

The Systematics of *Solanum* Section *Allophyllum* (Solanaceae)

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THE SYSTEMATICS OF  
*SOLANUM* SECTION  
*ALLOPHYLLUM*  
(SOLANACEAE)<sup>1</sup>

Lynn Bohs<sup>2</sup>

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ABSTRACT

Three species of *Solanum* are included in a new section, *Solanum* sect. *Allophyllum*. Two of the species, *S. allophyllum* and *S. mapiriense*, have been previously known; the third, *S. morellifolium* Bohs, is described as new. The combination of characters exhibited by members of this section, such as unbranched hairs, 2–3-leaved sympodial units, simple leaves with decurrent bases, and tapered anthers, is unique to this group and does not agree well with any existing subgenus of *Solanum*.

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A group of three species first attracted my attention during monographic work on the solanaceous genus *Cyphomandra* Sendtn. *Solanum allophyllum* (Miers) Standl., the most widespread and best-known species of the section, had been placed by various workers in *Cyphomandra* and in *Solanum*. Determination of the true affinities of this species entailed an examination of the validity of the characters separating the two genera. An account of the morphology of this species and its resultant exclusion from *Cyphomandra* is given in a separate paper (Bohs, 1989).

Bitter (1914) first noted the similarities between *S. allophyllum* (his *S. ellipsoideibaccatum* Bitter) and *S. mapiriense* Bitter (his *S. phytolaccoides* (Rusby) Bitter), but he did not create a formal taxonomic category to include them. Child (1984) erected sect. *Allophylla* to contain these two species and regarded the new section as belonging to *Cyphomandra* rather than to *Solanum*. He also surmised that *Cyphomandra chlorantha* Rusby belonged to sect. *Allophylla*, but Bohs (1986) confirmed that it belongs in *Cyphomandra* and that it has no close relationship to *S. allophyllum* or *S. mapiriense*. A recent analysis of *S. allophyllum* (Bohs, 1989) indicates that this species should be placed in *Solanum* instead of *Cyphomandra*. Accordingly, sect. *Allophylla* is here removed from *Cyphomandra* and placed in *Solanum*.

All three species of *Solanum* sect. *Allophyllum* share the following combination of characters: (1) upright herbs or shrubs (up to 2 m tall); (2) 2–3-

leaved sympodial units; (3) vegetative parts densely covered with “sand-punctae” (idioblasts containing crystal sand); (4) membranaceous leaf blades, usually with decurrent bases and winged petioles; (5) unbranched, few-flowered, relatively short inflorescences; (6) flowers with usually white or greenish white membranaceous corollas; (7) stamens with glabrous filaments, distally tapered anthers, and very small terminal pores; (8) glabrous, filiform styles with small truncate stigmas; and (9) glabrous, globose to ellipsoidal fruits with obtuse apices. Additional characters may further distinguish the section, but these are as yet imperfectly known for all three species. For instance, *S. allophyllum* and *S. mapiriense* have light-colored corollas and anthers both with darker spots at the base, but such spots have not been observed in *S. morellifolium*. Also, the fruits of *S. allophyllum* have a distinctive color and shape, being white to light orange marked with dark green or purple longitudinal stripes and being ovoid to ellipsoidal in outline but flattened on opposite sides (Bohs, 1989). The color and shape of mature fruits of *S. mapiriense* and *S. morellifolium* are unknown.

Most of the character states that define sect. *Allophyllum* are found in many other sections of *Solanum* and are probably plesiomorphic. These include (1) herbaceous habit; (2) exclusively simple, unbranched hairs; (3) absence of prickles; (4) presence of sand-punctae; (5) cuneate and decurrent leaf bases; (6) glabrous filaments; (7) glabrous, filiform styles with small truncate stigmas; (8) gla-

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<sup>1</sup> I thank the herbaria listed for loans of specimens, M. Nee, W. G. D’Arcy, and S. Knapp for helpful discussions and specimens, Julie Mitchell for the illustration of *S. morellifolium*, and G. McPherson for helping me search, albeit unsuccessfully, for *S. allophyllum* in Panama.

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brous, obtuse fruits; (9) stone granules in the fruits; and (10) small, flattened seeds. Probable derived character states manifested by members of the section include (1) tapered anthers with small terminal pores; (2) 2–3-leaved sympodial units; and (3) self-compatible breeding system (known only for *S. allophyllum*). The evolutionary significance of the laterally compressed fruits seen in *S. allophyllum* (and possibly present in the other two species) is uncertain, but compressed fruits occur in other subgroups of *Solanum*, such as the subgenera *Potatoe* (G. Don) D'Arcy and *Bassovia* (Aubl.) Bitt. The distribution of flattened fruits among other solanaceous genera is unknown to me. Perhaps this character is relatively insignificant taxonomically and may be related to the enlargement of the ovary wall and septum during fruit development.

In summary, sect. *Allophyllum* seems to combine a host of primitive features with a few seemingly derived character states, most notably tapered anthers.

#### PLACEMENT OF THE SECTION WITHIN *SOLANUM*

*Solanum* is one of the largest genera of flowering plants, containing an estimated 1,500 species (D'Arcy, 1979; Hunziker, 1979). Substantial taxonomic problems still exist with regard to *Solanum* and related genera. At present, *Solanum* is loosely defined and consists of plants with poricidally dehiscent anthers that lack the specialized features of associated segregate genera, such as enlarged anther connectives in *Cyphomandra* Sendtn., sterile anther beaks in *Lycopersicon* Mill., and distinctive calyx morphology in *Lycianthes* (Dun.) Hassl. Although each of these segregate genera may be monophyletic, monophyly has not been established for *Solanum*. Poricidal anther dehiscence may have evolved more than once in *Solanum* and its allies, and may thus not be a synapomorphy uniting these taxa. Certainly our understanding of phylogenetic relationships within *Solanum* is hampered by the lack of basic taxonomic and morphological information for many subgenera and sections within the genus. It seems inevitable that *Solanum* will be broken up into smaller monophyletic genera, but taking such a step now would be premature based on our current state of knowledge. The infrageneric classification of *Solanum* and the boundaries between *Solanum* and its related genera have not been firmly established, and the taxonomy of this group is likely to remain in a state of flux for many years to come.

The placement of sect. *Allophyllum* in *Solanum*

is enigmatic. No existing group in *Solanum* has the combination of tapered anthers, simple hairs, upright habit, simple leaves, and spinelessness seen in sect. *Allophyllum*. In fact, the anthers of this group resemble those of some species of *Lycianthes*, but sect. *Allophyllum* does not have the truncate calyx with subapical lobes, reduced inflorescences, and large stone cell aggregates in the fruits that distinguish *Lycianthes* (D'Arcy, 1986). Section *Allophyllum* may represent a new genus with characters intermediate between *Solanum* and *Lycianthes*, but no synapomorphies are known that distinguish sect. *Allophyllum* from *Solanum*. Given the possible polyphyly, or at least paraphyly, of *Solanum*, sect. *Allophyllum*, differentiated on the basis of a combination of characters but with no obvious synapomorphies, must be placed in *Solanum*. Further work on generic limits between *Solanum* and its allies will undoubtedly shed light on the proper generic placement of this section. Additional problems surface when the affinities of sect. *Allophyllum* within *Solanum* are considered, because the infrageneric classification scheme in *Solanum* leaves much to be desired.

Several attempts have been made to divide *Solanum* into subgenera and sections (e.g., Dunal, 1852; Seithe, 1962; Gilli, 1970; Danert, 1970; D'Arcy, 1972). The most widely used recent scheme is that of D'Arcy (1972), who accepted seven subgenera of *Solanum*, in a classification with basic elements derived from earlier literature. I will refer exclusively to his classification in the discussion below.

Although many well-defined sections can be discerned within *Solanum*, the circumscription of subgenera is more problematic. Most of the subgenera consist of one or several well-defined or well-studied sections along with a number of sections whose affinities are less certain. Thus, D'Arcy's subgenera are often clearly defined with respect to one or a few component sections, but the boundaries between the subgenera are less clear when all the associated sections are considered.

The large number of species in *Solanum* and the relative paucity of adequate taxonomic treatments for many infrageneric groups hampers understanding the genus. Because I lack the facilities for an exhaustive survey of morphology and variation in the entire genus, it is possible that I have overlooked existing groups in *Solanum* that might be allied with sect. *Allophyllum*. Nevertheless, I will attempt to enumerate the possibilities for placement of sect. *Allophyllum* within the existing subgenera of *Solanum* as I understand them.

Section *Allophyllum* probably does not belong to the subgenera *Archaeosolanum* Marz. (aneu-

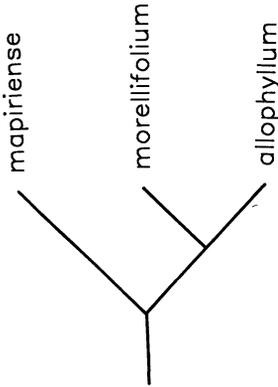


FIGURE 1. Hypothesis of phylogenetic relationships in *Solanum* sect. *Allophyllum*.

ploid-polyploid South Pacific species), *Lyciosolanum* Bitt. (restricted to a single South African species, *S. aggregatum* Jacq., with sessile inflorescences, short shoots, and very long filaments), or *Brevantherum* (Seithe) D'Arcy (exemplified by sect. *Brevantherum* Seithe, which contains species with entire leaves, elliptic to oblong anthers with blunt apices, and stellate hairs).

Bitter (1913) and Morton (1944) postulated an alliance of *S. allophyllum* with subg. *Leptostemonum* (Dun.) Bitt. because both groups have tapered anthers with small terminal pores. Such a relationship is doubtful, however, because all species of sect. *Allophyllum* lack the stellate hairs and prickles characteristic of subg. *Leptostemonum*.

Members of sect. *Allophyllum* resemble vegetatively those of sect. *Solanum* of subg. *Solanum* and have often been identified as members of sect. *Solanum* in herbaria. Both sections contain herbaceous plants with ovate to ellipsoidal leaf blades having decurrent bases; usually extra-axillary, relatively few-flowered inflorescences with an obvious peduncle; and often small aggregates of stone cells in the fruits. The lobed leaves of *S. allophyllum* also resemble those of *S. dulcamara* L., which D'Arcy placed in subg. *Potatoe* (G. Don) D'Arcy but which probably belongs to subg. *Solanum*. However, all species of subg. *Solanum* have oblong to ellipsoidal anthers that dehisce by large terminal pores opening into longitudinal slits rather than the tapered anthers with small pores that characterize sect. *Allophyllum*. Thus the resemblance of sect. *Allophyllum* to members of subg. *Solanum* appears to be superficial and based only on vegetative characters.

Section *Allophyllum* is not easily accommodated in subg. *Potatoe*. Although some members of this subgenus have more or less tapered anthers, they are also dehiscent by large terminal pores that

frequently develop into longitudinal slits. Many species of this group have twining stems and pinnately compound leaves, and self-incompatibility is common. None of these attributes suggests a relationship with sect. *Allophyllum*.

The remaining subgenus, subg. *Bassovia*, also does not appear to be a good candidate. Most members of this group have stout anthers with large apical pores that later open into longitudinal slits, and inflorescences located in leaf axils. These characteristics are not seen in sect. *Allophyllum*. Tapered anthers occur in *S. reptans* Bunb. of the monotypic sect. *Herposolanum* Bitt., but they open by longitudinal slits, and this species has no further morphological resemblance to sect. *Allophyllum*. (The inclusion of *Solanum reptans* in subg. *Bassovia* is itself doubtful.) Laterally compressed fruits occur in some species of this subgenus, but so little is known of the distribution and development of this character that it is not possible to determine whether this is an important link between sect. *Allophyllum* and subg. *Bassovia*.

The preceding considerations indicate that sect. *Allophyllum* does not fit well into any of the existing subgenera of *Solanum*. The group certainly deserves sectional rank, but given the problems already noted for its placement at both the generic and infrageneric levels, I am hesitant to create a new subgenus for it now.

#### INFRASECTIONAL RELATIONSHIPS

Within the section, *S. allophyllum* is most likely the most advanced species, exhibiting a suite of possible derived characters, such as pinnately lobed leaves, inflorescences situated in branch forks, rotate-stellate corollas, and large, ellipsoidal fruits. *Solanum mapiriense* may be the most primitive element of the section, exhibiting none of the derived features mentioned above for *S. allophyllum*. *Solanum morellifolium* shares with *S. allophyllum* few-flowered inflorescences, rotate-stellate corollas, and small ovate-elliptic leaf blades; on the other hand, *S. morellifolium* resembles *S. mapiriense* by having extra-axillary inflorescences, small globose fruits, and by lacking pinnately lobed leaves. The presence of gland-tipped finger hairs (unbranched multicelled stalks with a unicelled glandular tip) on the stems and inflorescences of *S. mapiriense* and some collections of *S. morellifolium* may be an indication of the relatively primitive status of these species, for gland-tipped finger hairs are thought by Seithe (1979), based on her ontogenetic studies, to be the most primitive hair type in *Solanum*. Finger hairs (without glandular tips) and multicellular glands (unicelled stalks with mul-

ticelled glandular tips) are the hair types found on the mature foliage and stems of *S. allophyllum*.

A preliminary hypothesis of the relationships among these three species is given in Figure 1. This should be interpreted only as a hypothesis for further examination and testing. A rigorous cladistic analysis can be attempted only when the proper placement of sect. *Allophyllum* within *Solanum* is known, when further information is gathered for many of the poorly characterized groups within the genus, and when appropriate hypotheses can be made concerning character polarity within and among the various lineages of *Solanum*.

#### TAXONOMIC TREATMENT

***Solanum* section *Allophyllum* (Child) Bohs, comb. nov. *Cyphomandra* section *Allophylla* Child, Feddes Repert. 95: 292. 1984. Type species: *Solanum allophyllum* (Miers) Standl.**

Herbae vel frutices fere glabra vel pilis simplicibus, omnibus partibus vegetativis abundanter areni-punctatis. Sympodia 2-3-foliata. Laminae foliorum simplices lobatae vel non lobatae basi subcordatae truncatae vel cuneatae plerumque in petiolum decurrentes. Inflorescentiae extra-axillares vel in furcis ramorum locatae non ramosae minus quam 10 cm longae floribus paucis; pedicelli 3-9 mm longi basi articulati. Corolla alba vel viridi-alba saepe basi maculis fuscatis. Stamina circum stylum conniventia; filamenta brevissima; thecae antherarum basi auriculatae apicem versus valde attenuatae, poris duobus apicalibus minimis dehiscentes. Stylus glaber filiformis; stigma truncatum. Bacca glabra ovoidea vel ellipsoidea apice obtusa.

*Herbs or shrubs* up to about 2 m tall. *Branches* glabrous to sparsely puberulent, abundantly sand-punctate. *Leaves* 2-3 per sympodial unit, the blades simple, lobed or unlobed, chartaceous to membranaceous, abundantly sand-punctate, the apex acuminate, the base subcordate to truncate or cuneate, decurrent along petiole, the midrib and major lateral veins prominent abaxially; petioles winged, glabrous to minutely puberulent, especially in adaxial channel. *Inflorescence* extra-axillary or located in a branch fork, unbranched, with up to 15 flowers, shorter than 10 cm long; pedicels 3-9 mm long, articulated at the base. *Calyx* membranaceous, veiny and sand-punctate. *Corolla* white or greenish (possibly blue?), usually with darker spots at the base, membranaceous, veiny and sand-punctate, glabrous to sparsely puberulent abaxially and adaxially, the margin glabrous to minutely tomentose, the apices acute. *Stamens* tightly connivent around style; filaments inserted about 1 mm above the corolla base, the free part of the filaments shorter than 1 mm and much shorter than the anthers; anther thecae narrowly triangular, strong-

ly tapered distally, sagittate at base, thickened abaxially in proximal half, the pores very small and directed distally. *Ovary* glabrous, ca. 1-3 mm long, 1-2 mm diam.; style glabrous, filiform, less than 0.5 mm diam., longer than the ovary; stigma truncate, the same diameter as style. *Fruit* glabrous, obtuse at apex, ovoid or ellipsoidal, laterally compressed in *S. allophyllum* and possibly also in the two other species.

#### KEY TO SPECIES OF *SOLANUM* SECTION *ALLOPHYLLUM*

- 1a. Leaf blades unlobed, elliptic, 10-27 cm long, 4-12 cm wide; inflorescences 8-15-flowered; corolla stellate, the lobes 6-8 mm long and 3-4 mm wide ..... 1. *Solanum mapiriense*
- 1b. Leaf blades lobed or unlobed, the unlobed leaves with blades ovate, ovate-elliptic, or triangular, 2.5-17 cm long, 1.3-7.5 cm wide; inflorescences 3-7-flowered; corolla rotate-stellate, the lobes 2-6 mm long and 1.5-3 mm wide.
  - 2a. Inflorescences 0.5-2.5 cm long; peduncles 0.3-1.5 cm long; corolla radius 4-5 mm long, the tube 1-2 mm long, the lobes 2-4 mm long; anther thecae 2.5-4 mm long; fruits globose, ca. 1 cm long and 1 cm in diameter; eastern Peru and adjacent Bolivia ..... 2. *Solanum morellifolium*
  - 2b. Inflorescences 1.5-7 cm long; peduncles 1-4.5 cm long; corolla radius 7-10 mm long, the tube 3-4 mm long, the lobes 4-6 mm long; anther thecae 5-6 mm long; fruits ovoid or ellipsoidal, 2.5-4 cm long, 1.5-2.5 cm wide; Central America and northwestern South America ..... 3. *Solanum allophyllum*

**1. *Solanum mapiriense* Bitter, Repert. Spec. Nov. Regni Veg. 11: 16. 1912. TYPE: Bolivia. La Paz: San Antonio near Mapiri, 850 m, Dec. 1907, *Buchtien 1434* (lectotype, US #1399273, here designated; isolectotype, US #1175838).**

*Bassovia phytolaccoides* Rusby, Bull. N.Y. Bot. Gard. 4: 317. 1907. *Solanum phytolaccoides* (Rusby) Bitter, Repert. Spec. Nov. Regni Veg. 13: 172. 1914, non *S. phytolaccoides* C. H. Wright, 1894. *Cyphomandra phytolaccoides* (Rusby) Child, Feddes Repert. 95: 292. 1984. TYPE: Bolivia. La Paz: Tipuani-Guanai, Dec. 1892, *Bang 1740* (lectotype, NY, here designated; isolectotypes, A, BM, E, GH, NY, US). Figure 2.

*Herb or shrub* ca. 1-2 m tall. *Branches* glabrous to sparsely puberulent with gland-tipped finger hairs. *Leaves* 2 per sympodial unit, the blades unlobed, elliptic, glabrous to sparsely puberulent or pubescent adaxially, nearly glabrous abaxially, (5-)10-27 cm long, (2-)4-12 cm wide, the length: width ratio ca. 2-3:1; major veins 5-11 on each side; petioles 1-5 cm long. *Inflorescence* extra-axillary, 8-15-flowered, 2-6 cm long; peduncle

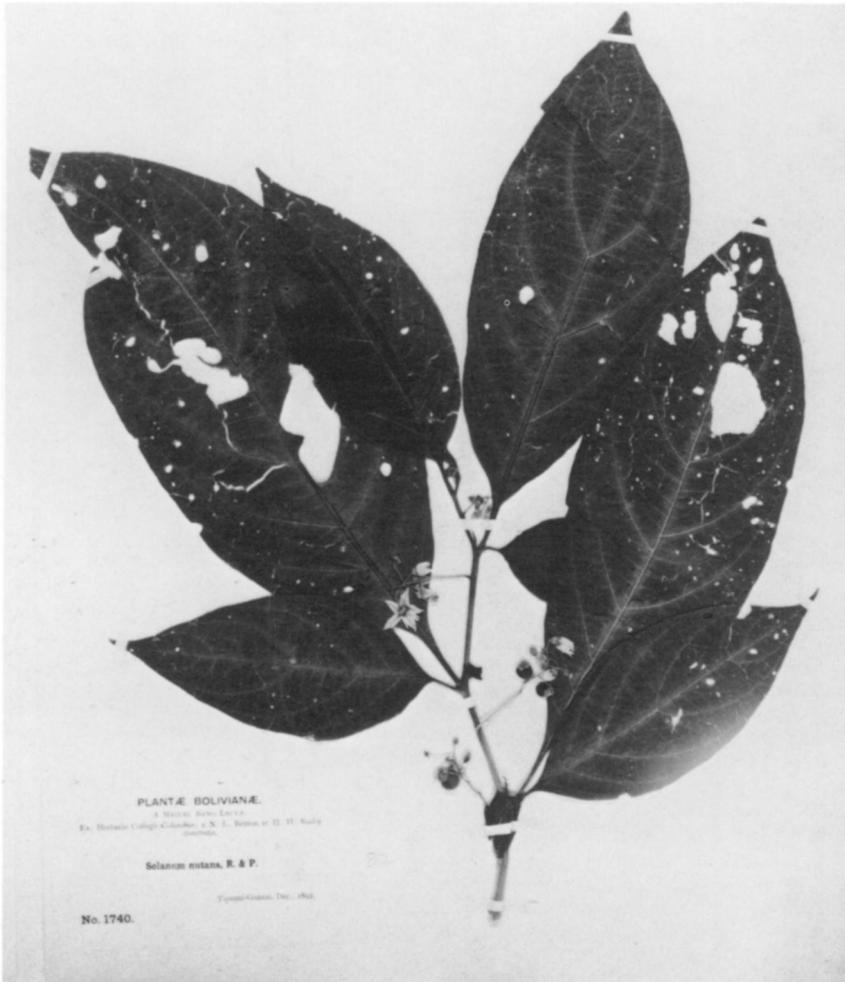


FIGURE 2. Isolectotype of *Bassovia phytolaccoides* (= *Solanum mapiriense*) (Bang 1740 BM).

1–3 cm long; rachis 1–4 cm long; pedicels 5–9 mm long, in fruit 7–9 mm long, spaced (1–)2–6 mm apart. Peduncle, rachis, and pedicels sparsely to moderately puberulent with curled gland-tipped finger hairs. *Calyx* glabrous to moderately glandular-puberulent, the radius 2 mm, the margin nearly entire with very shallow obtuse lobes. *Corolla* white to cream or greenish white with green spots at base (with deep blue center *fide* Rusby), stellate, the radius 8–10 mm, the tube 1–3 mm long, the lobes 6–8 mm long, 3–4 mm wide, elliptic to ovate, the apex short-tomentose. *Stamens* ca. 6 mm long; anther thecae yellow or white with green spots at base, (darker at the base *fide* Rusby), narrowly triangular, ca. 4–6 mm long, 1.5–2 mm wide at base, ca. 0.5 mm wide at apex. *Style* ca. 6 mm long, 0.2–0.5 mm diam.; stigma 0.2–0.5 mm diam. *Fruit* globose, 5–9 mm long, 4–9 mm

diam. (when immature?), the color when ripe unknown; presence of stone cell aggregates in mesocarp unknown (not present according to Bitter, 1912); seeds unknown.

*Distribution.* Known only from moist forest of western Bolivia in the Province of La Paz, 850–1,700 m (Figure 3).

*Additional specimens examined.* BOLIVIA. LA PAZ: Mapiri region, San Carlos, 850 m, 12 Dec. 1926, *Buchtien 1259* (NY); Prov. Nor Yungas, 10 km by road N and above Caranavi, ca. 15°47'S, 67°32'W, 1,400 m, 1 Nov. 1984, *Nee & Solomon 30305* (NY, UT); Prov. Nor Yungas, 4.6 km below Yolosa, then 19.1 km on road up the Rio Huarinilla, 16°12'S, 67°53'W, 1,700 m, 12 Nov. 1982, *Solomon 8757* (NY).

This species differs from the others of the section by its large elliptic leaves and relatively large stellate corollas with long lobes. The fruits are small

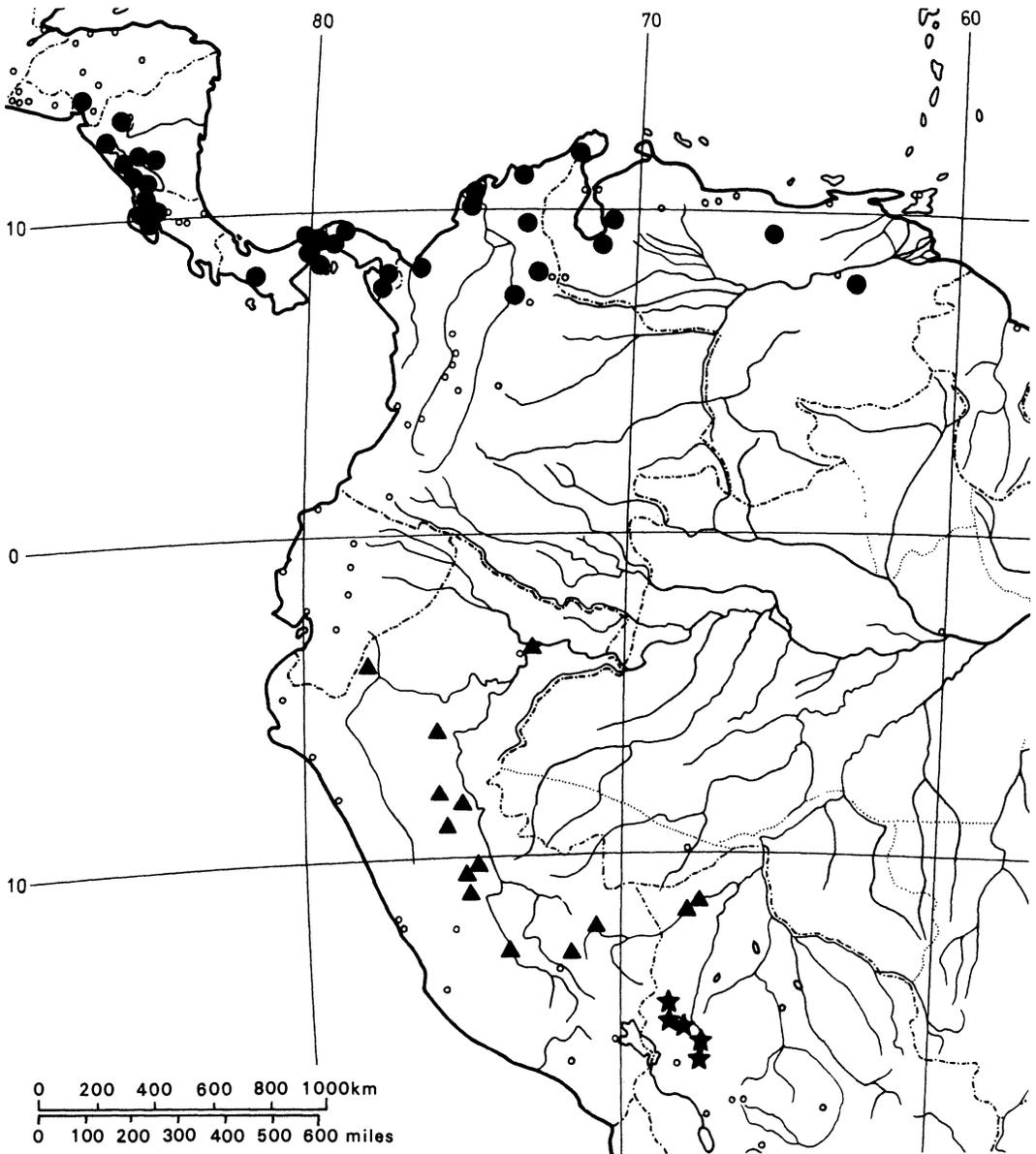


FIGURE 3. Distribution of *Solanum* sect. *Allophyllum*. Dots = *S. allophyllum*. Triangles = *S. morellifolium*. Stars = *S. mapiriense*. (Base map copyright 1979 by the University of Utrecht.)

and globose like those of *S. morellifolium*. Thus far *S. mapiriense* has only been collected from a restricted area of western Bolivia.

Although it is not possible to determine fruit shape from the herbarium specimens available, Rusby's description mentions that the fruits of *S. mapiriense* are slightly depressed and have two grooves. Laterally compressed fruits may therefore be characteristic of this species as well as of *S. allophyllum*.

*Solanum mapiriense* is the correct name for this species, as the combination *Solanum phytolaccoides* (Rusby) Bitter is a later homonym of *S. phytolaccoides* C. H. Wright.

Rusby did not specify the holotype for his *Bassovia phytolaccoides*, so a specimen at NY bearing his annotation has been chosen as the lectotype.

Bitter cited two syntypes for *S. mapiriense*, *Bang 1740* and *Buchtien 1434*. He stated in the protologue that he examined these specimens in

“herb. Buchtien.” Although most of Buchtien’s collections are at US, duplicates exist elsewhere, so “herb. Buchtien” does not precisely reveal the location of his types. The only specimens I have seen with a definite indication that Bitter examined them are *Buchtien 1434* (US #1399273) and *Bang 1740* (US #1175839) at US. The former sheet bears the annotation “*Solanum mapiriense* Bitter (det. Bitter),” but the handwriting does not appear to be Bitter’s. Furthermore, the label data do not precisely match that of the protologue; on the label it says “an Waldwegen,” whereas the protologue reads “in viis silvaticis.” The latter sheet has an annotation label in Bitter’s writing in the packet. However, this label reads “*Solanum phytolaccoides* (Rusby) Bitt.,” with *Bassovia phytolaccoides* Rusby and *Solanum mapiriense* Bitter given as synonyms. As Bitter was not aware of Rusby’s name when he described *S. mapiriense* in 1912, he must have examined this specimen at a later date, and it cannot be considered the type. In the absence of any better alternative candidates for the type of *S. mapiriense* Bitter, I have designated *Buchtien 1434* at US as the lectotype.

## 2. *Solanum morellifolium* Bohs, sp. nov. TYPE:

Peru. Ucayali: Prov. Coronel Portillo, Bosque von Humboldt Experimental Station, carretera marginal, km 86 toward Puerto Bermudez, 75°05’W, 8°45’S, ca. 330 m, 18 Apr. 1982, *D. Smith, Angulo & Lynch 1337* (holotype, MO; isotype, NY). Figure 4.

Herba fere glabra. Laminae foliorum non lobatae ovatae basi decurrentes. Inflorescentiae extra-axillares breves 3–7 floribus praeditae. Corolla rotato-stellata viridi-alba, lobi 2–4 mm longi. Thecae antherarum 2.5–4 mm longae. Stylus circa 3 mm longus. Bacca globosa circa 1 cm diametro.

*Herb or shrub* 0.5–1 m tall. *Branches* glabrous to very sparsely puberulent, rarely moderately puberulent with gland-tipped finger hairs. *Leaves* 2–3 per sympodial unit, the blades unlobed, ovate to ovate-elliptic or ± triangular, glabrous to sparsely puberulent adaxially and abaxially, 2.5–17 cm long, 1.3–7 cm wide, the length : width ratio ca. 2 : 1; major veins 4–8 on each side; petioles 0.5–7 cm long. *Inflorescence* extra-axillary, 3–7-flowered, 0.5–2.5 cm long; peduncle 3–15 mm long; rachis 3–10 mm long; pedicels 3–7 mm long, in fruit 5–8 mm long, spaced 1–4 mm apart. Peduncle, rachis, and pedicels glabrous to very sparsely and minutely puberulent, rarely moderately puberulent with gland-tipped finger hairs. *Calyx* glabrous, the radius 1–2 mm, the margin nearly entire except for 5 very short obtuse lobes or with deltate lobes

ca. 0.5–1 mm long and 1 mm wide. *Corolla* white or greenish white (blue *vide Smith et al. 1337*), rotate-stellate, the radius 4–5 mm, the tube 1–2 mm long, the lobes 2–4 mm long, 1.5–2 mm wide, triangular, the apex short-tomentose. *Stamens* 3.5–4 mm long; anther thecae yellow or white, 2.5–4 mm long, 1–1.5 mm wide at base, 0.3–0.5 mm wide at apex, triangular. *Style* ca. 3 mm long, ca. 0.2–0.5 mm diam. stigma ca. 0.2–0.5 mm diam. *Fruit* globose, 7–12 mm long, 6–12 mm diam. (when immature?), green or red (*Kayap 750*) or green with purple lines (*Smith et al. 1337; Knapp & Mallet 6642*); mesocarp with small aggregates of stone cells; seeds ca. 2 mm long, 1.5 mm wide.

*Distribution.* Forests or forest clearings of eastern Andean slopes and adjacent lowlands in Peru and Bolivia, 100–1,300 m (Fig. 3).

*Vernacular names.* *Chuagháteme* (*Kayap 750*).

*Additional specimens examined.* PERU. AMAZONAS: 12–15 km N of Huampami, 1,200 m, 2 Oct. 1972, *Berlin 156* (MO); Quebrada Huampami, Río Cenepa, 15 May 1973, *Kayap 750* (MO). AYACUCHO: Río Apurimac valley, near Kimpitiriki, 400 m, 10 May 1929, *Killip & Smith 22972* (NY, US). CUZCO: Prov. La Convención, Sahuayaco, Río Chalpimayo above Pacchar, 3,850 ft., 25 Jan. 1975, *Plowman & Davis 4858* (GH). HUÁNUCO: near Tingo María, ca. 600 m, 1 June 1977, *Hart 601* (A); Prov. Pachitea, Dist. Honoría, Bosque Nacional de Iparía, cerca del campamento Miel de Abeja, 300–400 m, 2 Mar. 1967, *Schunke 1706* (NY). JUNÍN: E of Quimiri Bridge, near La Merced, 800–1,300 m, 1–3 June 1929, *Killip & Smith 24015* (NY, US). LORETO: Prov. Maynas, trail from Indiana on Río Amazonas to Río Napo, 200 m, 24 May 1978, *Gentry et al. 22172* (MO); near Yurimaguas, 180–200 m, Nov. 1982, *Ochoa & Hooker 14885* (US). MADRE DE DIOS: Prov. Manú, Parque Nacional Manú, Cocha Cashu Station, 71°23’W, 11°53’S, 350 m, 12 Sep. 1986, *Foster 11363* (NY); same locality, 71°0’W, 11°45’S, 400 m, 15 Aug. 1986, *Núñez 5724* (NY). PASCO: Oxapampa, km 15 of Palcazu Road (km 73 Villa Rica–Iscozacín-Pto. Mairo) along Río Palcazu, 10°21’S, 75°10’W, 380 m, 17–18 Aug. 1984, *Knapp & Mallet 6642* (NY, US); Río Palcazu Valley, Iscozacín, 7 Oct. 1984, *Whalen & Salick 854* (NY). BOLIVIA. PANDO: Prov. Madre de Dios, along Río Madre de Dios, upstream and 22 km WSW of Florencia, 11°30’S, 67°34’W, 135 m, 23 Aug. 1985, *Nee 31505* (NY); Prov. Manuripi, along Río Madre de Dios, 3 km W of Humaita, 12°1’S, 68°18’W, 150 m, 30 Aug. 1985, *Nee 31658* (UT).

This species closely resembles *S. allophyllum*, but *S. morellifolium* has much smaller inflorescences, flowers, and fruits. The lobed leaves often seen in *S. allophyllum* apparently do not occur in this species. Although most collections are nearly glabrous, a few have glandular-puberulent inflorescence axes like those of *S. mapiriense*.

The specific epithet refers to the great similarity

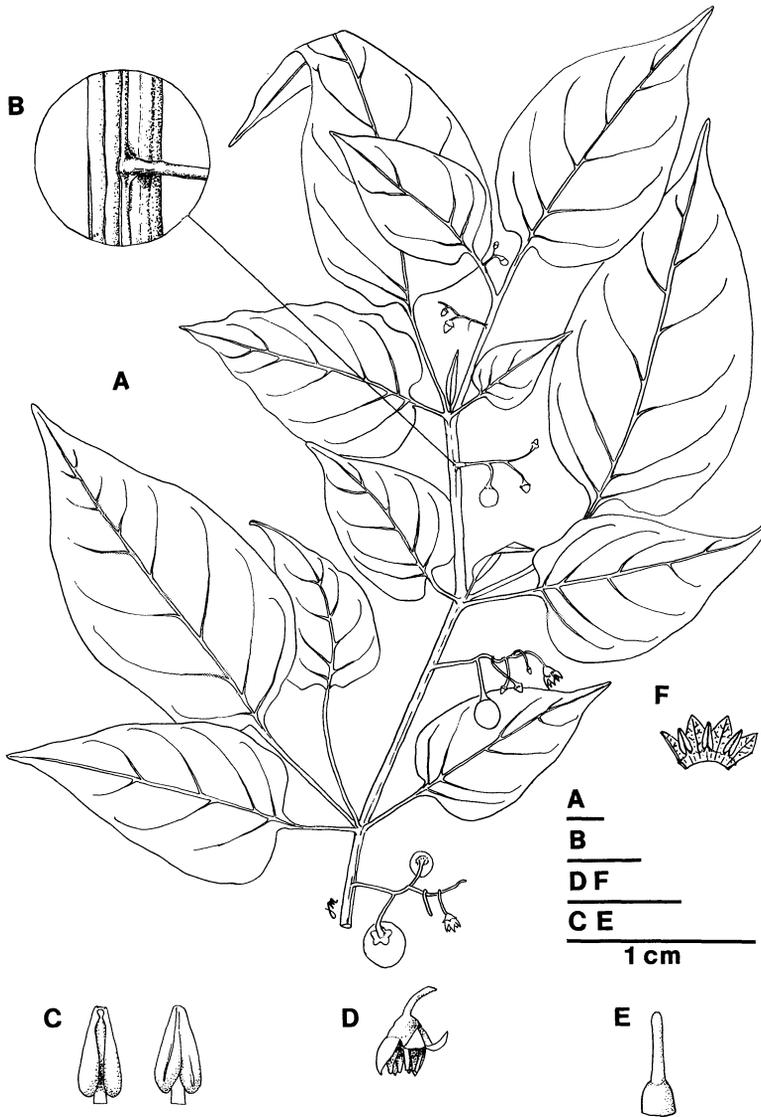


FIGURE 4. *Solanum morellifolium*.—A. Crown branch.—B. Stem and peduncle.—C. Stamens (left, abaxial view; right, adaxial view).—D. Flower.—E. Gynoecium—F. Corolla opened to show insertion of stamens. (A–E based on Smith et al. 1337 MO; F based on Nee 31505 NY.)

of the leaves of this species to those of *Solanum* sect. *Solanum*, which was formerly known as *Morella* or *Maurella* until the name was changed to sect. *Solanum* in accordance of the rules of botanical nomenclature (Seithe, 1962).

Data from Knapp & Mallet 6642 indicate that Ithomiine butterflies of the genus *Thyridia* oviposit on *S. morellifolium*. With this exception, all the known larval food plants for *Thyridia* belong to *Cyphomandra* (Drummond, 1986). If *S. morellifolium* indeed turns out to be a food source for these butterfly larvae, it may be indicative of a

closer relationship of sect. *Allophylla* to *Cyphomandra* than can be inferred on the basis of morphological characters (Knapp, pers. comm.).

**3. *Solanum allophyllum* (Miers) Standl., J. Wash. Acad. Sci. 17: 16. 1927. *Pionandra allophylla* Miers in Seem. Bot. Voy. Herald, 174. 1854. *Cyphomandra allophylla* (Miers) Hemsl., Biol. Cent.-Amer., Bot. 2: 417. 1882. TYPE: Panama: in waste places, Seemann 169 (lectotype, BM, here designated; isolectotype, K). Figure 5.**

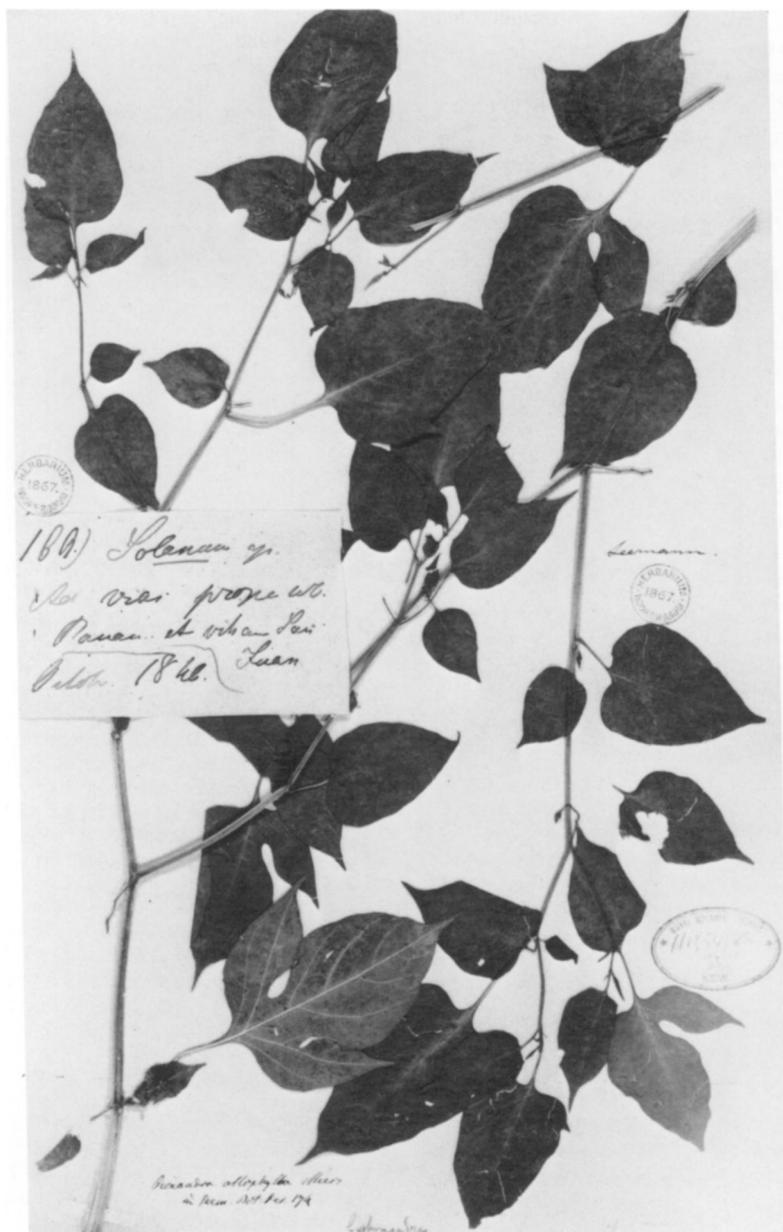


FIGURE 5. Isolectotype of *Pionandra allophylla* (= *Solanum allophyllum*) (Seemann 169 K).

*Solanum ellipsoideibaccatum* Bitter, *Repert. Spec. Nov. Regni Veg.* 11: 486. 1913. *Bassovia ellipsoideibaccatum* (Bitter) Pitt. *Cat. Fl. Venez.* 2: 356. 1947. TYPE: Colombia. Magdalena: Santa Marta, near Bonda, 150 ft., erect, branching, to 2.5 ft., rare in shady and somewhat damp places below 1,000 ft., corolla pale greenish, 12 Nov. 1898, H. H. Smith 1153 (distributed as *Solanum chenopodioides* Lam.?) (holotype, B, destroyed; isotypes, A, BM, E, F, GH, MO, NY, P, US, VT, WIS).

*Solanum ellipsoideibaccatum* var. *ficilobum* Bitter, *Repert. Spec. Nov. Regni Veg.* 13: 173. 1914. TYPE:

Panama. Chiriquí: near San Félix, 0–120 m, Pittier 5237 (holotype, US #715441; isotype, US).

*Herb or shrub* 0.4–1.5 m tall. *Branches* glabrous or sparsely puberulent, especially when young. *Leaves* 3 per sympodial unit, the blades unlobed or pinnately 2–5-lobed, sparsely eglandular-pubescent adaxially, glabrous abaxially; if unlobed, the blade ovate, 3–14 cm long, 1.5–7.5 cm wide, the length : width ratio ca. 2 : 1; if lobed, the blade

3–14 cm long, 2–12 cm wide, the terminal lobe elliptic to obovate, 2.5–12 cm long, 1–5.5 cm wide, the lateral lobes ascending, 1–10 cm long, 0.5–4 cm wide, the blade divided nearly to midrib, the sinuses rounded, acute; major veins 4–6 on each side; petioles 1–11 cm long. *Inflorescence* extra-axillary or located in a branch fork, 4–6-flowered, 1.5–7 cm long; peduncle 1–4.5 cm long; rachis 0.5–2.5 cm long; pedicels 4–6 mm long, in fruit 6–9 mm long, spaced 3–13 mm apart. Peduncle, rachis, and pedicels glabrous, or rarely sparsely puberulent. *Calyx* glabrous, the radius 2–3 mm, the lobes deltate, acute or obtuse, apiculate, 1–2 mm long, 1.5–2 mm wide. *Corolla* white or greenish, rotate-stellate, the radius 7–10 mm, the tube 3–4 mm long, the lobes 4–6 mm long, 3 mm wide, triangular. *Stamens* 6–6.5 mm long; anther thecae yellowish or white with a greenish patch near the base, narrowly triangular, 5–6 mm long, 1.5–2 mm wide at base, ca. 0.5 mm wide at apex. *Style* 4–5 mm long, 0.3–0.5 mm diam.; stigma 0.3–0.5 mm diam. *Fruit* ovoid or ellipsoidal, laterally compressed, 2.5–4 cm long, 1.5–2.5 cm wide, 1–1.8 cm thick, white or light yellow to orange, often with dark green or purple stripes; mesocarp with 3–6 stone cell aggregates ca. 2 mm diam.; seeds 2 mm long, 1.5 mm wide, rugose-verrucate.

*Distribution.* Forest and disturbed areas, especially in drier sites, Honduras to Panama, Colombia, and Venezuela, 0–900 m (Fig. 3). All collections from Panama are from Tropical Moist Forest, *sensu* Holdridge et al. (1971).

*Flowering and fruiting.* April through January.

*Vernacular names.* *Bleo de gallinazo* (Romero 6321) (probably a misprint for *bledo*, a Spanish term for herbs that can be used as food (Hunziker, pers. comm.), *cumapan* (Delascio & Liesner 6988), *hierba de gallinazo* (Standley 28138), *hierba gallota* (Pittier 6788), *yerba de gallote* (Bro. Paul 154), *zopilote* (Moreno 22030, Nee 28133).

*Uses.* Leaves used in salads, broths, and chopped meat dishes; ripe fruits used in stews (Colombia, from Romero-Castañeda, 1965).

*Additional specimens examined.* HONDURAS. CHOLUTECA: vicinity of Pespire, 160–200 m, 18–25 Oct. 1950, Standley 27108 (BM, F, US); same locality, 18–27 Oct. 1950, Standley 27237 (F). NICARAGUA. BOACO: Monte Grande, 12°25'N, 85°45'W, 200 m, 30 Sep. 1980, Moreno 3286 (MO); San Lorenzo, Sierra El Espino, 12°23'N, 85°39'W, 500–600 m, 11 Nov. 1982, Moreno

18544 (MO); Santa Cruz, 12°24'N, 85°49'W, 160–200 m, 15 Nov. 1982, Moreno 18608 (MO). CHONTALES: La Asunción, km 120 carretera Juigalpa, 12°9'N, 85°31'W, 120 m, 19 Oct. 1980, Moreno 3705 (MO); Hda. San Martín, near confluence of Río El Jordan and Río La Pradera, 12°17'N, 85°15'W, ca. 390 m, 30 July 1984, Stevens 22977 (MO, NY). GRANADA: Laguna de Apoyo, “Babilonia,” 11°55'N, 86°4'W, ca. 40–80 m, 30 May 1981, Moreno & Henrich 8898 (MO); camino de Casa Tejas, 11°46'N, 85°54'W, ca. 40–60 m, 21 June 1982, Moreno 16658 (MO). LEÓN: Isla de Momotombito, Lago de Managua, ca. 200 m, 21 Oct. 1979, Araquistain 362 (MO); same locality, ca. 150 m, 22 Oct. 1979, Araquistain 386 (MO). MANAGUA: El Carrizo, carretera a San Francisco, 12°23'N, 86°7'W, ca. 70–80 m, 10 Dec. 1980, Moreno 5080 (MO). MASAYA: Laguna de Apoyo, 11°56'N, 86°2'W, 100–140 m, 20 Sep. 1981, Moreno 11149 (MO). MATAGALPA: carretera a Jinotega, km 134, 800–900 m, July 1982, Bustos 44 (HNMN). RIVAS: Isla de Ometepe, 11°29'N, 85°29'W, 40–55 m, 14 Sep. 1983, Moreno 22030 (MO); above Balgue on facing slopes of Volcán Maderas, Isla de Ometepe, 11°28'N, 85°31'W, 600 m, 14 Sep. 1983, Nee & Téllez 28019 (MO, NY); same locality, 11°29'N, 83°31'W, 50–100 m, 15 Sep. 1983, Nee 28133 (MO, NY); Isla de Ometepe, Volcán Maderas, “La Palma,” 11°27–29'N, 85°28–30'W, 100–200 m, 21 Sep. 1984, Robleto 1221 (MO); Isla de Ometepe, entre Cuatro Esquinas y San Fernando, 11°30–32'N, 85°33–34'W, 17 July 1981, Sandino 1017 (MO). COSTA RICA. GUANACASTE: La Pacífica, Nov. 1976, Haber 57 (F, MO); between Las Cañas and Liberia, Pan American Highway, 100 ft., 12 Nov. 1953, Heiser 3719 (US); Santa Rosa National Park, 25 Sep. 1975, Janzen 10221 (MO); same locality, ca. 10°50'N, 85°37'W, 0–320 m, 1 July 1981, Janzen 12083 (MO); along Río Higuieron near agricultural experimentation area near Taboga, 10°20'N, 85°12'W, 0–100 m, 29–30 June 1977, Liesner et al. 2724 (MO); Finca La Pacífica, Cañas, Central Farm Road, 22 Oct. 1971, Opler 472 (MO). PANAMA. CANAL ZONE: Barro Colorado Island, 1931, Aviles 105 (F); vicinity Cerro Viejo on K16C, 13 Oct. 1965, Blum 1263 (MO); Farfan Beach, from Thatcher Hwy. to Palo Seco, 27 Dec. 1966, Burch et al. 1410 (MO, NY); Gatún, Nov. 1859, Hayes 563 (NY); vicinity of Madden Dam, 50 ft., 3 Dec. 1966, Lewis et al. 27 (M, MO); Madden Forest Preserve, along Las Cruces Trail and highway, 8 Apr. 1969, Lewis et al. 5315 (MO); Sosa Hill, Balboa, 27 Nov.–10 Dec. 1923, Standley 25289 (US); Balboa, Nov. 1923–Jan. 1924, Standley 25449 (US), 26109 (US); vicinity of Summit, 7 Jan. 1924, Standley 30142 (US); Barro Colorado Island, El Cermeño, 1 Dec. 1942, Zetek 5040 (F, MO). COLÓN: along Quebrada Bonita, 3 km NW of Salamanca, 13 km NE of Buena Vista, 150 m, 15 Sep. 1973, Nee 6970 (C, MO). DARIÉN: near mouth of Río Yapé, ca. 20 m, 12–14 July 1937, P. H. Allen 326 (F, MO); vicinity of Pinogana, ca. 20 m, 6 Oct. 1938, P. H. Allen 939 (F, MO, NY, US). PANAMÁ: Bayano, 24 Nov. 1973, Alvarado 42 (F); Cerro Campana, 12 Nov. 1975, D'Arcy 9613 (MO); ca. 6 mi. E of Chepo on Pan Am Highway, 28 Sep. 1961, Duke 4091 (MO); same locality and date, Duke 4092 (MO); vicinity of El Llano, 14–19 Oct. 1962, Duke 5798 (MO); Tumba Muerto antes del puente que queda cerca del Cicle Club, 24 Oct. 1974, Garrido 30 (MO); Natural Bridge, near Madden Lake, 3 Aug. 1972, Gentry 5604 (AAU, MO); Camino de Las Sabanas, 28 Nov. 1921, Bro. Heriberto 256 (US); Juan Díaz, 10 Nov. 1973, Herrera 42

(MO); same locality, 25 m, 30 Sep. 1917, *Killip 3100* (MO); along Tapia River, 75 m, 21 Oct. 1917, *Killip 3154* (MO); 1 km S of Madden Dam, 80 m, 20 Dec. 1973, *Nee 8900* (F—photos, MO), *8901* (MO); Sabanas, NE of Panama City, Oct. 1932, *Bro. Paul 154* (US); same locality, Nov. 1932, *Bro. Paul 175* (GH); Chepo, 60 m, Oct. 1911, *Pittier 4689* (BM, US); agricultural experiment station at Matías Hernández, 10 Sep. 1914, *Pittier 6788* (US); Taboga Island, Dec. 1923, *Standley 27089* (BM, US); Río Tapia, 7 Dec. 1923–11 Jan. 1924, *Standley 28138* (US); Río Tecumen, 3 Jan. 1924, *Standley 29461* (US). SAN BLAS: on mainland in front of Ustupo, 9 Nov. 1975, *D'Arcy 9472* (MO); cult. at Missouri Bot. Gard. from seed of *D'Arcy 9472*, 1976, *D'Arcy 9472a* (MO); on mainland in front of Ustupo, 9 Nov. 1975, *D'Arcy 9529* (MO, NY); Ailigandi area along trail from ocean to waterfall on river, 0–200 m, 7 Oct. 1978, *Hammel & D'Arcy 5002* (MO). COLOMBIA. BOLÍVAR: La Popa, near Cartagena, 50–175 m, 2 Nov. 1926, *Killip & Smith 14080* (GH, NY, US); Torrecilla, near Turbaco, 150–300 m, 7–19 Nov. 1926, *Killip & Smith 14647* (F, NY). CESAR: Rincón Hondo, 11 Aug. 1924, *C. Allen 373* (MO); same locality, 18 Aug. 1924, *C. Allen 423* (MO); same locality, 20 Aug. 1924, *C. Allen 451* (MO); Poponte, 23 Sep. 1924, *C. Allen 737* (MO); Becerril, ca. 100 m, 15 Sep. 1943, *Haught 3674* (US). CHOCÓ: alrededores de Tilupo, 21 June 1957, *Romero 6321* (F, MO, NY). GUAJIRA: Cerrejón, ca. 200 m, 3 Oct. 1949, *Haught 6637* (US). NORTE DE SANTANDER: valle del Río Peralonso en los alrededores de Santiago, 120 m, 21 Dec. 1948, *Molina & Barkley 86* (MO, US). SANTANDER: Barranca Bermeja, Magdalena Valley, between Sogamoso and Carare rivers, on Aguas Blancas Creek ca. 25 km S of El Centro, 150 m, 20 Nov. 1936, *Haught 2084* (F, GH). VENEZUELA. BOLÍVAR: Dist. Piar, La Camilera, 40 km al W de El Manteco, 250–260 m, July 1978, *Delascio & Liesner 6988* (MO, NY). GUÁRICO: ca. 39 km SSW of Calabozo on Hato Masaguaral, 100 m, 8°56'N, 67°60'W, 9 Nov. 1982, *Rondeau 123* (US). ZULIA: Dto. Bolívar, vía entre la carretera Lara–Zulia y Piedras Blancas (desviando en km 70 de la Lara–Zulia al SE del puente sobre el lago), entre km 1–3, 24 May 1979, *Bunting & Fucci 7651* (MO); San Martín, on Río del Palmar, Urdeneta, 15 Oct. 1922, *Pittier 10530* (US); vicinity of Mene Grande, 31 Oct. 1922, *Pittier 10610* (GH, NY, US).

*Solanum allophyllum* differs from the other species of the section by its large, ellipsoidal fruits and frequently pinnately lobed leaves. The unlobed leaves are very similar in size and shape to those of *S. morellifolium*. The flowers of *S. allophyllum*, though rather large like those of *S. mapiriense*, are rotate-stellate with short lobes like those of *S. morellifolium*. Details of the architecture, branching pattern, compatibility, and cytology of *S. allophyllum* may be found in Bohs (1989).

The herbarium sheet of *Seemann 169* at the British Museum (BM) bearing Miers's annotation has been chosen as the lectotype of *Pionandra allophylla* Miers.

Two collections are included here that show morphological features more characteristic of *S. morellifolium* than of *S. allophyllum*. I have iden-

tified them as *S. allophyllum* because of their occurrence in northwestern South America (Fig. 3). Haught's collection *2084* bears only flowers. The vegetative features conform to those of *S. allophyllum*, but the inflorescence is axillary, few-flowered, and has very small flowers, all characteristics more typical of *S. morellifolium* than of *S. allophyllum*. The collection *Rondeau 123* also resembles *S. allophyllum* in vegetative features, except for denser puberulence than is usual in that species. The fruits on this collection are globose and less than 1 cm in diameter. Although it is not known if these fruits are mature, their size and shape are more typical of *S. morellifolium* than of *S. allophyllum*. No flowers are present on this collection.

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