



Revision of *Solanum* Section *Cyphomandropsis* (Solanaceae)

Author(s): Lynn Bohs

Source: *Systematic Botany Monographs*, Vol. 61, Revision of *Solanum* Section *Cyphomandropsis* (Solanaceae) (Aug. 30, 2001), pp. 1-85

Published by: [American Society of Plant Taxonomists](#)

Stable URL: <http://www.jstor.org/stable/25027891>

Accessed: 02-03-2016 19:03 UTC

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



American Society of Plant Taxonomists is collaborating with JSTOR to digitize, preserve and extend access to *Systematic Botany Monographs*.

<http://www.jstor.org>

REVISION OF SOLANUM SECTION CYPHOMANDROPSIS (SOLANACEAE)

Lynn Bohs
Department of Biology
University of Utah
Salt Lake City, Utah 84112

ABSTRACT. *Solanum* section *Cyphomandropsis* (Solanaceae) includes 13 species native to South America. Plants of this section are woody shrubs to small trees that lack spines, are glabrous to pubescent with unbranched or dendritically branched trichomes, and have tapered anthers with small terminal pores. Section *Cyphomandropsis* is closely related to *Solanum* sect. *Pachyphylla* (formerly genus *Cyphomandra*), from which it differs by lacking discrete, enlarged connectives on the abaxial anther surfaces. Exceptionally large chromosomes characterize the *Cyphomandropsis/Pachyphylla* clade. The morphology, taxonomic history, nomenclature, ecology, distribution, economic value, reproductive biology, and evolutionary relationships of *Solanum* sect. *Cyphomandropsis* are reviewed. Four species groups, one new combination (*S. hutchisonii*), and one new name (*S. pelagicum*) are proposed. Dichotomous and synoptic keys are provided for the species of the section.

RESUMEN. *Solanum* sección *Cyphomandropsis* (Solanaceae) incluye 13 especies sudamericanas. Las plantas de esta sección son arbustos leñosos o arbolitos que carecen de espinas, son glabros o pubescentes con tricomas simples o dendriticamente ramificados, y tienen anteras atenuadas con pequeños poros terminales. Esta sección está estrechamente relacionada con la *Solanum* sección *Pachyphylla* (anteriormente incluida en el género *Cyphomandra*), del que se distingue por la falta de un conectivo engrosado en la superficie dorsal de las anteras. Las dos secciones *Cyphomandropsis* y *Pachyphylla* se caracterizan por sus cromosomas excepcionalmente grandes. Aquí se revisa la morfología, la historia taxonómica, la nomenclatura, la ecología, la distribución, la biología reproductiva, las relaciones filogenéticas, y el valor económico de las especies de *Solanum* sección *Cyphomandropsis*. Se proponen cuatro grupos de especies y dos nombres nuevos, *S. hutchisonii* (comb. nov.) y *S. pelagicum* (nom. nov.). Se proporciona una clave dicotómica y otra sinóptica para las especies de la sección.

INTRODUCTION

Solanum, with approximately 1000 to 1400 species, represents one of the largest genera of angiosperms. Because of its large size and morphological complexity, many infrageneric groups within *Solanum* are not well defined and their component species are poorly known. Recent taxonomic work using morphological and molecular approaches has led to a better understanding of broad-scale relationships within the genus and more precise knowledge of species limits in numerous sections, but a comprehensive view of the systematics of the entire genus is not yet within reach. This contribution aims to clarify the taxonomy of a poorly understood clade within *Solanum* by elucidating species relationships and generic placement of a formerly obscure section of the genus, *Solanum* sect. *Cyphomandropsis* Bitter. This section includes 13 species native to South America. The section is here defined in the traditional sense of Bitter (1913), Seithe (1962), Danert (1970), Morton (1976), and Child (1984). The goal of this treatment is to delimit and define the species of the section, clarify nomenclatural issues, and propose infrasectional species groups that can be used as hypotheses of relationships for further study.

MATERIALS AND METHODS

I have followed the morphological species concept in delimiting species of sect. *Cyphomandropsis*. Taxa are recognized as distinct if they possess a unique suite of characters and are separated from similar entities by morphological gaps. In nearly all cases, taxa also occupy geographically circumscribed ranges. No formal infraspecific taxa are recognized, and in fact many infraspecific names have been relegated to synonymy because they could not be defined by consistent morphological and/or geographic distinctions.

In general, measurements have been made from dried herbarium material with floral parts rehydrated in boiling water. Where possible, living and/or liquid-preserved material has been used to supplement measurements made on dried specimens. In species with cordate leaf bases, the length of the blade is given from the tip to the basalmost insertion point of the blade on the petiole. The petiole length is also measured from this point. Colors of corollas, fruits, etc., are described from living material or from herbarium label data. Conventions used in measuring and describing various organs follow Bohs (1994).

For SEM studies of pollen grains, dried pollen from herbarium specimens was mounted on a stub with double-stick tape and coated with gold-palladium. Sizes of grains were estimated from SEM photographs. Measurements in polar and equatorial view are combined in Table 1. Herbarium vouchers for pollen SEM are listed in Appendix 1.

Plants used in the crossing studies were grown from seed in the greenhouses at the University of Utah. Voucher information and original provenance data are given in Appendix 2. Pollinations were effected by shaking pollen onto a clean glass slide that was rubbed against the stigma of the female parent. All plants known or suspected to be self-compatible were emasculated in the bud before pollination. Success or failure of the cross was monitored, as well as fruit size, shape, color, and number of seeds in successful crosses. Seeds were initially judged to be viable or inviable based on their appearance, and full-sized seeds of successful combinations were germinated in the greenhouse to determine their viability. The number of accessions used, number of pollinations attempted, and outcome of crosses is given in Appendix 4.

Pollen tube growth was observed using the aniline-blue fluorescence technique described in Bohs (1991). At least three flowers were examined per crossing combination. In ambiguous cases, numerous flowers were examined for a given cross until a consistent pattern was observed.

Pollen viability was estimated in the parental plants using the aniline-blue-lactophenol technique of Hauser and Morrison (1964) as described in Bohs (1991). At least five flowers were observed per individual plant, and two to seven individual plants per accession were monitored. Pollen was allowed to stain for at least one hour before observation. The first 300 grains encountered were scored as either viable or inviable. Unshriveled grains staining deep blue were presumed to be viable. Pollen fertility is reported in Appendix 4.

SECTIONAL DELIMITATION AND RELATIONSHIPS

All species of *Solanum* sect. *Cyphomandropsis* share the following combination of characters: 1) they are woody shrubs or small trees lacking spines; 2) trichomes, if present, are simple to dendritically branched; 3) the anthers are relatively narrow and distally

tapered, with small terminal pores that usually do not enlarge into longitudinal slits; 4) a discrete enlarged connective region is lacking on the abaxial anther surface. At least eight of the 13 species of the section have thick, angled seeds and relatively few seeds per fruit.

Solanum sect. *Cyphomandropsis* is closely related to *Solanum* sect. *Pachyphylla* (Dunal) Dunal, which was formerly recognized as the segregate genus *Cyphomandra* Mart. ex Sendtn. (Bohs 1994). Plants of the two sections can be very similar morphologically, but all taxa of sect. *Pachyphylla* are distinguished by having an enlarged connective region on the dorsal anther surface that may function as a floral osmophore (Sendtner 1845; Sazima et al. 1993; Bohs 1994). All taxa of the two sections that have been investigated cytologically have very large chromosomes and/or large amounts of nuclear DNA (Roe 1967; Pringle & Murray 1991; Moscone 1992; Bohs 1994; see section "Chromosomes"). Previous authors (D'Arcy 1972; Child 1984; Moscone 1992; Bohs 1994) acknowledged the close relationship between sections *Cyphomandropsis* and *Pachyphylla*, and molecular data confirm that the sampled members of the two sections belong to the same clade (Olmstead & Palmer 1992, 1997; Bohs & Olmstead 1997, in press; Olmstead et al. 1999; Fig. 1). Other characters that may distinguish sect. *Cyphomandropsis* from sect. *Pachyphylla* include plant architecture (Leeuwenberg's to Chamberlain's model in sect. *Cyphomandropsis*, Prevost's model in sect. *Pachyphylla*), fruit texture (mesocarp scant and gummy in sect. *Cyphomandropsis*, abundant and juicy in sect. *Pachyphylla*), and habitat preferences (drier and cooler, often highland areas in sect. *Cyphomandropsis*, wetter and warmer regions at lower elevations in sect. *Pachyphylla*). These characters are described in more detail in the sections "Morphology" and "Habitats and Distribution" below.

Molecular data place the *Cyphomandropsis/Pachyphylla* group within a large clade composed of members of *Solanum* subg. *Leptostemonum* (Dunal) Bitter (the spiny solanums), some representatives of subg. *Minon* Raf. [sections *Brevantherum* Seithe, *Pseudocapsicum* (Moench) Bitter, *Extensum* D'Arcy, and *Holophylla* (G. Don) Walp., pro parte], sect. *Geminata* (G. Don) Walp., and two representatives of problematical groups, *S. allophyllum* (Miers) Standl. [sect. *Allophyllum* (A. Child) Bohs] and *S. wendlandii* Hook.f. (sect. *Aculeigerum* Seithe; Fig. 1). This clade, which includes nearly half of the currently recognized species in *Solanum*, is morphologically diverse, biogeographically widespread, and poorly understood. Likewise, the sister group to the *Cyphomandropsis/Pachyphylla* clade has not been identified with certainty. Trees resulting from combined nuclear and chloroplast sequence data sets place members of sections *Aculeigerum*, *Allophyllum*, *Brevantherum*, and *Extensum* as sister to the *Cyphomandropsis/Pachyphylla* clade (Bohs & Olmstead, in press; Fig. 1), but this clade has very low bootstrap support, and many members of potentially related groups have not been sampled.

TAXONOMIC HISTORY

Species of sect. *Cyphomandropsis* have been placed in the past in either *Solanum* or *Cyphomandra*. All species described before 1845, when Otto Sendtner established the genus *Cyphomandra*, were assigned to *Solanum*. Bitter set up the sect. *Cyphomandropsis* in 1913, which included two newly described species (*S. stuckertii* and *S. semicoalitum*) and one previously known species (*S. clavatum*), and transferred two species previously described as *Cyphomandra* to *Solanum* (*S. johannae* and *S. luridifuscescens*). Subsequent authors assigned the section to *Solanum* (Seithe 1962; Gilli 1970; Danert 1970; Morton

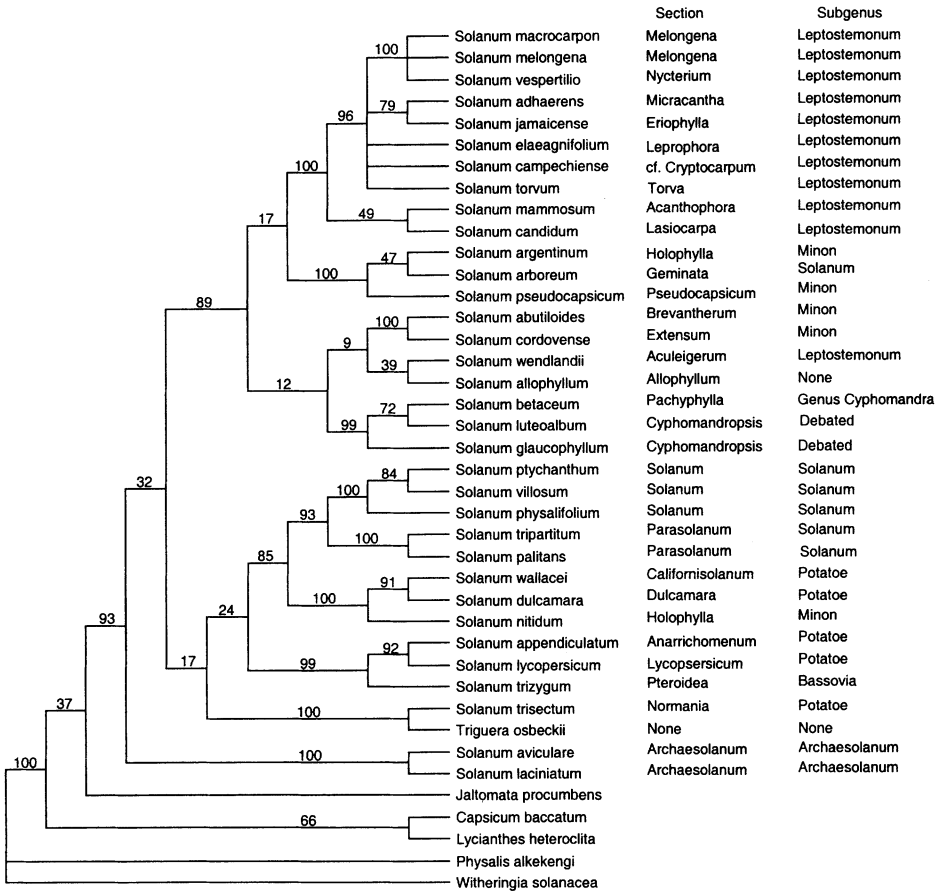


FIG. 1. Strict consensus of 16 most parsimonious trees of 1444 steps from parsimony analysis of combined data from chloroplast *ndhF* and nuclear ITS sequences (modified from Bohs and Olmstead, in press). Numbers above branches are bootstrap values (500 replicates; see Bohs and Olmstead, in press, for methodological details). Subgeneric and sectional assignments follow D'Arcy (1972, 1991), Child (1998), and Nee (1999). The generic and subgeneric taxonomy of sect. *Cyphomandropsis* has been controversial. Traditionally, the section has been placed most frequently in either *Solanum* subg. *Leptostemonum* or in the genus *Cyphomandra* (see text).

1976) or to *Cyphomandra* (D'Arcy 1972; Child 1984). All species of *Cyphomandra* were transferred to *Solanum* in 1995 (Bohs 1995).

The earliest description of a species that would later be assigned to sect. *Cyphomandropsis* is *S. pubescens* from Ruiz and Pavón's *Flora Peruviana et Chilensis* (1799), later renamed as *S. luteoalbum* by Persoon (1805). Desfontaines (1829) was the next to describe a new species of the section, *S. glaucophyllum*, the best-known and most widespread member of the group. His description was taken from a plant cultivated at the Botanic Garden in Paris. It is not known how or when *S. glaucophyllum* arrived in France, but herbarium records indicate that this showy species was cultivated in several European botanical gardens in the early 1800's, probably introduced from Argentina. Whereas most of the species now included within sect. *Cyphomandropsis* have been at least loosely associated with

each other in the past, *S. glaucophyllum* has been an exception owing to its aberrant morphology and striking convergence with *S. amygdalifolium* Steud., an unrelated non-spiny *Solanum* of the dulcamaroid group. Many authors since Sendtner (1846) and Dunal (1852) have considered *S. glaucophyllum* to be more closely related to *S. amygdalifolium* than to other species of sect. *Cyphomandropsis*. Dunal (1852) added to the confusion when he placed *S. glaucophyllum* and *S. malacoxylon*, here considered synonyms, into two separate groups within *Solanum* (“*Anthoresis*” and “*Subdulcamara*,” respectively). Child (1986) considered *S. glaucophyllum* to be unrelated to sect. *Cyphomandropsis* and removed it to its own section within *Solanum* subg. *Solanum*. Morphological, cytological, and molecular work (Morton 1976; Moscone 1992; Bohs & Olmstead, in press; Fig. 1) has confirmed the placement of *S. glaucophyllum* within sect. *Cyphomandropsis*, and has discounted its relationship with the superficially similar *S. amygdalifolium*.

Nearly concurrently with Desfontaines’s (1829) publication of *S. glaucophyllum*, Vellozo (1829) featured two new species, *S. ellipticum* and *S. cylindricum*, in his account of plants of the Rio de Janeiro region. Unfortunately, the plates and descriptions from this work are barely suitable for identification of many taxa, and no authentic herbarium material is known to exist. *Solanum ellipticum* is considered to be a synonym of *S. cylindricum* in the present work.

In 1846, Sendtner published his landmark treatment of Brazilian Solanaceae for Martius’s *Flora Brasiliensis*. He had established the genus *Cyphomandra* in the previous year and transferred to it a number of *Solanum* species, including *S. ellipticum* and *S. cylindricum*. In the same work, he also described two new species that would later be assigned to sect. *Cyphomandropsis*, one as a *Cyphomandra* (*C. velutina*, a synonym of *S. luridifuscenscens*) and one as a *Solanum* (*S. malacoxylon*, a synonym of *S. glaucophyllum*). Dunal’s (1852) treatment of Solanaceae for Candolle’s *Prodromus* basically followed Sendtner’s scheme, but Dunal added the new taxa *C. cornigera* (a synonym of *S. pelagicum*), *C. betacea* var. *velutina* (a synonym of *S. fallax*), and *S. glaucum* (a synonym of *S. glaucophyllum*). He considered *S. glaucum* and *S. malacoxylon* to represent two distinct species; they are treated as conspecific in the present work. Miers (1855) transferred *C. cylindrica*, *C. elliptica*, *C. cornigera*, and *C. velutina* to his genus *Pionandra*. Later authors (e.g., Smith & Downs 1966; D’Arcy 1973; Child 1984; Bohs 1994) did not recognize the distinction between *Cyphomandra* and *Pionandra*, and *Pionandra* was relegated to synonymy under *Cyphomandra*. *Cyphomandra* is currently treated as a synonym of *Solanum* (Bohs 1995).

The prolific taxonomist Georg Bitter published his works on Solanaceae during the early part of the 20th century. Bitter (1913) erected *Solanum* sect. *Cyphomandropsis* to include two new species (*S. stuckertii* and *S. semicoalitum*) and two species transferred from *Cyphomandra* (*C. velutina* and *C. elliptica*). The next year he described *S. narcoticum* (Bitter 1914), which he did not assign to sect. *Cyphomandropsis*, but noted that it occupied an isolated position among the non-spiny taxa of *Solanum*. The identity of *S. narcoticum* is in question, because Bitter’s type specimens were destroyed in the Second World War, and his description is not adequate to assign the name with certainty. In 1918, Bitter transferred *Cyphomandra lauterbachii* H. Winkler to *Solanum* and assigned it to sect. *Cyphomandropsis*. Its oblong rather than tapered anthers exclude this species from the section, and it actually belongs to *Solanum* sect. *Geminata*.

A few taxa were described during the next 40 years, but the more noteworthy developments did not occur until the 1960’s and 1970’s with the publication of floras by Macbride (1962), Smith and Downs (1964, 1966), and Morton (1976). *Solanum nitidum*

var. *hutchisonii* (now recognized as *S. hutchisonii*) and *S. luteoalbum* var. *tunya* (a synonym of *S. luteoalbum*) were first published in Macbride's (1962) *Flora of Peru*. Smith and Downs (1964, 1966), in their works cataloging the flora of Santa Catarina state in Brazil, proposed the novelties *S. fusiforme*, *S. matadori*, *C. maritima* (a synonym of *S. pelagicum*), and *S. catanduvae*, *S. iraniense*, and *S. subhastatum* (the latter three here considered synonyms of *S. cylindricum*). They maintained *Cyphomandra* as a separate genus, based on the enlarged anther connective. They assigned *S. fusiforme* and *S. matadori* to sect. *Cyphomandropsis*, and recognized two large subgenera within *Solanum*, subg. *Solanum* and subg. *Leptostemonum*. They considered sect. *Cyphomandropsis* to belong within *Solanum* subg. *Leptostemonum*, which otherwise includes the spiny solanums. In doing so, they emphasized the narrow tapered anthers with small pores and minimized the fact that species of sect. *Cyphomandropsis* have neither stellate hairs nor spines. In reality, it appears that there is no clear-cut division of *Solanum* into two large subgenera based on anther shape, trichome characters, and presence of spines (Bohs & Olmstead 1997).

Conrad V. Morton's contributions to our understanding of the Solanaceae included much herbarium work on *Solanum* as well as several publications (Morton 1944, 1976). Most noteworthy is his treatment of the genus *Solanum* in Argentina (Morton 1976). Morton also included sect. *Cyphomandropsis* within subg. *Leptostemonum* on the basis of its tapered anthers with small pores. He described *S. confusum* and *S. adelphum*, which are considered conspecific in the present treatment. He clarified the nomenclature of *S. confusum* and *S. clavatum*, and resolved some difficult problems of synonymy and typification in *S. glaucophyllum*.

The taxonomy of sect. *Cyphomandropsis* has received little attention until relatively recently. Many of the species occur largely outside the area of major published floras, and no revisionary or monographic studies have been available for sect. *Cyphomandropsis* or its close relative sect. *Pachyphylla*. In the last 15 years, Child (1984) and Bohs (1994) have published taxonomic conspecti or monographs that examined the *Pachyphylla/Cyphomandropsis* clade, and molecular data (Olmstead & Palmer 1992, 1997; Bohs & Olmstead 1997, in press) have elucidated the position of this clade within the larger picture of *Solanum*. Child (1984) included sections *Cyphomandropsis* and *Pachyphylla* in the genus *Cyphomandra*, and made a number of implicit transfers of *Solanum* taxa to *Cyphomandra*; however, most of these transfers are not validly published under Art. 33.2 of the ICBN (Greuter et al. 2000), because no reference was made to the basionyms. These combinations were validated in Bohs (1994). Child's concept of *Cyphomandra* was quite broad, and he included within it several elements that are now thought to belong to distinct clades of *Solanum* [e.g., *S. graveolens* Bunbury, a member of *Solanum* subg. *Potatoe* (D'Arcy 1972; Bohs 1994), and *S. allophyllum*, of *Solanum* sect. *Allophyllum* (Bohs 1990), which apparently belongs to an isolated clade along with *S. wendlandii* of *Solanum* sect. *Aculeigerum* (Bohs & Olmstead 1997)]. With these anomalous elements included, Child recognized six sections within *Cyphomandra*. Though his work is insightful, it did not examine species limits and nomenclature in the taxa under consideration.

In 1994, Bohs published a monograph of the genus *Cyphomandra*. She recognized 32 species and two insufficiently known taxa. She combined the sections *Cyphomandra* and *Ceratostemon* Miers recognized by Child, and defined five informal species groups. She excluded four of Child's six sections (*Allophylla*, *Rhynchantherum*, *Cornigera*, and *Cyphomandropsis*) from inclusion in the genus.

At about the same time, molecular data clearly established that the genus *Cyphomandra* is nested deeply within the genus *Solanum* (Olmstead & Palmer 1992,

1997; Bohs & Olmstead 1997, 1999), and thus recognition of *Cyphomandra* as a distinct genus is phylogenetically untenable. Accordingly, all species of *Cyphomandra* were transferred to *Solanum* (Bohs 1995). The infrageneric name of this group is now *Solanum* sect. *Pachyphylla* (Dunal) Dunal.

The present treatment aims to clarify the species limits of the remaining taxa in the *Pachyphylla/Cyphomandropsis* clade. Included are members of two of Child's sections, *Cyphomandropsis* and *Cornigera*, which are not recognized here as distinct sections. One species formerly considered to belong to sect. *Pachyphylla*, *S. fallax*, is now included in sect. *Cyphomandropsis*. Floral morphology and architectural characters serve to delimit the sections. Monophyly of each section has not been definitively established, however, and an explicit phylogenetic hypothesis of relationships within the entire clade awaits detailed molecular work.

MORPHOLOGY

HABIT, STEMS, AND ARCHITECTURE. Members of sect. *Cyphomandropsis* are generally small woody shrubs less than 3 m tall. An exception is *S. fallax*, which can be a small tree up to 5 m tall. The upright stems are usually slender with a narrow pith, in contrast to the thick fleshy stems of species of *Solanum* sect. *Pachyphylla*. Obvious elevated leaf scars are present on young stems. Older stems generally have smooth white to dark brown bark marked with longitudinal fissures and raised lenticels. Some species of the section (e.g., *S. confusum*, *S. glaucophyllum*, *S. hibernum*, *S. luteoalbum*, *S. stuckertii*) produce several to many upright stems from an underground rhizome. In *S. confusum* and *S. glaucophyllum*, this habit may result in large monospecific clumps composed of hundreds of stems.

Where known, the architecture of *Cyphomandropsis* species is similar to that of many other solanums (Fig. 2). Initially a single stem is produced with spirally arranged leaves. After reaching ca. 0.5 to 2 m in height, this upright stem ends in a terminal inflorescence. Two to three lateral shoots then develop from axillary buds just proximal to the inflorescence. These lateral shoots ascend at an acute angle, in contrast to the plagiotropic lateral shoots produced in the same morphological position in species of sect. *Pachyphylla* (see Bohs, 1989). Growth of the lateral shoots is sympodial, as in sect. *Pachyphylla*, but in general the sympodial units are plurifoliate and not clearly differentiated in leaf arrangement from the orthotropic axis. Thus, the trunk and branches are more or less equivalent in species of sect. *Cyphomandropsis*, whereas in sect. *Pachyphylla* the branches differ from the trunk in both orientation and leaf arrangement. The architecture exhibited by most species of sect. *Pachyphylla* conforms to Prevost's model in the scheme of Hallé et al. (1978). This is an uncommon model in the Solanaceae, and may be a synapomorphy that defines sect. *Pachyphylla*. Furthermore, species of sect. *Pachyphylla* that exhibit Prevost's model usually have 3–4-leaved sympodial modules on the plagiotropic (crown) branches, and early orders of branching on the plagiotropic shoots are generally dichasial; that is, two replacement shoots grow out from buds beneath the inflorescence so that the inflorescence appears to be situated in a branch fork. Sympodial modules in species of sect. *Cyphomandropsis* vary from 3- (in *S. fallax*) to 4- to many-foliate. Dichasial branching can also occur in sect. *Cyphomandropsis*, but monochasial branching is much more common, especially on later orders of branching. Thus, architecture in species of sect. *Cyphomandropsis* lies along a continuum between Leeuwenberg's and Chamberlain's



FIG. 2. *Solanum confusum* (Yungas de Mairana, Prov. Florida, Dept. Santa Cruz, Bolivia). Single upright stem showing branching pattern; scale bar = 10 cm.

model (Hallé et al. 1978), as illustrated by Bell and Dines (1995). Dichasial branching predominates in the former model, and monochasial in the latter model. This range of architectural forms is found in other species of *Solanum* and is common in the subfamily Solanoideae (Bell & Dines 1995).

TRICHOMES. Among the species of sect. *Cyphomandropsis*, trichomes can be sparse (e.g., *S. fusiforme*, *S. glaucophyllum*, *S. hutchisonii*, *S. matadori*) or abundant, and uniseriate and unbranched to branched. Unbranched trichomes may be eglandular or gland-tipped. Branched trichomes are always eglandular and can be forked, dendritically branched, or, in *S. cylindricum*, “substellate.” Dendritically branched hairs (sensu Roe, 1971; “branchlet hairs” of Seithe, 1979) are branched trichomes in which the lateral branches emerge at different places along the axis; frequently these have an antler-like appearance. They are found in *S. cylindricum*, *S. hibernum*, *S. pelagicum*, and in some populations of *S. amotapense* and *S. luteoalbum*. In *S. cylindricum*, the hairs are technically dendritic in form, but in some instances the lateral branches are arranged roughly in tiers. True stellate, echinoid, or dendritic-echinoid hairs have not been found in any species of

sect. *Cyphomandropsis*. [In the former hair type, all lateral rays emerge from one point on the axis. In the latter two types, the lateral rays are numerous, very short, and emerge at various points along the central axis (Roe 1971).] Likewise, prickles are absent in species of this section.

LEAVES. The majority of species of sect. *Cyphomandropsis* have entire, petiolate, elliptic to elliptic-ovate leaves. Most species have truncate, cuneate, or decurrent leaf blades, but in *S. amotapense*, *S. hibernum*, and *S. hutchisonii* the leaf base can be subcordate, and in *S. fallax* the leaf base is usually deeply cordate. *Solanum fallax* has the largest leaves in the section, with blades often reaching 20 cm or more in length and width. Leaves of the trunk and crown portion of the plants are more or less similar in shape and size, and do not exhibit the degree of morphological heterogeneity commonly seen in species of sect. *Pachyphylla*.

Solanum fusiforme and *S. pelagicum* frequently have both pinnately compound and simple leaves on a single plant, with the compound leaves especially common on the trunk. A few specimens of *S. cylindricum* have small hastate lateral lobes near the base of the blade.

Leaf texture in the group is generally chartaceous; subcoriaceous or fleshy leaves are found only in *S. hutchisonii* and *S. glaucophyllum*. The latter species is notable because most plants are covered with a dense glaucous bloom.

INFLORESCENCES. Inflorescences in sect. *Cyphomandropsis* are ebracteate, pedunculate, scorpioid cymes. As in all other species of *Solanum*, the inflorescence is developmentally terminal, and shoots distal to the first inflorescence are composed of sympodial modules. Most species have unbranched to forked inflorescences. Branched inflorescences occur in *S. confusum*, *S. glaucophyllum*, and *S. matadori*; *S. luteoalbum* and *S. stuckertii* rarely have branched inflorescences. In *S. fusiforme*, the inflorescence axis is noticeably zigzag between adjacent pedicels. The inflorescences are generally nodding to pendent.

In all species, except *S. fallax*, the pedicels are articulated at the base and after abscission leave scars or short pegs up to 1 mm long on the rachis. In *S. fallax*, the pedicels can have an articulation some distance above the point at which the pedicel joins the rachis, and upon abscission can leave remnants up to 6 mm long (see Fig. 16). This pattern is also seen in some species of sect. *Pachyphylla* (Bohs 1994).

In some specimens of *S. cylindricum*, the flowers are borne in subumbellate clusters with the pedicels inserted on a swollen platform. Pedicel platforms are a synapomorphy found in some groups of *Solanum* sect. *Holophylla* (Knapp 1989). Because the groups that possess this character have no close phylogenetic connection with sect. *Cyphomandropsis* (cf. the position of *Solanum nitidum* Ruiz & Pav. with the two representatives of sect. *Cyphomandropsis* in Fig. 1), the pedicel platform in *S. cylindricum* appears to be an example of convergence.

FLOWERS. The flowers of species of sect. *Cyphomandropsis* are all perfect, actinomorphic, and 5-merous. The calyx is green or greenish white and cupulate, with five lobes up to 3 mm long (up to 6 mm long in *S. cylindricum*). In *S. amotapense* and *S. fallax* the calyx tube is somewhat inflated, then constricted at the point where the lobes emerge. This morphology is not common in members of the *Pachyphylla*

Cyphomandropsis clade, but it occurs in at least a few species of *Solanum* sect. *Brevantherum* (e.g., *S. hazenii* Britton) and is apparently convergent in the two groups.

Corollas in sect. *Cyphomandropsis* are chartaceous in texture and stellate, rotate-stellate, or stellate-campanulate in outline. Corolla color is most commonly white or purple, with both color morphs appearing in several species. *Solanum glaucophyllum* and *S. confusum* frequently have pinkish corollas, often with a darker or lighter central star. In general, corolla shape, texture, and color are much more homogeneous in sect. *Cyphomandropsis* than in sect. *Pachyphylla*, which exhibits a remarkable diversity in floral color and morphology.

The stamens of sect. *Cyphomandropsis* are narrow and distally tapered, with small terminal pores that do not open into longitudinal slits with age. *Solanum cylindricum* is an exception, for older anthers in this species often have pores that extend into slits. This character is also seen in several groups thought to be related to the *Pachyphylla/Cyphomandropsis* clade, such as sections *Geminata*, *Pseudocapsicum*, and *Holophylla* pro parte (Knapp, in press). Whether this indicates that *S. cylindricum* might be relatively basal in the *Pachyphylla/Cyphomandropsis* clade remains to be investigated.

Previous workers, such as Bitter (1913) and Morton (1976), attached much significance to the degree of anther connation in distinguishing species. This is not a reliable character at the specific level, for both connivent and free anthers can occur within a single taxon or within a single plant. Connivent anthers in *Solanum* occur due to interlocking papillae or hairs on the lateral anther surfaces (cf. Bonner & Dickinson 1989). Environmental factors or developmental stage may thus affect the degree of anther connation in a particular flower.

In contrast to members of sect. *Pachyphylla*, species of sect. *Cyphomandropsis* lack a discrete enlarged connective region on the dorsal surface of the anthers (Bohs 1994; Fig. 3). The presence of this connective is the primary defining characteristic of sect. *Pachyphylla* and serves to differentiate it from sect. *Cyphomandropsis* regardless of variation in other characters. However, some species of sect. *Pachyphylla* can have small or inconspicuous connectives [e.g., *S. corymbiflorum* (Sendtn.) Bohs, *S. pinetorum* (L. B. Sm. & Downs) Bohs], and some taxa of sect. *Cyphomandropsis* may have anthers that are dorsally thickened or elaborated (e.g., *S. fallax*, *S. luridifuscescens*). The key to distinguishing between the two situations is whether the connective is discrete and clearly differentiated from the thecal tissue (sect. *Pachyphylla*) or whether it covers nearly all of the dorsal anther surface and is not clearly demarcated from the thecae (sect. *Cyphomandropsis*).

The gynoecium of species of sect. *Cyphomandropsis* consists of a conical bicarpellate ovary, a straight, slender, cylindrical style, and a truncate to subcapitate stigma more or less the same diameter as the style. This conforms to gynoecia in many other groups of *Solanum*, and contrasts with species of sect. *Pachyphylla*, which may have greatly expanded stigmas or distinctive stylar morphology (see Bohs, 1994, for examples). Most species of sect. *Cyphomandropsis* have glabrous ovaries and glabrous to sparsely puberulent styles; exceptions include *S. fallax* and some collections of *S. amotapense*, *S. cylindricum*, and *S. stuckertii*.

POLLEN. Pollen grains were examined with SEM in the species listed in Table 1; herbarium vouchers for the pollen studies are given in Appendix 1. Pollen of these species is tricolporate, with the colpi not fused at the poles (Fig. 4). The grains are spheroidal to prolate-spheroidal in equatorial view; in polar view the apertures often protrude so that the

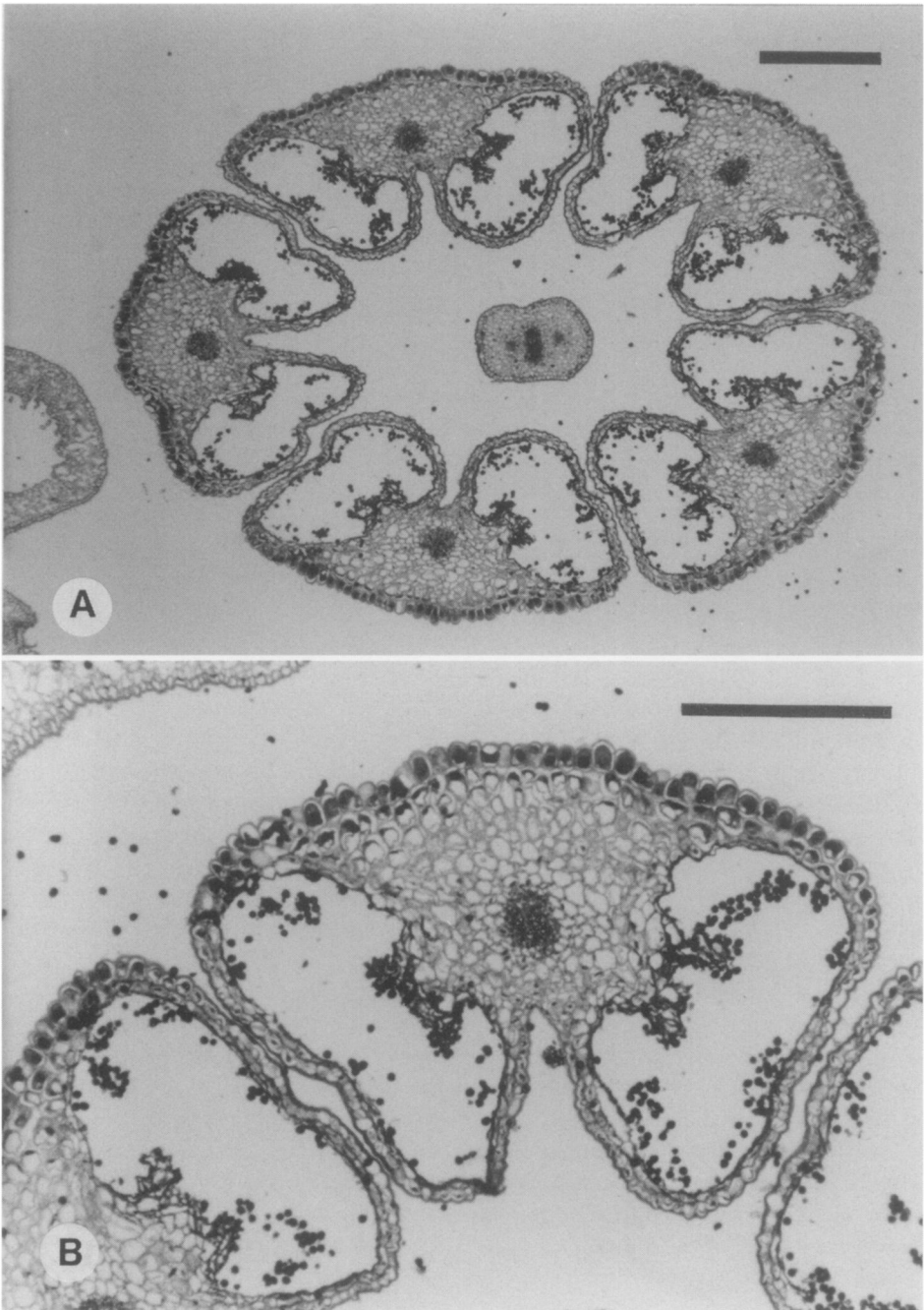


FIG. 3. *Solanum luteoalbum*. A. Transverse section through anther cone and style. B. Cross section of anther. (Scale bars = 0.5 mm.)

TABLE 1. Pollen of *Solanum* section *Cyphomandropsis* examined with SEM. Herbarium vouchers are listed in Appendix 1.

Species	Sculpturing	Size (μm)
<i>S. amotapense</i>	Granulate	15–16.25
<i>S. confusum</i>	Granulate	13.75–16.25
<i>S. cylindricum</i>	Granulate	11.25–11.75
<i>S. fusiforme</i>	Granulate	11.25–12.5
<i>S. glaucophyllum</i>	Psilate	12.5–13.75
<i>S. pelagicum</i>	Granulate	11.25–12.5

outline is semiangular. Grain diameter is approximately 10–20 μm . In most of the species examined, the pollen grains are finely ornamented with small bumps or granules less than 1 μm in diameter. The only exception is *S. glaucophyllum*, in which the grains are nearly smooth (psilate).

Passarelli (1999) examined pollen grains of three Argentine species of sect. *Cyphomandropsis*, *S. glaucophyllum*, *S. stuckertii*, and *S. confusum* (as *S. adelphum*). Her results were similar to those reported here, except she found the surface sculpturing of grains of *S. glaucophyllum* to be granulate rather than psilate. The diameter of acteoelyzed grains was 16–20 μm in *S. glaucophyllum*, 17–20 μm in *S. stuckertii*, and 17–24.5 μm in *S. confusum*. The number of pollen grains per flower estimated using a hemacytometer ranged from about 1.1 to 1.3×10^6 in the three species.

Pollen size and surface sculpturing in sect. *Cyphomandropsis* are very similar to that of species of sect. *Pachyphylla* and to many other species of *Solanum* (Anderson & Gensel 1976; Edmonds 1984; Bohs 1989, 1994; Passarelli 1999; Knapp, in press) and do not appear to provide useful taxonomic characters at the sectional or specific level.

FRUITS. The fruits in sect. *Cyphomandropsis* are usually globose berries ca. 1–2 cm in diameter. The fruit pulp in most species is sparse and much drier in texture than in the succulent, juicy berries common in sect. *Pachyphylla*. The surface of the berry can be shiny (e.g., *S. amotapense*, *S. hibernum*, *S. stuckertii*) or dull (e.g., *S. glaucophyllum*, *S. luteoalbum*). Ripe fruits are most commonly yellow or orange, but *S. amotapense* has bright red fruits. *Solanum glaucophyllum* is distinctive in producing dark purple or blackish fruits usually covered with a glaucous bloom. The yellowish or pale green mesocarp is juicier than in other members of the section and is extremely bitter. In one collection of this species from lowland Bolivia (Nee 37532) the fruits are described as green when they abscise. I have only seen blue-black mature fruits on plants of *S. glaucophyllum*.

Solanum fusiforme is also very unusual in its fruit morphology. As the name implies, the fruits are elongated and distally pointed. They turn yellow when ripe (Dottori 1995).

Solanum fallax is distinctive in having fruits that are densely pubescent with unbranched eglandular hairs. Several authors (Smith & Downs 1966; Child 1984) have described the fruits of *S. pelagicum* as being dendritically pubescent, but I have only seen glabrous fruits in herbarium material of this species.

Stone cell aggregates are commonly found in the fruits of species of sect. *Pachyphylla*. These are macroscopic sclerified structures that often occur in the distal and medial parts of the fruit. Large stone cell aggregates occur in just a few species of sect. *Cyphomandropsis* (e.g., *S. fusiforme*, *S. pelagicum*). Dottori (1995) reports that the fruits

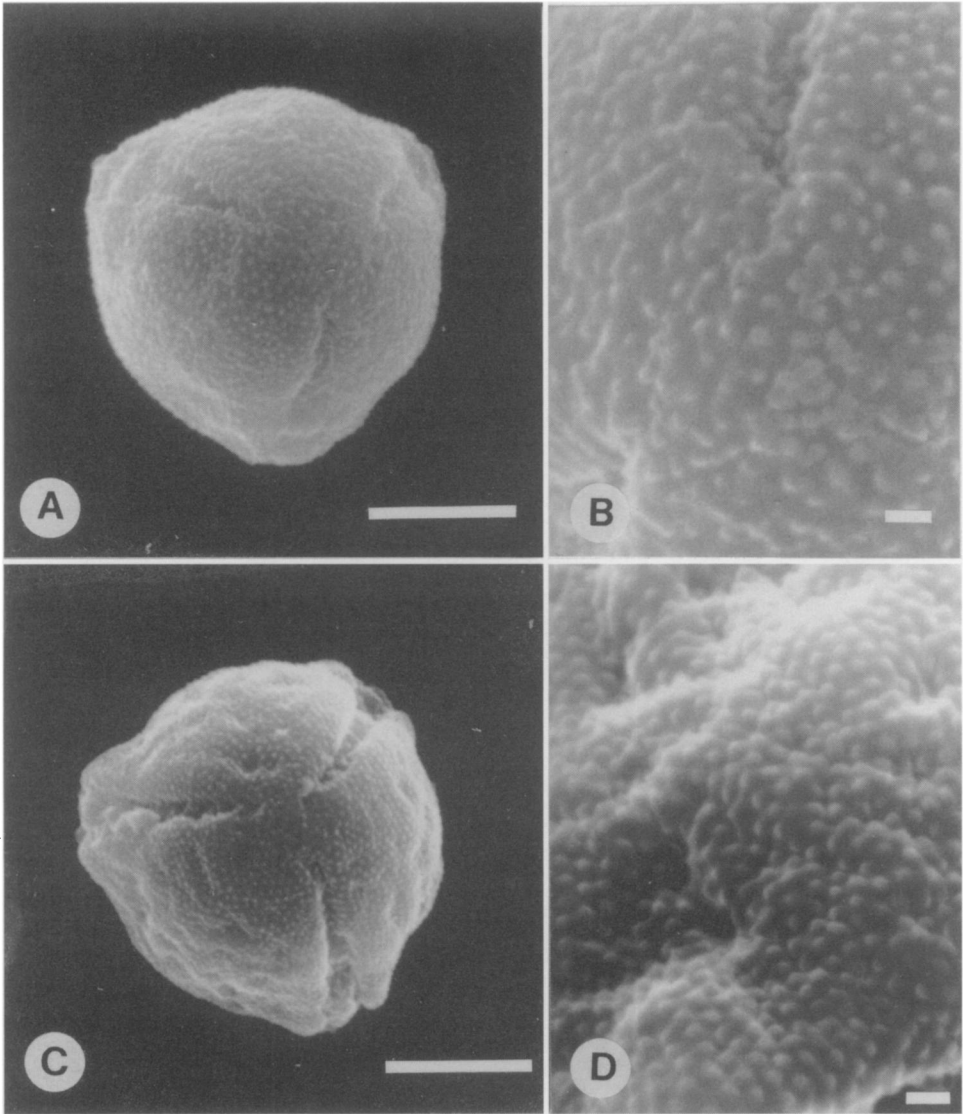


FIG. 4. Pollen grains of *Solanum* sect. *Cyphomandropsis* observed with the SEM. A,B. *S. pelagicum*. C,D. *S. fusiforme*. A, C. Polar view, $\times 3500$ (scale bars = 5 μm). B, D. Exine surface, $\times 10,000$ (scale bars = 0.5 μm).

of *S. confusum* and *S. stuckertii* also contain aggregations of sclereids, but I have not observed them in these species. The taxonomic utility and functional significance of this character are unknown. It would be useful to examine the distribution of stone cell aggregates in members of the sister group(s) of the *Pachyphylla/Cyphomandropsis* clade when they have been identified with certainty to determine if this character is primitive or derived in the group.

There are only two known reports of fruit dispersal in the group, both for *S. glaucophyllum* (q.v.). Observations of fruit and seed dispersal of *Cyphomandropsis* species are urgently needed. This dearth of information regarding dispersal agents also extends to

species of *Solanum* in general, where few well-documented studies exist (see Symon, 1979, for an exception).

SEEDS. Two basic seed morphologies occur in sect. *Cyphomandropsis*. At least four species have relatively small seeds (ca. 2–3 mm in diameter) that are lenticular, strongly flattened, and rounded in outline. The rest of the species have large seeds, ca. 4–5 mm long and 3–5 mm wide, which are rather thick, not very flattened, and angled in outline. Whether these two seed types define monophyletic lineages remains to be determined. Taxa known to have each of these seed types are listed in the synoptic key. Large-seeded species usually have fruits with very sparse mesocarp, and seeds occupy most of the volume of the fruit. These taxa also contain only on average about 10–50 seeds per fruit. Small-seeded taxa have more abundant mesocarp and may contain hundreds of seeds.

As is common in many species of *Solanum*, the outer walls of the cells of the seed coat are very thin and easily rub off. The anticlinal walls of these cells are thickened in comblike ridges that remain after the outer wall has disappeared (Souèges 1907; Edmonds 1983; Lester & Durrands 1984; Bohs 1994; Dottori 1995). Thus, many *Solanum* seeds appear to be “pubescent,” but the apparent hairs (termed “pseudohairs”) are not composed of cells but rather of the remnants of the thickened anticlinal walls.

CHROMOSOMES

All species of sect. *Cyphomandropsis* that have been investigated cytologically have a chromosome number of $n = 12$ ($2n = 24$; Appendix 3). The base chromosome number in *Solanum* and in most other genera of the subfamily Solanoideae is $x = 12$ (Moscone, 1992, and references cited therein). All species of sect. *Pachyphylla* investigated thus far also have $n = 12$ and $2n = 24$ chromosomes (Bohs 1994). Polyploidy does not appear to be a factor in the evolution of the *Pachyphylla/Cyphomandropsis* clade, as it has been in some groups, such as the potatoes (*Solanum* sect. *Petota* Dumort.; Hawkes 1990) and the nightshades (*Solanum* sect. *Solanum*; Edmonds 1972, 1977).

Although chromosome number is not unique in the *Pachyphylla/Cyphomandropsis* clade, the group is cytologically distinctive due to its large chromosome size and high amounts of nuclear DNA. All species from this clade that have been investigated have chromosomes that range in length from about 3 to 14 μm , making them on the order of 2 to 5 times larger than those of other species of *Solanum* (Roe 1967; Pringle & Murray 1991; Moscone 1992; Bohs 1994). Pringle and Murray (1991), using flow cytometry, included *S. luteoalbum* from sect. *Cyphomandropsis* in their investigation of DNA content in the *Pachyphylla/Cyphomandropsis* group. DNA content in this species was measured at 15.2 picograms per 2C nucleus. This value falls within the range reported for species of sect. *Pachyphylla* (Pringle & Murray 1991) and is substantially greater than that reported for other species of *Solanum* (including formerly recognized genus *Lycopersicon* Mill.; range = 1.7–4.2 pg per 2C nucleus; Bennett & Smith 1976; Bennett et al. 1982; Arumuganathan & Earle 1991). The functional significance of this remarkable difference in chromosome size and DNA content is unclear, but it may represent a synapomorphy that defines the *Pachyphylla/Cyphomandropsis* clade. Efforts should be made to examine chromosome number, size, and morphology in all the species of this clade with respect to its sister group(s) in order to establish a hypothesis of chromosomal evolution in sect. *Cyphomandropsis* and its relatives, and to gain insight into the possible adaptive significance of increased chromosome size and DNA content in flowering plants.

BREEDING SYSTEMS AND CROSSING STUDIES

Limited crossing experiments have been done to determine breeding systems and interspecific compatibility in sect. *Cyphomandropsis*. All species are hermaphroditic and monomorphic in floral form. Appendix 4 documents the distribution of self-incompatibility and self-compatibility in species of the section as determined by fruit and seed set and pollen tube growth in self- vs. sib- or outcrosses. Pollen tube growth was arrested in the style in incompatible pollinations, conforming to the pattern seen in other Solanaceae with gametophytic self-incompatibility (Nettancourt 1977). Self-compatibility may be more widespread in sect. *Cyphomandropsis* than in sect. *Pachyphylla*: two out of five species investigated in sect. *Cyphomandropsis* were self-compatible, whereas only two out of ten species were self-compatible in sect. *Pachyphylla* (Appendix 4; Bohs 1994). No fruits were set without manipulation, which indicates that biotic vectors must be present for pollination. *Solanum glaucophyllum* and *S. hibernum* occasionally set some fruits with seeds after selfing in greenhouse crosses. This probably indicates pseudocompatibility resulting from environmental conditions in the greenhouse (cf. Pandey 1959).

Passarelli (1999) calculated the pollen/ovule (P/O) ratio for three Argentine species of sect. *Cyphomandropsis* (*S. confusum*, *S. glaucophyllum*, and *S. stuckertii*). The pollen/ovule ratio is thought to reflect efficiency of pollen transfer and thus be a rough indicator of breeding system (Cruden 1977). The P/O ratios obtained for the three species were very high (37,875 in *S. confusum*, 25,309 in *S. glaucophyllum*, and 23,220 in *S. stuckertii*) and are consistent with xenogamy (Cruden 1977). Passarelli (1999) reports that the three *Cyphomandropsis* species are self-incompatible. These P/O ratios are equal to or greater than the highest ratios calculated by Mione and Anderson (1992) for species of *Solanum* sect. *Basarthrum* Bitter known to be self-incompatible.

Artificial interspecific intrasectional crosses were attempted using four species of sect. *Cyphomandropsis* (*S. glaucophyllum*, *S. hibernum*, *S. luteoalbum*, and *S. stuckertii*). Appendix 4 summarizes the results of these crosses. Some combinations (e.g., *S. luteoalbum* × *glaucophyllum*, *S. stuckertii* × *hibernum*) produced hybrid plants that were intermediate in morphology between the parental species; in the case of *S. luteoalbum* × *glaucophyllum*, the cross was successful only in one direction. Pollen tube growth into the ovary was observed in several crossing combinations that did not produce fruits or seeds, which implies that post-zygotic crossing barriers may be present. Both pre- and post-zygotic barriers appear to be effecting isolation among species of sect. *Cyphomandropsis*, as they are in sect. *Pachyphylla* (Bohs 1991, 1994).

Artificial intersectional crosses were attempted in both directions between four species of sect. *Cyphomandropsis* (*S. glaucophyllum*, *S. hibernum*, *S. luteoalbum*, and *S. stuckertii*) and seven species of sect. *Pachyphylla* (*S. betaceum*, *S. circinatum*, *S. corymbiflorum*, *S. diploconos*, *S. diversifolium*, *S. roseum*, and *S. unilobum*; Appendix 4). Small seedless fruits developed in many of these crosses, but none produced viable seeds. Pollen tube growth in intersectional crosses ranged from very good (many tubes around ovules) to poor (abnormal tube growth, few to no tubes in ovary), depending on the crossing combination. Reproductive isolation appears to be complete or nearly so between sections *Cyphomandropsis* and *Pachyphylla*. This is perhaps to be expected, given the strong crossing barriers between many species within sect. *Pachyphylla* (Bohs 1991).

SPECIES GROUPS AND INFRASECTIONAL RELATIONSHIPS

Phylogenetic relationships among the species of sect. *Cyphomandropsis* have not been established using rigorous analytical methods. It is likely that extensive convergence will confound cladistic analyses based on morphological characters, as is evident in other *Solanum* groups (Bohs & Olmstead 1997, 1999). Molecular studies are in progress to examine evolutionary relationships among species in the *Pachyphylla/Cyphomandropsis* clade (Bohs, unpubl.).

In the absence of cladistic analyses, the following species groups are proposed based on my intuitive interpretation of overall morphological similarity. Though not intended to represent well-supported and rigorously analyzed statements of relationship, they will serve as hypotheses for further testing.

I. *S. luteoalbum* group (*S. hibernum*, *S. luteoalbum*, *S. stuckertii*). These three species share 1) stellate corollas, 2) long narrow anthers unelaborated on the dorsal surface, 3) usually unbranched inflorescences, 4) globose, yellow to orange fruits, and 5) very large angled seeds. Dendritically branched hairs are present in *S. hibernum* and in some populations of *S. luteoalbum*. Corollas are white in *S. stuckertii* and deep purple (rarely white) in the other two species.

II. *S. amotapense* group (*S. amotapense*, *S. fallax*). This group is probably most closely related to the *S. luteoalbum* group with which it shares large angled seeds. The two species are similar in their cordate leaf bases and in having the calyx tube swollen at the base of the lobes. *Solanum fallax* is morphologically distinctive in sect. *Cyphomandropsis* due to its large stature, long pedicel remnants, large leaves, and pubescent fruits. Few-leaved sympodial units may also distinguish it from other species in the section.

III. *S. glaucophyllum* group (*S. confusum*, *S. glaucophyllum*, *S. luridifuscescens*, *S. matadori*). The taxa of this group all have elliptic and often rather narrow leaves with tapered bases, stellate to stellate-campanulate corollas, and relatively broad anthers, often with the dorsal surface roughened by scaly papillae. Branched inflorescences occur in all species, except *S. luridifuscescens*. The seeds of *S. confusum* and *S. glaucophyllum* are large and angled, as in the species groups described above. Fruits and seeds are unknown in *S. matadori*, and poorly known in *S. luridifuscescens*; the latter appears to have small lenticular seeds. *Solanum confusum* and *S. glaucophyllum* range from central Bolivia to the mouth of the Río de La Plata; *S. luridifuscescens* and *S. matadori* are found in south-eastern Brazil. Further investigation may reveal this group to be non-monophyletic.

IV. *S. cylindricum* group (*S. cylindricum*, *S. pelagicum*). These two species from southeastern Brazil are distinctive due to their usually abundant pubescence of dendritically branched hairs. Although *S. cylindricum* is morphologically variable, at least some dendritic hairs are present on most specimens. Other species in sect. *Cyphomandropsis*, such as *S. luteoalbum* and *S. amotapense*, can have populations with dendritically branched pubescence, but they differ from *S. cylindricum* and *S. pelagicum* in other morphological characters. Lobed or compound leaf blades may also link the two species; *S. pelagicum* has pinnately lobed trunk leaves, and some specimens of *S. cylindricum* have small hastate lobes at the base of the leaf blades.

V. Species not placed in a group (*S. fusiforme*, *S. hutchisonii*). *Solanum fusiforme* and *S. hutchisonii* are each morphologically distinctive, and their affinities to other species in the section are not obvious. Both species are nearly glabrous, but otherwise they are dissimilar. *Solanum fusiforme* is found in mesic areas of southeastern Brazil and adjacent Argentina and Paraguay, whereas *S. hutchisonii* occurs in dry valleys of northern Peru.

Solanum fusiforme can be recognized by its pinnately compound leaf blades and fusiform fruits. No other species in the section has fruits with this morphology. Although *S. pelagicum* also has pinnately compound leaves, it differs from *S. fusiforme* in many characters.

Solanum hutchisonii has distinctive fleshy leaf blades, often with subcordate bases. It may be most closely related to species of the *S. amotapense* group, which also have cordate leaf bases and large angled seeds, and are found in nearby areas of Ecuador and northern Peru.

HABITATS AND DISTRIBUTION

Species of sect. *Cyphomandropsis* are found at a range of elevations from sea level to snow line (ca. 4000 m). Although they occupy several distinct habitat types, in general they prefer sunny areas, such as light gaps and clearings in primary forest, and disturbed sites, such as roadsides or ravines in secondary vegetation. Approximately half the species in the group are typically found in seasonally arid inter-Andean valleys, often on rocky slopes or in canyons. Some of them may lose their leaves during dry periods. These species include *S. amotapense*, *S. fallax*, *S. hibernum*, *S. hutchisonii*, *S. luteoalbum*, and *S. stuckertii*. *Solanum confusum*, in contrast, is generally found in wetter cloud forest areas, especially in groves of *aliso* (*Alnus acuminata*). In the southern part of its range, *S. confusum* is found in the bosque tucumano-boliviano floristic province (Cabrera 1976; Killeen et al. 1993). *Solanum confusum* occupies the highest elevations of any species of the group (up to ca. 4000 m), tolerating at least short periods of frost and snow.

Some species of *Cyphomandropsis*, such as *S. cylindricum*, *S. fusiforme*, and *S. mata-dori*, typically occur in clearings in *Araucaria* forests in southeastern Brazil and adjacent areas at mid-elevations (300–1200 m). These regions are warmer and more humid than those described above, but can experience cold or frost in winter. A unique Brazilian endemic, *S. pelagicum*, is found at lower elevations and typically occupies *restinga* (coastal scrub or dune habitats) along the coast of the state of Santa Catarina. Some populations of this species also occur inland in forest clearings and margins. Another Brazilian endemic, *S. luridifuscescens*, grows in higher elevation rain forest (ca. 1100–2600 m) and prefers waterlogged or swampy ground.

Among the more unusual habitats exploited by species of sect. *Cyphomandropsis* are the seasonally inundated depressions in clay or sandy soil frequented by *S. glaucophyllum*. These are found throughout the Chaco floristic province in south-central Bolivia, Paraguay, north-central Argentina and adjacent areas, and in the Pampas floristic province of Argentina (Cabrera 1976). *Solanum glaucophyllum* can form dense monospecific thickets in isolated low-lying areas (called “curiches” in Bolivia and “duraznilares” in the Argentine pampas) and on flooded or waterlogged river banks and islands (Okada et al. 1977). This species is apparently deciduous during the winter dry season and can tolerate frost in at least some parts of its range.

In contrast to species of sect. *Pachyphylla*, which range from Mexico to Argentina, all species of sect. *Cyphomandropsis* are restricted to South America (Fig. 5). Only the ornamental species *S. glaucophyllum* has been taken to the Old World; cultivated specimens have been recorded from various European botanic gardens as well as from two sites in Asia. *Solanum glaucophyllum* was collected in Florida around 1900. It is thought that these plants were adventive from seeds carried in ships’ ballast (D’Arcy 1974). Whether the Asian collections of *S. glaucophyllum* also represent adventive plants is not known.

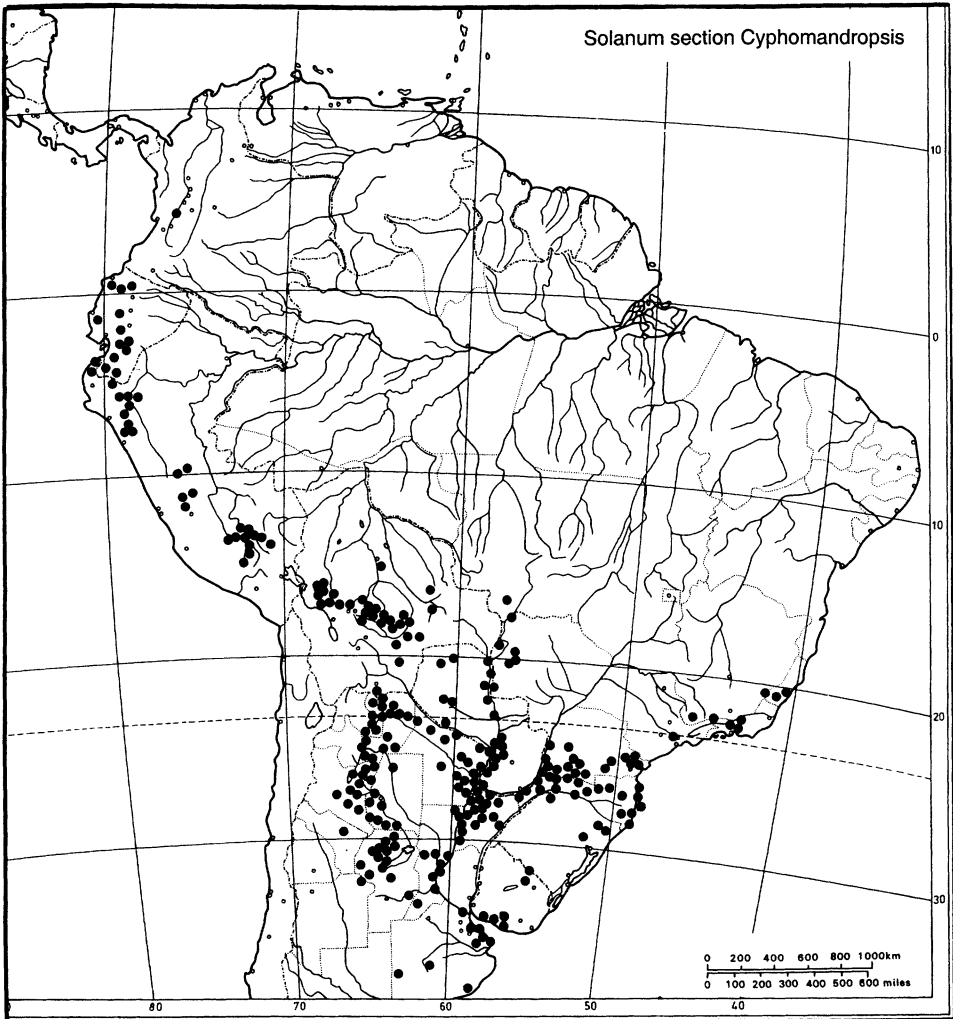


FIG. 5. Distribution of *Solanum* sect. *Cyphomandropsis*. This map is a composite of all the species maps included in the systematic treatment.

In comparison to the members of sect. *Pachyphylla*, species of sect. *Cyphomandropsis* exhibit a pronounced tolerance of drier and cooler conditions. The ranges of species of this section extend further south than those of sect. *Pachyphylla*, and, in general, encompass higher elevations. They exclude the more tropical parts of South America, such as the Amazon and Orinoco basins, Guayana highlands, Planalto de Mato Grosso in Brazil, and the northern and western coasts of Colombia. *Solanum glaucophyllum* and, to a lesser extent, *S. stuckertii*, are found in the seasonally dry Chaco and pampas regions from which sect. *Pachyphylla* is absent. The distribution of species by country is given in Appendix 5. Brazil has the largest number of endemics (3), followed by Peru and Bolivia with one each.

In terms of the species groups outlined above, the *S. luteoalbum* group is Andean in distribution, ranging from southern Ecuador to approximately 32°S in Argentina. The three species constituting this group are more or less allopatric and replace each other as one moves from north to south. Hybrid plants have resulted from artificial crosses between *S. hibernum* and *S. stuckertii* (see section "Breeding Systems and Crossing Studies"). The ranges of these two species partially overlap in south-central Bolivia, but in general they occupy different habitat types and occur at different elevations; thus, eco-geographic factors may prevent them from exchanging genes. Morphologically differentiated geographical variants are found in *S. luteoalbum*. Species and even populations within this group are likely isolated by distance and by ecological factors, such as unfavorably hot and dry conditions in intervening Andean valleys.

Solanum amotapense and *S. fallax* both occur west of the Andes from Ecuador to northern Peru; an isolated collection of *S. fallax* is known from the Cauca Valley of Colombia. Both are adapted to seasonally arid sites, but *S. fallax* is found in the more mesic Jauneche forest of northern and central Ecuador. *Solanum amotapense* has a disjunct distribution, and its range abuts that of *S. fallax* in southern Ecuador. It is possible, however, that additional field work will expand the ranges of these little-known species.

Solanum hutchisonii is restricted to a small area of the Río Marañón valley in northern Peru, where it is sympatric or nearly so with *S. amotapense*. Altitudinal differences appear to separate the two species; *S. hutchisonii* occurs below 600 m and *S. amotapense* above 700 m in elevation.

Species of the *S. glaucophyllum* group are almost completely allopatric, and, where their ranges approach each other, are separated by obvious ecological differences. This is most pronounced in the case of *S. glaucophyllum* and *S. confusum*, which occupy totally different habitats, even in areas where their ranges abut. *Solanum glaucophyllum* is found in seasonally inundated depressions in Chaco forest, whereas *S. confusum* occurs in the cloud forest understory. Both *S. matadori* and *S. luridifuscescens* are native to southeastern Brazil, but the two species are separated by geographic, ecological, and elevational differences. *Solanum matadori* restricted to mid-elevation *Araucaria* forests of Santa Catarina state, and *S. luridifuscescens* found at higher elevations and more northerly latitudes in the Atlantic coastal rain forest.

Likewise, *S. cylindricum* and *S. pelagicum* are species of southeastern Brazil and adjacent areas. Their known ranges barely overlap, however, and they are likely separated by ecological preferences; *S. pelagicum* is restricted to low elevation coastal areas, and *S. cylindricum* occurs in *Araucaria* groves in more upland areas. The range of *S. cylindricum* extends into Prov. Misiones, Argentina, where it overlaps with the enigmatic *S. fusiforme*, another species of *Araucaria* forest.

POLLINATION

The function of the anther connective or dorsal anther surface in providing rewards for pollinators needs further study in sections *Pachyphylla* and *Cyphomandropsis*. In most members of sect. *Pachyphylla* that have been investigated, the swollen anther connective acts as an osmophore to secrete volatile compounds that are gathered by male euglossine bees (Gracie 1993; Sazima et al. 1993). Although this indicates that pollination in sect. *Pachyphylla* may primarily be accomplished by passive pollen deposition on fragrance-gathering male bees, the only taxa that have been well studied are those with large anther

connectives. It remains to be determined what role female buzz-pollinating bees play in the reproductive biology of sect. *Pachyphylla*. At least one member of sect. *Pachyphylla*, *S. pinetorum*, is not visited by male euglossines but is buzzed by several genera of female bees (Sazima et al. 1993). Similarly, it is not known whether species of sect. *Cyphomandropsis*, especially those with elaborated anther surfaces, also produce volatile compounds that attract male bees. Pollination has been studied in only two species of sect. *Cyphomandropsis*, *S. glaucophyllum* and *S. stuckertii*, and they were found to be buzz-pollinated by female bees (L. Passarelli, pers. comm.). Field observations are needed to document flower visitors and to distinguish between two rather different pollination syndromes that might occur in the section (buzz-pollination by female pollen-collecting bees vs. fragrance gathering by male euglossine bees).

HERBIVORY

Little is known about herbivory in sect. *Cyphomandropsis*. Okada et al. (1977) note that the caterpillars of *Antarctia fusca* Esler burrow in the pith of *S. glaucophyllum* and cause damage to the aerial stems. They have also been seen on the leaves, but it is not known if they feed on them. Aside from this account, there are only two published reports of herbivores on species of the section; both are ithomiine butterflies in the genus *Mechanitis* [*M. polymnia casabranca* Haensch and *M. lysimnia lysimnia* (Fabricius)] that use *S. luridifuscescens* as a larval host plant in Brazil (Drummond & Brown 1987; species cited as *Cyphomandra velutina* Sendtn.). These butterflies are specialists on many species of Solanaceae, where they may discriminate in choosing oviposition sites among a rich array of phytochemicals produced by the plants (see Brown 1987; Drummond & Brown 1987; Vasconcellos-Neto 1986, 1991). Although they may use these secondary compounds to locate and identify potential solanaceous host plants, they rely upon other alkaloid sources, such as species of Boraginaceae and Asteraceae, to render the adults distasteful to predators. This extremely interesting interrelationship needs further study, and it is hoped that the present taxonomic treatment, by facilitating identification of the plants, will stimulate observations of use of *Cyphomandropsis* species by ithomiines and other herbivores. Such studies may in turn provide insight into the phytochemistry and evolutionary ecology of the *Pachyphylla/Cyphomandropsis* group.

USES

Unlike taxa in the related sect. *Pachyphylla*, few uses have been reported for species of sect. *Cyphomandropsis*. The fruits are small and unpalatable to humans, and there are no instances of their being used as food. *Solanum glaucophyllum* is the only species in the group with any recorded uses by people: it has been employed medicinally as a purgative, and the stems have been used as firewood and building materials (see notes under species treatments in section "Taxonomy"). Yet, the deleterious effects of this species far outweigh its usefulness, for *S. glaucophyllum* has been responsible for many cases of livestock poisoning in South America (Okada et al. 1977). Because its toxicity is due to increased calcification of soft tissues after ingestion, *S. glaucophyllum* is currently being investigated as a source of bone growth stimulants useful in medicine (Morris 1977; B. Barr, pers. comm.).

TAXONOMY

Solanum L., Sp. pl. 1: 184. 1753.—TYPE: *Solanum nigrum* L.

See D'Arcy (1972, 1973) for generic synonymy.

Herbs, shrubs, trees, or vines, with or without spines, glabrous or pubescent with unbranched or branched, often glandular hairs. Leaves alternate or paired and frequently unequal in size, simple to pinnately lobed or compound, petiolate or sessile, without stipules. Inflorescences cymose, branched or unbranched. Flowers usually perfect, (4–) 5-merous, actinomorphic or zygomorphic; calyx campanulate, sometimes accrescent in fruit; corolla rotate, campanulate, stellate, or urceolate, white, green, yellow, pink, or purple; stamens equal or unequal, the filaments generally short and inserted at the corolla base, the anthers basifixed, blunt or tapered toward apex, opening by terminal pores (sometimes expanding into longitudinal slits); ovary 2-carpellate; ovules many; style articulated at base, usually slender; stigma capitate. Fruit a berry, usually fleshy but occasionally dry, usually many-seeded, the seeds often flattened; embryo curved, embedded in abundant endosperm. Chromosome number: $n = 12, 23$.

Solanum section **Cyphomandropsis** Bitter, Repert. Spec. Nov. Regni Veg. 12: 461. 1913.

Cyphomandra section *Cyphomandropsis* (Bitter) D'Arcy, Ann. Missouri Bot. Gard. 59: 277. 1972.—LECTOTYPE, designated by Seithe, 1962: *Solanum stuckertii* Bitter.

Cyphomandra section *Cornigera* Child, Repert. Spec. Nov. Regni Veg. 95: 293. 1984.—TYPE: *Cyphomandra cornigera* Dunal [= *Solanum pelagicum* Bohs].

Solanum section *Glaucophyllum* Child, Repert. Spec. Nov. Regni Veg. 97: 144. 1986.—TYPE: *Solanum glaucophyllum* Desfontaines.

Herbs, shrubs, or small trees, sometimes rhizomatous, lacking spines. Stems glabrous to densely pubescent with unbranched glandular, unbranched eglandular, and/or dendritically branched eglandular hairs. Leaves 3 to many per sympodial unit, the blades chartaceous to subcoriaceous or succulent, simple and elliptic to ovate or pinnately compound, acute to acuminate at apex, cuneate to decurrent to deeply cordate at base, glabrous to densely pubescent, the petioles glabrous to densely pubescent. Inflorescence unbranched or forked to highly branched; pedicels articulated at or above the base, leaving scars or pedicellar remnants; inflorescence glabrous to densely pubescent. Flowers perfect, actinomorphic, 5-merous. Calyx campanulate, not accrescent in fruit, glabrous to densely pubescent, sometimes inflated below lobes, the lobes deltate to narrowly triangular with obtuse to acuminate tips. Corolla white, pink, purple, or bluish, membranaceous to subcoriaceous, stellate, rotate-stellate, or stellate-campanulate, the lobes narrowly triangular to ovate, subacute to apiculate at apex, glabrous to densely pubescent abaxially with branched or unbranched hairs, glabrous to moderately pubescent adaxially. Stamens equal, filaments very short, glabrous, inserted in corolla tube near its base; anthers connivent or free, yellow to greenish, reddish, or purplish, ovate to narrowly triangular, tapered toward apex, the pores directed distally and occasionally adaxially, not (or rarely) opening into longitudinal slits. Ovary glabrous to densely puberulent; style glabrous to moderately puberulent, cylindrical to subclavate; stigma truncate to subcapitate, the same diameter as the style. Fruits globose, ellipsoidal, ovoid, or fusiform, obtuse, acute, or apiculate at apex, glabrous to densely puberulent, yellow, orange, red, brownish, or blue-black

when ripe; stone cell aggregates present or absent. Seeds thick and angled to lenticular or strongly flattened, smooth to felty-pubescent. Chromosome number: $n = 12$.

SYNOPTIC LIST OF CHARACTERS OF SOLANUM SECTION CYPHOMANDROPSIS

The following is a list of distinctive character states found among species of section *Cyphomandropsis*. Numbers correspond to the species number in the taxonomic treatment. Numbers in parentheses indicate that the character state is uncommon or insufficiently studied in that species. In most cases, diagnostic character states are listed, but the alternatives are not. This is not intended to be an exhaustive list of characters, but an aid to identification of distinctive taxa.

Plants found in seaside habitats of southeastern Brazil: 12

Plants glabrous or nearly so: 2, 3, 5, 6, 8, 9, 11

Plants pubescent: 1, 2, 3, 4, (6), 7, 9, 10, 12, 13

Plants with branched hairs: 1, 3, 7, 10, 12

Plants glaucous: 6

Leaf surfaces strongly discoloured: 7

Pinnately compound leaves present: 5, 12

Leaf bases cordate or subcordate: 1, 4, 7, 8, 12

Inflorescences branched, with more than two rachises: 2, 4, 6, (10), 11, (13)

Pedicels articulated above the base, leaving remnants more than 1 mm long: 4

Calyx tube swollen at base of lobes: 1, 4

Corolla stellate-campanulate: 2

Corolla rotate-stellate: 1, 6

Fruits pubescent: 4, (12)

Fruits fusiform, much longer than wide: 5

Fruits dark blue or black when ripe: 6

Seeds very large and angled: 1, 2, 4, 6, 7, 8, 10, 13

KEY TO THE SPECIES OF SOLANUM SECTION CYPHOMANDROPSIS

1. Plants glabrous or nearly so; if pubescent, the hairs sparse and/or minute and only visible under high magnification (10× or more).
 2. Plants often with some pinnately compound as well as simple leaves; fruits elongate-fusiform. *5. S. fusiforme.*
 2. Plants with simple leaves only; fruits globose.
 3. Leaf bases rounded to subcordate; leaf blades somewhat thick and fleshy; northern Peru. *8. S. hutchisonii.*
 3. Leaf bases cuneate, truncate, or decurrent; leaf blades membranaceous to fleshy; Bolivia, Argentina, Paraguay, Uruguay, and southeastern Brazil.
 4. Leaves usually glaucous; corollas rotate-stellate and plicate, the tube 5–8 mm long, the lobes 5–10 mm wide; ripe fruits dark blue-black and glaucous. *6. S. glaucophyllum.*
 4. Leaves green, not glaucous; corollas stellate or stellate-campanulate, not plicate, the tube 2–6 mm long, the lobes 2–5 mm wide; ripe fruits yellow or orange.
 5. Abaxial surface of anthers smooth to roughened, but not obviously papillate; Bolivia and northwestern Argentina. *2. S. confusum.*
 5. Abaxial surface of anthers with band of scaly papillae (these most obvious in dried material); southeastern Brazil.
 6. Adaxial corolla surfaces pubescent; petioles glabrous; inflorescence branches three or more. *11. S. matadori.*

- 6. Adaxial corolla surfaces glabrous or nearly so; petioles pubescent; inflorescences unbranched or at most forked.
- 7. Abaxial surface of anthers with a dense band of scaly papillae; hairs, if present, unbranched; leaf blades 2–7 (–9) cm wide. 9. *S. luridifuscescens*.
- 7. Abaxial surface of anthers at most with very fine or inconspicuous papillae; branched hairs frequently present; leaf blades 0.5–3.5 cm wide. 3. *S. cylindricum*.
- 1. Plants obviously pubescent, the hairs visible without magnification.
 - 8. Pedicels articulated above the base, leaving remnants more than 1 mm long; fruits pubescent; leaf bases deeply cordate (rarely shallowly truncate to subcordate). 4. *S. fallax*.
 - 8. Pedicels articulated at or very near the base; fruits glabrous; leaf bases cuneate or at most shallowly cordate.
 - 9. Vegetative pubescence of unbranched hairs only.
 - 10. Leaf blades glaucous, very narrow, the length:width ratio generally more than 4.5:1. 6. *S. glaucophyllum*.
 - 10. Leaf blades green, not glaucous, length:width ratio usually less than 4.5:1.
 - 11. Calyx tube inflated at base of lobes; corollas rotate-stellate, the tube 5–7 mm long; leaf bases often subcordate, rarely cuneate. 1. *S. amotapense*.
 - 11. Calyx tube not noticeably swollen; corollas stellate to stellate-campanulate, the tube 2–4 (–6) mm long; leaf bases cuneate, truncate, rounded, or decurrent.
 - 12. Abaxial surface of anthers with an obvious band of scaly papillae; southeastern Brazil. 9. *S. luridifuscescens*.
 - 12. Abaxial surface of anthers smooth or roughened, but not obviously scaly-papillose; Andean Ecuador, Peru, Bolivia, and northwestern Argentina.
 - 13. Pubescence sparse to dense, with many of the hairs 1 mm long or more; corollas stellate to stellate-campanulate. 2. *S. confusum*.
 - 13. Pubescence moderate to dense, the hairs generally less than 1 mm long; corollas stellate.
 - 14. Corollas white; south-central Bolivia to northwestern Argentina. 13. *S. stuckertii*.
 - 14. Corollas purple (rarely white); southern Ecuador to southern Peru. 10. *S. luteoalbum*.
 - 9. Vegetative pubescence at least partly of branched hairs.
 - 15. Calyx tube inflated at base of lobes; corollas rotate-stellate, the tube 5–7 mm long. 1. *S. amotapense*.
 - 15. Calyx tube not inflated; corollas stellate, the tube 2–4 mm long.
 - 16. Leaves strongly discoloured, the adaxial surface green with sparse pubescence, the abaxial surface densely white-pubescent with branched hairs; central Bolivia. 7. *S. hibernum*.
 - 16. Leaves not strongly discoloured, green on both sides or with pubescence evenly distributed throughout; Ecuador, Peru, Argentina, and southeastern Brazil.
 - 17. Leaves often pinnately compound or lobed; if simple, the bases truncate to subcordate; seaside habitats in Santa Catarina, Brazil. 12. *S. pelagicum*.
 - 17. Leaves simple or with 1–2 small basal lobes, the bases cuneate to decurrent; inland and upland Ecuador, Peru, Argentina, and southeastern Brazil
 - 18. Peduncles 0.5–3.5 cm long; inflorescence unbranched or forked, 1–15-flowered; southeastern Brazil and adjacent Argentina. 3. *S. cylindricum*.
 - 18. Peduncles 3.5–6.5 cm long; inflorescence unbranched, forked, or further branched, (5–) 10–25-flowered; Andean Ecuador and Peru. 10. *S. luteoalbum*.

1. *Solanum amotapense* Svenson, Amer. J. Bot. 33: 483. 1946. *Cyphomandra amotapensis* (Svenson) A. Child ex Bohs, Fl. Neotrop. Monogr. 63: 153. 1994.—
 TYPE: PERU. Piura: Amotape Hills, near summit of Cerro Prieto, 81°15'W, 4°45'S, 2300 ft, 28–30 Mar 1941, *Haught & Svenson 11634* (holotype: BKL!; isotype: US! #1832594).

Cyphomandra villosa Steyermark, Phytologia 9: 348. 1964.—TYPE: ECUADOR. Loja: Las Chinchas, 2250 m, 12 Apr 1944, *Acosta Solís* 7743 (holotype: F!; photo of holotype [F neg #51366]: F!).

Shrub 0.5–2 m tall. Stems densely pubescent with unbranched eglandular hairs and often also some short-stalked glands (dendritically branched hairs occasionally present). Leaves 7—many per sympodial unit, the blades 4–23 cm long, 2–14 cm wide, length:width ratio ca. 1.5–2.5:1, simple, ovate to elliptic-ovate, acuminate at apex, cuneate to subcordate at base, chartaceous, nearly glabrous to densely pubescent adaxially with hairs like those of the stem, moderately pubescent to densely so on veins and abaxial surface, the petioles 1–8 cm long, densely pubescent. Inflorescence unbranched or forked, ca. 6–30-flowered, 2.5–14 cm long; peduncle 1–6.5 cm long; rachis 1.5–9 cm long; pedicels 5–15 mm long, 10–15 mm long in fruit, spaced 1–25 mm apart, articulated at the base; inflorescence axes moderately to densely pubescent. Calyx moderately pubescent with unbranched eglandular hairs and stalked glands, constricted at apex of inflated tube, the radius 2.5–5 mm, the lobes 1–3 mm long, 1–1.5 mm wide, deltate to triangular-subulate, acute at tips. Corolla white or purple, chartaceous to membranaceous, rotate-stellate, the radius 10–25 mm, the tube 5–7 mm long, the lobes 6–13 mm long, 4–12 mm wide at base, triangular-ovate, acute at apex, sparsely to moderately puberulent abaxially, especially near tips of lobes, glabrous adaxially. Anthers connivent or not, yellow or greenish yellow, ovate, 4–6 mm long, 2–2.5 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous (moderately pubescent in *Acosta Solís* 7743), cylindrical, 6–10 mm long, 0.5 mm in diameter; stigma truncate. Fruits 1.5–2 cm long, 1.5–2 cm in diameter, globose, obtuse at apex, glabrous, pale orange, red, or brownish when ripe; stone cell aggregates absent. Seeds 4–5 mm long, 4 mm wide, angled, smooth to rugose. Chromosome number: $2n = 24$. Figs. 6, 7.

Phenology. Flowering and fruiting in January through April and in November.

Distribution (Fig. 8). Southwestern Ecuador and northwestern Peru; cliff edges, dry and rocky stream beds, and under deciduous vegetation, primarily in seasonally arid areas; 600–2300 m.

Local name. Ecuador: Sabalucu (*Acosta Solís* 7743).

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** LOJA: road Celica–El Empalme, ca. 12 km from Celica, *Harling & Andersson* 22510 (GB, NY); road Cariamanga–Yambaca–El Toldo–Chaco, Km 10–20, *Harling & Ståhl* 26473 (NY). **Peru.** CAJAMARCA: Prov. Jaén, Pucará (on the Río Huancabamba), vicinity of town, Km 127 E of Olmos, Mesones–Muro hwy between Olmos and Jaén, *Hutchison & Wright* 3548 (F, MO, NY, US); Prov. Contumazá, near San Benito, *López & Sagástegui* 7894 (MO); Prov. Cajamarca, Chilete–Magdalena, *Sagástegui* 9614 (MO, NY); Prov. Contumazá, between Chilete and El Rupe, W of road Chilete–Contumazá, *Sánchez Vega* 4220 (NY).—TUMBES: Prov. Tumbes, mountains E of Hacienda Chicama, *Weberbauer* 7634 (F).

Cultivated. Cult. at Royal Botanic Gardens, Edinburgh, Scotland, *Child* C9469 (E, G).

Solanum amotapense can be distinguished from the other species in the section by its inflated calyx tube, rotate-stellate corolla, long slender filaments, and subcordate leaf bases. The only other species of sect. *Cyphomandropsis* occurring in arid areas of northern Peru is *S. hutchisonii*. *Solanum amotapense* differs from it in its abundant pubescence and chartaceous rather than succulent leaf blades.

All specimens of *S. amotapense* have unbranched eglandular hairs on the stems, leaves, and inflorescences, except the type collections of *S. amotapense* and *C. villosa*, which have a few dendritically branched hairs, especially on the leaf margins. Corolla

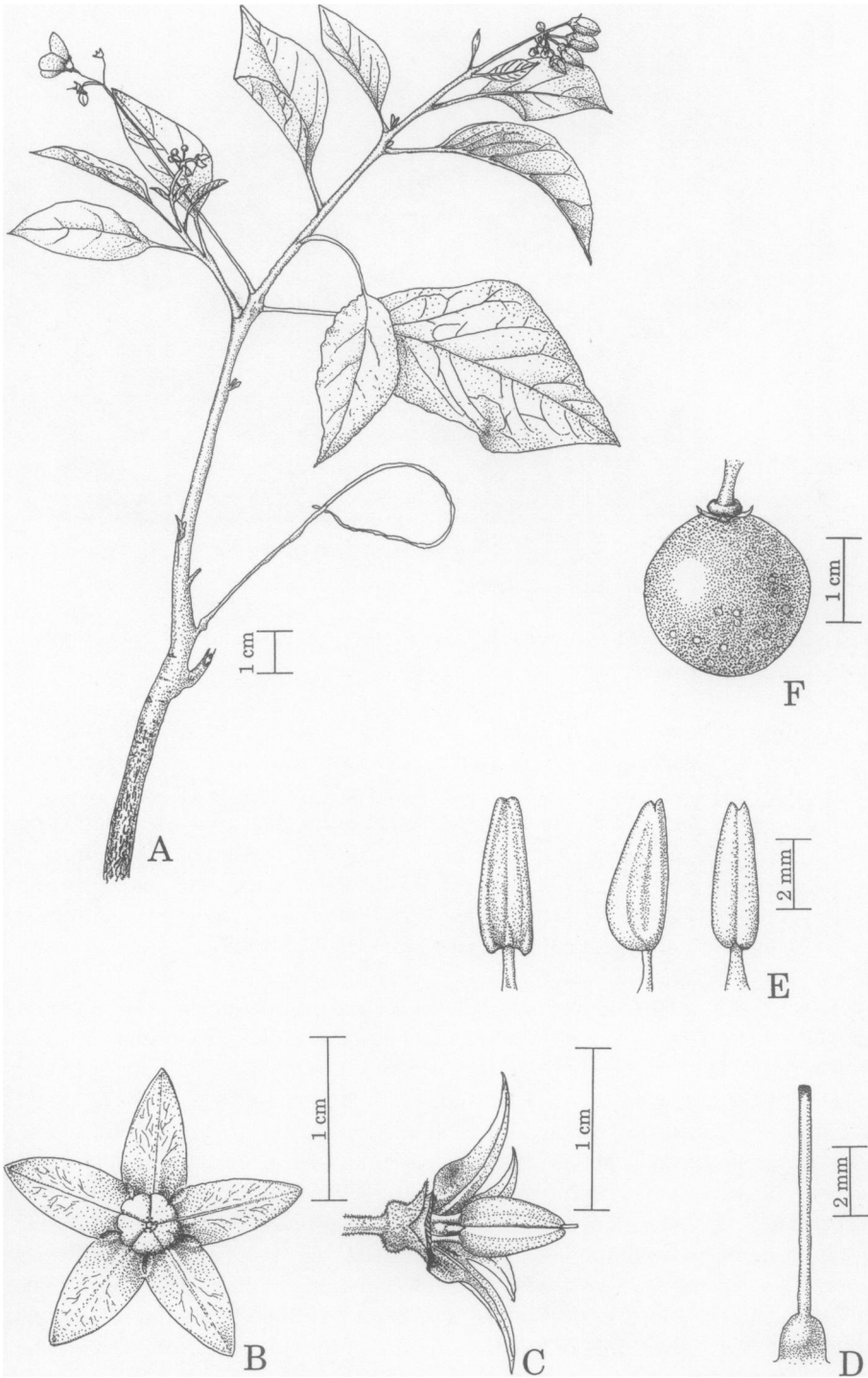


FIG. 6. *Solanum amotapense*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, and adaxial views). F. Fruit. (Based on: A, F, Child C9469; B–E, greenhouse material of Bohs 2479.)



FIG. 7. Flowers of *S. amotapense*. Scale bar = 1 cm.

color varies from white to light blue or purple in this species, and the style is puberulent rather than glabrous in the type of *C. villosa*.

2. *Solanum confusum* C. V. Morton, Contr. U.S. Natl. Herb. 29: 70. 1944.—TYPE: BOLIVIA. Cochabamba: Mount Tunari, near snow line, 1891, *Bang 1118* (holotype: US! #1177847; isotypes: C! F! G! L! LD! M! NY! WU! Z!).

Solanum adelphum C. V. Morton, A Revision of the Argentine Species of *Solanum*, 185. 1976. *Cyphomandra adelpha* (C. V. Morton) A. Child ex Bohs, Fl. Neotrop. Monogr. 63: 153. 1994.—TYPE: ARGENTINA. Tucumán: Depto. Burruyacú, Cerro del Campo, 1800 m, 14 Dec 1928, *Venturi 7732* (holotype: US! #1441095; photos of holotype: GH! NY!; isotypes: GH! S! SI! US).

Shrub 1–3.5 m tall. Stems glabrous to densely pubescent-pilose with glandular and eglandular hairs. Leaves 4–5 per sympodial unit, the blades 5–19 cm long, 1.5–6.5 (–8) cm wide, length:width ratio ca. 2–4.5:1, simple, elliptic, acute or acuminate at apex, cuneate or decurrent at base, chartaceous to subcoriaceous, nearly glabrous to moderately pubescent-pilose adaxially and abaxially, the petioles 0.5–4 cm long, glabrous to moderately pubescent-pilose, with pubescence denser in adaxial channel. Inflorescence unbranched to twice forked or further branched, 5–30 (–40 or more)-flowered, 3–20 cm long; peduncle 1.5–9 cm long; rachis 1–10 cm long; pedicels 5–30 mm long, 15–35 mm long in fruit, expanded distally below calyx, spaced 1–14 (–40) mm apart, articulated at or near base, leaving scars or short pegs up to 1 mm long; inflorescence axes glabrous to densely pubescent-pilose with glandular and eglandular hairs. Calyx nearly glabrous to densely pubescent, the radius 2–8 mm, the lobes 1–7 mm long, 1–2 mm wide, triangular-deltate, often narrowed into acuminate tips. Corolla white to pink or violet, chartaceous to membranaceous, stellate or stellate-campanulate, the radius 8–15 mm, the tube 2–4 mm long, the lobes 6–12 mm long, 2–5 mm wide at base, narrowly triangular to ovate, acute

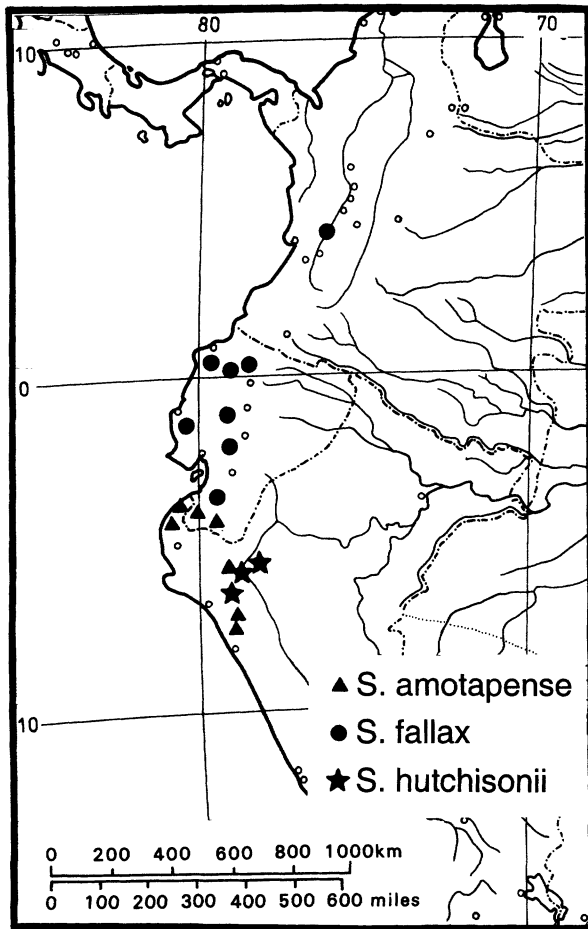


FIG. 8. Distribution of *S. amotapense*, *S. fallax*, and *S. hutchisonii*.

or subacute at apex, nearly glabrous to densely pubescent abaxially, nearly glabrous adaxially except on midribs and tips of lobes. Anthers connivent or not, greenish white to purplish, yellowish, or reddish brown, ovate to lanceolate, 5–9 mm long, 1.5–3.5 mm wide, glabrous, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous or sparsely puberulent, cylindrical, 6–10 mm long, ca. 0.5–1 mm in diameter; stigma truncate. Fruits ca. 0.8–2 cm long, 0.8–2 cm in diameter, globose, obtuse at apex, glabrous, yellow to orange when ripe; stone cell aggregates present or absent. Seeds 4–6 mm long, 3–5 mm wide, angled, glabrate and rugose or pubescent with dense white pseudohairs, especially along margin. Chromosome number: $n = 12$. Figs. 9, 10.

Phenology. Flowering in all months except July and August; fruiting in all months except July, August, and September.

Distribution (Fig. 11). Bolivia and northwestern Argentina; cloud forest, open areas, or secondary vegetation, often on slopes and in groves of *aliso* (*Alnus acuminata*); ca. 900–4000 m.

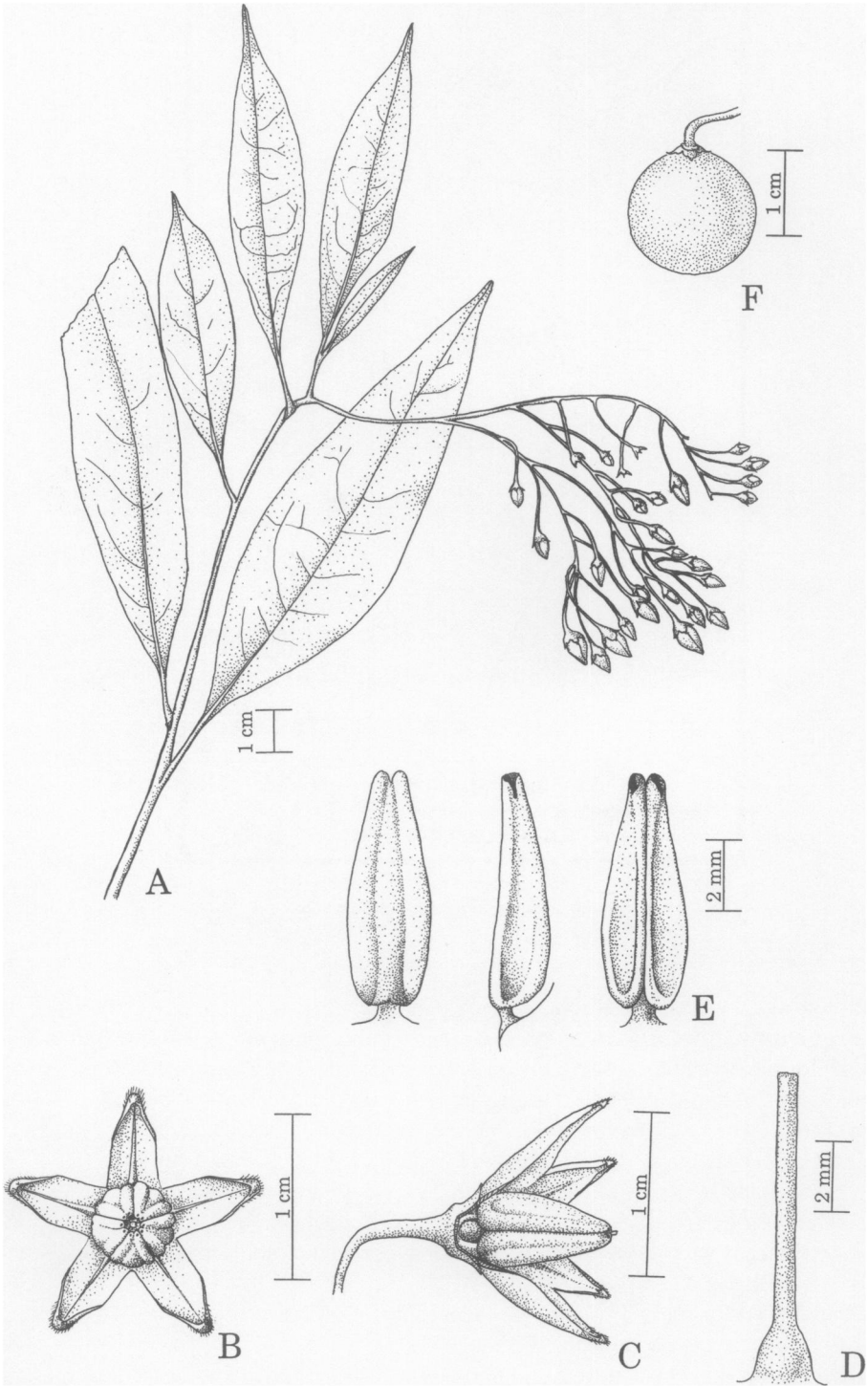


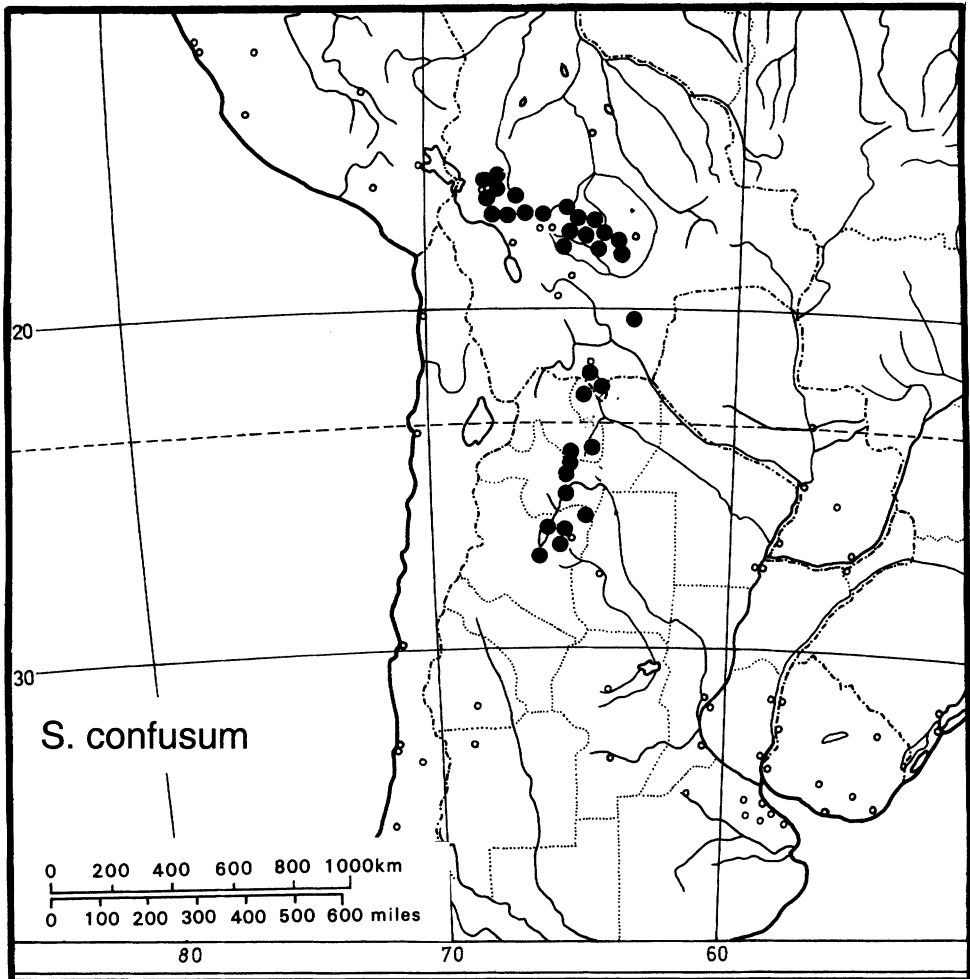
FIG. 9. *Solanum confusum*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial views). F. Fruit. (Based on: A, Meyer 15442; B–F, Sleumer 3056.)



FIG. 10. Inflorescence of *S. confusum* (Yungas de Mairana, Prov. Florida, Dept. Santa Cruz, Bolivia). Scale bar = 1 cm.

Local name. Bolivia: Tanta sachá (*Beck & Seidel 14478*).

REPRESENTATIVE SPECIMENS. **Bolivia.** CHUQUISACA: Prov. Sud Cinti, base oriental del Cerro Bufete, approx. 200 m al E del campamento Rinconada del Bufete, 20°49'49"S, 64°22'28"W, *Arroyo et al. 931* (USZ); Prov. Sud Cinti, camino entre campamento Rinconada del Bufete y la cumbre del Cerro Bufete, en al lado N del Cerro Bufete, 20°49'49"S, 64°22'28"W, *Serrano et al. 1299* (USZ); Prov. Sud Cinti, approx. 500 m al N del campamento Rinconada del Bufete, transecto 4-B-13, 20°49'49"S, 64°22'28"W, *Serrano et al. 1385* (USZ).—COCHABAMBA: Prov. Apopaya, ca. 10 km al NW de Independencia, *Beck & Seidel 14478* (LPB); Tako Tako, farm near Miske, 18°00'S, 65°15'W, *Brooke 5947* (BM, F, NY); Prov. Chapare, Incachaca, small power station about 80 mi NE of Cochabamba, 17°00'S, 65°30'W, *Brooke 6806* (BM); Prov. Ayopaya, Sailapata, *Cárdenas 3260* (US); Siberia, *Cárdenas 5741* (US); above Pojo, *Cárdenas 5773* (K, US); Prov. Carrasco, Jatún Pino, *Cárdenas 5936* (K, US); Prov. Carrasco, Com. Lachujmayu, *Hensen 936* (NY); Prov. Chapare, Centr. Hidroel. Corani, Km 61.4 Cochabamba–Chapare road, *Kessler & Kelschbach 233* (NY); Prov. Mizque, camino K'uri K'asa–Lagunas, 23°S, *López & Saravía 427* (USZ); Prov. Carrasco, on road from Comarapa to Cochabamba, 4 km W of border with Depto. Santa Cruz, 20 km (by air) and 28 km (by road) NW of Comarapa, 17°49'S, 64°41'W, *Nee & Solomon 34038* (LPB, NY); Prov. Carrasco, "Churro," 7 km (by air) ESE of Siberia, 8.5 km SW of limit with Depto. Santa Cruz, 17°50'S, 64°42'W, *Nee et al. 36494* (LPB, UT); Prov. Carrasco, narrow canyon of Río Monte Puncu, 5 km NE of Monte Puncu, 10 km (by air) NW of Epizana, 17°33'S, 65°16'W, *Nee & Solomon 36628* (LPB, USZ, UT); Prov. Mizque, comunidad Kehuñal, *Saravía & López 1171* (USZ); Pocona, *Steinbach 8660* (BM, GH, K, NY).—LA PAZ: Prov. Sud Yungas, debajo de Unduavi, subiendo al valle de Cerromarca, *Beck 14665* (NY); Prov. Nor Yungas, ca. 4.5 km al S de Coroico, *Beck 17219* (NY); Prov. Nor Yungas, ca. 2 km al S de Coroico, 16°11'S, 67°43'W, *Beck 21830* (LPB); Prov. Inquisivi, unos 8 km de Quime hacia Inquisivi, Camillaya, arriba del pueblo, 16°58'S, 67°12'W, *Beck 24352* (LPB); Prov. Inquisivi, first large waterfall above Circuata (16°38'S, 67°15'W) on road to Inquisivi, *Dorr et al. 6932* (LPB, UT); Prov. Inquisivi, Río Pavimani, 7 km NNE of Choquetanga, 16°47'S, 67°17'W, *Lewis 38693* (LPB); Prov. Inquisivi, Tambo Pata, 7 km S of Choquetanga, 16°54'S, 67°17'W, *Lewis 38954* (LPB); Prov. Nor Yungas, 9 km by road (ca. 4 km by air) down from and NE of Chuspipata, 16°16'S, 67°47'W, *Nee & Solomon 30226* (LPB, NY); Prov. Sud Yungas, Cantón Lambate, Chillkani, 16°35'S, 67°44'W, *Pizarro 91* (LPB); Prov. Nor Yungas, road from Unduavi to Sacramento, *Plowman & Davis 5150* (GH, K, MO); Prov. Sud Yungas, 3.1 km SE of Unduavi bridge (below) on old road, 16°19'S, 67°53'W, *Solomon 8694* (LPB, NY); Prov. Nor Yungas, 7.8 km SE (above) Yolosa on road

FIG. 11. Distribution of *S. confusum*.

to San Juan de La Miel, 16°16'S, 67°43'W, *Solomon* 9347 (K, LPB, NY); Prov. Nor Yungas, 10 km NE of (below) Chuspipata on road to Yolosa, 16°16'S, 67°47'W, *Solomon* 12566 (LPB, NY).—SANTA CRUZ: Prov. Caballero, just S of Parque Nacional Amboró, Cerro Bravo area, 4–10 map km N of Comarapa, ca. 17°51'S, 64°32'W, *Abbott & Jardim* 17232 (USZ); Prov. Caballero, Cantón San Juan del Potrero, Yungas de Tablar, *Coimbra* 2619 (LPB); Prov. Florida, Valle de "El Fuerte," Samaipata, ca. 65°50'W, 18°12'S, *Ibsch et al. xx.effl* (USZ); Prov. Vallegrande, between Mataralcito and El Palmar on road from Vallegrande to Tierras Nuevas, 17 km by air ESE of Vallegrande, 18°32'30"S, 63°57'30"W, *Nee et al.* 37398 (LPB, NY, UT); Prov. Vallegrande, between "Mataralcito" and "El Palmar" on road from Vallegrande to Tierras Nuevas, 17 km by air ESE of Vallegrande, 18°32'30"S, 63°57'30"W, *Nee et al.* 37409 (NY); Prov. Florida, 5 km SW of Yerba Buena, top of ridge at upper reaches of Quebrada Agua Blanca, 18°01'S, 64°03'W, *Nee & Vargas* 38292 (LPB, USZ, UT); Prov. Vallegrande, ca. 6 km S of Abra Tablas on road to Los Sitanos, ca. 1 km N of Lagunillas and 5 km N of Khasa Monte, 18°39'S, 64°02'W, *Nee* 38389 (LPB, USZ, UT); Prov. Vallegrande, Aguadita, 8 km (by air) S of Khasa Monte on road to Los Sitanos, 18°47'S, 64°02'W, *Nee* 38427 (LPB, USZ, UT); Prov. Vallegrande, 5 km (by air) NW of Los Sitanos, 1 km N of turnoff to Sitanos Altos on road from Abra Tabla to Los Sitanos, 18°50'30"S, 64°0'W, *Nee* 38546 (LPB, NY, UT); Prov. Florida, 7 km (by air) NE of Mairana, 18°4'S, 63°55'W, *Nee* 40633 (LPB, USZ, UT); Parque Nacional Amboró, SW region of park, N of Comarapa, in tree plot of I. Vargas C., 17°49'45"S,

64°33'05"W, *Skinner et al. 15, 30* (USZ); Prov. Caballero, 5.7 km al SE de San Isidro, 18°04'S, 64°24'W, *Solomon & Nee 17969* (LPB); Comarapa, *Steinbach 8383* (BM, F, GH, K, MO, NY), 8384 (A, BM, F, GH, K, MO, NY); Prov. Caballero, Parque Nacional Amboró, San Juan del Potrero, entre Yunguillas y cabeceras del Río Zapallar, 17°52'S, 64°25'W, *I. Vargas et al. 1362* (NY, USZ), *1363* (NY, USZ); Prov. Florida, Parque Nacional Amboró, La Yunga, trayecto entre Chape y El Corral (8–10 km al NE de Mairana, senda de la Yunga hacia el Río San Rafael), 18°04'S, 63°53'W, *I. Vargas et al. 2514* (USZ); Prov. Caballero, Parque Nacional Amboró, proximidades del Cerro Bravo a 10 km al N de Comarapa, alrededores de la parcela permanente, 17°49.5'S, 64°32.5'W, *I. Vargas & Jardim 3001, 3017* (USZ, UT); Prov. Vallegrande, tramo entre la comunidad El Palmar y Peñones, 10 km al E de la ciudad de Vallegrande, siguiendo el camino Vallegrande–Tierras Nuevas, 18°32.5'S, 63°57.5'W, *I. Vargas et al. 3043* (USZ, UT); Prov. Florida, Parque Nacional Amboró, La Yunga, trayecto entre Chape y el Corral (8–10 km al NE de Mairana, senda de la Yunga hacia el Río San Rafael), 18°04'S, 63°53'W, *I. Vargas 3714, 3718* (USZ, UT); La Yunga above Mairana (Amboró Park), *Wood 8672* (LPB, USZ).—TARIJA: Prov. Arce, 43 km hacia Padcaya, Huancanqui, *Beck 14092* (LPB); Prov. Arce, valley of Río Chillaguatas, below Rancho Nogalar on trail between Sidras and Tariquia, 22°5'S, 64°25'W, *Solomon 11274* (LPB, NY).—Without locality: *Bang 2618* (NY, US). **Argentina.** CATAMARCA: Esquina Grande, *Jørgensen 1472* (GH, MO, SI); Depto. Andalgalá, Esquina Grande, *Jørgensen 10788* (G).—JUJUY: Depto. Capital, Cerro Zapla, road to the antenna, *Ahumada 5316* (CTES); Depto. Capital, Sierra de Zapla, Mina 9 de Octubre, camino a la antena, *Cabrera et al. 32059* (SI); Depto. Santa Bárbara, cerca de El Fuerte, *Kiesling et al. 8295* (SI); Depto. Ledesma, road to Valle Grande, 4 km before Abra de Cañas, *Legname & Cuezco 8220* (LIL); Ruta 5 km al W de Perico de San Antonio, contra el valle del río, *Novara 247* (MCNS); Depto. Santa Bárbara, ascent to Centinela, *Rotman 944* (CTES).—SALTA: Parque Nacional El Rey, *Brown & Malmierca 1571* (CTES); Coronel Moldes, La Hoyada, *Burkart 13219* (SI); Depto. Orán, entre Río Pescado y Solazati, *Cocucci 36* (CORD); Depto. Santa Victoria, road from Los Toldos to Lipeo, ca. 15 km from Los Toldos, *Legname & Cuezco 9938* (CTES); Depto. Capital, Quebrada de San Lorenzo, *Lotti 86* (CTES); Depto. La Caldera, Vaqueros, cuenca del Arroyo Chaile, 3–4 km al W del pueblo, *Marmol & Núñez 5567* (MCNS); Depto. Santa Victoria, camino de Baritú a Porongal, *Marmol et al. 8773* (MCNS); Depto. Santa Victoria, Los Toldos, *Meyer et al. 20370* (CTES); Depto. La Caldera, Vaqueros, streambed of Arroyo Chaile, 3–4 km W of town, *Novara et al. 5567* (G, NY); Depto. Caldera, road to Corniza, El Lapachar, *Schiavone et al. 11849C* (LIL); Depto. Chicoana, Tilián, *Varela 155* (MCNS); Depto. Guachipas, Alemania, *Venturi 9837* (A, BM, GH, MO).—TUCUMÁN: Depto. Burruyacú, *Bailetti 269* (LIL); Quebrada de los Sosa, Alisales, *Cabrera 13658* (CTES, LP); Depto. Tafí, Quebrada de Caínzo, *Grassi & Vervoort s.n.* (W); Depto. Chicligasta, in front of the gauging station of Río Cochuna, slightly before beginning of Cuesta del Clavillo, *Hunziker 19508* (UT); Depto. Monteros, road to Tafí del Valle, Km 36 (Ruta prov. 307), *Hunziker 24871* (UT); Sierra San Javier, Alto San Pablo, *Lillo 4543* (A, LIL, NY); Depto. Chicligasta, Puesto Santa Rosa, *Meyer 15442* (B, W), *15445* (B); road from Tafí del Valle to Nogalar, *Meyer 16374* (L); Depto. Chicligasta, between Pte. Santa Rosa and Aser. Jaya, *Meyer 18911* (W); Depto. Chicligasta, Cochuna, *O'Donnell 70* (F, GH, LIL); Depto. Tafí, Siambón, *Olea 89* (A, NY); Río Loro, *Olea s.n.* (BM, LIL, NY); Depto. Tafí, Parque Aconquija, *Petersen & Hjerting 565* (C, MO, NY); Depto. Tafí, Raco, *Petersen & Hjerting 618* (C, MO); Depto. Chicligasta, bridge over Río Cochuna, *Schreiter 10393* (GH), *Schreiter & O'Donnell 35090* (F, GH, NY); Quebrada de los Sosa, Km 39 to Tucumán on Ruta 307 to Tafí del Valle, *Schulz 11433* (CTES); Depto. Burruyacú, Sa. El Nogalito, *Slanis et al. S124* (LIL); Depto. Tafí, Parque Aconquija, Quebrada de Cainzo, *Sleumer 2094* (G, NY, P, W); Depto. Tafí, Puerta de San Javier, *Sleumer 3056* (G, LIL); Depto. Monteros, Valle de los Sosas, road to Tafí del Valle, *Sleumer 3067* (G); Depto. Chicligasta, Estancia Las Pavas, *Venturi 4589* (A, F, GH, GOET, LP, NY, SI); Depto. Tafí, La Hoyada, *Venturi 5688* (A).

Solanum confusum is characterized by its unbranched and often sparse hairs, elliptic leaves, long peduncles and pedicels, and usually campanulate-stellate corollas. It is most similar to *S. glaucophyllum* and to *S. hibernum*, *S. luteoalbum*, and *S. stuckertii* in the *S. luteoalbum* species group. *Solanum glaucophyllum* differs from *S. confusum* in its purplish black fruits, narrower glaucous leaves, and rotate-stellate corollas. The collection *Schreiter 11214* mentioned by Morton (1976) as similar to *S. confusum* actually belongs to *S. glaucophyllum*. *Solanum confusum* differs from species of the *S. luteoalbum* group in its more campanulate corollas and in its often sparse and shaggy pubescence.

Morton (1976) distinguished *S. confusum* and *S. adelphum* in part on the basis of connate vs. free anthers, respectively, but this character is difficult to evaluate critically in herbarium material. I can find no consistent morphological distinctions between the two

taxa. Collections from southern Bolivia (Depto. Tarija) and Argentina are morphologically homogeneous, with sparse pubescence and usually branched inflorescences. These populations have been recognized as *S. adelphum*. Collections from elsewhere in Bolivia can vary widely in degree of pubescence, inflorescence branching, and corolla size and shape. Plants that are glabrous or nearly so were assigned to *S. confusum*; however, glabrous and densely pubescent individuals are found growing side by side in several Bolivian localities and apparently represent morphological variants of the same species. Therefore, the name *S. confusum* is particularly appropriate for this taxon.

Solanum confusum is confined to cloud forest areas above 1700 m in western and central Bolivia, whereas it is often found at lower elevations in southern Bolivia and northwestern Argentina. In these regions, it occurs in the forest type known as the "selva subtropical boliviano-tucumana" or "bosque tucumano-boliviano" (Cabrera 1983; Killeen et al. 1993).

The type collection of *S. confusum*, *Bang 1118*, is a mixture of two species separated on different sheets. Rusby based his description of *Solanum clavatum* on one of the elements, which has obtuse anthers with large terminal pores; this element is *S. aligerum* Schldl. of sect. *Holophylla* (*S.* Knapp, pers. comm.). The other element has tapered anthers with small terminal pores and belongs to sect. *Cyphomandropsis*. Bitter (1913) re-described what he thought was Rusby's *S. clavatum*, remarking that Rusby's description contained many inaccuracies; however, Bitter had the *Cyphomandropsis* element rather than the *Holophylla* element. Morton (1944) described the *Cyphomandropsis* element as a new species, *Solanum confusum*. Sleumer (1957) provided a description of what he called "*Solanum clavatum*," but his description refers to *S. confusum*. He provided unpublished information from the Bolivian botanist M. Cárdenas that the snow line on Mt. Tunari is at approximately 4000 m in elevation, which is the source for the maximum elevation reached by *S. confusum* given above under "Distribution."

- 3. *Solanum cylindricum*** Vellozo, Fl. flumin. 2: 87. 1829 (text); 2: t. 119. 1831 (icones). *Cyphomandra cylindrica* (Vellozo) Sendtner in Martius, Fl. bras. 10: 121. 1846. *Pionandra cylindrica* (Vellozo) Miers, Ann. Mag. Nat. Hist. 15, ser. 2: 199. 1855.—TYPE: BRAZIL. Locality unknown, *Vellozo s.n.* (holotype: unknown).
- Solanum ellipticum* Vellozo, Fl. flumin. 2: 84. 1829 (text); 2: t. 100. 1831 (icones), non *Solanum ellipticum* R. Brown, 1810. *Cyphomandra elliptica* (Vellozo) Sendtner in Martius Fl. bras. 10: 121. 1846. *Pionandra elliptica* (Vellozo) Miers, Ann. Mag. Nat. Hist. 15, ser. 2: 199. *Solanum johannae* Bitter, Repert. Spec. Nov. Regni Veg. 12: 465. 1913.—TYPE: BRAZIL. Rio de Janeiro: seaside forest of Pharmacopolis [Parati], *Vellozo s.n.* (holotype: unknown).
- Solanum subhastatum* Smith & Downs, Phytologia 10: 432. 1964. *Cyphomandra subhastata* (Smith & Downs) A. Child ex Bohs, Fl. Neotrop. Monogr. 63: 154. 1994.—TYPE: BRAZIL. Santa Catarina: Lauro Müller-Urussanga, Pinhal da Companhia, 300 m, 23 Aug 1958, *Reitz & Klein 7053* (holotype: US! #2323379; isotypes: HBR, L!).
- Solanum catanduvae* Smith & Downs, Fl. Illustr. Catar., Solanáceas, 1: 135, fig. 14a, a–c. 1966.—TYPE: BRAZIL. Santa Catarina: Mpio. Catanduvas, E of Catanduvas, ruderal, ca. 27°3'S, 51°45'W, 700–800 m, 7 Nov 1964, *Smith & Klein 12980* (holotype: US! #2568831; isotypes: B! F! HBR, R, US!).
- Solanum iraniense* Smith & Downs, Fl. Illustr. Catar., Solanáceas, 1: 137, fig. 14a, d–f. 1966.—TYPE: BRAZIL. Santa Catarina: Irani, Campo de Irani, ca. 26°57'S,

51°50'W, 700–900 m, 13 Oct 1964, *Smith & Reitz 12457* (holotype: US! #2568834; isotypes: HBR, NY! R, US!).

Shrub ca. 1–2 (–5) m tall. Stems glabrous to densely pubescent with unbranched or dendritically branched hairs, the branched hairs often long-stalked and with three or more terminal rays. Leaves 4—many per sympodial unit, the blades 3–12.5 cm long, 0.5–3.5 cm wide, length:width ratio ca. 2–10:1 or more, simple, elliptic-ovate to narrowly elliptic or lanceolate, acute to acuminate at apex, cuneate to decurrent and occasionally subhastate at base with 1–2 small lobes, chartaceous to subcoriaceous, glabrous to moderately pubescent adaxially, glabrous to densely pubescent abaxially with simple or branched hairs, the pubescence denser on margins and veins, petioles 0.3–2.5 cm long, sparsely to densely pubescent. Inflorescence unbranched or forked, 1–15-flowered, 0.5–5 cm long; peduncle 0.5–3.5 cm long; rachis up to 3 cm long; pedicels 5–15 (–20) mm long, nearly contiguous or spaced ca. 1–15 mm apart, articulated at the base; inflorescence axes glabrous to densely pubescent with unbranched, forked, or dendritically branched hairs and sometimes also with small stalked glands. Calyx sparsely to densely pubescent, the radius 2–9 mm, the lobes 1–6 mm long, 1–2 mm wide, deltate to narrowly triangular and often abruptly narrowed distally, acute to acuminate at tips. Corolla purple or white with a lighter or darker star at base, chartaceous, stellate, the radius 8–13 mm, the tube 2–3 mm long, the lobes 5–10 mm long, 2–4 mm wide at base, triangular to narrowly triangular, acute at apex, sparsely to densely puberulent abaxially with unbranched or branched hairs, nearly glabrous adaxially except for a few hairs on midveins. Anthers usually connivent, yellow, lanceolate to narrowly oblong, 4–6 mm long, 1.5–2 mm wide, abaxial surface at most with very fine or inconspicuous scaly papillae, the pores directed distally and adaxially. Ovary glabrous; style glabrous to moderately puberulent, cylindrical, 5–6 mm long, ca. 0.5 mm in diameter; stigma truncate to subcapitate. Fruits 1.5–2.5 cm long, 0.8–2 cm in diameter, globose, ellipsoidal, or ovoid-fusiform, obtuse or acute at apex, glabrous, color unknown; stone cell aggregates absent. Seeds 2–2.5 mm long, 2 mm wide, lenticular, puberulent on margin but otherwise nearly glabrous. Chromosome number unknown. Figs. 12, 13.

Phenology. Collected in flower in January, February, May, June, and August through December; collected in fruit in January, February, September, November, and December.

Distribution (Fig. 14). Southeastern Brazil (Paraná, Rio Grande do Sul, Santa Catarina), and perhaps Rio de Janeiro and in adjacent areas of Misiones, Argentina; clearings in *Araucaria* forest; 300–1100 m.

Local names. Brazil: Juá, joá manso, joá manso de fôlha comprida (all from Smith & Downs, 1966).

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Marichal Mallet, *Dusén 3056* (S, US); Itaperussú, *Dusén 7081* (F, GH, NY); Tres Barras, *Dusén 17508* (GH, S); Mpio. Bocaiuva do Sul, Varginha do Carumbê, *Hatschbach 9668* (MBM, US); Laranjeiras do Sul, *Hatschbach 10538 & Pereira 7924* (US); Mpio. Palmas, *Hatschbach 15436* (F, L, LIL, NY, US); Mpio. Dois Vizinhos, Rio Chopim, prox. a barra, *Hatschbach 19384* (F, MBM, Z); Mpio. Laranjeiras do Sul, Rio Iguaçú, prox. a barra do Desengano, *Hatschbach & Guimarães 19391* (F); Mpio. Ortiguera, Serra dos Mulatos, *Hatschbach 22933* (C, CTES, MBM, NY, Z); Mpio. São Mateus do Sul, Vargem Grande, *Hatschbach 23255* (MBM, Z); Planalto, *Hatschbach 26472* (UT); near Palmas, *Hatschbach 43491* (F, MBM); Mpio. Irati, Riozinho, *Hatschbach 45519* (C, MBM, Z); Mpio. Rio Branco do Sul, Rod. PR-092, *Hatschbach 48833* (UT); Itaperussú, *Jönsson 1009a* (F, GH, K, NY); Laranjeiras do Sul, *Klein & Eskuhe 19-50* (Z); Mpio. Rio Branco do Sul, Bromado, *Kummrow et al. 3067* (UT); near source of Rio Tigre Preto, ca. 25 km S of Marmaleiro, *Lindeman & de Haas 1355* (NY); N of Campo Novo, *Lindeman & de Haas 2839* (NY); Cascavel, *Rambo 53509* (B).—RIO GRANDE DO SUL: Neu-Württemberg, *Bornmüller 384*

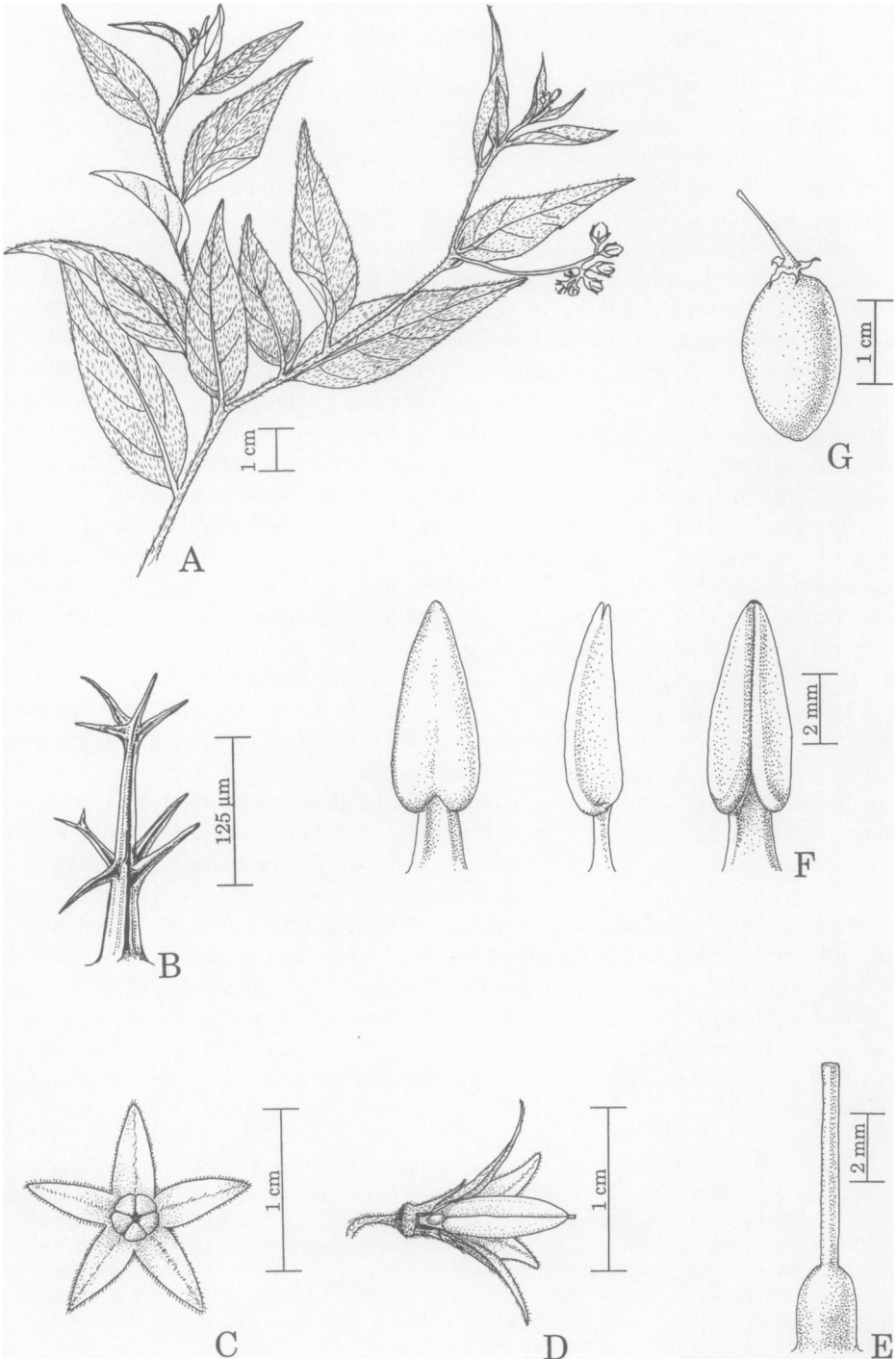


FIG. 12. *Solanum cylindricum* (element 4; see text). A. Habit. B. Dendritically branched trichome. C. Flower, seen from above. D. Lateral view of partially sectioned flower. E. Gynoecium. F. Stamen (left to right: abaxial, lateral, adaxial views). G. Fruit. (Based on: A, *Hatschbach 15436*; B–G, *Smith & Klein 12982*.)

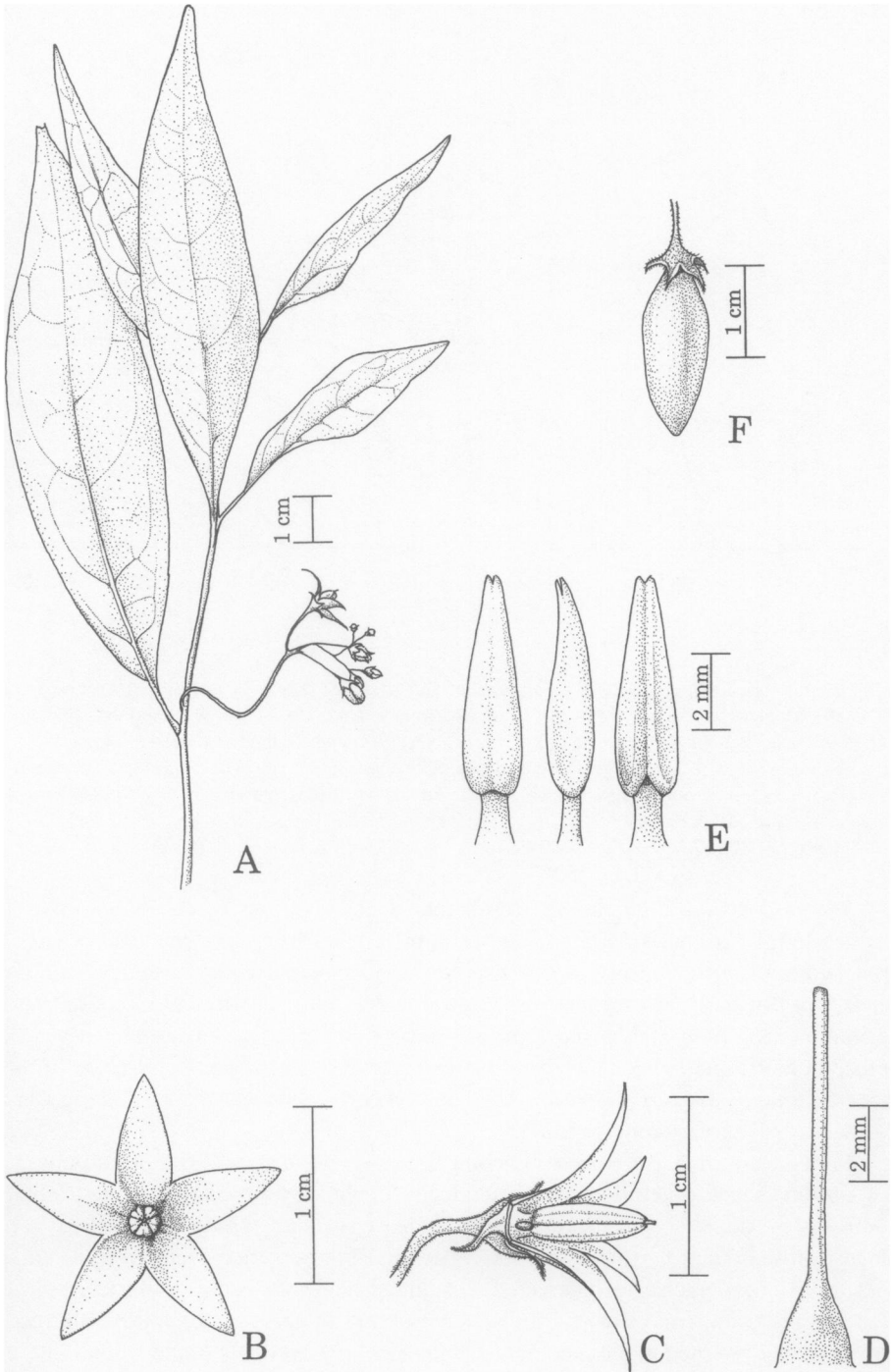


FIG. 13. *Solanum cylindricum* (element 5; see text). A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial views). F. Fruit. (Based on *Hatschbach* 22933.)

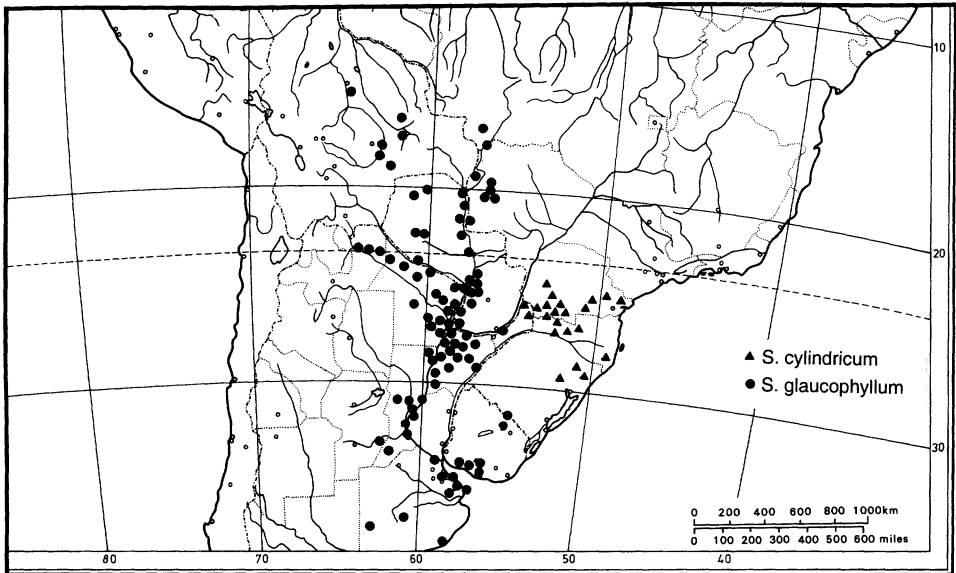


FIG. 14. Distribution of *S. cylindricum* and *S. glaucophyllum*.

(GH); Farroupilha, *Camargo 2101* (B); Farroupilha, *Rambo 40302* (LIL); Santa Rita p. Farroupilha, *Rambo 45760* (B); Montenegro, *Sehnem 3859* (B); Gramado, *Sehnem 4162* (US).—SANTA CATARINA: Mpio. Caçador, 8 km N of Caçador, *Smith & Reitz 8956* (US); Mpio. Chapecó, Fazenda Campo São Vicente, 24 km W of Campo Erê, *Smith & Klein 11572* (US); Mpio. Catanduvas, E of Catanduvas, ca. 27°03'S, 51°45'W, *Smith & Klein 12982* (NY, US). **Argentina.** MISIONES: ca. 5 km de Bernardo de Irigoyen, *Bernardi 18835* (BM); Parque Nac. Iguazú, Ao. Yacuí, *Klein & Eskuche 1-38* (US); San Antonio-S., Ao. Guayuvira, *Klein & Eskuche 7-27* (US, Z); San Antonio, C.E.B.S., *Klein & Eskuche 9058* (US); Iguazú, *Osten & Rojas 8262* (K).

Solanum cylindricum differs from other species of sect. *Cyphomandropsis* from southeastern Brazil in its relatively narrow, simple leaf blades and frequent occurrence of branched hairs. *Solanum pelagicum* also has stems covered with dense dendritic pubescence, but it usually has pinnately compound leaves and is restricted to coastal restinga vegetation. *Solanum luridifuscescens* has generally larger, wider simple leaves, lacks branched hairs, and has a dense band of scaly papillae on the abaxial surface of the anthers. *Solanum matadori* is glabrous, and has subcoriaceous leaf blades and branched inflorescences with very long peduncles.

My concept of *S. cylindricum* encompasses a great deal of variation in pubescence, leaf size and shape, and inflorescence and fruit morphology. Specimens range from nearly glabrous to densely pubescent with dendritic to substellate hairs. Leaf blades range from long and narrow to elliptic-ovate, and inflorescences vary from raceme-like with an extended rachis to contracted and umbel-like with pedicels clustered close together at the distal end of the axis. Fruits are obtuse to acute at the apices. Six morphotypes can be discerned in the material of *S. cylindricum* available to me, but all intergrade in morphological features and geographical distribution, which argues against recognition of separate taxa. Most specimens from Rio Grande do Sul have very narrow coriaceous leaves (length:width ratio ca. 3–10:1) with the blades nearly glabrous above and moderate to dense dendritic pubescence on the axes and abaxial leaf surfaces. The inflorescence

is raceme-like and lacks swellings at the bases of the pedicels. Many collections from Paraná and Santa Catarina also have very narrow leaf blades with sparse adaxial pubescence, but differ in inflorescence structure: the flower pedicels emerge at nearly the same point on the axis (umbel-like) and are subtended by a swelling or sleeve. Another element, represented by *Smith & Klein 11572, 12980, 12982*, and *Hatschbach & Pereira 10538* from Paraná and Santa Catarina, has rather broad leaf blades with a length:width ratio of ca. 2–3.5:1. Pubescence is relatively sparse in these collections, and the inflorescences are raceme-like, without pedicel swellings. This element was described as *Solanum catanduvae* by Smith and Downs (1966), who differentiated it on the basis of its supposedly woody habit and relatively broad leaf blades with obvious lateral veins. The fourth morphotype also has rather broad leaves, but is notable in its extremely dense dendritic pubescence that nearly obscures the stems and abaxial leaf surfaces. This element has raceme-like inflorescences without an obvious pedicel swelling or sleeve. Specimens with sparse to moderate branched pubescence, mostly from western parts of Paraná and Santa Catarina, were described as *S. subhastatum* Smith & Downs and constitute a fifth morphotype (Fig. 13). The sixth morphotype consists of nearly glabrous plants, usually with narrow leaves, ellipsoidal to ovoid and sometimes pointed fruits, and short, few-flowered inflorescences; it was segregated as *S. iraniense* Smith & Downs. Though each of these elements is somewhat distinctive when viewed in isolation, I cannot discern consistent morphological or geographical disjunctions that separate them, and therefore I have subsumed all these variants under one taxon.

Solanum cylindricum may be relatively basal in the *Cyphomandropsis* clade, for it has a number of characters that may link it to putative sister groups in *Solanum* subg. *Minon*. These include anther pores that eventually open into longitudinal slits, pedicels often inserted in a basal sleeve, collar, or platform, and branched pubescence that resembles the stellate hairs seen in some groups within subg. *Minon*. Although most of the hairs of *S. cylindricum* are dendritically branched, some specimens have the lateral branches arranged in several tiers (“substellate”; Fig. 12). Seithe (1979) postulated that dendritically branched and stellate hairs are derived from different developmental pathways, and thus discounted an ontogenetic relationship between the two types of branched hairs seen in *Solanum* species. This question should be re-examined in light of phylogenetic evidence that shows complex patterns of hair types throughout the genus (Bohs & Olmstead 1999).

Though highly stylized, Vellozo’s plates evidently represent variants of this polymorphic species, and thus his names have been adopted. Vellozo’s plate of *Solanum ellipticum* depicts a plant with narrowly elliptic leaves, racemose inflorescences, and ellipsoidal, obtuse fruits. He describes this species as pubescent (“sericeis”). Vellozo’s *Solanum cylindricum* is very similar, with narrowly elliptic leaves but with somewhat pointed fruits and 3–4-flowered, subumbellate inflorescences. Vellozo describes the stems of this species as glabrous (“laevi”). It may conform to the sixth morphotype of *S. cylindricum* as described above. The one point that is difficult to reconcile with recent specimens is Vellozo’s collecting locality in Rio de Janeiro. No other herbarium material of *S. cylindricum* has been seen from this state, nor from intervening areas in São Paulo.

- 4. *Solanum fallax*** Bohs, Taxon 44: 585. 1995. *Cyphomandra hypomalaca* Bitter, Repert. Spec. Nov. Regni Veg. 17: 346. 1921, non *Solanum hypomalacum* (Bitter) C. V. Morton, 1944.—TYPE: ECUADOR. Gualea, subtropical woods, May 1886, *Sodiro*

114/60 (holotype: B, destroyed; photo of holotype, F neg. 2934: F! G! GH!; isotype: P!).

Cyphomandra betacea var. *velutina* Dunal in DC., Prodr. 13(1): 394. 1852.—TYPE: PERU. Pavón s.n. (holotype: G!).

Shrub or small tree 3–5 m tall. Stems moderately to densely pubescent with unbranched glandular and eglandular hairs. Leaves 3 per sympodial unit, the blades 6–37 cm long, 4–25 cm wide, length:width ratio 1–2:1, simple, ovate, acute at apex, truncate to deeply cordate at base, chartaceous, sparsely to moderately pubescent adaxially, more densely so abaxially, the petioles 2–15 cm long, moderately to densely pubescent with hairs like those of the stem. Inflorescence usually forked or further branched, 20–50-flowered or more, 5–20 cm long; peduncle 2–8 cm long; rachis 2–12 cm long; pedicels 10–20 mm long, 15–30 mm long in fruit, spaced 2–9 mm apart, articulated above the base, leaving pedicellar remnants 1–6 mm long; inflorescence moderately pubescent. Calyx inflated distally, moderately pubescent, the radius 2–3 mm, the lobes 0.5–1 mm long, 2 mm wide, truncate, with acuminate tips. Corolla purple, chartaceous to subcoriaceous, stellate, the radius 10–15 mm, the tube 1–2 mm long, the lobes 8–13 mm long, 1.5–3 mm wide at base, narrowly triangular, acute at apex, sparsely pubescent abaxially, nearly glabrous adaxially. Anthers not connivent, yellow or purplish, narrowly triangular, 4–5 mm long, 1.5–3 mm wide, abaxial surface with thickened discrete papillate connective, the pores directed distally. Ovary densely puberulent; style sparsely puberulent, cylindrical, 7–9 mm long, 0.5–1 mm in diameter; stigma truncate. Fruits 1–1.5 cm long, 1–1.5 cm in diameter, globose, obtuse at apex, densely puberulent, color unknown; stone cell aggregates absent. Seeds 4–5 mm long, 3–4 mm wide, angled, whitish puberulent, reticulate on margin. Chromosome number unknown. Figs. 15, 16.

Phenology. Collected in flower in January, April through June, and August, September, and November; collected in fruit in January, February, May, June, August through October, and December.

Distribution (Fig. 8). Colombia and western Ecuador; forest pockets in dry savanna or scrub, Jauneche forest (tropical moist forest); 20–1300 m.

REPRESENTATIVE SPECIMENS. **Colombia.** VALLE: Mpio. Zarzal, Carretera Panamericana between La Paila and Zarzal, Hacienda El Medio, *Silverstone-Sopkin et al.* 2606 (NY). **Ecuador.** CHIMBORAZO: Valle Pallatanga, *Sodiro s.n.* (P).—ESMERALDAS: Hacienda Timbre, ca. 25 km S of Esmeraldas, *Sparre 15248* (S).—IMBABURA: Collapi, *Acosta Solís 12847* (F); Tercer Paso on the San Lorenzo R.R., *Madison et al.* 4972 (AAU, F).—MANABÍ: Cerro Montecristo, S. Manta, *Sparre 19484* (S); El Recreo, 30'S, *Eggers 15069* (C, F, GH, K, M, S, US).—EL ORO: ravine above Piñas on W slope of Andes, 03°09'S, 79°08'W, *Knight 673* (WIS).—PTCHINCHA: Cantón Quito, Reserva Maquipucuna, trail from Hacienda El Carmen to Hacienda Esparragos, ca. 5 km airline SE of Nanegal, 00°7.5'N, 78°38'W, *Webster & Hebert 27710* (TEX).—LOS RÍOS: Cantón Vinces, between Mocachi and Palenque on Estero Peñafiel, *Dodson & Valverde 6952* (MO); Hacienda Clementina, between Babahoyo and Montalve, *Sparre 17919* (S).

The affinities of *S. fallax* are problematical. This species was originally described as a member of the genus *Cyphomandra* (now *Solanum* sect. *Pachyphylla*) and was treated as such by Bohs (1994). However, the anther connective is not greatly enlarged in this species, and its flower and fruit structure, especially its distally swollen calyx and thick angled seeds as well as its tolerance of drier sites, are more suggestive of species of sect. *Cyphomandropsis*. It is anomalous in the latter section due to its very large cordate leaves, its pedicels articulated above the base leaving prominent pedicellar remnants, and its

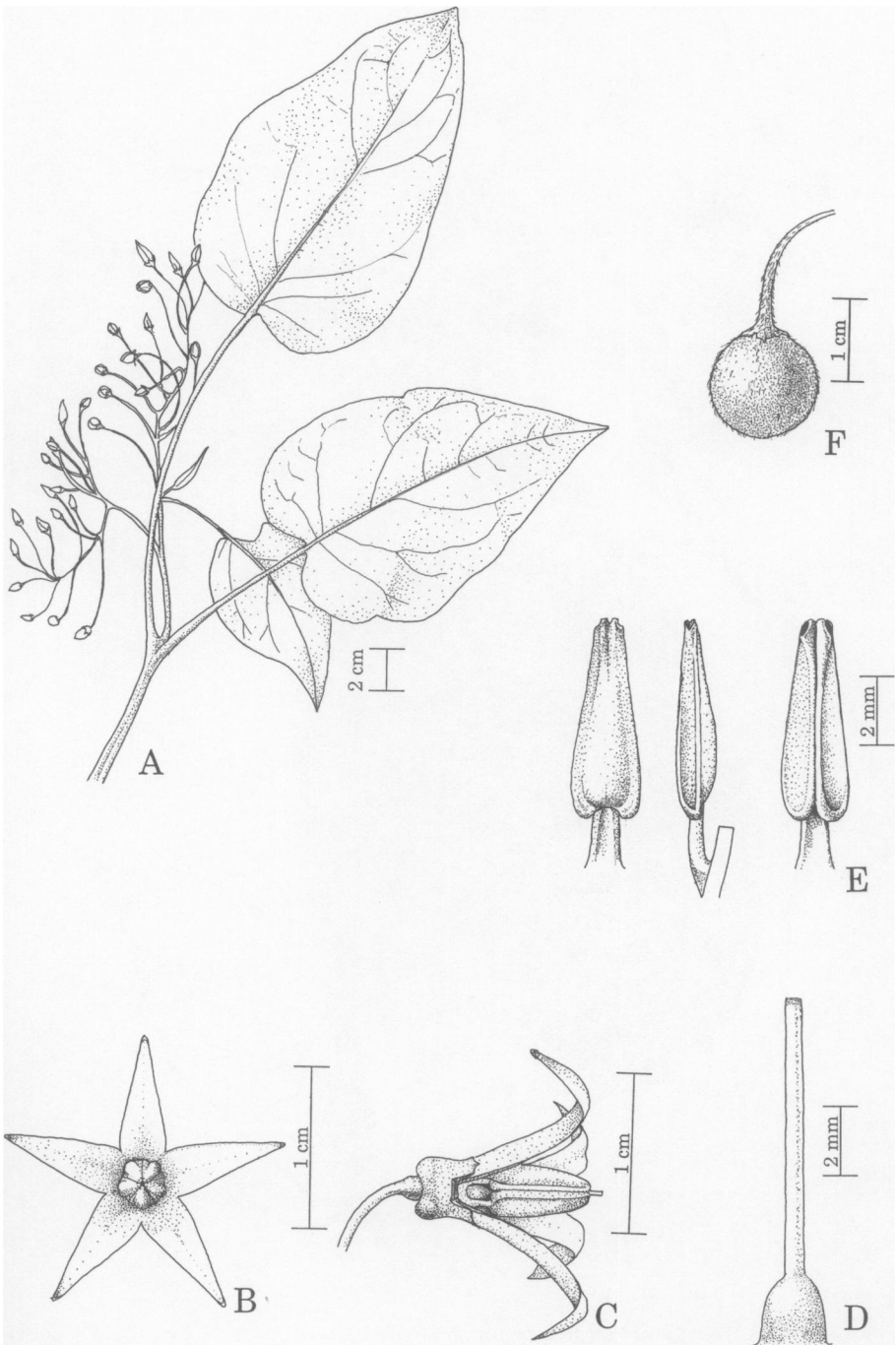


FIG. 15. *Solanum fallax*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial views). F. Fruit. (Based on: A–E, Webster & Hebert 27710; F, Silverstone-Sopkin et al. 2606.)

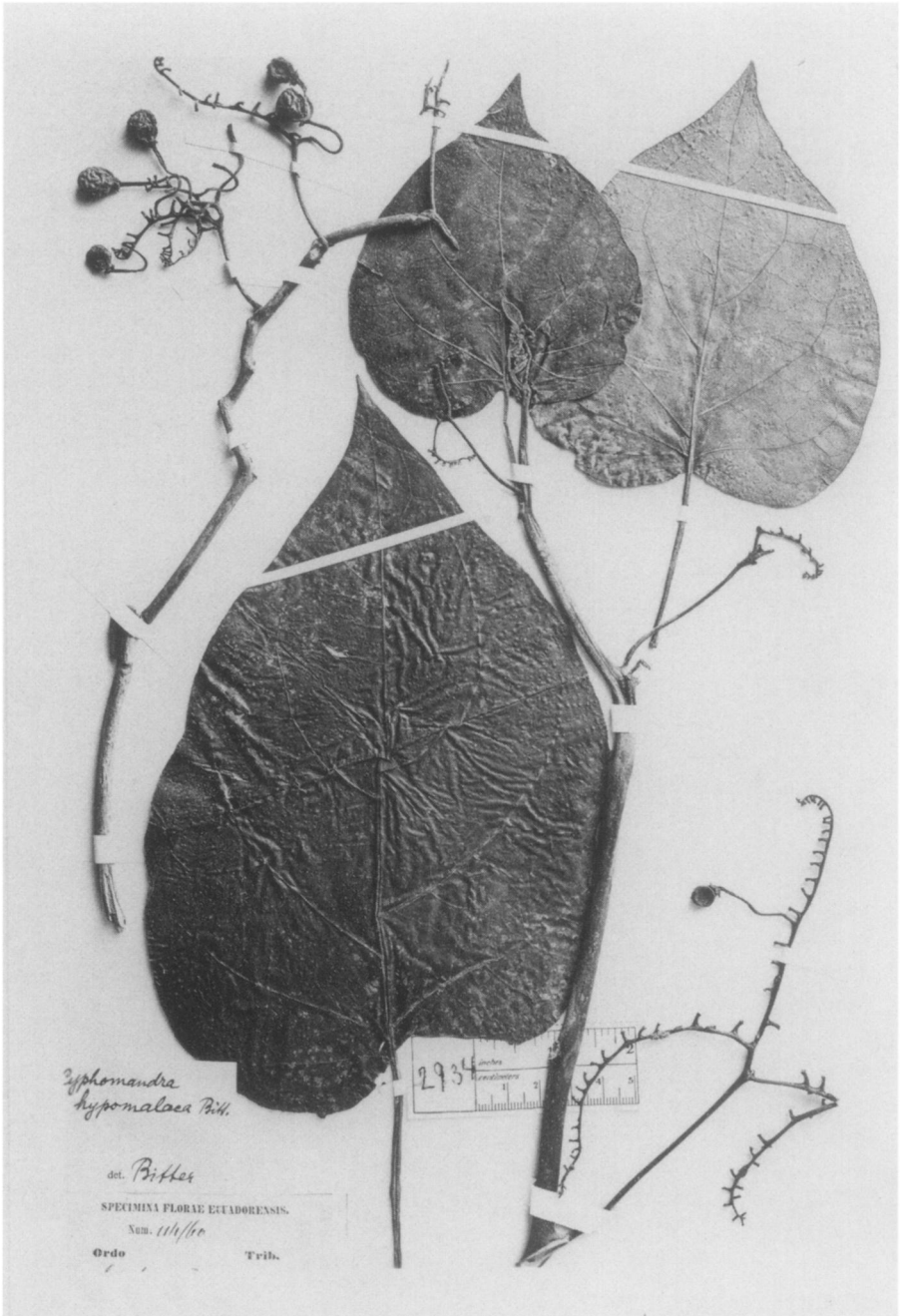


FIG. 16. Photo of holotype of *Cyphomandra hypomalaca* Bitt. (Sodiro 114/60, B; F neg. 2934) [= *Solanum fallax*]. Note prominent pedicellar remnants on inflorescence.

pubescent fruits. If it indeed belongs to sect. *Cyphomandropsis*, *S. fallax* may be most closely related to *S. amotapense* from coastal Ecuador and Peru. Characters that the two species share include cordate leaf bases, swollen calyces, and Ecuadorian distributions.

5. **Solanum fusiforme** Smith & Downs, *Phytologia* 10: 431. 1964. *Cyphomandra fusiformis* (Smith & Downs) A. Child ex Bohs, *Fl. Neotrop. Monogr.* 63: 154. 1994.—TYPE: BRAZIL. Santa Catarina: Mpio. Dionísio Cerqueira, near Dionísio Cerqueira, 800–850 m, 30 Dec 1956, *Smith & Reitz 9658* (holotype: US! #2423799; isotype: HBR).

Shrub 0.5–2 m tall. Stems glabrous to sparsely puberulent with unbranched hairs. Leaves 4 per sympodial unit, the blades 7–20 cm long, 3–17 cm wide, simple and elliptic-ovate to pinnately 7–11-compound, the simple leaves with length:width ratio 2–3:1, acute to acuminate at apex, truncate to cuneate at base, the compound leaves with the upper lateral leaflets often basiscopically decurrent, subcoriaceous, glabrous to sparsely (rarely moderately) puberulent adaxially and abaxially, especially along midribs, the petioles 1–7 cm long, glabrous to sparsely (rarely moderately) puberulent. Inflorescence unbranched, 6–12-flowered, 6–18 cm long; peduncle 3–7 cm long; rachis 1–11 cm long, often zigzag; pedicels 10–25 mm long, spaced 1–10 (–30) mm apart, articulated at or slightly above the base, leaving pedicellar remnants up to 1 mm long; inflorescence axes glabrous or nearly so. Calyx glabrous, the radius 3–5 mm, the lobes 1–2 mm long, 1–3 mm wide, triangular-deltate, often unequal, obtuse to acute at tips. Corolla pink to dark purple, chartaceous, stellate, the radius 10–15 mm, the tube 2–3 mm long, the lobes 8–13 mm long, 3–4 mm wide at base, narrowly triangular, acute at apex, glabrous abaxially and adaxially. Anthers usually connivent, the color unknown, narrowly triangular, 5–7 mm long, 1.5–2.5 mm wide, abaxial surface with an obvious band of scaly papillae, the pores directed distally. Ovary glabrous; style glabrous to sparsely puberulent, cylindrical, 7–9 mm long, 0.5–1 mm in diameter; stigma truncate. Fruits 3–5 cm long, 0.5–1.5 cm in diameter, elliptic-fusiform, acute at apex, glabrous, yellow when ripe; stone cell aggregates several per fruit, small. Seeds 2.5–3 mm long, 2 mm wide, strongly flattened, tomentulose. Chromosome number: $2n = 24$. Fig. 17.

Phenology. Collected in flower in January, February, April, and October through December, with a peak in December and January; collected in fruit in January through April, October, and December.

Distribution (Fig. 18). Argentina, Paraguay, and southeastern Brazil in drainages of the rivers Paraná and Uruguay; *Araucaria* forests, clearings, and thickets in “mata branca” zone (fide Smith & Downs, 1966), riparian forests, and disturbed areas; 500–850 m.

Local names. Brazil: Joá manso, juá (Smith & Downs 1966).

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** PARANÁ: Laranjeiras do Sul, *Hatschbach 18384* (Z); Mpio. Mal. Candido Rondón, Bom Jardim, *Hatschbach 40573* (C, CTES, HBG, UT, Z); Parque Nacional do Iguazu, *Pereira 5373* (US).—RIO GRANDE DO SUL: Herval Seco (NW), Sr. Leib., *Sehnm 10884* (US).—SANTA CATARINA: Liso, Guaraciaba, *Reitz & Klein 16873* (L, NY, US).—SÃO PAULO: Vale do Paranapanema, *Loefgren 4421* (SP, US). **Paraguay.** ALTO PARANÁ: Río Itabó, *Caballero Marmorì 281* (CTES). **Argentina.** MISIONES: San Antonio, C.E.B.S., *Ahumada & Eskuiche 3498* (Z); Posadas, Bonpland, *Ekman 845* (G, LD, S, US); San Pedro, Caragatay (Centro), *Montes 1573* (W); Iguazú, Puerto Segundo, Km 17, *Montes 9500* (BH, G); Depto. Iguazú, Puerto Wanda, *Montes 10404* (LP); Depto. San Pedro, Parque Provincial Cruce Caballero, Ruta Nac. 14, 14 km de San Pedro, camino a Tobuna, 26°31'S, 53°59'W, *Morrone et al. 799* (SI); Depto. Gral. M. Belgrano, 8 km de

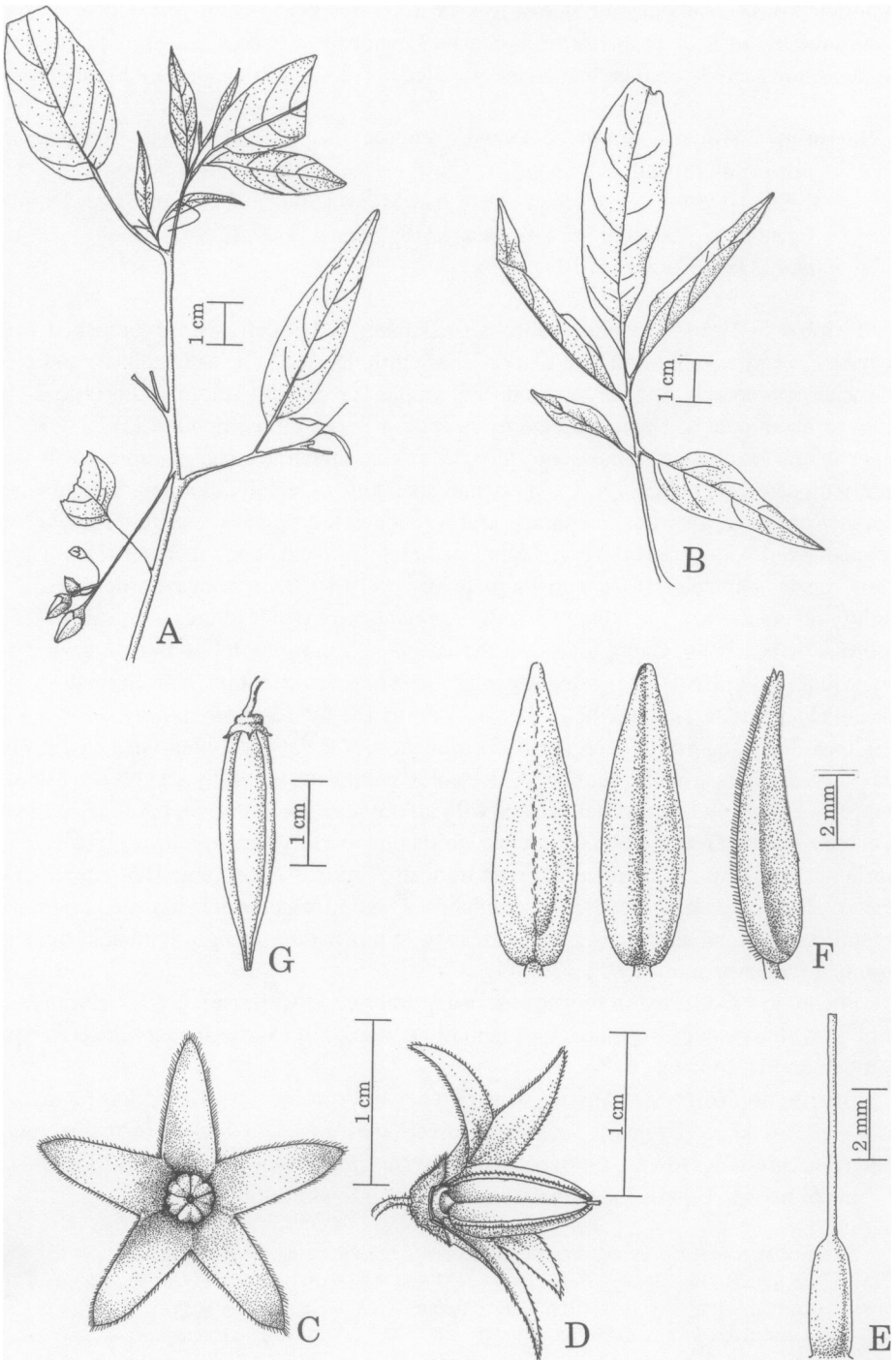


FIG. 17. *Solanum fusiforme*. A. Habit. B. Compound leaf. C. Flower, seen from above. D. Lateral view of partially sectioned flower. E. Gynoecium. F. Stamen (left to right: abaxial, adaxial, lateral views). G. Fruit. (Based on: A, C–G, *Smith & Reitz 9658*; B, *Hatschbach 18384*.)

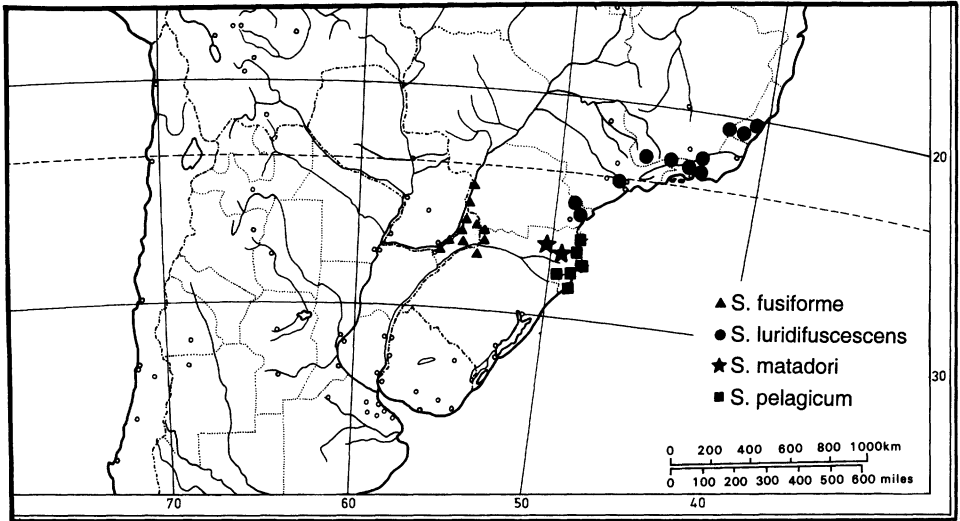


FIG. 18. Distribution of *S. fusiforme*, *S. luridifuscescens*, *S. matadori*, and *S. pelagicum*.

San Antonio, 26°01'S, 53°47'W, *Morrone et al.* 2073 (SI); Santa Ana, *Rodríguez* 745 (A, BM, SI); Depto. San Pedro, Parque Provincial Cruce Caballero, 26°31'S, 53°59'W, *Zuloaga et al.* 5538 (SI).

This distinctive species has several unusual morphological characters not commonly found in the other species of sect. *Cyphomandropsis*, including pinnately compound leaves, fusiform fruits, and nearly complete lack of pubescence. Some species of *Solanum* sect. *Pachyphylla* exhibit these characters, and *S. fusiforme* may have a closer relationship with sect. *Pachyphylla*, especially the Brazilian species *S. melissarum* Bohs, *S. diploconos* (Mart.) Bohs, *S. pinetorum* (Smith & Downs) Bohs, and *S. sciadostylis* (Sendtn.) Bohs, than with members of sect. *Cyphomandropsis*. *Solanum fusiforme*, however, completely lacks the swollen anther connective that defines sect. *Pachyphylla* and has stamens typical of sect. *Cyphomandropsis*.

Solanum fusiforme is uncommon and restricted to southeastern Brazil and areas of adjacent Argentina (Misiones) and Paraguay. Efforts should be made to relocate and preserve populations of this interesting species.

6. *Solanum glaucophyllum* Desfontaines, Cat. Pl. Hort. Paris, ed. 3: 396. 1829.—TYPE: based on living plants cultivated in the Botanical Garden at Paris (holotype: unknown).

Solanum malacoxylon Sendtner in Martius, Fl. bras. 10: 51. 1846. *Solanum malacoxylon* var. *genuinum* Hassler, Repert. Spec. Nov. Regni Veg. 15: 120. 1918.—TYPE: BRAZIL. *Sellow s.n.* (holotype: B, destroyed; fragment of holotype: F!; photos of holotype, F neg. 2837: F! G!; lectotype, designated by Morton, 1976: K!).

Solanum glaucum Bertoloni, Mem. Accad. Sci. Ist. Bologna 3: 188, t. 13. 1851, nec *Solanum glaucum* Dunal, 1852, nec *Solanum glaucum* Rojas, 1897.—TYPE: based on living plants cultivated at the Botanical Garden of the University of Bologna (holotype: unknown).

Solanum glaucum Dunal in DC., Prodr. 13(1): 100. 1852, nec *Solanum glaucum* Bertoloni, 1851, nec *Solanum glaucum* Rojas, 1897.—TYPE: ARGENTINA. Buenos Aires, *Bacle 43* (lectotype, designated by Morton, 1976: G!; photo of lectotype, Morton neg. 8586: F! GH!; isolectotype: G-DC!; photo of isolectotype: F neg. 6796 F! GH!).

Solanum malacoxylon (“*melanoxylon*”) var. *angustissimum* Kuntze, Rev. gen. pl. 3(2): 227. 1898. *Solanum malacoxylon* var. *subvirescens* f. *vulgare* subf. *angustissimum* (Kuntze) Hassler, Repert. Spec. Nov. Regni Veg. 15: 120. 1918.—TYPE: PARAGUAY. Río Tebicuary, *Kuntze s.n.* (lectotype, here designated: NY!).

Solanum malacoxylon (“*melanoxylon*”) var. *latifolium* Kuntze, Rev. gen. pl. 3(2): 227. 1898.—TYPE: PARAGUAY. Sep 1982 (fr), *Kuntze s.n.* (lectotype, here designated: NY!; isolectotype: US!).

Solanum malacoxylon var. *albo-marginatum* Chodat, Bull. Soc. Bot. Genève, sér. 2, 8: 153. 1916. *Solanum malacoxylon* var. *subvirescens* f. *albo-marginatum* (Chodat) Hassler, Repert. Spec. Nov. Regni Veg. 15: 121. 1918.—TYPE: PARAGUAY. Lago Ypacarai, Tuilerie, San Bernardino, *Chodat & Vischer 36* (holotype: G!).

Solanum malacoxylon var. *subvirescens* Hassler, Repert. Spec. Nov. Regni Veg. 15: 120. 1918. *Solanum malacoxylon* var. *subvirescens* f. *vulgare* Hassler, Repert. Spec. Nov. Regni Veg. 15: 120. 1918.—TYPE: PARAGUAY. Margin of Lake Ypacarai, *Hassler 3201* (lectotype, here designated: NY!; isolectotypes: BM! W!).

Rhizomatous shrub or slender treelet ca. 0.5–4 m tall. Stems glabrous (rarely moderately to densely puberulent-pubescent), usually light-colored and smooth. Leaves many per sympodial unit, the blades 6–18 cm long, 0.6–3.5 (–5) cm wide, length:width ratio 4.5–10 (–15):1, simple, narrowly elliptic, acute at apex, tapered to decurrent at base, succulent or fleshy with the midrib and margin often thickened and whitish, glabrous adaxially and abaxially (rarely moderately to densely puberulent-pubescent), surfaces glaucous in fresh material, the petioles 1.5 cm long or less, glabrous, often slightly winged. Inflorescence branched, sometimes highly so, ca. 20–50-flowered or more, 3.5–9 cm long; peduncle 1–3.5 cm long; rachis 2–7 cm long; pedicels 12–15 mm long, ca. 15–20 mm long in fruit, spaced 1–15 mm apart, articulated at the base; inflorescence axes glabrous (rarely moderately puberulent-pubescent). Calyx glabrous except for some sparse puberulence at margin, the radius 2–3 mm, the lobes 0.5–1.5 mm long, 1.5–2.5 mm wide, deltate, acute. Corolla whitish to pink or violet, often with a white central star, chartaceous, rotate-stellate and plicate, the radius 10–30 mm, the tube 5–8 mm long, the lobes 4–10 mm long, 5–10 mm wide at base, broadly triangular, apiculate at apex, moderately to densely puberulent abaxially, especially on distal parts of lobes and plicae, glabrous adaxially except for a few sparse hairs at tips of lobes. Anthers usually connivent, yellow to orange-yellow, ovate, 5–7 mm long, 2 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous, cylindrical, 5–7 mm long, 0.25–0.5 mm in diameter; stigma truncate. Fruits 0.75–2 cm long, 0.75–2 cm in diameter, globose, sometimes apiculate at apex when young, obtuse at apex when mature, glabrous, dark purple or blue-black and glaucous when ripe; stone cell aggregates absent. Seeds ca. 4–6 mm long, 3.5–4 mm wide, angled, smooth or with minute scalloped ridges. Chromosome number: $n = 12$. Figs. 19, 20.

Phenology. Flowering and fruiting throughout the year, with a peak in November through March.

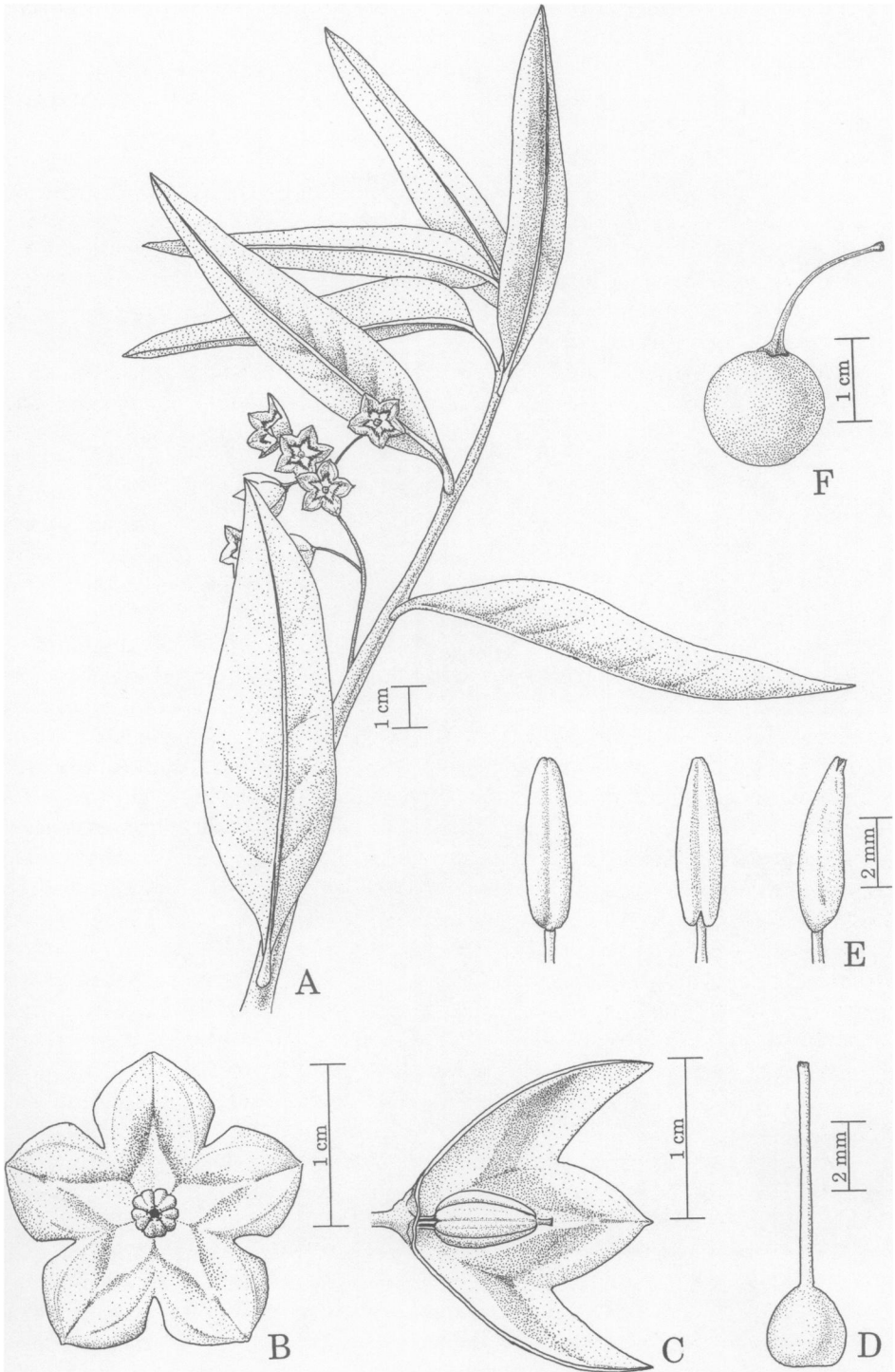


FIG. 19. *Solanum glaucophyllum*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, adaxial, lateral views). F. Fruit. (Based on: A, B, C, F, greenhouse material of *Bohs 2530*; D, E, *Cristóbal et al. 1437*.)



FIG. 20. *Solanum glaucophyllum*. A. Flowering branch; scale bar = 2 cm. B. Flowers with rotate-stellate corollas; scale bar = 1 cm.

Distribution (Fig. 14). Bolivia, southern Brazil, Paraguay, northern Argentina, and Uruguay; low, swampy ground at margins of marshes and ponds in seasonally inundated areas; ca. 0–600 m.

Local names and uses. Argentina: Corcho del agua (*Torres 9*), duraznillo (*Boffa 133*; *Gibson s.n.*; *Huidobro 1452*; *Schulz 2053*; *Tweedie s.n.*), duraznillo blanco (*Gibson s.n.*; *Lefèbre s.n.*), duraznillo de bañado (*Schinini 9033*), duraznillo hediondo (*Hunziker 310*), duraznillo negro (*Cordini 61*), na'kyet (*Arenas 2000*), palo hediondo (*Boelcke 1396*), palo-né or paloné (*Boelcke 1396*; *Irigoyen 221*), varilla (*Burkart 8727*, *Hunziker 25304*), yaa'tuk or ye'tuk (*Maranta & Arenas 153*). Bolivia: Bobo (*Murquia 502*). Paraguay: sin-hejúk (*Arenas 714*). Uruguay: duraznillo blanco (*Gallinal et al. A831*; *Gibert 140*), duraznillo negro (*Osten 21883*). Brazil: espichadeira (*Prance et al. 26173*), espixadeiro (*Macedo et al. 1209*).—The dried stems are used for firewood and for wattling (*Burkart 8727*; *Gibson s.n.*). Plants are used medicinally as a purgative (Morton, 1976; *Gibert 140*; *Tweedie s.n.*). Foliage is very toxic for cattle and other animals (*Prance et al. 26173*; *Schulz 2053*).

REPRESENTATIVE SPECIMENS. **Brazil.** MATO GROSSO: Mpio. Paconé, Fazenda Cassange, *Döbereiner & Tokarnia 699* (US); Transpantaneira Highway, Pocone, Fazenda Santa Rosa, Km 40, *Macedo et al. 1209* (NY); Transpantaneira Highway, Fazenda Jofre, 17°10'–17°S, 56°30'W, *Prance et al. 26173* (NY); Transpantanal Highway, Fazenda Jofre, *Schaller 258* (NY).—MATO GROSSO DO SUL: Mpio. Corumbá, Fazenda São Sebastião, *Döbereiner & Tokarnia 717* (L, US); Mpio. Aquidauana, Fazenda Tabaco, *Döbereiner & Tokarnia 794* (F, US); Mpio. Corumbá, Fazenda Brasil Fronteira, *Döbereiner & Tokarnia 797* (US); Mpio. Aquidauana, Fazenda Tupacireta, *Döbereiner & Tokarnia 800* (F, US); Mpio. Aquidauana, Fazenda Santa Cruz, *Hatschbach & Guimarães 21941* (F); Mpio. Miranda, Rio Miranda, *Hatschbach 38640* (F, US); Porto Murтинho, *Hatschbach & da Silva 49222* (NY, US); Pantanal, Fazenda Miranda, *Schaller 301* (NY); Mpio. de Miranda, Marimondo, 60 km N de Guaicurus, *Silva 80* (SP).—RIO GRANDE DO SUL: I.A.S., Pelotas, margem do Canal do I.A.S., São Gonçalo, *Sacco 816* (F, NY). **Bolivia.** BENI: Prov. Cercado, 7 km SW of Trinidad, vic. Puerto Almacén, along the Río Ibare, 14°52'S, 64°57'W, *Nee 37532* (G, LPB, NY, USZ).—CHUQUISACA: Prov. Luis Calvo, margenes del lugar "Arbol Solo," *Murquia 502* (LPB); Prov. Luis Calvo, El Salvador, Laguna Seca, Campo Quemado, a orillas de represa, *Penseiro & Marino 4423* (SI).—SANTA CRUZ: Prov. Velasco, San Miguelito, *Arnold s.n.* (K, US); Prov. Andrés Ibañez, Jardín Botánico de Santa Cruz, 12 km E of center of Santa Cruz on road to Cotoca, 17°47'S, 63°04'W, *Bohs & Nee 2767* (USZ, UT); Prov. Nufflo de Chávez, Estancia San Miguelito, 200 km NE de Santa Cruz, Puesto Corrales, 4 km NW del puesto, 17°9'S, 61°43'W, *Fuentes 586* (USZ); Curuyuyqui, trail along Río Parapetí ca. 8 km SW of airstrip, 18°50'S, 62°20'W, *Gentry & Foster 75300* (NY, USZ); Bañados de Izozog, *Navarro et al. 19* (LPB); Prov. Cordillera, Bañados de Izozog, Monte Alto, bosque inundado del Río Parapetí, *Navarro & Vargas 346* (LPB); Prov. Andrés Ibañez, Jardín Botánico de Santa Cruz, 12 km E of center of Santa Cruz on road to Cotoca, 17°47'S, 63°04'W, *Nee 35186* (JBSC, LPB, NY); Prov. Andrés Ibañez, 12 km SE of Comunidad Don Lorenzo, Estancia Caracore, 0.5 km W of the Río Grande [Río Guapaf], 17°51'S, 62°47'W, *Nee & Coimbra 39996* (JBSC, LPB); Prov. Andrés Ibañez, 7 km SE of comunidad Don Lorenzo, 17°50'S, 62°49'W, *Nee 40174* (LPB, USZ); Prov. Andrés Ibañez, 10 km S de Cotoca, camino a la localidad de Paurito, 17°49'0"S, 62°57'05"W, *I. Vargas 518* (USZ); Prov. Cordillera, Bañados de Izozog, 500 m al N de las instalaciones de Estancia Cachari, 18°55'S, 62°25'W, *I. Vargas et al. 1935* (USZ); Misiones Guarayos–Santa Cruz de la Sierra, *Werdermann 2625* (K, LPB, MO, S). **Paraguay.** ALTO PARAGUAY: Puerto Diana, 5 km de Bahía Negra, *Arenas 1407* (CTES).—BOQUERÓN: cerca y al S de Mariscal Estigarribia, *Casas & Molero 4434* (MO, NY); Zinfunké, orillas del Río Pilcomayo, *Mereles 704* (CTES); Puerto Casado and vicinity, *Pedersen 4198* (BR, C).—CAPITAL: Ascunción, *Morong 181* (BM, F, GH, K, MO, NY, US, WIS); Puerto Itá Enramada, *Schinini & Bordas 13344* (CTES, G, MO).—CENTRAL: Piquete-cué (Jukyty), *Bordas 4061* (CTES); Salado, Laguna Ypacaraí, *Chodat 33* (G); Laguna Ypoa, *Chodat 35* (G); Laguna Ipacarary, *Fiebrig 463* (E, F, G, GH); orillas del Lago Ypacaraí, *Mereles 163* (CTES, NY); Areguá, costa del Lago Ypacaraí, *Mereles 1017* (G); Nueva Italia, Compañía Jukyty, cercanías del arroyo ka'a ñave, *Pérez et al. 496* (CTES); Simpio a Emboscada, cerca del Cruce del Salado, *Schinini 3919* (G); Trinidad, Bahía P. Caballero, *Sparre & Vervoort 67* (S).—CHACO: Laquerenza, cauce seco del Río Zimane, *Mereles & Ramella 2692* (CTES); Mayor Pedro Lagerenza, cauce seco del Río Timane, 20°0'S, 60°45'W, *Schinini & Bordas 14871* (CTES); Cerro León, 20°26'S, 60°15'W, en Laguna Nueva Misión, *Schinini & Bordas 17881* (CTES, F, G, MO, NY).—CONCEPCIÓN: Chaco y prope Concepción,

Chodat 34 (G); near Concepción, shores of Río Paraguay, *Hassler 7483* (BM, G, GH, K, LIL, MO, NY, S, W).—CORDILLERA: Altos, Cnia. Bernal Cué, orillas del arroyo Itagaza, *Schinini 6721* (CTES); Río Salado, 25°13'S, 57°22'W, *Schinini & Mereles 24560* (CTES, G).—ÑEEMBUCÚ: Curupayty, Humaitá, *Bernardi 18517* (BM, F, MO, NY); Dist. Cambacu, Albera, *Walter 93* (BM).—PRESIDENTE HAYES: Estancia Loma Pyta, 23°40'S, 59°35'W, *Arenas 714* (NY); Colonia Menno, Paratodo, *Arenas 1490* (CTES); Villa Hayes, Estancia La Golondrina, 24°55'S, 57°40'W, *Hahn 671* (BH, NY); Km 120, Ruta Trans Chaco, *Mereles 2592* (CTES); Chacoí, campo inundable del Río Negro, 25°12'S, 57°38'W, *Schinini 26770* (CTES, NY).—SAN PEDRO: Puerto Rosario, island in Río Paraguay, *Woolston 937* (C, K, S, SP, U, US). **Argentina.** BUENOS AIRES: Pdo. Maipu, Ruta 74 a 7 km de Las Armas, *Boelcke et al. BAA 5888* (CTES); Pdo. Magdalena, Punta Indio, *Boelcke et al. BAA 12613* (CTES); Depto. La Plata, Berisso, *Boffa 133* (F); alrededores de La Plata, Los Talas, *Cabrera 2795* (NY); Tigre, *Castro BAB 52328* (K); Laguna de Monte, *Cordini 6* (SI); Laguna La Adela, *Dawson 663* (NY); Depto. Campana, Campana, *Eyerdam & Beetle 23064* (BH, G, GH, MO); Los Yngleses, Ajó, near Cape San Antonio, mouth of the Río de La Plata, *Gibson s.n.* (BM); Depto. La Plata, Punta Lara—La Plata, *Gómez Sosa 61* (CTES); Azul, *Huidobro 1452* (NY, S); Partido de Campana, Otamendi, *Hunziker 310* (NY); La Plata, *Lefèbre s.n.* (BR); Miramar, Partido Gral. Alvarado, *Pedersen 1045* (C, BR, S, US); Quilmes, Plátanos, *Rodríguez 111* (A, SI); 2 km SW of Ensenada on Ruta Provincial 10, *Solomon & Solomon 4026* (CTES, MO); outskirts of Buenos Aires, *Tweedie s.n.* (K); Buenos Aires, Barracas al Sud, *Venturi 76* (K, S).—CHACO: Depto. Resistencia, Margarita Belén, *Aguilar 1212* (BR, MO); Makallé, *Birabén 63* (LP); Depto. Primero de Mayo, Antequera Cerrito, *Charpin & Eskuche 20145* (G); Las Palmas, *Jørgensen 2204* (GH, MO, US); Depto. Gral. Güemes, Zaparínqui, 13 km S de J. J. Castelli, 26°04'S, 60°33'W, *Piccinini & Hilfer 4230* (CTES); Colonia Benítez, *Schinini 9033* (CTES); Depto. Donovan, 13 km N de La Verde, Estancia Dos Tranqueras, *Schinini 22746* (CTES); Colonia Benítez, *Schulz 2053* (CTES).—CÓRDOBA: Depto. Marcos Juárez, unos 8 km al SE de Camilo Aldao, a casi 20 km al W del límite con Santa Fé, *Hunziker 18957* (UT).—CORRIENTES: Depto. Bella Vista, Ruta 117, 7 km E de Ruta 27, *Ahumada 309* (CTES, MO); Depto. Itatí, Ruta Nac. 12, 60 km E de Itatí, Arrocería Rzepecki, *Ahumada et al. 858* (CTES, F); Depto. Esquina, 47 km W de Sauce, Ruta 126, *Ahumada et al. 1449* (CTES, LP); Depto. San Cosme, 28 km E de Corrientes, *Ahumada 1653* (CTES); Depto. San Miguel, 12 km S de Caa-Catí, Ruta 5, *Ahumada 1762* (CTES, MO, WIS); Depto. General Paz, 29 km S de Caa-Catí, Ruta 13, *Ahumada 2021* (CTES); Depto. Esquina, sobre Ruta 25, 29°48'S, 59°15'W, *Ahumada et al. 3458* (CTES); Depto. San Cosme, 4 km E de Paso de la Patria (desvío a Pto. González), *Arbo et al. 721* (CTES, MO, WIS); Depto. San Roque, Estancia Caaguazú, 11 km NE de Chavarría, camino a Tacuaritas, approx. 4 km al S del casco, orillas del Río Corriente, *Arbo et al. 6675* (LPB); Goya, *Boelcke 1396* (SI); Depto. San Roque, San Roque, bajos del Santa Lucía, *Cristóbal et al. 1437* (AAU, G, CTES); Depto. Itatí, Pueblo Cercanía, *Ibarrola 890* (NY, S); Depto. Empedrado, 4 leguas al E de El Pollo, *Ibarrola 3205* (F, L); Depto. Bella Vista, camino de Bella Vista a San Roque, 6 km del empalme a Bella Vista, *Irigoyen 221* (AAU, CTES, G, WIS); Depto. San Cosme, Paso de La Patria, orillas del Río Paraná, *Krapovickas & Cristóbal 12964* (CTES); Depto. Empedrado, Río Empedrado, Ruta Nacional 12, *Krapovickas et al. 19897* (CTES); Depto. Esquina, Esquina, costa del Río Corriente, *Krapovickas et al. 26742* (CTES, G, MO); Depto. Esquina, islas frente a Esquina, *Krapovickas et al. 26861* (CTES, G, MO); Depto. Goya, Ruta 12, 40 km S de Goya, *Krapovickas et al. 27317* (CTES, G, MO); Depto. Esquina, 26 km SE de Libertador, Estancia La Blanca, 30°20'S, 59°20'W, *Krapovickas et al. 27503* (CTES); Depto. Bella Vista, Ruta 23 y Río Santa Lucía, *Lourteig et al. 2678* (CTES); Depto. Capital, Capital, *Meyer 6458* (A); Depto. Mburucuyá, Estancia Santa María, *Pedersen 2595* (BR, C, G, GH, K, MO, S, US); Saladas, road to Mburucuyá, *Plowman 2724* (F, GH, L, S, US); Depto. San Luis del Palmar, Arroyo Riachuelito, 25 km E de San Luis de Palmar, *Quarín et al. 383* (CTES, US, WIS); Depto. Mercedes, Cnia. Pellegrini, *Quarín & Schinini 1044* (CTES, WIS); Depto. Capital, Riachuelo, 10 km S de Corrientes, *Schinini et al. 6915* (CTES); Depto. Capital, Corrientes, *Schinini et al. 9659* (CTES, G, MO); Depto. Bella Vista, Ruta 27, 10 km S de Bella Vista, Toropí, orilla del Río Paraná, *Schinini & Cristóbal 9870* (CTES); Depto. Saladas, Saladas, *Schinini et al. 11059* (CTES); Depto. Mercedes, 75 km N de Mercedes, Laguna Trin, Estancia Culantrillar, sobre la orilla inundable de la Laguna Trin, *Schinini et al. 11829* (CTES); Depto. San Roque, San Roque, orillas de la ciudad, Río Santa Lucía, *Schinini & Ahumada 12666* (CTES); Depto. Curuzú Cuatiá, 13 km NW de Perugorria, Ruta 12, *Schinini 13956* (CTES); Depto. San Martín, 6 km SW de La Cruz, sobre el Río Uruguay, *Schinini et al. 16868* (CTES, MO); Depto. Goya, 36 km S de Goya por Ruta 12, *Schinini et al. 18929* (CTES); Depto. Curuzú Cuatiá, Ruta 12, 8 km E de Paso López, *Tressens et al. 531* (CTES, G); Depto. Mercedes, Laguna Iberá, Paso Picada, Reserva Natural Provincial de Iberá, *Tressens et al. 3580* (CTES).—ENTRE RÍOS: Islas de Victoria, *Burkart 8727* (F); Depto. Paraná, Paraná, un poco al S de la ciudad, a orillas del Río Paraná, Bajada Grande, *Hunziker 25304* (UT); Isla Puentes (frente a Paraná), *Meyer 10094* (B); Constanza, brazo largo del Río Paraná, *Walter & Walter 216* (B).—FORMOSA: Depto. Patiño, Pozo Navagán, Reducción de Indígenas Pilagás, 24°15'S, 60°0'W, *Arenas 2000* (CTES); camino de Pilcomayo a la Esmeralda, *Cordini 61* (SI); Depto. Formosa, Formosa, *Eyerdam & Beetle 22974* (BH, G, GH, K);

Depto. Patiño, 3 km al N de Las Lomitas, *Filipov 110* (SI); Depto. Pilcomayo, Parque Nacional Pilcomayo, alrededores de Laguna Blanca, 25°10'S, 58°06'W, *Fortunato et al. 2041* (SI); Depto. Laishi, Ruta 11, 10 km N de Puerto Velaz, *Krapovickas & Cristóbal 13196* (CTES, MO, US, WIS); Depto. Pirané, 3 km W of Pirané, *Morel 305* (L, MO); Depto. Pirané, Los Matacos, *Morel 655* (G); Depto. Pilcomayo, Ruta 11, Km 6, *Morel 1346* (F); Depto. Pilcomayo, Puente Ceibo, *Morel 3592* (B); Depto. Pilcomayo, Isla Pé, *Morel 3739* (BR, MO); Depto. Pilcomayo, 2 km NW of Riacho Negro, *Morel 4072* (B); Depto. Pilcomayo, Puente Sastre, *Morel 5087* (C); Depto. Pilcomayo, Ruta 86 al Km 50, *Morel 5174* (C); Depto. Bermejo, Las Lomitas, *Pierotti 4085* (F, K); Depto. Pirané, Chacras, *Pierotti 4157* (BR, G); 5 km E of Capitán J. Page, *Renvoize 3546* (C, K, MO, NY, S, US); Ing. Juárez, *Torres 9* (CTES).—MISIONES: Depto. Candelaria, Puerto Santa Ana, *Schwarz 599* (F, NY).—SALTA: Orán, Laguna del Palmar, *Hieronymus s.n.* (Z); Depto. San Martín, 12 km de Hickmann, *Krapovickas & Schinini 30853* (CTES); Depto. Rivadavia, J. Solá (Morillo), Barrio Mataco, 23°28'S, 62°53'W, *Maranta & Arenas 153* (CTES, NY); Depto. San Martín, Fca. "Marianito de los llanos" entre Ruta 81 y el Río Bermejo, unos 10 km al E de Hickmann, antes de llegar a Dragones, *Novara 500* (MCNS); Depto. Orán, Km 58, Vespucio a Hickmann, *Schreiter 11214* (F, GH, SI); Depto. Orán, Embarcación, orilla del Río Bermejo, *Venturi 5158* (A, SI, US).—SANTA FE: Depto. Gral. López, Chapuy, *Franceschi 762* (CTES); Depto. Castellanos, Rafaela, *Huidobro 3419* (G); Depto. San Jerónimo, autopista Rosario-Santa Fe, Km 115, cerca del desvío a Coronda, *Hunziker et al. 24857* (UT); Depto. San Lorenzo, entre La Salada e Ibarlucea, Ruta 34, a 1 km al E de la ruta, *Moscone & Barboza 113* (UT); Depto. Gral. Obligado, Mocoví, *Quarín 590* (CTES, WIS); Depto. General Obligado, La Reserva, Arroyo Las Garzas, *Quarín 3058* (CTES); Depto. La Capital, camino a Guadalupe, *Ragonese 2139* (US); Depto. Gral. Obligado, entre San Juan y Adelaida Vieja, *Ragonese 3255* (US); Depto. Garay, Colonia Mascias, *Spegazzini BAB 64608* (K); Depto. Capital, El Puerto, *Terribile 563* (L). **Uruguay.** CANELONES: Barra Arroyo, *Osten 21883* (GH, S).—CERRO LARGO: Río Negro, estancia Palleros, *Gallinal et al. A831* (US); Sierra del Aceguá, *Herter 18512* (K).—COLONIA: Aerodromo, *Herter 659a* (US, Z).—MONTEVIDEO: Montevideo, *Gibert 140* (K, W); Carrasco, *Osten 5281* (GOET, US).—SAN JOSÉ: Barra, *Herter 659* (B, F, G, GH, HBG, MO, NY, S, SI, U, US, WIS, Z).

Introductions. **Japan.** Koyasan, *Wilson & Suzuki s.n.* (A). **Nepal.** Kathmandu, 27°42'N, 85°19'E, *Do-bremez 616* (BM). **U.S.A. FLORIDA:** Pensacola, *Curtiss 6862* (BH, G, HBG, NY, WU, Z).

Solanum glaucophyllum can be distinguished from other species in sect. *Cyphomandra* by its usually glabrous, glaucous, lanceolate to elliptic leaves with decurrent bases and short, slightly winged petioles, its rotate-stellate corolla with a relatively long tube and broad lobes, and its globose, purple-black, glaucous fruits. The stems are smooth and usually light yellowish or whitish, and the leaf midribs and margins are often thickened, inrolled, and whitish or cream-colored. Throughout its range, *S. glaucophyllum* exhibits great morphological variability, especially in leaf shape, which ranges from elliptic to nearly linear, and in corolla and fruit size. Narrow-leaved plants generally have smaller flowers and fruits than those with broader leaves, and narrow-leaved forms seem more common in the northern part of the geographical range of this species.

This species grows commonly in flooded or swampy ground, where it forms thickets, known as "varillales" or "duraznillales," of virgate stems from spreading rhizomes (Okada et al. 1977; Cabrera & Zardini 1978). It is reportedly deciduous in winter (Okada et al. 1977). The fruits apparently float readily and may be dispersed by water (*Nee 37532*); they are also eaten by birds (*Gibson s.n.*).

Solanum glaucophyllum is of economic importance mainly because it causes a disease, "enteque seco" or "espichamento," of grazing animals (D'Arcy 1974; Wasserman 1974; Morris 1977; Okada et al. 1977). The disease is characterized by calcification of soft tissues, frequently leading to death, and has caused losses of millions of dollars annually to livestock ranchers in Argentina (Cabrera 1983). The active principle of *S. glaucophyllum* has been shown to be a vitamin D-like substance that increases calcium and phosphorous absorption (Wasserman 1974; Morris 1977). Extracts of *S. glaucophyllum* are currently being tested for activity as bone growth factors useful in human and veterinary medicine (Morris 1977; B. Barr, pers. comm.).

Solanum glaucophyllum is most similar to *S. confusum* of northwestern Argentina and adjacent Bolivia, and to *S. matadori* of southeastern Brazil. *Solanum confusum* differs from *S. glaucophyllum* in being commonly pubescent, and by having leaves with longer petioles, shorter corolla tubes with narrower corolla lobes, and yellow to orange fruits. *Solanum matadori* is glabrous, like most plants of *S. glaucophyllum*, but it has stellate corollas, green rather than glaucous leaves, and is known only from Santa Catarina, Brazil.

On the basis of morphological characters, Child (1986) considered *S. glaucophyllum* to be unrelated to sect. *Cyphomandropsis*. He removed it to its own section, *Solanum* sect. *Glaucophyllum* Child, included within *Solanum* subg. *Solanum*. Dottori (1995) investigated fruit and seed morphology of this species and concluded that there were significant differences in fruit and seed characters between *S. glaucophyllum* and the other species of sect. *Cyphomandropsis* (*S. confusum*, *S. fusiforme*, and *S. stuckertii*) she investigated. These differences included epicuticular wax covering the fruit exocarp, ventilation cracks rather than stomata in the fruit surface, and seed coat cells with a distinct shape and pattern of wall thickening. Although *S. glaucophyllum* exhibits some unique characters and may represent an isolated clade within the section, its tapered anthers, large angled seeds, and large chromosomes establish it as a member of sect. *Cyphomandropsis*.

A few collections (Arenas 1407, Döbereiner & Tokarnia 794, 797, 800, Hatschbach & Guimarães 21941, Schaller 301) from ca. 20°S latitude in the Río Paraguay drainage are anomalous in having moderately to densely puberulent-pubescent axes and leaves. Morton segregated the pubescent plants in the herbarium but never published the varietal name he assigned them. Because they conform to typical representatives of *S. glaucophyllum* in all other respects and occur within the range of the glabrous forms, I do not consider them to be taxonomically distinct.

Solanum glaucophyllum has often been confused with *S. amygdalifolium* Steud. (also known under the synonyms *S. angustifolium* Lam., *S. persicifolium* Mart., *S. handelianum* Morong, *S. brittonianum* Morong), which is sympatric and is found in similar habitats. *Solanum amygdalifolium*, however, is a twining or scandent vine with strongly ridged stems and ovate-lanceolate leaves. The anthers dehisce by broad pores that open into longitudinal slits, and the seeds are much smaller than those of *S. glaucophyllum*. *Solanum amygdalifolium* belongs to the dulcamaroid group of *Solanum* (sections *Dulcamara* (Moench) Dumort., *Jasminosolanum* Seithe, and relatives) and, though strikingly convergent in several morphological features, is not closely allied to sect. *Cyphomandropsis*.

Desfontaines (1829) published the name *S. glaucophyllum* in reference to plants in cultivation in the Paris Botanic Garden. I was unable to locate a type specimen for this name, and a search of the collections at P by Sandra Knapp in 1998 failed to turn up any candidates. D'Arcy (1974) cited a specimen at MPU labelled as "*S. glaucophyllum* Hort. Paris Cat. Ann. 1829, p. 396" and speculated that it may be a type. Sandra Knapp in 1998 found this specimen at MPU, but with the additional annotation "h.m. Jul 1840," indicating that it was grown at the Montpellier Botanic Garden in 1840 and thus cannot be a type. Specimens from BR, FI, and G attest to the cultivation of this species in the Paris Botanic Garden in the early nineteenth century. Bertoloni (1851) and Dunal (1852) indicate that both of the names *S. glaucophyllum* and *S. glaucum* were in use to refer to this species. Because *S. glaucophyllum* was described from living material, it is likely that no type specimen exists; however, Desfontaines's original description is adequate to fix the application of the name.

Kuntze (1898), Chodat (1916), and Hassler (1918) proposed a number of infraspecific taxa based on leaf color and size. All of these taxa are subsumed within the range of variation that is encompassed in my concept of the species.

Solanum glaucophyllum was cultivated in French botanical gardens at Angers, Hyeres, and Dijon in the mid-nineteenth and early twentieth century, and specimens are also known from Japan, Nepal, and the United States (Pensacola, Florida). It is not known whether the Asian plants were cultivated or adventive, but probably at least the Nepal collection was a deliberate introduction. D'Arcy (1974) speculates that *S. glaucophyllum* was introduced to Florida in ship's ballast. It has not been collected from Florida since 1901.

7. *Solanum hibernum* Bohs, Novon 4: 203. 1994.—TYPE: BOLIVIA. Santa Cruz: Prov. Florida, 3 km S of Mataral, valley of Río Ciénega, 18°08'S, 64°13'W, 1400 m, 1 Feb 1987, *Nee & Coimbra 33970* (holotype: US! #3146788; isotypes: K! LPB, NY! TEX!).

Small shrub 0.5–1.5 m tall. Stems densely pubescent with mostly unbranched eglandular hairs mixed with some short-stalked glands, dendritically branched hairs occasionally present. Leaves 6—many per sympodial unit, the blades 4–11 cm long, 1.5–5.5 cm wide, length:width ratio ca. 1.5–3.3:1, simple, ovate or elliptic, acute at apex, cuneate to subcordate at base, chartaceous to subcoriaceous, sparsely pubescent adaxially with curled, white, usually dendritically branched hairs, these more abundant on midvein and margin, densely white-pubescent abaxially with dendritically-branched hairs, the petioles 1–2.5 cm long, densely pubescent with hairs like those of the stem. Inflorescence unbranched (rarely forked), ca. 10-flowered, 1.5–3.5 cm long; peduncle 0.5–1 cm long; rachis 0.5–2.5 cm long; pedicels 10–15 mm long, spaced 1–5 (–10) mm apart, articulated at or near the base, leaving scars or short pegs less than 1 mm long; inflorescence axes sparsely to moderately pubescent with mostly unbranched hairs. Calyx sparsely to moderately pubescent, the radius 3–5 mm, the lobes 1–3 mm long, ca. 2 mm wide, often unequally divided, deltate, with apiculate tips. Corolla violet, chartaceous, stellate, the radius 9 mm, the tube 2 mm long, the lobes 7 mm long, 2.5 mm wide at base, narrowly triangular, acute at apex, moderately to densely puberulent abaxially, sparsely puberulent adaxially. Anthers usually connivent, yellow, lanceolate, 5–7 mm long, 1.5–2 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous, cylindrical to subclavate, 7–8 mm long, 0.5 mm in diameter; stigma truncate to subcapitate. Fruits 1.5–2 cm long, 1.5–2 cm in diameter, globose, obtuse or slightly apiculate at apex, glabrous, yellow to orange when ripe; stone cell aggregates very small or absent. Seeds 4–5 mm long, 3–4 mm wide, angled, felty-pubescent with white pseudohairs. Chromosome number: $2n = 24$. Figs. 21, 22.

Phenology. Collected in flower in January, February, May, and December; collected in fruit in February, March, June, August, September, and December.

Distribution (Fig. 23). Central Bolivia in Deptos. Chuquisaca, Cochabamba, and Santa Cruz; sandy or rocky soil in semiarid inter-Andean valleys, often in thorn scrub communities; 1250–2600 m.

Local names and uses. Bolivia: Andres huaylla (Spanish; *I. García 71B*), bolo bolo (*Nee & Coimbra 33970*), kita (Quechua; *I. García 30*).—Used as an antidote for snake bites in cattle (*Nee 46611*). Fruits said to not be eaten due to their bitter taste (*Nee & Coimbra 33970*).

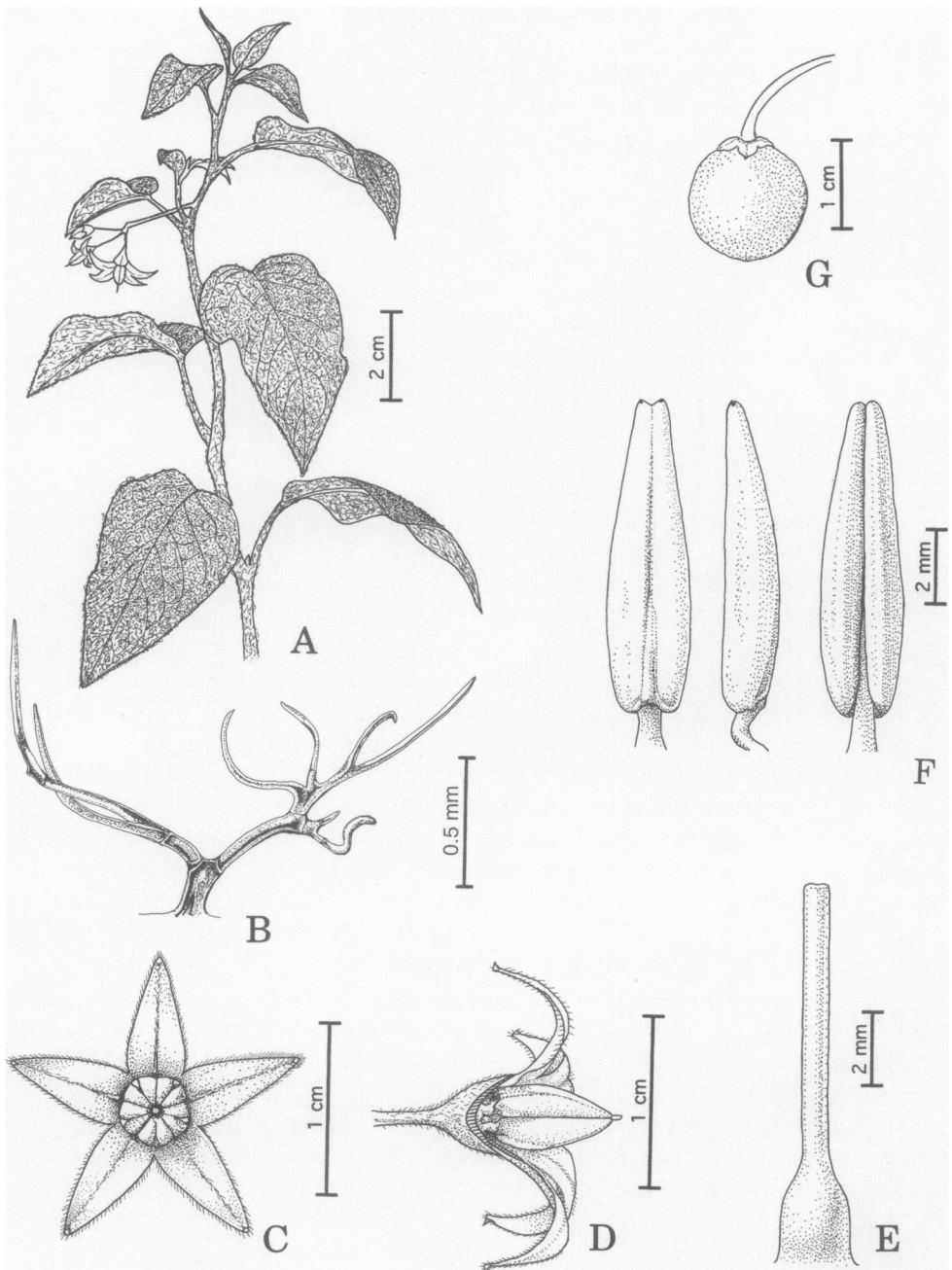


FIG. 21. *Solanum hibernum*. A. Habit. B. Dendritically branched trichome. C. Flower, seen from above. D. Lateral view of partially sectioned flower. E. Gynoecium. F. Stamen (left to right: abaxial, lateral, adaxial views). G. Fruit. (Based on greenhouse material of *Bohs 2443*.)



FIG. 22. Flowers of *S. hibernum*; scale bar = 1 cm.

ADDITIONAL SPECIMENS EXAMINED. **Bolivia.** CHUQUISACA: Prov. Zudañez, Rodeo Monte Espinoso, 20 km E de Zudañez, *Mühlbauer s.n.* (LPB).—COCHABAMBA: Prov. Camparo, Rumicancha (Aiquile), *I. García 30, 71B* (LPB).—SANTA CRUZ: Prov. Caballero, Saipina, Estancia Buena Vista, 6 km NW del pueblo, 18°03'18"S, 64°39'44"W, *Balcazar 385* (LPB, USZ); Prov. Florida, along road from Mairana to Yunga de Mairana, 2 km NE of central square in Mairana, 18°07'S, 63°56'W, *Bohs et al. 2770* (USZ, UT); Prov. Vallegrande, 10 km by air NNW of Vallegrande, 18°23'S, 64°8'W, *Nee & Coimbra 33945* (NY); Prov. Vallegrande, Quebrada Llullucha, 14 km by air SSE of Mataral, 18°14'S, 64°11'W, *Nee & Coimbra 33950* (LPB, NY); Prov. Florida, 7 km NNE of Los Negros, along road from Mairana to Comarapa, ca. 18°00'S, 64°05'W, *Nee 35544* (LPB, NY); Prov. Vallegrande, 6.5 km NNW of center of Vallegrande, 18°26'S, 64°7'W, *Nee & Solomon 36559* (LPB, NY); Prov. Vallegrande, Lagunillas, 5 km N of El Trigal on road to Mataral, 18°15'S, 64°09'W, *Nee 38328* (LPB, NY, USZ, UT); Prov. Caballero, 6.5 km (by road) SW of Mataral on highway to San Isidro, narrow gorge at confluence of Río Karikari and Quebrada Seca, 18°08'S, 64°16'W, *Nee 46524* (USZ); Prov. Caballero, 10 km (by road) SE of Comarapa on highway to San Isidro, just NW of turnoff to Pulquina Arriba, along Quebrada Pujio (a dry wash), 17°59'S, 64°29'W, *Nee 46611* (USZ); Prov. Vallegrande, tramo entre Santa Rosita, Blanquiscal y San Antonio (2–3 km al S de Vallegrande), 18°30'32"S, 64°06'12"W, *I. Vargas et al. 1999* (USZ).

This species is most similar to *S. luteoalbum* of Peru and *S. stuckertii* of south-central Bolivia and Argentina. *Solanum hibernum* is distinctive in having strongly discoloured leaf surfaces with the lower surface densely covered with dendritically branched hairs. Many specimens of *S. luteoalbum* also have dendritically branched pubescence, but the hairs are more evenly distributed on both leaf surfaces. *Solanum hibernum* and

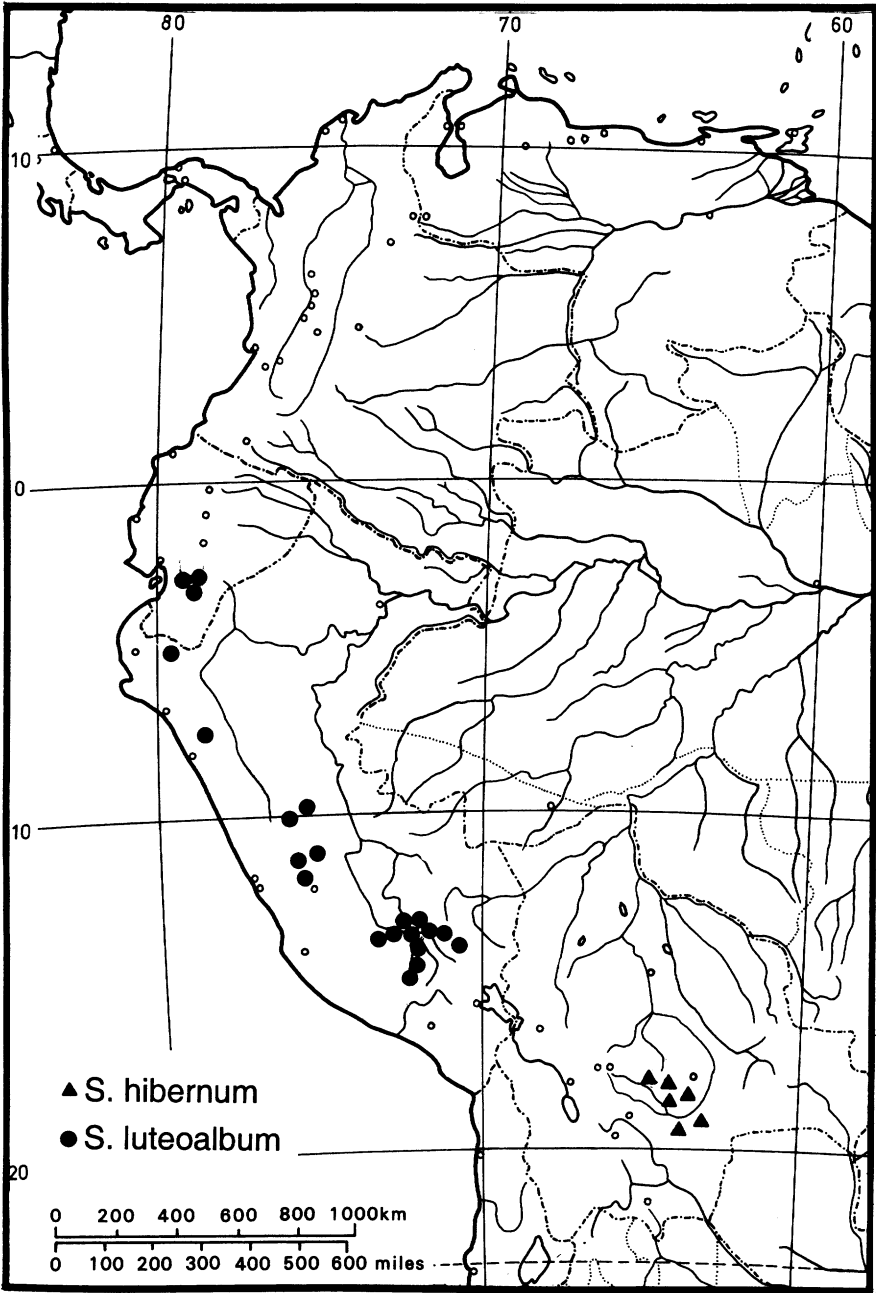


FIG. 23. Distribution of *S. hibernum* and *S. luteoalbum*.

S. luteoalbum are geographically disjunct, and no hybrids resulted from greenhouse crossing attempts.

In general, *S. hibernum* can be distinguished from *S. stuckertii* by hair morphology and corolla color. *Solanum stuckertii* invariably has unbranched hairs and whitish corollas. All specimens of *S. hibernum* have dendritically branched hairs (at least on the abaxial leaf surfaces) and most have purplish corollas. However, in *Nee 46524* the collector described the corollas as white with a yellow central vein. Polymorphism for blue and white flowers, even within a single population, has been noted in species of *Solanum* sections *Petota* and *Solanum* (Correll 1962; Henderson 1974; Edmonds 1977), but the frequency of white corollas in *S. hibernum* needs further investigation. Furthermore, hybrids have been produced between *S. hibernum* and *S. stuckertii* in greenhouse crosses. The F₁ hybrid plants resembled *S. hibernum* in pubescence characters, but had whitish or very light lavender corolla lobes with a yellowish central star.

Many individuals of *S. hibernum* become leafless during the dry season, but remain conspicuous because of their persistent bright orange fruits that hang like tiny Halloween pumpkins from the bare branches (M. Nee, pers. obs.).

8. *Solanum hutchisonii* (Macbride) Bohs, comb. nov. *Solanum nitidum* var. *hutchisonii* J. F. Macbride, Field Mus. Publ. Bot. 13, pt. V-B, no. 1: 209. 1962.—TYPE: PERU. Amazonas: Prov. Bagua, “St. Julian” hill, on the Río Utcubamba, Hacienda Marerilla near Bagua Grande, 600 m, 1 Oct 1957, *Hutchison 1490* (lectotype, here designated: F! #1559946; photo of lectotype, F neg #51398: F!; isolecotypes, G! K! NY! US!). [The type was cited erroneously in the protologue as *Hutchison 1243*.]

Herb or shrub up to 3 m tall. Stems glabrous and white-punctate with cells containing crystal sand. Leaves ca. 4–5 per sympodial unit, the blades 2.5–9 cm long, 1–3 cm wide, length:width ratio 1.75–3.5:1, simple, elliptic-ovate, acute at apex, rounded to subcordate at base, subcoriaceous or somewhat succulent, glabrous and white-punctate adaxially and abaxially, the petioles 1–2.5 cm long, glabrous. Inflorescence unbranched or rarely forked, 5–25-flowered, 1.5–6 cm long; peduncle 1–4 cm long; rachis 0.2–2 cm long; pedicels 5–15 mm long, 15–20 mm long in fruit, unevenly spaced 1–5 mm apart, articulated at base, leaving scars on the axis; inflorescence glabrous. Calyx glabrous abaxially except for a few sparse hairs at tips of lobes, veiny and sand-punctate, irregularly splitting, the radius 3–6 mm, the lobes 2–5 mm long, 1.5–3 mm wide, deltate, with apiculate tips. Corolla purple, chartaceous, stellate, the radius 8–15 mm, the tube 2–3 mm long, the lobes 6–12 mm long, 2–4 mm wide at base, triangular-ovate, acute at apex, glabrous abaxially and adaxially except for the ciliolate margins. Anthers not connivent, color unknown, narrowly triangular, 5–8 mm long, 1.5–2.5 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous, cylindrical, 6–11 mm long, 0.5–1 mm in diameter; stigma truncate. Fruits 1–2.5 cm long, 1–2.5 cm in diameter, globose, obtuse at apex, glabrous, dark-colored when ripe; stone cell aggregates absent. Seeds 4 mm long, 3 mm wide, angled, whitish pubescent and reticulate. Chromosome number unknown. Fig. 24.

Phenology. Collected in flower in February, October, and November; collected in fruit in February.

Distribution (Fig. 8). Northern Peru, Río Marañón valley in Deptos. Amazonas and Cajamarca; dry slopes; 450–600 m.

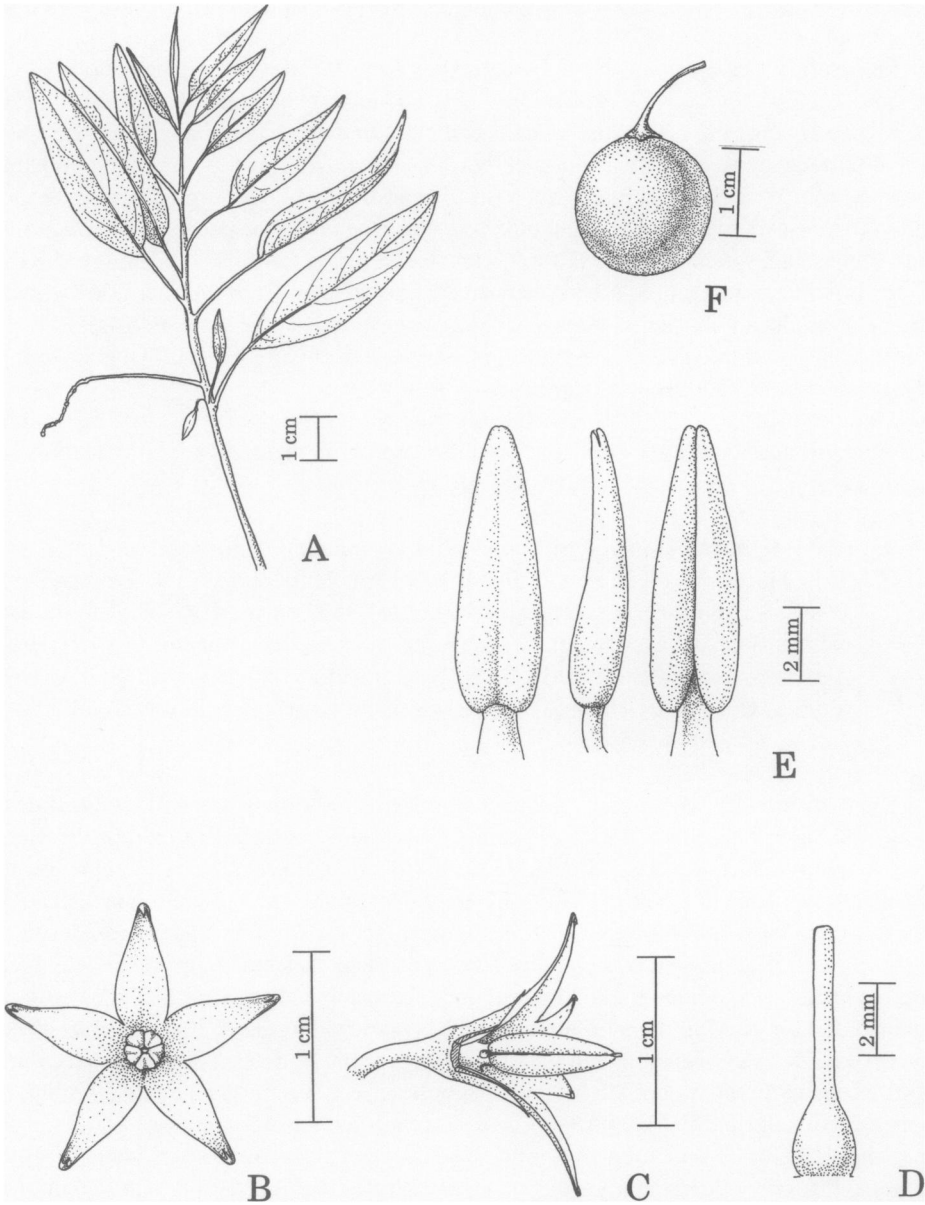


FIG. 24. *Solanum hutchisonii*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial view). F. Fruit. (Based on *Hutchison 1490*.)

ADDITIONAL SPECIMENS EXAMINED. **Peru.** AMAZONAS: Prov. Bagua, cerca a Corral Quemado, laderas que convergen al Río Marañón, *Sánchez Vega* 3970 (F, NY).—CAJAMARCA: Prov. Jaén, confluencia del Chamaya con Marañón, *Sagástegui* 5862 (US); Prov. Chota, Huambos, 9 Nov 1956, *Soukup* 4531 (US).

Solanum hutchisonii can be distinguished from the other species in sect. *Cyphomandropsis* by its fleshy subcordate leaves and lack of pubescence. Some other species of the section, such as *S. glaucophyllum* and *S. fusiforme*, are glabrous or nearly so, but they occur far to the south in Brazil, Argentina, and adjacent areas.

Macbride (1962) cited the type of *S. nitidum* var. *hutchisonii* as *Hutchison* 1243. It is obvious from herbarium notations that the correct type number of *S. nitidum* var. *hutchisonii* is *Hutchison* 1490, and that the citation in Macbride's protologue is an error. Consequently, *S. nitidum* var. *hutchisonii* should not be considered as a synonym of *S. nitidum*, contrary to Knapp's (1989) treatment. The collection *Hutchison* 1243 is *S. nitidum* Ruiz & Pav., a species of the *S. nitidum* group of *Solanum* sect. *Holophylla* (Knapp 1989). According to molecular data, *S. nitidum* belongs to a clade consisting of *S. dulcamara* L., *S. wallacei* (A. Gray) Parish, and relatives, and is unrelated to sect. *Cyphomandropsis* (Bohs & Olmstead, in press; Fig. 1).

9. *Solanum luridifuscescens* Bitter, Repert. Spec. Nov. Regni Veg. 12: 466. 1913.

Cyphomandra velutina Sendtner in Martius, Fl. bras. 10: 120, t. 17. 1846, non *Solanum velutinum* Dunal, 1814. *Pionandra velutina* (Sendtner) Miers, Ann. Mag. Nat. Hist. 15, ser. 2: 199. 1855.—TYPE: BRAZIL. Goiás: ad Fazendam S. Cruz da Donna Tereza, *Pohl* 3455 (lectotype, here designated: W!; photos of lectotype, US neg. 8531: F! GH! LL! NY!, US neg. 8758: GH! LL! NY!; isolectotypes: BR! F! G, M! W!).

Cyphomandra glaberrima Dusén, Ark. Bot. 9(5): 19. 1909.—TYPE: BRAZIL. Rio de Janeiro: Serra do Itatiaia, ca. 1200 m, Oct 1903, *Dusén* 2057 (lectotype, here designated: S!).

Perennial herb or shrub up to 2 m tall. Stems nearly glabrous to densely puberulent-pubescent with stalked glandular and unbranched eglandular hairs. Leaves 4–5 per sympodial unit, the blades 4.5–23 cm long, 2–7 (–9) cm wide, length:width ratio 1.5–3 (–4):1, simple, elliptic to elliptic-ovate, acute to acuminate at apex, cuneate to decurrent at base, chartaceous, nearly glabrous to moderately puberulent-pubescent adaxially and abaxially with unbranched eglandular hairs, the pubescence denser on veins, the petioles 0.3–2.5 cm long, sparsely to densely puberulent-pubescent. Inflorescence unbranched, 5–12 (–25)-flowered, 4–20 cm long; peduncle 2–6 cm long; rachis 2–18 cm long; pedicels (10–) 20–30 mm long, 20–30 mm long and thickened distally in fruit, spaced 3–14 mm apart, articulated at or slightly above the base, leaving pedicellar remnants up to 1 mm long; inflorescence axes sparsely to densely puberulent-pubescent with hairs like those of the stem. Calyx sparsely to moderately puberulent-pubescent, the pubescence denser on margins and tips of lobes, the radius 4–6 mm, the lobes 1.5–3 mm long, 1.5–2.5 mm wide, deltate, narrowed to acute or acuminate tips. Corolla white to purple, subcoriaceous, stellate, the radius 13–18 mm, the tube 3–4 mm long, the lobes 9–15 mm long, 3–5 mm wide at base, narrowly triangular, acute at apex, sometimes with a small subapical projection, glabrous to moderately puberulent-pubescent abaxially, with the pubescence denser distally, glabrous adaxially. Anthers connivent or free, yellow, lanceolate, 7–9 mm long, 1.5–2 mm wide, abaxial surface with an obvious band of scaly papillae, the pores directed

distally. Ovary glabrous; style glabrous, cylindrical, 5–8 mm long, 0.5–1 mm in diameter; stigma truncate. Fruits 1–2 cm long, 1–2 cm in diameter, globose, obtuse at apex, glabrous, the color when ripe unknown; stone cell aggregates absent. Seeds 3–4 mm long, 2–3 mm wide, lenticular, densely puberulent with whitish pseudohairs. Chromosome number unknown. Fig. 25.

Phenology. Collected in flower in February and June through November; collected in fruit in October, November, and February.

Distribution (Fig. 18). Eastern to southeastern Brazil (Espírito Santo, Goiás, Minas Gerais, Paraná, Rio de Janeiro, and São Paulo); moist forest, often in wet or swampy areas; 1100–2650 m.

REPRESENTATIVE SPECIMENS. **Brazil.** ESPIRITO SANTO: arredores de Muniz Freire, *Hatschbach & Guimarães 46879* (UT); SE slopes of Serra da Caparaó, *Mexia 4039* (BM, GH, MO, NY, US), *4043* (G, S, US); Mpio. Serra, perto de Vitória, Estação Biológica do Mestre Álvaro, subida para o Morro do Mestre Álvaro, *Pirani et al. 164* (SP).—MINAS GERAIS: Serra do Caparaó, *Brade 16926* (RB); Sapucaí-Mirim, Serraria Boa Vista, *Kuhlmann 2597* (SP); Ervália, Serra do Gongo, 7 km do Careço (arraial), fazenda das Olivieras, propriedade de Maurício Ferreira Fernandes, *Vieira 630* (GH, VIC).—PARANÁ: Mpio. Cerro Azul, Morro Grande, *Hatschbach 8302* (L, US); Mpio. Campina Grande do Sul, Serra Capivari Grande, *Hatschbach 20327* (CTES, Z).—RIO DE JANEIRO: Teresópolis, Serra dos Orgãos, Pedra do Frade, *Brade 16604* (RB, UT); environs of Rio de Janeiro, Serra do Coelho et Nova Friburgo an Conego, *Glaziou 13084* (BR, C, F [fragment], G, K).—SÃO PAULO: Alto Tiete, Rio Claro, *Loefgren 5880* (US); Serra dos Orgãos, *Ule 4314* (HBG).

This species is distinctive in having rather large elliptic leaves with a tapered base and a dense obvious band of scaly papillae on the abaxial anther surfaces. Vegetative pubescence is quite variable in *S. luridifuscescens*; plants range from nearly glabrous to densely pubescent on axes and leaf surfaces. *Solanum luridifuscescens* is superficially similar to and has been confused with *S. melissarum* of *Solanum* sect. *Pachyphylla*. It can be distinguished from the latter species by its stellate corollas with very short tubes and by its papillose anther surfaces.

The epithet *velutina* cannot be used when *Cyphomandra velutina* is transferred to *Solanum*, because the name is already occupied by *S. velutinum* Dunal in Poiret (1814). Bitter provided a new name in *Solanum*, *S. luridifuscescens*, which refers to the dark brown tobacco color of the dried plants. He pointed out several discrepancies in Sendtner's original description (Sendtner 1846) and provided a new diagnosis based solely on the collection *Ule 4314* from the Organ Mountains near Rio de Janeiro.

Dusén (1909) did not specify a holotype for *C. glaberrima*; his specimen at S, which matches the protologue, has been chosen as the lectotype.

- 10. *Solanum luteoalbum*** Persoon, Syn. 1: 221. 1805. *Solanum pubescens* Ruiz & Pavón, Fl. peruv. 2: 36, pl. 169, fig. b. 1799, non *Solanum pubescens* Willdenow, 1794. *Cyphomandra luteoalba* (Persoon) A. Child ex Bohs, Fl. Neotrop. Monogr. 63: 154. 1994.—TYPE: PERU. "In Peruviae nemoribus ad Cuchero tractus, floret Januario et Februario," Ruiz & Pavón s.n. (lectotype, here designated: MA; fragment of lectotype: F!; photo of lectotype, F neg. 29723: F! GH!).
- Solanum semicoalitum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 463. 1913.—TYPE: ECUADOR. Azuay: hills above Gualaceo, Sep 1864, Jameson s.n. (holotype: W!; photo of holotype, F neg. 33110: F! G!).
- Solanum luteoalbum* var. *tunya* Macbride, Field Mus. Publ. Bot. 13, pt. V-B, no. 1: 206. 1962.—TYPE: PERU. Cuzco: Ollantaytambo, ca. 3000 m, 18 May 1915, Cook & Gilbert 804 (lectotype, here designated: US! #603970).

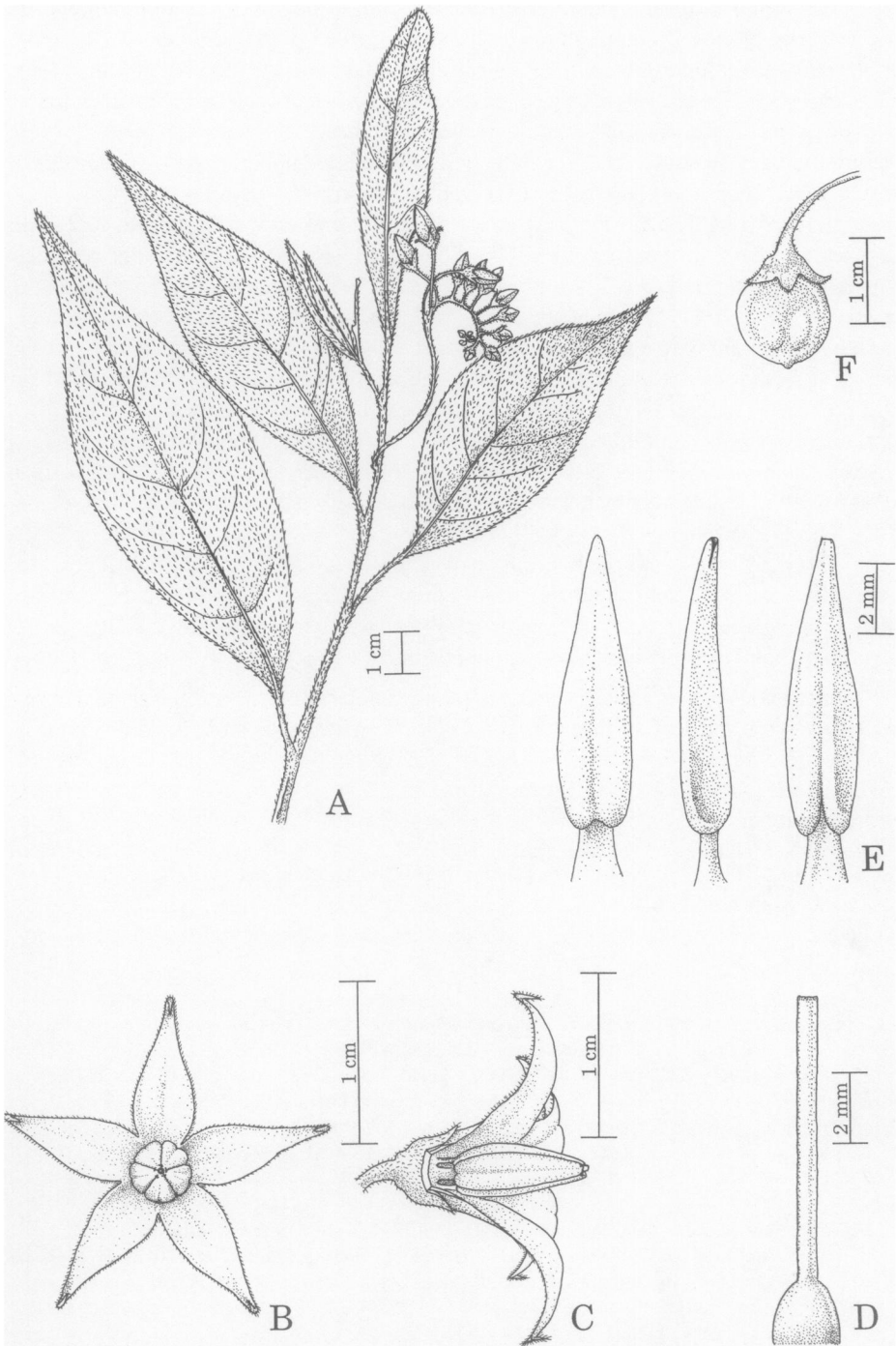


FIG. 25. *Solanum luridifuscescens*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial views). F. Fruit. (Based on: A, Brade 16926; B–F, Hatschbach 20327.)

Shrub 1–3 m tall. Stems moderately to densely pubescent with eglandular unbranched or dendritically branched hairs and also with short-stalked glands; tips of shoots sometimes densely glandular. Leaves 6 to many per sympodial unit, the blades 3.5–18 cm long, 1.5–7.5 cm wide, length:width ratio 2–3:1, simple, elliptic or ovate-elliptic, acute to acuminate at apex, cuneate to slightly decurrent at base, chartaceous, moderately to densely pubescent adaxially and abaxially with eglandular unbranched or dendritically branched hairs and often also with short-stalked glands, the petioles 1–4.5 cm long, densely pubescent with hairs like those of the stem. Inflorescence unbranched, forked, or sometimes further branched, ca. (5–) 10–25-flowered, 4–10 (–15) cm long; peduncle 3.5–6.5 cm long; rachis 1–5 (–10) cm long; pedicels 10–25 mm long, 10–35 mm long in fruit, spaced ca. 2–10 (–15) mm apart, articulated at base; inflorescence axes moderately to densely puberulent with eglandular unbranched and/or dendritically branched hairs and often also densely beset with glands. Calyx moderately puberulent with glandular and eglandular hairs, the radius 3–4 mm, the lobes 1.5–2 mm long, 1.5–2 mm wide, deltate, often abruptly narrowed into acuminate tips. Corolla purple (rarely white), chartaceous, stellate, the radius 11–20 mm, the tube 3–4 mm long, the lobes 8–17 mm long, 3–4 mm wide at base, narrowly triangular, acute at apex, sparsely to densely puberulent abaxially with eglandular unbranched and/or dendritically branched hairs and often also glandular hairs, nearly glabrous adaxially except for some hairs on midrib and near apices of lobes. Anthers usually connivent, yellow, lanceolate, 5–8 mm long, 1.5–2 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous or sometimes with a few hairs, cylindrical, 7–9 mm long, 0.5 mm in diameter; stigma truncate. Fruits 1.5–2 cm long, 1.5–2 cm in diameter, globose, obtuse at apex, glabrous, orange or red when ripe; stone cell aggregates absent. Seeds 5–6 mm long, 4–5 mm wide, angled, smooth to rugose. Chromosome number: $2n = 24$. Figs. 26, 27, 28.

Phenology. Collected in flower in August through March; collected in fruit in all months except July.

Distribution (Fig. 23). Andean slopes from southern Ecuador to southern Peru; gravelly or rocky slopes and cliffs to moist river valleys; 2200–3300 m.

Local names. Peru: Pajarito (*Macbride & Featherstone 1038*), tunya (*Herrera 3346*), tunya-tunya (*Marin 159, Cook & Gilbert 804*).

REPRESENTATIVE SPECIMENS. **Ecuador.** AZUAY: 4–6 km N of Sevilla de Oro, *Camp E-4675* (NY); partido sitio denominado Llantera–Chiquintad–Saucay, Guandum–La Represa de agua, sector NW de Cuenca, 02°47'S, 79°08'W, *Ortiz & Jaramillo 140* (NY). **Peru.** APURIMAC: valley of Río Colcachaca at Cotarusi–Colca ca. 1 km above junction with Río Chalhuanca, ca. 15 km (air) S of Chalhuanca, *Ilitis et al. 528* (BM, F, WIS); valley of Río Chalhuanca, 5–15 km (air) S and SW from Chalhuanca on road to Carabamba, Carabamba, junction of two rivers, *Ilitis et al. 582* (BM, F, WIS), *Ilitis et al. 584* (WIS), *Ilitis et al. 589* (BM, F, WIS), *Ilitis et al. 591* (WIS); vicinity of Acobamba, valley of Río Chalhuanca, 5 km NW of Chalhuanca, *Ilitis et al. 601* (WIS); Prov. Abancay, Curahuasi, valley of Río Apurimac, ENE of Abancay near Catholic Church, *Ilitis et al. 736* (WIS); Prov. Abancay, Curahuasi, *Marin 1872* (F); Chalhuanca, Aymaraes, 14°03'S, 73°15'W, *Núñez 7137* (MO); Prov. Andahuaylas, W of Pincos, *Stork & Horton 10711* (F, GH, K).—CAJAMARCA: Prov. Contumazá, ca. 16 km S of Contumazá en route to Cascas, Bosque Cachil, 07°24'S, 78°46.5'W, *Dillon & Sagástegui 6088* (NY, UT), *López et al. 9089* (MO), *Sagástegui et al. 15117* (UT).—CUZCO: Ollantaytambo, *Cook & Gilbert 387a* (NY); 13 km N of Písaq on road to Ollantaytambo, *A. Gentry et al. 19785* (F, MO, NY); near Cuzco, *Herrera 921* (W); valley of Río Urubamba, Ollantaytambo, *Herrera 3346* (F); Prov. Calca, bottom of Río Urubamba valley, Km 56 on road Cuzco–Urubamba ca. 6 km W of Calca (6 km E of Yucay), *Ilitis et al. 923* (BM, F, K, WIS); valley of Río Urubamba, Pachar, 4 km below Urubamba, *Ilitis & Ugent 1141* (WIS); Prov. Urubamba, just SE of Urcos at Km 57 from Cuzco, 13°40'S, 71°40'W, *Ilitis & Ugent 1213* (WIS); Prov. Urubamba, near Ollantaytambo, Río Vilcanota valley, 13°15'S, 72°20'W, *Knapp & Mallet 6465* (F, K, MO, NY);

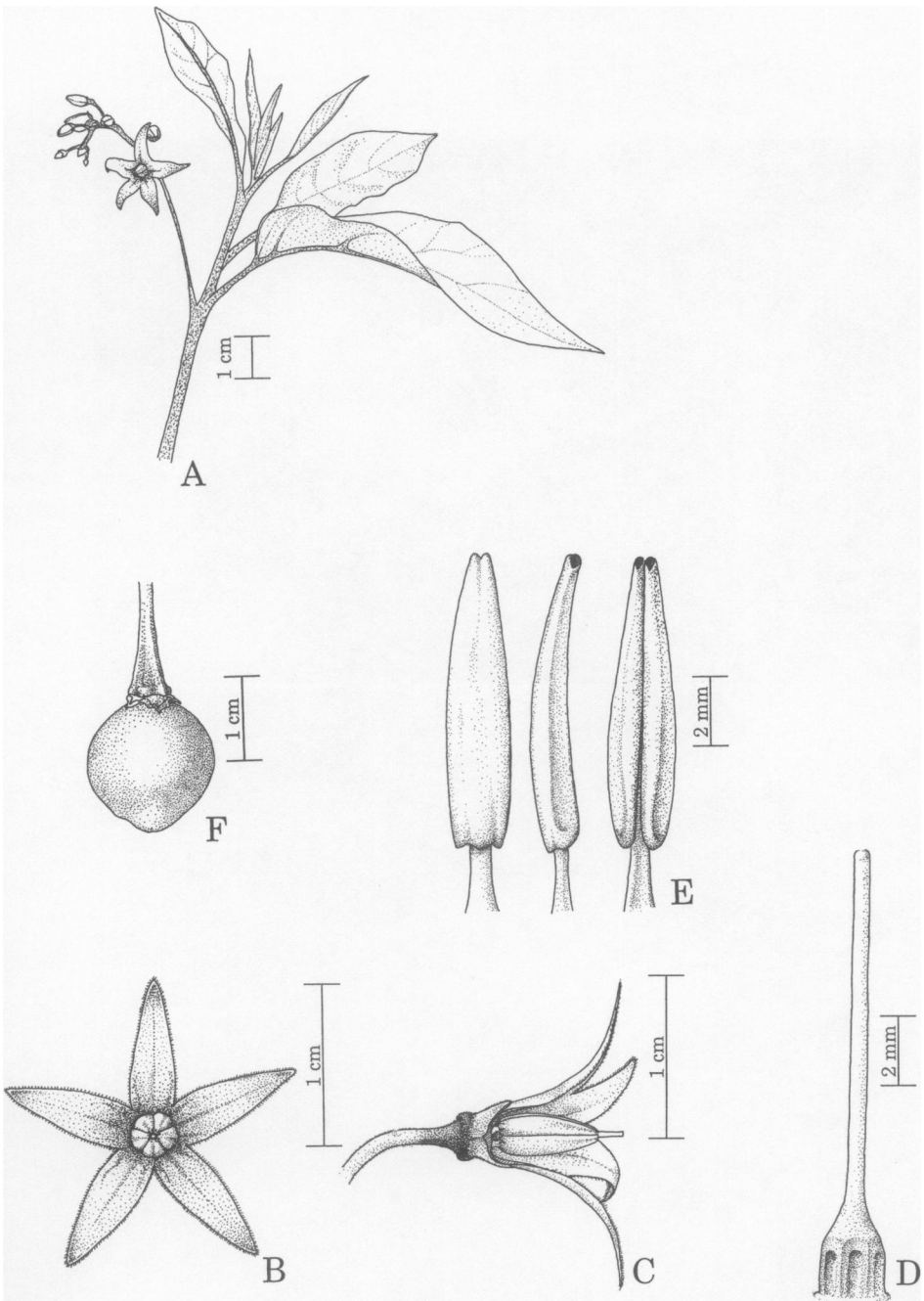


FIG. 26. *Solanum luteoalbum*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial views). F. Fruit. (Based on greenhouse material of *Bohs* 2336.)



FIG. 27. *Solanum luteocalbum*. A. Habit; scale bar = 2 cm. B. Fruits, showing rough dull surface; scale bar = 1 cm.



FIG. 28. Inflorescence of *S. luteoalbum* showing stellate corollas; scale bar = 1 cm.

Prov. Calca, Pisac, *Marin 159* (F); Huayocari to Yanacocha, Urubamba, NW from Cuzco, 13°16'S, 72°4'W, *Núñez et al. 7040* (F, NY); Yaurisque, Paruro, SW of Cuzco on road from Cuzco to Paruro, *Núñez 7361* (MO); Prov. Urubamba, 67 km from Cuzco, from Río Calicanto to Chacchapara, Muris and environs, 13°16'S, 72°16'W, *Núñez & Bengoa 8667* (NY); Prov. Paucartambo, near Paucartambo on road to Abra Acanacu, *Plowman & Davis 4913* (F, K, GH); Río Urubamba, Pisac, hillsides around ruins, *Solomon 3030* (F, MO); Prov. Anta, Limatambo, *Vargas 200* (GH); Prov. Calca, Hacienda Urco, *Vargas 686* (GH); Prov. Urubamba, Yanahuara, *Vargas 9325* (WIS); ruins of Ollantaytambo, *West 6476* (GH, MO).—HUÁNUCO: near Huánuco, *Kanehira 79* (GH).—JUNÍN: Prov. Tarma, 1.5 km above (W of) Palca, *Iltis et al. 221* (BM, F, NY, WIS), *222* (BM, F, WIS); Tarma, *Macbride & Featherstone 1038* (F); Mito, *Macbride 3273* (F, G).—PIURA: Prov. Ayabaca, Bosque de Huamba, *Cano 1557* (NY).—PUNO: Prov. Carabaya, Ollachea, across San Gaban river from town, *Boeke & Boeke 3173* (NY, TEX).—Department unknown: Yanano, *Macbride 3795* (F).

Solanum luteoalbum is similar to *S. stuckertii* and *S. hibernum*; all have elliptic leaves, stellate corollas, orange globose fruits, and large angled seeds. *Solanum luteoalbum* can be distinguished from *S. stuckertii* by its purple rather than white corollas and more northerly distribution. Hairs of *S. stuckertii* are exclusively unbranched, whereas those of *S. luteoalbum* can be either unbranched or dendritically branched. *Solanum luteoalbum* and *S. hibernum* are very similar morphologically. Both species have purple corollas and are often covered with dendritically branched trichomes, but in *S. hibernum* the leaf surfaces are strongly discoloured due to the dense whitish covering of dendritically branched hairs on the lower surface, whereas the pubescence of *S. luteoalbum* is more or less evenly distributed.

Solanum luteoalbum is also similar to pubescent forms of *S. confusum*, but can be distinguished from the latter by its stellate and usually deep purple corollas, shorter and often branched trichomes, and its more northerly geographical range.

Peruvian specimens of *S. luteoalbum* from the Departments of Apurimac and Cuzco have an obvious, often dense indumentum of forked or dendritically branched trichomes on the axes and leaf undersides, especially on young parts. Macbride (1962) differentiated these collections as *S. luteoalbum* var. *tunya*. Plants from further north in Deptos. Huánuco and Junín usually have a few branched hairs on the axes and leaf midribs, but these are not nearly as noticeable as in the collections from southern Peru. Collections from Ecuador and Deptos. Cajamarca and Piura in Peru, as well as the types of *S. pubescens* and *S. semicoalitum*, have exclusively unbranched hairs and numerous stalked glands. Whether these variants merit taxonomic recognition is debatable. Herbarium specimens from these areas do not have any obvious morphological differences except for indumentum characters.

Ruiz and Pavón's description and plate of *S. pubescens* place it in sect. *Cyphomandropsis*. A specimen at MA annotated as *S. pubescens* is very similar to plate 169 in Ruiz and Pavón's Flora (1799) and here designated the lectotype. The only discrepancy is their description of the corolla color as "albo-lutescens"; the plants listed here have purple corollas.

A single specimen of *Cook & Gilbert 804* representing the type collection of *S. luteoalbum* var. *tunya* Macbride was examined from US. This specimen is not annotated by Macbride, and he gives no indication of the type location in his protologue. Nonetheless, since this is the only specimen that has been located of this number, it has been designated as the lectotype.

11. *Solanum matadori* Smith & Downs, *Phytologia* 10: 432. 1964.—TYPE: BRAZIL.

Santa Catarina: Rio do Sul, Alto Matador, *Araucaria* forest, 800 m, 16 Oct 1958, *Reitz & Klein 7254* (holotype: US! #2323440; isotypes: HBR, L! NY!).

Shrub up to 2 m tall. Stems glabrous. Leaves many per sympodial unit, the blades 6–16 cm long, 1–2.5 cm wide, length:width ratio 4–8:1, simple, narrowly elliptic, acute at apex, tapered at base, somewhat fleshy, glabrous adaxially and abaxially, the margins ciliolate, often thickened and inrolled, the petioles 0.5–2 cm long, glabrous. Inflorescence branched, 15–30-flowered or more, 8–15 cm long; peduncle 4–6 cm long; rachises 4–7 cm long; pedicels 5–25 mm long in flower, spaced 2–10 mm apart, articulated at the base, leaving scars on the rachis; inflorescence axes nearly glabrous, with a few simple or forked hairs at base of pedicels. Calyx glabrate to sparsely pubescent with simple or forked hairs, the pubescence denser on margins and tips of lobes, the radius 3–5 mm, the lobes 2–3 mm long, 2–3 mm wide, deltate, narrowed to acute or acuminate tips. Corolla violet, chartaceous, stellate, the radius 11–17 mm, the tube 3–6 mm long, the lobes 7–11 mm long, 3–4 mm wide at base, triangular, acute at apex, sparsely to moderately pubescent abaxially and adaxially with simple and forked hairs. Anthers connivent or free, color unknown, lanceolate, 7–9 mm long, 2–3 mm wide, abaxial surface with an obvious band of scaly papillae, the pores directed distally. Ovary glabrous; style glabrous, cylindrical, 7–8 mm long, 0.5–1 mm in diameter; stigma truncate. Fruits and seeds unknown. Chromosome number unknown.

Phenology. Collected in flower in October.

Distribution (Fig. 18). Southeastern Brazil (Santa Catarina); *Araucaria* forest; 800–1200 m.

Local names. Brazil: Joá manso de fôlhas compridas, juá (Smith & Downs 1966).

ADDITIONAL SPECIMENS EXAMINED. **Brazil.** SANTA CATARINA: Alto da Serra do Espigão, pr. Vale Campos do Areão, *Pabst 6086 & Pereira 6259* (F, RB).

Solanum matadori is known from only two collections from Santa Catarina, Brazil. It is most similar to two other southeastern Brazilian species, *S. fusiforme* and *S. luridifuscescens*. All three species have the abaxial anther surface scaly or papillose; these papillae are most obvious in *S. luridifuscescens*. *Solanum matadori* and *S. fusiforme* are similar in having branched inflorescences and in being nearly glabrous vegetatively. *Solanum fusiforme* has distinctive elongated ovaries and fruits. Fruits of *S. matadori* are unknown, but the ovaries appear to be elongated. *Solanum matadori* differs from *S. fusiforme* in its narrower and strictly simple leaves, pubescent corollas, and glabrous petioles. *Solanum matadori*, unlike *S. luridifuscescens*, has very narrow leaves, branched inflorescences, and corolla lobes that are pubescent adaxially as well as abaxially.

12. *Solanum pelagicum* Bohs, nom. nov. *Cyphomandra cornigera* Dunal in DC., Prodr. 13(1): 401. 1852, non *Solanum cornigerum* Dunal, 1852. *Pionandra cornigera* (Dunal) Miers, Ann. Mag. Nat. Hist., ser. 2, 15: 199. 1855.—TYPE: BRAZIL. Santa Catarina, *Gaudichaud 160* (lectotype, here designated: P!; photo of lectotype, F neg. 39255: WIS!; isolectotype: P!; fragment of lecto- or isolectotype: F!).

Cyphomandra maritima Smith & Downs, Phytologia 10: 436, pl. 9, fig. 7. 1964, non *Solanum maritimum* Meyen ex Nees, 1843.—TYPE: BRAZIL. Santa Catarina: Mpio. Pôrto Belo, Bombas, strand, 1–5 m, 31 Mar 1957, *Smith et al. 12322* (lectotype, here designated: US! #2423787; isolectotypes: HBR, R, US!).

Herb or shrub 0.5–1 m tall. Stems moderately to densely pubescent with forked or dendritically branched eglandular hairs and some scattered long-stalked glands. Leaves 4–6 (–many?) per sympodial unit, the blades 2–10 cm long, 1.5–10 cm wide, simple and elliptic-ovate to pinnately (2–) 3–9 (–11) compound, the simple leaves with length:width ratio ca. 1.5–2.5:1, the compound leaves with the upper lateral leaflets often basiscopically decurrent, acute at apex, truncate to subcordate at base, chartaceous to subcoriaceous, moderately pubescent adaxially with unbranched or dendritically branched hairs, moderately to densely pubescent abaxially with dendritic hairs and often with scattered stalked glands, the petioles 1–4 cm long, densely dendritic-pubescent. Inflorescence unbranched or forked, ca. 7–40-flowered, 2–12 cm long; peduncle 1–5.5 cm long; rachis 1–10 cm long; pedicels ca. 10–15 mm long, spaced 1–15 mm apart, articulated at or slightly above base, leaving pedicellar scars up to 1 mm long; inflorescence axes moderately to densely puberulent with dendritic hairs and sparser stalked glands. Calyx moderately puberulent with glandular and eglandular hairs, the radius 2–5 mm, the lobes 1–3 mm long, 1–3 mm wide, deltate, acute at tips. Corolla purple, lilac, or bluish, chartaceous to membranaceous, stellate, the radius 8–13 mm, the tube 3 mm long, the lobes 5–10 mm long, 2.5–4 mm wide at base, triangular, acute at apex, sparsely to moderately puberulent abaxially, glabrous to sparsely puberulent adaxially. Anthers often connivent, yellow, lanceolate to narrowly oblong, 4.5–6 mm long, 1–2 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous; style glabrous, cylindrical, 4–5 mm long, 0.5–1 mm in diameter; stigma truncate to subcapitate. Fruits 1–2.5 cm long, 1–2 cm in diameter, ovoid or ellipsoidal, obtuse at apex, glabrous (dendritically pubescent, fide Smith & Downs, 1966), color unknown; stone cell

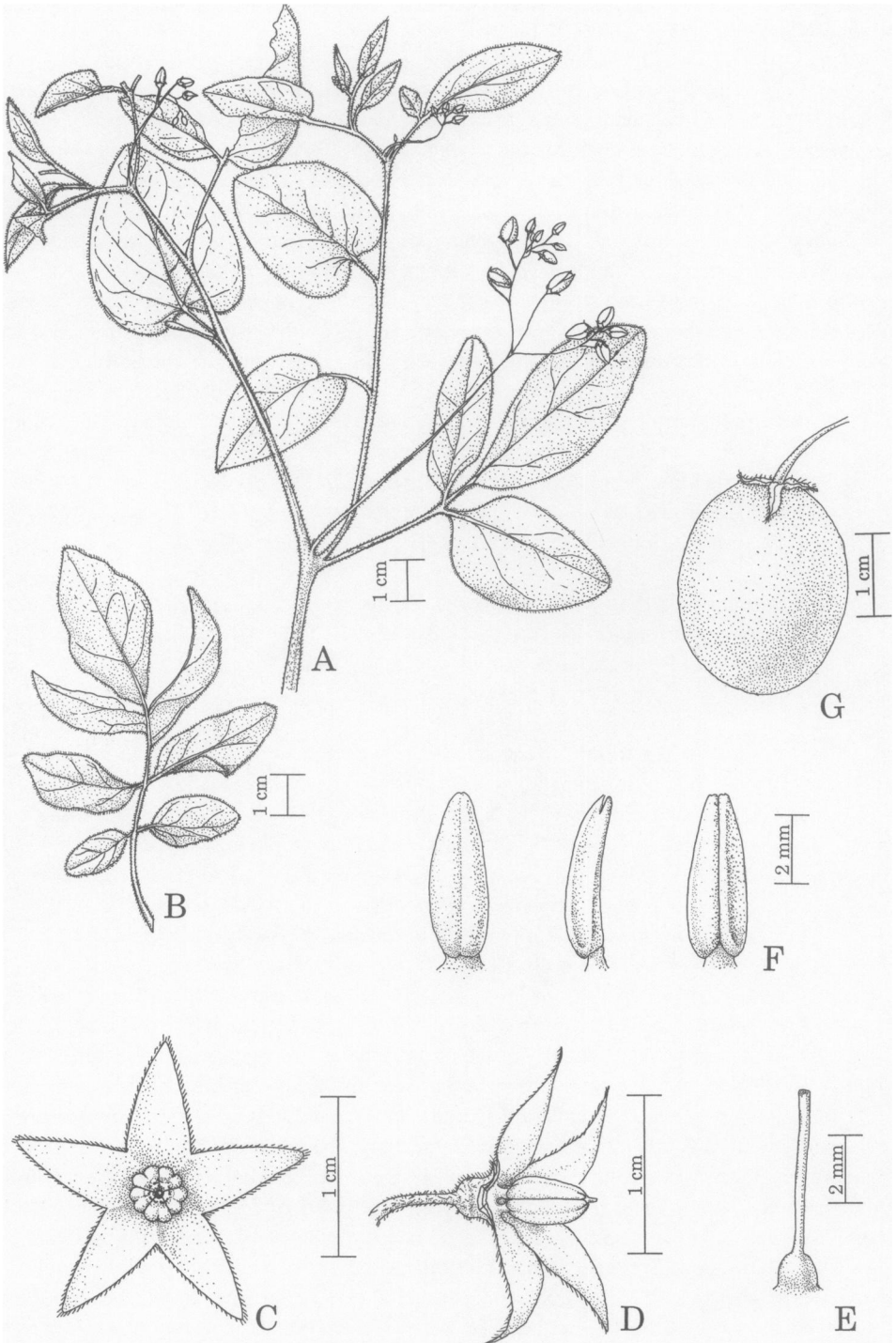


FIG. 29. *Solanum pelagicum*. A. Habit. B. Compound leaf. C. Flower, seen from above. D. Lateral view of partially sectioned flower. E. Gynoecium. F. Stamen (left to right: abaxial, lateral, adaxial views). G. Fruit. (Based on: A, *Occhioni 5307*; B–F, *Hatschbach & Forero 40366*; G, *Reitz & Klein 6770*.)

aggregates present. Seeds ca. 3 mm long, ca. 2 mm wide, strongly flattened, rugulose. Chromosome number unknown. Fig. 29.

Phenology. Collected in flower in July and October through December; collected in fruit in March, July, October, and December. A peak of flowering and fruiting occurs in October.

Distribution (Fig. 18). Southeastern Brazil (Santa Catarina); sandy beaches along coast (*restinga* vegetation) and inland in pastures; 0–300 m.

Local names. Brazil: Baga de urubú (*Reitz & Klein 6770*); baga de bugre da praia (Smith & Downs 1966).

REPRESENTATIVE SPECIMENS. **Brazil.** SANTA CATARINA: Garopaba, *Eskuche 1251-11* (Z); Laguna, *Hatschbach & Kozicki 27529* (BH, C); Mpio. Laguna, Praia do Gi, *Hatschbach & Forero 40366* (BH, C, CTES, LL, NY, Z); Praia de Laguna, *Hoehne 24447* (US); Itajaí, Praia Braba, *Hunt 6360* (US); Pântano do Sul, Ilha de Santa Catarina, *Klein et al. 5817* (US); Pântano do Sul, *Klein & Bresolin 6289* (US); Morro das Pedras, *Klein & Bresolin 6386* (US); Garopaba, *Klein & Bresolin 8834* (US); Barra da Lagôa, Rio Vermelho, *Occhioni 5307* (F); Laguna, *Reitz & Klein 4* (US); Orleães, *Reitz 1732* (US); Campeche, Ilha Santa Catarina, *Reitz 5081* (US); Bom Retiro, Braco do Norte, *Reitz & Klein 6770* (NY, US); mainland opposite Desterro, *Ule s.n.* (HBG, US).

Solanum pelagicum can be distinguished by its often pinnately compound leaves with subcordate bases, stalked glands on the stem and inflorescence axes, stone cell aggregates in the fruits, and by its specialized habitat and restricted distribution. The dendritic hairs of this species are similar to those of *S. cylindricum*.

Smith and Downs (1966) distinguished between *C. cornigera* and *C. maritima* on the basis of leaf morphology and ecological characteristics. According to them, *C. cornigera* had pinnately compound leaves, whereas their new species *C. maritima* had simple or rarely few-lobed leaves. In reality, both variants occupy the same habitat and localities, and some specimens have both simple and pinnately compound leaves on the same plant, which argues against recognition as two separate taxa.

Smith and Downs (1966) describe the fruits as minutely pubescent, but this character was not obvious in the herbarium material I examined.

Three sheets of the type collection of *C. cornigera* Dunal (*Gaudichaud 160*) exist at P. Two are annotated by Dunal, and one of these has been chosen as the lectotype of this name.

Two sheets at US are annotated by Smith and Downs as "*C. maritima*-Type." One of them, #2423787, is here selected as the lectotype.

Solanum pelagicum occupies the unusual habitat of beach dune formations (*restinga*) along the coast of southeastern Brazil. The herbarium label of *Hunt 6360* indicates that the plants were collected "above the high water mark." Several other collectors noted finding this species along forest margins and cleared pastures. A new name is required because *S. cornigerum* and *S. maritimum* are already occupied. The epithet "pelagicum," from Greek *πελαγος* (sea) has been chosen in reference to the seaside habitat of this species.

13. *Solanum stuckertii* Bitter, Repert. Spec. Nov. Regni Veg. 12: 461. 1913. *Cyphomandra stuckertii* (Bitter) D'Arcy, Ann. Missouri Bot. Garden 59: 277. 1972.—
TYPE: ARGENTINA. Tucumán: Burreuyacú, 20 Apr 1910, *Stuckert 21589* (lectotype, here designated: G!; photo of lectotype, F neg. # 23159: F!; isolectotypes: CORD! GOET! [fragment]).

- Solanum stuckertii* var. *angustifrons* Bitter, Repert. Spec. Nov. Regni Veg. 12: 463. 1913.—TYPE: ARGENTINA. Córdoba: Los Cocos, Punilla, *Stuckert 16234* (lectotype, here designated: CORD!).
- Solanum stuckertii* var. *atrichostylum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 463. 1913.—TYPE: ARGENTINA. Tucumán: Burreyacú, 1 Apr 1900, *Stuckert 9138* (lectotype, here designated: CORD!; isolectotype: GOET! [fragment]).
- Solanum stuckertii* var. *trichostylum* Bitter, Repert. Spec. Nov. Regni Veg. 12: 463. 1913.—TYPE: ARGENTINA. Córdoba: Salto, Rio Tercero, *Stuckert 915a* (lectotype, here designated: CORD!; isolectotype: GOET! [fragment]).
- Solanum stuckertii* var. *obrutum* C. V. Morton, A Revision of the Argentine Species of *Solanum*, p. 192. 1976.—TYPE: ARGENTINA. Salta: Depto. La Viña, Coronel Moldes, ca. 1200 m, 2 Feb 1941, *Hunziker 1223* (holotype: US! #1804101).
- Solanum stuckertii* var. *pilosistylum* C. V. Morton, A Revision of the Argentine Species of *Solanum*, p. 193. 1976.—TYPE: ARGENTINA. Tucumán: Depto. Trancas, Vipos, 850 m, 9 Nov 1921, *Venturi 1424* (holotype: US! #1548854; isotype: GH!).

Shrub 0.3–3 (–7 fide *Venturi 5613*) m tall. Stems moderately to densely pubescent with unbranched eglandular hairs. Leaves 6—many per sympodial unit, the blades 3–15 (–25) cm long, (1–) 1.5–7 (–10) cm wide, length:width ratio ca. 1.7–3.5 (–6):1, simple, ovate to elliptic, acute to acuminate at apex, truncate, cuneate, or rounded to slightly decurrent at base, chartaceous, sparsely to moderately pubescent adaxially with curled unbranched uniseriate hairs, more densely so on veins, moderately to densely pubescent abaxially, the petioles 0.5–4 cm long, densely pubescent with unbranched hairs. Inflorescence unbranched or forked (rarely further branched), ca. 5–30-flowered, 2.5–10 cm long; peduncle 1–5 cm long; rachis 1.5–8 cm long; pedicels ca. 6–15 mm long, spaced 1–7 mm apart, articulated at the base; inflorescence axes sparsely to densely pubescent with eglandular unbranched hairs and occasionally with a few stalked glands. Calyx moderately to densely pubescent with eglandular hairs, the radius 3–6 mm, the lobes 1.5–3 mm long, 1.5–2 mm wide, often unequal, deltate, abruptly narrowed distally into acute or acuminate tips. Corolla white, chartaceous, stellate, the radius 10–19 mm, the tube 3–6 mm long, the lobes 7–15 mm long, 3–4 mm wide at base, narrowly triangular, acute at apex, moderately to densely pubescent abaxially with mostly unbranched hairs, glabrous adaxially except for a few hairs toward tips. Anthers usually connivent, yellow, lanceolate, 6–7 (–10) mm long, 1–2.5 mm wide, abaxial surface smooth to roughened but not obviously papillate, the pores directed distally. Ovary glabrous or sparsely puberulent at apex; style glabrous or sparsely to moderately pubescent, cylindrical to subclavate, 7–10 mm long, 0.5–1 mm in diameter; stigma truncate to subcapitate. Fruits 1–3 cm long, 1–3 cm in diameter, globose, obtuse at apex, glabrous, orange to reddish when ripe; stone cell aggregates present or absent. Seeds 3–5 mm long, 3–4 mm wide, angled, rugose-pubescent. Chromosome number: $n = 12$. Figs. 30, 31.

Phenology. Collected in flower in October through May; collected in fruit in October through August.

Distribution (Fig. 32). Southern Andes of Argentina (Catamarca, Córdoba, Jujuy, La Rioja, Salta, San Luis, Santiago del Estero, and Tucumán); clearings, thickets, and open woodland, often at the borders of streams, in relatively dry areas; 250–2000 m. Several specimens have also been collected in Bolivia in low-lying areas east of the Andean slopes in Chaco forest, and populations of *S. stuckertii* are to be expected from suitable habitats

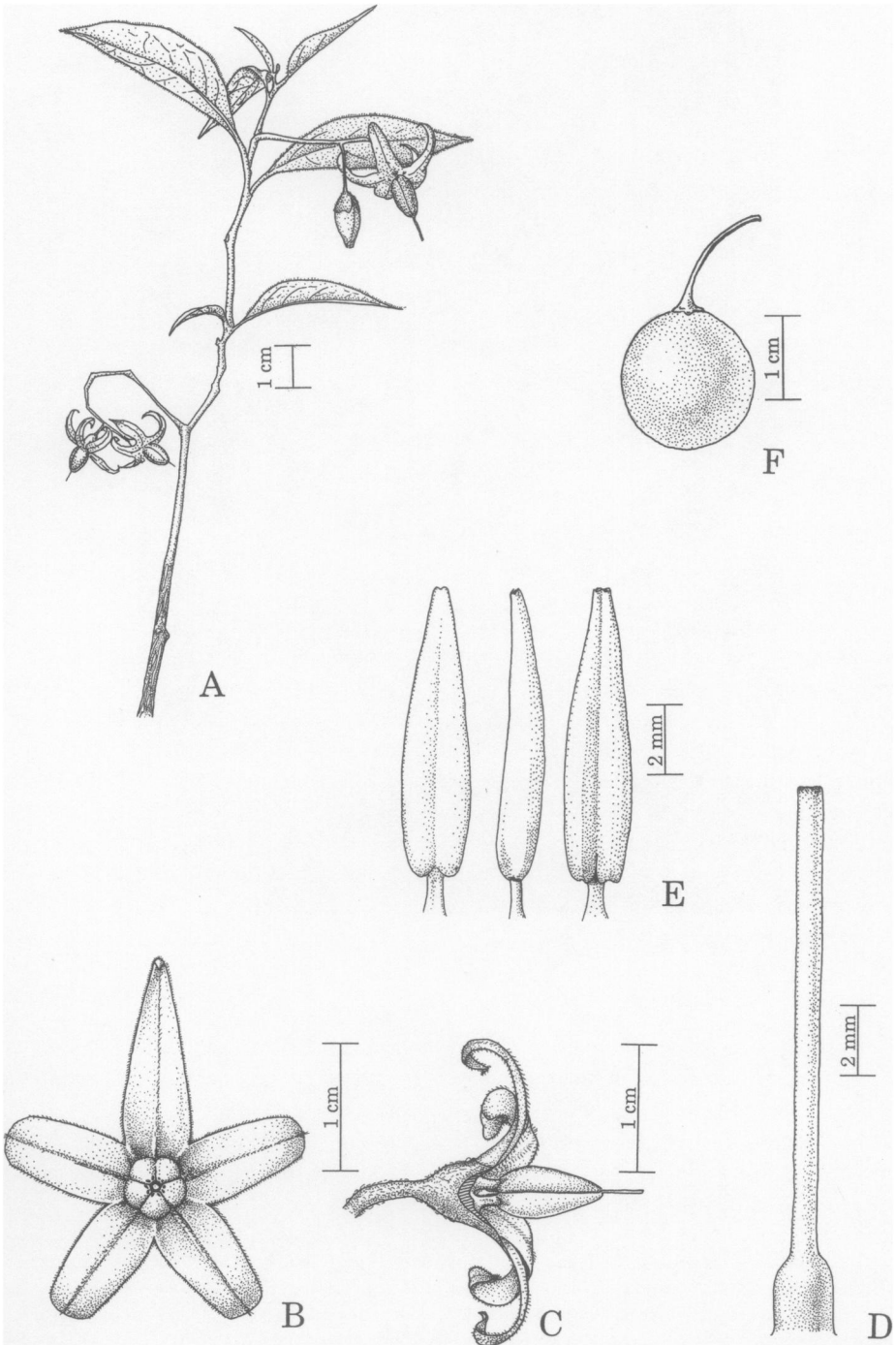


FIG. 30. *Solanum stuckertii*. A. Habit. B. Flower, seen from above. C. Lateral view of partially sectioned flower. D. Gynoecium. E. Stamen (left to right: abaxial, lateral, adaxial views). F. Fruit. (Based on greenhouse material of *Bohs* 2522.)

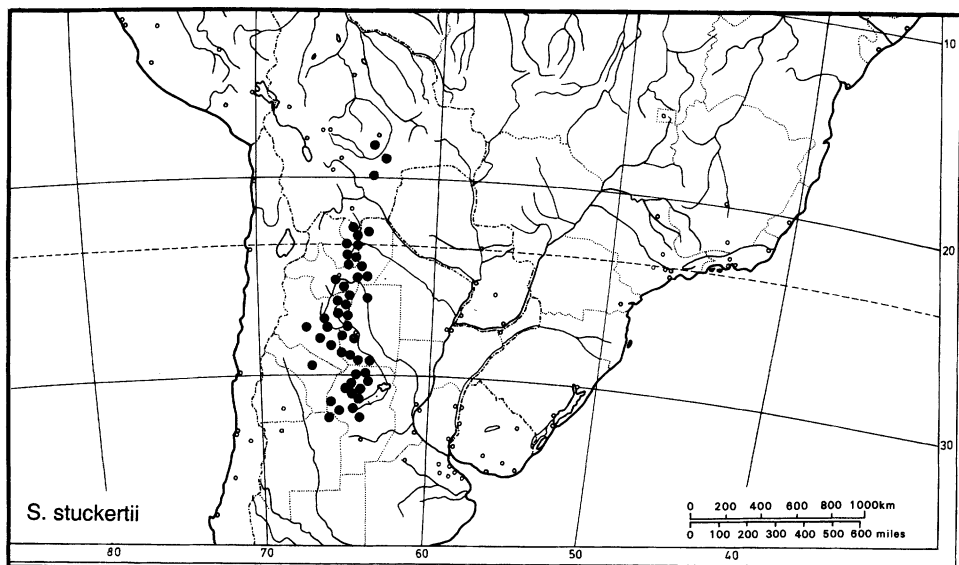


FIG. 31. Flowers of *S. stuckertii* with white, deeply stellate corollas; scale bar = 1 cm.

in intervening areas of southern and perhaps southeastern Bolivia. According to Cabrera (1983), this species is found in the phytogeographic provinces of Chaco forests and in the transition zone between the Chaco and Yungas provinces.

Local names. Bolivia: Malva (*Muñoz 565*), pereremi grande (*Vargas & Tapia 1055*). Argentina: Bolillos del perro (*Bartlett 20453*), comida de víbora (*Stuckert 9138*), duraznillo (*Villafañe 361*), hediondillo negro (*Schuel 36*).

REPRESENTATIVE SPECIMENS. **Bolivia.** CHUQUISACA: Prov. Luis Calvo, 2 km al NE de Prop. Inti, *Muñoz 565* (LPB).—SANTA CRUZ: Prov. Cordillera, *Cárdenas 2731* (F); Prov. Cordillera, Charagua, *Coimbra 336* (JBSC); Prov. Cordillera, La Brecha, Bañados de Izozog, alrededores del hospital y 3 km E camino hacia Río Parapetí, 19°35'S, 62°35'W, *I. Vargas & Tapia 1055* (NY, USZ). **Argentina.** CATAMARCA: Depto. Ancasti, El Potrero, *Brizuela 1113* (BH, G); Depto. Andalgalá, along Río Andalgalá, 4 km N of Andalgalá, *Cantino 669* (GH); Catamarca, *Lorentz & Hieronymus s.n.* (F); Depto. Andalgalá, Capillitas, *O'Donnell 4163* (B, G); Yacutula, *Schickendantz 162* (CORD); Carrizal de Augier, Villavil, *Schickendantz 297* (CORD); Depto. Belén, Sierra de Belén, Las Faldas, *Schreiter 35083* (GH); Depto. Belén, Quebrada de Belén, *Sleumer & Vervoort 2356* (G, US, W).—CÓRDOBA: Cuesta de Tala Cañada, cerca a Taninga, *Burkart 20832* (SI); San Javier, slope of Cerro

FIG. 32. Distribution of *S. stuckertii*.

Champaquí, *Fabris & Pérez Moreau* 6769 (LP); Depto. Punilla, Puerto Punilla, *Gutiérrez* 333 (BH, G, W); near city of Córdoba, *Hieronymus s.n.* (BR, NY); Depto. Santa María, Alta Gracia, banks of arroyo Alta Gracia, *Hunziker* 639 (US); La Falda, Río Grande, *Job* 480 (GH); Estancia Germania near Córdoba, *Lorentz* 15 (BM, GOET, W, WU), *Lorentz* 29 (BM, BR, G, GOET, M, W); cercanías de Córdoba, *Lorentz* 101 (CORD); Sierra Chica, *Lossen* 194 (BH, F, GH, M, Z); between Cosquin and Santa María, *Rodrigo* 395 (F); Pampa de Arhala, between La Posta and Mesillas, *Rodrigo* 486 (F); Depto. Capital, Puesto del Paraíso, *Stuckert* 843 (CORD); General Paz, *Stuckert* 1112 (CORD, G); Sierra Chica, *Stuckert* 2146 (CORD); prope Córdoba, *Stuckert* 5641 (G); Cruz de Eje, *Stuckert* 8246 (CORD); Sierra S. Miguel, *Stuckert* 8884a (CORD); falda de Mina Alnera, S. Alberto, *Stuckert* 10992 (CORD); Sierra de Córdoba, *Stuckert* 15196 (CORD, G); Depto. Punilla, Charbonier, *Villafañe* 361 (B, W).—JUJUY: Depto. Santa Bárbara, El Fuerte, *Cabrera et al.* 22208 (NY, US); Depto. Santa Bárbara, between Santa Clara and Abra de los Morteros, *Cabrera et al.* 23358 (LP, SI); Depto. Ledesma, Río de Las Piedras (NE de Yuto), *Fabris et al.* 3116 (LP, SI).—LA RIOJA: Huaco, *Burkart* 12584 (SI); Alto de Sanogasta, *Job de Francis* 1830 (GH).—SALTA: Joaquín V. Gonzales, *Aguilar* 211 (NY); Depto. Anta, camino San Severo a San Javier, *Del Costillo & Varela* 695, 699 (MCNS); Depto. Orán, Río Tarija on Bolivian border, S of Volcán, 50 km NE of Orán, *Eyerdam & Beetle* 22825 (BH, G, GH, MO); Depto. Anta, Río Dorado, 39 km NE of Las Lajitas, 24°25'S, 64°W, *Krapovickas & Schinini* 38643 (CTES); Depto. Rosario de la Frontera, between Balboa and Almirante Brown, *Legname & Cuezco* 7454 (GH); Pasaje del Río Juramento, *Lorentz & Hieronymus* 360 (F, GOET, US); Depto. Ledesma, between Chalicán and Ledesma, *de Marco et al.* 10225C (CTES); Depto. José de San Martín, Coronel Cornejo, *Maruñak et al.* 595 (G); Depto. Orán, El Tabacal, *Meyer* 4543 (F); Orán, El Tabacal, *Rodríguez* 1087 (NY); Depto. Anta, Joaquín V. González, *Varela* 29 (CORD); Depto. Orán, Abra Grande, *Venturi* 5613 (A, F, GH, K, SI, US); Depto. Guachipas, Alemania, *Venturi* 10001 (A, BM, F, GH, LP, US).—SAN LUIS: Merlo, Arroyo Piedra Blanca, *Gerth s.n.* (L).—SANTIAGO DEL ESTERO: S of Sumampa, *Bartlett* 19855 (F, GH, NY, SI, US); Depto. Choya, La Punta to Choya, *Bartlett* 20453 (F, GH, NY, SI, US); Sierra de San Luis, Quebrada del Tigre, Ruta 5, entre Santa Rosa y Bañado de Cautana, *Hunziker & Cocucci* 14877 (CORD); Depto. Ojo de Agua, Pozo Cavado, *Maldonado* 981 (LP); Depto. Río Hondo, Río Hondo—El Alto, *Ousset* 82 (GH); Depto. Pellegrini, Taco Pozo, *Peirano s.n.* (GH); Depto. Guasayán, El Cevilar, *Pierotti s.n.* (A, US); Depto. Pellegrini, La Armonia, Ruta 3, *Renolfi* 414 (CTES).—TUCUMÁN: Depto. Leales, Los Puestos, Ruta Nac. 9, *Krapovickas & Cristóbal* 17367 (CTES, LP); Vipos, *Lillo* 7284 (A, US, U); Tapia, *Rodríguez* 543 (A, CTES, SI); Cañada Alegre, Burreyacu, *Stuckert* 19328 (CORD); Depto. Leales, Santa Rosa, *Venturi* 633 (A, US); Depto. Cruz Alta, K. 754 C.N., *Venturi* 1603 (SI); Depto. Trancas, Vipos, *Venturi* 2366 (US); Depto. Trancas, Tapia, *Venturi* 5808 (GH, US); Depto. Burreyacu, Cerro del Campo, *Venturi* 7756 (GH, US).

Solanum stuckertii is most similar to *S. luteoalbum* and *S. hibernum*. All three species have stellate corollas and persistent showy orangish fruits with large angled seeds. *Solanum stuckertii* can be distinguished from *S. luteoalbum* by its indumentum of exclusively unbranched hairs and its white corollas. *Solanum stuckertii* is found in southern Bolivia to central Argentina, whereas *S. luteoalbum* occurs in Ecuador and Peru. *Solanum hibernum* differs in having purple corollas and a dense covering of dendritically branched hairs on the abaxial leaf surfaces. In Bolivia, *S. hibernum* is generally found in the arid vegetation of interandean valleys, whereas *S. stuckertii* occurs in lowland Chaco vegetation, and thus the two species may be separated by ecogeographic differences.

Bitter (1913) and Morton (1976) divided *S. stuckertii* into several varieties based mainly on leaf and flower size, styler pubescence, and number of flowers per inflorescence. All of these characters vary within the species; there is no justification for recognizing infraspecific taxa.

D'Arcy (1972) designated *Stuckert 21589* as the lectotype collection of *S. stuckertii* from among the many syntypes cited by Bitter (1913) in the protologue. He gave the location of the lectotype as "B?, not seen; photo NY"; this specimen is no longer extant. I have seen duplicates of *Stuckert 21589* at CORD, G, and GOET (a fragment) and a photo of the G specimen at F (neg. # 23159), but none at NY. Therefore, I amend D'Arcy's choice by designating the G specimen as the lectotype. Morton (1976) designated another of Bitter's syntypes, *Stuckert 5641* (G), as the lectotype of *S. stuckertii*, but D'Arcy's earlier choice must be followed under Art. 9.13 of the ICBN (Greuter et al. 2000). Bitter did not specify the herbarium location of the specimens he examined for his description of *S. stuckertii* and its varieties. Many of these sheets were likely at B and have been destroyed. Duplicates of some of these collections exist in other herbaria, such as GOET and CORD, and have been used to designate as lectotypes.

Specimens of *S. stuckertii* have sometimes been misidentified as *S. sordidum* Sendtn. The latter species belongs to *Solanum* subg. *Leptostemonum* and has the characteristic stellate hairs that usually occur in members of that subgenus.

DOUBTFUL AND EXCLUDED NAMES

Solanum clavatum Rusby, Mem. Torrey Bot. Club 6: 87. 1896. *Cyphomandra clavata* (Rusby) A. Child ex Bohs, Fl. Neotrop. Monogr. 63: 154. 1994.—TYPE: BOLIVIA. Cochabamba: Mt. Tunari, 1891, *Bang 1118* (E! NY! US!). = *Solanum aligerum* Schtdl.—*Bang 1118* is a mixture of two different species separated on different herbarium sheets. One element, represented by sheets at C, F, G, L, LD, M, NY, US, WU, and Z belongs to *Solanum confusum* of sect. *Cyphomandropsis* (q.v.). The other element is the basis of Rusby's *Solanum clavatum*. This name is a synonym of the widespread species *S. aligerum* Schtdl. of *Solanum* section *Holophylla* (Knapp, in press).

Solanum foetidum Ruiz & Pavón, Fl. peruv. 2: 39. 1799, non *Solanum foetidum* Rottbøll, 1778. *Solanum maleolens* J. F. Macbride, Publ. Field Mus. Nat. Hist., Bot. ser. 8: 111. 1930.—TYPE: PERU. "In Tarmae oppidi versuris et ruderatis, floret Julio et Augusto," Ruiz & Pavón s.n. (holotype: not located).—The application of Ruiz and Pavón's name is uncertain. The brief description is too vague to fix the name and not accompanied by an illustration; no authentic material is known. Dunal (1852) placed *S. foetidum* Ruiz & Pav. among members of *Solanum* sect. *Geminata* and postulated that

its affinities are with *S. caavurana* Vell. of that section; however, he included many disparate elements in his circumscription of *S. foetidum*. Macbride (1930) accepted *S. foetidum* Ruiz & Pav. as a species and, because the name is a later homonym, provided the new name *S. maleolens*. Subsequently, he considered it conspecific with *S. luteoalbum* but indicated in his discussion that more than one taxon may be included (Macbride 1962).

Solanum glaucescens Bacle ex Dunal in DC., Prodr. 13(1): 100. 1852, pro syn., non *Solanum glaucescens* Zuccarini, 1835.

Solanum lauterbachii (H. Winkler) Bitter, Repert. Spec. Nov. Regni Veg. 15: 155. 1918. *Cyphomandra lauterbachii* H. Winkler, Repert. Spec. Nov. Regni Veg. 7: 247. 1909.—TYPE: BOLIVIA. La Paz: San Antonio bei Mapiri, 850 m, Dec 1907, *Buchtien 1436* (holotype: WRSL; isotype: US!). = *Solanum corumbense* S. Moore.—Bitter (1918) assigns this species to *Solanum* sect. *Cyphomandropsis*, but its oblong anthers do not fit with the definition of this section. Instead, it belongs to sect. *Geminata* and is a synonym of *Solanum corumbense* S. Moore (S. Knapp, pers. comm.). Knapp (in press) notes that the flowers of *S. corumbense* superficially resemble those of *Solanum* sect. *Pachyphylla*.

Solanum narcoticum Bitter, Repert. Spec. Nov. Regni Veg. 13: 97. 1914.—TYPE: BOLIVIA. Toldos prope Bermejo, ca. 1900 m, 26 Nov 1903 (fl), *Fiebrig 2261* (holotype: B, destroyed; photos of holotype, Morton neg. 2717: F! G! NY!).—The description is not sufficient to assign the name with certainty, and no isotypes have been found. Possibly this name applies to *S. confusum*, but this cannot be ascertained from the photograph.

ACKNOWLEDGMENTS

I thank Solanaceae specialists G. Anderson, G. Bernardello, A. Child, W. G. D'Arcy, A. Hunziker, S. Knapp, R. N. Lester, E. Moscone, R. G. Olmstead, and D. Spooner for technical help, patience, and insight into many aspects of *Solanum* biology. Special thanks are due to Michael Nee for his unfailing support, vast knowledge, and invaluable assistance in the field. Financial support was provided by NSF grants DEB-9207359 and DEB-9726511, National Geographic Society Grant 6189-98, the University of Utah Research Committee, the University of Utah Bioscience Undergraduate Research Program, and the Department of Biology, University of Utah. Distribution maps were prepared from Flora Neotropica Base Map No. 1, ©University of Utrecht. I also thank A. Purgue for the line drawings; C. Christensen for help with the chromosome counts; C. Nepi at FI for information on possible types of *S. glaucophyllum*; the Botanic Garden at Nijmegen, the Netherlands, for providing *Solanum* seeds; the staff of the University of Utah greenhouses for maintaining my living collections; A. Kelsey of the Garrett Herbarium for help with herbarium loans; and C. Anderson, G. Bernardello, and D. Spooner for their comments on the manuscript. I also acknowledge the help and companionship of Bolivian colleagues S. Beck, F. Mamani, M. Moraes, Y. Roca, M. Saldías, and I. Vargas and Argentine botanists G. Bernardello, A. Cocucci, A. Hunziker, E. Moscone, L. Novara, and A. Sérsic for facilitating field work in South America. I thank the curators and staff of the following herbaria for providing me with access to their specimens and/or facilities: A, AAU, B, BH, BKL, BM, BR, C, COL, CR, CTES, DUKE, E, ECON, F, G, GB, GH, GOET, HBG, INB, K, L, LD, LIL, LL, LP, M, MA, MBM, MO, NY, RB, S, SI, SP, TEX, U, US, USM, UT, VIC, W, WIS, WU, and Z.

LITERATURE CITED

- Anderson, G. J., and P. G. Gensel. 1976. Pollen morphology and the systematics of *Solanum* section *Basarthrum*. *Pollen & Spores* 18: 533–552.
- Arumuganathan, K., and E. D. Earle. 1991. Nuclear DNA content of some important plant species. *Pl. Molec. Biol. Reporter* 9: 208–218.
- Bell, A. D., and T. D. Dines. 1995. Branching patterns in the Solanaceae. In *Experimental and molecular approaches to plant biosystematics*, ed. P. C. Hoch and A. G. Stephenson, 53: 157–171. St. Louis, Missouri: Missouri Botanical Garden.
- Bennett, M. D., and J. B. Smith. 1976. Nuclear DNA amounts in angiosperms. *Philos. Trans. Royal Soc. London, ser. B*, 274: 224–274.
- Bennett, M. D., J. B. Smith, and J. S. Heslop-Harrison. 1982. Nuclear DNA amounts in angiosperms. *Proc. Royal. Soc. London, ser. B*, 216: 179–199.
- Bertoloni, A. 1851. *Miscellanea Botanica Duodecima*. *Mem. Accad. Sci. Ist. Bologna* 3: 145–191, pl. 12–17.
- Bitter, G. 1913. *Solana nova vel minus cognita XII. XXXVII. Sectio Cyphomandropsis* Bitter, nov. sect. *Repert. Spec. Nov. Regni Veg.* 12: 461–467.
- _____. 1914. XXIX. *Solana nova vel minus cognita. XIV. Repert. Spec. Nov. Regni Veg.* 13: 88–98.
- _____. 1918. XXIII. *Solanaceae quattuor austro-americanae adhuc generibus falsis adscriptae*. *Repert. Spec. Nov. Regni Veg.* 15: 149–155.
- Bohs, L. 1989. *Solanum allophyllum* (Miers) Standl. and the generic delimitation of *Cyphomandra* and *Solanum* (Solanaceae). *Ann. Missouri Bot. Gard.* 76: 1129–1140.
- _____. 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.
- _____. 1994. *Cyphomandra* (Solanaceae). *Fl. Neotrop. Monogr.* 63: 1–175.
- _____. 1995. Transfer of *Cyphomandra* (Solanaceae) and its species to *Solanum*. *Taxon* 44: 583–587.
- Bohs, L., and R. G. Olmstead. 1997. Phylogenetic relationships in *Solanum* (Solanaceae) based on *ndhF* sequences. *Syst. Bot.* 22: 5–17.
- _____. 1999. *Solanum* phylogeny inferred from chloroplast DNA sequence data. In *Solanaceae IV: advances in biology and utilization*, ed. M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop, 97–110. Kew: Royal Botanic Gardens.
- _____. In press. A reassessment of *Normania* and *Triguera* (Solanaceae). *Pl. Syst. Evol.*
- Bonner, L. J., and H. G. Dickinson. 1989. Anther dehiscence in *Lycopersicon esculentum* Mill. I. Structural aspects. *New Phytol.* 113: 97–115.
- Brown, K. S., Jr. 1987. Chemistry at the Solanaceae/Ithomiinae interface. *Ann. Missouri Bot. Gard.* 74: 359–397.
- Cabrera, A. L. 1976. *Regiones fitogeográficas argentinas*. Buenos Aires: Editorial Acme.
- _____. 1983. Solanaceae. In *Flora de la provincia de Jujuy*, ed. A. Cabrera, 292–493. Buenos Aires: Instituto Nacional de Tecnología Agropecuaria.
- Cabrera, A. L., and E. M. Zardini. 1978. *Manual de la flora de los alrededores de Buenos Aires*. Buenos Aires: Editorial Acme.
- Child, A. 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.
- _____. 1998. Studies in *Solanum* and related genera (6). New infrageneric taxa for the genus *Solanum* L. (Solanaceae). *Feddes Repert.* 109: 407–427.
- Chodat, R. 1916. II. B. Géobotanique et Etude critique de quelques Solanées paraguayennes. *Bull. Soc. Bot. Genève, ser. 2*, 8: 142–160.
- Correll, D. S. 1962. *The potato and its wild relatives*. Renner, Texas: Texas Research Foundation.
- Cruden, R. W. 1977. Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32–46.
- Danert, S. 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. In "Flora of Panama," ed. R. E. Woodson and R. W. Schery. *Ann. Missouri Bot. Gard.* 60: 573–780.
- _____. 1974. *Solanum* and its close relatives in Florida. *Ann. Missouri Bot. Gard.* 61: 819–867.
- _____. 1991. The Solanaceae since 1976, with a review of its biogeography. In *Solanaceae III: taxonomy, chemistry, evolution*, ed. J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada-R., 75–137. Kew: Royal Botanic Gardens.
- Desfontaines, R. 1829. *Tableau de l'école de botanique*, 3rd ed. *Catalogus plantarum horti regii parisiensis*. Paris: J. S. Chaudé.
- Dottori, N. 1995. Desarrollo y estructura de fruto y semilla en *Solanum* sect. *Cyphomandropsis* (Solanaceae) de Argentina. *Kurtziana* 24: 83–104.
- Drummond, B. A., III, and K. S. Brown, Jr. 1987. Ithomiinae (Lepidoptera: Nymphalidae): summary of known larval food plants. *Ann. Missouri Bot. Gard.* 74: 341–358.
- Dunal, M. F. 1852. Solanaceae. In *Prodromus systematis naturalis regni vegetabilis*, ed. A. L. P. P. de Candolle, 13(1): 1–690. Paris: Victor Masson.
- Dusén, P. 1909. Beiträge zur Flora des Itatiaia. *Ark. Bot.* 9(5): 1–50.
- Edmonds, J. M. 1972. A synopsis of the taxonomy of *Solanum* sect. *Solanum* (*Maurella*) in South America. *Kew Bull.* 27: 95–114.
- _____. 1977. Taxonomic studies on *Solanum* section *Solanum* (*Maurella*). *Bot. J. Linn. Soc.* 75: 141–178.
- _____. 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*. *Bot. J. Linn. Soc.* 88: 237–251.
- Federov, A. 1974. *Chromosome numbers of flowering plants*. Koenigstein: Otto Koeltz Science Publishers.
- Gilli, A. 1970. Bestimmungsschlüssel der Subgenera und Sektionen der Gattung *Solanum*. *Feddes Repert.* 81: 429–435.
- Gracie, C. 1993. Pollination of *Cyphomandra endopogon* var. *endopogon* (Solanaceae) by *Eufriesea* spp. (Euglossini) in French Guiana. *Brittonia* 45: 39–46.
- Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland, and D. L. Hawksworth. 2000. International code of botanical nomenclature (St. Louis Code). *Regnum Veg.* 138: 1–474.
- Hallé, F., R. A. Oldeman, and P. B. Tomlinson. 1978. *Tropical trees and forests: an architectural analysis*. Berlin: Springer-Verlag.
- Hassler, E. 1918. XVIII. Solanacea paraguayensi critica vel minus cognita. *Repert. Spec. Nov. Regni Veg.* 15: 113–121.
- Hauser, E. J. P., and 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. 1990. *The potato: evolution, biodiversity, and genetic resources*. Washington, D.C.: Smithsonian Institution Press.
- Henderson, R. J. F. 1974. *Solanum nigrum* L. (Solanaceae) and related species in Australia. *Contr. Queensland Herb.* 16: 1–78.
- Killeen, T. J., E. García E., and S. G. Beck. 1993. *Guía de árboles de Bolivia*. St. Louis, Missouri: Missouri Botanical Garden.
- Knapp, S. 1989. A revision of the *Solanum nitidum* group (section *Holophylla* pro parte): Solanaceae. *Bull. Brit. Mus. Nat. Hist. (Bot.)* 19: 63–112.
- _____. In press. *Solanum* section *Geminata* s.l. [sections *Geminata*, *Pseudocapsicum*, *Holophylla* pro parte, and *Indubitaria* pro parte] (Solanaceae). *Fl. Neotrop. Monogr.*
- Kuntze, O. 1898. *Revisio generum plantarum*. Vol. 3(2). Leipzig: Arthur Felix.
- Lester, R. N., and P. Durrands. 1984. Enzyme treatment as an aid in the study of seed surface structures of *Solanum* species. *Ann. Bot.* 53: 129–131.
- Macbride, J. F. 1930. Peruvian Solanaceae. *Publ. Field Columbian Mus., Bot. Ser.* 8: 105–112.
- _____. 1962. Solanaceae. In "Flora of Peru," *Field Mus. Nat. Hist., Bot. Ser.* 13(5B, 1): 1–267.
- Miers, J. 1855. On the genera *Pionandra*, *Cliocarpus*, and *Paecilochroma*. *Pionandra*. *Ann. Mag. Nat. Hist., ser. 2*, 15: 196–200.
- Mione, T., and G. J. Anderson. 1992. Pollen-ovule ratios and breeding system evolution in *Solanum* section *Basarthurum* (Solanaceae). *Amer. J. Bot.* 79: 279–287.
- Morris, M. 1977. A drug from a disease-causing plant? *New Scientist* 73: 135–136.
- Morton, C. V. 1944. Some South American species of *Solanum*. *Contr. U.S. Natl. Herb.* 29: 41–72.

- _____. 1976. *A revision of the Argentine species of Solanum*. Córdoba, Argentina: Academia Nacional de Ciencias.
- Moscone, E. A. 1992. Estudios de cromosomas meióticos en Solanaceae de Argentina. *Darwiniana* 31: 261–297.
- Nee, M. 1999. Synopsis of *Solanum* in the New World. In *Solanaceae IV: advances in biology and utilization*, ed. M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop, 285–333. Kew: Royal Botanic Gardens.
- Nettancourt, D. de. 1977. *Incompatibility in angiosperms*. Berlin: Springer-Verlag.
- Okada, K. A., B. J. Carrillo, and M. Tilley. 1977. *Solanum malacoxylon* Sendtner: a toxic plant in Argentina. *Econ. Bot.* 31: 225–236.
- Olmstead, R. G., and J. D. Palmer. 1992. A chloroplast DNA phylogeny of the Solanaceae: subfamilial relationships and character evolution. *Ann. Missouri Bot. Gard.* 79: 346–360.
- _____. 1997. Implications for the phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. *Syst. Bot.* 22: 19–29.
- Olmstead, R. G., J. A. Sweere, R. E. Spangler, L. Bohs, and J. D. Palmer. 1999. Phylogeny and provisional classification of the Solanaceae based on chloroplast DNA. In *Solanaceae IV: advances in biology and utilization*, ed. M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop, 111–137. Kew: Royal Botanic Gardens.
- Pandey, K. K. 1959. Mutations of the self-incompatibility gene (S) and pseudo-compatibility in angiosperms. *Lloydia* 22: 222–234.
- Passarelli, L. M. 1999. Morphology, reserves, and pollen viability of some *Solanum* sect. *Cyphomandropsis* species. *Grana* 38: 284–288.
- Persoon, C. H. 1805. *Synopsis plantarum seu enchiridium botanicum*. Paris: C. F. Cramer.
- Poiret, J. L. M. 1814. *Encyclopédie methodique. Botanique. Supplément*, Vol. 3. Paris: H. Agasse.
- Pringle, G. J., and B. G. Murray. 1991. Karyotype diversity and nuclear DNA variation in *Cyphomandra*. In *Solanaceae III: taxonomy, chemistry, evolution*, ed. J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada-R., 247–252. Kew: Royal Botanic Gardens.
- Ratera, E. L. 1954. Número de cromosomas de *Solanum stuckertii* Bitter. *Bol. Soc. Arg. Bot.* 5: 153–154.
- Roe, K. E. 1967. Chromosome size in *Solanum* and *Cyphomandra*: taxonomic and phylogenetic implications. *Amer. Nat.* 101: 295–297.
- _____. 1971. Terminology of hairs in the genus *Solanum*. *Taxon* 20: 501–508.
- Ruiz, H., and J. A. Pavón. 1799. *Flora peruviana, et chilensis*. Madrid: Gabriel de Sancha.
- Sazima, M., S. Vogel, A. Cocucci, and G. Hauser. 1993. The perfume flowers of *Cyphomandra* (Solanaceae): pollination by euglossine bees, bellows mechanism, osmophores, and volatiles. *Pl. Syst. Evol.* 187: 51–88.
- 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*. In *The biology and taxonomy of the Solanaceae*, ed. J. G. Hawkes, R. N. Lester, and A. D. Skelding, 307–319. London: Academic Press.
- Sendtner, O. 1845. De *Cyphomandra*, novo Solanacearum genere tropicae Americae. *Flora* 28: 161–176.
- _____. 1846. Solanaceae. In *Flora brasiliensis*, ed. C. P. F. v. Martius, 10: 1–228. Munich: C. Wolf.
- Sleumer, H. 1957. Notas sobre la Flora Argentina. III. *Darwiniana* 11: 272–282.
- Smith, L. B., and R. J. Downs. 1964. Notes on the Solanaceae of southern Brazil. *Phytologia* 10: 422–453.
- _____. 1966. Solanáceas. In *Flora Ilustrada Catarinense*, ed. P. R. Reitz, 1–321. Itajaí, Brasil.
- Souèges, R. 1907. Développement et structure du tégument séminal chez les Solanacées. *Ann. Sci. Nat. Bot.*, ser. 9, 6: 1–124.
- Symon, D. E. 1979. Fruit diversity and dispersal in *Solanum* in Australia. *J. Adelaide Bot. Gard.* 1: 321–331.
- Vasconcellos-Neto, J. 1986. Interactions between Ithomiinae (Lepidoptera: Nymphalidae) and Solanaceae. In *Solanaceae: biology and systematics*, ed. W. G. D'Arcy, 364–377. New York: Columbia University Press.
- _____. 1991. Interactions between Ithomiine butterflies and Solanaceae: feeding and reproductive strategies. In *Plant-animal interactions: evolutionary ecology in tropical and temperate regions*, ed. P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, 291–313. New York: John Wiley and Sons, Inc.
- Vellozo, J. M. C. 1829. *Flora fluminensis*. Vol. 2. Rio de Janeiro.
- Wasserman, R. H. 1974. Calcium absorption and calcium-binding protein synthesis: *Solanum malacoxylon* reverses strontium inhibition. *Science* 183: 1092–1094.

APPENDIX 1

HERBARIUM VOUCHERS FOR SEM STUDIES OF POLLEN GRAINS

- S. amotapense*: Harling & Andersson 22510, NY.
S. confusum: Petersen & Hjerting 618, MO.
S. cylindricum: Hatschbach 15436, NY.
S. fusiforme: Hatschbach 40573, UT.
S. glaucophyllum: Arbo et al. 721, MO.
S. pelagicum: Hatschbach & Forero 40366, LL.

APPENDIX 2

VOUCHERS FOR CHROMOSOME AND CROSSING STUDIES

Solanum sect. *Cyphomandropsis*.

- S. amotapense*. Voucher: *Bohs* 2479 (UT). From seeds of *Hawkes* 2422, collected in Peru, Dept. Cajamarca, Prov. Cajabamba, valley of Condebamba (Birmingham seed accession S.43).
S. fusiforme. Voucher: *Moscone & Daviña* 218 (CORD). Collected in Argentina, Prov. Misiones, Dept. Libertador General San Martín, Ruta Nac. 12, Tres de Mayo.
S. glaucophyllum. Voucher: *Bohs* 2530 (UT). From seeds of *Hunziker and Pastoriza* 25304, collected in Argentina, Prov. Entre Ríos, Dept. Paraná, Paraná.
S. hibernum. Voucher: *Bohs* 2443 (UT). From seeds of *Nee s.n.*, collected in Bolivia, Dept. Santa Cruz, Mairana.
S. luteoalbum. Voucher: *Bohs* 2336 (GH). From seeds of *Hawkes et al.* 5416, collected in Peru, Dept. Cuzco, Prov. Calca, Pisac (Birmingham seed accession S.1543).
S. stuckertii. Voucher: *Bohs* 2522 (UT). From seeds of *Moscone* 122, collected in Argentina, Prov. Córdoba, Córdoba.—Voucher: *Bohs* 2523 (UT). From seeds of *Vargas* 1055, collected in Bolivia, Dept. Santa Cruz, Bañados del Izozog.

Solanum section *Pachyphylla*.

- S. betaceum* Cav. Voucher: *Bohs* 2274 (GH). From seeds of *Sperling s.n.*, collected in Ecuador, Pichincha, Quito, purchased in La Vincentina market.—Voucher: *Bohs* 1599 (GH). From seeds of *Bohs* 1599, collected in Colombia, Putumayo, valley of Sibundoy.—Voucher: *Bohs* 2468 (UT). From seeds of *Nee* 30359, collected in Bolivia, Cochabamba, purchased in Cochabamba market.
S. circinatum Bohs. Voucher: *Bohs* 2301 (GH). From seeds of *Buch s.n.*, collected in Colombia, Huila, Fundación Merenberg.—Voucher: *Bohs* 2442 (UT). From seeds of *Debouck et al.* 2948, collected in Colombia, Dept. Tolima, Chaparral.
S. corymbiflorum (Sendtn.) Bohs. Voucher: *Bohs* 2343 (GH). From seeds sent by G. Pringle, DSIR, New Zealand (NZ IP #27772), originally collected in southeastern Brazil, exact provenance unknown.
S. diploconos (Mart.) Bohs. Voucher: *Bohs* 2335 (GH). From seeds sent by A. Child, Yorkshire, England, originally collected in Brazil, Paraná, city of Curitiba.
S. diversifolium Dunal. Voucher: *Bohs* 2341 (GH). From seeds of *Benítez de Rojas* 2744, collected in Venezuela, Aragua, Parque Nacional Henri Pittier.
S. roseum Bohs. Voucher: *Bohs* 2338 (GH). From seeds of *Solomon & Escobar* 12458, collected in Bolivia, Dept. Nor Yungas, 8.7 km below Chuspipata on road to Yolosa.
S. unilobum (Rusby) Bohs. Voucher: *Bohs* 2284 (GH). From seeds of *Sperling & King* 5500, collected in Bolivia, Dept. La Paz, Larecaja, between Consata and Mapiri.

APPENDIX 3

CHROMOSOME NUMBERS IN SOLANUM SECT. CYPHOMANDROPSIS

References to previously published reports are cited in parentheses. Information on vouchers is given in Appendix 2.

- S. amotapense*: 2n = 24, voucher: *Bohs 2479*.
S. confusum: n = 12 (Moscone 1992).
S. fusiforme: 2n = 24, voucher: *Moscone & Daviña 218* (Moscone, pers. com.).
S. glaucophyllum: 2n = 24 (Federov 1974); n = 12 (Moscone 1992).
S. hibernum: 2n = 24, voucher: *Bohs 2443*.
S. luteoalbum: 2n = 24, voucher: *Bohs 2336*; 2n = 24 (Pringle & Murray 1991).
S. stuckertii: n = 12 (Ratera 1954; Moscone 1992).

APPENDIX 4

ACCESSIONS USED IN CROSSING STUDIES

Collection numbers in parentheses refer to vouchers listed in Appendix 2. Numbers in brackets refer to number of plants used, number of selfs/outcrosses attempted, number of fruit set containing viable seeds in selfs/outcrosses, pollen tubes in self pollinations growing into ovary (+) or inhibited in upper style (-), average pollen stainability of parents, compatibility (SC = self-compatible, SI = self-incompatible). nt = not tested.

INTRASPECIFIC CROSSES

- S. amotapense* (2479) [2, 11/0, 11/0, +, 98.0%, SC]
S. glaucophyllum (2530) [6, 31/28, 0/25, -, 76.0%, SI]
S. hibernum (2443) [4, 35/1, 1/0, -, 90.0%, SI]
S. luteoalbum (2336) [4, 31/68, 19/47, +, 73.0%, SC]
S. stuckertii (2522) [7, 14/15 0/10, -, 76.8%, SI]
S. stuckertii (2523) [2, 8/2, 0/2, nt, nt, SI]

CROSSES BETWEEN SPECIES OF SECT. CYPHOMANDROPSIS

The female parent is listed first. Numbers in brackets indicate number of crossing attempts, number of fruits set, number of fruits produced with full-sized seeds, F₁s produced (y) or not (n), pollen tube growth into ovary (+) or not (-) or not tested (nt).

- S. glaucophyllum* (2530) × *S. hibernum* (2443) [17, 9, 0, n, +]
S. glaucophyllum (2530) × *S. luteoalbum* (2336) [25, 0, 0, n, -]
S. glaucophyllum (2530) × *S. stuckertii* (2522) [17, 7, 0, n, +]
S. hibernum (2443) × *S. stuckertii* (2522) [2, 2, 2, y, nt]
S. luteoalbum (2336) × *S. glaucophyllum* (2530) [37, 29, 29, y, +]
S. luteoalbum (2336) × *S. hibernum* (2443) [22, 10, 0, n, +]
S. luteoalbum (2336) × *S. stuckertii* (2522) [19, 11, 6, n, +]
S. stuckertii (2522) × *S. glaucophyllum* (2530) [18, 8, 8, n, -]
S. stuckertii (2522) × *S. hibernum* (2443) [19, 10, 7, y, +]
S. stuckertii (2522) × *S. luteoalbum* (2336) [18, 0, 0, n, -]

CROSSES BETWEEN SPECIES OF SECT. CYPHOMANDROPSIS AND SECT. PACHYPHYLLA

Number in brackets indicate number of crossing attempts, number of fruits produced, pollen tube growth into ovary (+) or not (-) or not tested (nt). No seeds resulted from any of the following crosses.

- S. betaceum* (2468) × *S. glaucophyllum* (2530) [19, 5, +]
S. betaceum (2468) × *S. hibernum* (2443) [6, 0, -]
S. betaceum (2274) × *S. hibernum* (2443) [4, 0, +]

- S. betaceum* (1599) × *S. hibernum* (2443) [10, 0, nt]
S. betaceum (2468) × *S. luteoalbum* (2336) [12, 0, -]
S. betaceum (2274) × *S. luteoalbum* (2336) [9, 0, nt]
S. betaceum (2274) × *S. stuckertii* (2522) [3, 0, +]
S. circinatum (2301) × *S. glaucophyllum* (2530) [20, 0, +]
S. circinatum (2442) × *S. glaucophyllum* (2530) [14, 0, +]
S. circinatum (2301) × *S. hibernum* (2443) [10, 0, nt]
S. circinatum (2442) × *S. hibernum* (2443) [21, 0, +]
S. circinatum (2301) × *S. luteoalbum* (2336) [30, 0, -]
S. circinatum (2442) × *S. luteoalbum* (2336) [21, 0, -]
S. circinatum (2301) × *S. stuckertii* (2522) [15, 0, nt]
S. circinatum (2442) × *S. stuckertii* (2522) [18, 0, +]
S. corymbiflorum (2343) × *S. glaucophyllum* (2530) [20, 0, -]
S. corymbiflorum (2343) × *S. hibernum* (2443) [18, 0, -]
S. corymbiflorum (2343) × *S. luteoalbum* (2336) [20, 0, -]
S. corymbiflorum (2343) × *S. stuckertii* (2522) [20, 0, -]
S. diploconos (2335) × *S. glaucophyllum* (2530) [19, 0, +]
S. diploconos (2335) × *S. luteoalbum* (2336) [20, 0, -]
S. diploconos (2335) × *S. stuckertii* (2522) [0, 0, +]
S. diversifolium (2341) × *S. glaucophyllum* (2350) [10, 0, +]
S. diversifolium (2341) × *S. hibernum* (2443) [20, 0, -]
S. diversifolium (2341) × *S. luteoalbum* (2336) [23, 0, -]
S. diversifolium (2341) × *S. stuckertii* (2522) [20, 0, +]
S. glaucophyllum (2530) × *S. betaceum* (2468) [15, 7, +]
S. glaucophyllum (2530) × *S. betaceum* (2274) [5, 0, nt]
S. glaucophyllum (2530) × *S. circinatum* (2442) [16, 4, +]
S. glaucophyllum (2530) × *S. circinatum* (2301) [25, 5, +]
S. glaucophyllum (2530) × *S. corymbiflorum* (2343) [20, 2, +]
S. glaucophyllum (2530) × *S. diploconos* (2335) [20, 7, +]
S. glaucophyllum (2530) × *S. diversifolium* (2341) [24, 9, +]
S. glaucophyllum (2530) × *S. roseum* (2338) [4, 0, -]
S. glaucophyllum (2530) × *S. unilobum* (2284) [5, 0, +]
S. luteoalbum (2336) × *S. betaceum* (2468) [10, 0, +]
S. luteoalbum (2336) × *S. betaceum* (2274) [10, 0, nt]
S. luteoalbum (2336) × *S. circinatum* (2442) [24, 12, +]
S. luteoalbum (2336) × *S. circinatum* (2301) [20, 1, -]
S. luteoalbum (2336) × *S. corymbiflorum* (2343) [22, 0, +]
S. luteoalbum (2336) × *S. diploconos* (2335) [20, 4, +]
S. luteoalbum (2336) × *S. diversifolium* (2341) [21, 0, -]
S. luteoalbum (2336) × *S. roseum* (2338) [5, 0, +]
S. luteoalbum (2336) × *S. unilobum* (2284) [20, 0, +]
S. roseum (2338) × *S. glaucophyllum* (2530) [0, 0, +]
S. roseum (2338) × *S. luteoalbum* (2336) [0, 0, -]
S. roseum (2338) × *S. stuckertii* (2522) [0, 0, +]
S. stuckertii (2522) × *S. betaceum* (2468) [0, 0, +]
S. stuckertii (2522) × *S. circinatum* (2442) [0, 0, +]
S. stuckertii (2522) × *S. corymbiflorum* (2343) [0, 0, -]
S. stuckertii (2522) × *S. diversifolium* (2341) [0, 0, -]
S. unilobum (2284) × *S. glaucophyllum* (2530) [8, 0, +]
S. unilobum (2284) × *S. luteoalbum* (2336) [20, 0, -]

APPENDIX 5

DISTRIBUTION OF SPECIES OF SOLANUM SECT. CYPHOMANDROPSIS BY COUNTRY

Asterisks indicate species endemic to the country listed.

Colombia: *S. fallax*

Ecuador: *S. amotapense*, *S. fallax*, *S. luteoalbum*

Peru: *S. amotapense*, *S. hutchisonii**, *S. luteoalbum*

Brazil: *S. cylindricum*, *S. fusiforme*, *S. glaucophyllum*, *S. luridifuscens**, *S. matadori**, *S. pelagicum**

Bolivia: *S. confusum*, *S. glaucophyllum*, *S. hibernum**, *S. stuckertii*

Paraguay: *S. fusiforme*, *S. glaucophyllum*

Argentina: *S. confusum*, *S. cylindricum*, *S. fusiforme*, *S. glaucophyllum*, *S. stuckertii*

Uruguay: *S. glaucophyllum*

NUMERICAL LIST OF SPECIES

- | | |
|----------------------------|----------------------------|
| 1. <i>S. amotapense</i> | 8. <i>S. hutchisonii</i> |
| 2. <i>S. confusum</i> | 9. <i>S. luridifuscens</i> |
| 3. <i>S. cylindricum</i> | 10. <i>S. luteoalbum</i> |
| 4. <i>S. fallax</i> | 11. <i>S. matadori</i> |
| 5. <i>S. fusiforme</i> | 12. <i>S. pelagicum</i> |
| 6. <i>S. glaucophyllum</i> | 13. <i>S. stuckertii</i> |
| 7. <i>S. hibernum</i> | |

INDEX TO NUMBERED COLLECTIONS

The numbers in parenthesis refer to the corresponding species in the text and in the Numerical List of Species presented above.

- | | |
|--|--|
| Abbott, J. R., & A. Jardim 17232 (2). | Bodenbender, W. SI 26573 (13). |
| Acosta Solís, M. 7743 (1), 12847 (4). | Boeke, J. D., & S. Boeke 3173 (10). |
| Aguilar, R. M. 211 (13), 280 (13), 1212 (6). | Boelcke, O. 1396 (6). |
| Ahumada, O. 309 (6), 1653 (6), 1762 (6), 2021 (6), 2105 (6), 5316 (2). | Boelcke, O., et al. BAA-5888 (6), BAA-12613 (6). |
| Ahumada, O., & U. Eskuche 3498 (5). | Boffa, P. 133 (6), 1009 (13). |
| Ahumada, O., et al. 858 (6), 1449 (6), 3458 (6). | Bohs, L. 2336 (10), 2337 (10), 2443 (7), 2479 (1), 2522 (13), 2523 (13), 2530 (6). |
| André, E. 4450 (1). | Bohs, L., & M. Nee 2767 (6). |
| Arbo, M. M., et al. 721 (6), 6675 (6). | Bohs, L., et al. 2770 (7), 2776 (2), 2780 (2), 2790 (2), 2836 (2), 2844 (2). |
| Arechavaleta, J. 140 (6), 3057 (6). | Bordas, E. 4061 (6). |
| Arenas, P. 714 (6), 1407 (6), 1490 (6), 2000 (6). | Bornmüller, A. 384 (3). |
| Arroyo, L., et al. 931 (2). | Brade, A. C. 16604 (9), 16926 (9). |
| Bacle 43 (6). | Brizuela, J. 1113 (13). |
| Bailletti, E. 269 (2). | Brooke, W. M. A. 5947 (2), 6806 (2). |
| Balansa, B. 2105 (6). | Brown & Malmierca 1571 (2). |
| Balcazar, J. 385 (7). | Burkart, A. 7737 (13), 8727 (6), 12584 (13), 13219 (2), 20832 (13), 22103 (2). |
| Bang, M. 1118 (2, <i>S. aligerum</i>), 2618 (2). | Caballero Marmorì, G. 281 (5). |
| Bartlett, H. H. 19855 (13), 20453 (13). | Cabrera, A. 2795 (6), 13658 (2). |
| Beck, S. G. 14092 (2), 14665 (2), 17219 (2), 21830 (2), 24352 (2). | Cabrera, A., et al. 22208 (13), 23358 (13), 32059 (2). |
| Beck, S. G., & R. Seidel 14478 (2). | Cadifuerel, J. 1198 (2). |
| Bernardi, M. 18517 (6), 18835 (3). | Camargo 2101 (3), 2150 (3). |
| Billiet, F., & B. Jadin 3036 (6), 3244 (6). | Camp, W. H. E-4675 (10). |
| Birabén, M. 63 (6). | |

- Cano, A. 1557 (10).
 Cantino, P. 669 (13).
 Cárdenas, M. 2731 (13), 3260 (2), 5741 (2), 5773 (2), 5936 (2).
 Carter, G. F. 42 (6).
 Casas & Molero 4434 (6).
 Castro, R. BAB-52328 (6).
 Charpin, A., & U. Eskuche 20145 (6).
 Child, A. C9469 (1).
 Chodat, R. 32 (6), 33 (6), 34 (6), 35 (6), 36 (6).
 Cocucci, A. 36 (2).
 Coimbra, G. 336 (13), 601 (13), 1006 (6), 2320 (6), 2358 (2), 2618 (2), 2619 (2), 2893 (2).
 Cook, O., & G. Gilbert 387a (10), 804 (10).
 Cordini, R. 6 (6), 61 (6).
 Crespo, N. E. 132 (13).
 Cristóbal, C. L., et al. 1437 (6).
 Cuezco, A., et al. 11271C (6).
 Curtiss, A. H. 6862 (6).
 Dawson 663 (6).
 Del Costillo, A. de, & F. Varela 695 (13), 699 (13).
 DiFulvio, T. E. 473 (13).
 Dillon, M. O., & A. Sagástegui 6088 (10).
 Dionisi e Otavio 237 (9).
 Döbereiner, J. 820 (6).
 Döbereiner, J., & Tokarnia 687 (6), 690 (6), 699 (6), 717 (6), 794 (6), 797 (6), 800 (6).
 Dobremez, J. F. DBR Nep #616 (6).
 Dodson, C. H., & F. M. Valverde 6952 (4).
 Dodson, C. H., et al. 8731 (4).
 Dorr, L., et al. 6932 (2).
 Duarte, A. P., & J. Façao 3206 (12).
 Dusén, P. 2057 (9), 3056 (3), 7081 (3), 17508 (3).
 Eggers, H. 15069 (4).
 Ekman, E. L. 845 (5).
 Eskuche, U. 1251-11 (12).
 Eyerdam, W. J., & A. A. Beetle 22825 (13), 22974 (6), 23064 (6).
 Fabris, H. A., & R. L. Pérez Moreau 6769 (13).
 Fabris, H. A., et al. 3116 (13), 5038 (13).
 Felippone, F. 5947 (6).
 Ferreyra, R. 9141 (1).
 Fiebrig, K. 463 (6), 1249 (6), 2261 (2).
 Filipov, A. 110 (6).
 Flossdorf, A. 14 (6).
 Fortunato, R., et al. 2041 (6).
 Franceschi, E. A. 762 (6).
 Friedrichs 32880 (3).
 Fries, R. E. 1640 (6).
 Fuentes, A. 586 (6).
 Gallinal et al. A-831 (6).
 García, I. H. 30 (7), 71B (7).
 Gaudichaud, C. 160 (12), 1833 (6).
 Gentry, A. 30988 (4).
 Gentry, A., & R. Foster 75300 (6).
 Gentry, A., et al. 19785 (10).
 Giardelli, M. L. 878 (13).
 Gibert, M. 140 (6).
 Glaziou, A. 13084 (9).
 Gómez Sosa, E. 61 (6).
 Gutiérrez, J. 333 (13).
 Hahn, W. 671 (6).
 Harling, G., & L. Andersson 22510 (1).
 Harling, G., & B. Stahl 26473 (1).
 Hassler, E. 317 (6), 3201 (6), 7483 (6).
 Hatschbach, G. 8302 (9), 9668 (3), 15436 (3), 18384 (3, 5), 19384 (3), 19391 (3), 20327 (9), 22240 (9), 22933 (3), 23255 (3), 26472 (3), 38640 (6), 40573 (5), 43491 (3), 45519 (3), 48833 (3).
 Hatschbach, G., & E. Forero 40366 (12).
 Hatschbach, G., & O. Guimarães 21941 (6), 46879 (9).
 Hatschbach, G., & C. Kozicki 27529 (12).
 Hatschbach, G., & E. Pereira 10538 (3).
 Hatschbach, G., & da Silva 49222 (6).
 Haught, O., & H. K. Svenson 11634 (1).
 Hensen, I. 936 (2).
 Herrera, F. L. 921 (10), 3346 (10).
 Herter, W. 659 (6), 659a (6), 18512 (6).
 Hieronymus, G. 3057 (6).
 Hoehne, F. C. 24447 (12).
 Huber 111 (6).
 Huidrobo, A. R. M. 1452 (6), 3419 (6).
 Hunt, D. R. 6360 (12).
 Hunziker, A. T. 310 (6), 639 (13), 1223 (13), 6290 (13), 7630 (13), 7980 (13), 18957 (6), 19508 (2), 24871 (2), 25304 (6).
 Hunziker, A. T., & A. E. Cocucci 14877 (13).
 Hunziker, A. T., et al. 24857 (6), 25325 (13).
 Hutchison, P. 1490 (8).
 Hutchison, P., & J. Wright 3548 (1).
 Ibarrola, T. S. 890 (6), 3205 (6).
 Ibsch, P., et al. xx.ef1 (2).
 Iltis, H. H., & D. Ugent 1141 (10), 1213 (10).
 Iltis, H. H., et al. 221 (10), 222 (10), 528 (10), 582 (10), 584 (10), 589 (10), 591 (10), 601 (10), 736 (10), 923 (10).
 Irigoyen, J. 221 (6).
 Juárez, F. 2023 (2).
 Job, M. M. 480 (13), 737 (6).
 Job de Francis 1830 (13).
 Jönsson, G. 1009a (3).
 Jörgensen, P. 1472 (2), 2204 (6), 10788 (2).
 Kanehira, R. 79 (10).
 Kessler, M., & M. Kelschbach 233 (2).
 Kiesling, R., et al. 8295 (2).
 Klein & U. Eskuche 1-38 (3), 7-27 (3), 19-50 (3), 9058 (3).
 Klein, R., & A. Bresolin 6289 (12), 6386 (12), 8834 (12).
 Klein, R., et al. 5817 (12).
 Knapp, S., & J. Mallet 6465 (10).
 Knight, D. H. 673 (4).
 Krapovickas, A. 1711 (13).

- Krapovickas, A., & C. Cristóbal 12964 (6), 13196 (6), 17367 (13), 44389 (6).
- Krapovickas, A., & J. Irigoyen 17844 (6).
- Krapovickas, A., & A. Schinini 30853 (6), 38643 (13).
- Krapovickas, A., et al. 19897 (6), 26742 (6), 26861 (6), 27317 (6), 27503 (6), 27517 (6).
- Kuhlmann, M. 2597 (9).
- Kummrow, R., et al. 3067 (3).
- Legname, P. R., & A. R. Cuzzo 7454 (13), 8220 (2), 9938 (2).
- Lewis, M. 38693 (2), 38954 (2).
- Lillo, M. 4543 (2), 7284 (13).
- Lindeman, J. C., & J. H. de Haas 1355 (2), 2839 (3).
- Lindeman, J. C., et al. ICN # 21246 (3).
- Loefgren, A. 4421 (5), 5880 (9).
- López, A., & A. Sagástegui 7894 (1).
- López, A., & E. Saravia 427 (2).
- López, A., et al. 9089 (10).
- Lorentz, P. G. 15 (13), 29 (13), 101 (13), 101b (13), 180a (13), 323 (6), 1018 (6).
- Lorentz, P. G., & G. Hieronymus 360 (13), 568 (6).
- Lossen, W. 194 (13).
- Lotti, J. 86 (2).
- Lourteig, A., et al. 2678 (6).
- Luna, T. E. 555 (13).
- Luti, R. 4628 (13).
- Macbride, J. F. 3273 (10), 3795 (10).
- Macbride, J. F., & Featherstone 1038 (10).
- Macedo et al. 1209 (6).
- Madison, M., et al. 4972 (4).
- Maldonado, R. 981 (13), 1013 (13).
- Malme, G. A. 840 (6).
- Malvarez, M. R. 28 (13).
- Maranta & Arenas 153 (6).
- Marco, N. E. de, et al. 10225C (13).
- Marin 159 (10), 1872 (10).
- Marmol, L., & V. Núñez 5567 (2).
- Marmol, L., et al. 8773 (2).
- Martínez Crovetto, R. 1230 (6).
- Maruñiak, V., et al. 595 (13).
- Mereles, F. 163 (6), 704 (6), 1017 (6), 2592 (6).
- Mereles, F., & L. Ramella 2692 (6).
- Mexia, Y. 4039 (9), 4043 (9).
- Meyer, T. 4543 (13), 6458 (6), 10094 (6), 15442 (2), 15445 (2), 16374 (2), 18911 (2).
- Meyer, T., et al. 20370 (2).
- Montes, J. E. 1573 (5), 9500 (5), 10404 (5).
- Morel, I. 305 (6), 655 (6), 898 (6), 1158 (6), 1346 (6), 1624 (6), 1670 (6), 2286 (6), 2602 (6), 3592 (6), 3650 (6), 3739 (6), 4072 (6), 4910 (6), 5087 (6), 5174 (6), 5268 (6), 6566 (6).
- Morong 181 (6), 1530 (6).
- Morrone, O., et al. 799 (5), 2073 (5).
- Moscone, E. A., & G. Barboza 113 (6).
- Moscone, E. A., & J. R. Daviña 217 (5), 218 (5).
- Múñoz, T. 565 (13).
- Murquia, O. 502 (6).
- Navarro, G., & I. Vargas 346 (6).
- Navarro, G., et al. 19 (6).
- Nee, M. 25505 (6), 35186 (6), 35544 (7), 37532 (6), 38328 (7), 38389 (2), 38427 (2), 38546 (2), 40174 (6), 40633 (2), 46524 (7), 46611 (7).
- Nee, M., & G. Coimbra 33945 (7), 33950 (7), 33970 (7), 39996 (6).
- Nee, M., & J. Solomon 30226 (2), 34038 (2), 36559 (7), 36628 (2).
- Nee, M., & I. Vargas 38292 (2).
- Nee, M., et al. 36494 (2), 37398 (2), 37409 (2).
- Novara, L. 247 (2), 500 (6), 8171 (2).
- Novara, L., et al. 5567 (2).
- Núñez, P. 7137 (10), 7361 (10).
- Núñez, P., & E. Bengoa 8667 (10).
- Núñez, P., et al. 7040 (10).
- Núñez, V. 155 (2).
- Occhioni, P. 5307 (12).
- O'Donell, C. A. 70 (2), 4163 (13).
- Olea, D. 89 (2).
- Ortíz, F. I., & J. Jaramillo 140 (10).
- Ortíz, M. 510 (6).
- Osten, C. 5281 (6), 21883 (6).
- Osten, C., & Rojas 8262 (3).
- Ousset 82 (13), 106 (13).
- Pabst, G., & E. Pereira 6086 (11).
- Passarelli, L. M. 1 (6), 2 (6).
- Pedersen, T. M. 1045 (6), 2595 (6), 4198 (6).
- Penseiro, J., & G. Marino 4423 (6).
- Pereira, E. 5373 (5).
- Pérez, L., et al. 496 (6).
- Peter, A. 54 (6).
- Petersen, E., & J. P. Hjerting 565 (2), 618 (2).
- Piccinini, B., & J. Hilfer 4230 (6).
- Pierotti, S. 4063 (6), 4085 (6), 4157 (6).
- Pirani, J. R., et al. 164 (9).
- Pizarro, L. 91 (2).
- Plowman, T. 2724 (6).
- Plowman, T., & E. W. Davis 4913 (10), 5150 (2).
- Pohl, J. 3455 (9).
- Porto, P. C. 772 (9).
- Prance, G., et al. 26173 (6).
- Quarín, C. 590 (6), 3058 (6).
- Quarín, C., & A. Schinini 1044 (6).
- Quarín, C., & S. Tressens 1436 (6).
- Quarín, C., et al. 383 (6).
- Ragonese 2139 (6), 3255 (6).
- Rambo, B. 40302 (3), 45760 (3), 53509 (3).
- Reitz, R. 1732 (12), 5081 (12).
- Reitz, R., & R. Klein 4 (12), 6770 (12), 7053 (3), 7254 (11), 16873 (5).
- Renolfi, R. R278 (13), 414 (13).
- Renoize, S. A. 3546 (6).
- Rizzini 268 (9).
- Rodrigo, A. P. 395 (13), 486 (13), 994 (6).
- Rodríguez 111 (6), 464 (3), 543 (13), 745 (5).

- Rodríguez, D. 1087 (13).
 Rodríguez, V. 774 (6).
 Rojas, T. 318 (6), 13694 (6).
 Rotman, A. 944 (2).
 Sacco, J. da Costa 816 (6).
 Sagástegui, A. 5862 (8), 9614 (1).
 Sagástegui, A., et al. 15117 (10).
 Saint-Yves, A. 156 (6).
 Sánchez Vega, I. 3970 (8), 4220 (1).
 Santesson, R. 75 (6).
 Saravía, E., & A. López 1171 (2).
 Schaller 258 (6), 301 (6).
 Schiavone, M., et al. 11849 (2).
 Schickendanz, F. 162 (13), 165 (13), 288 (13), 297 (13).
 Schinini, A. 3919 (6), 5350 (6), 6721 (6), 9033 (6), 12611 (6), 13956 (6), 22746 (6), 26770 (6), 28827 (13).
 Schinini, A., & O. Ahumada 12666 (6).
 Schinini, A., & E. Bordas 13344 (6), 14871 (6), 17881 (6).
 Schinini, A., & C. Cristóbal 9870 (6).
 Schinini, A., & F. Mereles 24560 (6).
 Schinini, A., et al. 6915 (6), 9659 (6), 11059 (6), 11829 (6), 12048 (6), 16868 (6), 18929 (6).
 Schmeda, G. 192 (6), 706 (6).
 Schreiter 3387 (13), 10393 (2), 11214 (6), 35083 (13).
 Schreiter & O'Donell 35090 (2).
 Schuel 36 (13).
 Schulz, A. G. 2053 (6), 9033 (6), 11433 (2).
 Schulz, C. L. 62 (6).
 Schwabe, H. 558 (13).
 Schwarz 599 (6).
 Sehnem, A. 3859 (3), 4162 (3), 10884 (5).
 Sellow, F. 127 (6), 134 (3).
 Serrano, M., et al. 1299 (2), 1385 (2).
 Silva, J. S. 80 (6).
 Silverstone-Sopkin, P., & N. Paz 3581 (4).
 Silverstone-Sopkin, P., et al. 2606 (4).
 Skinner, N., et al. 15 (2), 30 (2).
 Slanis, A., et al. S124 (2).
 Sleumer, H. 1994 (13), 2094 (2), 3056 (2), 3067 (2).
 Sleumer, H., & F. Vervoort 2356 (13).
 Smith, L. B., & R. Klein 11572 (3), 12980 (3), 12982 (3).
 Smith, L. B., & R. Reitz 8956 (3), 9658 (5), 12457 (3).
 Smith, L. B., et al. 12322 (12).
 Soares, A. A. VIC 11.220 (9).
 Sodiro, L. 114/60 (4).
 Solomon, J. 3030 (10), 8694 (2), 9347 (2), 11274 (2), 12566 (2).
 Solomon, J., & M. Nee 17969 (2).
 Solomon, J., & A. Solomon 4026 (6).
 Soria, N. 4181 (6).
 Sota, E. de la 1739 (2).
 Soukup, J. 1180 (10), 2023 (10), 4531 (8).
 Sparre, B. 362 (6), 15248 (4), 17919 (4), 19484 (4).
 Sparre, B., & Vervoort 67 (6), 124 (6).
 Spegazzini, P. L. 33867 (13).
 Spegazzini, R. A. BAB 64608 (6).
 Steinbach, J. 8383 (2), 8384 (2), 8660 (2).
 Stork, H. E., & O. B. Horton 10711 (10).
 Stuckert, T. 843 (13), 915a (13), 1112 (13), 2146 (13), 5641 (13), 5923 (13), 8246 (13), 8884a (13), 9138 (13), 10992 (13), 12614 (13), 13093 (13), 13093a (13), 15196 (13), 16234 (13), 19328 (13), 21589 (13).
 Sucre, D., & P. Krieger 6664 (9).
 Terribile, M. 563 (6).
 Torres, I. 9 (6).
 Tressens, S. G., et al. 531 (6), 3580 (6).
 Ule, E. 4314 (9).
 Varela, F. 29 (13), 1520 (2).
 Varela, F., & A. del Castillo 1261 (2).
 Vargas, C. 200 (10), 686 (10), 9325 (10).
 Vargas, I. 518 (6), 3714 (2), 3718 (2).
 Vargas, I., & A. Jardim 3001 (2), 3017 (2).
 Vargas, I., & E. Tapia 1055 (13).
 Vargas, I., et al. 1362 (2), 1363 (2), 1935 (6), 1999 (7), 2514 (2), 3043 (2).
 Venturi, S. BAB 41593 (2), 76 (6), 312 (6), 633 (13), 1424 (13), 1451 (2), 1603 (13), 2366 (13), 3336 (2), 3922 (2), 4071 (2), 4589 (2), 5081 (2), 5158 (6), 5613 (13), 5688 (2), 5808 (13), 6337 (6), 7732 (2), 7756 (13), 9837 (2), 10001 (13).
 Vieira, M. F. 630 (9).
 Villafañe, M. 361 (13).
 Wall, E., & B. Sparre 31 (6, *S. boerhaavifolium* Sendtn.).
 Walter, H., & E. Walter 216 (6).
 Walter, M. 93 (6).
 Weberbauer, A. 7634 (1).
 Webster, G. L., & L. Hebert 27710 (4).
 Werdermann, E. 2625 (6).
 West, J. 6476 (10), 8448 (13).
 White, E. W. 96 (13).
 Wood, J. R. I. 8672 (2).
 Woolston, A. L. 937 (6).
 Zuloaga, F., et al. 5538 (5).

INDEX TO SCIENTIFIC NAMES

Accepted names are in Roman type; the main entry for each is in **boldface**. Synonyms are in italics.

Alnus

- acuminata 17, 27
 Antarctica fusca Esler 20
 Araucaria 19, 41
 Asteraceae 20
 Boraginaceae 20
 Capsicum
 baccatum L. 4
 Cyphomandra Mart. ex Sendtn. 3, 4, 5, 6, 7
 sect. *Allophylla* A. Child 6
 sect. *Ceratostemon* (Miers) A. Child 6
 sect. *Cornigera* A. Child 6, 7, 21
 sect. *Cyphomandra* 6
 sect. *Cyphomandropsis* (Bitter) D'Arcy 6, 7, 21
 sect. *Rhynchantherum* (Bitter) A. Child 6
 adelpa (C. V. Morton) A. Child ex Bohs 26
 amotapensis (Svenson) A. Child ex Bohs 23
 betacea
 var. *velutina* Dunal 5, 38
 clavata (Rusby) Bohs 72
 cornigera Dunal 21, 65, 67
 cylindrica (Vell.) Sendtn. 32
 elliptica (Vell.) Sendtn. 5, 32
 fusififormis (L. B. Sm. & Downs) A. Child ex Bohs 41
 glaberrima Dusén 57, 58
 hypomalaca Bitter 37, 40
 lauterbachii H. Winkl. 73
 luteoalba (Pers.) A. Child Bohs 58
 maritima L. B. Sm. & Downs 6, 65, 67
 stuckertii (Bitter) D'Arcy 67
 subhastata (L. B. Sm. & Downs) A. Child ex Bohs 32
 velutina Sendtn. 5, 20, 57
 villosa Steyererm. 24, 26, 58
 Jaltomata
 procumbens (Cav.) J. L. Gentry 4
 Lycianthes
 heteroclita (Sendtn.) Bitter 4
 Lycopersicon Mill. 14
 Mechanitis 20
 lysinnia lysinnia (Fabricius) 20
 polymnia casabranca Haensch 20
 Physalis
 alkekengi L. 4
 Pionandra Miers 5
 cornigera (Dunal) Miers 65
 cylindrica (Vell.) Miers 32
 elliptica (Vell.) Miers 32
 velutina (Sendtn.) Miers 57
 Solanaceae 5, 7, 20
 Solanoideae 8, 14

Solanum L. 21

- subg. *Archaeosolanum* Marzell 4
 subg. *Bassovia* (Aubl.) Bitter 4
 subg. *Leptostemonum* (Dunal) Bitter 3, 4, 6, 72
 subg. *Minon* Raf. 3, 4, 37
 subg. *Potatoe* (G. Don) D'Arcy 4, 6
 subg. *Solanum* 4, 5, 6, 50
 sect. *Acanthophora* Dunal 4
 sect. *Aculeigerum* Seithe 3, 4, 6
 sect. *Allophyllum* (A. Child) Bohs 3, 4, 6
 sect. *Anarrichomenum* Bitter 4
 sect. *Archaeosolanum* (Marzell) Danert 4
 sect. *Basarthrum* Bitter 15
 sect. *Brevantherum* Seithe 3, 4, 10
 sect. *Californisolanum* A. Child 4
 sect. *Cryptocarpum* Dunal 4
 sect. *Cyphomandropsis* Bitter 21–22
 sect. *Dulcamara* (Moench) Dumort. 4, 50
 sect. *Eriophylla* Dunal 4
 sect. *Extensum* D'Arcy 3, 4
 sect. *Geminata* (G. Don) Walp. 3, 4, 5, 10, 72, 73
 sect. *Glaucophyllum* A. Child 21, 50
 sect. *Holophylla* (G. Don) Walp. 3, 4, 9, 10, 32, 57, 72
 sect. *Jasminosolanum* Seithe 50
 sect. *Lasiocarpa* (Dunal) D'Arcy 4
 sect. *Leprophora* Dunal 4
 sect. *Lycopersicum* Wettst. 4
 sect. *Melongena* (Mill.) Dunal 4
 sect. *Micracantha* Dunal 4
 sect. *Normania* (Lowe) Bitter 4
 sect. *Nycterium* (Vent.) Dunal 4
 sect. *Pachyphylla* (Dunal) Dunal 3, 4, 6, 7, 9, 10, 12, 13, 14, 15, 16, 17, 18, 19, 20, 38, 43, 58, 73, 77, 78
 sect. *Parasolanum* A. Child 4
 sect. *Petota* Dumort. 14, 55
 sect. *Pseudocapsicum* (Moench) Bitter 3, 4, 10
 sect. *Pterodea* Dunal 4
 sect. *Solanum* 4, 14, 55
 sect. *Torva* Nees 4
 [unranked] *Anthoresis* Dunal 5
 [unranked] *Subdulcamara* Dunal 5
 abutiloides (Griseb.) Bitter & Lillo 4
adelpum C. V. Morton 6, 12, 26, 31, 32
adhaerens Roem. & Schult. 4
aligerum Schldtl. 32, 72
allophyllum (Miers) Standl. 3, 4, 6
amotapense Svenson 8, 9, 10, 12, 16, 17, 19, 23–26, 27, 41, 77, 78, 80
amygdalifolium Steud. 5, 50
angustifolium Lam. 50

- appendiculatum* Dunal 4
arboreum Dunal 4
argentinum Bitter & Lillo 4
aviculare G. Forst. 4
betaceum Cav. 4, 5, 77, 78, 79
brittonianum Morong 50
caavurana Vell. 73
campechiense L. 4
candidum Lindl. 4
catanduvae L. B. Sm. & Downs 6, 32, 37
circinatum Bohs 5, 77, 79
clavatum Rusby 3, 6, 32, 72
confusum C. V. Morton 6, 7, 8, 9, 10, 12, 13, 15, 16, 17, 19, 22, 23, 26–32, 50, 63, 72, 73, 77, 78, 80
cordovense Sessé & Moc. 4
cornigerum Dunal 5, 67
corymbiflorum (Sendtn.) Bohs 10, 15, 77, 79
corumbense S. Moore 73
cylindricum Vell. 5, 6, 8, 9, 10, 12, 16, 17, 19, 23, 32–37, 67, 77, 80
diploconos (Mart.) Bohs 15, 42, 77, 79
diversifolium Dunal 15, 77, 79
dulcamara L. 4, 57
elaeagnifolium Cav. 4
ellipticum R. Br. 32
ellipticum Vell. 5, 32, 37
fallax Bohs 5, 7, 9, 10, 12, 16, 17, 19, 23, 27, 37–41, 80
foetidum Rottb. 72
foetidum Ruiz & Pav. 72, 73
fusifforme L. B. Sm. & Downs 6, 8, 9, 12, 13, 16, 17, 19, 22, 41–43, 50, 57, 65, 77, 78, 80
glaucescens Bacle ex Dunal 73
glaucescens Zucc. 73
glaucophyllum Desf. 4, 5, 6, 7, 8, 9, 10, 12, 13, 15, 16, 17, 18, 19, 20, 21, 22, 23, 31, 36, 43–51, 77, 78, 80
glaucum Bertoloni 43, 44
glaucum Dunal 5, 43, 44, 50
glaucum Rojas 43, 44
graveolens Bunbury 6
handelianum Morong 50
hazenii Britton 10
hibernum Bohs 7, 8, 9, 12, 15, 16, 17, 19, 23, 31, 51–55, 63, 72, 77, 78, 79, 80
hutchisonii (J. F. Macbr.) Bohs 6, 8, 9, 16, 17, 19, 22, 24, 27, 55–57, 80
hypomalacum (Bitter) C. V. Morton 37
iraniense L. B. Sm. & Downs 6, 32, 37
jamaicense Mill. 4
johannae Bitter 3, 32
laciniatum Aiton 4
lauterbachii (H. Winkl.) Bitter 5, 73
luridifuscescens Bitter 3, 5, 10, 16, 17, 19, 20, 23, 26, 43, 57–58, 59, 65, 80
lutealbum Pers. 4, 6, 7, 8, 9, 11, 12, 14, 16, 17, 19, 23, 31, 53, 54, 55, 58, 60–64, 72, 73, 77, 78, 79, 80
var. tunya J. F. Macbr. 6, 58, 64
lycopersicon L. 4
macrocarpon L. 4
malacoxylon Sendtn. 5, 43
var. albo-marginatum Chodat 44
var. angustissimum Kuntze 44
var. genuinum Hassl. 43
var. latifolium Kuntze 44
var. subvirescens Hassl. 44
f. albo-marginatum (Chodat) Hassl. 44
f. vulgare Hassl. 44
subf. angustissimum (Kuntze) Hassl. 44
maleolens J. F. Macbr. 72, 73
mammosum L. 4
maritimum Meyen ex Nees 65, 67
matadori L. B. Sm. & Downs 6, 8, 9, 16, 17, 19, 22, 36, 43, 50, 64–65, 80
melanoxylo 44
melissarum Bohs 42, 58
melongena L. 4
narcoticum Bitter 5, 73
nigrum L. 21
nitidum Ruiz & Pav. 4, 9, 57
var. hutchisonii J. F. Macbr. 6, 55, 57
palitans C. V. Morton 4
pelagicum Bohs 5, 6, 8, 9, 12, 13, 16, 17, 19, 21, 23, 36, 43, 65–67, 77, 80
persicifolium Mart. 50
physalifolium Rusby 4
pinetorum (L. B. Sm. & Downs) Bohs 10, 20, 42
ptychanthum Dunal 4
pubescens Ruiz & Pav. 4, 58, 64
pubescens Willd. 58
roseum Bohs 15, 77, 79
sciadostylis (Sendtn.) Bohs 43
semicoalitum Bitter 3, 5, 58, 64
sordidum Sendtn. 72
stuckertii Bitter 3, 5, 7, 9, 10, 12, 13, 15, 16, 17, 18, 19, 20, 21, 23, 31, 53, 55, 63, 67–72, 77, 78, 79, 80
var. angustifrons Bitter 68
var. atrichostylum Bitter 68
var. obrutum C. V. Morton 68
var. pilosistylum C. V. Morton 68
var. trichostylum Bitter 68
subhastatum L. B. Sm. & Downs 6, 32, 37
torvum Sw. 4
tripartitum Dunal 4
trisectum Dunal 4
trizygum Bitter 4
unilobum (Rusby) Bohs 15, 77, 79
velutinum Dunal 57, 58
vespertilio Aiton 4
villosum Mill. 4
wallacei (A. Gray) Parish 4, 57
wendlandii Hook. f. 3, 4, 6
Triguera osbeckii (L.) Willk. 4
Witheringia solanacea L'Hér. 4