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Solanum maternum (Solanaceae), a New Bolivian Relative of the Tree Tomato

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ABSTRACT. A new species endemic to Bolivia, *Solanum maternum*, is described. *Solanum maternum* belongs to a group of taxa formerly recognized as the genus *Cyphomandra*. *Solanum maternum* is morphologically very similar to the tree tomato, *Solanum betaceum*, and may be its closest wild relative.

The former genus *Cyphomandra* Sendtner encompasses a group of about 30 species of shrubs and small trees with usually large, pendent fruits. The group is characterized by the presence of an enlarged connective region on the abaxial anther surface; this structure may play a role in pollination by secreting volatile compounds that attract male euglossine bees (Gracie, 1993; Sazima et al., 1993; Soares et al., 1989). Other characteristics of the *Cyphomandra* group that occur in most, but not all, species include Prévost's architectural model, very large chromosomes, and gametophytic self-incompatibility (Bohs, 1994).

Recent molecular evidence indicates that the *Cyphomandra* group is nested within *Solanum* (Bohs & Olmstead, 1997; Olmstead & Palmer, 1992, 1997; Spooner et al., 1993), and all *Cyphomandra* species have now been transferred or returned to *Solanum* (Bohs, 1995), where the first described species were placed. The infrageneric taxonomy of *Solanum* is currently under study and no infrageneric rank is consistently used at present for the *Cyphomandra* group. The monophyly of the *Cyphomandra* group and the relationship of this group to others within *Solanum*, particularly its putative sister group, *Solanum* sect. *Cyphomandropsis* Bitter, are issues that need to be examined before a taxonomic designation is made.

Species of the *Cyphomandra* group have been of interest because many produce edible fruits that are gathered from the wild or grown as minor crops. The most important in this regard is *Solanum betaceum* Cavanilles, the tree tomato, which is frequently cultivated in Latin America and commonly sold in Andean markets. *Solanum betaceum* has

also been an item in international commerce, usually sold under the name "tamarillo." Until recently, little was known about the place of origin of the tree tomato, which is usually regarded as being a cultigen. A group of species from Bolivia has now been identified as the closest wild relatives of *S. betaceum*, based on morphological and crossing data (Bohs, 1991, 1994). The species described here is a new member of this species complex and bears great morphological similarity to *S. betaceum*. Evidence presented below indicates that the new species is interfertile with *S. betaceum* and with two other members of the *S. betaceum* species complex.

Solanum maternum Bohs, sp. nov. TYPE: Bolivia. Santa Cruz: Prov. Caballero, Siberia-El Empalme, 5 km entrando hacia Khara Huasi, carretera entre Comarapa-Cochabamba, 17°50'S, 64°43'W, 2300 m, 8-9 May 1992 (fl, fr), I. Vargas & E. Prado 1273 (holotype, NY; isotypes, DUKE, MO not seen, USZ not seen). Figure 1.

Solano betaceo Cavanilles affine, a quo differt corollis albo-purpureis, fructibus maturis luteis, pube paulo sparsiore, connectivis antherarum paulo latioribus.

Small tree or shrub 1-4 m tall. Branches and petioles moderately to densely puberulent with glandular and eglandular unbranched hairs less than 1 mm long. Leaf blades simple, unlobed, chartaceous, acuminate at apex, moderately puberulent adaxially, more densely so on veins, densely puberulent abaxially. Trunk leaves with blade ovate, 19-34 cm long, 15-24 cm wide, length:width ratio ca. 1.5:1, the base cordate with basal lobes 1-4 cm long; petioles 11-22 cm long. Crown leaves 4 per sympodial unit, the blade ovate, 6.5-21 cm long, 5-14 cm wide, length:width ratio ca. 1-1.5:1, the base cordate to auriculate with basal lobes 1-3 cm long; petioles 2.5-11 cm long. Inflorescence unbranched or branched, ca. 20-60-flowered, 5-10 cm long; peduncle 3-4 cm long; rachis 2-8 cm long; pedicels ca. 15-20 mm long, 20-35 mm long in fruit, ca. 1-10 mm apart, articulated above the



Figure 1. *Solanum maternum* Bohs. —A. Flower. —B. Gynoecium. —C. Habit. —D. Stamens (left to right, abaxial, side, adaxial, top view). —E. Fruit. All based on living material of *I. Vargas & Prado 1273*.

base, leaving pedicellar remnants up to 2 mm long; peduncle, rachis, and pedicels moderately to densely puberulent with glandular and eglandular unbranched hairs. Flower buds ellipsoidal to ovoid, obtuse to acuminate at apex. Calyx fleshy, sparsely to moderately glandular-puberulent, the radius 6–9 mm, the lobes deltate, somewhat apiculate, ca.

2–3 mm long, 2.5–3 mm wide. Corolla white to pink with a darker pink to purple star toward center, subcoriaceous, stellate, the radius 15–25 mm, the tube 2–4 mm long, the lobes triangular, 8–12 mm long, 3–5 mm wide at base, glabrous abaxially and adaxially, the margin tomentose, the apex acute. Anther thecae light yellow to cream, 5–6 mm

long, 2–3 mm wide, the pores directed distally; connective lemon yellow to light orange, ca. 4–5 mm long, 1.5–2 mm wide, narrowly triangular, abaxially somewhat shorter than the thecae at apex, slightly shorter than them at base, adaxially absent. Ovary glabrous; style cylindrical, glabrous, not dilated distally, 6–8 mm long, 0.5–1 mm wide, exerted up to 2 mm beyond anthers; stigma truncate, 0.5–1 mm diam. Fruit ellipsoidal, acute or apiculate at apex, 3–8.5 cm long, 2–5 cm diam., glabrous, yellow to orange when ripe with dark green longitudinal mottling; mesocarp with stone cell aggregates; seeds 3–4 mm long, 2.5–3 mm wide, appearing densely pubescent.

Phenology. Flowering specimens have been collected in May, September, October, and December; fruiting specimens have been collected in January, May, June, and December.

Distribution. Cloud forest at 1350–2600 m elevation in Depts. Cochabamba, La Paz, and Santa Cruz, Bolivia.

Local uses and names. Fruits edible. N.v. “pepinillo” (Vargas & Vargas 710), “pepino del monte” (Nee 38493), “tomate de monte” (Eriksson & Vargas 3523, 3524, 3525, 3527, Vargas & Prado 1273), “tomate lima” (Vargas 1460), “tomatillo” (Eriksson & Vargas 3503).

Etymology. The epithet “maternum” is taken from the Latin for “mother,” because of the possibility that this species represents the wild ancestral form of the tree tomato.

Solanum maternum apparently belongs to a complex of closely related taxa from Bolivia, which includes *S. roseum* Bohs [formerly *Cyphomandra acuminata* Rusby], *S. unilobum* (Rusby) Bohs [formerly *Cyphomandra uniloba* Rusby], and *S. betaceum* [formerly *Cyphomandra betacea* (Cavanilles) Sendtner], the cultivated tree tomato. *Solanum maternum* is morphologically very similar to *S. betaceum*, and the two species are difficult to distinguish from herbarium material alone. Differences include slightly longer and less dense pubescence, more shallowly cordate leaves, and slightly wider anther connectives in *S. maternum*. Living material differs from *S. betaceum* in flower and fruit color. *Solanum maternum* has purplish or pinkish corollas with a deep purple star at base, whereas *S. betaceum* has uniformly white or pinkish corollas. The fruits of *S. maternum* are yellow or light orange, not dark orange or reddish as is typical of *S. betaceum*, although some forms of *S. betaceum* may have yellowish or light orange fruits. Fruits of *S. maternum* usually have a prominent apiculum or “nipple” at the distal end; those of *S. betaceum* may be acute

distally, but usually lack an obvious apiculum. The reddish or purplish corollas of *S. maternum* resemble those of *S. roseum*, but the latter species is nearly glabrous and has much larger seeds than *S. maternum*. *Solanum maternum* differs from *S. unilobum* in its corolla color (*S. unilobum* has greenish corollas), its unexpanded style and small stigma, and its more abundant pubescence.

Solanum maternum grows wild in upland areas of Bolivia in the Departments of La Paz, Cochabamba, and Santa Cruz. *Solanum unilobum* also occurs in this area, but is generally found at lower elevations (300–1700 m). *Solanum roseum* has been found only farther to the northwest in the Department of La Paz, and its range is probably not sympatric with that of *S. maternum*. Thus far, definitively wild populations of *S. betaceum* have not been found. Occasional plants may persist around abandoned dwellings or sporadically escape from cultivation, but the only reports of more extensive wild stands of this species are from southern Bolivian and northwestern Argentina (Bohs, 1989; Brücher, 1968, 1977; J. Solomon, pers. comm.; E. Zardini, pers. comm.). Fieldwork is needed to fully document the wild status of these plants.

In addition to morphological similarity, crossing data have indicated a close relationship among *S. betaceum*, *S. roseum*, and *S. unilobum*. Previous crossing studies have shown that *S. betaceum* will form fertile hybrids with *S. roseum* and *S. unilobum* (Bohs, 1991), although each of these crossing combinations is successful in only one direction. Crossing data thus suggest that *S. roseum* and *S. unilobum* may have played a role in the origin of the cultivated species, *S. betaceum*. *Solanum roseum* and *S. unilobum* are self-incompatible, but all plants of *S. betaceum* examined are self-compatible. This is consistent with the observation that cultivated taxa have often evolved self-compatible breeding systems from self-incompatible ancestors (de Nettancourt, 1977; Rick, 1988).

To further understand the placement of *S. maternum*, we collected data on breeding systems and crossability of *S. maternum* with other members of the complex. These data are presented below.

Greenhouse crosses were performed with two accessions each of *S. maternum*, *S. betaceum*, and *S. unilobum* using the methods described in Bohs (1991). Provenance and voucher data can be found in Table 1. Living material of *S. roseum* was unavailable for the crossing study.

Pollen viability. Pollen viability of the *S. maternum* plants, as measured by staining in aniline blue/lactophenol, was high (91–99%) throughout the study period, with the exception of one Vargas

Table 1. Voucher information for plants used in the crossing study.

Species	Collector and locality	Bohs voucher number
<i>S. betaceum</i>	<i>Sperling s.n.</i> Ecuador. Pichincha: Quito, purchased in La Vincentina market	2274, 2275
	<i>Nee 30359</i> Bolivia. Cochabamba: purchased in Cochabamba market	2468
<i>S. maternum</i>	<i>I. Vargas & Prado 1273</i> Bolivia. Dept. Santa Cruz: zona de San Juan del Potrero, Los Sagüintales, lado SW del Parque Nacional Amboró	2694
	<i>I. Vargas 1460</i> Bolivia. Dept. Santa Cruz: Prov. Caballero, Cerro Bravo	2547
<i>S. unilobum</i>	<i>Sperling & King 5500</i> Bolivia. Dept. La Paz: Larecaja, between Consata and Mapiri	2283, 2284
	<i>Eriksson & I. Vargas 3530</i> Bolivia. Dept. Santa Cruz: cultivated in Jardín Botánico, Santa Cruz	2549

1460 plant whose pollen stainability was 58%. Pollen stainability of the *S. betaceum* and *S. unilobum* accessions averaged 71% and 78%, respectively, lower than reported previously (Bohs, 1991).

Intraspecific crosses. No fruits were produced from 120 self-pollinations of both accessions of *S. maternum*. In contrast, 7.2% of the intraspecific sib crosses yielded fruits. Pollen tube observations were consistent with these results, with good pollen tube growth into the ovaries in sib crosses, but all pollen tube growth inhibited in the style in self-pollinations. These results indicate that the *S. maternum* accessions are self-incompatible.

A new accession of *S. unilobum* was examined during this study. Only one plant of this accession flowered during the study period, so sib crosses could not be performed. Unsuccessful pollen tube growth and lack of fruit set following self-pollinations suggest that this accession is self-incompatible.

Interaccession crosses of *S. maternum* were successful in both directions, yielding fruits with many viable seeds that subsequently germinated into F₁ hybrid plants. Many pollen tubes were seen growing into the ovary and around the ovules in these crossing combinations.

Interspecific crosses. Full-sized fruits were set in all interspecific crossing combinations among *S. maternum*, *S. betaceum*, and *S. unilobum*, but fruit set was often low (ca. 4–20% success). Likewise, pollen tube growth was uniformly successful in all

directions. Vigorous F₁ hybrid plants were produced from the interspecific combinations *S. maternum* (♀) × *S. betaceum* (♂), *S. maternum* (♀) × *S. unilobum* (♂), and *S. unilobum* (♀) × *S. maternum* (♂). Seeds from the *S. betaceum* (♀) × *S. maternum* (♂) crosses usually appeared flat and misshapen, and only 3 seeds of this combination germinated from 13 fruits produced.

When these results are considered along with those of Bohs (1991), the following conclusions emerge: (1) the wild members of the complex, *S. maternum*, *S. unilobum*, and *S. roseum*, are self-incompatible, whereas all accessions of the putative cultigen *S. betaceum* that have been examined are self-compatible, and (2) all species of the complex that have been tested are interfertile to some extent. The high degree of morphological similarity among the taxa on herbarium sheets precludes speculation about the degree of natural hybridization among members of the complex. Additional fieldwork is needed to sort out morphological differences among living plants that are not evident in dried material, and other accessions, particularly of *S. maternum* and *S. betaceum*, should be examined for self-incompatibility. The geographical distributions of the taxa of the complex also need to be documented in detail to determine if plants of these taxa are indeed sympatric and can thus exchange genes in nature.

Accumulating evidence suggests that *S. maternum*, *S. unilobum*, and/or *S. roseum* may have been

involved in the origin of the tree tomato, *S. beta-ceum*. Questions that remain concern the status of *S. beta-ceum* as a cultigen and the exact series of events that have led to its evolution. The close morphological resemblance of *S. maternum* to *S. beta-ceum* and its self-incompatible breeding system suggests that *S. maternum* may be the wild ancestral form of the tree tomato. However, more field, greenhouse, and laboratory work needs to be done to support this hypothesis. *Solanum maternum* should be explored as a source of useful genes for improvement of the tree tomato, and may itself be valuable as an economic fruit crop.

Paratypes. BOLIVIA. **Cochabamba:** Prov. Carrasco, Serranía Siberia, 20–35 km W of Comarapa on the old Cochabamba–Santa Cruz road (Hwy. 4), ca. 2000 m, 14–15 Jan. 1990 (fr), *Dorr & Barnett 7038* (MO, NY). **La Paz:** Prov. Sud Yungas, 7 km de Huancané en carretera a San Isidro, 16°21'S, 67°31'W, 2300 m, 13 Dec. 1989 (fr), *D. N. Smith et al. 13920* (NY). **Santa Cruz:** Prov. Caballero, Santa Rosa, 17°52'S, 64°12'W, 2100 m, 3 May 1993 (fr), *Eriksson & I. Vargas 3503, 3504* (NY), 5 km NE Río Lapacha, 1900 m, 4 May 1993 (fr), *Eriksson & I. Vargas 3507* (NY), 1800 m, *Eriksson & I. Vargas 3508* (NY); Prov. Caballero, Verdesillo, 17°50'S, 64°33'W, 2400 m, 10 May 1993 (fr), *Eriksson & I. Vargas 3523, 3524, 3525* (NY); Prov. Caballero, Locotal, 17°45'S, 64°45'W, 2230 m, 10 May 1993 (fl, fr), *Eriksson & I. Vargas 3527* (NY); Prov. Caballero, Parque Nacional Amorbó, Cerro Bravo, cerca Comarapa, 2600 m, 17 June 1995 (fr), *Jardim et al. 1987* (MO, NY); Prov. Caballero, entre 15 y 25 km al N de San Juan de Potrero, hacia Cerro Bravo, 17°48'S, 64°15'W, 2000–2500 m, 6 June 1992 (fr), *Killeen & I. Vargas 4068* (MO, NY), *4112* (MO, 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, 1900–1950 m, 23 Dec. 1989 (fl), *Nee & I. Vargas 38287* (NY); Prov. Vallegrande, SW side of Los Sitanos and along Quebrada Seca, 18°52'S, 63°57'30"W, 1350 m, 27 Dec. 1989 (fl, fr), *Nee 38493* (NY); Prov. Florida, 7 km (by air) NE of Mairana, on dirt road NE of “Yungas,” 18°05'S, 63°55'W, 2100 m, 2 June 1991 (fr), *Nee 40694* (NY); Prov. Vallegrande, Alto Seco, 21 km SE (línea recta) de Pucará, 18°53'S, 64°05'W, 2163 m, 13 May 1988 (fl, fr), *Saldias 351* (NY); Prov. Caballero, 50 km al N de Mataral (en la carretera Santa Cruz–Comarapa) pasando por San Juan del Potrero y bajando a la cuenca del alto Río Ichilo, 2000–2100 m, 26 May 1989 (fl, fr), *Quintana & García 13429* (NY); Prov. Vallegrande, La Centinela y Tupiriqui (La Yunga), 15 km SE línea recta de Piraimirí, 18°40'S, 63°48'W, 1500 m, 3 Sep. 1990 (fl), *I. Vargas & E. Vargas 710* (NY); zona de San Juan del Potrero, Los Saggiintales, lado SW del Parque Amorbó, *I. Vargas 1322* (NY, USZ); Prov. Caballero, Cerro Bravo, ca. 2000 m, 10 June 1992, *I. Vargas 1460* (NY, USZ); Prov. Florida, Parque Nacional Amorbó, 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, 2300 m, 23 May 1993 (fr), *I. Vargas et al. 2513* (NY); Prov. Caballero, Parque Nacional Amorbó, proximidades del Cerro Bravo a 10 km al N de Comarapa, alrededores de la Parcela permanente, 17°49.5'S, 64°32.5'W, 2400–2600 m, 18–25 Oct. 1993

(fl), *I. Vargas & Jardim 2947* (NY); Prov. Vallegrande, Monte Paulo, 4–5 km SE de Piraimirí sobre la carretera a Mascicurí, 18°39.4' S, 63°56'W, 2160 m, 27 Dec. 1994 (fl), *I. Vargas & V. Vargas 3688* (NY).

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