ruiz and Pavón (1799).

overlap in Bolivia. *Cyphomandra pendula* can be differentiated from *C. benensis* primarily by its long corolla tube and glabrous fruits.

Cyphomandra viridiflora (Ruiz & Pavón) Sendtner appears to be closely related to *C. pendula*, as pointed out by Ruiz and Pavón in the original description of the two species. From their illustrations in the *Flora Peruviana* (1799), the species seem to differ in that *C. viridiflora* has entire leaves and villous fruits whereas *C. pendula* has ternate or pinnate leaves and glabrous fruits. Since pinnate, ternate, or simple leaves can occur on a single plant of *C. pendula*, leaf shape must be ruled out as a diagnostic character to separate the two species. The illustrations also indicate that *C. viridiflora* is pubescent on the leaves and stems and *C. pendula* is not, but the description accompanying *C. pendula* refers to it as being hirsute or pubescent. Without type material or photos of *C. viridiflora* it is difficult to evaluate its position, and this taxon is included in the DOUBTFUL NAMES section.

Lectotypes have been chosen for *Solanum pendulum* Ruiz & Pavón, *Cyphomandra arborea* H. Winkler, and *Cyphomandra subcordata* Rusby. Three sheets of *S. pendulum* collected by Ruiz and Pavón exist at MA. None of them matches the plate that accompanies the protologue (Fig. 60), and none of them has the fruits pictured on the plate. A typical specimen representing the diagnostic features of this taxon was chosen as the lectotype from among the three specimens (Fig. 61).

21. Cyphomandra pilosa Bohs, Syst. Bot. **13:** 265. 1988. Type. Peru. San Martín: Prov. Mariscal Cáceres, region of Tocache Nuevo, Cerro de Palo Blanco, near the bridge over the Río Tocache, side of path in virgin forest, 600–800 m, 27 Apr 1983 (fl), *Bohs & Schunke 2169* (holotype, GH; isotypes, COL, F, G, K, MO, NY, S, US, USM). Figs. 62, 63.

Small *tree* 1–5 m tall. *Branches* densely pubescent-pilose with hairs up to 3 mm long. *Leaf blades* simple, unlobed, chartaceous to rather fleshy, abruptly short-acuminate at apex, moderately pubescent and also pilose adaxially with hairs 1–3 mm long, more densely pubescent on veins, densely pubescent-pilose abaxially; petioles densely pilose. *Trunk leaves* simple, unlobed, the blade elliptic-ovate, 22–45 cm long, 11–20 cm wide, length:width ratio (1.5–)2(–3):1, the base truncate to cordate with basal lobes (0.5–)1–2(–3) cm long; petioles 4–12 cm long. *Crown leaves* 3 per sympodial unit, simple, unlobed, the blade elliptic-ovate to elliptic-oblong, 4–30 cm long, 2.5–12 cm wide, length:width ratio 1–3(–4):1, the base cuneate to truncate or shallowly cordate with basal lobes up to 1 cm long; petioles 1–4 cm long. *Inflorescence* unbranched, rarely forked or further branched, 15–35(–50)-flowered, 3–18 cm long; peduncle 1–6 cm long; rachis 1.5–12 cm long; pedicels 10–20(–25) mm long, 20–30 mm long in fruit, 1–5 mm apart, articulated near the base, leaving pedicellar remnants less than 1 mm long; peduncle, rachis, and pedicels densely pubescent-pilose. *Flower buds* ovoid, acute at apex. *Calyx* fleshy,

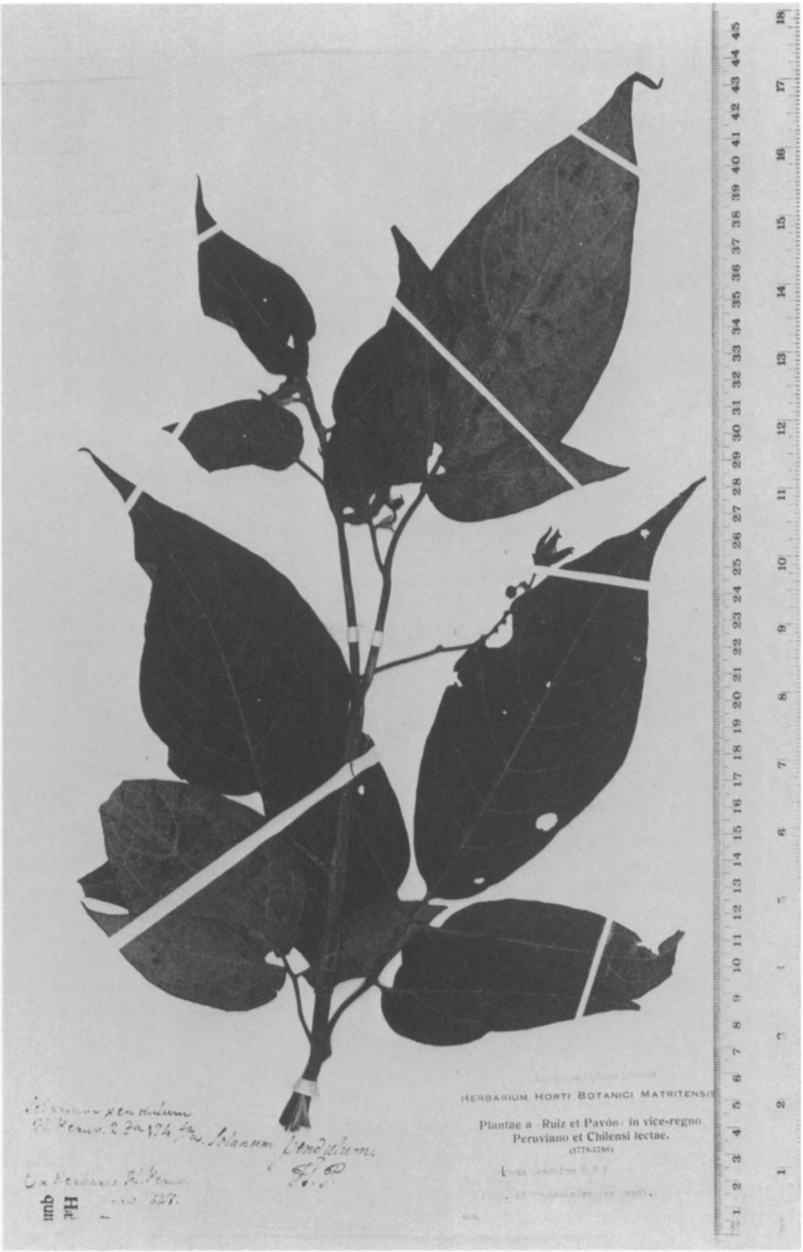


FIG. 61. Lectotype of *Solanum pendulum*. Specimen at MA.

moderately pilose, the radius 2–3 mm, the lobes 1–2 mm long, 1.5–2 mm wide, deltate, apiculate. *Corolla* white to yellow green or purplish abaxially, greenish-brown, violet, or black adaxially, coriaceous or fleshy, campanulate to stellate, the radius 8–16 mm, the tube 1.5–2.5 mm long, the lobes narrowly triangular, 7–15 mm long, 2–4 mm wide, nearly glabrous to moderately pilose abaxially, papillose to glabrous adaxially, the margin tomentose, the apex acute. *Anther thecae*

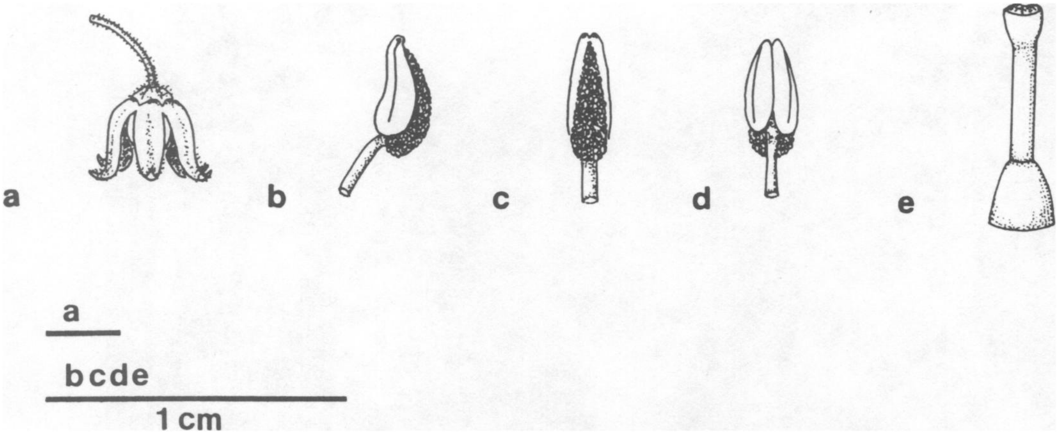


FIG. 62. *Cyphomandra pilosa.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Bohs & Schunke 2169.*

white, lanceolate, 3–4 mm long, 1 mm wide, the pores directed distally and somewhat laterally; connective yellow, narrowly triangular, 3–5 mm long, 1 mm wide, abaxially equal to thecae at apex, exceeding them by 1 mm at base, adaxially present or absent. *Ovary* glabrous or finely pubescent; style cylindrical, glabrous, slightly dilated distally, 4–5 mm long, 1 mm in diam., exserted 2 mm beyond stamens; stigma truncate or capitate, 1–1.5 mm in diam. *Fruit* ellipsoidal or globose, obtuse or rarely acute at apex, 2.5–5 cm long, 1.5–2.5 cm in diam., moderately to densely pilose, green when immature with darker green or whitish stripes, possibly white when ripe; presence of stone cell aggregates in mesocarp unknown; seeds ca. 3–4 mm long, 3.5–4 mm wide, densely pubescent.

Distribution (Fig. 59B) and phenology. Clearings, paths, and light gaps in primary forest, 100–1850 m in elevation, eastern slope of the Andes from southern Colombia to Ecuador and Peru. Flowering specimens have been collected in all months of the year. Fruiting specimens have been collected in June through October and December.

Additional specimens examined. COLOMBIA. CAQUETA: Quebrada del Río Hacha, Cajón de Pulido, 1700 m, 26 Mar 1940 (fl), *Cuatrecasas 8751* (COL, F); Morelia, 150 m, 11 Oct 1941 (fl), *von Sneidern A1121* (S). **PUTUMAYO:** Río San Miguel, Quebrada de la Hormiga, 290 m, 15 Dec 1940 (fl), *Cuatrecasas 11085* (COL, F, US); Umbría, 0° 54'N, 76° 10'W, 325 m, Dec 1930 (fl), *Klug 1857* (BM, F, GH, MO, NY, S, US).

ECUADOR. MORONA-SANTIAGO: Puerto Santana, ca. 5–6 km from Shell-Mera, 16 Sep 1968 (fl), *Lugo 454* (GB, MO); Macuma, ca. 50 km NE of Macas, 21 Mar 1973 (fl), *Lugo 3613* (GB, MO); Tunantza, Jíbaro settlement in vic. Macuma, ca. 50 km NE of Macas, 25 Mar 1973 (fl), *Lugo 3727* (GB, MO); Macuma, path to Tunantza, 18 Dec 1976 (fl), *McElroy 94* (BH). **NAPO:** Parque Nacional Yasuní, pozo petrolero Daimi, 0° 55'S, 76° 11'W, 200 m, 26 May–8 Jun 1988 (fl), *Cerón & Hurtado 4203* (UT); Estación Biológica Jatun Sacha, 8 km E of Misahualli, 1° 4'S, 77° 36'W, 450 m, 24 Aug 1988 (fl, fr), *Cerón & Cerón 4654* (UT); same locality, 17–21 Nov 1988 (fl), *Cerón & Iguago 5603* (UT); same locality, 23–31 Jan 1989 (fl), *Cerón 6090* (UT); ca. 2 km W of Muyuna, ca. 5.7 km W of Tena, vic. bridge over Río Tena, ca. 0° 01'S, 77° 51'W, ca. 500 m, 1 May 1984 (fl), *Croat 58835* (GH); roadside above Tena, 10 Jan 1981 (st), *D'Arcy 14047* (MO); 43–47 km S of Coca, end of Aucas oil field near Río Tiputini, ca. 300 m, 5 Nov 1974 (fl), *A. Gentry 12517* (GH); road Coca-Auca oilfields, 3 km along the road to Yucca, 76° 55'W, 0° 28'S, 400 m, 20 Aug 1979 (fr), *Holm-Nielsen et al. 19625* (AAU); road Hollín-Loreto, km 25, Comunidad Challua Yacu, S slopes of Volcán Sumaco, 0° 43'S, 77° 36'W, 1100 m, 27 Dec 1988 (fr), *Hurtado et al. 1287* (MO); San José de Payamino, 40 km W of Coca, 0° 30'S, 77° 20'W, 300–600 m, 29 Sep 1982 (fl, fr), *Irvine 149* (F); same locality, 16 Dec 1983 (fl, fr), *Irvine 435* (F, GH); Apuya, ca. 10 km S of the Puerto Misahualli turn-off on Puyo-Tena road, 1° 7'S, 77° 50'W, ca. 500 m, 23 Jan 1984 (fl), *Knapp & Mallet 6187* (BH, US); Río Hollín, ca. 10 km E of Archidona, 16 May 1972 (fl), *Lugo 2313* (GB, MO); Cotundo, ca. 15 km N of Tena, 18 May 1972 (fl), *Lugo 2327* (GB, MO); Lago Agrio, 4 Feb 1973 (fl), *Lugo 3104* (GB, MO); Finca Tipán, 5 km N of Coca and Coca-Payamino road, 0° 25'S, 77° 0'W, 250 m, 22 Oct

FIG. 63. *Cyphomandra pilosa.* **A.** Flowering branches. Scale bar = 10 cm. **B.** Inflorescence. Scale bar = 1 cm. From *Bohs & Schunke 2169.*

1988 (fl), *Palacios 3184* (UT); Estación Biológica Jatun Sacha, Río Napo, 8 km E of Misahualli, 1° 4'S, 77° 36'W, 400 m, 14 Dec 1989 (fl), *Palacios 4767* (UT); Cantón El Chaco, Río Granadillo, Campamento of INECEL "Codo Alto," 77° 28'W, 0° 8'S, 1300 m, 13–15 Sep 1990 (fl), *Palacios 5607* (UT); El Chaco Canton, slopes S of Volcán Reventador, left bank of Río Reventador, 1600–1850 m, 77° 36'W, 0° 7'S, 11 Oct 1990 (fl), *Palacios 6170* (UT); Cantón Tena, Estación Biológica Jatun Sacha, 1° 4'S, 77° 36–37'W, 375–400 m, 30 Jul 1990 (fl), *Webster 28485* (TEX). Pastaza: Curaray (Jesús Pitishka), near the posto militar, ca. 200 m, 18 Mar 1980 (fl), *Harling & Andersson 17372* (GB, MO); Canelos, 7 Mar 1971 (fl), *Lugo 1548* (GB, MO); Río Pacayacu, vic. Canelos, 10 Mar 1971 (fl), *Lugo 1577* (GB, MO); Montalvo, Río Bobonaza, 300 m, 26 Dec 1976 (fl), *McElroy 197* (BH); village of Canelos on the Bobonaza River, ca. 500 m, 24 Jul 1980 (fl, fr), *Shemluck 319* (ECON, F); vic. Puyo, 750–1000 m, Aug

1939 (fl), *Skutch 4401* (A, F, NY, US). ZAMORA-CHINCHIPE: road in construction Zamora-Zumba (along Río Jamboe), ca. km 30, S of Finco Cruz-Kaya, 1400–1500 m, 22 Apr 1974 (fl), *Harling & Andersson 13858* (GB, MO).

PERU. HUÁNUCO: Prov. Leoncio Prado, Dist. Rupa Rupa, E of Tingo María, near Cerro Quemado, 700–800 m, 11 Jun 1978 (fr), *Schunke 10211* (NY). LORETO: Andoas, 100 m, 23 Oct 1979 (fr), *Ayala 2140* (TEX); Prov. Loreto, Pampa Hermosa and vic., Río Corrientes, 1 km S of junction with Río Macusari, 3° 15'S, 75° 50'W, 160 m, 3–20 Dec 1985 (fr), *Lewis et al. 10126* (Lewis-pers. coll.); Prov. Loreto, Marsella, Río Tigre, 2° 30'S, 75° 50'W, 250 m, 13–14 Mar 1987 (fl), *Lewis et al. 12683* (Lewis-pers. coll.); Prov. Loreto, Pampa Hermosa and vic., Río Corrientes, 75° 50'W, 3° 15'S, 160 m, 9–11 Dec 1988 (fl, fr), *Lewis et al. 14406* (Lewis, pers. coll.); Brillo Nuevo, Yaguasyacu River (affluent of Ampiyacu River), Dist. Pebas, ca. 150 km ENE of Iquitos, 75° 5'W, 3° 0'S, ca. 106 m, 22 Sep 1981 (fr), *Treacy & Alcorn 67* (WIS). SAN MARTÍN: Prov. Mariscal Cáceres, region of Tocache Nuevo, Palo Blanco, above Río Tocache, 500–550 m, 29 Jun 1978 (fr), *Plowman & Schunke 7458* (F); Dist. Tocache Nuevo, Quebrada de Canuto, near Chacra of Lizardo Aliaga, 500 m, 7 May 1979 (fl), *Schunke 10940* (MO, TEX).

Local names and uses. Ecuador: Asua manga cushnichina yura ("chicha-pot-smoking tree"-Quechua)(*Irvine 149*), manga caspi ("pot tree"-Quechua)(*Irvine 149*), pungi huanduj (*Shemluck 319*). Peru: Chupo sacha macho (*Schunke 10211*), tsuna (Mayna Jívaro) (*Lewis et al. 10126*), tsuná japimiarman (Mayna Jívaro) (*Lewis et al. 14406*), wantsaunik (Achuar Jívaro) (*Lewis et al. 12683*).

The lowland Quechua in Prov. Napo, Ecuador use the leaves of this species to smoke clay pots used for storing chicha, a fermented beverage (*Irvine 149*). A poultice of the leaves is used for muscle cramps in Prov. Pastaza, Ecuador (*Shemluck 319*). In Loreto, Peru, the Boras crush the leaves and mix them with water for bathing (*Treacy & Alcorn 67*). The Mayna Jívaro of Loreto, Peru, apply the leaves to the chest as a poultice to relieve respiratory congestion, especially in children (*Lewis et al. 10126, 14406*).

Both *C. pilosa* and *C. foetida* of the eastern Andean slope have shallowly cordate leaves, pubescent fruits, and abundant long hairs on the leaves and branches. Despite these similarities, it is doubtful that the two species are closely related. *Cyphomandra pilosa* differs from *C. foetida* in its longer and narrower leaves, very short pedicellar remnants, and globose fruits with obtuse apices.

The long hairs, fleshy campanulate corollas, and usually unbranched inflorescences of *C. pilosa* resemble those of *C. tenuisetosa*. *Cyphomandra pilosa* differs from this species in its pubescent fruits, truncate to very shallowly cordate and exclusively unlobed leaves, and shorter anthers, styles, and calyces. A close relationship between *C. pilosa* and *C. tenuisetosa* is possible, but at present the true affinities of *C. pilosa* are obscure.

22. Cyphomandra pinetorum Smith & Downs, Phytologia **10:** 436. Tab. 9, fig. 8–10. 1964; Smith & Downs, Fl. Illustr. Catar. pp. 207–208. Fig. 28, c–e. 1966. Type. Brazil. Santa Catarina: Campo and pinheiral, 4 km S of Campo Alegre on road to Jaraguá do Sul, elev. 900–1000 m, 6 Nov 1956 (fl), *Smith & Klein 7339* (holotype, US 2423790, isotype, HBR, n.v.). Fig. 64.

Cyphomandra hispida Smith & Downs, Phytologia **10:** 437. Tab. 10, fig. 5–7. 1964; Smith & Downs, Fl. Illustr. Catar. pp. 212–213. 1966. Type. Brazil. Santa Catarina: Vidal Ramos, Sabía, forest, elev. 750 m, 31 Dec 1957 (fl), *Reitz & Klein 5982* (holotype, US 2271853; isotype, HBR, n.v.).

Cyphomandra angustifolia Smith & Downs, Phytologia **10:** 438. Tab. 10, fig. 8–10. 1964; Smith & Downs, Fl. Illustr. Catar. pp. 214–215. Fig. 29, i–k. 1966. Type. Brazil. Santa Catarina: Pôrto União, ruderal near Pôrto União on road to Santa Rosa, elev. 750–800 m, 18 Dec 1956 (fl), *Smith & Reitz 8736* (holotype, US 2423801; isotypes, HBR (n.v.), NY, R (n.v.), S).

Shrub or small *tree* 0.5–4 m tall. *Branches* densely glandular- and eglandular puberulent (-pubescent) and often also moderately to densely eglandular-pilose. *Leaf blades* simple, lobed or unlobed, chartaceous to subcoriaceous, acuminate at apex, sparsely to densely glandular-puberulent and also sparsely to densely eglandular pubescent-pilose adaxially, more so on veins, moderately to densely pubescent abaxially; petioles densely puberulent(-pubescent) and often also sparsely to moderately pubescent-pilose. *Trunk leaves* simple, unlobed or (2–)3-lobed; if unlobed, the blade ovate to elliptic-ovate, 6–14.5 cm long, 2.5–7 cm wide, length:width ratio ca. 1.5–3(–4):1, the base cordate with basal lobes up to 1 cm long; if lobed, the blade 5.5–11 cm long, 3.5–7.5 cm wide, divided 1/2 to 7/8 to midrib, the sinuses acute to obtuse, the base cordate with

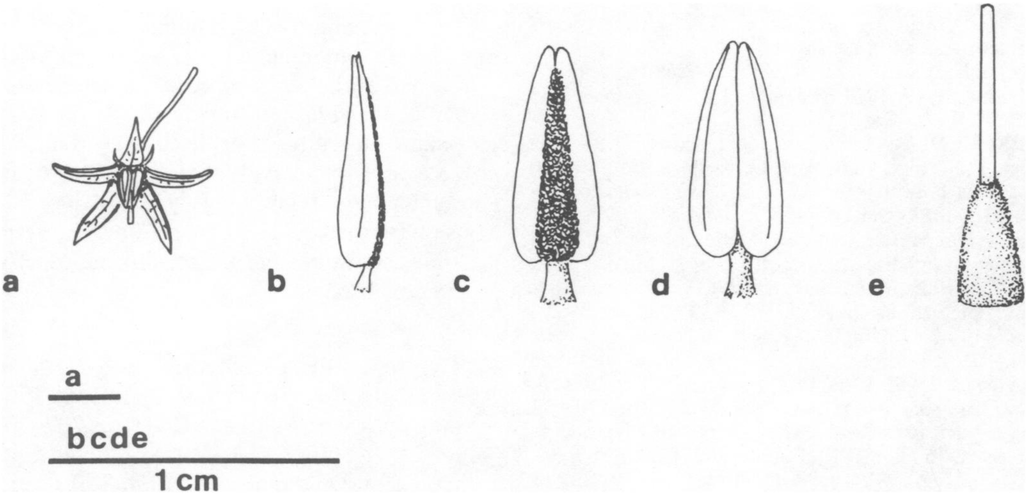


FIG. 64. *Cyphomandra pinetorum*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Hatschbach 13144*; b–e, based on *Kuhlmann 2168*.

basal lobes up to 1 cm long; petioles 1.5–8 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade ovate, 2–13 cm long, 1–7 cm wide, length:width ratio 1–3(–3.5):1, the base (truncate to) cordate with basal lobes up to 1(–2) cm long; petioles 0.5–6 cm long. *Inflorescence* unbranched or rarely forked, 5–15(–20)-flowered, 2–9 cm long; peduncle 1–4 cm long; rachis 1–6 cm long; pedicels (10-)15–25(–30) mm long, 10–25(–35) mm long in fruit, (1–)2–6(–9) mm apart, articulated above the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachis, and pedicels densely glandular- and eglandular-puberulent and often also sparsely to moderately pubescent-pilose. *Flower buds* ellipsoidal, obtuse at apex. *Calyx* chartaceous, moderately to densely pubescent-pilose, the radius 2–5 mm, the lobes 1–4 mm long, 1–2 mm wide, deltate, acute. *Corolla* purple, chartaceous, stellate, the radius 7–22 mm, the tube 2–3 mm long, the lobes narrowly triangular to lanceolate, (5–)7–19 mm long, (2–)3–7 mm wide, sparsely to densely puberulent-pubescent abaxially, glabrous adaxially, the margin tomentose, the apex acute. *Anther thecae* yellow or purple, lanceolate, (5–) 6–7 mm long, 1.5–3 mm wide, the pores directed distally; connective dark purple or dark yellow, narrowly triangular, 5–6 mm long, 1–2 mm wide, triangular, abaxially shorter than thecae at apex, nearly equal to them at base, adaxially absent. *Ovary* glabrate to sparsely puberulent; style cylindrical, glabrous, not dilated distally, 4–7 mm long, 0.5–1 mm in diam., exserted 1–2 mm beyond stamens; stigma truncate, 0.5–1 mm in diam. *Fruit* ellipsoidal, elongated, acute at apex, 1.5–5 cm long, (0.5-)1–1.5 cm in diam., densely glandular-puberulent and densely pilose with eglandular hairs 2–3 mm long, the color when ripe unknown; mesocarp with stone cell aggregates; seeds unknown.

Distribution (Fig. 65A) and phenology. Secondary vegetation and disturbed areas in primary forest, coastal cloud forest and *Araucaria* forests of southeastern Brazil at elevations of 750–2100 m in the provinces of Minas Gerais, Rio de Janeiro, São Paulo, Paraná, and Santa Catarina. Flowering specimens have been collected in January, March, July, and September through December with a flowering peak in October through January. Fruiting specimens have been collected in January, June, July, November, and December.

Additional specimens examined. BRAZIL. MINAS GERAIS: Mun. Itamonte, Serra da Mantiqueira, 1600 m, 8 Oct 1982 (fl), *Hatschbach & Kummrow 45544* (MBM, Z); Sapucai-Mirim, Serra da Mantiqueira, 6 Nov 1953 (fl), *Kuhlmann 2927* (SP). **PARANÁ:** Itaperussú, 16 Nov 1908 (fl), *Dusén 7098* (S); Calmo, 12 Mar 1910 (fl), *Dusén 9404* (GH, NY, S); Itaperussú, 27 Sept 1914 (fl), *Jönsson 1008a* (F, GH, K, NY, P, S); Mun. Bocaiuva do Sul, Campina

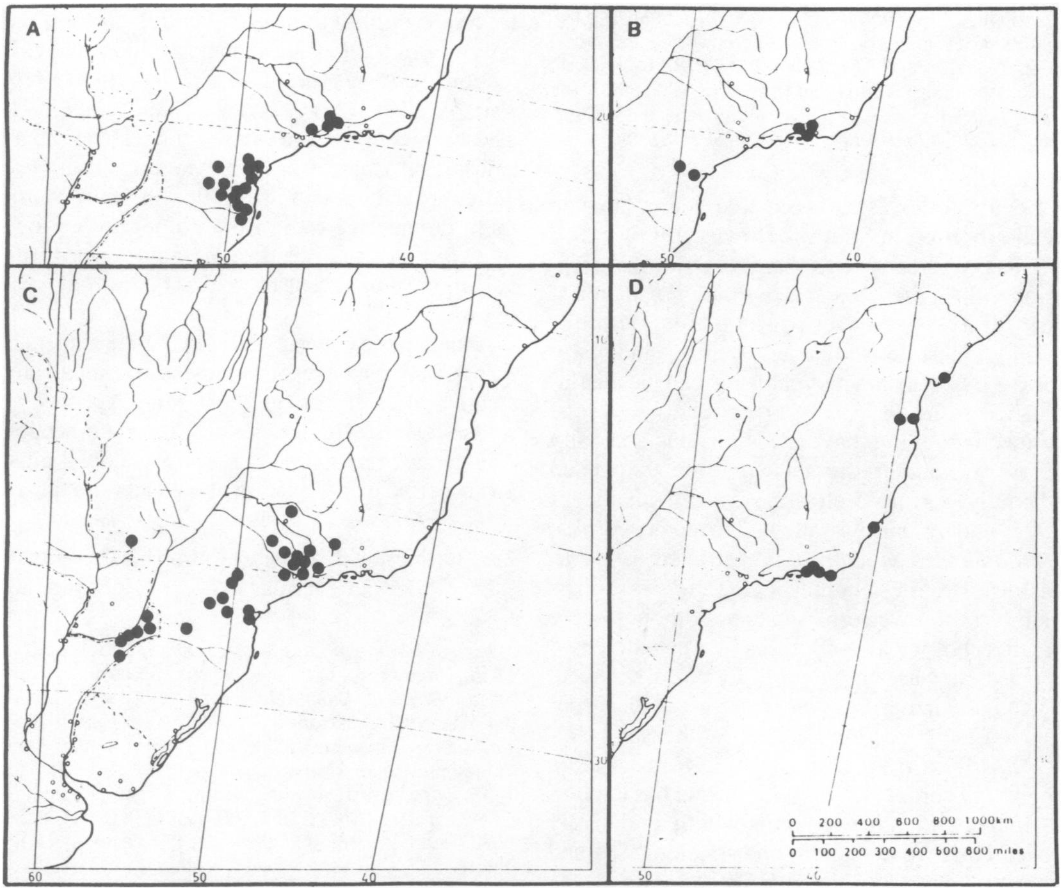


FIG. 65. Distributions of **A.** *C. pinetorum.* **B.** *C. premnifolia.* **C.** *C. sciadostylis.* **D.** *C. sycocarpa.*

dos Tavares, 11 Nov 1959 (fl), *Hatschbach 6470* (MBM, US); Mun. Bocaiuva do Sul, Passa Vinte, 27 Dec 1963 (fl, fr), *Hatschbach 10818* (MBM, US); Mun. Cerro Azul, Descida do Itupava, 18 Jul 1964 (fl, fr), *Hatschbach 11328* (MBM); Mun. Piraquara, Novo Tirol, 900 m, 27 Nov 1964 (fl), *Hatschbach 11903* (MBM); Mun. Bocaiuva do Sul, Passa Vinte, 18 Nov 1965 (fl, fr), *Hatschbach 13144* (F, K, M, NY, US, WIS); Mun. Campina Grande do Sul, Pico Caratuva, 1950 m, 15 Nov 1967 (fl), *Hatschbach 17834* (F, MBM, Z); Mun. Campina Grande do Sul, Serra Capivari Grande, 1700 m, 15 Jan 1969 (fl), *Hatschbach & Koczicki 20757* (MBM); Mun. Cerro Azul, Vila Branca, 20 Nov 1970 (fl, fr), *Hatschbach & Guimares 25577* (MBM, UT, Z); Mun. Colombo, Capivari, 4 Nov 1971 (fl), *Hatschbach 27625* (BH, C); Irati, 16 Dec 1977 (fl, fr), *Hatschbach 40631* (MBM, UT); Tijuca do Sul, Represa Vassoroca, 6 Dec 1988 (fl), *Kummrow 3118* (GH, UT, Z). **Rio de Janeiro:** Serra do Itatiaia, ca. 2100 m, 18 Oct 1902 (fl), *Dusén 2029* (S); Mun. Resende, W side of base of Mt. Itatiaia, 22° 23'S, 44° 45'W, ca. 1650 m, 7 Nov 1965 (fl, fr), *Eiten & Eiten 6688* (MO, NY, SP, US); Itatiaia, 1200 m, 26 Jan 1975 (fl), *Hatschbach et al. 35852* (MBM); Itatiaia, km 12, 22–28 Nov 1938 (fl), *Markgraf 3749* (SP); Itatiaia, 10 Dec 1903 (fl), *Moreira 26* (US); Parque Nac. do Itatiaia, 17 Nov 1980 (fl), *Occhioni 9209* (MBM); Parque Nac. Itatiaia, Estrada Registro-Agulhas Negras, 17 Jan 1979 (fl), *Occhioni s.n.* (MBM); Itatiaia, 14 Nov 1975 (fl), *Peixoto 697* (RB); Itatiaia, Macieiras, 1860 m, 19 Oct 1922 (fl), *Porto 1109* (SP); same locality, ca. 1900–2000 m, 23 Oct 1927 (fl), *Zerny s.n.* (W). **Santa Catarina:** Bom Retiro, Riozinho, 1100 m, 15 Dec 1948 (fl), *Reitz 2363* (L, NY, US); Bom Retiro, Figueiredo, 1000 m, 28 Dec 1948 (fl), *Reitz 2870* (US); Vidal Ramos, Sabía, 750 m, 7 Mar 1958 (fl), *Reitz & Klein 6596* (L, NY, US); Rio do Sul, Alto Matador, 800 m, 26 Jan 1959 (fl), *Reitz & Klein 8317* (L, US); São José, Serra da Boa Vista, 900 m, 25 Jan 1961 (fl), *Reitz & Klein 10743* (US); Santa Cecilia, Campo do Areão, 1100 m, 3 Jan 1962 (fl, fr), *Reitz & Klein 11391* (B, L, NY, US); Pôrto União, Carazinho, 1100 m, 7 Jan 1962 (fl), *Reitz & Klein 11710* (US); São Bento, 18 Jun 1885 (fr), *Schwacke s.n.* (P, US); Mun. Papanduva, km 136 N of Papanduva on Estrada de Rodagem Federal, ca. 800 m, 7 Dec 1956 (fl, fr), *Smith & Klein 8416* (US). **São Paulo:** Campos do Jordão, Fazenda da Guarda, 1600 m, 25 Nov 1949 (fl), *Kuhlmann 2168* (SP); Campos do Jordo, ascending towards peak of Itapeva, 1800 m, 27 Nov 1949 (fl) *Kuhlmann 2206* (SP); São Francisco dos Campos, 22 Dec 1896 (fl), *Lofgren 3483* (SP, US).

Local names. Brazil: Baga de bugre, baga de veado (both from Smith & Downs, 1966).

This Brazilian species shares the following features with *C. foetida* and *C. corymbiflora*: pubescent leaves with cordate bases, slender cylindrical styles, truncate stigmas, and hairy fruits. *Cyphomandra pinetorum* can be distinguished from *C. foetida* by its relatively broad connective region that does not extend abaxially below the anther thecae and is not expanded adaxially, its more elongate fruits with longer hairs, and its purple rather than green corolla. *Cyphomandra pinetorum* is restricted to southeastern Brazil, whereas *C. foetida* is found mainly in the western Amazon. Although there are morphological similarities between these two species, they are only doubtfully closely related. *Cyphomandra pinetorum* is more obviously allied to *C. corymbiflora*, also of southeastern Brazil. It differs from *C. corymbiflora* in its more shallowly cordate leaves with shorter basal lobes, its longer and narrower anthers with a relatively broad connective region, and its elongated and pointed fruits. The inflorescences of *C. pinetorum* are usually unbranched and few-flowered, unlike the branched and many-flowered inflorescences of *C. corymbiflora*.

Smith and Downs (1966) recognized three species, based mainly on differences in pubescence and leaf size and shape, whereas I recognize only one. Pubescence and leaf size vary considerably within *C. pinetorum* (the occurrence and density of longer eglandular hairs is especially variable), and the criteria used by Smith and Downs (1966) for distinguishing these species do not hold up when the entire range of collections is examined. *Cyphomandra pinetorum*, as circumscribed here, has a disjunct distribution, with populations in the northern area in the states of Minas Gerais, Rio de Janeiro, and São Paulo separated from those of the southern area in Paraná and Santa Catarina by about 250 km. The northern populations typically have larger leaves and corollas than those from the southern region. The element segregated as *C. angustifolia* by Smith and Downs (1964) occupies the north central part of the province of Santa Catarina and includes the collections *Smith & Reitz 8736*, *Smith & Klein 8416*, *Reitz & Klein 11710*, and *Reitz & Klein 11391*. These collections have smaller and relatively narrower leaves, narrower corolla lobes, and shorter, narrower anthers with a smaller and less prominent connective region than other collections of *C. pinetorum*, but do not seem to be to be sufficiently different to justify taxonomic recognition.

Although the connective region of the anthers is quite prominent on most specimens, it is not greatly swollen dorsally as in most other species of *Cyphomandra*. This species may belong in section *Cyphomandropsis*, but certain placement must await a critical examination of the latter group.

23. Cyphomandra premnifolia (Miers) Dunal, DC. Prodr. 13(1): 392. 1852. Fig. 66.

Pionandra premnifolia Miers, London J. Bot. **4:** 360. 1845, 'premnaefolia.' Type. Brazil. São Paulo (from Miers), *Bowie & Cunningham s.n.* (lectotype, BM, here designated. Chosen from syntypes *Bowie & Cunningham s.n.* and *Luccombe s.n.*).

Pionandra pubescens Miers, London J. Bot. **4:** 356. 1845. Type. Brazil. Rio de Janeiro: Organ Mountains, Cook's Waterfall on Paraíba road, Feb 1838 (fl, fr), *Miers 4538* (lectotype, BM, here designated; isolectotype, K).

Shrub about 1–2 m tall. *Branches* moderately to densely puberulent and often also moderately to densely pilose with hairs 1–2 mm long. *Leaf blades* simple, unlobed, chartaceous to subcoriaceous, acute to acuminate at apex, sparsely to moderately pubescent-pilose and often also sparsely to densely glandular-puberulent adaxially, densely puberulent-pubescent abaxially; petioles densely puberulent and often also sparsely to densely pubescent-pilose. *Trunk leaves* not represented. *Crown leaves* 4 per sympodial unit, the blade ovate or ovate-elliptic, 3–12 cm long, 3–8 cm wide, length:width ratio 1–2:1, the base truncate to cordate with basal lobes 0–2 cm long; petioles 1–4 cm long. *Inflorescence* unbranched, (4–)10–40-flowered, 3–12 cm long; peduncle 1–3.5 cm long; rachis 1–10 cm long; pedicels 10–20 mm long, 20–25(–30) mm long in fruit, (1–)2–6(–12) mm apart, articulated above the base, leaving pedicellar remnants 1–5 mm long; peduncle, rachis, and pedicels moder-

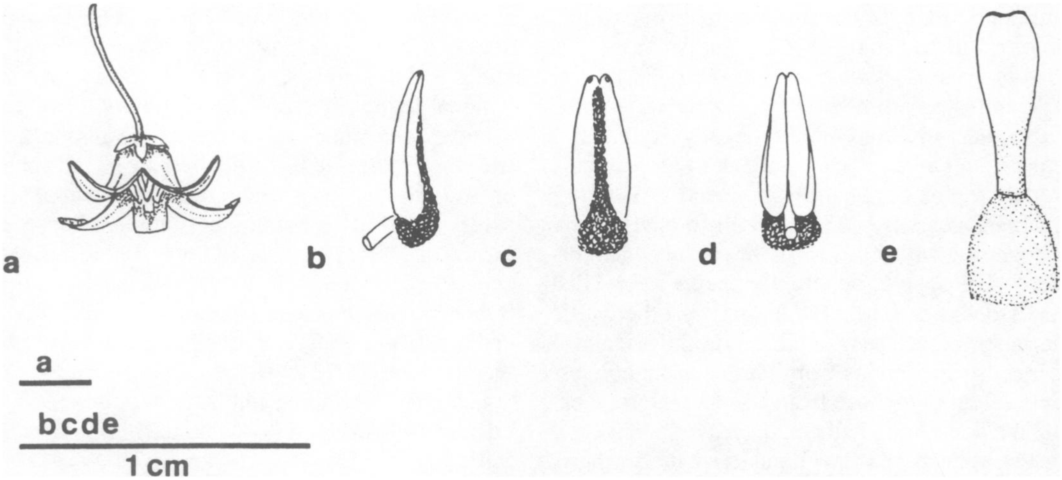


FIG. 66. *Cyphomandra premnifolia.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Brade 11131.*

ately to densely puberulent and often also moderately (to densely) pubescent-pilose. *Flower buds* ellipsoidal to ovoid, acute or obtuse at apex. *Calyx* chartaceous, moderately to densely puberulent, the radius (3–)4–7 mm, the lobes (1.5–) 2.5–5 mm long, (1.5–)2–3 mm wide, triangular-elliptic, acute or obtuse at apex. *Corolla* blue or violet fading to yellowish, fleshy, campanulate (to stellate), the radius 9–20 mm, the tube 3–5 mm long, the lobes narrowly triangular, 5–17 mm long, 2.5–4(–5) mm wide, glabrous to moderately puberulent abaxially, glabrous to papillose adaxially, the margin tomentose, the apex acute. *Anther thecae* lanceolate, the color unknown, 4–5 mm long, 2 mm wide, the pores directed abaxially and laterally; connective 5–6 mm long, 2 mm wide, the color unknown, broad at base, abruptly narrowed distally, abaxially slightly shorter than thecae at apex, exceeding them by ca. 1 mm at base, adaxially absent. *Ovary* sparsely to densely puberulent; style clavate, sparsely glandular-puberulent, narrow at base, dilated distally, then narrowed again at apex, (4–)5–6 mm long, 0.5–1 mm in diam. at base, widening distally to 1–2 mm, about equal to or exserted up to 1 mm beyond stamens; stigma truncate to concave and bilobed, 1–2 mm in diam. *Fruit* oblong-fusiform or globose, acute or obtuse at apex, 1–2.5 cm long, 0.6–1.5 cm in diam., densely puberulent, the color when ripe unknown; mesocarp with small round stone cell aggregates (seen only in *Martinelli et al. 4138*); seeds unknown.

Distribution (Fig. 65B) and phenology. Secondary vegetation and openings or margins of primary forest, southeastern Brazil in Paraná and Rio de Janeiro and possibly also in Bahia and São Paulo, at about 50–700 m in elevation. Flowering specimens have been collected in February, April, and September through December. Fruiting specimens have been collected in February, April, and December.

Additional specimens examined. BRAZIL. Bahia: without locality, *Lockhart s.n.* (BM). **Paraná:** Colônia São Nicolau, Curitiba, *Capriglione s.n.* (NY, US); Capão Grande, 23 Dec 1903 (fl, fr), *Dusén 2923* (F, GH, NY, S); Capão Grande, 4 Feb 1909 (fl), *Dusén 7525* (S); Ponta Grossa, 20 Feb 1910 (fl, fr), *Dusén 9522* (GH, NY, S). **Rio de Janeiro:** Mata de Sacupa, 17 Oct 1945 (fl), *Azanbuja 34* (B, E); Pilar, Sep 1931 (fl), *Brade 11131* (BH, GH, US); Guanabara, Sacopã, Lagoa Rodrigo de Freitas, 8 Nov 1960 (fl), *Duarte 5424* (RB, US); Mun. Rio de Janeiro, Campo Grande, Serra do Mendanha, floresta sobre Regime de Preservacão Permanente IBDF, 600–700 m, 4 Apr 1978 (fl, fr), *Martinelli et al. 4138* (RB); Guanabara, Serra da Mendanha, 50 m, 27 Nov 1969 (fl), *Sucre 6405 = Braga 1795* (RB).

Cyphomandra premnifolia belongs to the *C. diploconos* complex by virtue of its fleshy campanulate corollas, broad, curved stamens with the connective abruptly constricted above the base, expanded style, and puberulent fruits. It closely resembles *C. calycina*; the stigma in both species, although broad, is not nearly as wide or abruptly expanded as that of *C. diploconos* or *C. sciadostylis. Cyphomandra premnifolia* can be distinguished from *C. calycina* by its smaller calyx, narrower and more elongated style that is constricted at the apex, and lack of an adaxially visible region of the anther connective.

This species is rather difficult to characterize morphologically because of the paucity of collections. The species apparently occurs in two disjunct localities, one in Paraná and the other in Rio de Janeiro, and these exhibit morphological differences. Specimens from Paraná are much less puberulent than those from Rio de Janeiro, lacking the dense long hairs on the leaves, stems, and inflorescence axes that characterize the northerly populations. In addition, the specimens from Paraná have much shorter pedicellar remnants (ca. 1 mm long) than those from Rio (ca. 3–5 mm long). Several collections from Paraná have immature fruits that are elongated with acute apices; no stone cell aggregates are discernable. In contrast, one collection (*Martinelli et al. 4138*) from Rio has nearly mature fruits that are globose and obtuse with small stone cell aggregates in the mesocarp. However, *Miers 4538* from the Organ Mountains of Rio (the type of *Pionandra pubescens* Miers) shows characteristics more typical of the Paraná collections: short pedicellar remnants, nearly glabrous corollas, and elongated, pointed fruits. This collection also has a smaller calyx (radius ca. 3 mm) than other accessions of this species (calyx radius 4–7 mm). It is clear that more collections, especially of fruiting material, will shed much light upon the critical characters of *C. premnifolia.*

It is surprising that no collections are available from the intervening area in São Paulo. Only one specimen, *Bowie & Cunningham s.n.*, has been purportedly collected from this state, but even this information is in doubt. Miers (1845) reports that this specimen was collected in São Paulo, but the sheet itself contains no locality information. The occurrence of this species in Bahia is also questionable. The Lockhart specimens in BM were supposedly collected there, but no additional locality information is available.

Although no etymology is available, it is assumed that the specific epithet is derived from *Premna*, a genus in the Verbenaceae, and "folium," or leaf. The correct compounding form should be "premnifolium." This is treated as an orthographic error (Art. 73.8; Greuter et al., 1988) and is corrected here.

Dunal first used "*Solanum premnaefolium*" as a herbarium name on an otherwise unmarked specimen in the De Candolle herbarium at G and on the Bowie and Cunningham sheet at BM. Miers used this name as the basis of his *Pionandra premnaefolia* (Miers, 1845). Miers cites the collections at BM of Luccombe from Bahia and Bowie and Cunningham from São Paulo as representatives of his new species. A search of the holdings of BM failed to turn up the "Luccombe" specimen, although one gathered by Lockhart was supposedly collected in Bahia. Accordingly, the Bowie and Cunningham sheet at BM has been designated as the lectotype. The sheet annotated as *Solanum premnaefolium* by Dunal at G bears no indication that it is a duplicate of the Bowie and Cunningham collection and therefore is not considered an isolectotype.

Miers (1845) did not specify the location of the type of his *Pionandra pubescens*, so his specimen at BM bearing the annotation "*Cerastemon* (sic) *pubescens*" is designated as the lectotype.

24. Cyphomandra rojasiana Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. **22:** 377. 1940; Gentry & Standley Fieldiana, Bot. **24:** 36, fig. 7. 1974. Type. Guatemala. Suchitepequez: Finca Moca, in ravine, 3300 ft, 20 Oct 1934 (fl), *Skutch 1472* (holotype, F 934375 [F neg. 49360 F, WIS]; isotypes, A, US). Fig. 67.

Shrub 2–3.5 m tall. *Branches* densely puberulent. *Leaf blades* simple, unlobed, chartaceous, acuminate at apex, densely puberulent adaxially and abaxially, more so on veins; petioles densely puberulent. *Trunk leaves* (only one represented) simple, unlobed, the blade ovate, 28–31(–45 ex descr.) cm long, 22–27 cm wide, length:width ratio ca. 1.5:1, the base deeply cordate with basal lobes 3–6 cm long; petiole ca. 12 cm long. *Crown leaves* 3? per sympodial unit, simple, unlobed, the blade ovate, 6.5–22 cm long, 7–18 cm wide, length:width ratio 1–1.5:1, the base deeply cordate with basal lobes 1–2.5 cm long; petiole 3–11 cm long. *Inflorescence* unbranched, 5–10-flowered, 2.5–3.5 cm long; peduncle 2–3 cm long;

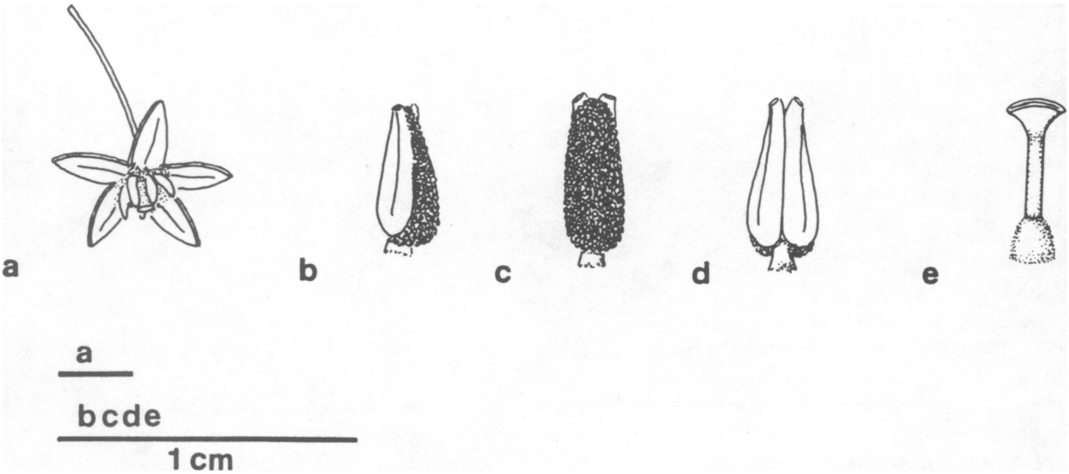


FIG. 67. *Cyphomandra rojasiana*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Skutch 1472*; b–e, based on *Steyermark 33743*.

rachis 0.5–1 cm long; pedicels 10–20 mm long, 20–25(–45 ex descr.) mm long in fruit, 1–3 mm apart, articulated at the base, leaving pedicellar remnants less than 1 mm long; peduncle, rachis, and pedicels densely puberulent. *Flower buds* ovoid or globose, obtuse at apex. *Calyx* coriaceous, puberulent, the radius 2–3 mm, the lobes 1–2 mm long, 2 mm wide, triangular, mucronate. *Corolla* green outside, bronze to purple inside, coriaceous, stellate, the radius ca. 10–13 mm, the tube 2 mm long, the lobes narrowly triangular, 8–11 mm long, 3–4 mm wide, glabrous adaxially and abaxially, the margin tomentose, the apex acute. *Anther thecae* white or yellow?, oblong, 4–5 mm long, 2 mm wide, the pores slightly extrorse and directed upward; connective light orange, oblong, 4–5 mm long, 1.5–2 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 0.5 mm, adaxially absent. *Ovary* puberulent; style glabrous, obconical, strongly dilated distally, 3–4 mm long, 0.3–0.5 mm in diam., exserted 1 mm beyond stamens; stigma peltiform, 1.5–2 mm in diam. *Fruit* ellipsoidal, acute at apex, 5–6.5 cm long, 3–5 cm in diam., glandular-puberulent, yellow with green stripes and splotches at end; mesocarp with stone cell aggregates; seeds 4–5 mm long, 3.5–4 mm wide, densely pubescent.

Distribution (Fig. 68) and phenology. Thickets and forested slopes, 1000–1500 m in elevation, in Belize, Guatemala, and Chiapas, Mexico. Flowering specimens have been collected in January, March through May, and October. Fruiting specimens have been collected in January, February, and November.

Additional specimens examined. MEXICO. CHIAPAS: Escuintla, along roadside to Finca California Turquia, 15 May 1947 (fl), *Matuda 16553* (F); Col. Turquia, near Esperanza, 23 Feb 1948 (fr), *Matuda 17600* (F, K).

GUATEMALA. PETEN: La Cumbre, ca. 4 km E of Porcela José León, 26 Mar 1977 (fl), *Lundell & Contreras 20681* (LL). **QUEZALTENANGO:** lower south-facing slopes on Volcán Santa María, between Finca Pirineos and Los Positos, between Santa María de Jesús and Calahuaché, 1300–1500 m, 8 Jan 1940 (fl, fr), *Steyermark 33743* (F, US). **PROV. UNKNOWN:** San Francisco Miramare, Apr 1878 (fl), *Bernoulli & Cario 2333* (GOET).

BELIZE. Toledo district, between Monkey River and Cockscomb, 20 Nov 1942 (fr), *Gentle 4237* (LL, MO).

Local names. Mexico: Huevo de gato (*Matuda 17600*). Belize: Wild cucumber (*Gentle 4237*).

The expanded stigma and the short, broad anthers of this species are typical of the *C. obliqua* group. It most closely resembles *C. obliqua* of the eastern Andean slope, but can be distinguished from it by its puberulent fruits and few-flowered inflorescences.

Standley and Steyermark (1940), in their original description of this species, refer to it as being related to *C. costaricensis* Donn. Sm. (=*C. hartwegii*) of Central and northern South Amer-

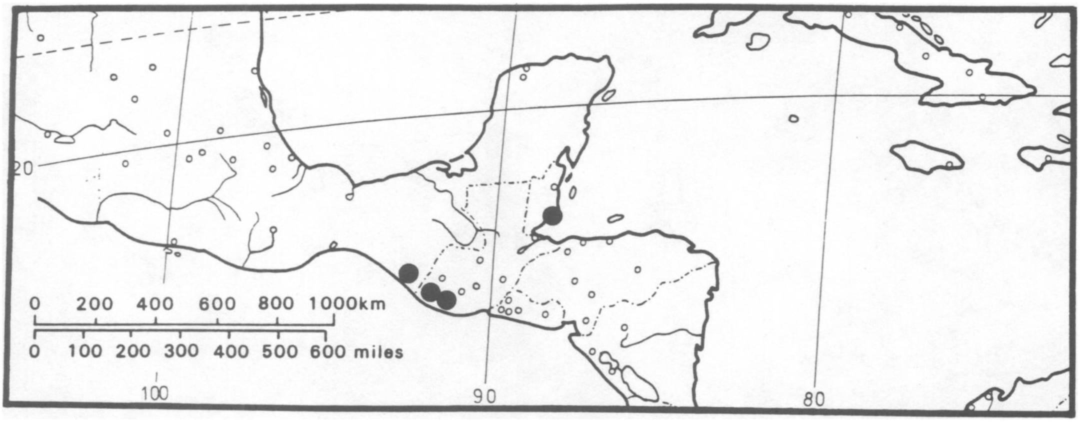


FIG. 68. Distribution of *C. rojasiana.*

ica. They erroneously refer to the anthers of *C. costaricensis* as being shorter than those of *C. rojasiana*, though their statement that *C. costaricensis* has narrower buds and longer corollas is correct. *Cyphomandra rojasiana* does not seem to be at all related to the *C. hartwegii* complex but rather to the *C. obliqua* group of Peru and Brazil. Gentry and Standley's assertion in the *Flora of Guatemala* (1974) that *C. rojasiana* is closely related to and perhaps a variety of *C. betacea* is incorrect. The two species differ greatly in the morphology of the anthers and gynoecium, though they have some vegatative similarities in their velutinous puberulence and deeply cordate, rather thin leaves.

25. Cyphomandra sciadostylis Sendtner, Flora **28:** 170. Tab. 4, fig. 1–10. 1845. Type. Brazil. São Paulo: circa Mogyguacu, Aug 1834 (fl), *Martius 330* (lectotype, BR, here designated. Chosen from syntypes *Martius 330* and *Sellow 179*). Figs. 69, 70.

Cyphomandra sciadostylis var. *ovato-lanceolata* Dunal, DC. Prodr. **13(1):** 392. 1852. Type. Brazil. São Paulo, *Gaudichaud 315* (holotype, P [F neg. 39257 F, WIS]).

Cyphomandra sciadostylis var. *trichocarpa* Hassler, Repert. Spec. Nov. Regni Veg. **9:** 119. 1911. Type. Paraguay. Esperanza, Sierra de Amambay, Dec 1907 (fl) & Jun 1908 (fr), *Rojas 10863* (lectotype, G, here designated; isolectotypes, G, NY).

Cyphomandra sciadostylis var. *hirsuta* Witasek, Denkschr. Kaiserl. Akad. Wiss., Math.-Naturwiss. Kl. **79:** 363. 1931. Type. Brazil. São Paulo: Campinas, Oct 1900 (fl), *Campos Novaes 199* (lectotype, WU, here designated).

Cyphomandra reitzii Smith & Downs, Phytologia **10:** 437. Plate 10, fig. 1–4. 1964. Type. Brazil. Santa Catarina: Mun. Xanxerê, 17 km N of Abelardo Luz, elev. 500–600 m, 25 Dec 1956 (fl, fr), *Smith & Reitz 9216* (holotype, US 2423791; isotypes, HBR [n.v.], R [n.v.]).

Small *tree* or *shrub* 1–3 m tall. *Branches* densely puberulent and often also sparsely to densely pilose with hairs 2–4 mm long. *Leaf blades* simple, pinnately lobed, or pinnately compound, subcoriaceous, acuminate at apex, sparsely to densely puberulent and also frequently pilose adaxially, moderately to densely puberulent to pubescent abaxially; petioles densely puberulent and often also sparsely to moderately pilose. *Trunk leaves* unlobed to (2–)5–9-pinnate or pinnatifid, occasionally irregularly lobed with smaller interstitial leaflets; if unlobed, the blade ovate-elliptic, 7–18 cm long, 5–10.5 cm wide, length:width ratio ca. 1.5–2:1, the base cordate with basal lobes 0.5–2 cm long; if lobed or compound, the blade 8–28 cm long, 6.5–23 cm wide, the terminal leaflet elliptic or oblong, 6–11.5 cm long, 1.5–5 cm wide, the base cuneate, the petiolule 0–3 mm long, the lateral leaflets 3–11 cm long, 1.5–4 cm wide, sessile, the upper lateral leaflets basiscopically decurrent, oblique; petioles 3–10 cm long. *Crown leaves* 4 per sympodial unit, unlobed or (2–)3–5-pinnate or pinnatifid; if unlobed, the blade ovate or elliptic, 2.5–18 cm long, 2–12 cm wide, length:width ratio ca. 1–2.5:1, the base truncate to cordate with basal lobes 0–2 cm long; if lobed or compound, the blade 6–15 cm long, 8–15 cm wide, the ter-

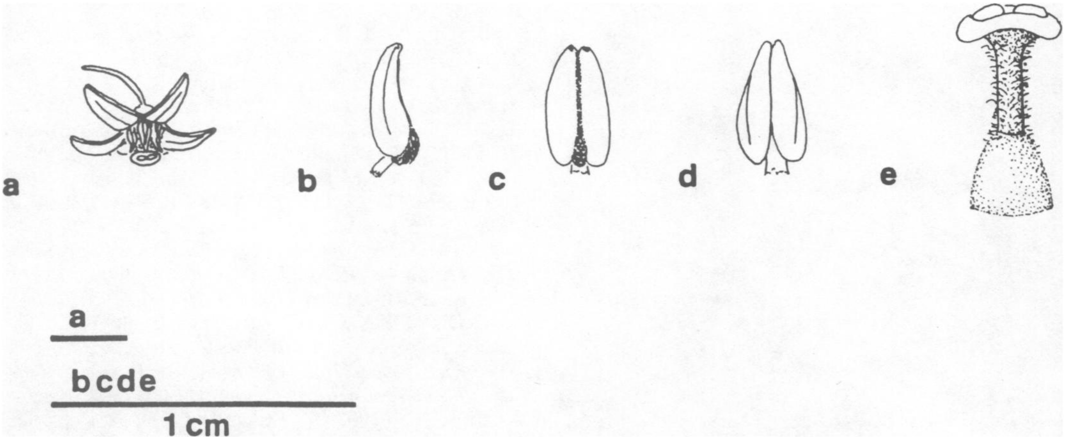


FIG. 69. *Cyphomandra sciadostylis.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Krapovickas & Cristobal 35365.*

minal leaflet elliptic, 6–14 cm long, 1.5–3.5 cm wide, the base cuneate, the petiolule absent, the lateral leaflets spreading or ascending, 4–9 cm long, 1.5–3 cm wide, sessile; petioles 1–6 cm long. *Inflorescence* unbranched, 10–20-flowered, 3.5–12 cm long; peduncle 1.5–3 cm long; rachis 1.5–9 cm long; pedicels 10–20 mm long, ca. 15–30 mm long in fruit, deflexed, (1–)3–10 mm apart, articulated above the base, leaving pedicellar remnants 1–4 mm long; peduncle, rachis, and pedicels densely puberulent and often also sparsely to moderately pilose. *Flower buds* oblong, obtuse at apex. *Calyx* chartaceous, densely pubescent to pilose, the radius 3–5 mm, the lobes 2–3 mm long, 1.5–2 mm wide, deltate, acute. *Corolla* pink, purple, or white, fleshy, campanulate, the radius 7–15 mm, the tube 1–3 mm long, the lobes triangular, 5–11 mm long, 2–5 mm wide, glabrous to densely pubescent abaxially, especially along midrib and toward apex, glabrous to densely papillose adaxially, the margin tomentose, the apex acute. *Anther thecae* violet, oblong, 4–5 mm long, 2–3 mm wide, the pores directed abaxially and laterally; connective 4–5 mm long, 0.5–2 mm wide, the color unknown, broad at base, narrowed distally, abaxially slightly shorter than thecae at apex, about equal to or slightly exceeding them at base, adaxially present or absent. *Ovary* densely puberulent; style densely puberulent, cylindrical to obconical, strongly dilated distally, 3–4 mm long, 1–1.5 mm in diam., exserted ca. 1 mm beyond stamens; stigma peltiform, biglandular, 2–4 mm in diam. *Fruit* ellipsoidal, ovoid, or fusiform, acute at apex, 2.5–3.5 cm long, 0.7–2 cm in diam., densely glandular- and eglandular-pubescent, apparently whitish when ripe with darker green longitudinal stripes; mesocarp with ellipsoidal stone cell aggregates about 3–7 mm long and 3–4 mm wide; seeds unknown.

Distribution (Fig. 65C) and phenology. Thickets, margins of fields, and *Araucaria* stands at ca. 200–1600 m in elevation, southeastern Brazil and adjacent areas of Argentina and Paraguay. Flowering specimens have been collected in all months of the year except March and July, with a flowering peak in August through January. Fruiting specimens have been collected in January through April, June, and October through December.

Additional specimens examined. BRAZIL. Minas Gerais: Poços de Caldas, Represa Bertolán, 19 Jan 1980 (fl, fr), *Krapovickas & Cristóbal 35365* (C, CTES, MO, NY); Lavras, 9 Dec 1980 (fr), *Leitão et al. 11815* (MBM); Caldas, Dec 1854 (fl), *Lindberg 172* (BR); Caldas, 20 Oct 1873 (fl), *Mosén 659* (LD), *660* (S); Poços de Caldas, Escubre de Santa Rosália, 21° 50'S, 46° 33'W, 16 Mar 1981 (fl), *Pereira et al. 873* (RB); Caldas, 1846–1875, *Regnell III 992* (BR, C, F, GH, P, S, U, US, WU); Caldas, 9 Nov 1845 (fl), *Widgren 1144* (BR). **Paraná:** Jaguariaíva, 29 Nov 1914 (fl, fr), *Dusén 15890* (GH, NY, S); Mun. Piraí-Mirim, road from Cerne, beginning of Serra dos Furnas, 3 Nov 1946 (fl), *Hatschbach 511* (B, SP); Mun. Guarapuava, Rio das Mortes, Rod. BR–277, 5 Dec 1968 (fl), *Hatschbach & Guimarães 20494* (MBM,

FIG. 70. *Cyphomandra sciadostylis* pictured in Tab. 16 from Martius' *Flora Brasiliensis*, vol. 10 (1846).

UT, Z); Mun. S. Mateus do Sul, Vargem Grande, 780 m, 16 Dec 1969 (fl, fr), *Hatschbach 23256* (C, MBM, MO, NY); Mun. Curitiba, Centro Civico, 19 Dec 1977 (fl, fr), *Hatschbach 40309* (MBM, UT); Mun. Candido Rondon, Bom Jardim, 10 Dec 1977 (fl, fr), *Hatschbach 40568* (MBM, UT, Z); Mun. Tijucas do Sul, Campina 46 km S of Curitiba, 14 Feb 1979 (fl, fr), *Krapovickas & Cristobal 33649* (C, CTES, MO); Curitiba, Parque Iguaçu, 2 Dec 1988 (fl), *Kummrow 3117* (GH, UT); same locality, 16 Dec 1987 (fl), *Soares s.n.* (VIC 10286)(GH). São Paulo: Fazenda Sete Quedas, Campinas, 20 Nov 1938 (fl), *Costa 2927* (SP); Fazenda Cascata, Estação Alfores Rodrigues, Oct 1899 (fl, fr), *Edwall 4422* (SP, US); Serra da Bocaina, 9 Sep 1879 (fl), *Glaziou 11387a* (P); Serra da Cantareira, sitio Pedro Doll., 19 Oct 1901 (fl), *Hammar 5882* (SP, US); Campinas, 25 Sep 1904 (fl), *Heiner 221* (S); Cascata, 21 Nov 1938 (fr), *Kiehl 4016* (SP); between Juqueira and Campos do Jordão, 18 Nov 1938 (fl), *Krug 4883* (SP); Amparo, Monte Alegre, Estação Experimental, 16 Dec 1942 (fl, fr), *Kuhlmann 75* (SP); Ibití, Estaco Experimental, 1 Aug 1946 (fr), *Kuhlmann 1400* (SP); Campos do Jordão, Oct 1945 (fl), *Leite 3666* (A); Rio Claro, 13 Jun 1888 (fl), *Löfgren 644* (C, SP); Araraquara, 20 Nov 1888 (fr), *Löfgren 1023* (C, SP); Franca, 3 Jan 1893 (fl), *Löfgren & Edwall 2016* (C, SP, US); Atibáia, Serra da Itapetinga, Pedra Grande, 1100 m, 29 Nov 1961 (fl), *Mattos & Handro 9523* (SP); Aguas da Prata, 3 km NW of Cascata, road Cascata-São Roque da Fartura, 9 Nov 1966 (fl), *Mattos & Mattos 14188* (SP); Serra de Caracol, 25 Dec 1873 (fr), *Mosén 1559* (S); Campinas, *Campos Novaes 197* (US, WU); Barreiro Co., Serra da Bocaina, Lageado Farm, 1600 m, Mar 1951 (fr), *Sagadas-Vianna 2840* (NY); Serra Ubatuba, 29 Sep 1938 (fl), *Viegas & Costa 4885* (SP); Sorocaba, 1902, *Wacket s.n.* (W, WU, Z).

PARAGUAY. Mbuneva, Nov 1931 (fl, fr), *Jorgensen 4374* (A, C, F, LP, MO, NY, S, US); Cantera, Puerto Cantera, 230 m, 20 Nov 1948 (fl), *Montes 3303* (K, SI).

ARGENTINA. Corrientes: Dept. Santo Tomé, Estancia Garruchos, potrero Puente, 11 Feb 1972 (fl), *Krapovickas et al. 21557* (LP). Misiones: Posadas, Bonpland, 7 Jan 1908 (fl, fr), *Ekman 842* (G, S, US); same locality, 6 Feb 1908 (fl), *Ekman 843* (LD, S); Dept. San Pedro, Ruta 102, ± 10 km antes de San Pedro, 29 Oct 1960 (fl), *Hunziker et al. 15458* (UT); Dept. San Ignacio, San Igancio, 224 m, 21 Oct 1946 (fl), *Medina 210* (B, G, TEX); Dept. Candelaria, Santa Ana, 10 Jan 1946 (fl), *Montes 1744* (LP); Dept. Iguazú, Puerto Wanda, km 9, 28 Oct 1950 (fl, fr), *Montes 9605* (LD, NY, TEX); Dept. Iguazú, Puerto Istuete, 7 Oct 1950 (fl, fr), *Montes 10110* (CTES, LP); Dept. Candelaria, Loreto, 220 m, 22 Apr 1958 (fl, fr), *Montes 27483* (MO, NY, TEX); Dept. Cainguás, Cásis, 17 Nov 1948 (fl), *Schwindt 901* (BH, C, G).

Local names and uses. Brazil: Baga de bugre (Smith & Downs, 1966), baga de veado (*Kummrow 3117*; Smith & Downs, 1966). Like *C. diploconos*, this species has ornamental potential.

Cyphomandra sciadostylis can be distinguished from all other species in the genus by its densely puberulent style. It belongs to the *C. diploconos* group by virute of its fleshy campanulate corolla, broad curved stamens with the connective abruptly narrowed above the base, expanded style and stigma, and puberulent fruits. *Cyphomandra sciadostylis* most closely resembles *C. diploconos*. Both species share the traits enumerated above, as well as frequently pinnately lobed trunk leaves, paired crown leaves, and strongly dilated stigmas and styles. It differs from *C. diploconos* in its puberulent style, abundant vegetative pubescence, and acute fruits with stone cell aggregates.

A few collections from Paraná and São Paulo, namely *Hatschbach 23256*, *Hatschbach 40309*, *Krapovickas & Cristobal 33649*, and *Hammar 5882*, are distinctive in having elongated fusiform fruits and abundant long (3–4 mm) hairs on the the stem, leaves, and inflorescences. The anther connective in these collections is somewhat broader than is usual and is very pronounced on the adaxial side, but otherwise the floral structure conforms to *C. sciadostylis*.

Dunal, Hassler, and Witasek described varieties of *C. sciadostylis*. Dunal's variety *ovato-lanceolata* and Hassler's variety *trichocarpa* have no detectable differences from "typical" *C. sciadostylis*. The type of Witasek's variety *hirsuta* is also alike in all particulars except that it has a larger number of long eglandular hairs on the leaves and stems. Although the longer hairs are denser on this specimen than is usual in *C. sciadostylis*, long hairs are not uncommon in this species. For this reason, I do not feel that Witasek's variety should be recognized as a distinct taxon.

Sendtner did not cite any collection numbers for his syntypes of *C. sciadostylis*. One specimen at BR, *Martius 330*, bears the same locality data as the collection cited by Sendtner and has been designated as the lectotype. The only sign of the Sellow syntype that I could find is a fragment at F labelled *Sellow 179* taken from a B sheet that has apparently been destroyed.

Rojas 10863, the type of *C. sciadostylis* variety *trichocarpa* Hassler, probably consists of several specimens collected at different times and all given the same number. The specimen at G bearing Hassler's label and annotations is here chosen as the lectotype. Unfortunately, this specimen has neither fruits nor flowers, so the isolectotypes should also be consulted to gain a concept of the critical characters of this taxon.

Witasek did not specify a single sheet to serve as the holotype of her variety *hirsuta*, so the collection at WU annotated by her has been chosen as the lectotype.

Vellozo possibly pictured this species as *Solanum conicum* in Plate 96 of his *Flora Fluminensis*. A type specimen is lacking, and therefore a critical identification cannot be made. For further details of *Solanum conicum* Vell., a synonym of *S. fluminense* Steud., see DOUBTFUL NAMES.

26. Cyphomandra sibundoyensis Bohs, Syst. Bot. **13:** 273. 1988. Type. Colombia. Putumayo: Valley of Sibundoy, 2 km E of Sibundoy, finca of Gomercindo Rodriguez, planted here among agricultural crops, but grows wild in the surrounding mountains, 2200 m, 20 Aug 1983 (fl), *Bohs & Juajibioy 2222* (holotype, COL; isotypes, CAUP, F, GH, MO). Fig. 71.

Small *tree* 4–8 m tall. *Branches* glabrous or sparsely puberulent with glandular and eglandular hairs less than 0.5 mm long. *Leaf blades* simple, unlobed, subcoriaceous, acuminate at apex, glabrous to sparsely eglandular-pilose and glandular-puberulent adaxially, glabrous to sparsely glandular-puberulent abaxially; petioles glabrous or minutely papillose. *Trunk leaves* simple, unlobed, the blade ovate-elliptic, 20–37 cm long, 15–28 cm wide, length:width ratio ca. 1.5:1, the base cordate with basal lobes 3–4 cm long; petioles 10–22 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade ovate, 5–18 cm long, 4–13 cm wide, length:width ratio 1–2:1, the base cordate, sometimes oblique, with basal lobes 1–3.5 cm long; petioles 2–7.5 cm long. *Inflorescence* branched, 40–100+ -flowered, 8–20 cm long; peduncle 3–5 cm long; rachises 3–14 cm long; pedicels 15–25 mm long, 40 mm long in fruit, 1–2(–5) mm apart, articulated at the base, leaving pedicellar remnants 0.5–1 mm long; peduncle, rachises, and pedicels glabrous or sparsely glandular-puberulent. *Flower buds* ovoid to ellipsoidal, acuminate at apex. *Calyx* succulent, glabrous, the radius 4–5 mm, the lobes 1–3 mm long, 3 mm wide, obtuse, minutely apiculate. *Corolla* lavender or greenish-purple mottled with dark violet, coriaceous, stellate, the radius 10–19 mm, the tube 1–2 mm long, the lobes narrowly triangular, 8–17 mm long, 2.5–3 mm wide, glabrous abaxially, sparsely to moderately puberulent adaxially especially toward apex, the margin tomentose, the apex acute. *Anther thecae* purple, lanceolate, 6–7 mm long, 2–2.5 mm wide, the pores introrse and directed distally; connective dark purple, lanceolate, 5–7 mm long, 1–2 mm wide, abaxially slightly shorter than thecae at apex, equal to or slightly exceeding them at base, adaxially present between bases of thecae. *Ovary* glabrous; style cylindrical, glabrous, not dilated distally, 6–7 mm long, 0.5–1 mm in diam., slightly shorter than to exserted 1–2 mm beyond stamens; stigma truncate, 0.5–1 mm in diam. *Fruit* ellipsoidal, ovoid, or globose, obtuse at apex, 6–10 cm long, 5.5–7 cm in diam., glabrous, yellow or orange when ripe; mesocarp with stone cell aggregates; seeds 6–9 mm long, 4–7 mm wide, densely pubescent.

Distribution (Fig. 72) and phenology. Cloud forest, 1400–2300 m in elevation, endemic to Sibundoy, Colombia and surrounding areas. Flowering specimens have been collected in Jan-

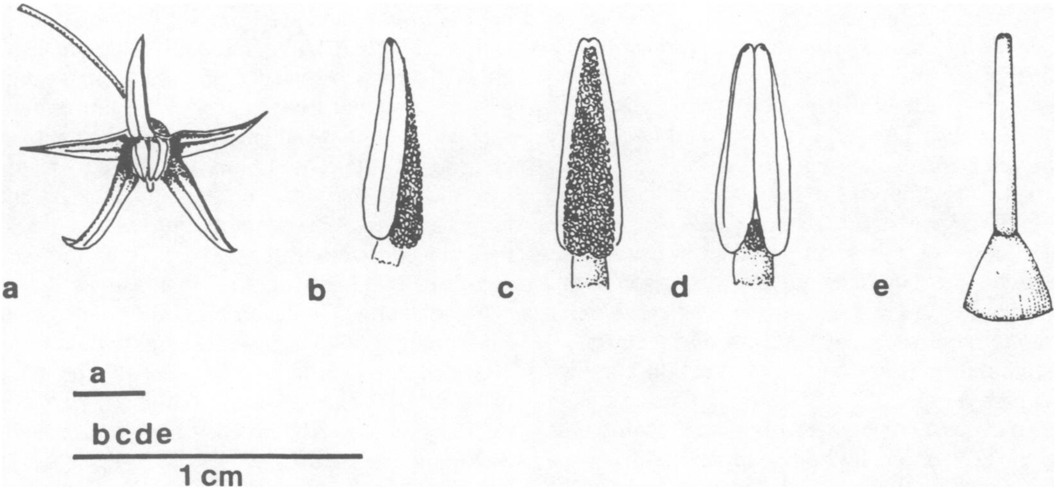


FIG. 71. *Cyphomandra sibundoyensis*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Bohs & Juajibioy 2222*.

uary, May, and August. Fruiting specimens have been collected in January, June, and August.

Additional specimens examined. COLOMBIA. HUILA: confluence of Rios Villalobos and Cauchos, 1400 m, Jan 1943 (fl, fr), *Schultes & Villarreal 5271* (ECON). PUTUMAYO: Valle de Sibundoy, 5 km S of Sibundoy, 2200 m, 12 Jun 1963 (fr), *Bristol 1119* (COL, ECON); 1 km S Balsayaco, 2200 m, 20 Aug 1963 (fl, fr), *Bristol 1316* (ECON); Sibundoy, ca. 2225–2300 m, 29 May 1946 (fl), *Schultes & Villarreal 7650* (ECON, F, GH, K, US).

Local names and uses. Colombia: Tomate salvaje, tomate silvestre (*Bohs & Juajibioy 2222*). The fruits are edible and have a pleasant acidulous taste (*Bristol 1316*; *Bohs & Juajibioy 2222*). This species was formerly used as the source of a black, blue, or yellow dye by the natives of the Sibundoy Valley of southern Colombia (*Bohs & Juajibioy 2222*). The placenta of fruit may be used as a cure for intestinal worms (*Bohs & Juajibioy 2222*). Schultes & Raffauf (1990) report that the Kamsá Indians of the Sibundoy Valley use a decoction of the leaves as a vermifuge, and use the pulp of the fruit to dye wool black (probably *Schultes & Villarreal 7650*, erroneously cited in Schultes and Raffauf as *7450*).

Cyphomandra sibundoyensis has stellate corollas, slender anthers, truncate stigmas, and fruits with stone cell aggregates as are typical of the *C. hartwegii* group. It most closely resembles *C. hartwegii*, but the corollas are purplish instead of green and it does not have lobed trunk leaves. This species is difficult to distinguish from *C. hartwegii* on herbarium sheets.

Cyphomandra sibundoyensis produces some of the largest fruits known in the genus. The fruit pulp is sweet, juicy, and pleasant-tasting, and the seeds are surrounded by an attractive purplish layer. Although a good candidate for trial as a fruit crop, it may be difficult to successfully cultivate this species outside the specialized climate of southern Colombia where it is native.

27. Cyphomandra stellata Bohs, sp. nov. Type. Colombia. Putumayo: selva higrófila del Río Putumayo en Puerto Ospina, 230 m, "arbusto 3–4 m, ramas horizontales con largos racimos péndulos paucifiores, corola blanco verdosa o blanco violáceo sucio, fruto 4–5 cm diam.," 25 Nov 1940 (fl, fr), *Cuatrecasas 10792* (holotype, US 1799572; isotypes, COL, F). Figs. 73, 74.

Cyphomandrae endopogi proxima, a qua differt alabastris acutis, radiis corollarum 14–20 mm longis, thecis antherarum 6–7 mm longis, fructibus subtiliter glanduloso-puberulis saltem ubi juvenibus, et inflorescentiis plerumque valde ramosis.

Small *tree* 1–8 m tall. *Branches* glabrous to

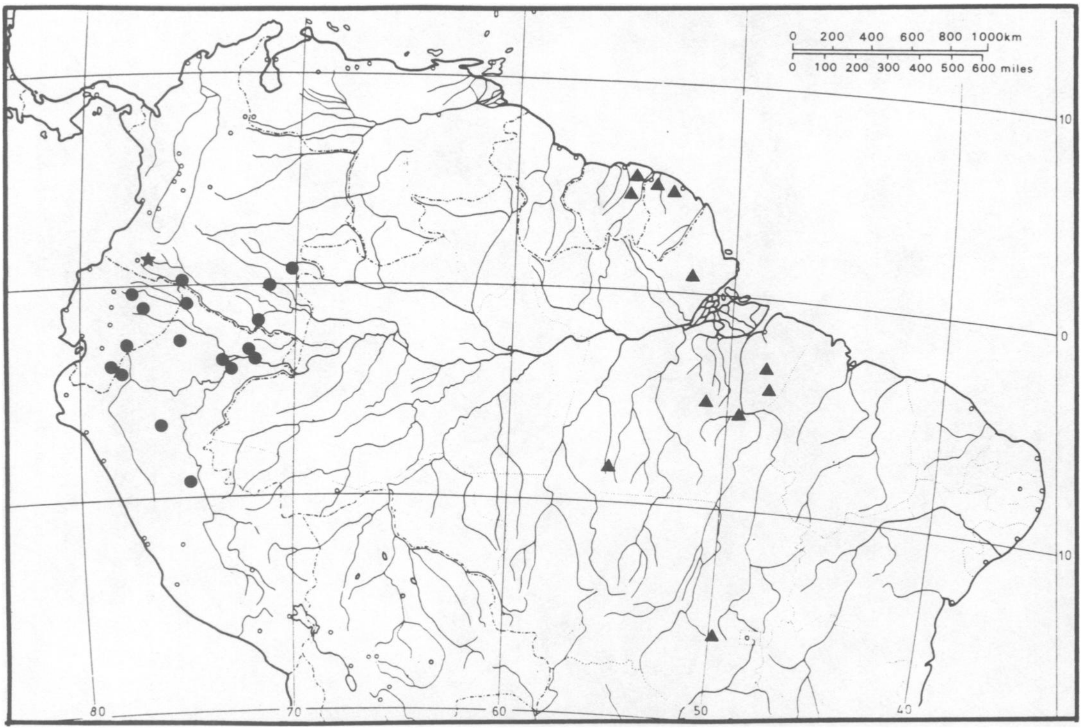


FIG. 72. Distributions of *C. sibundoyensis* (star), *C. stellata* (dots), and *C. tegore* (triangles).

finely puberulent, occasionally moderately to densely pubescent. *Leaf blades* simple, unlobed, subcoriaceous, acute to short-acuminate at apex, glabrous to sparsely pubescent adaxially except for denser pubescence on main veins, glabrous to moderately pubescent abaxially, more so on veins; petioles glabrous to moderately pubescent-pilose. *Trunk leaves* simple, unlobed, the blade elliptic, 17–26 cm long, 10–15 cm wide, length:width ratio 1.5–2:1, the base cuneate to truncate, without basal lobes; petioles 5–7 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, elliptic to ovate, 6–22 cm long, 5–16 cm wide, length:width ratio (1–)1.5–2:1, the base cuneate or truncate to deeply cordate, often oblique, with basal lobes up to 5 cm long; petioles 1.5–5 cm long. *Inflorescence* occasionally unbranched or forked but usually highly branched, ca. 50–100+ -flowered, (10-)30–50+ cm long; peduncle 4–12 cm long; rachises (5–)11–40+ cm long; pedicels 10–25 mm long, 20–30 mm long in fruit, (1–)4–10 mm apart, articulated near the base, leaving pedicellar remnants up to 1 mm long; peduncle, rachises, and pedicels glabrous to moderately puberulent, occasionally pubescent. *Flower buds* lanceolate, acute at apex. *Calyx* fleshy, glabrous to glandular-puberulent, the radius 2–3 mm, the lobes 1 mm long, 2 mm wide, truncate, apiculate. *Corolla* purplish- or greenish-white, membranaceous, stellate, the radius 13–20 mm, the tube 1–2 mm long, the lobes narrowly triangular, 12–18 mm long, 1.5–2 mm wide, glabrous to sparsely puberulent abaxially, sparsely villous adaxially, the margin densely ciliate with hairs ca. 1 mm long, the apex acute. *Anther thecae* yellowish, narrowly oblong to triangular, 6–7 mm long, 1 mm wide, the pores directed distally and adaxially; connective narrowly oblong to triangular, the color unknown, 6–7 mm long, 1 mm wide, abaxially slightly shorter than thecae at apex, exceeding them by up to 1 mm at base, adaxially present as a narrow swelling especially prominent at base. *Ovary* finely glandular-puberulent; style cylindrical, glabrous, somewhat dilated distally, 7–9 mm long, 0.5–1 mm in diam., exserted 2–3 mm be-

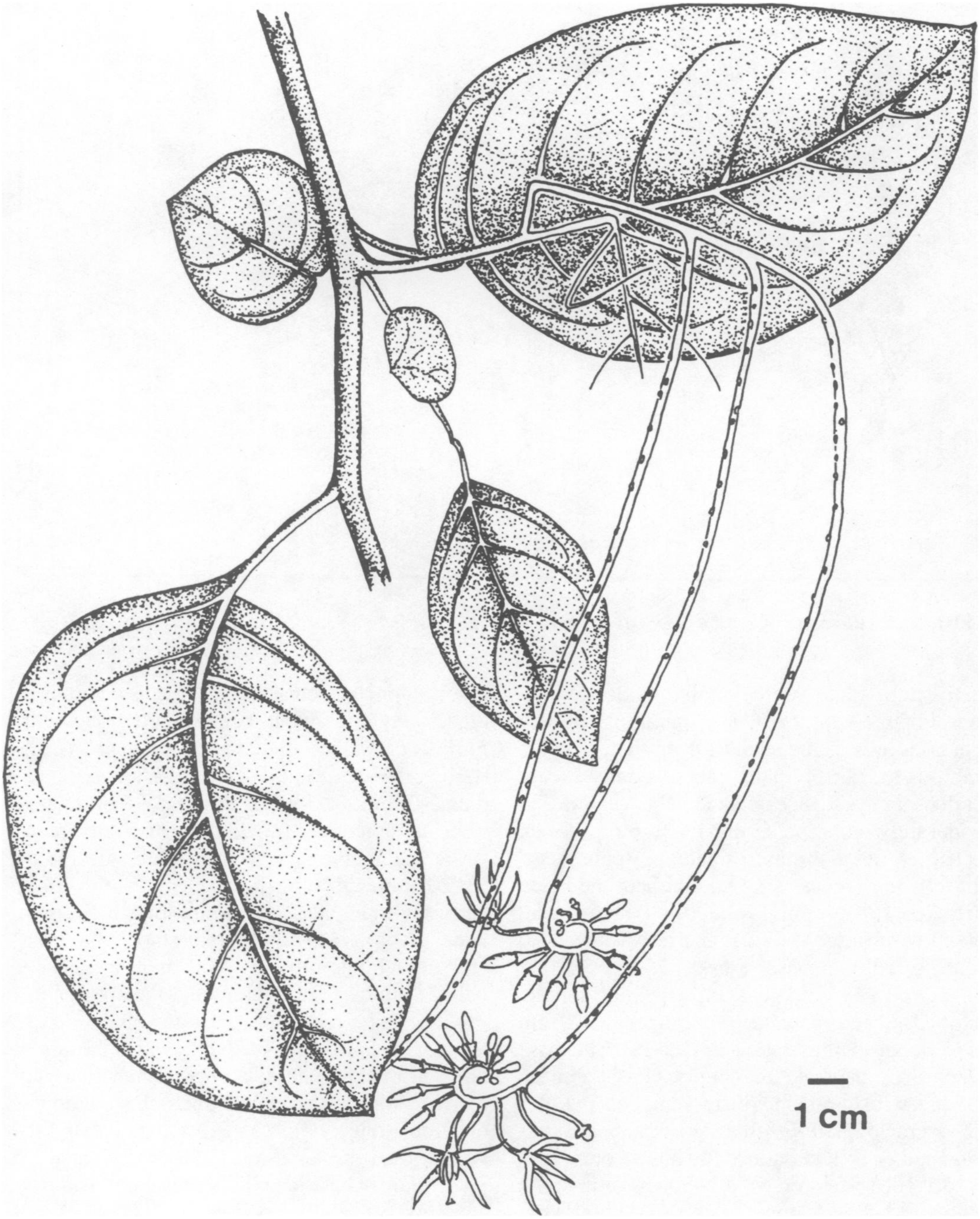


FIG. 73. *Cyphomandra stellata*. Crown branch with inflorescence. Based on *Cuatrecasas 10792*.

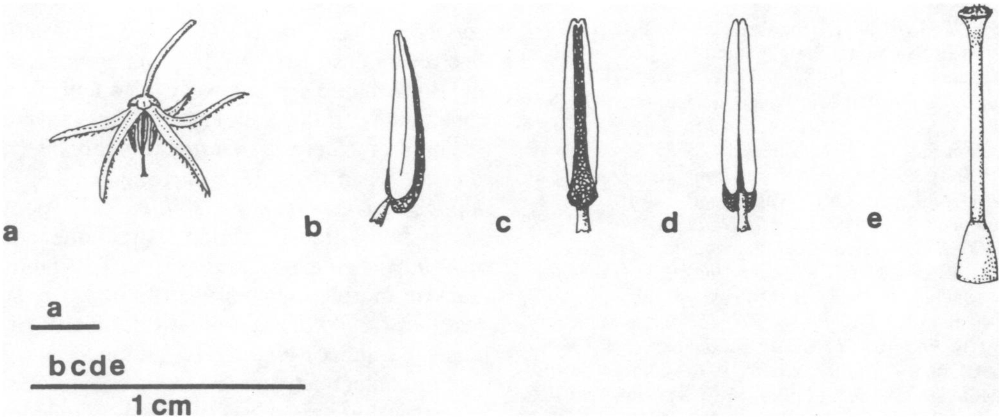


FIG. 74. *Cyphomandra stellata.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Schunke 10455*; b–e based on *Cuatrecasas 10792*.

yond stamens; stigma peltiform to capitate, ca. 1 mm in diam. *Fruit* ellipsoidal or globose, obtuse at apex, 3–5 cm long, 3–4.5 cm in diam., finely glandular-puberulent, especially when young, the color when ripe unknown, but probably yellowish; mesocarp with stone cell aggregates; seeds 5–6 mm long, 4 mm wide, puberulent.

Distribution (Fig. 72) and phenology. Disturbed areas of tropical rain forest, sometimes on inundated soil, 100–1200 m in elevation, western Amazon basin of southern Colombia, eastern Ecuador, and northeastern Peru. Flowering specimens have been collected in March and August through November, with a flowering peak in August and September. Fruiting specimens have been collected in all months of the year except April, June, and July.

Additional specimens examined. COLOMBIA. Amazonas: Leticia, 22 Aug 1946 (fl), *Blacke 46-62* (SP); Río Igara-Parana, Bella Vista, summit of plateau, 8 Sep 1973 (fl, fr), *Sastre 2162* (COL, MO); Amazon River, Leticia, ca. 100 m, 20 Sep 1945 (fl), *Schultes 6541* (GH, US); same locality, Sep 1946 (fl), *Schultes 8232* (US); Río Apaporis, Soratama, near mouth of Río Pacoa, 17 Aug 1951 (fl, fr), *Schultes & Cabrera 13044* (GH, US); Río Apaporis, Soratama, between Río Pacoa and Rio Kananarí, ca. 250 m, 15 Sep 1951 (fl, fr), *Schultes & Cabrera 13993* (U); La Victoria on the Amazon River, Aug-Sep 1929 (fl), *Ll. Williams 2564* (F, US); same locality, 29 Aug 1929 (fl), *Ll. Williams 2917* (F). **Vaupés:** Río Vaupés, Cerro de Mitú, ca. 250 m, 7 Sep 1951 (fl), *Schultes & Cabrera 13903* (GH, U, US); vic. Mitú, 200 m, 30 Mar 1970 (fl), *Soejarto & Lockwood 2468* (COL, F, K).

ECUADOR. Morona-Santiago: Bomboiza, 800 m, 24 Aug 1977 (fl), *Hart 1211* (A, MO, US); Gualaquiza, Misión, Bomboiza, Misión Salesiana, 700–800 m, 28 Sep 1967 (fl, fr), *Sparre 19118* (S); Bomboiza, 17 km SE of Gualaquiza, 3° 27'S, 78° 34'W, 700 m, Jul-Oct 1985 (fl), *Zaruma 313* (GH). **Napo:** Tena, 10 Oct 1939 (fl), *Asplund 9221* (S); Parque Nacional Yasuní, vic. Helipuerto de Amo Sur, 230 m, 0° 52'S, 75° 5'W. 16–19 Jan 1988 (fr), *Cerón 3485* (UT); Estación Biológica Jatun Sacha, 450 m, 1° 4'S, 77° 36'W, 24 Aug 1988 (fl), *Cerón & Cerón 4518* (UT), *4632* (UT); road Coca-Loreto, between community of 10 de Agosto and Río Pinguillo, 1000 m, 0° 43'S, 77° 28'W, 20 Oct 1988 (fr), *Cerón & Iguago 5280* (UT); Estación Biológica Jatun Sacha, Río Napo, 8 km E of Misahualli, 450 m, 1° 4'S, 77° 36'W, 22 Oct 1988 (fr), *Cerón & Iguago 5418* (UT); road Coca-Auca oilfields, km 53, 76° 52'W, 0° 50'S, 400 m, 20 Aug 1979 (fl), *Holm-Nielsen et al. 19662* (AAU); same locality and date (fl), *Holm-Nielsen et al. 19668* (AAU); road Coca-Loreto, 10 km W of Río Payamino, 275 m, 0° 35'S, 77° 10'W, 10 Oct 1987 (fl), *Neill et al. 7878* (UT); road Hollín-Loreto, km 32, 8 km W of Guamaní, 0° 43'S, 77° 38'W, 1200 m, 20 Sep 1988 (fl), *Neill et al. 8611* (UT); Estación Biológica Jatun Sacha, 8 km E of Misahualli, 450 m, 1° 8'S, 77° 30'W, 2–5 Sep 1988 (fl), *Palacios 2851* (UT). **Pastaza:** Pastaza Canton, pozo petrolero "Namoyacu" de UNOCAL, 30 km S of Curaray, 76° 57'W, 1° 40'S, 13–30 Nov 1990 (fr), *Espinoza & Coba 684* (UT). **Zamora Chinchipe:** Estación Experimental "El Palmi", 52 km NE of Zamora, 900 m, 3° 43'S, 78° 38'W, 11 Sep 1975 (fl), *Little et al. 303* (COL, MO, US).

PERU. Amazonas: Rio Cenepa, vic. Huampami, ca. 5 km E of Chávez Valdívia, next to Kayamas entsa, ca. 78° 30'W, 4° 30'S, 200–250 m, 7 Aug 1978 (fl), *Kujikat 168* (MO). **Huánuco:** Prov. Leoncio Prado, Dist. Rupa Rupa, E of Tingo María, near Cerro Quemado, 700–800 m, 5 Aug 1978 (fl), *Schunke 10445* (MO). **Loreto:** Prov. Maynas, Pucaurtillo-Pevas, 100 m, 16 Dec 1980 (fr), *Ayala 2976* (NY, TEX); Prov. Maynas, Explorama Tourist Camp, Quebrada Sucusari, 3° 15'S, 72° 55'W, 130 m, 18 Jan 1983 (fr), *A. Gentry et al. 39539* (MO); Mishuyacu, near Iquitos, ca. 100 m, 24–28 Sep 1929 (fl), *Killip &*

Smith 29863 (F, NY, US); Prov. Maynas, Dist. Napo, environs of Río Santa María, garden E of Secoya village of "Vencedor," ca. 1° 10'S, 74° 44'W, 100 m, 16 May 1982 (fr), *King 511* (GH); Mishuyacu, near Iquitos, Oct-Nov 1929 (fl), *Klug 52* (F, NY, US); Prov. Loreto, Nueva Jerusalem and vic., Río Macusari, 2° 55'S, 76° 15'W, 220–300 m, 29 Dec 1985–3 Jan 1986 (fr), *Lewis et al. 10499* (Lewis, pers. coll.); Valencia, Río Corrientes near Platanoyacu, 21 Sep 1968 (fl), *McDaniel & Marcos 11170* (F, MO); Río Ampiyacu, 2 km above Pucu Orquilla, ca. 100 m, 11 Feb 1969 (fr), *Plowman 2462* (GH, NY, USM); Prov. Maynas, Mishana, Río Nanay, 73° 30'W, 3° 50'S, ca. 140 m, 1978 (fl), *Ramírez 65* (MO); same locality, 1978 (fl), *Ramírez 117* (MO); Río Nanay, near Caserio Santa Clara, vic. Iquitos, 25 Oct 1976 (fr), *Revilla 1645* (F, MO, USM); Dist. Iquitos, Río Momón, trib. Río Nanay, trail from caserio of San Andrés, 24 Mar 1977 (fr), *Rimachi 2923* (F, MO, NY). SAN MARTÍN: near Tarapoto, on slopes of Guayrapurima mountains, Sep 1856 (fl), *Spruce 4616* (BM, BR, K, W).

Local names and uses. Colombia: Mee ooḿ be te ka (Kubeo)(*Schultes & Cabrera 13993*), wa só a (Tukano)(*Schultes & Cabrera 13993*). Ecuador: nemponcan (Huaorani) (*Espinoza & Coba 684*), yodil (*Little et al. 303*). Peru: Chupo sacha macho (*Schunke 10445*), ko pi (*King 511*), mun nejendas (*Kujikat 168*), pákupkus (Mayna Jívaro) (*Lewis et al. 10499*).

The Mayna Jívaro of Peru heat the leaves on a fire and apply them to the chest as a poultice to treat respiratory congestion, especially in children (*Lewis et al. 10599*). A specimen from the Peruvian Amazon (*King 511*) records the use of the seeds as food.

Cyphomandra stellata closely resembles *C. endopogon* in its narrow corolla lobes bordered by conspicuous hairs, long narrow anthers, and slender styles dilated at the apices into expanded peltiform stigmas. As in *C. endopogon*, the inflorescences can become elongated and often bear leaflike bracts near the base, but those of *C. stellata* are highly branched whereas those of *C. endopogon* are usually unbranched or only forked. The floral parts of *C. stellata* are smaller than those of *C. endopogon* and the flower buds are acute rather than obtuse. Both *C. stellata* and *C. endopogon* subspecies *guianensis* have puberulent fruits.

Cyphomandra stellata is sympatric with *C. endopogon* subspecies *endopogon* in the western Amazon. Because of the morphological similarities between the two species, *C. stellata* was previously considered to be a variety of *C. endopogon* (Bohs, 1986). *Cyphomandra stellata* also resembles *C. hartwegii* in many vegetative and floral features, particularly in its acute flower buds, acute corolla lobes, and smaller floral parts. Stigma diameter in *C. stellata* is roughly intermediate between that of *C. hartwegii* and *C. endopogon*. *Cyphomandra stellata* also occurs largely in the area of overlap between the ranges of *C. hartwegii* and *C. endopogon*. The intermediacy in morphology and distribution may suggest that *C. stellata* is a hybrid derivative of *C. hartwegii* and *C. endopogon* established in the area of contact between the latter two species.

To test this hypothesis, pollen was examined from herbarium sheets of *C. stellata*, *C. hartwegii*, and *C. endopogon* collected in areas where all three species co-occur in eastern Ecuador and Peru. Pollen stainability, as assessed by treatment with aniline blue/lactophenol, did not differ significantly between the three species (*C. stellata*: x = 88.8%, s = 9.57, n = 14; *C. endopogon*: x = 90.0%, s = 6.26, n = 6; *C. hartwegii*: x = 94.3%, s = 4.48, n = 4). These results do not support the idea of a hybrid origin of *C. stellata*. If it is indeed a hybrid, it has high pollen fertility. Further biosystematic studies in the field and greenhouse should be undertaken to elucidate the relationships between these three putatively related species.

The epithet *stellata* has been chosen to reflect the star-shaped corolla of this species.

28. Cyphomandra sycocarpa (Martius & Sendtner) Sendtner in Martius Fl. Bras. 10: 113. Tab. 15. 1846. Figs. 75, 76.

Solanum sycocarpum Martius & Sendtner, Flora **24(2)**, Beibl. 6, p. 85. 1841; Martius Herb. Fl. Bras. p. 325, 1841. Type. Brazil. Bahia: In umbrosis silvis ad Ilheus, *Martius 621* (lectotype, L, here designated; isolectotypes, BM, BR, G [F neg. 8496 F, GH, LL, NY], GH, K, L, M [F neg. 6515 F, NY, WIS], MO, P, W).

Cyphomandra lobata Sendtner in Martius Fl. Bras. **10**: 115. 1846. Type. Brazil. Rio de Janeiro: Ponte Negra, *Schott 5405* (lectotype, W, here designated [F neg. 33017 F, GH, US, WIS]).

Shrub or small *tree* 1–6 m tall. *Branches* glabrous, succulent. *Leaf blades* simple, unlobed or lobed, succulent, acute to obtuse at apex, glabrous adaxially and abaxially; petioles glabrous. *Trunk leaves* simple, unlobed or 7–9-lobed; if unlobed, the blade elliptic, 30–60 cm long, 18–24 cm wide, length:width ratio 2–2.5:1, the base cuneate, without basal lobes; if lobed, the blade ca. 20–30 cm long, 15–22 cm wide, divided ca. 5/6 to midrib, the sinuses rounded, obtuse, the base cuneate, without basal lobes; petioles 5–10 cm long. *Crown leaves* 3 per sympodial unit, simple, unlobed or (2–)3–5-lobed; if unlobed, the blade elliptic to obovate, 4.5–25 cm long, 3–12.5 cm wide, length:width ratio ca. 2–3:1, the base cuneate, without basal lobes; if lobed, the blade 8.5–15 cm long, 6.5–12 cm wide, divided ca. 3/4 to midrib, the sinuses rounded, obtuse, the base cuneate, without basal lobes; petioles 1–7 cm long. *Inflorescence* unbranched or forked (occasionally two inflorescences emerging from same point on branch), ca. 10–30-flowered, 1–6 cm long; peduncle 0.5–3 cm long; rachis 0.4–3 cm long; pedicels 10–25 mm long, 20–25 mm long in fruit, nearly contiguous, articulated at the base, leaving conspicuous pedicellar scars on the rachis; peduncle, rachis, and pedicels glabrous and succulent. *Flower buds* ellipsoidal, obtuse at apex. *Calyx* fleshy, glabrous, 4–6 mm high, the lobes 1.5–3 mm long, 2.5–4 mm wide, deltate to shallowly triangular, obtuse or apiculate. *Corolla* green to brownish, very fleshy, campanulate to stellate, ca. 15–25 mm high, the tube 3–5 mm long, the lobes 8–20 mm long, 3–5 mm wide, triangular, glabrous abaxially, puberulent or papillose adaxially, the margin minutely tomentose, the apex acute. *Anther thecae* yellow, elliptic, 3–5 mm long, 1.5–2 mm wide, the pores directed distally and laterally; connective dark brown, elliptic-ovate, 4–6 mm long, 2 mm wide, abaxially exceeding thecae at apex by 0.5–1 mm, equal to or exceeding them at base by ca. 0.5 mm, adaxially absent. *Ovary* glabrous; style obconical, glabrous, strongly dilated distally, 4–6 mm long, ca. 1 mm in diam. at base, barely exserted beyond stamens; stigma truncate and bilobed, 2–3 mm in diam. *Fruit* globose to obovate, obtuse at apex, 1.3–3 cm long, 1.3–3 cm in diam., glabrous, yellow or orange when ripe; mesocarp without stone cell aggregates; seeds 4–5 mm long, 4 mm wide, reticulate, puberulent around margin.

Distribution (Fig. 65D) and phenology. Restinga vegetation along the seashore in Bahia, Espírito Santo, and Rio de Janeiro, Brazil at 10–50 m in elevation. Flowering specimens have been collected in February, March, August, September, and November. Fruiting specimens have been collected in September and October.

Additional specimens examined. BRAZIL. Bahia: Mun. de Camacari, Guarajuba, Loteamento Canto do Mar, 20 Feb 1982 (fl), *Bautista 530* (NY, RB); Mun. de Ilhéus, area do CEPEC, km 22 da Rodovia Ilhéus-Itabuna (BR 415), 50 m, 27 Oct 1981 (fr), *Hage & dos Santos 1490* (F); Mun. de Itamaraju, ca. 5 km W of Itamaraju, 20 Sep 1978 (fl), *Mori et al. 10758* (US); Almadina, Serra da Pancadinha, Faz. Beija, 3 Aug 1971 (fl), *Pinheiro 1536* (US). **Espírito Santo:** Vitória, 20 Mar 1934 (fl), *Kuhlmann 3* (SP); same locality, Sep 1957 (fr), *Kuhlmann s.n.* (SP). **Rio de Janeiro:** Jurujuba, *Miers 3683* (BM); Recreio dos Bandeirantes, 4 Nov 1969 (fl), *Sucre 6200* (RB); Mun. de Cabo Frio, entre os loteamentos Nova California e Frecheiras, ca. 10 m, 23 Aug 1972 (fl), *Sucre et al. 9542* (RB).

This species is one of the most unusual in the genus. It is a small tree of the seacoast with succulent stems, leaves, and flowers. The leaf-opposed inflorescences resemble those of *Solanum* section *Geminata*. The inflorescence axis is rather short for a *Cyphomandra*, and the small, obovate fruits are atypical in the genus. These fruits are said to resemble small figs, hence the name "sycocarpa" or "fig-like fruit." In floral features, however, this species certainly belongs to *Cyphomandra*. The anther connective is obvious and discrete; furthermore, it is prolonged beyond the apices of the anther thecae as a rostrate or beaked structure similar to that of *C. heterophylla* and *C. uniloba*.

Three collections from the area around Rio de Janeiro have pinnately lobed leaves, in contrast to the elliptic or obovate leaves of the more northerly collections. Sendtner (1846) considered the plants with lobed leaves as a separate species, *C. lobata* Sendtner, but mentioned that the taxon might better be regarded as a variety of *C. sycocarpa*. Because both lobed and unlobed leaves may be present on a single plant (e.g., *Sucre et al. 9542*) and because the flowers of both segregates are similar in all respects, I regard them as conspecific. Further field work is needed to ascertain whether the differences in leaf morphology are consistent with geographical location.

A single specimen was not designated as the type of *Solanum sycocarpum* Martius & Sendtner. Many sheets exist annotated with this name and Martius No. 621. The sheet at M also has a small tag attached to the twig with the number 503. Only one specimen I have seen, at L, bears the locality information

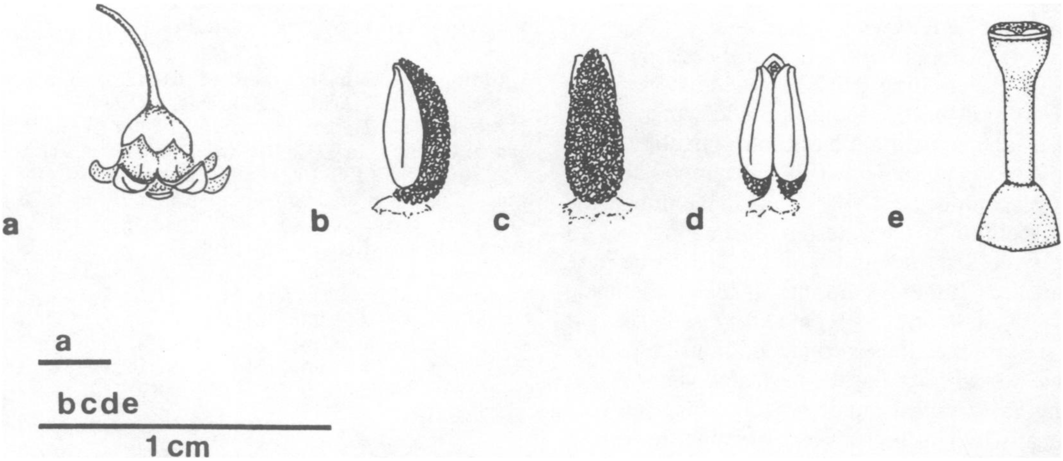


FIG. 75. *Cyphomandra sycocarpa.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on *Martius 621.*

given in the protologue in Martius' handwriting, and has been chosen as the lectotype.

Sendtner (1846) did not choose a single specimen as the holotype of his *C. lobata.* The only sheet I have been able to find that matches the information in his protologue is *Schott 5405* at W, which is here chosen as the lectotype.

Although several authors (e.g., Child, 1984; D'Arcy, 1973; Smith & Downs, 1966) have claimed that Sendtner designated *C. sycocarpa* as the type species for his genus *Cyphomandra,* this supposition is in error, as was noted by Benitez de Rojas (1974, 1981). She rightly points out that *C. sycocarpa* was not one of the species included in Sendtner's original description of the genus in 1845, but was only later described in his treatment for Martius' *Flora Brasiliensis* in 1846. In accordance with this fact, *C. sycocarpa* should not be chosen as the lectotype species of the genus, and her recommendation of designating *C. betacea* as the lectotype species should be followed.

29. Cyphomandra tegore (Aublet) Walpers, Repert. Bot. Syst. **6:** 579. 1847. Figs. 77, 78.

Solanum tegore Aublet, Hist. Pl. Guiane **1:** 212. Pl. 84. 1775. Type. French Guiana. River Sinemari, cultivated by the Galibis, *Aublet s.n.* (lectotype, BM, here designated).

Pionandra tegore (Aublet) Miers, London J. Bot. **4:** 362. 1845.

Small *tree* 1.5–5 m tall. *Branches* moderately to densely puberulent and sparsely pilose with hairs 1–2 mm long. *Leaf blades* simple, lobed or unlobed, chartaceous to subcoriaceous, acuminate at apex, sparsely puberulent and pilose adaxially, densely puberulent abaxially; petioles densely puberulent and sparsely pilose. *Trunk leaves* simple, pinnately 9-lobed (one leaf represented), the blade 34 cm long, 28 cm wide, divided 3/4 to 4/5 to midrib, the sinuses acute, the base cordate with basal lobes ca. 2 cm long; petiole ca. 5 cm long (fide Aublet). *Crown leaves* 3–4 per sympodial unit, simple, unlobed, the blade ovate, 4–15 cm long, 2–6 cm wide, length:width ratio (1–)1.5–2.5:1, the base truncate to cordate with basal lobes 0–1.5 cm long; petioles 1–4 cm long. *Inflorescence* unbranched, 15–50-flowered, 2–12 cm long; peduncle 0.5–1.5 cm long; rachis 1–10 cm long; pedicels 10–20 mm long, 15–20 mm long in fruit, 1 mm apart, articulated near the base, leaving pedicellar remnants ca. 1 mm long; peduncle, rachis, and pedicels densely puberulent and sparsely pilose. *Flower buds* lanceolate, acute at apex. *Calyx* subcoriaceous to fleshy, glandular-puberulent, occasionally sparsely pilose, the radius 1.5–2 mm, the lobes 1 mm long, 1–1.5 mm wide, rounded, acute or apiculate. *Corolla* green, greenish-brown, or whitish, membranaceous to subcoriaceous, stellate, the radius ca. 10 mm, the

FIG. 76. *Cyphomandra sycocarpa* illustrated in Tab. 15 of Martius' *Flora Brasiliensis*, vol. 10 (1846).

tube 0.5 mm long, the lobes narrowly triangular, ca. 10 mm long, 1.5–2 mm wide, glabrous abaxially, often sparsely pubescent toward apex, glabrous adaxially, the margin ciliate, the apex acute. *Anther thecae* white or yellow, narrowly triangular, 4.5–5 mm long, 1 mm wide, the pores directed distally and adaxially; connective purple or yellow, narrowly triangular, 5–6 mm long, 0.5–1 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 1 mm, adaxially absent or present at base. *Ovary* glandular-puberulent; style cylindrical, glabrous, not dilated distally, 6 mm long, 0.3–0.5 mm in diam., exserted 1–2 mm beyond stamens; stigma truncate, 0.3–0.5 mm in diam. *Fruit* ovoid or globose, obtuse at apex, 1.5–3.5 cm long, 1.5–2.5 cm in diam., moderately glandular-puberulent, yellow when mature (fide Aublet); mesocarp with stone cell aggregates; seeds 4 mm long, 4 mm wide, glabrous.

Distribution (Fig. 72) and phenology. Forest clearings, 70–700 m, Suriname, French Guiana, and eastern Brazil. Flowering specimens have been collected in March and June through December. Fruiting specimens have been collected in March, June, August, September, November, and December.

Additional specimens examined. SURINAME. B.S.H. ekspl. Patamacca, 8 Nov 1967 (fl, fr), *Boerboom (LBB)12032* (U); near Moengo tapoe, 14 Jun 1954 (fl, fr), *Lindeman 6176* (GH, U); Lely Mountains, 175 km SSE of Paramaribo, on N edge of plateau no. 1, 500–700 m, 11 Oct 1976 (fl), *Mori & Bolten 8444* (MO).

FRENCH GUIANA. Region of Paul Isnard, Massif of Décou Décou, N slope 2 km S of Boeuf, 410 m, 14 Nov 1982 (fl), *de Granville 5335* (BR); exploitation forestière au S de St. Laurent du Maroni, 26 Mar 1968 (fr), *Sastre & Sastre 295* (MO).

BRAZIL. AMAPÁ: Serra do Navio, Rio Amapari, lower slopes of Observatorio Ore Body, 70–300 m, 8 Nov 1954 (fl, fr), *Cowan 38154* (NY, US). **AMAZONAS:** Presidente Figueiredo, Represa de Balbina on Rio Uatamã, ca. 4 km NW of dam on D-1 road, 1° 50'S, 59° 32'W, 5 Jul 1986 (fl), *Thomas et al. 5360* (NY). **GOIÁS:** Goiânia, Morro da Agua Branca, 10–15 km from Centro de Goiânia, 17 Dec 1975 (fl), *Guimarães & Peixoto 323* (RB, UT). **PARÁ:** Mun. Itaituba, estrada Santarém-Cuiabá, BR 163, km 794, 7° 25'S, 55° 20'W, 5 Dec 1983 (fl, fr), *Amaral et al. 1250* (GH); Rodovia Belém-Brasília, km 93, 20 Aug 1959 (fl), *Kuhlmann & Jimbo 60* (SP); Belém-Brasília highway, 5 km N of Gurupi, vic. Paragominas, km 161, 12–13 Aug 1964 (fl, fr), *Prance & Silva 58675* (B, F, K, NY, S, U, US); Santarem, km 35 da estrada do Palhao, arredores do Acampamento do Igarape Curupira, 30 Aug 1969 (fl), *Silva & Souza 2448* (TEX); Marabá, Serra dos Carajás, 30 Mar 1977 (fl, fr), *Silva & Bahia 2949* (NY); Serra dos Carajás, 7–11 km NW of AMZA camp 3-Alfa on road to camp 4-Alfa, 5° 47'S, 50° 34'W, 250 m, 10 Jun 1982 (fl, fr), *Sperling et al. 6058* (GH); Taperinha bei Santarem, 4 Sep 1927 (fl, fr), *Zerny 796* (WU); same locality and date (fl, fr), *Zerny s.n.* (W).

Local names and uses. Suriname: Forestiki (*Boerboom (LBB)12032*). French Guiana: Mananga mâle" (Boni)(*Sastre 295*), tegoré (Galibi)(Aublet, 1775). Aublet (1775) states that this species was cultivated by the Galibis of French Guiana but does not mention any uses of the plants.

Cyphomandra tegore belongs to the *C. hartwegii* complex and manifests some of the typical characteristics of that group: pinnately lobed trunk leaves, greenish stellate corollas with narrow lobes, long narrow anthers, and slender cylindrical styles with small truncate stigmas. Its abundant pubescence, unbranched inflorescences, ciliate corolla margins, and pubescent

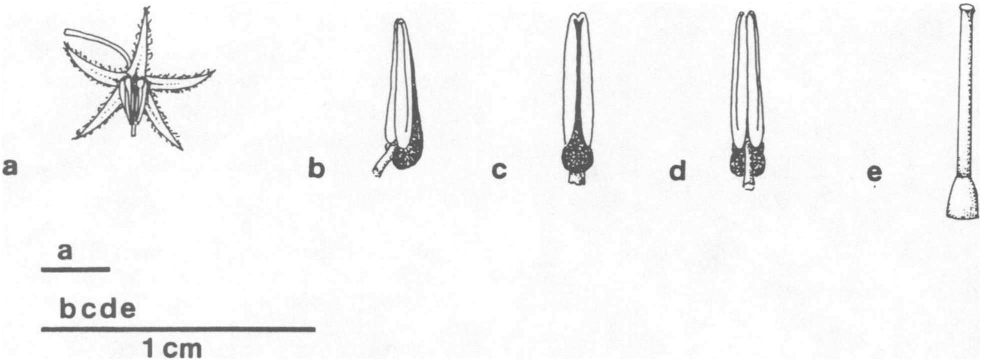


FIG. 77. *Cyphomandra tegore.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Sperling et al. 6058*; b-e, based on *Mori & Bolten 8444.*

fruits closely resemble those of *C. foetida*, but *C. tegore* differs in having lobed rather than entire trunk leaves and fruits with obtuse rather than acute apices. These two species are very similar, however, and further research may show that they are conspecific.

A single specimen representing Aublet's type is located at BM and has been chosen as the lectotype of *Solanum tegore* Aublet. It is probable that this specimen was used to prepare the plate for Aublet's description (Aublet, 1775; Fig. 78). However, the flowers pictured in the plate are not present on the BM specimen. Howard (1983) notes that many of Aublet's drawings and descriptions are mixtures of discordant elements. The provenance and fate of the flowers pictured in his illustration are unknown, but the leaves and distinctive puberulent fruits present on the type specimen are sufficient to identify it to species.

30. Cyphomandra tenuisetosa Bitter, Repert. Spec. Nov. Regni Veg. **17:** 352. 1921. Type. Brazil or Peru. Acre-Gebiet, im Walde bei Porto Carlos, *Ule 9753* (type, B, destroyed [F neg. 2937 F, G, GH, NY, US, WIS]). Neotype. Peru. Huánuco: Dist. Churubamba, Hacienda San Carlos, trail Exito to San Carlos, open woods, 1650 m, 18 Sep 1936 (fl, fr), *Mexia 8209* (type, US 1705382; duplicates, B, BH, BM, F, GH, K, MO, NY, S, U). Fig. 79.

Small *tree* or *shrub* 1.5–8 m tall. *Branches* moderately to densely puberulent and also moderately pilose-hirsute with hairs up to 5 mm long, often with hard and broadened bases. *Leaf blades* simple, unlobed or lobed, chartaceous to subcoriaceous, abruptly acuminate at apex, glabrescent to moderately glandular-puberulent and sparsely to moderately pilose adaxially with eglandular hairs 1–3 mm long, moderately to densely puberulent-pubescent abaxially; petioles moderately to densely puberulent and also sparsely to densely pilose-hirsute. *Trunk leaves* simple, unlobed or with 1–2 lateral lobes at base; if unlobed, the blade ovate, 12–20 cm long, 7–12 cm wide, length:width ratio 1.5–2:1, the base cordate with basal lobes 1–2 cm long; if lobed, the blade 10–19 cm long, 10–19 cm wide, divided 1/3–1/2 to midrib, the sinuses rounded, obtuse, the base cordate with basal lobes up to 1.5 cm long; petioles 6–9 cm long. *Crown leaves* 4 per sympodial unit, the blade simple, unlobed, ovate, 5–15 cm long, 3–10 cm wide, length:width ratio ca. 1.5:1, the base cordate and sometimes oblique with basal lobes 0.5–1.5 cm long; petioles 1–5 cm long. *Inflorescence* unbranched or occasionally branched, 10–35-flowered, 6–20 cm long; peduncle 3–7 cm long; rachises 3–17 cm long; pedicels 20–30 mm long, 30–40 mm long in fruit, 3–10 mm apart, articulated above the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachises, and pedicels moderately to densely glandular-puberulent and sparsely eglandular-pilose with hairs 1–3 mm long. *Flower buds* ovoid, acute at apex. *Calyx* somewhat fleshy, glabrate to sparsely pilose, the radius 4–5 mm, the lobes 2–5 mm long, 2–4 mm wide, ovate to oblong, acute

FIG. 78. *Cyphomandra tegore* pictured in Plate 84 of Aublet (1775).

or obtuse and apiculate, often unequal. *Corolla* deep purple to lavender or greenish, fleshy, campanulate, the radius (10–)15–20 mm, the tube 4–5 mm long, the lobes (7–)10–15 mm long, (3-)4–6 mm wide, triangular, glabrous to sparsely puberulent abaxially, moderately pubescent adaxially, the margin tomentose, the apex acute. *Anther thecae* yellow or purplish, narrowly triangular, 5–7 mm long, ca. 2 mm wide, the pores directed laterally; connective lilac?, lanceolate, 6–8 mm long, 1.5–2 mm wide, abaxially slightly shorter than thecae at apex, exceeding them at base by 1 mm, occasionally present adaxially as a slight swelling. *Ovary* glabrous; style cylindrical, glabrous, slightly dilated apically, 6–10 mm long, 0.5–1 mm in diam., exserted 2–4 mm beyond stamens; stigma capitate, 1–2 mm in diam. *Fruit* ellipsoidal, acute or obtuse at apex, 4–10 cm long, 2.5–5 cm in diam., glabrous, green mottled with dark green stripes when immature, the color when ripe unknown; mesocarp with stone cell aggregates; seeds 4–6 mm long, 4–5 mm wide, moderately pubescent.

Distribution (Fig. 80) and phenology. Open to dense rain forest, eastern slopes of Andean Cordillera in eastern Peru east to Amazonian Brazil at 135–1850 m in elevation. Flowering specimens have been collected in all months of the year except February and April. Fruiting specimens have been collected in January, March, April, July, and September through December.

Additional specimens examined. PERU. Ayacucho: Río Apurimac Valley, near Kimpitiriki, 400 m, 10–11 May 1929 (fl), *Killip & Smith 22924* (NY, US); Prov. de La Mar, trail between Santa Rosa and Sanabamba, along Río Santa Rosa, vic. Santa Rosa bridge, 700 m, 9 Jun 1975 (fl), *Wasshausen & Encarnación 528* (K, US). **Huánuco:** Prov. Huánuco, Tingo María, 29 Aug 1940 (fl), *Asplund 13386* (S); along Río Huallaga ca 13.7 km S of Tingo María, 18 Nov 1979 (fl), *Jones & Davidson 9260* (F, NY); Prov. Leoncio Prado, Dist. Rupa Rupa, E of Tingo María, 680 m, 2 Dec 1971 (fr), *Schunke 5209* (G, MO, NY, US); W of Tingo María, hill in front of airport, 700–800 m, 7 Aug 1978 (fl), *Schunke 10465* (MO); Prov. Huamalies, 13 km N of Tingo María, 610 m, 31 Oct 1938 (fl, fr), *Stork & Horton 9559* (F, G, K). **Junín:** San Ramón, 900 m, 17 Jul 1962 (fl, fr), *Woytkowski 7406* (GH, MO). **Loreto:** Yurimaguas, lower Río Huallaga, ca. 135 m, 23 Aug–7 Sep 1929 (fl), *Killip & Smith 28005* (F, NY, US); same locality and date (fl, fr), *Killip & Smith 28703* (F, NY, US), (fr) *29093* (F, NY, US); Fortaleza, Yurimaguas, lower Río Huallaga, 155–210 m, 30 Oct 1929 (fl, fr), *Ll. Williams 4370* (F); same locality, 6 Nov 1929 (fl, fr), *Ll. Williams 4687* (F). **Madre de Dios:** Prov. Tambopata, Tambopata Nature Reserve, ca. 30 air km or 70–80 river km SSW Puerto Maldonado at effluence Río La Torre (Río D'Orbigny)/Río Tambopata (SE bank), 12° 49'S, 69° 17'W, ca. 260 m, 25 Jun 1980 (fl), *Barbour 5788* (MO); same locality, 6 Mar 1981 (fl), *A. Gentry & Young 32038* (MO, USM); Manu, 6–10 km W of Shintuya on road to Salvación, ca. 500 m, 12° 40'S, 71° 15'W, 14 May 1984 (fl), *Knapp & Mallet 6448* (BH, US); Explorer's Inn, near the confluence of Río Tambopata and Río La Torre, 12° 50'S, 69° 20'W, 15 Jul 1987 (fl, fr), *S. F. Smith et al. 1047* (US). **Pasco:** Puerto Bermudez, 375 m, 14–17 Jul 1929 (fl, fr), *Killip & Smith 26605* (F, NY, US). **San Martín:** Prov. Mariscal Cáceres, Dist. Tocache, Pueblo Mantención, property of Hernán Ortíz, ca. 10 km S of Tocache Nuevo, 400–700 m, 26 Apr 1983 (st), *Bohs & Schunke 2161* (GH, MO, USM); same locality and date (fr), *Bohs & Schunke 2163* (F, GH, NY, USM); Fundo Curareland near Tinanta, 20 km NW of Tocache at N edge of palm plantation, 500 m, 14 Mar 1979 (fl), *A. Gentry et al. 25674* (MO); Juan Jui, upper Río Huallaga, ca. 400 m, Oct 1934 (fl), *Klug 3873* (BM, F, GH, K, MO, NY, S, US); km 28 of Tarapoto-Yurimaguas road, 650 m, 6° 25'S, 76° 15'W, 20 Jun 1984 (fl), *Knapp & Mallet 6527* (BH, US); Lamas, km 68 on Tarapoto-Yurimaguas road, 6° 16'S, 76° 17'W, ca. 270 m, 23 Jun 1984 (fl), *Knapp & Mallet 6536* (BH, MO, US); Prov. Mariscal Cáceres, Dist. Tocache Nuevo, Río Cañuto, "Curarelandia," near km 23 along

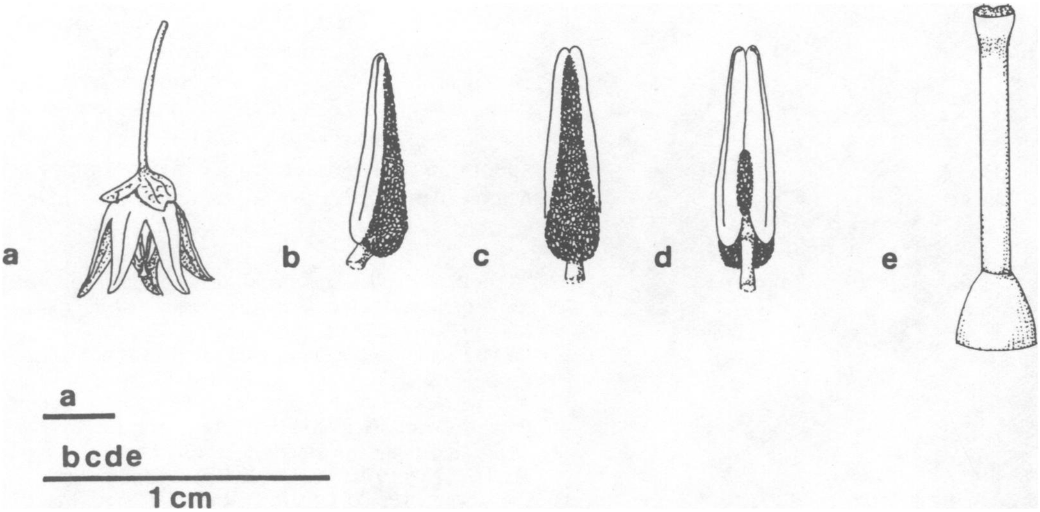


FIG. 79. *Cyphomandra tenuisetosa.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, e, based on *Klug 3873*; b, c, d, based on *Wasshausen & Encarnación 528.*

road from Tocache Nuevo to Puerto Pizano, 8° 06'S, 76° 36'W, 475 m, 19 Dec 1981 (fl), *Plowman & Schunke 11495* (F, GH); Dist. Campanilla, Río Sión, SW of village of Sión, 5 Oct 1969 (fl), *Schunke 3481* (F, G, NY, US); Dist. Tocache Nuevo, road to Pueblo Viejo from Tocache, 18 Jan 1970 (fl, fr), *Schunke 3736* (F, G, NY, US); Quebrada de Huaquisha (right bank of Río Huallaga), 400–450 m, 1 Jul 1974 (fl), *Schunke 7085* (GH); Quebrada de Mantención (E of bridge), 500 m, 27 Jul 1974 (fl, fr), *Schunke 7806* (GH); Prov. Lamas, Dist. Alonso de Alvarado, San Juan de Pacaizapa, km 72 on Tarapoto-Moyobamba road, 1000–1050 m, 9 Jun 1977 (fl), *Schunke 9668* (MO, U).

BRAZIL. Acre: Mun. de Sena Madureira, road from Bonsucesso km 7, left bank of Rio Caeté, 10 Jan 1980 (fr), *Cid & Nelson 2659* (NY); vic. km 7, road Sena Madureira to Rio Branco, 10 Sep 1968 (fr), *Prance et al. 7683* (NY, U, WIS).

Local names and uses. Peru: Chupo sacha macho (*Schunke 10465*), chupo sacha silvestre (*Plowman & Schunke 11495*), gallinaso huasca (*Schunke 3481*), huasca chuposacha (*Schunke 7806*), pepino del campo (*Mexia 8209*). The leaves stain bluish-black (*Woytkowski 7406*).

This species can be recognized by its rather large calyces, large campanulate corollas, and the abundant long hairs found on the vegetative parts. Many specimens have distinctive two- or three-lobed leaves.

Some collectors have described *C. tenuisetosa* as being a vine, and very young plants do have twining stems. When older, though, a weakly woody trunk is formed and tiers of spreading branches develop as is typical for many other species in the genus. It is likely that these spreading branches do not really twine, but sprawl across the surrounding vegetation. The growth habit of mature plants needs to be investigated in more detail in the field, for if *C. tenuisetosa* is indeed a vine, it is unique in the genus in this respect.

The affinities of *C. tenuisetosa* are unclear, but its campanulate corolla, large calyx, and slightly dilated style suggest a relationship with *C. pendula. Cyphomandra tenuisetosa* also resembles *C. pilosa* and *C. foetida* in its copious long hairs, but differs from these two species in flower and fruit characters. The large calyx, campanulate corolla, and lobed trunk leaves may also indicate a relationship with *C. oblongifolia*, but the two species differ in pubescence, leaf shape, and anther morphology.

Bitter cites two sheets of *Ule 9753* in the protologue, both of which were presumably lost in Berlin during World War II. Photographs of this type are extant, and owing to the distinctive leaf form often seen in this species, the identity of the name *C. tenuisetosa* is clear from these photo-

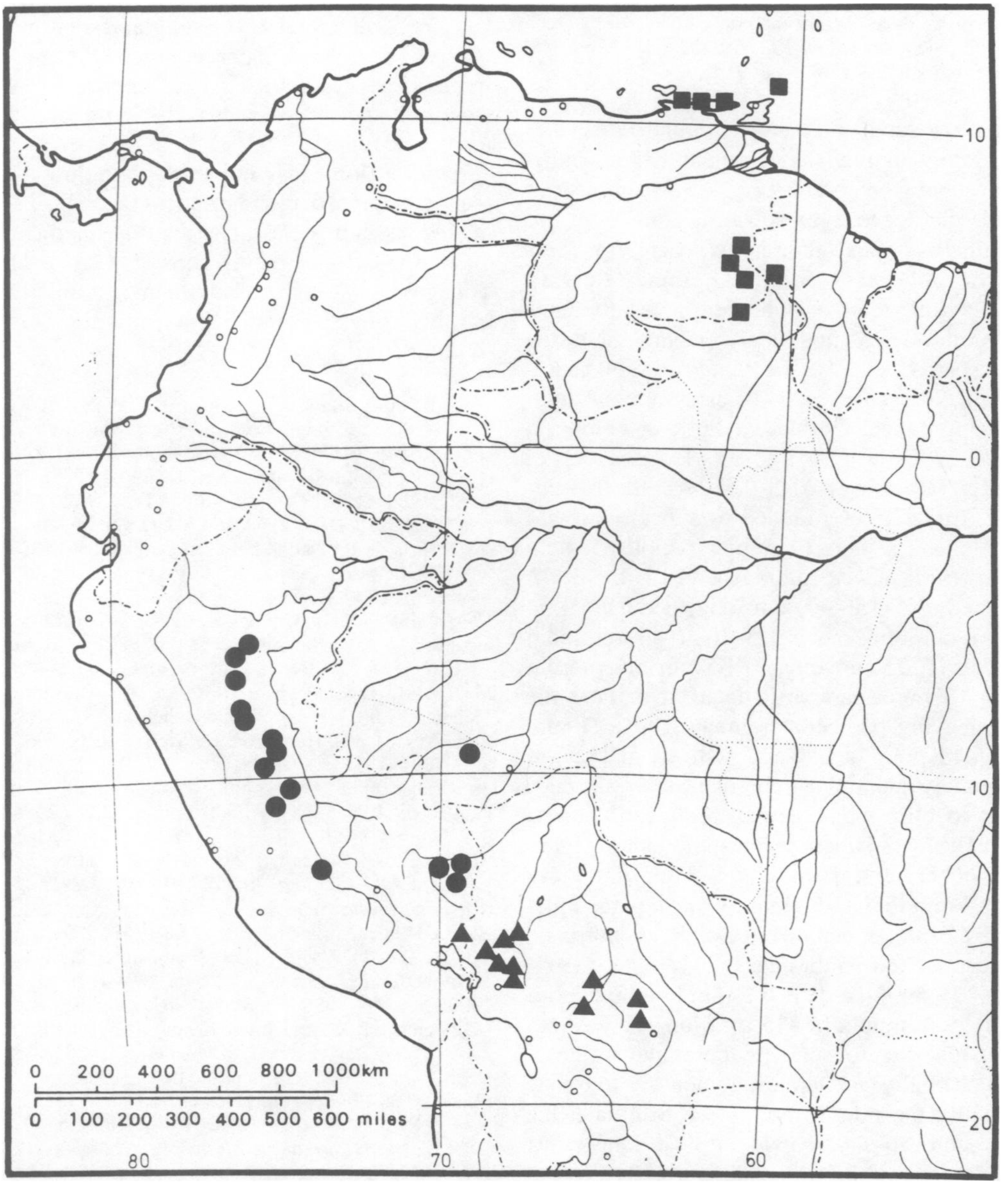


FIG. 80. Distributions of *C. tenuisetosa* (dots), *C. tobagensis* (squares), and *C. uniloba* (triangles).

graphs. No duplicates of the Ule collection have been found, so a neotype has been selected.

31. Cyphomandra tobagensis Sandwith, Kew Bull. **9:** 370. 1938. Type. Tobago. Englishman's Bay near Parlatuvier, "plant shrubby, flowers have a disagreeable penetrating odor, fruit *Passiflora*-like," 15 Apr 1912 (fl, fr), *Broadway 3879* (holotype, K). Fig. 81.

Cyphomandra bolivarensis Steyermark, Bol. Soc. Venez. Ci. Nat. **26:** 441, fig. 10. 1966. Type. Venezuela. Bolívar: woods in draw, on summit, Sororopan-tepui, "branching herb 5–6 ft tall, flowers with odor of dung, pendent, corolla lobes white, anthers lilac, tipped brownish, leaves firmly membranaceous, deep green above, pale green below," 2225- 2255 m, 13 Nov 1944, *Steyermark 60094* (holotype, VEN, n.v.).

Shrub or small *tree* 2–5(–10) m tall. *Branches* moderately glandular-puberulent when young, glabrescent when older. *Leaf blades* simple, unlobed, chartaceous to subcoriaceous, acute to acuminate at apex, glabrate to sparsely puberulent or pubescent adaxially, moderately to densely puberulent or pubescent abaxially; petioles glabrous to moderately puberulent, often with stalked glands. *Trunk leaves* not represented. *Crown leaves* 3–4 per sympodial unit, simple, unlobed, the blade elliptic or oblong to ovate, 5–23 cm long, 3–11.5 cm wide, length:width ratio (1–)1.5–2.5(–3):1, the base cuneate, truncate, or rounded to subcordate with basal lobes less than 1 cm long; petioles 1–4 cm long. *Inflorescence* unbranched, 15–40(–100)-flowered, 3.5–15(–47) cm long; peduncle 1.5–3.5(–6) cm long; rachis 1.5–10.5(–44) cm long; pedicels 15–25 mm long, 20–35 mm long in fruit, 1–3(–10) mm apart, articulated at or near the base, leaving pedicellar remnants up to 1 mm long; peduncle, rachis, and pedicels glabrate to moderately glandular-puberulent. *Flower buds* ovoid to ellipsoidal, acute or obtuse at apex. *Calyx* fleshy or subcoriaceous, moderately glandular-puberulent, the radius 2–3 mm, the lobes 0.5–1.5 mm long, 1.5–2 mm wide, deltate, apiculate. *Corolla* green, white, pink, or purplish, chartaceous to membranaceous, stellate, the radius 9–16 mm, the tube 1–2 mm long, the lobes narrowly triangular, 8–15 mm long, 2–2.5 mm wide, glabrate to sparsely puberulent(-pubescent) abaxially, moderately tomentose to ciliate adaxially, the margin tomentose to ciliate, the apex acute. *Anther thecae* purplish, lanceolate, 5–6 mm long, 1–1.5 mm wide, the pores directed distally; connective purple, lanceolate, 5–6 mm long, 0.5–1 mm wide at base, abaxially nearly equal to thecae at apex, slightly exceeding them at base by 0.5–1 mm, adaxially present as a linear swelling near base of thecae. *Ovary* glabrous or glandular-puberulent; style cylindrical, glabrous, not to very slightly dilated distally, 5–8 mm long, 0.5–1 mm in diam., exserted 1–2 mm beyond stamens; stigma truncate, 0.5–1 mm in diam. *Fruits* ellipsoidal to fusiform, acute at apex, 3–7 cm long, 1.5–3 cm in diam., sparsely to moderately puberulent when young, glabrescent when older, light green with darker green stripes when immature, yellow when ripe; mesocarp with stone cell aggregates; seeds 3.5–5 mm long, 3–4 mm wide, rugose.

Distribution (Fig. 80) and phenology. Primary wet forest or cloud forest, 400–1300(–2255) m elev., eastern Venezuela (distribution disjunct due to the Orinoco delta), adjacent Guyana, and Tobago. Flowering and fruiting most prolifically in July through December, but continuing at least through April.

Additional specimens examined. VENEZUELA. **Bolívar:** Dist. Sifontes, bosques en la base de los tepuyes (Peraytepuy y Guytepuy) del sector "La Hoyada" (Parytepuy), 7 km NW del Caserío "El Pilón,", 58 km W de Sta. Elena de Uairén, ca. 4° 40'N, 61° 33'W, 850–1100 m, 23 Oct 1986 (fl), *Aymard 4782* (MO), (fl, fr) *4799* (MO); Fila de La Danta, between campamento 125 and km 127, between Luepa and Cerro Venamo, 1200 m, 15–17 Apr 1960 (fl, fr), *Steyermark & Nilsson 183* (NY, US); drainage of Río Cuyuní, along Río Anawaray-parú, vic. km 134 and campamento 134 S of El Dorado, 1300–1350 m, 25 Dec 1970 (fl, fr), *Steyermark et al. 104421* (F, M, NY, U). **Sucre:** Peninsula de Paria, Dist. Mariño, entre Manacal y Los Pocitos de Santa Isabel, ca. 25 km NW de Irapa, W de Cerro Humo, 62° 38'W, 10° 40'N, 700–900 m, 9–10 Jul 1972 (st), *Dumont et al. 7489* (NY); Peninsula de Paria, Cumbre La Estrella, W of Manacal, N of El Paujil, 10° 40'N, 62° 41'W, 800–850 m, 17 Oct 1984 (fl, fr), *Knapp & Mallet 6762* (BH, NY, US); entre Manacal y Los Pocitos de Sta. Isabel, 25 km NW of Irapa, 62° 38'W, 10° 40'N, 700–900 m, 9–10 Jul 1972 (st), *Morillo 2551* (F); Peninsula de Paria, Cerro Patao, N de Puerto de Hierro, NE de Guiria, 1020 m, 19 Jul 1962 (fl, fr), *Steyermark & Agostini 91077* (K, US); Peninsula de Paria, Cerro de Humo, entre La Laguna y Roma, NW de Irapa, 800–1000 m, 5 Mar 1966 (fl), *Steyermark 95044* (F, K, NY, US); Peninsula de Paria, Cerro Espejo, 700–750 m, 6 Aug 1966 (fl, fr), *Steyermark & Rabe 96064* (G, GH, NY, S, US); Peninsula de Paria, Cumbre de Las Estrellas, W of Manacal, ca. 15 km (by air) NW of Irapa, E of El Sanche, N of El Paujil, 10° 40'N, 62° 40'W, 800–830 m, 30 Nov 1979 (fl, fr), *Steyermark & Liesner 120808* (MO, NY).

TOBAGO. Parlatuvier-Roxborough trace, Bloody Bay to road-head above Roxborough, 550 m, 8 Apr 1959 (fl, fr), *Cowan 1476* (GH, NY, US); Bloody Bay-Roxborough road, 550 m, 10 Jan 1970 (fr), *Kalloo B1061* (NY); Roxborough-Parlatuvier road, near 5th milepost, 1300 ft, 14 Oct 1937 (fl), *Sandwith 1773* (K); Roxborough-Parlatuvier road, between 4th and 5th mileposts, ca. 1200–1400 ft, 20 Aug 1959 (fl, fr), *Webster et al. 9802* (A, S, TEX, U, US).

GUYANA. W side of Kamarang River, Utschi mouth, 24 Oct 1960 (fl, fr), *Tillett & Tillett 45781* (MO, NY, US).

Cyphomandra tobagensis belongs to the *C. hartwegii* group by virtue of its elongated anthers

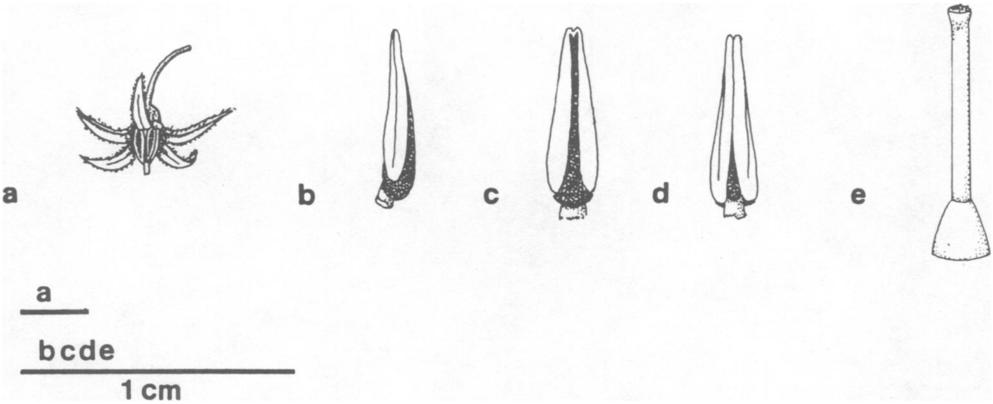


FIG. 81. *Cyphomandra tobagensis*. **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. a, based on *Steyermark & Agostini 91077*; b–e, based on *Steyermark et al. 104421*.

and style and its large seeds. No lobed leaves have yet been observed in this species. Like *C. dolichocarpa*, *C. tobagensis* has truncate to subcordate leaf bases, tomentose to ciliate corolla margins, and acute fruits. The puberulent fruits of *C. tobagensis* distinguish it from *C. dolichocarpa*. In addition, the leaves of *C. dolichocarpa* appear to be larger and more coriaceous than those of *C. tobagensis*, and *C. dolichocarpa* is restricted to Central America, whereas *C. tobagensis* is found only in northern South America. *Cyphomandra tobagensis* is also similar to *C. hartwegii*, and is distinguished from it by its exclusively unlobed leaves with truncate to subcordate bases, and its puberulent, acute fruits. The taxonomic distinctions between the species of the *C. hartwegii* complex are problematical, and the validity of the recognized species and their relationships with each other need to be investigated more intensively.

Cyphomandra tobagensis has a disjunct distribution, and some morphological differentiation seems to have taken place between the two areas. *Steyermark & Nilsson 183* and *Steyermark & Dunsterville 104421*, both from Edo. Bolívar, Venezuela, have a much denser and longer indumentum on the lower leaf surfaces than any of the other collections. In general, the collections from Edo. Bolívar and Guyana have longer inflorescences than those from Tobago and coastal Venezuela. Examples of other plant taxa showing disjunct distributions between coastal Venezuela and lowland forests to the south are given by Steyermark (1979, 1982).

The specimen of *Broadway 3879* at K is annotated by Sandwith as "Typus!" No duplicates of this collection have been found in other herbaria. Accordingly, I consider this specimen the holotype in spite of the fact that Sandwith did not specify the location of the type as K in the protologue.

32. Cyphomandra uniloba Rusby, Mem. Torrey Bot. Club **6:** 90. 1896. Type. Bolivia. La Paz: Mapiri, Jul-Aug 1892 (fl), *Bang 1535* (lectotype, NY, here designated; isolectotypes, A, BM, E, F, G, GH, K, M, MO, NY, US, WIS). Figs. 82, 83.

Small *tree* 2–6 m tall. *Branches* glabrescent to moderately puberulent. *Leaf blades* simple, unlobed, chartaceous to subcoriaceous, acute to acuminate at apex, sparsely to moderately puberulent adaxially, more so on veins, glabrescent to sparsely puberulent abaxially; petioles glabrous to moderately puberulent. *Trunk leaves* simple, unlobed, the blade ovate, 18–25 cm long, 10–18 cm wide, the length:width ratio ca. 1.5:1, the base cordate to almost truncate with basal lobes 1–2 cm long; petioles 8–15 cm long. *Crown leaves* 4 per sympodial unit, simple, unlobed, the blade ovate, 6–20 cm long, 4–14 cm wide, the length:width ratio 1–2:1, the base cordate to almost truncate with basal lobes 0.3–2 cm long; petioles 2–8 cm long. *Inflorescence* unbranched or branched, 20–100+ -flowered, 5–16 cm long; peduncle 2–5.5 cm long; rachises 3–15 cm long; pedicels 10–15 mm

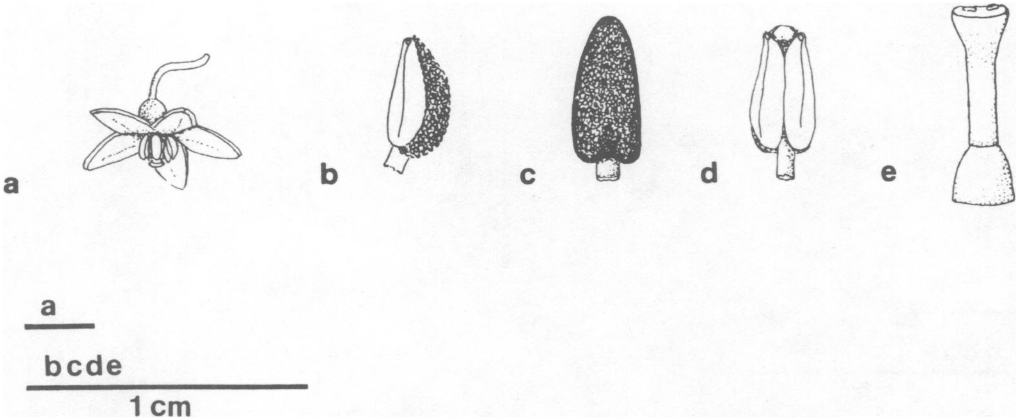


FIG. 82. *Cyphomandra uniloba.* **a.** Flower. **b–d.** Stamens (b. side view. c. abaxial view. d. adaxial view.). **e.** Gynoecium. All based on greenhouse material of *Sperling & King 5500.*

long, 25–40 mm long in fruit, 2–6 mm apart, articulated slightly above the base, leaving pedicellar remnants 1–3 mm long; peduncle, rachises, and pedicels glabrous to glandular-puberulent. *Flower buds* globose to ellipsoidal, obtuse at apex. *Calyx* fleshy, glabrate to puberulent, the radius 4–7 mm, the lobes 1–2 mm long, 2.5–4 mm wide, shallowly triangular, obtuse. *Corolla* green or yellow-green, coriaceous, stellate, the radius 10–15 mm, the tube 2–4 mm long, the lobes narrowly triangular, 8–12 mm long, 3–5 mm wide, glabrous abaxially, puberulent adaxially, especially toward apices, the margin tomentose, the apex acute. *Anther thecae* white, oblong, 3–5 mm long, 1.5–2.5 mm wide, the pores directed adaxially and somewhat laterally; connective yellow to yellow-orange or brown, oblong, 3–4.5 mm long, 1–2 mm wide, abaxially slightly exceeding thecae and bent over tip into an adaxial projection, equal to or shorter than thecae at base, adaxially absent. *Ovary* glabrous; style cylindrical, glabrous, dilated distally, 5–6 mm long, 1–1.5 mm in diam., exserted 0–2 mm beyond stamens; stigma subpeltiform, convex, biglandular, ca. 2–3 mm in diam. *Fruit* ellipsoidal to ovoid, acute at apex, 4–5 cm long, 2–3 cm in diam., glabrous (glandular-puberulent in *Fleischmann 157*), yellow or orange with dark green or purple longitudinal stripes; mesocarp with or without stone cell aggregates; seeds 3.5–4 mm long, 3–4 mm wide, densely pubescent.

Distribution (Fig. 80) and phenology. Moist forest in Bolivia and southern Peru on eastern slopes of the Andes and adjacent lowlands, 300–1700 m in elevation. Flowering specimens have been collected in March, June, July, August, October, and November. Fruiting specimens have been collected in January through March, July, and October through December.

Additional specimens examined. PERU. PUNO: near San Juan de Oro, 1400 m, 23 Oct 1976 (fl), *Bernardi et al. 16817* (MO).

BOLIVIA. BENI: Rurrenabaque, 1000 ft., 7 Oct 1921 (fr), *Cárdenas 1555* (NY); Vic. Reyes, Rurrenabaque on the Río Beni, 10 Dec 1930 (fl, fr), *Fleischmann 155* (S), *157* (S). **COCHABAMBA:** Antahuacana, Espírito Santo, ca. 160 km NE of Cochabamba, 750 m, Jun 1909 (fl), *Buchtien 2233* (NY, US); Prov. Chapare, road to Todos Santos, 120 km NE of Cochabamba, near Chimore, S side of Río San Mateo, 800 m, 10 Mar 1939 (fr), *Eyerdam 24747* (F, K); Prov. Chapare, Todos Santos, 300 m, 25 Oct 1966 (fl), *R. F. Steinbach 436* (F, GH, MO, NY, S, U, US, WIS). **LA PAZ:** Prov. Murillo, 55 km NNE in a straight line from La Paz, Valle de Zongo, Cahua (end of the road), 1450–1550 m, 1 Feb 1981 (fr), *Beck 6079* (ECON); Prov. Nor Yungas, N of Caranavi, above Carrasco, 1550 m, 1 Jul 1983 (fr), *Beck 9284* (GH); Polo-Polo near Coroico, Nordyungas, 1100 m, Oct-Nov 1912 (st), *Buchtien 3900* (E, G, US); Prov. Nor Yungas, 10 km by road N and above Caranavi, ca. 15° 47'S, 67° 32'W, 1400 m, 1 Nov 1984 (fr), *Nee & Solomon 30301* (MO); Prov. Nor Yungas, 4.6 km below Yolosa, then 19.1 km on road up the Río Huarinilla, 16° 12'S, 67° 53'W, 1700 m, 12 Nov 1982 (fl, fr), *Solomon 8792* (MO); Prov. Nor Yungas, Serranía de Bella Vista, 16 km N of Carrasco (37 km N of Caranavi) on road to Palos Blancos, 15° 35'S, 67° 34'W, 1500 m, 31 Oct 1984 (fl, fr), *Solomon & Nee 12717* (MO); Prov. Larecaja, near trail along the Río Consata between villages of Consata and Mapiri, 68° 20'W, 15° 15'S, 1350 m, 17 Dec 1981 (fr), *Sperling & King 5500* (GH); San Buena

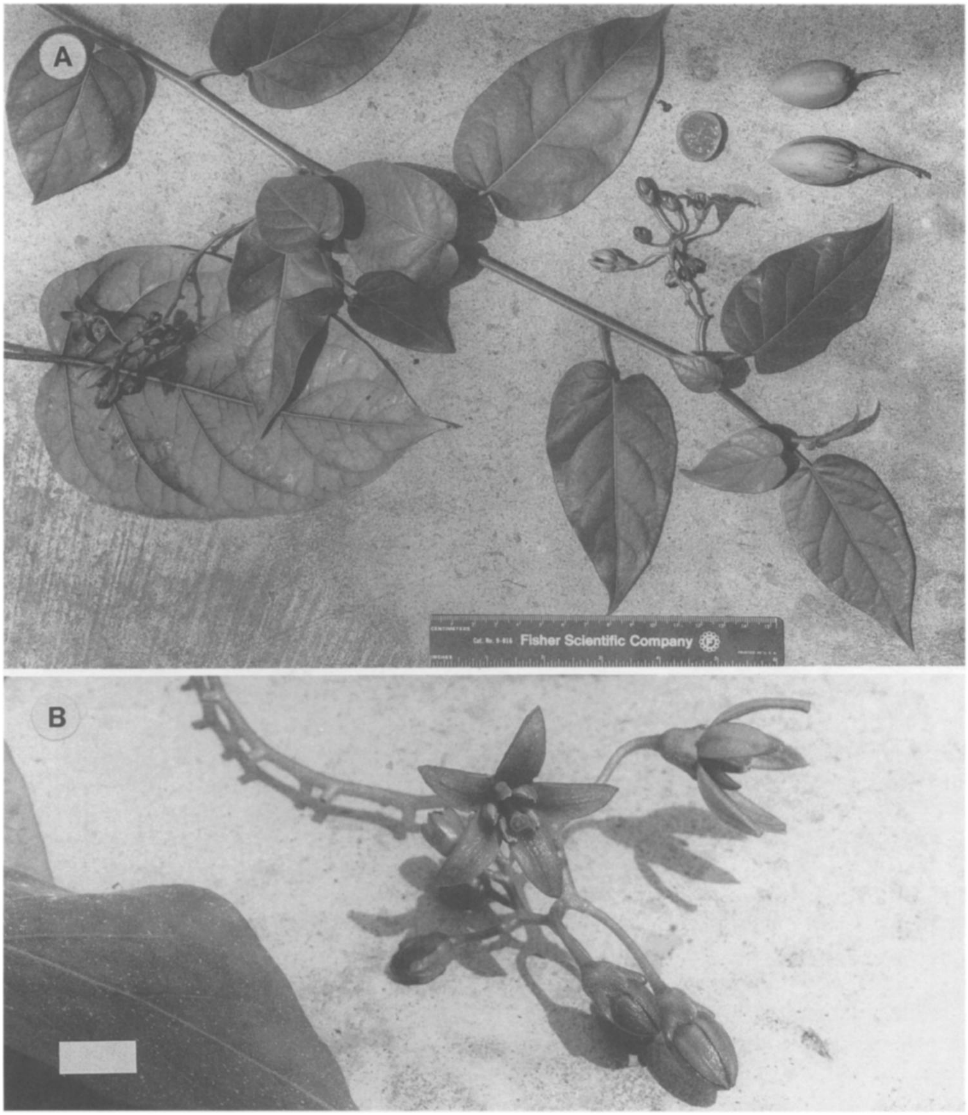


FIG. 83. *Cyphomandra uniloba.* **A.** Trunk leaf, crown branch with inflorescence, and fruits. **B.** Inflorescence. Scale bar = 1 cm. From greenhouse material of *Sperling & King 5500.*

Ventura, 1500 ft, 29 Nov 1901 (fl, fr), *R. S. Williams 373* (BM, K, NY, US). Santa Cruz: Prov. Ichilo, Estancia San Rafael de Amboro, 15 km (by air) SSE of Buena Vista, 17° 35'S, 63° 37'W, 375 m, 28 Jul 1987 (fl, fr), *Nee et al. 35368* (NY); Prov. Ichilo, W side of Río Surutu across from "Terminal" area of Huaytu, 16 km (by air) S of Buena Vista, 17° 36'S, 63° 38'30"W, 350 m, 2 Aug 1987 (fl), *Nee 35491* (NY); Prov. Ichilo, between Río Chonta (Río Ancho) and Río Saguayo, Parque Nacional Amboro, 17° 39'S, 63° 42'W, 425 m, 22 Jan 1988 (fr), *Nee & Saldias 36047* (NY); Prov. Sara, Buenavista, 500 m, 1–30 Mar 1921 (fl), *J. Steinbach 5382* (A, F, MO, NY); same locality, 9 Jul 1924 (fl), *J. Steinbach 6217* (A); Río Surutú, 400 m, 2 Oct 1924 (fl), *J. Steinbach 6544* (A). Without Department: Calopampa, 11 Jul 1894 (fl), *Bang 2337* (BM, F, G, GH, K, MO, NY, US)(a mixed collection; the other element is *C. betacea*).

Local names and uses. Bolivia: Tomate de monte (*Nee et al. 35368*; *Steinbach 436*).

Fruits grown in the greenhouse at the University of Vermont were acid, sweet, and juicy and may be a substitute for the tree tomato, *C. betacea*. Others (*Nee & Solomon 30301*) report that the fruits are pleasant-tasting but leave a bitter aftertaste. The leaves said to be used as kidney medicine in Santa Cruz, Bolivia (*Nee et al. 35368*).

This species belongs to the *C. obliqua* group because of its expanded stigma, short thick anthers, and coriaceous, stellate corolla. It most closely resembles *C. acuminata*; both species are nearly glabrous and have similar anthers and gynoecia. *Cyphomandra uniloba* may be distinguished from *C. acuminata* by its relatively broader leaves, greenish rather than reddish corollas, and smaller seeds. The two species are often nearly impossible to distinguish on herbarium sheets when mature fruits are not present. Both occur in the Bolivian uplands.

Cyphomandra uniloba also resembles *C. obliqua* from the eastern Andean slope of Peru. It differs from the latter species in its nearly glabrous leaves and broadly spaced pedicels articulated above the base.

Three collections show some anomalous features. *Fleischmann 157* has pointed, glandular-puberulent fruits, unlike the glabrous ones usually seen in *C. uniloba*. *Williams 373* and *Bernardi et al. 16817* are rather densely puberulent on the vegetative parts, thus resembling *C. obliqua* more than *C. uniloba*. All these collections occur well within the distributional range of typical *C. uniloba*, and they are here considered as that species.

Cyphomandra uniloba will form hybrids with *C. betacea* in greenhouse crosses (Bohs, 1991). The two species are very similar vegetatively, but they differ in corolla and fruit color and in the morphology of the stamens and gynoecium. The occurrence or extent of natural hybridization between the two species is unknown.

INSUFFICIENTLY KNOWN TAXA

The following taxa probably represent new species of *Cyphomandra*, but the available material does not provide enough details of their essential characteristics. They will be described in a later publication if better material is collected.

1. Unnamed taxon 1

Shrub or small *tree* 1–2.5 m tall. *Branches* densely pubescent. *Leaf blades* simple, unlobed, chartaceous, acuminate at apex, sparsely to moderately pubescent adaxially, moderately to densely pubescent abaxially; petioles densely pubescent. *Trunk leaves* unknown. *Crown leaves* simple, unlobed, the blade elliptic, 10–20 cm long, 5–11 cm wide, length:width ratio 2–2.5:1, the base truncate, tapered or rounded, without basal lobes; petioles 0.5–2 cm long. *Inflorescence* unbranched, 20–45-flowered, 12–42 cm long; peduncle (3–)6–15 cm long; rachis 4.5–27 cm long; pedicels 5(–10) mm long, 10–20 mm long in fruit, 2–10 mm apart, articulated at the base, leaving pedicellar remnants up to 1 mm long; peduncle, rachis, and pedicels moderately to densely pubescent. *Flower buds* unknown. *Calyx* chartaceous, moderately to densely pubescent, the radius 2 mm, the lobes 1–3 mm long, 1–2 mm wide, deltate to narrowly triangular, acute. *Corolla* lilac, white, cream or green, chartaceous, moderately puberulent abaxially. *Fruit* ellipsoidal, ca. 3–5 cm long, 1.5–4 cm in diam.; seeds 5–6(–8) mm long, 4–5(–8) mm wide, glabrate to densely pubescent.

Specimens examined. COLOMBIA. AMAZONAS: márgen izquierda del Río Amazonas, 3 km arriba de Leticia, 100 m, 12 Oct 1961 (fr), *Idrobo 4737* (COL); Río Caquetá, Isla de Mirití, 160 m, 1 Jun 1984 (fr), *Jaramillo et al. 7998* (COL). **CHOCÓ:** slopes of Serranía del Darién E of Unguia, 300–1300 m, 19 July 1976 (fl), *A. Gentry et al. 16771* (COL).

FRENCH GUIANA. Route Regina-Saint Georges D.Z.5-P.K.43, Bassin du Ba, 52° 1'W, 4° 3'N, 20 m, 8 Apr 1991 (fl, fr), *Cremers & Gautier 12071* (NY).

PERU. LORETO: Yanomono, Explorama Tourist Camp, trail to Río Napo, 72° 48'W, 3° 25'S, 130 m, 19 Feb 1981 (fr), *A. Gentry et al. 31535* (MO); same locality, 72° 50'W, 3° 22'S, 120 m, 22 Mar 1982 (st), *A. Gentry et al. 36553* (MO); same locality, 72° 48'W, 3° 28'S, 130 m, 25 Jun 1982 (fl, fr), *A. Gentry et al. 37193* (MO); Mishuyacu, near Iquitos, 100 m, Oct-Nov 1929 (fr), *Klug 93* (F, NY, US); Prov. Maynas, Puerto Almendras, Río Nanay above Iquitos, 73° 25'W, 3° 50'S, 120 m, 17 Apr 1980 (fl, fr), *Vásquez & Jaramillo 174* (MO); Prov. Maynas, Yanamono tourist camp, 50 mi NE of Iquitos, 3° 30'S, 72° 50'W, ca. 106 m, 18 Oct 1980 (fl, fr), *Vásquez & Jaramillo 547* (MO).

BRAZIL. MARANHÃO: FUNAI, 40 km from city of Arame, 13 Mar 1983 (fr), *Vilhena et al. 1016* (GH).

This taxon is distinctive in its elliptical leaves with truncate bases, abundant vegetative pubescence, and very long, slender inflorescences. Fruits of the Brazilian collection are pubescent, blunt at the apex, and have obvious rounded stone cell aggregates. All other collections have glabrous pointed fruits without obvious stone cell aggregates. All flowering collections except *Vásquez & Jaramillo 174* and *Cremers & Gautier 12071* have urceolate corollas with tubes ca. 6 mm long and deltate lobes ca. 3–5 mm long and wide. *Vásquez & Jaramillo 547* has a style that is dilated distally into a truncate stigma ca. 1 mm in diameter. In other collections, the style is apparently not dilated distally and the stigma is the same diameter as the style. *Vásquez & Jaramillo 174* and *Cremers & Gautier 12071* have stellate corollas with tubes only 1–3 mm long and narrowly triangular lobes ca. 10–13 mm long and 1–3 mm wide. The anthers are long and slender (ca. 5–7 × 0.5–1.5 mm) and the narrow style is not dilated distally. More than one element may be represented by these collections. Because of these apparent conflicts in floral and fruiting characters, I am not confident in describing this taxon as a new species.

2. Unnamed taxon 2

Shrub 3 m tall. *Branches* densely puberulent. *Leaf blades* simple, unlobed, chartaceous, acute at apex, moderately to densely puberulent adaxially and abaxially, more so on veins; petioles densely puberulent. *Trunk leaves* (only one seen) simple, unlobed, the blade ovate, 34 cm long, 23 cm wide, length:width ratio ca. 1.5:1, the base cordate with basal lobes 2–3 cm long; petiole 19 cm long. *Crown leaves* simple, unlobed, the blade ovate or elliptic, 8.5–28 cm long, 7.5–19 cm wide, length:width ratio ca. 1–1.5:1, the base cordate with basal lobes up to 1(–3) cm long; petioles 1.5–10 cm long. *Inflorescence* forked, 10–30-flowered, 3–4 cm long; peduncle 2–3 cm long; rachis 0.5–1.5 cm long; pedicels 7–15 mm long, ca. 35 mm long in fruit, ca. 1 mm apart, articulated near the base, leaving pedicellar remnants 1–2 mm long; peduncle, rachis, and pedicels densely puberulent. *Flower buds* ellipsoidal or globose, obtuse at apex. *Calyx* subcoriaceous, densely puberulent-pubescent, the radius 3 mm, the lobes 1.5 mm long, 2–2.5 mm wide, deltate, apiculate. *Corolla* olive green within, subcoriaceous, stellate, the radius ca. 7 mm, the tube ca. 1 mm long, the lobes narrowly triangular, ca. 6 mm long, 2–2.5 mm wide, abaxially glabrous at base, densely tomentose to villous toward apex, adaxially glabrous with a few hairs near apex, the margin tomentose, the apex acute. *Anther thecae* dull yellow, ovoid to oblong, ca. 4 mm long, ca. 2.5 mm wide, the pores directed laterally; connective oblong, ca. 4 mm long, 1–1.5 mm wide, abaxially shorter than thecae at apex. *Style* obconical, strongly dilated distally, 0.5–1 mm in diam. at base; stigma peltiform with two apical glands, 2 mm in diam. *Fruit* ovoid, acute at apex, 3.5–4 cm long, 1.5–2.5 cm in diam., densely puberulent.

Specimens examined. VENEZUELA. MIRANDA: Guinand Estate (Cárdenas), Siquire Valley, 500–1000 m, 19–24 Mar 1913 (fl), *Pittier 5987* (MO, NY, US). **PORTUGUESA:** along Cerro Seco, cloud forest contiguous with Cerro Córdoba, 17–20 km E of Chabasquén, 9° 26–27'N, 69° 54–55'W, 1520 m, 31 Oct 1982 (fr), *Steyermark & Liesner 126896* (MO, NY).

This taxon is known only from two collections from northern Venezuela, one in fruit and the other with a single mature flower. This is probably the species pictured in Fig. 17 of Benitez de Rojas (1974). It is probably allied to *C. rojasiana* from Central America. Characters in common include stellate coriaceous corollas, broadly expanded stigmas, dense vegetative puberulence, short inflorescences with nearly contiguous pedicel scars, and puberulent fruits.

DOUBTFUL NAMES

Cyphomandra argentea Bull, Catalogue of New, Beautiful, and Rare Plants, 3. 1880. Type. Unknown.

This name is validly published in a seed catalogue (Greuter et al., 1988), but no specimens are extant and the description does not suffice to identify the species in question.

Cyphomandra cornucopia Dunal *in* DC. Prodr. **13(1):** 400. 1852. Type. Brazil. Prov. São Paulo, *Gaudichaud 46* (holotype, P [F neg. 39256 F, WIS]).

The type is a poor specimen that lacks fruits or flowers. The shoot architecture, with the leaves

FIG. 84. Plate 96 from Icones of Vellozo's *Flora Fluminensis* showing *Solanum conicum* Vell.

paired and very unequal in size and the inflorescences in the axils of the leaf pairs, does not suggest *Cyphomandra*, but a positive placement of this species cannot be made on the basis of such scanty material.

Solanum fluminense Steudel, Nom. Bot. p. 602. 1841, nom. nov. for *Solanum conicum* Vellozo.

Solanum conicum Vellozo, Fl. Flumin. **2:**83. 1829 (text); **2:** Tab. 96. 1831 (Icones), non *Solanum conicum* Ruiz & Pavón (1799). Type. Brazil. Prov. Rio de Janeiro, "habitat campis apricis mediterraneis ad Praedium derelictum vulgo dictum Paricão, floret Jul. Aug.," *Vellozo s.n.* (No specimen extant; Plate 96 from Vellozo's *Flora Fluminensis* is chosen here as the lectotype. Fig. 84).

The unfortunate fact that none of Vellozo's type specimens are in existence prevents the unequivocal identification of many of his taxonomic entities. Plate 96 of Vellozo's *Flora Fluminesis* definitely represents a *Cyphomandra*, but it is not possible to positively establish its identity. Plate 96 could represent either *Cyphomandra sciadostylis*, *C. diploconos*, or *C. calycina*, all of which have expanded stigmas and pubescent stems and leaves. The plate most closely resembles *C. sciadostylis*, which has pointed fruits like the illustration, but the distinctive pubescent style of *C. sciadostylis* is not pictured in the plate nor mentioned in Vellozo's protologue. Furthermore, *C. sciadostylis* has not been documented as occurring in the state of Rio de Janeiro. *Cyphomandra calycina* also has pointed fruits and pubescent stems and leaves, but the illustration does not emphasize the extremely large calyx of this species, its outstanding distinguishing feature. The plate could also represent *C. diploconos*. Pubescent collections of this species have been found in Rio de Janeiro, but the leaves are usually not as deeply cordate at the bases and the fruits are generally obtuse rather than acute at the apices.

Cyphomandra velloziana Sendtner, Flora **28:** 175. 1845, nom. nov. for *Solanum elegans* Vellozo.

Solanum elegans Vellozo, Fl. Flumin. **2:** 83. 1829 (text); **2:** Tab. 95. 1831 (Icones), non *Solanum elegans* Dunal (1813). Type. Brazil. Presumably Rio de Janeiro, "habitat tum mediterraneis, cum maritimis, floret Jan. Jul.," *Vellozo s.n.* (No specimen extant; Plate 95 of Vellozo's *Icones* is here designated as the lectotype [Fig. 85]).
Solanum arrabidae Steudel, Nom. Bot., ed. 2. **2:** 600. 1841, nom. nov. for *Solanum elegans* Vellozo.

The identification of Vellozo's Plate 95 is problematical. Pictured is a plant with pubescent stems, leaves, petioles, and inflorescence axes, deeply cordate leaves, unbranched inflorescences, flowers with slender styles and truncate, unexpanded stigmas, and ellipsoidal, obtuse fruits. Its general appearance is that of a *Cyphomandra*. Most likely it corresponds to *C. premnifolia*, a species known from Rio de Janeiro. *Cyphomandra premnifolia* has dense pubescence, deeply cordate leaves, unbranched inflorescences, and ellipsoidal or globose fruits (in the Rio de Janeiro region). The illustration does not picture the obconical (but still relatively slender) style and stigma, the usually prominent and long pedicellar remnants, and the pubescent fruits that are characteristic of *C. premnifolia*.

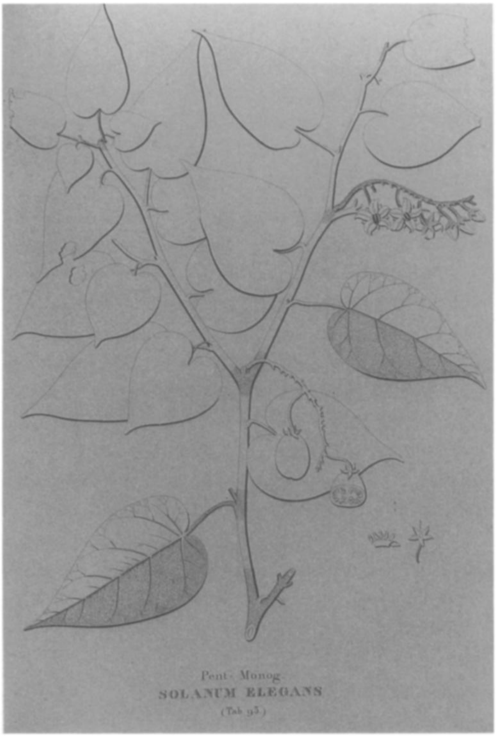


FIG. 85. Plate 95 from Icones of Vellozo's *Flora Fluminensis* showing *Solanum elegans* Vell.

Without an actual specimen at hand, it seems the most prudent course to regard Vellozo's *Solanum elegans* as a name of uncertain affinity.

Cyphomandra viridiflora (Ruiz & Pavón) Sendtner, Flora **28:** 175. 1845.

Solanum viridiflorum Ruiz & Pavón, Fl. Peruv. **2:** 38, pl. 173, fig. b. 1799. Type. Peru. "Ad Sancti Antonii de Playa grande vicum," *Ruiz & Pavón* (no specimen located).

Pionandra viridiflora (Ruiz & Pavón) Miers, London J. Bot. **4:** 359. 1845.

Ruiz and Pavón describe and figure this species in their *Flora Peruviana* (1799) (Fig. 86) and state that it is allied to *Solanum pendulum* (= *Cyphomandra pendula*), but that it differs from the latter in having unlobed leaves and pubescent fruits. A search of the holdings at MA failed to turn up a sheet of this species. Miers (1845) reported seeing a specimen of *C. viridiflora* in herb. Hooker, but no specimens were found after a search at K. I cannot identify this taxon without type specimens.

Though Hemsley (1882) and Pittier (1908) mention *C. viridiflora* in Central America, they are almost certainly referring to *C. hartwegii.*

Papaya tunariensis O. Kuntze, Rev. Gen. **3,** part 2: 102. 1898. Type. Bolivia. Cochabamba: Tunari, 3000 m, *Kuntze s.n.* (US).

Although originally described by Kuntze as a species of *Papaya* and placed in the Passifloraceae, this is definitely a *Cyphomandra.* Kuntze's type has only leaves and fruits. The leaves are cordate and densely pubescent, and the fruits are large (ca. 12 × 5 cm), obovate, pubescent, and borne on thick woody inflorescences. This specimen conforms to no other species of *Cyphomandra*, but it may be identical to the problematical *C. viridiflora* (see above). *Tate 661* (NY) from Nequejahuira, Bolivia may also represent this species.

The following taxa belong to *Solanum* section *Cyphomandropsis.* The generic placement of the section is uncertain, and assignment of the section and its species to *Cyphomandra*, *Solanum*, or another taxon is deferred until systematic studies of the group are completed.

Cyphomandra section *Cyphomandropsis* (Bitter) D'Arcy, Ann. Missouri Bot. Gard. **59:** 277. 1972. Lectotype species. *Cyphomandra stuckertii* (Bitter) D'Arcy.

Solanum section *Cyphomandropsis* Bitter, Repert. Spec. Nov. Regni Veg. **12:** 461. 1913. Lectotype species. *Solanum stuckertii* Bitter, designated by Seithe, 1962.

Cyphomandra adelpha (C. Morton) Child, Feddes Repert. **95:** 295. 1984.

Solanum adelphum C. Morton, A Revision of the Argentine Species of *Solanum*, p. 185. 1976. Type. Argentina. Tucumán: Dept. Burruyacú, Cerro del Campo, 1800 m, 14 Dec 1928, *Venturi 7732* (holotype, US 1441095; isotypes, GH, S, SI, US).

Cyphomandra amotapensis (Svenson) Child, Feddes Repert. **95:** 295. 1984.

Solanum amotapense Svenson, Amer. J. Bot. **33:** 483. 1946. Type. Peru. Piura: Amotape Hills, near summit of Cerro Prieto, 2300 ft., *Haught and Svenson 11634* (holotype, BKL; isotype, US).

FIG. 86. Plate 173 from Ruiz & Pavón's *Flora Peruviana* showing *Solanum viridiflorum* (bottom).

Cyphomandra clavata (Rusby) Child, Feddes Repert. **95:** 295. 1984.

Solanum clavatum Rusby, Mem. Torrey Bot. Club **6:** 87. 1896. Type. Bolivia. Cochabamba: Mt. Tunari, *Bang 1118*. The type collection is a mixture, as noted by Morton (1944). One element, represented by specimens from E, NY, and US, belongs to *Solanum* section *Geminata*. The other element, represented by specimens at G, NY, and US, belongs to *Solanum* section *Cyphomandropsis*. This latter element was renamed *Solanum confusum* C. Morton (Morton, 1944).

Cyphomandra section *Cornigera* Child, Feddes Repert. **95:** 293. 1984. Type species. *Cyphomandra cornigera* Dunal.

Cyphomandra cornigera Dunal in DC. Prodr. **13(1):** 401. 1852. Type. Brazil. Prov. Santa Catarina, *Gaudichaud 160* (types, P [F neg. 39255 WIS], F).

Pionandra cornigera (Dunal) Miers, Ann. Mag. Nat. Hist. ser. 2, **15:** 199. 1855.

Cyphomandra maritima Smith & Downs, Phytologia **10:** 436. Plate 9, fig. 7. 1964. Type. Brazil. Santa Catarina: Mun. Pôrto Belo, Bombas, 31 Mar. 1957, *L. Smith, Reitz, & Klein 12322* (types, US, HBR, R).

Cyphomandra cylindrica (Vellozo) Sendtner in Mart. Fl. Bras. **10:** 121. 1846.

Solanum cylindricum Vellozo, Fl. Flumin. **2:** 87. 1829 (text); **2:** Tab. 119. 1831 (Icones). Type. Brazil. Rio de Janeiro, "habitat campis apricis mediterraneis," *Vellozo s.n.* (No specimen extant).

Pionandra cylindrica (Vellozo) Miers, Ann. Mag. Nat. Hist., ser. 2, **15:** 199. 1855.

Cyphomandra elliptica (Vellozo) Sendtner, in Mart. Fl. Bras. **10:** 121. 1846.

Solanum ellipticum Vellozo, Fl. Flumin. **2:** 84. 1829 (text). **2:** tab. 100. 1831 (Icones), non *Solanum ellipticum* R. Br. (1810). Type. Brazil. Rio de Janeiro, "habitat silvis maritimis Pharmacopolitanis," *Vellozo s.n.* (No specimen extant).

Pionandra elliptica (Vellozo) Miers, Ann. Mag. Nat. Hist., ser. 2, **15:** 199. 1855.

Solanum johannae Bitter, Repert. Spec. Nov. Regni Veg. **12:** 465. 1913, nom. nov. for *Cyphomandra elliptica* (Vellozo) Sendtner.

Cyphomandra fusiformis (Smith & Downs) Child, Feddes Repert. **95:** 295. 1984.

Solanum fusiforme Smith & Downs, Phytologia **10:** 431, t. 3, fig. 13–17. 1964. Type. Brazil. Santa Catarina, near Dionisio Cerqueira, 800–850 m, 30 Dec 1956, *Smith & Reitz 9658* (holotype, US; isotype, HBR).

Cyphomandra luteoalba (Persoon) Child, Feddes Repert. **95:** 295. 1984.

Solanum luteoalbum Persoon, Syn. Pl. **1:** 221. 1805. Type. Unknown at present.

Cyphomandra stuckertii (Bitter) D'Arcy, Ann. Missouri Bot. Gard. 59: 277. 1972.

Solanum stuckertii Bitter, Repert. Spec. Nov. Regni Veg. **12:** 461. 1913; C. Morton, Revis. Arg. Sp. *Solanum* 191. 1976. Lectotype. Argentina. *Stuckert 21589* (?B, photo NY, chosen by D'Arcy, 1972). Superfluous lectotype. Argentina. *Stuckert 5641* (G, chosen by Morton, 1976).

Cyphomandra subhastata (Smith & Downs) Child, Feddes Repert. **95:** 295. 1984.

Solanum subhastatum Smith & Downs, Phytologia **10:**

432. 1964. Type. Brazil. Santa Catarina: Lauro Müller-Urussanga, Pinhal da Companhia, 300 m, 23 Aug 1958, *Reitz & Klein 7053* (holotype, US; isotype, HBR).

Cyphomandra velutina Sendtner, in Mart. Fl. Bras. **10:** 120. Tab. 17. 1846. Type. Brazil. Goiás: Fazenda Santa Cruz da Donna Tereza, *Pohl 3455* (types, BR, F, G, M, W; photos of types, GH, NY).

Pionandra velutina (Sendtner) Miers, Ann. Mag. Nat. Hist. **15,** ser. 2: 199. 1855.
Cyphomandra glaberrima Dusén, Ark. Bot. **9:** 19. 1909. Type. Brazil. Rio de Janeiro: Serra do Itatiaia, Oct. 1903, *Dusén 2057* (type, S).
Solanum luridifuscescens Bitter, Repert. Spec. Nov. Regni Veg. **12:** 466. 1913. Type. Brazil. Rio de Janeiro: Serra dos Orgãos, Oct 1896, *Ule 4314* (type, HBG).

Cyphomandra villosa Steyermark, Phytologia **9:** 348. 1964. Type. Ecuador. Loja: region central, Las Chinchas, 2250 m, 12 Apr 1944, *Acosta-Solís 7743* (holotype, F [F neg. 51366 F]).

EXCLUDED TAXA

Cyphomandra abutiloides Grisebach, Abh. Konigl. Ges. Wiss. Gottingen **24:** 249. 1879. Type. Argentina. Jujuy: Prope urbem Jujuy, *Lorentz & Hieronymus 995* (lectotype, CORD (n.v.), designated by Morton, 1976; isolectotypes, B, destroyed, G; photo of isolectotype, F).
=*Solanum abutiloides* (Grisebach) Bitter & Lillo, Repert. Spec. Nov. Regni Veg. **12:** 136. 1913.

The stellate hairs and anther morphology exclude this species from *Cyphomandra.* It belongs to *Solanum* section *Anthoresis* according to Bitter (1913b) and Morton (1944) and to *Solanum* section *Brevantherum* according to Roe (1972) and Morton (1976).

Cyphomandra aculeata J. D. Smith, Bot. Gaz. (Crawfordsville) **57:** 423. 1914. Type. Guatemala. Alta Verapaz, prope Cobán, Apr 1882, *Lehmann 1334* (type, US 1324994).
=*Solanum cobanense* J. L. Gentry, Phytologia **26:** 276. 1973.

The epithet change was necessary because the names *Solanum aculeatum* St. Lag. and *Solanum aculeatum* O. E. Schulz already exist.

Child (1983) tentatively places this species in *Solanum* section *Nemorense* because of its simple leaves, equal stamens, and recurved prickles on the abaxial midvein of the leaves.

Cyphomandra adenotricha (Dunal) Dunal, in DC. Prodr. **13(1):** 400. 1852.
Solanum adenotrichum Dunal, Hist. Sol., p. 236. 1813. Type. Unknown.

I have not located any specimen associated with this name, or found any description of the species other than the brief one given by Vandelli and repeated by Dunal. This description was first published by Vandelli (1788) under *Solanum* without a specific epithet. Dunal validly published the name *Solanum adenotrichum* in 1813 along with the same description, which he attributed to Vellozo. Dunal later (1852) tranferred it to *Cyphomandra* with a query. Both Dunal (1852) and Sendtner (1846) indicate an affinity of this species with *Solanum concinnum* Schott. *Solanum adenotrichum* is apparently from Brazil (Dunal, 1813). It is unknown why *Solanum adenotrichum* was associated with *Cyphomandra*; perhaps it is because of the cordate leaves referred to in the description.

Cyphomandra section *Allophylla* Child, Feddes Repert. **95:** 292. 1984. Type species. *Cyphomandra allophylla* (Miers) Hemsley.
=*Solanum* section *Allophyllum* (Child) Bohs, Ann. Missouri Bot. Gard. **77:** 401. 1990. Type species. *Solanum allophyllum* (Miers) Standley.
Cyphomandra allophylla (Miers) Hemsley, Biol. Cent.-Amer., Bot. **2:** 417. 1882.
Pionandra allophylla Miers, *in* Seem. Bot. Voy. Herald, 174. 1854. Type. Panama. In waste places, *Seemann 169* (lectotype, BM, designated by Bohs, 1990; isolectotype, K).
=*Solanum allophyllum* (Miers) Standley, J. Wash. Acad. Sci. **17:** 16. 1927.

This species has recently been examined in detail and placed in *Solanum* section *Allophyllum* (Child) Bohs (Bohs, 1990). A complete description and synonymy can be found in Bohs (1989a, 1990).

Cyphomandra bassovioides Rusby, Descrip. 300 So. Amer. Pl. 116. 1920. Type. Colombia. Santa Marta, Sierra del Libano, 6000 ft, 20 Jan 1899, *H.H. Smith 1181* (types, A, BM, F, G, GH, K, L, NY, P, S, U, US).

This species belongs to *Solanum* section *Geminata* on the basis of its paired anisophyllous leaves, short, thick anthers, and globose fruits.

Cyphomandra crotonifolia (Dunal) Walpers, Repert. Bot. Syst. **6:** 579. 1847.
Pionandra crotonifolia (Dunal) Miers, London J. Bot. **4:** 364. 1845.
=*Solanum crotonifolium* Dunal, Solan. Syn. 18. 1816; H.B.K., Nov. Gen. Sp. **3:** 24. 1818. Type. Nova Granada, circa Carthagenam, *Humboldt & Bonpland* (holotype, P herb. HBK).

The stellate hairs and tapered anthers of this species are typical of *Solanum* subgenus *Leptostemonum* (Dun.) Bitt. This species may be identical to *Solanum trachyphyllum* Dunal (see below). The differences noted by Humboldt and Bonpland between the two species are minor.

Cyphomandra dichotoma Rusby, Mem. Torrey Bot. Club **4:** 231. 1895. Type. Bolivia. La Paz: Yungas, 1890, *Bang 519* (types, BM, E, GH, MO, NY, US, W, WIS).
Witheringia dichotoma (Rusby) D'Arcy, Phytologia **25:** 116. 1973.
=*Vassobia dichotoma* (Rusby) Bitter, Repert. Spec. Nov. Regni Veg. **15:** 150. 1918; Hunziker, Kurtziana **10:** 23, fig. 6. 1977; Hunziker, Kurtziana **17:** 96. 1984.

The anthers of *C. dichotoma* dehisce by longitudinal slits. Bitter (1918) placed it in the genus *Vassobia*, which was monographed by Hunziker (1984).

Cyphomandra flagrans (Tenore) Walpers, Repert. Bot. Syst. **6:** 579. 1847.
Pionandra flagrans (Tenore) Miers, London J. Bot. **4:** 364. 1845.
Solanum flagrans Tenore, Sem. Ort. Bot. Nap. 12. 1839; Tenore, Ann. Sci. Nat. Bot., ser. 2, **13:** 381. 1840. Type. Not extant? Originally from Brazil; plant on which protologue is based was grown in botanic garden at Naples, Italy.
=*Solanum pseudoquina* St. Hilaire, Pl. Usuelles des Brasiliens, part. **5:** t. 21, 1. 1825.

Dunal (1852) gives this name as a synonym of *Solanum inaequale* Vellozo, which in turn is regarded as a synonym of *Solanum pseudoquina* St. Hil. (*Solanum* section *Geminata*) by Knapp (1986a). Although no specimen is known, the description coincides in all particulars to this species.

Cyphomandra fraxinella Sendtner, *in* Mart. Fl. Bras. **10:** 122. 1846. Syntypes. Brazil. Rio de Janeiro: "Ad viam publicam Paulinam, ad praedium Tacasava, Dec. florens," *Martius 407* (M); "In umbrosis Parahybunae," Jan 1839, *Martius Herb. Fl. Bras. 1256*, attributed to Luschnath by Sendtner (1846) (BR; possibly G, M); "Brasilia australiore," *Sellow 78* (B [destroyed], K).
Pionandra fraxinella (Sendtner) Miers, Ann. Mag. Nat. Hist., ser. 2, **15:** 199. 1855.
Pionandra pinnata Miers, Ann. Mag. Nat. Hist., ser. 2, **15:** 199. 1855; Ill. S. Amer. Pl. **2:** 142. Plate 61. 1857. Type. Brazil. Rio de Janeiro: Serra dos Orgãos, Jan 1838 (fl), *Miers 4539* (types, BM, K).
Cyphomandra pinnata (Miers) Wagner, Ann. K.K. Naturhist. Hofmus. **31:** 150. 1917.
=*Solanum graveolens* Bunbury, Proc. Linn. Soc. London **1:** 110. 1841; Bunbury, Ann. Mag. Nat. Hist. **7:** 532. 1841; Bitter, Repert. Spec. Nov. Regni Veg. **12:** 62. 1913; Bitter, Repert. Spec. Nov. Regni Veg. **12:** 136. 1913 (erroneously given as *Solanum suaveolens* by Bitter). Type. Brazil. Minas Gerais: near Gongo Soco, Nov 1834, *Bunbury s.n.* (type, CGE, n.v.).

Although the shoot architecture of *Solanum graveolens* is reminiscent of *Cyphomandra*, with 3–4-leaved sympodial units and the inflorescences often emerging from branch forks, this species must be excluded from the genus on the basis of anther structure. The entire abaxial surface of the anther is thickened and extends apically to form a short beak at the tip of the anther. The pores are adaxial and subterminal; they at first open into large pores, than extend into longitudinal slits. This species has been placed in the section *Rhynchantherum* Bitter (Bitter, 1913c) and belongs to *Solanum* subgenus *Potatoe* (G. Don) D'Arcy (D'Arcy, 1972).

Rusby's assignments of two Bolivian collections to *Cyphomandra fraxinella* (Rusby, 1899, 1907) are erroneous. *Rusby 800* represents *Cyphomandra benensis*, and *Bang 2248* belongs to *Solanum* section *Pteroidea.*

Cyphomandra godefroyi Bonati, in Lecomte, Fl. Indo-Chine **4:** 336. 1915. Type. Cochinchina. *Godefroy s.n.* (type, P).

This specimen has the opposite leaves and interpetiolar stipules characteristic of the Rubiaceae.

Cyphomandra homalophylla Standley, Trop. Woods **10:** 50. 1927; Standl. Publ. Field Mus. Nat. Hist., Bot. Ser. **18:** 1054. 1938. Type. Panama. Bocas del Toro: Almirante region, 1927, *Cooper & Slater 39* (Yale 10139) (holotype, US 1269809; isotype, F).
=*Solanum rovirosanum* J. D. Sm., Bot. Gaz. (Crawfordsville) **48:** 297. 1909; D'Arcy, Ann. Missouri Bot. Gard. **60:** 749. 1973. 1984. Type. Guatemala. *Turckheim 11021* (=J.D. Sm., Pl. Guat. 8716) (holotype, US, n.v.).

This species belongs to *Solanum* section *Geminata* according to Knapp (1986a, 1991).

Cyphomandra itabirensis Dunal, in DC. Prodr. **13(1):** 400. 1852. Type. Brazil. Minas Gerais: Itabira, *Lund s.n.* (holotype, G-DC) [F neg. 6854 GH, NY, US, WIS]).

The type specimen consists of a single leafy branch bearing only fruits. All the vegetative parts of the plant are densely pubescent with uniseriate glandular and eglandular hairs. Without flowers it is difficult to ascertain the affinities of this species, but the very short, few-flowered inflorescences and globose, shining fruits almost certainly preclude inclusion in *Cyphomandra.*

Cyphomandra lauterbachii H. Winkler, Repert. Spec. Nov. Regni Veg. **7:** 247. 1909. Type. Bolivia. La Paz: San Antonio near Mapiri, 850 m, Dec 1907, *Buchtien 1436* (holotype, WRSL, n.v.; isotype, US).
=*Solanum lauterbachii* (H. Winkler) Bitter, Repert. Spec. Nov. Regni Veg. **15:** 155. 1918.

This species has poricidal anther dehiscence, but the anthers lack the thickened connective characteristic of *Cyphomandra.* Bitter (1918) placed this species in *Solanum* section *Cyphomandropsis*, but its oblong anthers do not resemble the tapered ones typical of the section.

Cyphomandra narensis (Dunal) Walpers, Repert. Bot. Syst. **6:** 579. 1847.
Pionandra narensis (Dunal) Miers, London J. Bot. **4:** 364. 1845.
=*Solanum narense* Dunal, Solan. Syn. 18. 1816; H.B.K., Nov. Gen. Sp. **3:** 24. 1818; Dunal *in* DC. Prodr. **13(1):** 116. 1852; Whalen, Gentes Herb. **12:** 237. 1984. Type. Colombia. "Inter Nares et Honda, in ripa obrumbrata fluvii Magdalenae," *Humboldt & Bonpland s.n.* (holotype, P-HBK).

The stellate pubescence and tapered anthers of this species are typical of *Solanum* subgenus *Leptostemonum.* Whalen (1984) places it in the *Solanum torvum* group of this subgenus.

Cyphomandra physaloides Dunal, *in* DC. Prodr. **13(1):** 388. 1852. Type. Brazil. *Sellow 132* (holotype, BM).

The type of this species is very poor, but from the fragmentary material available and from Dunal's protologue, it apparently has anthers that dehisce by longitudinal slits, a calyx that is accrescent in fruit, and a corolla with fairly long lobes. These characteristics, along with its location in Brazil, make it most likely a species of *Athenaea.*

Cyphomandra phytolaccoides (Rusby) Child, Feddes Repert. **95:** 292. 1984.
Bassovia phytolaccoides Rusby, Bull. N.Y. Bot. Gard. **4:** 317. 1907. Type. Bolivia. La Paz: Tipuani-Guanai, Dec 1892, *Bang 1740* (lectotype, NY, designated by Bohs (1990); isolectotypes, A, BM, E, GH, NY).
Solanum phytolaccoides (Rusby) Bitter, Repert. Spec. Nov. Regni Veg. **13:** 172. 1914, non *S. phytolaccoides* C.H. Wright, 1894.
=*Solanum mapiriense* Bitter, Repert. Spec. Nov. Regni Veg. **11:** 16. 1912. Type. Bolivia. La Paz: San Antonio near Mapiri, 850 m, Dec 1907, *Buchtien 1434* (lectotype, US 1399273,

designated by Bohs (1990); isolectotype, US 1175838).

This species is allied to *Solanum allophyllum* and has been placed in *Solanum* section *Allophyllum* by Bohs (1990).

Cyphomandra section *Rhynchantherum* (Bitter) Child, Feddes Repert. **95:** 293. 1984 (as *Rhyncantherum*). Type species. *Cyphomandra fraxinella* Sendtner (=*Solanum graveolens* Bunbury).
=*Solanum* section *Rhynchantherum* Bitter, Repert. Spec. Nov. Regni Veg. **12:** 61. 1913. Type species. *Solanum graveolens* Bunbury.

Cyphomandra trachyphylla (Dunal) Sendtner, Walp. Repert. Bot. Syst. **6:** 579. 1847.
Pionandra trachyphylla (Dunal) Miers, London J. Bot. **4:** 364. 1845.
=*Solanum trachyphyllum* Dunal, Solan. Syn. 18. 1816; H.B.K., Nov. Gen. Sp. **3:** 25. 1818; Dunal, *in* DC. Prodr. **13(1):** 117. 1852; Whalen, Gentes Herb. **12:** 237. 1984. Type. Colombia. "In Provincia Popayanensi, inter Buga et Carthago, 3000 ft," *Humboldt & Bonpland s.n.* (holotype, P-HBK).

This species belongs to *Solanum* subgenus *Leptostemonum.* Whalen (1984) regards it as a synonym of *Solanum narense* Dunal (see above) and places it in the *Solanum torvum* group. This species appears to be the same as *Solanum crotonifolium.*

Cyphomandra verruculosa Hassler, Repert. Spec. Nov. Regni Veg. **9:** 118. 1911. Syntypes. Paraguay. *Fiebrig 4726* (BM, G, M), *Fiebrig 4461* (BM, G), *Fiebrig 4824* (BM, G).
=*Solanum verruculosum* (Hassler) Hassler, Repert. Spec. Nov. Regni Veg. **15:** 218. 1918.

The anther structure of this species is that of a *Solanum.* It probably belongs in *Solanum* section *Geminata* or *Solanum* section *Indubitaria.*

Cyphomandra yungasense Rusby, Bull. Torrey Bot. Club **26:** 195. 1984. Type. Bolivia. La Paz: Yungas, 6000 ft, 1885, *Rusby 2475.*

This species definitely belongs to the genus *Solanum.* According to Child (1984), it is a member of *Solanum* section *Jasminosolanum.*

The name *Solanum yungasense* Hawkes has already been applied to a species in the subgenus *Potatoe.*

ACKNOWLEDGMENTS

Expressing my gratitude individually to all those who have helped me in this work would be an impossible task. To all those who provided help but are not individually mentioned here, I give my sincerest thanks. Dr. R. E. Schultes first suggested this project and provided much helpful support and advice. Financial assistance was provided by Sigma Xi, the World Wildlife Fund, the University of Utah Research Committee, and the Anderson-Atkins Garden Fund and a Sheldon Fellowship, both from Harvard University. The following institutions and individuals helped with field work: Instituto de Ciencias Naturales, Bogotá, Colombia; Insituto de Ciencias, Pontificia Universidad Católica del Ecuador, Quito, Ecuador; Universidad Nacional Mayor de San Marcos, Lima, Peru; Herbario Nacional de Bolivia, La Paz, Bolivia; Instituto Miguel Lillo, Tucumán, Argentina; Universidad Nacional de Córdoba, Córdoba, Argentina; Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil; Museu Botânico Municipal, Curitiba, Brazil; Smithsonian Tropical Research Institute, Panama; and Señores Gunther Buch, Pedro Juajibioy, José Schunke, and Gert Hatschbach. Luis Bernardello, Alan Child, W. G. D'Arcy, Armando Hunziker, Sandra Knapp, Eduardo Moscone, Michael Nee, Greg Pringle, Arlete Soares, and Stefan Vogel shared insights into various aspects of *Cyphomandra* biology. W. G. D'Arcy, George Rogers, and two anonymous reviewers critically read the manuscript. Diana Valencia and Alejandro Purgue corrected the Spanish abstract. The greenhouse staff at Harvard University, the University of Vermont, and the University of Utah maintained my Solanaceae living collections. Thanks are due the curators and staff of the following herbaria for providing loans of specimens: A, AAU, B, BH, BM, BR, C, COL, CR, CTES, E, ECON, F, G, GB, GH, GOET, HBG, K, L, LD, LIL, LL, LP, M, MA, MBM, MO, NY, P, RB, S, SI, SP, TEX, U, US, USM, W, WU, WIS, and Z.

LITERATURE CITED

Ackerman, J. D., M. R. Mesler, K. L. Lu & A. M. Montalvo. 1982. Food-foraging behavior of male Euglossini (Hymenoptera: Apidae): vagabonds or trapliners? Biotropica **14:** 241–248.

Anderson, G. J. & P. G. Gensel. 1976. Pollen morphology and the systematics of *Solanum* section *Basarthrum*. Pollen & Spores **18:** 533–552.

Andrade-Lima, D. de. 1982. Present-day forest refuges in northeastern Brazil. Pages 245–251 *in* G. T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

Armstrong, J. E. 1986. Comparative floral anatomy of Solanaceae: a preliminary survey. Pages 101–113 *in* W. G. D'Arcy (ed.), Solanaceae: biology and systematics. Columbia University Press, New York.

Aublet, J. B. C. F. 1775. Hist. pl. Guiane. Vol. 1. Didot, Paris.

Basak, R. K. 1967. The pollen grains of Solanaceae. Bull. Bot. Soc. Bengal **21:** 49–58.

Benitez de Rojas, C. E. 1974. Los géneros de las Solanaceae de Venezuela. Rev. Fac. Agron. (Maracay) **7(3):** 25–108.

———. 1981. Sobre el tipo del género *Cyphomandra* Mart. ex Sendt. Ernstia **1:** 6.

Bernardello, L. M. & G. J. Anderson. 1990. Karyotypic studies in *Solanum* section *Basarthrum* (Solanaceae). Amer. J. Bot. **77:** 420–431.

Bitter, G. 1913a. Solana nova vel minus cognita XII. XXXVII. Sectio *Cyphomandropsis* Bitter nov. sect. Repert. Spec. Nov. Regni Veg. **12:** 461–467.

———. 1913b. XXVII. Solana nova vel minus cognita. XI. XXIX. Solana erronee generi Cyphomandrae adscripta. Repert. Spec. Nov. Regni Veg. **12:** 136–137.

———. 1913c. Solana nova vel minus cognita X. XXIII. Sectio *Rhynchantherum* Bitter, nov. sect. Repert. Spec. Nov. Regni Veg. **12:** 61–65.

———. 1914. Weitere Untersuchungen über das Vorkommen von Steinzellkonkretionen im Fruchtfleisch beerentragender Solanaceen. Abh. Naturwiss. Vereine Bremen **23:** 114–163.

———. 1918. XXIII. Solanaceae quattuor austro-americanae adhuc generibus falsis adscriptae. Repert. Spec. Nov. Regni Veg. **15:** 149–155.

Bohs, L. 1986. The biology and taxonomy of *Cyphomandra* (Solanaceae). Ph.D. thesis, Harvard University, Cambridge, Massachusetts.

———. 1988a. Four new species of *Cyphomandra* (Solanaceae) from South America. Syst. Bot. **13:** 265–275.

———. 1988b. The Colombian species of *Cyphomandra*. Revista Acad. Colomb. Ci. Exact. **16:** 67–75.

———. 1989a. *Solanum allophyllum* (Miers) Standl. and the generic delimitation of *Cyphomandra* and *Solanum* (Solanaceae). Ann. Missouri Bot. Gard. **76:** 1129–1140.

———. 1989b. IOPB chromosome data I: Solanaceae. IOPB Newsletter **13:** 17.

———. 1989c. Ethnobotany of the genus *Cyphomandra* (Solanaceae). Econ. Bot. **43:** 143–163.

———. 1990. The systematics of *Solanum* section *Allophyllum* (Solanaceae). Ann. Missouri Bot. Gard. **77:** 398–409.

———. 1991. Crossing studies in *Cyphomandra* (Solanaceae) and their systematic and evolutionary significance. Amer. J. Bot. **78:** 1683–1693.

Brewbaker, J. L. 1957. Pollen cytology and self-incompatibility systems in plants. J. Heredity **48:** 271–277.

Brown, K. S., Jr. 1982. Paleoecology and regional patterns of evolution in neotropical forest butterflies. Pages 255–308 *in* G. T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

———. 1987a. Chemistry at the Solanaceae/Ithomiinae interface. Ann. Missouri Bot. Gard. **74:** 359–397.

———. 1987b. Biogeography and evolution of neotropical butterflies. Pages 66–104 *in* T. C. Whitmore & G. T. Prance (eds.), Biogeography and Quaternary history in tropical America. Oxford University Press, New York.

Brücher, H. 1968. Die genetischen Reserven Südamerikas für die Kulturpflanzenzuchtung. Theoret. Appl. Genet. **38:** 9–22.

———. 1977. Tropische Nutzpflanzen. Springer-Verlag, Berlin.

Buchmann, S. L. 1983. Buzz pollination in angiosperms. Pages 73–113 *in* C. E. Jones & R. J. Little (eds.), Handbook of experimental pollination biology. Van Nostrand Reinhold Co., Inc., New York.

Cabrera, A. L. 1976. Regiones fitogeograficas Argentinas. Editorial Acme, Buenos Aires, Argentina.

Cavanilles, A. J. 1799. Descripción de cinco géneros nuevos y de otras plantas. Ann. Hist. Nat. **1:** 33–45.

———. 1801. Icones et descriptiones plantarum, quae aut sponte in Hispania crescent. Vol. 6. Regia Typographia, Madrid.

Child, A. 1979. A review of branching patterns in the Solanaceae. Pages 345–356 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

———. 1983. Taxonomic studies in *Solanum* L. 1. Section *Nemorense* Child, sectio nova. Feddes Repert. **94:** 35–42.

———. 1984. Studies in *Solanum* L. (and related genera). 3. A provisional conspectus of the genus *Cyphomandra* Mart. ex Sendtner. Feddes Repert. **95:** 283–298.

———. 1986. Taxonomic studies in *Solanum* L. (and related genera) 4. *Cyphomandra casana* Child sp. nov. and *Solanum* sect. *Glaucophyllum* Child sect. nov. Feddes Repert. **97:** 143–146.

Coccuci, A. A. 1991. Pollination biology of *Nierembergia* (Solanaceae). Pl. Syst. Evol. **174:** 17–35.

Corrêa, M. P. 1975. Dicionario das plantas úteis do Brasil. Vol. 6. Ministerio da Agricultura, Rio de Janeiro.

Cruden, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. Evolution **31:** 32–46.

Danert, S. 1958. Die Verzweigung der Solanaceen im Reproduktiven Bereich. Abh. Deutsch. Akad. Wiss. Berlin, Kl. Chem. **6:** 1–183.

———. 1967. Die Verzweigung als infragenerische Gruppenmerkmal in der Gattung *Solanum*. Kulturpflanze **15:** 275–292.

———. 1970. Infragenerische Taxa der Gattung *Solanum* L. Kulturpflanze **18:** 253–297.

D'Arcy, W. G. 1972. Solanaceae studies II: typification of subdivisions of *Solanum.* Ann. Missouri Bot. Gard. **59:** 262–278.

———. 1973. Solanaceae. Pages 573–780 *in* R. E. Woodson & R. W. Schery (eds.), Flora of Panama. Ann. Missouri Bot. Gard. Vol. 60.

———. 1979. The classification of the Solanaceae. Pages 3–47 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

———. 1991. The Solanaceae since 1976, with a review of its biogeography. *In* J. G. Hawkes, R. N. Lester, M. Nee & N. Estrada (eds.), Solanaceae III: taxonomy, chemistry, evolution. Royal Botanic Garden, Kew, U.K.

Davis, P. H. & V. H. Heywood. 1963. Principles of angiosperm taxonomy. D. Van Nostrand Co., Inc., New York.

DeVries, P. J. 1985. Hostplant records and natural history notes on Costa Rican butterflies (Papilionidae, Pieridae & Nymphalidae). J. Res. Lepid. **24:** 290–333.

Dinerstein, E. 1986. Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. Biotropica **18:** 307–318.

Dodson, C. H., A. H. Gentry & F. M. Valverde. 1985. La Flora de Jauneche. Banco Central del Ecuador, Quito, Ecuador.

Don, G. 1837. Gen. hist. Vol. 4. London.

Dressler, R. L. 1968. Pollination by euglossine bees. Evolution **22:** 202–210.

———. 1979. *Eulaema bombiformis, E. meriana,* and Müllerian mimicry in related species (Hymenoptera: Apidae). Biotropica **11:** 144–151.

———. 1982. Biology of the orchid bees (Euglossini). Ann. Rev. Ecol. Syst. **13:** 373–394.

Drummond, B. A., III. 1986. Coevolution of Ithomiine butterflies and solanaceous plants. Pages 307–327 *in* W. G. D'Arcy (ed.), Solanaceae: biology and systematics. Columbia University Press, New York.

——— **& K. S. Brown, Jr.** 1987. Ithomiinae (Lepidoptera: Nymphalidae): summary of known larval food plants. Ann. Missouri Bot. Gard. **74:** 341–358.

Dunal, M. F. 1813. Hist. nat. *Solanum.* Paris, Strasbourg, & Montpellier.

———. 1816. Solan. syn. Ed. 2. Renaud, Montpellier.

———. 1852. Solanaceae. Pages 1–690 *in* A. P. DeCandolle, Prodr. **13(1).** Victoris Masson, Paris.

Edmonds, J. M. 1982. Epidermal hair morphology in *Solanum* L. section *Solanum.* Bot. J. Linn. Soc. **85:** 153–167.

———. 1983. Seed coat structure and development in *Solanum* L. section *Solanum* (Solanaceae). Bot. J. Linn. Soc. **87:** 229–246.

———. 1984. Pollen morphology of *Solanum* L. section *Solanum.* J. Linn. Soc., Bot. **88:** 237–251.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Almqvist & Wiskell, Stockholm.

———. 1969. Handbook of palynology. Munksgaard, Copenhagen.

Evans, W. C. 1979. Tropane alkaloids of the Solanaceae. Pages 241–254 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

———, **A. Ghani & V. A. Woolley.** 1972. Alkaloids of *Cyphomandra betacea* Sendt. J. Chem. Soc. Perkin Trans. **1:** 2017–2019.

——— **& A. Somanabandhu.** 1980. Nitrogen-containing non-steroidal secondary metabolites of *Solanum, Cyphomandra, Lycianthes,* and *Margaranthus.* Phytochemistry **19:** 2351–2356.

Gentry, A. H. 1978. Floristic knowledge and needs in Pacific tropical America. Brittonia **30:** 134–153.

Gentry, J. L., Jr. & P. C. Standley. 1974. Solanaceae. Flora of Guatemala. Fieldiana, Bot. **24,** part 10, No. 1–2: 1–151.

Gibson, R. W. 1971. Glandular hairs providing resistance to aphids in certain wild potato species. Ann. Appl. Biol. **68:** 113–119.

Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. Pages 210–240 *in* L. E. Gilbert & P. H. Raven (eds.), Coevolution of animals and plants. University of Texas Press, Austin, TX.

Gilli, A. 1970. Bestimmungsschlüssel der Subgenera und Sektionen der Gattung *Solanum.* Feddes Repert. **81:** 429–435.

Greuter, W., H. M. Burdet, W. G. Chaloner, V. Demoulin, R. Grolle, D. L. Hawksworth, D. H. Nicolson, P. C. Silva, F. A. Stafleu, E. G. Voss & J. McNeill. 1988. International code of botanical nomenclature. Koeltz Scientific Books, Konigstein, West Germany.

Haber, W. A. 1978. Evolutionary ecology of tropical mimetic butterflies (Lepidoptera: Ithomiinae). Ph.D. thesis, University of Minnesota.

———. 1983. *Solanum ochraceo-ferrugineum* and *S. siparunoides.* Pages 324–328 *in* D. H. Janzen (ed.), Costa Rican natural history. University of Chicago Press, Chicago, IL.

Haffer, J. 1969. Speciation in Amazonian forest birds. Science **165:** 131–137.

———. 1987a. Quaternary history of tropical America. Pages 1–18 *in* T. C. Whitmore & G. T. Prance (eds.), Biogeography and Quaternary history in tropical America. Oxford University Press, New York.

———. 1987b. Biogeography of neotropical birds. Pages 105–150 *in* T. C. Whitmore & G. T. Prance (eds.), Biogeography and Quaternary history in tropical America. Oxford University Press, New York.

Hallé, F., R. A. A. Oldeman & P. B. Tomlinson. 1978. Tropical trees and forests: an architectural analysis. Springer-Verlag, Berlin.

Harborne, J. B. 1986. Systematic significance of variations in defense chemistry in the Solanaceae. Pages 328–344 *in* W. G. D'Arcy (ed.), Solanaceae: biology and systematics. Columbia University Press, New York.

Hauser, E. J. P. & J. H. Morrison. 1964. The cytochemical reduction of nitro blue tetrazolium as an index of pollen viability. Amer. J. Bot. **51:** 748–752.

Hawkes, J. G. & J. P. Hjerting. 1969. The potatoes of Argentina, Brazil, Paraguay, and Uruguay. Oxford University Press, London.

——— **& P. Smith.** 1965. Continental drift and the age of angiosperm genera. Nature **207:** 48–50.

Heithaus, E. R., T. H. Fleming & P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology **56:** 841–854.

Hemsley, W. B. 1882. Biol. cent.-amer., Bot. Vol. 2. R. H. Porter & Dulau & Co., London.

Hickey, L. J. 1979. A revised classification of the architecture of dicotyledonous leaves. Pages 25–39 *in* C. R. Metcalfe & L. Chalk (eds.), Anatomy of the dicotyledons, ed. 2, vol. 1. Clarendon Press, Oxford.

Holdridge, L. R., W. C. Grenke, W. H. Hatheway, T. Liang & J. A. Tosi, Jr. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, Oxford.

Hooker, W. J. 1839. *Solanum fragrans*: fragrant South American nightshade. Bot. Mag., new Ser. **12:** 3684.

Howard, R. A. 1983. The plates of Aublet's Histoire des Plantes de la Guiane Françoise. J. Arnold Arbor. **64:** 255–292.

Hsaio, T. H. 1986. Specificity of certain chrysomelid beetles for Solanaceae. Pages 345–363 *in* W. G. D'Arcy (ed.), Solanaceae: biology and systematics. Columbia University Press, New York.

Humboldt, A., A. Bonpland & C. S. Kunth. 1818. Nov. gen. sp. Vol. 3. Librairie Grecque-Latine-Allemande, Paris.

Hunziker, A. T. 1979a. South American Solanaceae: a synoptic survey. Pages 49–85 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

———. 1979b. The Solanaceae in the Neotropics: a critical appraisal. Pages 355–364 *in* K. Larsen & L. B. Holm-Nielsen (eds.), Tropical botany. Academic Press, London.

———. 1984. Estudios sobre Solanaceae. XIX. Sinopsis de *Vassobia*. Kurtziana **17:** 91–118.

Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. Science **171:** 203–205.

Knapp, S. 1983. Sectional nomenclature in *Solanum* (Solanaceae). Taxon **32:** 635–636.

———. 1986a. A revision of *Solanum* section *Geminata* (G. Don) Walpers. Ph.D. thesis, Cornell University, Ithaca, NY.

———. 1986b. Reproductive biology of *Solanum* section *Geminata* in a Costa Rican cloud forest. Pages 253–263 *in* W. G. D'Arcy (ed.), Solanaceae: biology and systematics. Columbia University Press, New York.

———. 1989. A revision of the *Solanum nitidum* group (section *Holophylla* pro parte): Solanaceae. Bull. Br. Mus. Nat. Hist. (Bot.) **19:** 63–112.

———. 1991. A revision of the *Solanum sessile* species group (section *Geminata pro parte*: Solanaceae). Bot. J. Linn. Soc. **105:** 179–210.

Kuntze, O. 1898. Revis. gen. pl. Pars III.II. Arthur Felix, Leipzig.

Levin, D. A. 1976. The chemical defenses of plants to pathogens and herbivores. Ann. Rev. Ecol. Syst. **7:** 121–159.

Lewis, D. H. 1985. Pollination and fruit set in the tamarillo, *Cyphomandra betacea* (Cav.) Sendt. M.Sc. thesis, University of Auckland, Auckland, New Zealand (cited in Pringle, 1991).

Lowe, R. T. 1867. Some account of the fruits and vegetables of Madeira, the Canaries, and Cape Verdes. J. Roy. Hort. Soc. **1:** 161–187.

———. 1868. Man. fl. Madeira. John Van Voorst, London.

Macbride, J. F. 1930. Peruvian Solanaceae. Publ. Field Columbian Mus., Bot. Ser. **8:** 105–112.

———. 1962. Solanaceae. Flora of Peru. Field Mus. Nat. Hist. Bot. Ser. **13(5B):** 1–267.

Mahlberg, P. G. 1985. Trichome morphogenesis on leaves of *Cyphomandra betacea* Sendt. (Solanaceae). Israel J. Bot. **34:** 253–264.

Martius, C. P. F. de. 1829. Nov. Gen. sp. pl. Vol. 3. C. Wolf, Munich.

———. 1838. Herb. fl. bras. Munich. Pages 129–160 reprinted from Flora **21(2),** Beibl. 4–5: 49–80.

Mey, J. A. M. van der, G. A. M. van Hasselt & D. E. Elsevier. 1969. Idiogram of *Cyphomandra betacea* Sendt., the tree tomato or tamarillo. Genetica **40:** 413–416.

Michener, C. D. 1962. An interesting method of pollen collecting by bees from flowers with tubular anthers. Rev. Biol. Trop. **10:** 167–175.

Miers, J. 1845. Contributions to the botany of South America. London J. Bot. **4:** 319–371.

———. 1850. Illus. S. Amer. pl. Vol. 1. H. Bailliere, London.

———. 1854. Solanaceae. Pages 172–176 *in* B. Seemann, Bot. voy. Herald. Lovell Reeve, London.

———. 1855. XVII. On the genera *Pionandra, Cliocarpus,* and *Paecilochroma. Pionandra.* Ann. Mag. Nat. Hist. ser. 2 **15:** 196–200.

Morton, C. V. 1944. Taxonomic studies of tropical American plants. Some South American species of *Solanum.* Contr. U.S. Natl. Herb. **29:** 41–72.

———. 1976. A revision of the Argentine species of *Solanum.* Academia Nacional de Ciencias, Córdoba, Argentina.

Morton, J. F. 1982. The tree tomato, or "tamarillo," a fast-growing, early-fruiting small tree for subtropical climates. Proc. Florida State Hort. Soc. **95:** 81–85.

Muller, J. 1970. Palynological evidence on early differentiation of angiosperms. Biol. Rev. Cambridge Philos. Soc. **45:** 417–450.

Murray, K. G. 1987. Selection for optimal fruit-crop size in bird-dispersed plants. Amer. Naturalist **129:** 18–31.

Murry, L. E. & W. H. Eshbaugh. 1971. A palynological study of the Solaninae (Solanaceae). Grana **11:** 65–78.

National Research Council. 1989. Lost crops of the Incas. National Academy Press, Washington, D.C.

Nettancourt, D. de. 1977. Incompatibility in angiosperms. Springer-Verlag, Berlin.

Olmstead, R. G. & J. D. Palmer. 1992. A chloroplast DNA phylogeny of the Solanaceae: subfamilial relationships and character evolution. Ann. Missouri Bot. Gard. **79:** 346–360.

Ortega, C. G. 1800. Nov. pl. descr. dec. Vol. 9. Typographia Mariniana, Madrid.

Pandey, K. K. 1960. Evolution of gametophytic and sporophytic systems of self-incompatibility in angiosperms. Evolution **14:** 98–115.

Pijl, L. van der. 1982. Principles of dispersal in higher plants. Ed. 3. Springler-Verlag, Berlin.

Pittier, H. 1908. Ensayo pl. usual. Costa Rica. H. L. & J. B. McQueen, Inc., Washington, D.C.

———. 1910. Two new species of *Cyphomandra* from Colombia. Contr. U.S. Natl. Herb. **13:** 116–117.

———. 1947. Catálogo de la flora venezolana. Vol. 2. Solanaceae, pp. 347–382. Caracas, Venezuela.

Prance, G. T. 1973. Phytogeographic support for the theory of Pleistocene forest refuges in the Amazon Basin, based on evidence from distribution patterns in Caryocaraceae, Chrysobalanaceae, Dichapetalaceae, and Lecythidaceae. Acta Amazonica **3(3):** 5–28.

———. 1982. Forest refuges: evidence from woody angiosperms. Pages 137–157 *in* G. T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

———. 1987. Biogeography of neotropical plants. Pages 46–65 *in* T. C. Whitmore & G. T. Prance (eds.), Biogeography and Quaternary history in tropical America. Oxford University Press, New York.

Prévost, M.-F. 1978. Modular construction and its distribution in tropical woody plants. Pages 223–231 *in* P. B. Tomlinson & M. H. Zimmermann (eds.), Tropical trees as living systems. Cambridge University Press, Cambridge, England.

Pringle, G. J. 1991. The cytogenetics of the tamarillo, *Cyphomandra betacea* (Cav.) Sendt., and its wild relatives. Ph.D. thesis, University of Auckland, Auckland, New Zealand.

——— **& B. G. Murray.** 1991a. Karyotype diversity and nuclear DNA variation in *Cyphomandra.* Pages 247–252 *in* J. G. Hawkes, R. Lester, M. Nee & N. Estrada (eds.), Solanaceae III: taxonomy, chemistry, evolution. Royal Botanic Gardens, Kew, U.K.

——— **&** ———. 1991b. Interspecific hybridisation involving the tamarillo, *Cyphomandra betacea* (Cav.) Sendt. (Solanaceae). New Zealand J. Crop Hort. Sci. **19:** 103–111.

——— **&** ———. 1991c. Reproductive biology of the tamarillo, *Cyphomandra betacea* (Cav.) Sendt. (Solanaceae), and some wild relatives. New Zealand J. Crop Hort. Sci. **19:** 263–273.

Rao, V. N. M. & A. A. Rauoof. 1970. Pollen and pollination studies in tree tomato (*Cyphomandra betacea* Sendt.). J. Palynology **6:** 70–72.

Raven, P. H. & D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. **61:** 539–673.

Reitsma, T. 1969. Size modification of recent pollen grains under different treatments. Review of Paleobotany and Palynology **9:** 175–202.

Roe, K. E. 1967. Chromosome size in *Solanum* and *Cyphomandra*: taxonomic and phylogenetic implications. Amer. Naturalist **101:** 295–297.

———. 1972. A revision of *Solanum* section *Brevantherum* (Solanaceae). Brittonia **24:** 239–278.

Roubik, D. W. & J. E. Moreno P. 1991. Pollen and spores of Barro Colorado Island. Missouri Botanical Garden, St. Louis, MO.

Ruiz, H. & J. A. Pavón. 1799. Fl. peruv. Vol. 2. Gabrielis de Sancha, Madrid.

Rusby, H. H. 1896. On the collections of Mr. Miguel Bang in Bolivia–Part III. Mem. Torrey Bot. Club **6:** 1–130.

———. 1899. An enumeration of the plants collected by Dr. H. H. Rusby in South America, 1885–1886 - XXVII. Bull. Torrey Bot. Club **26:** 189–200.

———. 1907. An enumeration of the plants collected in Bolivia by Miguel Bang. Part 4. Bull. New York Bot. Gard. **4:** 309–470.

———. 1912. New species from Bolivia, collected by R. S. Williams–2. Bull. New York Bot. Gard. **8:** 89–135.

———. 1920. Descriptions of three hundred new species of South American plants. Publ. by the author, N.Y.

Safford, W. E. 1917. Food plants and textiles of ancient America. Pages 12–30 *in* Proc. 19th Intl. Congress of Americanists, Washington, D.C.

Sandwith, N. Y. 1938. The correct name of the "tree tomato." Chron. Bot. **4:** 225.

Sazima, M. & S. Vogel. 1989. *Cyphomandra* species (Solanaceae) visited by male euglossine bees: floral fragrances as a reward for pollen dispersal. Abstract 9, p. 52. Symposium Morphologie, Anatomie und Systematik, Wien.

Schreiber, K. 1979. The steroid alkaloids of *Solanum.* Pages 193–202 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

Schultes, R. E. & R. F. Raffauf. 1990. The healing forest. Dioscorides Press, Portland, Oregon.

Seithe, A. 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. Bot. Jahrb. Syst. **81:** 261–335.

———. 1979. Hair types as taxonomic characters in *Solanum.* Pages 307–319 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

Sendtner, O. 1845. De *Cyphomandra,* novo Solanacearum genere tropicae Americae. Flora **28:** 161–176.

———. 1846. Solanaceae. Pages 1–228 *in* C. P. F. von Martius, Fl. bras. Vol. 10. C. Wolf, Munich.

Simpson, B. B. & J. Haffer. 1978. Speciation patterns in the Amazonian forest biota. Ann. Rev. Ecol. Syst. **9:** 497–518.

——— **& J. L. Neff.** 1981. Floral rewards: alternatives to pollen and nectar. Ann. Missouri Bot. Gard. **68:** 301–322.

Smith, J. D. 1899. Undescribed plants from Guatemala and other Central American republics. XXI. Bot. Gaz. (Crawfordsville) **27:** 434–443.

———. 1903. Enum. pl. guatem. Part 6. H. N. Patterson, Illinois.

Smith, L. B. 1965. Herbarium Notes, II. Phytologia **12:** 249–251.

——— **& R. J. Downs.** 1964. Notes on the Solanaceae of southern Brazil. Phytologia **10:** 422–453.

——— **&** ———. 1966. Solanáceas. Pages 1–321 *in* P. R. Reitz (ed.), Flora Ilustrada Catarinense. Itajaí, Brasil.

Soares, A. A., L. A. de O. Campos, M. F. Vieira & G. A. R. de Melo. 1989. Relações entre *Euglossa* (*Euglossella*) *mandibularis* Friese, 1899 (Hymenoptera, Apidae, Euglossini) e *Cyphomandra calycina* (Solanaceae). Ci. e Cult. **41:** 903–905.

Souèges, R. 1907. Développement et structure du tégument séminal chez les Solanacées. Ann. Sci. Nat. Bot., Ser. 9, **6:** 1–124.

Stafleu, F. A. & R. S. Cowan. 1979. Taxonomic literature. Vol. 2, H-Le. 2nd ed. Bohn, Scheltema & Holkema, Utrecht.

Standley, P. C. 1927. New trees collected in Panama by George P. Cooper and George M. Slater. Trop. Woods **10:** 47–51.

———. 1928. Solanaceae. Flora of the Panama Canal Zone. Contr. U.S. Natl. Herb. **27:** 327–333.

———. 1929. Studies of American plants. I & II. Publ. Field Columbian Mus., Bot. Ser. **4:** 197–345.

——— **& C. V. Morton.** 1938. Solanaceae. Pages 1035–1099 *in* P. C. Standley, ed., Flora of Costa Rica. Field Mus. Nat. Hist., Bot. Ser. **18(3).**

——— **& J. A. Steyermark.** 1940. Studies of Central American Plants. II. Field Mus. Nat. Hist., Bot. Ser. **22(5):** 323–396.

Stern, W. L., K. J. Curry & W. M. Whitten. 1986. Staining fragrance glands in orchid flowers. Bull. Torrey Bot. Club **113:** 288–297.

Steyermark, J. A. 1966. Botanical novelties in the region of Sierra de Lema, Estado Bolivar, Venezuela - III. Bol. Soc. Venez. Ci. Nat. **26:** 411–452.

———. 1979. Plant refuge and dispersal centres in Venezuela: their relict and endemic element. Pages 185–221 *in* K. Larsen & L. Holm-Nielsen (eds.), Tropical botany. Academic Press, New York.

———. 1982. Relationships of some Venezuelan forest refuges with lowland tropical floras. Pages 182–220 *in* G. T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

——— **& O. Huber.** 1978. Flora del Avila. Sociedad Venezolana de Ciencias Naturales, INCAFO, Caracas, Venezuela.

Symon, D. E. 1979. Sex forms in *Solanum* (Solanaceae) and the role of pollen collecting insects. Pages 385–397 *in* J. G. Hawkes, R. N. Lester & A. D. Skelding (eds.), The biology and taxonomy of the Solanaceae. Academic Press, London.

Tétényi, P. 1987. A chemotaxonomic classification of the Solanaceae. Ann. Missouri Bot. Gard. **74:** 600–608.

Toledo, V. M. 1982. Pleistocene changes in the vegetation of tropical Mexico. Pages 93–111 *in* G. T. Prance (ed.), Biological diversification in the tropics. Columbia University Press, New York.

Vandelli, D. 1788. Fl. lusit. bras. spec. Academico-Regia, Coimbra, Portugal.

Vasconcellos-Neto, J. 1991. Interactions between Ithomiine butterflies and Solanaceae: feeding and reproductive strategies. Pages 291–313 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes & W. W. Benson (eds.), Plant-animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley & Sons, New York.

Vellozo, J. M. C. 1829. Fl. flumin. Vol. 2. Rio de Janeiro, Brazil.

Vignoli, L. 1945. Sterilita e moltiplicazione vegetativa in *Jaborosa*, *Artemisia*, *Hemerocallis*. Nuovo Giorn. Bot. Ital., n. Ser. **52:** 1–10.

Vogel, S. 1990. The role of scent glands in pollination: on the structure and function of osmophores. Amerind Publishing Co., New Delhi, India.

Waisel, Y. 1972. Biology of halophytes. Academic Press, New York.

Walpers, W. G. 1844. Solanaceae. Repert. Bot. Syst. **3:** 5–126. Leipzig.

———. 1847. *Cyphomandra.* Repert. Bot. Syst. **6:** 576–579.

Wettstein, R. v. 1891. Solanaceae. Pages 4–38 *in* A. Engler & K. Prantl (eds.), Nat. Pflanzenfam., Div. 4, Vol. 3b. W. Engelmann, Leipzig.

Whalen, M. D. 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum.* Gentes Herb. **12:** 179–282.

Wheelwright, N. T., W. A. Haber, K. G. Murray & C. Guindon. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. Biotropica **16:** 173–192.

Whitaker, T. W. 1933. The chromosome complement of *Cyphomandra betacea.* J. Arnold Arbor. **14:** 113–117.

Whitmore, T. C. & G. T. Prance (eds.) 1987. Biogeography and Quaternary history in tropical America. Oxford University Press, New York.

Williams, N. H. 1978. A prelimiary bibliography on euglossine bees and their relationships with orchids and other plants. Selbyana **2:** 345–355.

———. 1982. The biology of orchids and euglossine bees. Pages 119–171 *in* J. Arditti (ed.), Orchid biology: reviews and perspectives, Volume 2. Cornell University Press, Ithaca, NY.

——— **& C. H. Dodson.** 1972. Selective attraction of male euglossine bees to orchid floral fragrances and its importance in long-distance pollen flow. Evolution **26:** 84–95.

Williams, W. G., G. G. Kennedy, R. T. Yamamoto, J. D. Thacker & J. Bordner. 1980. 2-Tridecanone: a naturally-occurring insecticide from the wild tomato *Lycopersicon hirsutum* f. *glabratum.* Science **207:** 888–889.

NUMERICAL LIST OF TAXA

1. *Cyphomandra acuminata* Rusby
2. *Cyphomandra benensis* Britton
3. *Cyphomandra betacea* (Cav.) Sendtn.
4. *Cyphomandra cajanumensis* (HBK) Walp.
5. *Cyphomandra calycina* Sendtn.
6. *Cyphomandra corymbiflora* Sendtn.
    a. subsp. *corymbiflora*
    b. subsp. *mortoniana* (Sm. & Downs) Bohs
7. *Cyphomandra diploconos* (Mart.) Sendtn.
8. *Cyphomandra divaricata* (Mart.) Sendtn.
9. *Cyphomandra diversifolia* (Dunal) Bitter
    a. subsp. *diversifolia*
    b. subsp. *chlorantha* (Rusby) Bohs
10. *Cyphomandra dolichocarpa* Bitter
11. *Cyphomandra endopogon* Bitter
    a. subsp. *endopogon*
    b. subsp. *guianensis* Bohs
12. *Cyphomandra foetida* Bohs

13. *Cyphomandra fragilis* Bohs
14. *Cyphomandra hartwegii* (Miers) Walp.
    a. subsp. *hartwegii*
    b. subsp. *ramosa* Bohs
15. *Cyphomandra heterophylla* Taubert
16. *Cyphomandra hypomalaca* Bitter
17. *Cyphomandra obliqua* (Ruiz & Pav.) Sendtn.
18. *Cyphomandra oblongifolia* Bohs
19. *Cyphomandra ovum-fringillae* Dunal
20. *Cyphomandra pendula* (Ruiz & Pav.) Sendtn.
21. *Cyphomandra pilosa* Bohs
22. *Cyphomandra pinetorum* Smith & Downs
23. *Cyphomandra premnifolia* (Miers) Dunal
24. *Cyphomandra rojasiana* Standl. & Steyermark
25. *Cyphomandra sciadostylis* Sendtn.
26. *Cyphomandra sibundoyensis* Bohs
27. *Cyphomandra stellata* Bohs
28. *Cyphomandra sycocarpa* (Mart. & Sendtn.) Sendtn.
29. *Cyphomandra tegore* (Aubl.) Walp.
30. *Cyphomandra tenuisetosa* Bitter
31. *Cyphomandra tobagensis* Sandwith
32. *Cyphomandra uniloba* Rusby

LIST OF EXSICCATAE

Acosta Solís, M., 6361 (14a); 8856, 9482 (3); 12715 (14a); 12847 (16); 13906, 13971 (14a).
Afriastini, J. 772 (3).
Agudelo, M. & J. Klevers, 78 (14a).
Albuquerque, B. de et al., 1384 (12).
Allen, C., 488 (14a).
Allen, P., 919, 5241, 6617 (14a).
Almeda, F., 344 (14a).
Almeda, F. & K. Nakai, 4019 (14a).
Almeida, J. & T. Santos, 233 (8).
Alston, A., 14158 (3).
Amaral, et al., 1250 (29).
Ancuash, E., 1273, 1512 (11a).
Andrade, J. de, 3357 (3).
Anglade, L., 818, s.n. (3).
Archer, W., 590, 1759 (14a).
Archer, W. & E. Mesa, 838 (3).
Argent, G. et al., 6378 (18).
Aristeguieta, L., 5934 (9a).
Aristeguieta, L. & F. Tamayo 4457 (14a).
Asplund, E., 9221 (27); 9432 (11a); 9524 (14a); 12136 (11a); 13019 (13); 13049 (20); 13386 (30); 14135, 14568 (17).
Asunción Leveau, J., 27, 278 (11a).
Atamparo, 1021 (7).
Aublet, J. B. C. F., s.n. (29).
Ayala, F., 2140 (21); 2976 (27).
Ayala, F. & E. Arevalo, 4230 (17).
Aymard, G., 4782, 4799 (31).
Azanbuya, D., 34 (23).
Bailey, L., s.n. (3).
Bailey, L. & E. Bailey, 302 (14a); 711 (7); 770 (14a); 9550 (3).
Bakhuizen van den Brink, R., 1560, 2786 (3).
Bang, M., 1535 (32); 2281 (1); 2337 (mixed collection of 3 & 32); s.n. (3); s.n. (32).
Baptista, L. et al., 27625 (6a); 34090 (7).
Barbour, P., 2704 (11); 4366 (11a); 4785 (13); 5788 (30).
Barros, F. de, 596 (7).
Barrus, M., 74 (3).
Bautista, H., 530 (28).
Beaman, J., 5138, 5620, 6127 (14a).
Beaman, J. & C. Alvarez, 5855 (14a).
Beck, S., 3605 (1); 6079 (32); 8782 (1); 9284 (32).
Beck, S. & M. Liberman, 9675 (3).
Benitez de Rojas, C., 1576 (14a); 2744 (9a).
Berlin, B., 44, 120, 284, 473, 1974, 2009, 3513 (11a).
Bernardi, A., 282 (9b); 548 (3); 1778 (9b); 5702 (14a).
Bernardi, L., 18825 (6a).
Bernardi, L. et al., 16817 (32).
Bernoulli & Cario, 2333 (24).
Bertero, D., 1325 (3).
Bertoni, M., 1962, 2087, 2787 (6a).
Billiet, F. & B. Jadin, 1343 (11b).
Blacke, G., 46–62 (27).
Blanchet, J., 124 (8); 2857 (19); s.n. (8).
Blum, K. & J. Duke, 2192 (14a).
Boerboom, J., 9564, 9564a, 9605 (14a); (LBB) 12032 (29).
Bohs, L., 1599 (3); 1643, 1644, 1645 (14b); 1687 (3); 2192 (3); 2210, 2211, 2214 (14a); 2335(7); 2338 (1); 2341 (9a); 2343(6a); 2442 (14a).
Bohs, L. & J. Schunke, 2159 (17); 2160 (11a); 2161 (30); 2162 (11a); 2163 (30); 2164 (12); 2165 (20); 2166 (11a); 2167 (20); 2169 (21).
Bohs, L. & P. Juajibioy, 2222 (26).
Bohs, L. & G. McPherson, 2312 (10); 2318 (14a).
Bohs, L. & J. Sperry, 2330 (9b).
Boom, B. K., 26628 (3).
Boom, B. M., 4054, 4978 (18).
Borgmann, E., 347 (3).
Bornmüller, A., 620 (6a).
Boschwezen (BW), 6686 (14a).
Boucher, D., 424 (14a).
Bowie & Cunningham, s.n. (23).
Brade, A., 8000 (8); 8002 (7); 11131 (23); 18611 (8).
Braga, R. & H. Moreira Filho, 221 (6a).
Brahe, C. et al., 18C703 (14a).
Brand, J. & A. Cogollo, 73, 151 (14a).
Brandbyge, J. & E. Asanza, 30136 (14a).
Brandbyge, J. et al., 33317, 33342, 33347B, 33465 (14a).
Bredemeyer, s.n. (9a).
Breedlove, D., 11695 (3).
Brenes, A., 4478, 5125, 6044, 16273, 23194 (14a).
Bristan, N., 1009 (14a).
Bristol, M., 777 (3); 1014 (14a); 1119, 1316 (26).
Broadway, W., 3879 (31).
Bruijn, J. de, 1439 (14a).
Buchtien, O., 340 (3); 1276, 1278 (14a); 1423 (20); 1444 (14a); 2233, 3900 (32).
Bunge, A. de, s.n. (3).
Bunting, G. & P. Drummond, 6287 (9b).
Burch, D., 4585 (14a); 6794, 6795 (3).
Burchell, W., 3434, 4731–8 (7).
Burger, W. & T. Antonio, 11005 (9b).
Burger, W. & R. Liesner, 7280 (14a).

Burger, W. & G. Matta, 4749 (14a).
Burger, W. & R. Stolze, 5584 (14a).
Busey, P., 613 (14a).
Buysman, M., 72 (3).
BW, 6686 (14a).
Cabrera, A. & H. Fabris, 16014 (3).
Cabrera, A. et al., 5023 (14b); 27868 (3); 28885 (6a); 30923 (3).
Cadena, M. & G. Pena, s.n. (3).
Calderon, et al., 2849 (11a).
Callejas, R. et al., 1997, 3575 (14a).
Calzada, J., 2411 (3).
Camp, W., E–984 (11a); E–1733 (4); E–3675 (14a).
Cantonspark, 195 (3).
Capriglioni, T., 1657 (7); s.n. (23).
Cardenas, M., 1555 (32); 5268 (2).
Carpenter, J., 488 (3).
Carrasquilla, L. & R. Mendoza, 1346 (14a).
Carvalho, L. de, 509 (8).
Castelnau, M. de, s.n. (17).
Castillo, G. et al., 216 (3).
Cavanilles, A., s.n. (3).
Cazalet, P. & T. Pennington, 5026 (14a).
Cedillo, R. & J. Calzada, 57 (14a).
Cerón, C., 1996 (27); 2143 (21); 2218 (3); 3485 (27); 6090 (21); 6702 (13).
Cerón, C. & M. Cerón, 4518, 4632 (27); 4654 (21); 4671 (13).
Cerón, C. & F. Hurtado, 4203 (21); 6667 (14a).
Cerón, C. & C. Iguago, 5280, 5418 (27); 5603 (21).
Cerón, C. et al., 4322 (11a).
Chacon, I. & G. Herrera, 1734 (14a).
Chase, N., 1246 (3).
Cid, C., 2894 (12).
Cid, C. & B. Nelson, 2659 (30).
Cid, C. et al., 4505, 5004 (11a).
Clewell, A. & E. Tyson, 3309 (14a).
Close, J., s.n. (14a).
Clute, W., 220 (3).
Coêlho, et al., 1688 (17).
Collins, G., 102 (3).
Conrad, J. & W. Dietrich, 2057 (7).
Cook, O. & C. Doyle, s.n. (14a).
Cook, O. & G. Gilbert, 770, 1101 (3).
Cooper, G., 398 (9b).
Cooper, G. & G. Slater, 181 (14a).
Cooper, J., 10215 (14a).
Cordeiro, J. & J. Silva, 474 (6a).
Córdoba, J., 385 (3).
Core, E., 1184 (3).
Correa, M. & R. Dressler, 1050, 1132 (14a).
Correa, M. et al., 3437 (14a).
Costa, A., 2927 (25).
Cowan, R., 1476 (31); 38154 (29).
Cremers, G., 7955, 8165 (14a).
Croat, T., 7628 (17); 9016, 10196, 11774, 12934, 13835, 14508, 16579 (14a); 18023 (11a); 18045 (17); 18620 (11a); 19407 (17); 20249 (11a); 21452 (9a); 22024 (14a); 43967 (3); 58189 (11a); 58835 (21).
Cuadros, H., 680, 1507 (14a).
Cuatrecasas, J., 8751 (21); 10792 (27); 11085 (21); 12896, 13421 (9b); 14382, 14826 (14a); 21969 (3); 23917 (4).
Cuatrecasas, J. & V. Patiño, 27469 (14a).
D'Alleizette, C., 5107 (25); s.n. (3).
Daniel, Bro., 3868 (14a).
Däniker, A., 3129 (3).
Danser, B., 6039 (3).
D'Arcy, W., 3973 (14a); 5910 (3); 14047 (21).
D'Arcy, W. & G. Bejarano, 13870 (3).
D'Arcy, W. & T. Croat, 13589 (14a).
D'Arcy, W. & J. D'Arcy, 6131, 6156 (14a).
D'Arcy, W. et al., 3949, 3958 (14a).
Davidse, G., 10418 (7).
Davidse, G. et al., 11077 (7).
Dawe, M., 805 (14a).
Dawkins, H., 721 (3).
Debouck et al., DGD2948 (14a).
Delforte, R., 7 (23).
Delgado, 7 (9a).
Denslow, J., 79–71 (14a).
Devia, W., 641 (3)
Devia, W. & E. Moreno, 70 (3).
Devia, W. & F. Prado, 2119 (14a).
DeVries, P., 36 (14a).
Díaz, C. & N. Jaramillo, 1 (18).
Díaz, C. & H. Osores, 2980 (20).
Díaz, S. et al., 484 (14b).
Dodson, C., 5136 (14a).
Dodson, C. & P. Dodson, 11794 (3); 15395 (4).
Dodson, C. & M. Fallen, 7765 (14a).
Dodson, C. & A. Gentry, 6554, 12367 (14a).
Dodson, C. & F. Valverde, 6952 (16).
Dodson, C. et al., 7223, 7531 (14a); 8731 (16).
Dombrowski, L., 2630 (8); 4922 (6a).
Dombrowski, L. & Y. Kuniyoshi, 1910 (6a); 2175 (8).
Dominguez, F., 150 (11a).
Dorantes, B., 3474 (14a).
Dorantes, B. & M. Cházaro, 3105 (14a).
Dorantes, J. et al., 3610 (14a).
Dosedlie-Grotovitz, H., 101 (3).
Dress, W., 9466, 9474, 9555 (3).
Dressler, R., 3070, 3586 (14a).
Drummond, B., 7312 (14a); 7348 (11a).
Drummond, R. & J. Hemsley, 2408 (3).
Dryer, V., 1480 (14a).
Duarte, A., 5424 (23).
Ducke, A., RB(22586) (18); RB(22588) (17).
Dugès, A., 393A (3).
Duke, J., 4107, 4847, 5396, 12167, 12896, 14260, 14739 (14a).
Duke, J. & N. Bristan, 8283 (14a).
Duke, J. & J. Kirkbride, 14026 (14a).
Dumont, K. et al., VE–7489 (31).
Dunal, M. F., s.n. (7).
Dunlap, V., 264 (14a).
Duque-Jaramillo, J., 1707, 2672-A (3).
Dusén, P., 2029 (22); 2485 (8); 2923 (23); 3011 (8); 3057 (6a); 7083 (8?); 7098 (22); 7284 (7); 7421 (8); 7422 (7); 7525 (23); 7526 (8); 7630 (7); 9312 (6a); 9404 (22); 9522 (23); 11861 (6a); 14400 (8); 15890 (25); 15949, 17509 (8); 17510 (7).
Duss, A., 4429 (3).
Dwyer, J., 6257 (3); 7065A (14a).
Dwyer, J. & J. Dwyer, 10273 (14a).

Dwyer, J. & A. Gentry, 9485 (14a).
Dwyer, J. & B. MacBryde, 9770 (13).
Eastwood, A., s.n. (3).
Ebinger, J., 605 (14a).
Edwall, G., 1729 (7); 4422 (25).
Eggeling, W., 3094 (3).
Eggers, H., 15069 (16).
Eiten, G. & L. Eiten, 6688 (22).
Ekman, E., 842, 843 (25); 844 (6a).
Emelen, A. van, 5 (7).
Encarnación, F., 26446 (11a).
Escobar, L., 965 (14a).
Espinal, S., 838 (14a), 1959 (14b).
Espinoza, S. & T. Coba, 684 (27).
Evinger, E. & W. Hodge, 441 (16?).
Eyerdam, W., 24747 (32); 25355 (3).
Fabris, H., 3411 (3).
Fagerlind, F. & G. Wibom, 686, 1634 (14a).
Fairchild, D. & Dorsett, 325 (7).
Fendler, A., 1009, 1015 (9a); 2097 (14a).
Fernández-Pérez, A., 6863 (11a).
Ferreyra, R., 959, 982 (11a); 2708 (3); 4407 (11a); 4523 (20); 4789 (17); 7109 (3).
Fiebrig, K., 5823, 5864, 6456 (7).
Fielding, s.n. (5).
Figureido, E., s.n. (7).
Filskov, P. et al., 37010 (3).
Fleischmann, E., 140 (2); 155, 157 (32).
Fleming, G., 925a (3).
Folsom, J., 3056, 3733 (14a).
Folsom, J. & L. Skog, 2471 (14a).
Fontella, J. & C. Moura, 110 (7).
Forero, E. et al., 1711, 1941 (14a); 5569 (9b); 5642, 6647, 7543 (14a).
Foresta, H. de, 669 (11b).
Fosberg, F., 19641 (9b); 20136 (14b); 28993 (17).
Foster, R., 1784 (14a); 2535, 5428 (18); 9267 (13).
Foster, R. & J. Terborgh, 5167 (18).
Foster, R. & E. Vivar, 13272 (12).
Foster, R. et al., 3455 (18); 10630 (20).
Fournet, 309 (14a).
Fournier, L., 575 (14a).
Frame, D. et al., 216 (11a).
Franck, C., 1198 (3).
Frankie, G., 11a (14a).
Freitas, 122 (18).
Fries, R., s.n. (3).
Friis, I. et al., 2187 (3).
Frodin, D., 657 (3).
Fróes, R., 20644, 21072 (17).
Gaczo, s.n. (7).
Gade, D., s.n. (3).
Gamerro, J., 1337 (3).
Gamerro & Toursakisian, 102 (6a).
García-Barriga, H., 5125A (14a); 10896 (3); 12464 (14a); 21286, 21339 (3).
García-Barriga, H. et al., 18935 (14a).
Gardner, G., 5041 (5).
Garwood, N. et al., 747 (14a).
Gaudichaud, C., 315 (25); 514, 516 (7).
Gay, H., 20945 (3).
Gehrt, A., 4661 (15).
Gentle, P., 4237 (24).
Gentry, A., 463, 1208, 4785, 9867, 10140 (14a); 12517 (21); 30988 (16).
Gentry, A. & J. Brand, 36902 (14a).
Gentry, A. & J. Dwyer, 4820 (14a).
Gentry, A. & H. Leon, 20213 (14a).
Gentry, A. & E. Renteria, 24003 (14a).
Gentry, A. & D. Smith, 35996 (27?).
Gentry, A. & K. Young, 31787, 32035 (13); 32038 (30).
Gentry, A. et al., 12088 (14a); 15689 (18); 17027 (14a); 22200, 25388 (17); 25674 (30); 32110 (11a); 32421 (14a); 36593 (11a); 39539 (27); 55935 (17); 56222 (18); 61315 (3).
Gentry, J., 3730 (14a).
Gentry, J. & W. Burger, 2741 (3); 2766, 2767, 2840, 2851, 2890, 3017 (14a).
Gevieski, A., 50 (7).
Gillett, J., 17583 (3).
Gilli, A., 427 (3).
Gines, H., 4078 (3).
Glaziou, A., 3079 (5); 3080 (7); 7789 (3); 8870 (8); 11387 (5); 11387a (25); 12096 (5); 12097 (15); 16293 (7); 18403 (8); 18404 (5); s.n. (15).
Gleason, H. & M. Cook, Y-3 (3).
Godfrey, R., 66847, 67278 (14a).
Godoy, J. de, s.n. (5).
Gomara, R., 5130 (3).
Gómez, L., 2209 (14a); 20734, s.n. (3).
Gómez-Pompa, A., 4450 (14a).
Gonçalves, P., s.n. (7).
González, J., 29 (6a).
Goudot, J., 101, s.n. (3); s.n. (4); s.n. (14a).
Granville, J. de, 2220, 4901, 4941 (11b); 5335 (29).
Grenand, P., 808 (11b).
Grierson, A. & D. Long, 3170 (3).
Guerra, et al., 275 (6a).
Guimarães, E. & L. Peixoto, 323 (29).
Gunther, E., 5851 (3).
Gurgel, 14608 (7).
Gutiérrez, G. & F. Barkley, 17C119 (14a).
Haenke, T., 1783 (17).
Hage, J. & E. dos Santos, 1490 (28).
Hahn, W., 220 (14a).
Hallier, H., 17 (3).
Hammar, A., 5882 (25).
Hammel, B., 1708 (14a); 2364 (10); 6010 (14a).
Handro, O., s.n. (8).
Hansen, B. & M. Nee, 7611 (14a).
Happel, R. & D. Neill, 01 (14a).
Harling, G., 4899 (4); 6072 (14a).
Harling, G. & L. Andersson, 11995 (12); 13858, 17372 (21); 17377 (12); 17743 (11a).
Harris, W., 484, s.n. (3).
Hart, J., 568 (17); 956 (3); 1211 (27).
Hart, J. H., s.n. (3).
Hartman, R., 12047 (14a).
Hartweg, C. T., 1297 (14a).
Hatschbach, G., 511 (25); 1514 (7); 1593 (6b); 2049 (8); 3485, 4132 (6a); 6470 (22); 9363 (6a); 9678 (7); 10097 (6a); 10818, 11328 (22); 11897 (7); 11903 (22); 11922 (6b); 13037 (6a); 13144 (22); 13204 (7); 14964 (6a); 15323 (8); 15393, 17440 (6a); 17820 (8); 17834 (22);

17980 (8); 19786 (6a); 20195 (8); 22306, 22369, 22693, 22700 (6a); 23256 (25); 23265 (7); 23266 (8); 24443, 24958 (6a); 26504 (6a); 27625 (22); 31001 (7); 32843, 35537, 37342, 37351 (6a); 40309 (25); 40426 (8); 40568 (25); 40631 (22); 41913 (8); 42696 (6a); 43280 (8); 43442 (6a).
Hatschbach, G. & J. Cordeiro, 52673 (6a).
Hatschbach, G. & J. Fontella, 20821 (7).
Hatschbach, G. & O. Guimarães, 19741, 20488 (6a); 20494 (25); 20496 (6a); 25577 (22).
Hatschbach, G. & C. Koczicki, 20757 (22); 20903 (8).
Hatschbach, G. & R. Kummrow, 45544 (22).
Hatschbach, G. & E. Pereira, 10383, 10572 (6a).
Hatschbach, G. & J. Silva, 51485 (6a).
Hatschbach, G. et al., 35852 (22).
Haught, O., 1617, 2063, 2482 (14a); 2859 (9b); 3786, 4701, 5542 (14a).
Hazlett, D. & F. Coe, 2745 (14a).
Heiner, A., 221 (25); s.n. (8).
Heiser, C., s.n. (3).
Hernandez, C. et al., 49 (3).
Hernández, H., 177 (14a).
Hernandez, H. & González, 1797 (14a).
Herrera, F., 2984 (3).
Herrera, G. et al., 421 (14a).
Hochreutiner, B., 2602 (3).
Hodge, W., 6713 (3).
Hoehne, F., 3480, 4702 (7); s.n. (3); s.n. (8).
Holm-Nielsen, L. et al., 19625 (21); 19662, 19668 (27); 21195 (14a); 21721 (11a); 22475, 25336 (14a).
Holton, I., 555 (14a); s.n. (3).
Hottle, W., 53 (14a).
Huashikat, V., 154 (11a); 949 (11a?).
Humbles, J., 6221 (14a).
Humboldt, A. & A. Bonpland, 3410 (4); s.n. (9a).
Hunnewell, F., 19065 (14a).
Hunziker, A. et al., 15458 (25).
Hurtado, F. & A. Alvarado, 335 (14a); 341, 343 (13); 945 (14a).
Hurtado, F. et al., 170 (14a); 1287 (21); 2092 (14a).
Hutchison, P. & K. von Bismarck, 6528 (4).
Ibarra, G., 20 (14a).
Ibarra, G. & R. Cedillo, 1012 (14a).
Ibarra, G. et al., 1609 (14a).
Idrobo, J., 1816, 1914 (14a); 4725 (17); 4760, 8382 (14a).
Idrobo, J. et al., 2901 (14b).
Iltis, H., s.n. (3).
Iltis, H. & M. Iltis, E–142 (14a).
Iltis, H. et al., 1068, s.n. (3).
Irvine, D., 149, 202, 287 (21); 354 (13); 435 (21); 628 (14a).
Jack, J., 7291 (3).
Jacobs, B., 2124 (14a).
Jacobs, M., 4440 (3).
Játiva, C. & C. Epling, 364 (14a).
Jenkins, R., 318 (14a).
Jiménez, A., 575, 3005, 3457, 4153 (14a).
Johnson, L., 8350 (3).
Jones, I., s.n. (7).
Jones, J. & C. Davidson, 9260 (30).
Jönsson, G., 1008a (22).
Jörgensen, P., 4374 (25).
Judziewicz, E., 3127 (3).
Juncosa, A., 1146 (14a).
Kalbreyer, W., 1019 (3); 1662 (14b).
Kalloo, M., B 1061 (31).
Kanhai (LBB), 13370 (14a).
Katende, A., 530 (3).
Kayap, R., 642 (27?); 1185, 1434, 2029 (11a).
Kenoyer, L., 511 (14a).
Kiehl, J., 4016 (25).
Kiesling, R. et al., 1155 (3).
Killip, E., 39617 (3); 39968 (14a).
Killip, E. & A. Smith, 22924, 26605 (30); 26829 (13); 26872 (17); 28005 (30); 28182 (11a); 28703, 29093 (30); 29863 (27).
King, S., 511 (27).
Klein & Eskuche, 9059 (6a).
Klein, R., 255 (7); 3746 (8); 3754 (7); 4207, 4223, 4371, 5733 (6a).
Klein, R. & A. Bresolin, 8064 (7).
Klug, G., 52 (27); 1685 (14a); 1776 (13); 1857 (21); 2560 (11a); 3600 (13); 3873 (30); 4192 (17).
Knapp, S. & J. Alcorn, 7558 (3).
Knapp, S. & J. Mallet, 5684, 6184 (14a); 6187 (21); 6293 (13); 6448, 6527, 6536 (30); 6560 (3?); 6762 (31); 6769 (9a).
Knapp, S. & R. Schmalzel, 5257 (14a).
Knapp, S. et al., 6314 (3); 6315 (17).
Knight, D., 673 (16).
Køie, M., 4844 (14a).
Kottsberg, s.n. (3).
Koyama et al., 16022 (3).
Krapovickas, A. & C. Cristobal, 33649, 35365 (25).
Krapovickas, A. & A. Schinini, 38319 (6a); 38854, 39059 (3).
Krapovickas, A. et al., 21557 (25).
Krug, 4883 (25).
Krukoff, B., 1456 (20?); 5461, 6319 (18); 6345, 8081 (11a).
Kuhlmann, J., 3 (28); 747 (17); 1769 (8); s.n. (5); s.n. (8); s.n. (28).
Kuhlmann, M., 75 (25); 1384 (7); 1400 (25); 2168, 2206, 2927 (22); 2928 (5); 3025 (7).
Kuhlmann, M. & S. Jimbo, 60 (29).
Kujikat, A., 168 (27); 252 (11a).
Kummrow, R., 136, 1262 (6a); 1647 (7); 1990 (6a).
Kummrow, R. & A. Soares, 2945, 3082, 3083 (6a); 3095 (7); 3102 (8); 3117 (25); 3118 (22); 3141 (25?).
Kuntze, O., s.n. (3)
Kvist, L., 40191 (14a).
Lalande, s.n. (5).
Landrum, L., 2444, 2711 (6a); 2865 (7); 3914 (8).
Langsdorff, G., s.n. (5).
Lanjouw, J. & J. Lindeman, 3239 (18).
Laskowski, C., 1456 (14a).
Lasser, T., 52 (3).
Lawrance, A., 118, 579 (14a).
LBB, 8285, 9313 (14a); 12032 (29); 13370 (14a).
Legname, P. & A. Cuezzo, 5872C (3).
Lehmann, F., 6433 (3); 6988, 7564 (14a); 7818 (3).
Leitão, H. et al., 11815 (25); 13119, 13135 (7).
Leite, J., 3666 (25).
Lent, R., 306, 1873 (14a).

Lent, R. et al., 3419 (14a).
León, H., 549 (14a).
León, J., 1239 (14a); 2855 (3).
Leon Arteta, R., s.n. (3).
Lewis, W. et al., 5293 (14a); 10126 (21); 10499 (27); 11660 (17); 12148 (11a); 12176 (17); 12281 (11a); 12683 (21); 13236 (17); 13326 (13); 13686, 14008 (11a); 14406 (21).
Lhotsky, J., s.n. (8).
Liesner, R., 226 (14a); 349 (9b); 510, 1063, 2189, 3036, 5094, 5128 (14a).
Liesner, R. & A. González, 10877 (9b).
Liesner, R. et al., 15388 (14a).
Lindberg, 171 (8); 172 (25).
Lindeman, J., 5535 (18); 6176 (29); 6812 (14a).
Lindeman, J. & J. de Haas, 2517 (6a); 4970 (7).
Lindeman, J. et al., 9436, (ICN)8164, (ICN)20847 (6a).
Linden, J., 7 (9a).
Lisbôa, A., s.n. (23?).
Little, E., 6173 (14a); 8108 (14b).
Little, E. et al., 303 (27).
Lleras, E. et al., P17459 (17).
Lockhart, s.n. (23).
Löfgren, A., 644, 1023 (25); 3482 (5); 3483 (22); 4088 (7).
Löfgren, A. & G. Edwall, 2016 (25); 2478 (5).
Lojtnant, B. & U. Molau, 14548 (11a).
López, L., 83–0621 (14b).
Lorentz, P. & G. Hieronymus, 251 (3).
Lot, N., 701 (14a).
Lourteig, A., 2129 (6b); 2222 (6a).
Loveridge, M., 207, 243 (3).
Lowe, R., s.n. (3).
Lowrie, S. et al., 347 (12); 424 (20).
Luederwaldt, H., s.n. (3); s.n. (5).
Lugo, H., 454 (21); 964 (11a); 1548, 1577, 2313, 2327 (21); 2603, 2709, (14a); 2829, 2865 (13); 3104 (21); 3114 (14a); 3613, 3727 (21); 3832, 3878, 4049, 4886, 4938, 5207, 5306, 5498 (11a).
Lundell, C. & E. Contreras, 20681 (24).
Luteyn, J. & T. Croat, 905 (14a).
Lyra, R. de, 67 (7).
Maas, P. & H. Maas, 416 (18).
Maas, P. & G. Martinelli, 3398 (8).
Maas, P. et al., 2359 (14a); P12713 (13); P12812, P13318 (11a).
Macbride, J., 3875 (3); 4141 (20).
MacBryde, B., 842 (20).
MacBryde, B. & J. Dwyer, 1298 (14a).
Macedo, A., 1129 (18).
Madison, M. et al., 4972 (16); 5481 (14a).
Maguire, B. et al., 56771 (11a).
Manara, B., s.n. (9a).
Mangieri, H., 24 (6a).
Mantovani, W., 145 (5).
Markgraf, F., 3122 (7); 3749 (22).
Marmol, L. et al., 8856C, 9242 (3).
Marsh, A., s.n. (3).
Martin, R., 1187 (11a).
Martinelli, G., 4070 (7).
Martinelli, G. et al., 4138 (23).
Martinez, G., 2114, 3001 (14a).
Martius, C., 245 (490 on tag) (7); 330 (25); 491, 492, 493 (7); 496, 497, 498 (8); 621 (28); 626 (8); 1260 (5); 2917 (489 on tag) (17); s.n. (8).
Maruñak, V., 378 (6a).
Mata, G., 367 (14a).
Mathews, 1971 (17); s.n. (3).
Mathias, M. & D. Taylor, 3979 (17).
Mattos, J., 12327 (6a); 12661, 13589 (7); 15502, 15598-b (18).
Mattos, J. & O. Handro, 9523 (25).
Mattos, J. & N. Mattos, 14188 (25); 15123 (8); 15716 (15); 15759 (5).
Matuda, E., 5195, 16215 (3); 16553, 17600 (24); 17746 (3).
Maya, 644 (14a).
McDaniel, S., 5122 (14a).
McDaniel, S. & B. Marcos, 11170 (27).
McDaniel, S. & M. Rimachi, 17800 (17).
McDaniel, S. et al., 2568 (12).
McDowell, T., 524 (14a).
McElroy, J., 93 (14a); 94 (21); 171 (13); 197 (21).
Medina, B., 210 (25).
Melin, D., 329 (17).
Mexia, Y., 5310, 5474a (8); 7161 (14a); 8209 (30); 8235 (17); 8245 (20).
Meyer, G., 237 (18).
Miers, J., 467 (7); 3683 (28); 4531 (8); 4537 (7); 4538 (23); s.n. (7); s.n. (8).
Miller, J. & Sandino, 1106, 1223 (14a).
Molina, A., 20844 (14a).
Molina, A. & A. R. Molina, 12046 (3).
Molina, A. et al., 17720 (14a).
Montes, J., 1744, 3303, 9605, 10110 (25); 27479 (6a); 27483 (25).
Moore, G. et al., 121 (11a).
Moraes, J. de, 735 (8).
Morales, G. & J. Abalo, 377 (14a).
Moreira, C., 26 (22).
Mori, S. & F. Benton, 12862 (8).
Mori, S. & A. Bolten, 8444 (29).
Mori, S. & B. Boom, 14709 (11b).
Mori, S. & R. Dressler, 7788 (10).
Mori, S. & J. Kallunki, 1826, 2348, 5146 (14a); 5905 (10).
Mori, S. et al., 6903 (14a); 10758 (28); 11513 (8); 15028 (11b).
Moricand, M., s.n. (3).
Morillo, G., 2551 (31).
Moritz, J., 1702 (9a).
Morton, J., K852 (3).
Mosén, H., 659, 660 (25); 661 (8); 1559 (25); 2907 (7); 4302 (8).
Mostacedo, B. & R. Foster, 50 (18).
Mowbray, R., 6993, 70231, 703113 (14a).
Muenscher, W., s.n. (3).
Muhlbauer, G., s.n. (3).
Mutis, J., 1973, 1985, 3566 (14b).
Nadruz, M. et al., 469, 563 (5).
Nee, M., 7596 (14a); 23344 (3); 29757 (14a); 30359 (3); 31543 (14a); 35491 (32); 38685 (18).
Nee, M. & M. Hansen, 18648 (3).
Nee, M. & S. Mori, 3557, 3564 (14a).

Nee, M. & Saldias, 36047 (32).
Nee, M. & G. Schatz, 19929 (14a).
Nee, M. & J. Solomon, 30301 (32).
Nee, M. & M. Whalen, 16798 (9a).
Nee, M. et al., 13994 (14a); 35368 (32).
Neill, D. & Zaruma, 7020 (11a).
Neill, D. et al., 7758, 7793 (11a); 7878 (27); 8095 (11 or 14); 8611 (27).
Nelson, B., 822 (20).
Nelson, C. et al., 3097 (14a).
Novaes, J., 197, 199 (25); 6153 (8).
Nunes, 121 (22).
Nuñez et al., 8257 (3).
Ocampo, R., 920, 1039, 2408 (14a).
Occhioni, P., 9209, s.n. (22).
Octavio, O., 68 (8).
Oldeman, R., T.358, T.982, B.1906 (11b).
Oliveira, P., 105 (6a); 704 (8); 813 (6a).
Øllgaard, B. et al., 39210 (13).
Opler, P., 256 (14a).
Orozco, C. et al., 660 (14a).
Pabst, G. & E. Pereira, 6073, 6687 (6a).
Palacios, W., 1961 (27); 2205, 2233 (13); 2851 (27); 3184, 4767 (21); 5225 (14a); 5607 (21); 5621, 5671 (14a); 6170 (21).
Palacios, W. et al., 264 (14a).
Palmer, E., 636 (3).
Pavón, J., s.n. (14a); s.n. (16).
Peckolt, T., 90 (5).
Peixoto, A., 697 (22); 3379 (8?).
Pennell, F., 4593, 4645, 10720 (14a).
Pereira, E., 5514 , 6246 (6a).
Pereira, E. & G. Hatschbach, 7767, 7960 (6a).
Pereira, S. et al., 873 (25).
Pickel, B., 3200 (19); 4319 (7).
Pinheiro, R., 1536 (28).
Pirani, J., et al., 181 (7); 185 (8).
Pires, J. & R. Martin, 9946 ((11a).
Pittier, H., 512, 914 (14a); 5988 (9a); 6097 (3); 7161 (9a); 9059, 10294 (14a); 13520 (9a); 15512 (14a).
Pittier, H. & M. Nakichenovich, 15428 (14a).
Plowman, T., 2180 (14a); 2462 (27); s.n. (3).
Plowman, T. & E. Davis, 4372 (14a); 4929 (1).
Plowman, T. & R. Ramírez, 11191 (20); 11211 (17).
Plowman, T. & J. Schunke, 7458 (21); 7513 (17); 11495 (30); 11550, 11724 (17).
Plowman, T. et al., 2332 (17); 4065 (14a); 6524 (17).
Poeppig, E., 1447B, s.n. (30); 1845 or D2127 (17).
Pohl, J., 500 (8); 504 (28); 3456 (5); s.n. (7).
Polania, 48 (14b).
Porto, M., 1523 (6a).
Porto, P., 1109 (22).
Poveda, L., 125 (14a); 1207 (9b).
Prance, G. & J. Ramos, 6922 (11a).
Prance, G. & N. Silva, 58675 (29).
Prance, G. et al., 2352, 2761, 2984, 5277 (18); 5620 (11a); 7683 (30); 8963 (11a); 11822 (14a or 27); 13740 (11a); 14392 (11a or 27); 16289 (18); 16402 (17); P25404 (12); 59094 (18).
Prévost, M., 1600 (11b).
Pring, G., s.n. (3).
Prior, A., s.n. (3).
Pulle, A., 3115 (3).
Purpus, C., 6903 (24).
Quiñones, H. & M. Barrero, s.n. (3).
Raben, F., 843 (5).
Rambo, B., 31117, 43076, 43388, 51898, 53204, 54611 (6a).
Ramírez, R., 65, 117 (27).
Ratter, J. et al., 626, 1977 (18).
Raven, P., 21585, 21605, 21749 (14a).
Regnell, A., II–218 1/8 (8); III–992 (25).
Reiss, R., 47A (6a).
Reitz, R., 2363 (22); 2364a (6b); 2870 (22).
Reitz, R. & R. Klein, 4084, 5455 (6b); 5692 (7); 5982, 6596 (22); 7044, 7517 (6a); 7636 (7); 7744 (6b); 8038 (7); 8317, 10743, 11391, 11710 (22); 12576 (6a); 12700 (7); 12873, 13533, 13593, 13912, 14101, 14138 (6a).
Rentería, E. et al., 1691 (14a).
Rentería, E. & A. Cogollo, 2652 (14a).
Restrepo-Mejía, R., 38 (14a).
Reuter, G., s.n. (3).
Revilla, J., 1645 (27).
Ribas, O. & J. Cordeiro, 99 (8).
Richter, E., 7890 (6a).
Riedel, L., 409 (8); 1081 (23); s.n. (5); s.n. (7).
Rimachi, M., 2923 (27).
Rodrigo, A., 2750 (3).
Rodriguez, 2270 (3).
Rojas, O., 8275 (6a).
Rojas, T., 10863 (25).
Romero-Castañeda, R., 1142, 2690, 5022, 6722 (14a); 6948, 9007 (3).
Rosa, N. & J. Pires, 3770 (7).
Rosa, N. & M. Santos, 2109 (11a).
Rosa & Vilar, 2876, 2932 (18).
Rose, J. & G. Rose, 21634, 21797 (3); s.n. (3).
Rowlee, W. & H. Stork, 704 (14a).
Rubio, D., 92 (14a).
Rudder, J., 4081 (3).
Ruiz, H. & J. Pavón, s.n. (17); s.n. (20).
Ruiz, J., 36 (11a).
Rury, P. 580 (14a).
Rusby, H., 800 (2); 805 (20); 840 (2); 2600 (1).
Rusby, H. & F. Pennell, 1003 (14b).
Rwaburindore, P., 368 (3).
Sagadas-Vianna, 2840 (25).
St. Hilaire, A., C1–15 (7).
Sandwith, N. 1773 (31).
Santos, T. dos, 1432 (15).
Santos, T. dos & L. Mattos Silva, 3129 (8).
Saravia et al., 880 (9b).
Sastre, C., 1430 (18); 2162 (27).
Sastre, C. & F. Sastre, 295 (29).
Schlechter, R., s.n. (7).
Schmidt, E., 18 (18).
Schott, H., 5405 (28); 5448 (7); 5449 (5); 5450 (8); s.n. (3); s.n. (5); s.n. (7).
Schultes, R., 3258 (3); 3652 (14a); 6541, 8232 (27).
Schultes, R. & I. Cabrera, 13044, 13903, 13993 (27); 18979 (11a).
Schultes, R. & M. Villarreal, 5271, 7650 (26); 7862 (3).
Schulz, A., 8421, 18402 (3).
Schulz, J., (LBB) 8285, 9313 (14a).

INDEX OF LOCAL NAMES

INDEX OF SCIENTIFIC NAMES

New names and combinations are in **boldface** and synonyms are in *italics*. Page numbers in **boldface** indicate primary page references. Page numbers with an asterisk (*) indicate pages with illustrations or maps.