



Solanum perlongistylum and *S. catilliflorum*, New Endemic Peruvian Species of *Solanum*, Section *Basarthrum*, Are Close Relatives of the Domesticated Pepino, *S. muricatum*

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ABSTRACT. Two species new to *Solanum* sect. *Basarthrum* (Bitter) Bitter are described. *Solanum perlongistylum* G. J. Anderson, Martine, Prohens & Nuez and *S. catilliflorum* G. J. Anderson, Martine, Prohens & Nuez are narrowly distributed species from southern Peru in the group that includes the Andean domesticate *S. muricatum* Aiton and are very closely related to the widespread *S. caripense* Dunal. *Solanum catilliflorum* bears small, dish-shaped flowers (for which it is named) and is self-compatible and autogamous, with short styles like those that characterize all self-compatible species in this section. It also has a low pollen:ovule ratio, which is characteristic of self-compatible species in the group. On the other hand, the style of the self-incompatible *S. perlongistylum* is the longest in the group, and its flowers have a higher pollen:ovule ratio. Both species are diploid at $n = 12$. We hypothesize that these two species may be peripheral isolates from the widespread and variable *S. caripense*.

Key words: IUCN Conservation Status: VU, pepino, pollen:ovule ratios, Solanaceae, *Solanum catilliflorum*, *Solanum perlongistylum*, *Solanum* sect. *Basarthrum*.

Some of the species in *Solanum* L. sect. *Basarthrum* (Bitter) Bitter are highly variable, a feature noted in a number of current biosystematic studies (e.g., Anderson, 1979a; Anderson & Jansen, 1998), as well as by the original monographer of the group, Donovan Correll (1962). In particular, the domesticated pepino, *Solanum muricatum* Aiton, displays great morphological diversity (e.g., Anderson et al., 1996; Anderson & Jansen, 1998; Prohens et al., 1996). This is not surprising, given the variability of many domesticates. However, some of the wild species in the section also show wide variation. Common garden (usually northern temperate greenhouse) studies have been useful in understanding some of that variation. For instance, growing plants from seeds to flowering has allowed the recognition of leaf variation (from 1- to 11-foliate) that characterizes developmental stages rather than distinguishes among species (Anderson et al., 1999). The results from interspecific hybridization studies revealed that anther, pistil, and pollen differences among three types of plants formerly recognized as distinct species actually characterized the sexes of a single dioecious species, *S. appendiculatum* Dunal (Anderson, 1979b; Anderson & Levine, 1982).

The variation within the series *Caripensia* Correll has been of special interest; there are a number of species in this group, and many are difficult to distinguish morphologically. Thus, the variation within any particular species can be great. However, some of that variation is not intraspecific, but rather interspecific. Thus, intensive studies of a broad range of data have led to the recognition of a number of new species (e.g., *Solanum cochoae* G. J. Anderson & Bernadello (Anderson & Bernadello, 1991) and *S. heiseri* G. J. Anderson (Anderson, 1975)). *Solanum caripense* Dunal is one of the most widespread wild species (distributed in mountainous regions from Costa Rica to Peru) and may be the plexus from which more local variants have become separated and isolated. Extensive studies of morphology, chromosomes, crossability, and lately, DNA have supported various elements as distinct entities, for example, *S. heiseri* and *S. cochoae* (Anderson & Jansen, 1998; Prohens et al., 2003). Most recently, a field expedition (Fernando Nuez, Jaime Prohens, and associates) identified populations from southern Peru that are morphologically clearly in the series *Caripensia* (*S. basendopogon* Bitter, *S. caripense*, *S. cochoae*, *S. filiforme* Pavón ex Dunal, *S. fraxinifolium* Dunal, *S. heiseri*, *S. trachycarpum* Bitter & Sodiro). However, DNA extractions from these presumed *S. caripense* variants were also part of a study of amplified length polymorphisms (AFLP) in section *Basarthrum* (Prohens et al., 2006). *Solanum perlongistylum* and *S. catilliflorum* proved to possess AFLP patterns more distinct from the plexus of the series *Caripensia* than any of the other species; in fact, the AFLP patterns of these new Peruvian populations are more distinct than most recognized species in section *Basarthrum*. Further study has confirmed that these elements merit recognition as distinct species, and they are so described below, along with additional data that provide some perspective on their biology and systematic position.

The bulk of the measurements for both species were made from a large number of living plants grown from seed collected in Peru in March 2001. Because the original field collections of Prohens and Nuez consisted only of seeds, the type material and herbarium specimens are from plants grown from those seeds and cultivated in the University of Connecticut Ecology and Evolutionary Biology Conservatory.

Solanum perlongistylum G. J. Anderson, Martine, Prohens & Nuez, sp. nov. TYPE: U.S.A. Connecticut: cultivated at Univ. Conn. Ecol. & Evol. Biol. Conservatory, Storrs, 19 Nov. 2004,

C. T. Martine 953 (holotype, CONN; isotypes, MO, MOL, NY, US, VAL) [Peru. Huancavelica: near Montacra, quebrada border, 16 Mar. 2001, seed collection, *J. Prohens* & *F. Nuez* 51]. Figure 1A–D.

Habitus semierectus; foliola base rotunda, plerumque tria; pubescentia densa, pili longi; sine pugiotis pilis glandulosis; stylus perlongus, extendens multo ultra columnam staminalem.

Trailing or viny shrub with arching-ascending branches to 1 m long or more, internodes 20–70 mm; stem woody or thick-herbaceous, moderately strigose when young, the older branches occasionally rooting at nodes. Leaves with mostly 3 (rarely 1 or 5) leaflets, 40–60 mm long, with petiole 10–20 mm long; leaflets lanceolate to lanceolate-elliptic, base obtuse, apex acute or acuminate, not glutinous, with moderately dense strigose vestiture of 2-celled bayonet hairs (ca. 0.8 mm) intermixed with short square gland hairs (ca. 0.08 mm) on both surfaces; gland-tipped finger hairs not present; terminal leaflet somewhat larger than the first pair of lateral leaflets, 27–44 × 14–24 mm, petiolule 3–7 mm long; first pair of lateral leaflets 9–20 × 6–14 mm, short-petiolulate; pseudostipules present. Inflorescence an indeterminate pseudoterminal cymose raceme with 1 axis and (5)6 to 8(13) hermaphrodite flowers; pedicels 8–13 mm long, basally articulate, with dense strigose vestiture of 2-celled bayonet hairs intermixed with short square gland hairs. Corolla white or purple and fading to white, rotate, moderately reflexed, the lobes 11–14 mm long, the sinuses 9–11 mm long, the lobe:sinus ratio about 1.4:1, glabrous or sparingly strigose adaxially, densely puberulent abaxially; calyx green, acute to acuminate, about 1/2 the length of the corolla lobes (6–7 mm long), the strigose vestiture heavy; anthers pale yellow, the apices rounded, 3.5–4.8 mm long, glabrous adaxially and abaxially, filaments 0.7–1.3 mm long, fused for less than 1/4 of their length, with scattered stiff hairs around base; style 7.3–12.8 mm long, sparingly to densely strigose over lower 2/3 of length, the stigma slightly capitate, exceeding staminal column by 3.6–4.4 mm. Fruits globose, mature fruits pale green or yellowish green with darker green or purple-black stripes, with darker maculae on the lighter areas, 22–27 × 23–27 mm, round in cross section, smooth, apex rounded, locules 2; soluble solids concentration 6.0%–7.5%; seeds 60 to 120 per fruit; fruits falling from plant when ripe. Pollen grains per anther ca. 133,765, pollen:ovule ratio ca. 4968:1 (Table 1); plants self-incompatible; *n* = 12 (*Martine* 953, CONN).

Habitat and distribution. Collections of the species have been made in Peru at elevations around

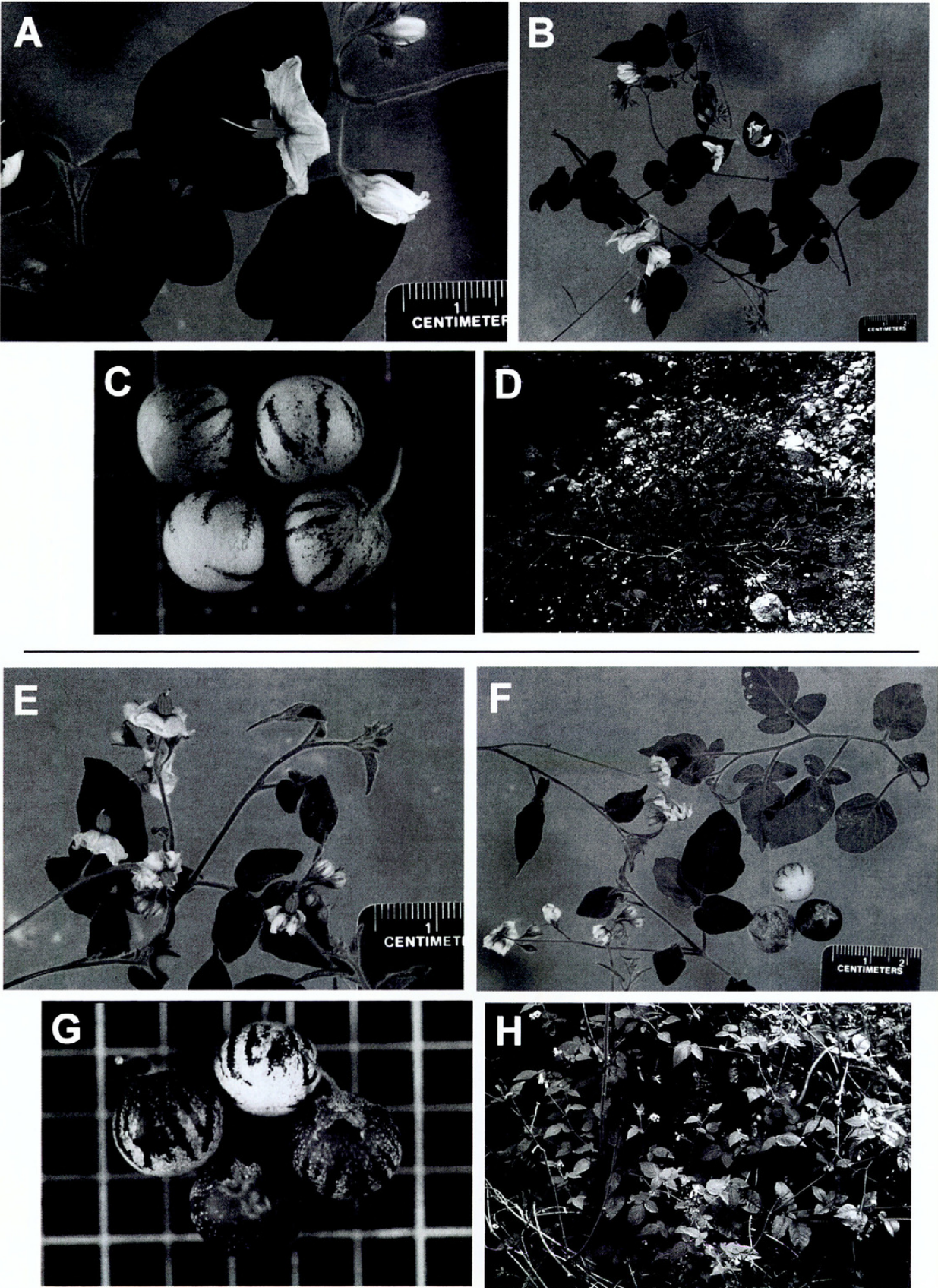


Figure 1. Photographs of *Solanum perlongistylum* (A–D) and *S. catilliflorum* (E–H). —A. Flowers. —B. Form. —C. Fruits. —D. Field habit. —E. Flowers. —F. Form. —G. Fruits. —H. Field habit. Scale as indicated, except for the fruits (C & G), where each square is 10 × 10 mm.

Table 1. Pollen:ovule ratios of *Solanum perlongistylum* and *S. catilliflorum*. Pollen:ovule ratios of the two species are significantly different; see text. GJA = G. J. Anderson numbers used to label greenhouse-grown plants from seeds of original field collections by Prohens and Nuez. PN = Prohens and Nuez original seed collection numbers. * Mean pollen:ovule ratio for all accessions of *S. perlongistylum* = 4968 ± 1719. ** Mean pollen:ovule ratio for all accessions of *S. catilliflorum* = 2170 ± 365.

<i>S. perlongistylum</i> *			<i>S. catilliflorum</i> **		
Accessions	Pollen grains per flower (5 anthers)	Ovules per flower	Accessions	Pollen grains per flower (5 anthers)	Ovules per flower
GJA 4561 (PN 51)	664,300	154	GJA 4565 (PN 71)	222,100	85
GJA 4561 (PN 51)	638,600	184	GJA 4565 (PN 71)	198,300	
GJA 4561 (PN 51)		172	GJA 4566 (PN 74)	183,800	88
GJA 4562 (PN 61)	862,000	120	GJA 4566 (PN 74)	185,000	70
GJA 4562 (PN 61)	805,000		GJA 4567 (PN 80)	172,100	124
GJA 4564 (PN 64)	497,800	117	GJA 4567 (PN 80)	186,100	94
GJA 4564 (PN 64)	545,000	117	GJA 4568 (PN 82)	217,100	116
GJA 4564 (PN 64)		145	GJA 4568 (PN 82)	227,500	67

2100–3200 m on field borders, road cuts, quebradas, and riverbanks. Local names for *Solanum perlongistylum* vary, as do perceptions of the edibility of the fruits. Near Montacra in Huancavelica, the fruit is known as nokai and is said to be poisonous to livestock. Locals in the area of Oeros in Ayacucho call the species alpunto and also consider the fruits inedible. However, around Ccochahuayjo, Apurimac, people consider the fruits edible and sweet, and call the species pepino de monte (Prohens, pers. obs.).

The new taxon is distinguished from morphologically similar species in *Solanum* sect. *Basarthrum* ser. *Caripensia* by bearing the longest styles, nearly 8.5 mm on average, versus about 6 mm for the other species with which it might be confused (i.e., the so-called Caripense complex including the widespread *S. caripense* (Central America to Peru) and the narrowly distributed *S. filiforme* (only in Peru), *S. fraxinifolium* (mostly in Venezuela), and *S. heiseri* (only in Colombia) (Anderson & Bernardello, 1991; Prohens et al., 2006)). Furthermore, the style of this new species extends beyond the staminal column by an average of about 4 mm, almost twice as much as the similar species in the Caripense complex. The flowers are generally larger as well (11–14 mm vs. ca. 8.0–8.5 mm in *S. caripense*). The anthers are lemon yellow in *S. perlongistylum*, versus the more orange-yellow of closely related species. The leaf hairs are long, yielding a white-downy appearance to the leaves. The hairs are about 40% longer than those of *S. catilliflorum*. Both of these new species bear two types of hairs: 2-celled bayonet hairs and short square gland hairs. All other species in the series have these plus a third type: gland-tipped finger hairs (these being the cause for viscid leaves in the other species). There are generally 3 leaflets, although that is not particularly distinctive, and the habit is a bit more

upright, similar to (but not as upright as) *S. basendopogon*.

Etymology. The epithet was selected to reflect the notably long styles.

Conservation status. Estimated IUCN rank: VU. Rare and known from a limited number of localities. Total wild population still unknown.

Paratypes. U.S.A. **Connecticut:** cultivated at Univ. Conn. Ecol. & Evol. Biol. Conservatory, Storrs, 18 July 2005, *C. T. Martine & M. R. Opel 1083* (CONN) [Peru, Apurimac, Ccochahuayjo, 18 Mar. 2001, seed collection, *J. Prohens & F. Nuez 62*], 18 July 2005, *C. T. Martine & M. R. Opel 1082* (CONN) [Peru, near Apurimac River, Ninabamba, 17 Mar. 2001, seed collection, *J. Prohens & F. Nuez 61*].

Solanum catilliflorum G. J. Anderson, Martine, Prohens & Nuez, sp. nov. TYPE: U.S.A. Connecticut: cultivated at Univ. Conn. Ecol. & Evol. Biol. Conservatory, Storrs, 19 Nov. 2004, *C. T. Martine 949* (holotype, CONN; isotypes, MO, MOL, NY, US, VAL) [Peru, Abancay: near Abancay, rubbish heap in wet terrain, 19 Mar. 2001, seed collection, *J. Prohens & F. Nuez 80*]. Figure 1E–H.

Habitus reptans; folia et foliola parva; folia in foliola pleraque 3 divisa; sine pugiotis pilis glandulosis; flores parvuli; stylus brevis, extendens vix ultra columnam staminalem; fertile secum; fructus parvi.

Viney or trailing shrub; branches to 1 m long; internodes 15–60 mm; stem woody or thick-herbaceous, moderately strigose when young, older branches commonly rooting at nodes. Leaves with mostly 3 (rarely 1) leaflets, 32–58 mm long, with petiole 7–14 mm long; leaflets lanceolate to elliptic, base obtuse, apex acute or acuminate, not sticky, with moderately dense strigose vestiture of 2-celled

bayonet hairs intermixed with short square gland hairs on both surfaces; bayonet hairs about 0.5 mm in length; short square gland hairs about 0.07 mm in length; gland-tipped finger hairs not present; terminal leaflet somewhat larger than the first pair of lateral leaflets, 23–36 × 14–22 mm, the petiolule 2–5 mm long; first pair of lateral leaflets 8–18 × 5–11 mm, short-petiolulate; pseudostipules present. Inflorescence an indeterminate pseudoterminal cymose raceme with 1 axis and 5(to 8) hermaphrodite flowers; pedicels 5–8 mm long, basally articulate, with dense strigose vestiture of 2-celled bayonet hairs intermixed with short square gland hairs. Corolla white, rotate, moderately reflexed, lobes 7–9 mm long, sinuses 4.0–6.5 mm long, the lobe:sinus ratio about 1.35:1, glabrous adaxially, sparsely strigose to hispid abaxially; calyx green, acute to acuminate, ca. 1/2 length of corolla lobes, strigose vestiture moderate to heavy; anthers pale yellow, 2.8–3.4 mm long, apices rounded, 2.8–3.4 mm long, glabrous adaxially and abaxially, filaments 0.7–1.1 mm long, fused for less than 1/4 length, with scattered stiff hairs at midpoint; style 4.7–6.1 mm long, sparingly to moderately strigose over lower half, stigma slightly capitate, exceeding staminal column by 1.6–2.4 mm. Fruits globose, the mature fruits pale green or yellowish green with darker green or purple-black stripes, with darker maculae on the lighter areas, 13–18 × 12–18 mm, round in cross section, smooth, apex rounded, locules 2; soluble solids concentration 5%–8%; seeds 100 to 175 per fruit; fruits falling from plant when ripe. Pollen grains per anther ca. 39,800, pollen:ovule ratio ca. 2170:1 (Table 1); plants self-compatible; $n = 12$ (Martine 949, CONN).

Habitat and distribution. Collections of this new species have been made at elevations near 2100 m on open, wet terrain in Peru. The ripened fruits of *Solanum catilliflorum* are eaten by locals. Near Auquibamba, Abancay, the species is known as pipino (Prohens, pers. obs.).

This new taxon is distinguished from morphologically similar species in *Solanum* sect. *Basarthurum* ser. *Caripensia* by its scrambling habit, small flowers (smallest in the Caripense complex), and short styles extending only slightly beyond the staminal column, similar to the other self-compatible species in section *Basarthurum*. However, these styles extend farther beyond the staminal column than any other self-compatible species in the series. Plants of this species are not only self-compatible, but autogamous, as demonstrated by greenhouse observations (G. Anderson, pers. obs.). The other self-compatible species in section *Basarthurum* are the domesticated pepino (*S. muricatum*), two herbaceous annuals (*S. canense*

Rydberg, *S. suaveolens* Kunth & Bouché), and one woody perennial (*S. trachycarpum*) limited to low-elevation xeric sites in Ecuador. *Solanum catilliflorum* is easy to distinguish from *S. trachycarpum* based on the small flowers, compound leaves (vs. simple), and scrambling habit (vs. erect). Likewise, *S. catilliflorum* lacks the gland-tipped finger hairs present in the majority of the species in series *Caripensia*.

Etymology. The epithet reflects the small flowers of this species, the Latin *catillus* being a small plate or dish.

Conservation status. Estimated IUCN rank: VU. Rare and known from a limited number of localities. Total wild population still unknown.

Paratypes. U.S.A. **Connecticut:** cultivated at Univ. Conn. Ecol. & Evol. Biol. Conservatory, Storrs, 18 July 2005, C. T. Martine & M. R. Opel 1084 (CONN) [Peru, Abancay/Apurimac, road cut near Auquibamba, 18 Mar. 2001, seed collection, J. Prohens & F. Nuez 71]; 18 July 2005, C. T. Martine & M. R. Opel 1085 (CONN) [Peru: Auquibamba, 18 Mar. 2001, seed collection, J. Prohens & F. Nuez 74]; 18 July 2005, C. T. Martine & M. R. Opel 1086 (CONN) [Peru, Abancay, 19 Mar. 2001, seed collection, J. Prohens & F. Nuez 82].

DISCUSSION

The chromosome number (Martine 949 & 953, CONN), which was determined from counts of meiosis of pollen mother cells using standard methodology with acetocarmine staining and phase microscopy, is $n = 12$, the same count as all the other species of *Solanum* sect. *Basarthurum* (Bernardello & Anderson, 1990). Furthermore, assessments of fertility (e.g., pollen stains, as in Anderson, 1975) showed high stainability, which further supports that meiosis is normal and that the new species are not segregating hybrids.

Crosses were performed in the greenhouses in Valencia, Spain, and Storrs, Connecticut, U.S.A., to determine compatibility of the new species. On both continents, the results show clearly that *Solanum catilliflorum* is self-compatible (38 of 54 self-pollinations resulted in fruits with viable seeds). In addition, abundant fruits were regularly set on this species in pollinator-free greenhouses in both Valencia and in Storrs, indicating that this species is not only self-compatible, but is also autogamous. The short styles on the flowers of this species, exceeding the staminal column by about 2 mm, support the style length generalization recognized previously for other self-compatible species in *Solanum* sect. *Basarthurum*, i.e., that species with styles that exceed the staminal column by ca. 2 mm or less are self-compatible

Table 2. Crossing results. All crosses were made between different plants (self crosses discussed in the text). The values reflect the percent fruit set. The numbers in parentheses are the number of fruits set divided by the number of crosses attempted. All fruits contained morphologically normal seeds.

	<i>S. perlongistylum</i> (♂)	<i>S. catilliflorum</i> (♂)	<i>S. caripense</i> (♂)	<i>S. basendopogon</i> (♂)	<i>S. canense</i> (♂)
<i>S. perlongistylum</i> (♀)	21% (4/19)	21% (6/28)	20% (6/24)	0% (0/14)	0% (0/15)
<i>S. catilliflorum</i> (♀)	43% (10/23)	63% (15/24)	25% (5/20)	0% (0/22)	0% (0/15)
<i>S. caripense</i> (♀)	9% (2/22)	16% (3/19)	25% (6/24)	—	—
<i>S. basendopogon</i> (♀)	0% (0/15)	0% (0/17)	—	22% (5/23)	—
<i>S. canense</i> (♀)	0% (0/22)	0% (0/27)	—	—	32% (8/25)

(Anderson, 1977). Thus, in this instance, compatibility could have been inferred without pollination experiments.

The other new species, *Solanum perlongistylum*, is fully self-incompatible. This very long-styled species never set fruit upon self-pollination of more than 100 flowers (in Valencia). The style length of this species is greater than that of any other recorded in *Solanum* sect. *Basarthurum*.

Since the seminal paper by Bob Cruden nearly three decades ago (1977) stimulated interest in the ratio of pollen grains to ovule number, it has become a widely used first estimate of breeding system. A comprehensive survey for *Solanum* sect. *Basarthurum* (Mione & Anderson, 1992) provided additional support for the generalization that self-compatible species have lower pollen:ovule ratios than out-crossing taxa. The two new species described here also support this generalization. *Solanum catilliflorum*—the self-compatible, autogamous species—bears about half the pollen per flower, and about 70% of the number of ovules per flower as the self-incompatible *S. perlongistylum* (Table 1). Thus, the pollen:ovule ratio of the autogamous species is about half that of the obligately xenogamous *S. perlongistylum* (and, significantly different: $P = 0.02$). The pollen grain numbers, ovule numbers, and pollen:ovule ratios of these two species are all in accord with the general patterns observed for other species in section *Basarthurum* (Mione & Anderson, 1992). However, for both new species the pollen:ovule ratios are higher in absolute value when compared to the ratios for self-compatible and self-incompatible species in the previous study (Mione & Anderson, 1992). The number of pollen grains per flower is about the same as previously assessed; the higher pollen:ovule ratios seem mostly to be due to the ovule number, which is about half that of the species reported by Mione and Anderson (1992).

In addition, a limited number of pollinations between species were performed in greenhouses in Valencia (Table 2). Crosses between the two new *Solanum* species were moderately successful, yielding 20%–40% fruit set. All fruits included seeds that

were morphologically normal, i.e., not flattened as sterile seeds in the group usually are (Anderson, 1975, 1977, 1979a); however, germination tests were not done and the vigor and fertility of F₁ plants were not tested. Successful fruit set from these interspecific crosses likely indicates some similarity between the genomes of the new species. Interestingly, the results of the reciprocal crosses between these two new species were different; when the self-incompatible species (*S. perlongistylum*) was used as the female parent, the fruit set was lower. As with the compatibility versus style length generalization above, this conforms to the generalization that self-incompatible species often perform less well as female parents in hybridization experiments (Anderson, 1979a; Lewis & Crowe, 1958; Onus & Pickersgill, 2004). Crosses with three other species from *Solanum* sect. *Basarthurum* were largely unsuccessful. Crosses with the more distant congeners (Prohens et al., 2006; Anderson & Bernardello, 1991) *S. basendopogon* and *S. canense* were, as one might expect for species as distinct as these, unsuccessful. Those crosses with the variable *S. caripense*, the most closely related species (Prohens et al., 2006), were somewhat more successful, yielding 9%–25% fruit set.

The new species described here are similar to *Solanum caripense* and are difficult to distinguish from it on the basis of morphology, as is also the case with some of the previously described species in series *Caripensia* (e.g., Anderson, 1975; Anderson & Bernardello, 1991; Prohens et al., 2006). *Solanum caripense* has the widest distribution of the species in section *Basarthurum* (Costa Rica through Peru) and is among the most widely distributed of any of the species closely related to the (tuberous or non-tuberous) potatoes (Anderson, 1975; Correll, 1962). It may well be that isolation of populations along the range of this widely distributed, montane species (or its ancestral forms) in mountain valleys may help explain the number of sibling species documented, of which *S. catilliflorum* and *S. perlongistylum* are the two most recently recognized. This pattern of speciation has also been proposed for an analogous self-compatible/incompatible species pair of tomatoes (*Solanum*

neorickii D. M. Spooner, G. J. Anderson & R. K. Jansen and *S. chmielewskii* (C. M. Rick, Kesicki, Fobes & M. Holle) D. M. Spooner, G. J. Anderson & R. K. Jansen), also from Peru (Rick et al., 1976).

Ongoing studies by Blanca et al. are assessing the relationships of these two new species to the domesticated pepino (*Solanum muricatum*). Like other members of the Caripense complex, *S. catilliflorum* and *S. perlongistylum* are closely related to this ancient Andean domesticate. Although there is no indication that either of the two new species was involved directly in the origin of the pepino, DNA sequence haplotype data (Blanca et al., unpublished data) imply that some introgression of *S. perlongistylum*, *S. catilliflorum*, or both, into the pepino may well have taken place. Such post-origin introgression is suggested for other close relatives of the pepino as well, in particular, *S. caripense* (Anderson & Jansen, 1998; Anderson et al., 1996).

Acknowledgments. We appreciate the support for this research from the Department of Ecology and Evolutionary Biology, The University of Connecticut, and Instituto para la Conservación y Mejora de la Agrodiversidad Valenciana (COMAV). We thank Ken Bernier, José M. Blanca, Toya Cuenca, Andrew Doran, Virge Kask, Clinton Morse, Paul Neal, Matthew R. Opel, Mariola Plazas, Adrián Rodríguez, Carl Schlichting, and Colin Young for help with various aspects of this work. Victoria Hollowell, Tom Mione, and an anonymous reviewer provided constructive comments on the manuscript. Special thanks to Michael Nee for advice on name selection, Nicholas Tippery for help with the names and the Latin diagnoses, and David Spooner for comments on an earlier version of the manuscript.

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