



Solanum lycopersicum L.

This mid-sixteenth century watercolor, part of unpublished manuscript materials of Leonhard Fuchs (Codex II, 122, p. 161), is probably the oldest illustration of the tomato plant prepared in Europe. It is morphologically inaccurate in its depiction of the inflorescences as axillary and single-flowered, but shows a variety of fruit morphologies and colors. The upper-left-hand marginal sketch of the 7-petaled flower is accurately detailed. [Reproduced with permission of the Österreichische Nationalbibliothek, Vienna.]

SYSTEMATIC BOTANY MONOGRAPHS

VOLUME 84

Taxonomy of Wild Tomatoes and their Relatives
(*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*,
sect. *Lycopersicon*; Solanaceae)

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THE AMERICAN SOCIETY OF PLANT TAXONOMISTS

2 June 2008

SYSTEMATIC BOTANY MONOGRAPHS
ISSN 0737-8211

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ISBN 978-0-912861-84-5

Printed in the United States of America

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TAXONOMY OF WILD TOMATOES AND THEIR RELATIVES (*Solanum* SECT. *Lycopersicoides*, SECT. *Juglandifolia*, SECT. *Lycopersicon*; SOLANACEAE)

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ABSTRACT. *Solanum* section *Lycopersicon* (Solanaceae) includes the cultivated tomato (*S. lycopersicum*) and 12 additional wild relatives, endemic to western South America from Ecuador to northern Bolivia and Chile, and with two endemic species in the Galápagos Islands; weedy escaped forms of *S. lycopersicum* are distributed worldwide. Two species in *Solanum* section *Juglandifolia*, distributed in Colombia, Ecuador, and Peru, are sister to section *Lycopersicon*, and two species of *Solanum* section *Lycopersicoides*, distributed in southern Peru and northern Chile, are sister to sections *Lycopersicon* and *Juglandifolia*. The delimitation and relationships of wild tomatoes have differed widely depending upon whether morphological or biological species concepts are considered more important. Our monograph summarizes recent morphological and molecular studies of section *Lycopersicon*, section *Juglandifolia*, and section *Lycopersicoides*, and utilizes data from herbarium specimens and observations of germplasm accessions of all species grown in gardens. We recognize four species from the previously polymorphic *S. peruvianum* sensu lato: *S. arcanum*, *S. corneliomulleri*, *S. huaylasense*, and *S. peruvianum* sensu stricto, and recognize section *Lycopersicoides* at sectional level for the first time. Full descriptions and synonymies (including designations of lectotypes), illustrations, distribution maps, and an extensive list of localities are provided for all of tomato and outgroup species.

INTRODUCTION

Solanum L., with approximately 1,500 species (J. Bennett & S. Knapp, pers. comm., Sep 2006), represents one of the largest genera of the angiosperms and is the largest genus in the Solanaceae. The genus is widespread, but circum-Amazonian tropical South America is the center of diversification and species richness (Knapp 2002d). *Solanum* traditionally has been recognized by the pentamerous flowers with partly fused sepals, usually persistent and often enlarged around the fruits, the petals variously fused with corollas stellate, pentagonal, to rotate, and with a short tube and spreading almost flat lobes to broadly campanulate; stamen filaments short and attached to the corolla tube; anthers connivent or connate around the style, opening by terminal pores sometimes expanding into longitudinal slits, or introrsely longitudinally dehiscent with age (sect. *Lycopersicon*); with fruits typically bicarpellate bilocular berries. In the most recent traditional

classification of the entire genus based on overall morphology D'Arcy (1972) distinguished seven subgenera and 52 sections. *Solanum* (in our expanded sense here) includes valuable crops, such as tomato (*S. lycopersicum*), eggplant (*S. melongena* L.), potato (*S. tuberosum* L.), other edible species like pepino (*S. muricatum* Ait.), naranjilla (*S. quitoense* Lam.), cocona (*S. sessiliflorum* Dunal), and species used for medicinal or ornamental purposes.

Wild tomatoes have traditionally been treated within the genus *Lycopersicon* Mill., mainly based on the anther morphology (D'Arcy 1972; Hunziker 2001). In this monograph, we treat tomatoes in *Solanum*, rather than as the segregate genus *Lycopersicon*, based on morphological and molecular evidence. In the past decade, several molecular phylogenetic studies of the Solanaceae unambiguously showed tomatoes to be deeply nested within *Solanum* (Spooner et al. 1993; Bohs & Olmstead 1997, 1999; Olmstead & Palmer 1997; Olmstead and al. 1999; Peralta & Spooner 2001; Bohs 2005; Spooner et al. 2005). We propose a phylogenetic classification philosophy that simply states the hypothesis that tomatoes may have more "predictivity" under *Solanum*, and also apply a Linnaean nomenclatural system (hierarchical) to provide the accepted names of wild species in *Solanum*.

We propose a formal classification of tomatoes in *Solanum* sect. *Lycopersicon* and recognize 13 species, all native to western South America, from Ecuador to northern Bolivia and Chile, with two endemic species in the Galápagos Islands; weedy escaped forms of the cultivated tomato (*S. lycopersicum*) are distributed worldwide (see Table 1 for authors of species and equivalent names of tomato in *Lycopersicon* and *Solanum*). *Solanum* section *Lycopersicon* comprises annuals or biennials to herbaceous perennials characterized by 2–3 leaves per sympodial unit, 1–2-branched (rarely 3–4-branched) inflorescences, and a distinctive androecium. The anthers are strongly coalescent by interlocking lateral hairs, forming a tube with a sterile apical appendage, and dehisce by longitudinal introrse slits (except in *S. pennellii* the anthers are separate to slightly connivent and without a sterile apical appendage). The fruits are berries, which are either red, orange, or yellow when carotenoid pigments are present, or green with purple mottling or purple stripes when anthocyanin pigments are present. We also provide an informal classification within sect. *Lycopersicon* by recognizing species groups that reflect our hypotheses of species relationships.

The immediate outgroups of tomatoes are treated in two sections: *Juglandifolia* and *Lycopersicoides*, both characterized by plurifoliate sympodial units with usually more than 3 leaves in each, inflorescences usually with more than 4–5 dichotomous branches, separate or moderately connivent anthers that lack a sterile apical appendage and that initially dehisce by apical pores and only later by introrse slits to the anther base, and by fruits that are usually uniformly green and lack darker stripes. *Solanum* sect. *Juglandifolia* is sister to sect. *Lycopersicon* and comprises two woody vining species distributed in Colombia, Ecuador, and Peru, *S. juglandifolium* and *S. ochranthum*, with ebracteate inflorescences, bright yellow anthers, and large fruits (>15 mm in diameter) with a thick, hard pericarp. *Solanum* sect. *Lycopersicoides*, sister to sections *Lycopersicon* + *Juglandifolia*, comprises two shrub or subshrub species distributed in southern Peru and northern Chile, *S. lycopersicoides* and *S. sitiens*, with bracteate inflorescences, pale yellow to almost white anthers, and fruits 10–15 mm in diameter with a thin, leathery pericarp.

Considering morphological characters, phylogenetic relationships, and geographic distribution, we recognize here four species within the highly polymorphic and taxonomically difficult green-fruited species *S. peruvianum* sensu lato: *S. arcanum*, *S. huaylasense*,

TABLE 1. Species list for *Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, and sect. *Lycopersicon*, with names in *Lycopersicon*, fruit color, and breeding system. SI = self-incompatible; SC = self-compatible.

NAME IN SOLANUM	NAME IN LYCOPERSICON	FRUIT COLOR	BREEDING SYSTEM
1. <i>S. lycopersicoides</i> Dunal	<i>L. lycopersicoides</i> (Dunal) A. Child ex J. M. H. Shaw	green-yellow when maturing, black when ripe	SI, allogamous
2. <i>S. sitiens</i> I. M. Johnst.	<i>L. sitiens</i> (I. M. Johnst.) J. M. H. Shaw	green-yellow when maturing, black when ripe	SI, allogamous
3. <i>S. juglandifolium</i> Dunal	<i>L. juglandifolium</i> (Dunal) J. M. H. Shaw	green to yellow-green	SI, allogamous
4. <i>S. ochranthum</i> Dunal	<i>L. ochranthum</i> (Dunal) J. M. H. Shaw	green to yellow-green	SI, allogamous
5. <i>S. pennellii</i> Correll	<i>L. pennellii</i> (Correll) D'Arcy	green	usually SI, some SC in southern part of range
6. <i>S. habrochaites</i> S. Knapp & D. M. Spooner	<i>L. hirsutum</i> Dunal	green with darker green stripes	typically SI, with SC populations at range margins
7. <i>S. chilense</i> (Dunal) Reiche	<i>L. chilense</i> Dunal	green to whitish green with purple stripes	SI, allogamous
8. <i>S. huaylasense</i> Peralta	partly <i>L. peruvianum</i> (L.) Miller	typically green with dark green stripes	typically SI, allogamous,
9. <i>S. peruvianum</i> L.	<i>L. peruvianum</i> (L.) Miller	typically green to greenish white, sometimes flushed with purple	typically SI, allogamous,
10. <i>S. corneliomulleri</i> J. F. Macbr. (1 geographic race: Misti near Arequipa)	partly <i>L. peruvianum</i> (L.) Miller; also known as <i>L. glandulosum</i> C. F. Mill.	typically green with dark green or purple stripes, sometimes flushed with purple	typically SI, allogamous,
11. <i>S. arcanum</i> Peralta (4 geographic races: humifusum, lomas, Marañón, Chotano-Yamatuc)	partly <i>L. peruvianum</i> (L.) Miller	typically green with dark green stripes	typically SI, allogamous, rarely SC, allogamous, facultative allogamous
12. <i>S. chmielewskii</i> (C. M. Rick et al.) D. M. Spooner et al.	<i>L. chmielewskii</i> C. M. Rick et al.	typically green with dark green stripes	SC, facultative allogamous
13. <i>S. neorickii</i> D. M. Spooner et al.	<i>L. parviflorum</i> C. M. Rick et al.	typically green with dark green stripes	SC, highly autogamous
14. <i>S. pimpinellifolium</i> L.	<i>L. pimpinellifolium</i> (L.) Miller	red	SC, autogamous, facultative allogamous
15. <i>S. lycopersicum</i> L.	<i>L. esculentum</i> Miller	red	SC, autogamous, facultative allogamous
16. <i>S. cheesmaniae</i> (L. Riley) Fosberg	<i>L. cheesmaniae</i> L. Riley	yellow, orange	facultative allogamous
17. <i>S. galapagense</i> S. C. Darwin & Peralta	partly <i>L. cheesmaniae</i> L. Riley	yellow, orange	SC, exclusively autogamous
			SC, exclusively autogamous

S. peruvianum, and *S. corneliomulleri*. The first two species were described as new from Peru (Peralta et al. 2005), and the last two were already named by Linnaeus (1753) and MacBride (1962), respectively. We also recognize the yellow- to orange-fruited species *S. galapagense*, segregated from *S. cheesmaniae* (Darwin et al. 2003; Knapp & Darwin 2006); both species are endemic to the Galápagos Islands.

We rely on clear morphological discontinuities to define the easily distinguished species *S. habrochaites*, *S. juglandifolium*, *S. lycopersicoides*, *S. pennellii*, *S. ochranthum*, and *S. sitiens*. The following closely related species are generally easy to distinguish but sometimes intergrade: 1) *S. lycopersicum*, *S. pimpinellifolium*, 2) *S. cheesmaniae*, *S. galapagense* (sometimes also with introduced *S. pimpinellifolium*), 3) *S. arcanum*, *S. chmielewskii*, *S. neorickii*, 4) *S. corneliomulleri*, *S. peruvianum*, 5) *S. chilense*, *S. huaylasense*. Specific characters used for recognition are detailed with each species description and in the keys.

We do not recognize taxa below the species level, most notably the small-fruited tomatoes known to many as “var. *cerasiforme*.” The name “*cerasiforme*” has been used to refer to putatively wild forms of *S. lycopersicum* that have been regarded as progenitors of the cultivated tomato. It is impossible to distinguish wild from cultivated forms using herbarium specimens, and we regard many specimens labeled as “var. *cerasiforme*” to be possible revertants from cultivation (i.e., feral plants) or possible hybrids of wild and weedy taxa.

Our monograph of the 17 species of sections *Lycopersicoides*, *Lycopersicon*, and *Juglandifolia* summarizes recent morphological and molecular studies and uses data from herbarium specimens and from germplasm accessions of all species grown in gardens. Full descriptions and synonymies (including designations of lectotypes), clarification of nomenclatural matters, illustrations, distribution maps, and an extensive list of localities are provided for all species. Our goal is to construct a predictive phylogenetic classification based on an integrative approach and to provide a useful taxonomy for all biologists working with tomatoes.

MATERIALS AND METHODS

Our taxonomic treatment of tomatoes and their relatives draws upon data from morphological, molecular, crossability, and field studies, as described in Relationships and Species Concepts below. We considered data from both molecular cladistic and morphological phenetic studies (Peralta & Spooner 2005); we used extensive germplasm collections from the C. M. Rick Tomato Genetic Resource Center (TGRC) in Davis, California, and from the USDA germplasm collection in Geneva, New York. Many of these collections lacked herbarium vouchers, and we grew plants of these unvouchered accessions to reproductive maturity in field plots in Mendoza, Argentina, in Hancock, Wisconsin, and in greenhouses in Madison, Wisconsin, and the Chelsea Physic Garden in London; vouchers of these specimens are deposited at BM, DAV, MERL, and WIS. Recently, the herbarium vouchers collected by Dr. Rick in his many years of field work obtaining germplasm were found in Davis, California (R. Chetelat, pers. comm., March 2007). These specimens are in the process of being labelled and mounted, and the data will be entered into a database and eventually made available in association with the germplasm collections of the TGRC (www.tgrc.com; R. Chetelat, pers. comm., March 2007). We also examined approximately 5000 collections from 49 herbaria (herbarium abbreviations in the text follow *Index herbariorum*, Holmgren et al. 1990; a complete list of the herbaria consulted is

given in the Acknowledgments). Cultivated collections sometimes show atypical morphology (often larger parts), and our species descriptions in this monograph are taken entirely from material collected in the wild. Many wild tomatoes and their relatives are cultivated in botanical gardens and agricultural stations for breeding purposes. We have examined many such collections (particularly of *S. lycopersicum*), but have excluded them from the specimen citations in this monograph; some can be found in the Index to Numbered Collections Examined, and the country distribution of *S. lycopersicum* is presented in Appendix 3. Many tomato specimens were collected by anonymous collectors or were not given numbers by their collectors. We have not included these in the Index to Numbered Collections Examined, although many can be found in the specimens cited for the relevant species. Complete specimen citations of all material examined for this treatment, with full label data, can be found on the Solanaceae Source website, established as part of the “PBI: *Solanum* Planetary Biodiversity Inventory” project (<http://www.nhm.ac.uk/solanaceaesource>). Where we have not specifically cited cultivated specimens, we list the countries in which specimens we have seen were collected in the discussion for each species (with the exception of *S. lycopersicum*, see above).

Morphological studies of anthers and seeds were undertaken at the Natural History Museum (London). Material was prepared from herbarium specimens, mounted on aluminum stubs and sputter-coated with gold palladium, then viewed in a field emission scanning electron microscope (Philips XL30) operated at 5kV.

PRE-LINNAEAN CONCEPTS OF TOMATOES AND THEIR RELATIVES

Tomatoes were introduced into Europe from the Americas and became known to botanists about the middle of the sixteenth century. Pietro Andrea Matthioli (Latinized as Petrus Andrea Matthiolus and sometimes also written as Mattioli) described tomatoes for the first time in the first edition of his *Di Pedacio Dioscoride Anazarbeo . . .* (Matthioli 1544), an Italian-language commentary upon the work of the 1st century Greek botanist Dioscorides of Anazarbos. Matthioli incorporated information from different sources into observations of Dioscorides (see Arber 1990), and his text was greatly enriched with Italian local and traditional knowledge, including the descriptions and uses of plants previously not known in Europe. The affinity of tomatoes to other solanaceous plants was well known to herbalists. Matthioli’s description indicates the tomato is a sort of mandrake. Tomatoes were classified and identified by comparison with plants already known in Europe and from classical Greek references, and, following this tradition, Matthioli (1544) described tomatoes in his section “Della Mandragorae,” as: “Portansi à i tempi nostri d’un’altra spetie in Italia stiacciante come le mele rose, & fatte a spicci, de color prima verdi & come son mature, di color d’oro, lequali pur si mangiano nel medesimo modo” (Another species has been brought to Italy in our time, flattened like the “mele rose” [variety of apple] and segmented, green at first and when ripe of a golden color, which is eaten in the same manner). In the same section on mandrakes he described the preparation of eggplants (“mele insane”) fried in oil with salt and pepper, as with mushrooms; apparently tomatoes were prepared in the same way.

Matthioli traveled widely in northern Italy and was a keen observer of plants cultivated and growing wild in the region (Raphael 1989). His description of the tomato almost certainly came from first-hand knowledge of live plants. In his first Italian edition Matthioli (1544) referred to the tomato as “pomi d’oro” (the Italian common name) and in the

first Latin edition (Matthioli 1554) as “mala aurea” (the Latin equivalent, later translated into English as “golden apples”). Many editions of Matthioli’s work were produced throughout Europe, in many languages (see Watson 1989), and additional information was included in these later versions—a 1572 French translation (Matthioli 1572) refers to eggplants as “pomme d’amour” and tomatoes as another type of these, both still associated with mandrakes. This translation bears no relation to the Latin from which it was said to have been taken and is certainly an addition of the translator; earlier works (e.g., Dodoens 1554) used the name “poma amoris” (see Fig. 1) only for the tomato.

The tomato was not illustrated in any of the many editions of the *Commentarii in sex libros Pedacii Dioscorides* produced during Matthioli’s lifetime (1501–1577). Even the monumental set of woodcuts made for the illustration of mid-16th century editions (Matthioli 1562, 1563, 1565; see Watson 1989; Bidwell 2003) did not include the tomato, although the eggplant (*Solanum melongena*) was illustrated, as were mandrakes (*Mandragora officinarum* L.). In the 1586 edition of Matthioli’s work, edited by Joachim Camerarius and published in Frankfurt, an illustration of the tomato was included for the first time (Matthioli 1586), and a different illustration was used in the edition edited by Caspar Bauhin in Basel (Matthioli 1598). The woodcuts representing *Solanum lycopersicum* were taken from other woodcut sets, not those used in editions of Matthioli’s work (see Watson 1989 and below); that in the Frankfurt edition from Camerarius’s own woodcuts prepared in the 1580s, and that in the Basel edition apparently based on the illustration of Dodoens (1554).

In the mid-sixteenth century the German physician and medical professor Leonhart Fuchs (1542) published his *De Historia Stirpium comentarii insignes* (or *Notable Commentaries on the History of Plants*). He broke with tradition by illustrating plants as they looked in nature instead of using conventional (and often bizarrely inaccurate) representations based on Greek and Roman sources. Tomatoes were not illustrated in the editions published during his lifetime, but his collected unpublished observations are held in Vienna and are referred to as the ‘Vienna Codex’ (Meyer et al. 1999). The Vienna Codex contains a large number of previously unpublished illustrations and descriptions of plants, one of which is the tomato, referred to as “De Mala Aurea.” Fuchs’s description is detailed and makes clear this is an unfamiliar plant: “This plant is one of the number that were not mentioned by the ancient Greeks or Romans, or even the Moors, so we must use the name known for it today. . . . The [golden] apple is not found in our region unless it is planted” (Meyer et al. 1999). The Vienna Codex also contains a watercolor (see frontispiece) that is certainly one of the earliest depictions of the tomato; it was executed sometime between 1542 and Fuchs’s death in 1560. Fuchs’s illustration is of a “composite” plant, bearing fruits of various colors and shapes. The herb is easily recognizable as a tomato plant but is morphologically incorrect in showing axillary and mostly single-flowered inflorescences; however, the flowers (both painted and sketched in the margin) are accurate representations of the “fasciated” flowers common in the cultivated tomato.

The first published illustration of the tomato is a woodcut, which certainly represents the cultivated species *Solanum lycopersicum*, in Dodoens’s herbal (1554) and was used again in subsequent editions and translations of that and many other works (Dodoens 1557, 1563). This rather crude woodcut (Fig. 1), labeled “poma amoris,” shows a plant with 8-parted flowers and highly fasciated fruits. It is clear that tomatoes first seen by European botanists were not wild plants, and that they had been introduced as already highly modified, cultivated plants (for a discussion of the introduction and early cultivation of tomatoes see below). Camerarius’s woodcut published in his edition of Matthioli (1586) is also of a modified, cultivated plant with many-parted flowers and lobulate fruits (Fig. 2).

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POMA AMORIS.

Pomum
amoris
et à nōc
nullis
Pomum
aureum
hic fru-
ctus no-
minatur
Germa.
Goldt
opffel.
Brabāt.
Wulde
appel.
Gallis
Pōme
d'a-
mours.

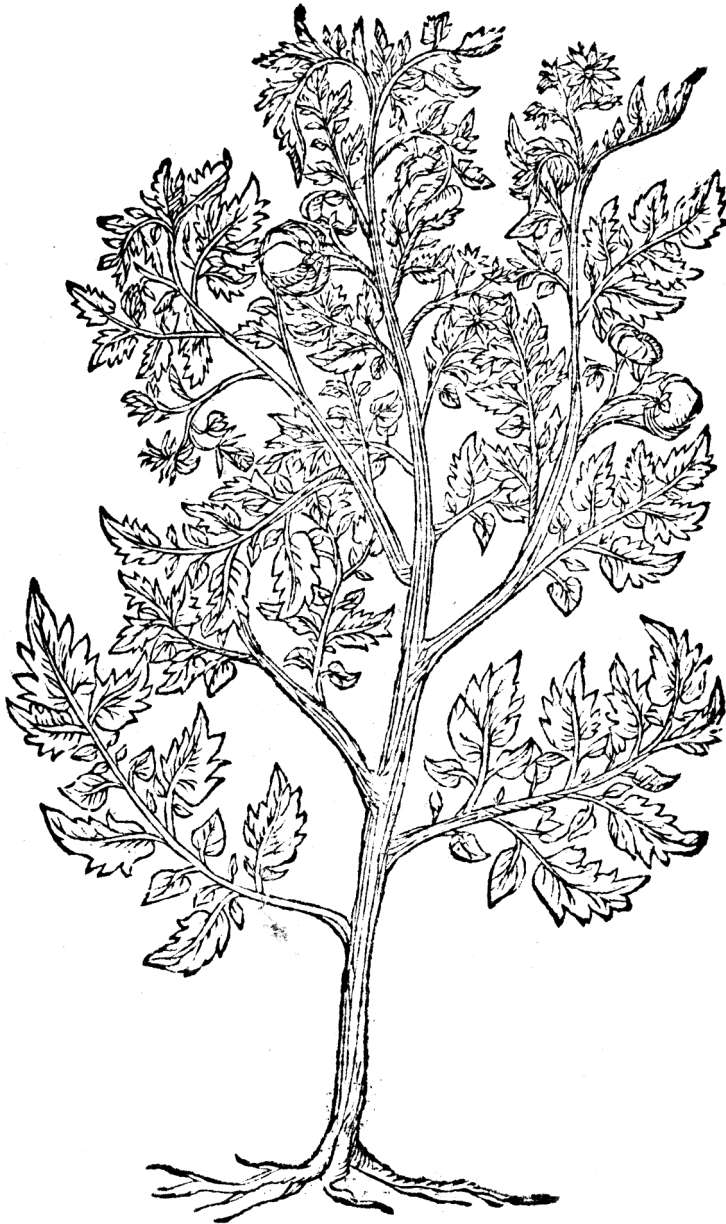


FIG. 1. The first published illustration of the tomato, *Solanum lycopersicum*, from Dodoens (1554). Reproduced with permission of the Natural History Museum Botany Library.

POMA AMORIS.



FORMA.

Herba late ramos spargit, grauitur olentes, fere vt Gariophyllorū Indicorum planta, crescit ad altitudinem humani corporis. fert poma magnitudine oui, primo viridia, vbi maturuerint, crocea, vel rubra.

LOCVS.

Habetur in hortis, locisque gaudet humidis.

QUALITATES,
ET VIRES.

Frigida est, & forte nō absq; maligna qualitate, Poma vero innoxie in Italia eduntur. Eadem oleo macerantur & infolantur, vel in fimum equinum infoduntur, ad scabiem inungendam, idque mirifice à quibusdam commendatur.*

FIG. 2. The woodcut of "Poma aurea" or "Goldapffel" (*Solanum lycopersicum*) from Matthioli (1586). Reproduced with permission of the Trustees of the Royal Botanical Gardens, Kew.

The herbalist Anguillara (1561) equated the tomato with a plant described fourteen centuries earlier by the Greek physician Galen called *Lycopersicon* (λυκοπεροτον, "wolf peach"), but of course it does not correspond to any form of tomato, which is native to the New World (Luckwill 1943a). Anguillara (1561) associated the tomato with "melanzane," the eggplant or aubergine (*Solanum melongena*); he recognized tomato and eggplant as belonging to the same group.

The earliest extant herbarium specimen of tomato is in the sixteen-volume herbarium of Ulisse Aldrovandi, now preserved in the herbarium of the Botanical Garden of Bologna. Aldrovandi was a student of the great Italian botanist and founder of the first botanical garden Luca Ghini, and his herbarium is regarded as the oldest extant collection of pressed plants (Mattiolo 1899). Aldrovandi collected in the area of Bologna and by 1570 had already amassed fourteen volumes of pressed plants (Mattiolo 1899). The specimen of the tomato (Fig. 3), labeled "Pomum amoris Mali insani species," was probably collected in the middle of the sixteenth century. Another early tomato specimen, attributed



FIG. 3. Oldest herbarium specimen of *Solanum lycopersicum*, from the Aldrovandi herbarium (Vol. 1, p. 368) in Bologna. The pair of leaves at the bottom of the page belongs to a species of Cucurbitaceae. Copyright Sistema Museale D'Ateneo, Università degli Studi di Bologna.

to Petrollini and mentioned by McCue (1952) as held in the Biblioteca Angelica in Rome, was not traced by us.

As noted above, the relationship of tomatoes with the genus *Solanum* was early recognized by botanists, who commonly referred to tomatoes as “*Solanum pomiferum*” or apple-bearing nightshade during the late sixteenth and early seventeenth century (Sabine 1820). Caspar Bauhin, in his edition of Matthioli (Matthioli 1598), labeled his illustration of the tomato “*Solanum pomiferum, fructu rotundo, molli*” (Fig. 4) and in his *Pinax Theatri Botanici* (1623), an index of plants in his own work and that of the Greek and Roman herbalists Theophrastus, Dioscorides, and Pliny, also referred to “*Solanum pomiferum*.” Tournefort (1694) was the first to consider cultivated tomatoes as distinct from *Solanum* and used the Greek term *Lycopersicon*. He placed plants with large multilocular fruits in a group he called *Lycopersicon* and those with bilocular fruits of in second group he called *Solanum*; however, tomatoes can have two or more locules, with the multilocular trait common in cultivated tomatoes. Within his *Lycopersicon*, Tournefort listed nine different taxa, two of which are now excluded from tomatoes. Tournefort’s “*Lycopersicon fructo striato duro*” most probably refers to some species of *Physalis* L. and his “*Lycopersicon americanum arborescens*” certainly corresponds to *Solanum betaceum* Cav., the tree tomato [formerly known as *Cyphomandra betacea* (Cav.) Sendtn., see Bohs 1995]. Using fruit color and fruit size, Tournefort distinguished seven taxa that correspond to what we recognize as cultivars of *S. lycopersicum*. As Jenkins (1948) noted concerning early nomenclature of the tomato: “The multitude of scientific names is a record of ideas on the taxonomy of tomatoes, but is of no significance in tracing their origin.” (see also Domestication of the Cultivated Tomato below).

In his first edition of *The gardener’s dictionary* (Miller 1731) Philip Miller, the English botanist and curator of the Chelsea Physic Garden, followed Tournefort in using the generic name *Lycopersicon* and included a number of taxa with multilocular fruits (“roundish, soft, fleshy Fruit which is divided into several Cells, wherein are contain’d many flat Seeds”), all color variants of the cultivated tomato (*S. lycopersicum*). In this same work he also recognized *Solanum*, and included within it the eggplant, as “*Solanum Americanum, spinosum, foliis Melongenae, fructu mammore,*” and the potato, as “*Solanum tuberosum, esculentum.*”

TAXONOMIC HISTORY

Linnaeus, in the first edition of *Species plantarum* (1753), classified tomatoes in the genus *Solanum*, and included two species, *S. lycopersicum* and *S. peruvianum*. He included within *S. lycopersicum* all the forms described by Tournefort as different taxa. Jussieu (1789), in his *Genera plantarum*, also included tomatoes in *Solanum*.

Philip Miller, in the abridged 4th edition of *The gardener’s dictionary* of 1754, expanded his definition of *Lycopersicon* by including “*Lycopersicon radice tuberosa, esculentum*” (the potato) and stated: “This Plant was always ranged in the Genus of *Solanum*, or Nightshade, and is now brought under that Title by *Dr. Linnaeus*; but as *Lycopersicon* has now been establish’d as a distinct Genus, on account of the Fruit being divided into several Cells, by intermediate Partitions, and as the Fruit of this Plant [the potato] exactly agrees with the Characters of the other species of this Genus, I have inserted it here.” In the 8th edition of the *Gardener’s dictionary* Miller (1768) adopted the binomial nomenclature introduced by Linnaeus (1753) and published binomials with descriptions for all



FIG. 4. The woodcut of "*Solanum pomiferum fructu rotundo molli*" (*Solanum lycopersicum*) from Matthioli (1598), a Latin edition edited by Caspar Bauhin. Reproduced with permission of the Natural History Museum Botany Library.

his recognized species of *Lycopersicon*: *L. Galeni*, *L. esculentum*, *L. aethiopicum* (the scarlet eggplant, *S. aethiopicum* L.), *L. pimpinellifolium*, *L. peruvianum*, *L. procumbens* (see Doubtful and Excluded Names), and *L. tuberosum*. In the posthumously published edition of *The gardener's and botanist's dictionary* (Miller 1807) the editor Thomas Martyn merged *Lycopersicon* and *Solanum*, and accepted all of Miller's species as members of *Solanum*. A number of classical and modern authors continued to recognize a separate genus for tomatoes and used the Tournefortian name *Lycopersion*, validated by Miller in 1768 (e.g., Dunal 1813, 1852; Bentham 1873; Müller 1940a, 1940b; Luckwill 1943a, 1943b; Correll 1958; D'Arcy 1972, 1987, 1991; Hunziker 1979, 2001; Rick 1979, 1988; Rick et al. 1990; Symon 1981, 1985; Taylor 1986; Warnock 1988; Hawkes 1990).

Michel-Félix Dunal was a nineteenth-century specialist of the family Solanaceae (see Knapp 2007a). In his doctoral thesis *Histoire naturelle, medicinale et économique des Solanum*, Dunal (1813) included tomatoes in *Lycopersicon* and described *L. cerasiforme* and *L. pyriforme* as new species based on the shape of the fruits. He expanded this treatment by publishing a synopsis of all taxa in *Solanum* and its relatives (Dunal 1816), and described three new species in the genus *Lycopersicon*: *L. hirsutum*, *L. regulare*, and *L. dentatum*. In this work he also described three relatives of the tomatoes as new species in the genus *Solanum*, *S. juglandifolium*, *S. ochranthum*, and *S. caldasii*. In his treatment of the Solanaceae for Candolle's *Prodromus*, Dunal (1852) further increased the number of species, subspecies, and varieties among taxa now recognized as tomatoes and their relatives. He included 10 species, and described *L. agrimoniifolium*, *L. chilense*, *L. philippinarum*, and *S. lycopersicoides* as new. Wettstein (1895), in his classical revision of the Solanaceae, included *Lycopersicon* as part of the genus *Solanum*, a treatment followed by a minority of later authors (MacBride 1962; Seithe 1962; Heine 1976; Fosberg 1987). Börner (1912) also recognized the close affinity between tomatoes and potatoes, and proposed a new genus *Solanopsis* to segregate them from the rest of *Solanum*. D'Arcy (1972, 1987) in his list of the types of sections of *Solanum* treated *Lycopersicon* as a distinct genus. He later discussed the differences in anther morphology thought to separate the two genera (D'Arcy 1987), and suggested that perhaps *Lycopersicon* should be merged with *Solanum*, but following convention kept the two genera separate. Lester (1991) studied the relationships among domesticated pepinos, potatoes, and tomatoes, and used seed coat characters and other data to show their close affinities. He concluded that these three groups could be included in a single genus segregated from *Solanum*, but decided for practical reasons to treat them in *Solanum* sect. *Basarthrum* (Bitter) Bitter (the pepino), *Solanum* sect. *Petota* Dumort (the potatoes), and *Lycopersicon* (the tomatoes).

The species of tomatoes have been treated quite differently by different authors, both in terms of species identity and in terms of group membership and relationships. Figure 5 depicts the differing classifications through the twentieth century and compares them to our classification adopted here. We have not included in the diagram those classifications that focused primarily on the cultivated tomatoes (e.g., Lehmann 1955; Brezhnev 1958) rather than on the group as a whole (see below).

Müller (1940a) and Luckwill (1943a) produced the two most complete taxonomic treatments of wild tomatoes based on morphological concepts, and recognized them under *Lycopersicon* (Fig. 5). Müller (1940a) divided *Lycopersicon* into two subgenera: subg. *Eulycopersicon* (two species) with glabrous, and red- to orange- to yellow-colored fruits, flat, obovate, and silky pubescent seeds, ebracteate inflorescences, and leaves without pseudostipules; and subg. *Eriopersicon* (four species) with pubescent or hirsute, green or greenish white to yellowish and purple-tinged fruits, frequently with a dark green,

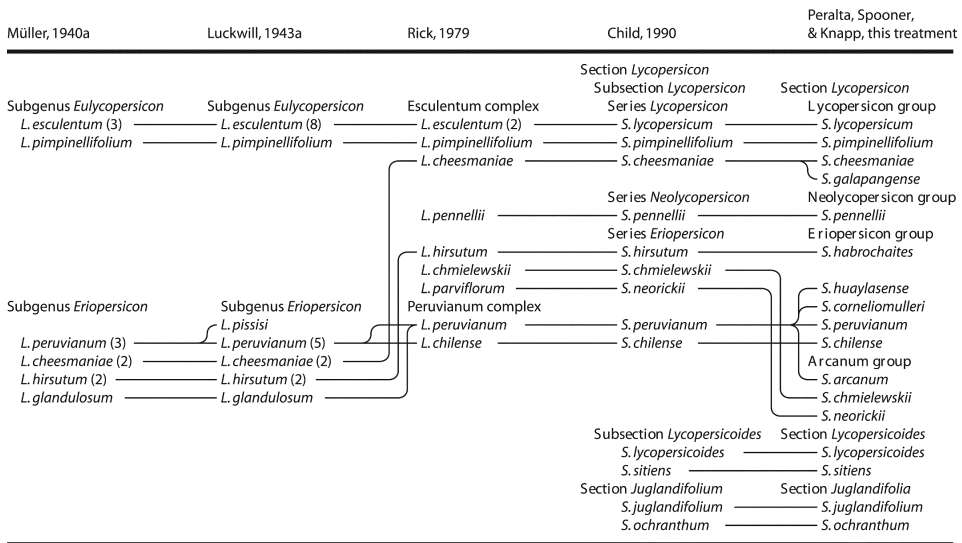


FIG. 5. Chronological flow chart of hypotheses of species boundaries and relationships of *Solanum* sect. *Lycopersicon*, sect. *Juglandifolia*, and sect. *Lycopersicoides* as recognized by Müller (1940a), Luckwill (1943a), Child (1990), and in the present treatment. The numbers in parentheses represent the number of infraspecific taxa recognized by these authors.

lavender, or purple stripe, thick, oblanceolate, glabrous (pilose only at the apex) seeds, bracteate inflorescences, and leaves usually with pseudostipules. Müller (1940a) also described a new species, *L. glandulosum*, and divided the highly polymorphic *L. peruvianum* into two varieties: var. *dentatum* and var. *humifusum*. Within the Galápagos Island endemic *L. cheesmaniae* he included two forms: f. *typicum* and f. *minor*, and also described two forms within the Andean *L. hirsutum*: f. *typicum* and f. *glabratum*.

Three years later, Luckwill (1943a) adopted Müller's (1940a) two subgenera but proposed different infraspecific taxa and recognized five species in the subg. *Eriopersicon* (see Fig. 5). He agreed with Müller (1940a) in the circumscription of subg. *Eulycopersicon*, but within *Eriopersicon* he considered *L. pissisi* a distinct species, and placed *L. peruvianum* var. *humifusum* as its synonym. He also proposed new infraspecific categories in *L. esculentum*, *L. cheesmaniae*, *L. hirsutum*, and *L. peruvianum*. He recognized four subspecies within *L. esculentum*: subsp. *galeni*, subsp. *humboldtii*, subsp. *intermedium*, and subsp. *typicum*, and described five varieties within the last subspecies: var. *commune*, var. *grandiflorum*, var. *pyriforme*, var. *typicum*, and var. *validum*. Luckwill elevated Müller's division of the Galápagos tomatoes to subspecific rank; subsp. *typicum* and subsp. *minor*. Tomatoes from the Galápagos Islands have yellow to orange fruits, bractless inflorescences, and leaves without pseudostipules. Based on these characters *L. cheesmaniae* belongs to subg. *Eulycopersicon*, as defined by both Müller and Luckwill, but was rather inexplicably assigned to subg. *Eriopersicon* by both authors (Müller 1940a; Luckwill 1943a). Luckwill recognized two varieties within *L. hirsutum*: var. *agrimoniifolium* and var. *glabratum*. In the polymorphic *L. peruvianum* he recognized four subspecies: subsp. *commutatum*, subsp. *dentatum*, subsp. *puberulum*, and subsp. *typicum*, and within the last subspecies he described var. *typicum* and var. *regulare*.

Lehmann (1954) developed his own classification system for the tomato plants cultivated at the Gatersleben Institute of Crop Plant Research in the former East Germany

(now known as the Leibniz Institute of Plant Genetics and Crop Plant Research, or IPK Gatersleben). He treated the wild species as had Müller (1940a), and recognized *L. esculentum*, *L. pimpinellifolium*, *L. peruvianum*, *L. cheesmaniae* (as *L. cheesmanii*), *L. hirsutum*, and *L. glandulosum*. For the cultivated tomato, *L. esculentum*, he devised a complex classification of convarieties and provarieties (which seem to be more or less equivalent to the rank of variety). Although these names are validly published under the ICBN and must be taken into account in synonymy (see *S. lycopersicum*), they are better considered as cultivar names; these names have been largely ignored by tomato breeders working in western Europe and the U.S.A. The germplasm lines from which these names were coined are still kept in cultivation in Gatersleben (H. Knupffer, pers. comm., November 2007), and will be of great interest for the study of cultivar relationships and character differentiation in the cultivated tomato.

In the former Soviet Union, a great deal of work was done on the systematics of cultivated plants, and tomatoes were no exception. Brezhnev (1958) produced a detailed account of the tomatoes for the *Cultivated Flora of the Soviet Socialist Republics (Kul'turnaia Flora SSSR vol. 20)* where he treated the three species available to him in the Soviet Union: *Lycopersicon peruvianum*, *L. esculentum*, and *L. hirsutum*. Within his *L. peruvianum* he recognized two varieties, Müller's var. *humifusum*, and var. *dentatum*, under which he placed in synonymy *L. dentatum*, *L. chilense*, *L. bipinnatifidum*, *L. atacamense*, *L. pissisi*, and *L. puberulum*. He did not record any of Luckwill's (1943a) names or combinations; he may not have had access to Luckwill's work. He recognized no infraspecific taxa for *L. hirsutum*. His treatments, both the 1958 *Flora* account and the later revised edition including just the tomato (Brezhnev 1964), were focused on the cultivated tomato, which he recognized as *L. esculentum*. He recognized the close relationship of *L. pimpinellifolium* and *L. esculentum*, and included the first as a variety of the latter. Within his concept of *L. esculentum*, he recognized three subspecies, 11 varieties, and many cultivars (as two categories, "grex conculorum" and cultivar). This classification is extremely complex, and is partly geographic and partly "phylogenetic"; it will be of great utility to those investigating the origins and relationships of tomato cultivars. We discuss Brezhnev's classification of *L. esculentum* more fully in the discussion of *S. lycopersicum* (p. 137). Many of the names he coined and combinations he proposed for infraspecific taxa were not validly published, because he did not follow the rules of the *Code* of the time. Although Brezhnev (1958, 1964) did not treat all the wild species, his detailed treatment of the morphology of the cultivars he studied was excellent. No American or western European treatments have made reference to this work (see discussion under *S. lycopersicum*).

More recently, Khrupalova (1999, 2001) treated tomatoes under *Lycopersicon* and recognized Müller's (1940a) two subgenera, and *Neolycopersicon*, at subgeneric level. She recognized ten species: *L. esculentum*, *L. cheesmaniae*, *L. pimpinellifolium*, *L. chmielewskii*, *L. parviflorum*, *L. pennellii*, *L. hirsutum*, *L. chilense*, *L. peruvianum*, and *L. glandulosum*. She basically followed Brezhnev's (1958, 1964) treatment and recognized many infraspecific taxa, all of which had been previously described, except those she named in *L. esculentum* (see below): one variety within *L. cheesmaniae*, *L. pennellii*, and *L. hirsutum*; two varieties within *L. pimpinellifolium* and *L. peruvianum*; and two subspecies (one autonymic), 17 varieties, and 60 subvarieties within *L. esculentum*. All of her names and combinations were published without reference to an original description or publication, Latin diagnoses, or designated type specimens, rendering them not validly published (*nomina nuda*, see Appendix 1); she used two categories, subspecies and

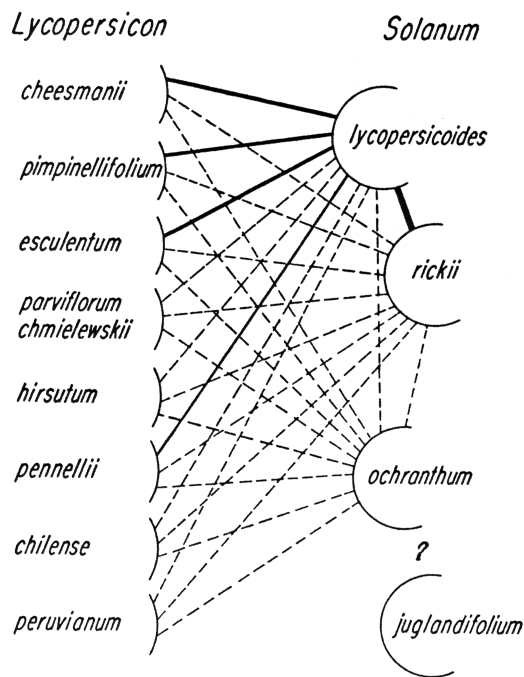


FIG. 6. Diagram of crossability relations among wild tomatoes and outgroups used by Rick (1979) to support the separation of *Lycopersicon* and *Solanum*. *Solanum lycopersicoides* hybridized unilaterally with *L. esculentum*, *L. pimpinellifolium*, *L. cheesmaniae*, and *L. pennellii*, and was compatible with *S. rickii* (= *S. sitiens*). *Solanum ochranthum* failed to cross in every combination; crossing tests with *S. juglandifolium* were not done due to failure of flowering. Solid lines indicates compatible combinations and dashed lines cross failures. Adapted from Rick (1979), reproduced with permission of Academic Press.

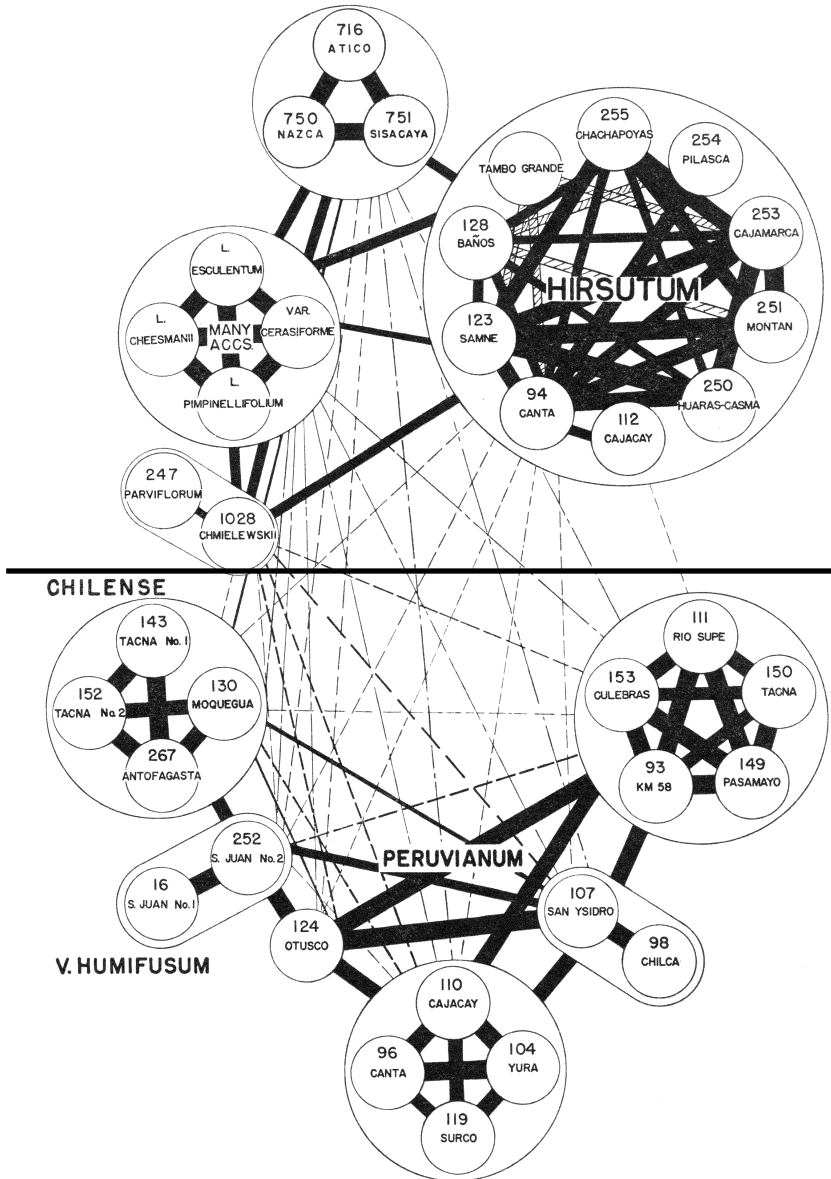
convariety, as equivalent, and we have assumed she intended these to be the same rank recognized in the *Code*, that of subspecies. The tomato collection preserved at the N. I. Vavilov Institute of Plant Industry of Saint Petersburg (VIR) is currently organized according Khrapalova's (1999, 2001) taxonomic treatment.

The noted tomato breeder and geneticist Charles Rick treated tomatoes in the genus *Lycopersicon*. Rick (1979; see Fig. 6) studied crossing relationships among wild tomatoes and other closely related species of the genus *Solanum*. He recognized *S. pennellii* as a member of the genus *Lycopersicon* and as belonging to his "Esculentum complex." Four *Solanum* species, considered related to tomatoes, were also studied by Rick (1979). *Solanum lycopersicoides* was compatible with its close relative *S. rickii* (here recognized as a synonym of *S. sitiens*), and also hybridized unilaterally (as a pollen donor) with *L. esculentum*, *L. pimpinellifolium*, *L. cheesmaniae*, and *S. pennellii*. *Solanum rickii* only crossed with its close relative *S. lycopersicoides*, while *S. ochranthum* failed to cross in every combination, and the crossability test with the closely related *S. juglandifolium* could not be performed. Based on these results, he concluded that the boundary between *Solanum* and *Lycopersicon* is profound and justified maintaining two genera (see Fig. 6).

Rick (1960, 1979) proposed an infrageneric classification based on crossing relationships discovered in his work with a large collection of wild-collected plants amassed for breeding purposes. He recognized nine wild tomato species, classified into two complexes

"Esculentum" Group

S. PENNELLII



"Peruvianum" Group

FIG. 7. Rick's (1979) polygon scheme showing his rationale for recognizing his "Esculentum" group (*Lycopodium cheesmaniae*, *L. chmielewskii*, *L. esculentum*, *L. parviflorum*, *L. pimpinellifolium*, *L. hirsutum*, and *L. pennellii*), and his "Peruvianum" group (*L. chilense*, *L. peruvianum*). Circles are labeled with TGRC accession numbers and localities; the width of connecting bands indicates the amount of seed produced by intrapopulation crosses, and dashed lines indicate crosses that failed to produce hybrids. Adapted from Rick (1979), reproduced with permission of Academic Press.

(Fig. 7). His “Esculentum complex” included seven species: *L. cheesmaniae*, *L. chmielewskii*, *L. esculentum*, *L. hirsutum*, *L. parviflorum*, *L. pennellii*, *L. pimpinellifolium*, mainly self-compatible except *L. hirsutum* and *L. pennellii*, and easily crossed with the cultivated tomato. Within this group, three species have mostly glabrous, pigmented fruits, while the others have pubescent, green fruits. His “Peruvianum complex” included the self-incompatible species with pubescent green fruits *L. chilense* and *L. peruvianum*, which seldom crossed with *L. esculentum*.

Rick and Lamm (1955) recognized *L. chilense* as a separate species based on intercrossability and morphological data, and included *L. glandulosum* within the broad concept of *L. peruvianum*. Rick (1986a) thought that *L. chilense* was probably derived from *L. peruvianum*; *L. chilense* could be hybridized with the northern *L. peruvianum* races but not with remainder of the central to southern races. Rick and Lamm (1955) also examined a photograph of the original type collection of *L. pissisi*, but could not ascertain whether *L. pissisi* was a synonym of *L. peruvianum* or the name of another, distinct taxon.

Using data from morphological characters, mating systems, ecological preferences, reproductive isolation and allozyme types, Rick, Kesicki, Fobes, and Holle (1976) described two new species, *L. parviflorum* and *L. chmielewskii*, from the central Peruvian Andes. These two species were previously referred to as “*L. minutum*,” a name never validly published (Chmielewski & Rick 1962). *Lycopersicon parviflorum* was shown to be strictly autogamous, with small flowers and style included in the anther tube or slightly exserted, whereas *L. chmielewskii* is autogamous and facultatively allogamous, with larger flowers and exserted styles and stigmas. *Lycopersicon chmielewskii* was considered as the ancestral species from which *L. parviflorum* evolved (Rick et al. 1976). Fertile hybrids among these two sibling species were obtained experimentally by reciprocal crosses, but no natural hybrids were found in sympatric populations (Rick et al. 1976).

Rick (1963) analyzed the morphological, ecological, and reproductive variability of *S. peruvianum*, the most polymorphic species that grows throughout much of the range of the wild tomatoes. He (1986a) later studied additional collections and recognized 40 races or ecotypes in *L. peruvianum*, some of them widespread coastal races but the majority locally distributed mountain races restricted to a single drainage system; none of these were formally described (Fig. 8). Rick (1963) characterized these races mainly by leaf shape, which he found to be correlated with variation in plant habit, pubescence, inflorescence branching, and anther tube shape. He observed that morphological differences among the restricted range mountain races are greater in magnitude than those among widespread coastal races; he proposed that strict gametophytic self-incompatibility and geographic isolation drove differentiation among these races and that, most likely, the responsible genes were fixed gradually over a long period of time. Rick (1963) suggested that the mountain races had less morphological diversity due to isolation and small population size, despite self-incompatibility. Rick (1963, 1986a) described a broad trend from south to north toward reduction in leaf form, unbranched inflorescences, and also the length and arching of the anther tube (short and straight in northern races of his broadly circumscribed *L. peruvianum*). He (1963, 1986a) concluded that *L. peruvianum* is one highly diverse species with morphological gradation and a geographic cline, and did not propose taxonomic segregation at subspecific level (Fig. 8). His ideas were based on relatively strict acceptance of the biological species concept. Nevertheless, Rick (1963) pointed out that if *L. glandulosum* (here recognized as *S. corneliomulleri*) were considered a different morphological species, then at least five more species should be recognized within his broadly defined *L. peruvianum*.

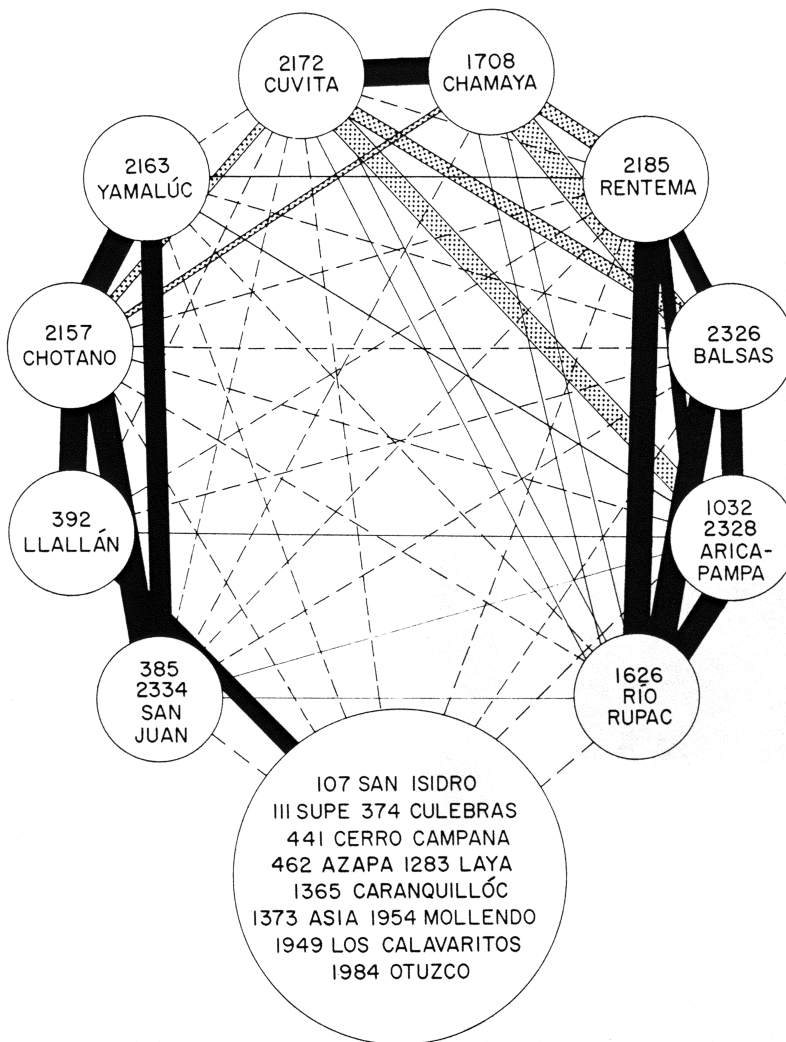


FIG. 8. Rick's (1986a) analysis of crossing relationships within his broadly defined *Solanum peruvianum* (as *Lycopersicon peruvianum*). Northern populations are represented by ten circles, southern populations by one large circle in the lower half of the figure. Our separation of these populations differs from Rick's (1986a) definition of crossing groups; see discussion of *S. arcanum* (page 116). Circles are labeled with TGRC accession numbers and localities; the width of connecting bands indicates the amount of seed produced by intrapopulation crosses, stippled bands correspond to hybrids with high gamete sterility, empty bands correspond to hybrids with unknown fertility, and dashed lines indicate crosses that failed to produce hybrids. Adapted from Rick (1986a), reproduced with permission of Columbia University Press.

D'Arcy (1972) treated tomatoes in the genus *Lycopersicon* but did not address sub-generic relationships. He placed *S. pennellii* in *Solanum* subg. *Potatoe* (G. Don) D'Arcy sect. *Neolycopersicon*. Hunziker (2001) also maintained *Lycopersicon* as a distinct genus. His decision was influenced by the lack of chromosome pairing in somatic fusion hybrids involving crosses with some *Solanum* species (Haider et al. 2000), differences in the androecium (Carrizo García 2003), and his desire to maintain traditional names.

Child (1990) placed tomatoes within the genus *Solanum* subg. *Potatoe* sect. *Lycopersicon* subsect. *Lycopersicon*, mainly characterized by anthers with sterile appendages, laterally connivent and forming a tube. He classified tomatoes in three series: series *Lycopersicon*, *Eriopersicon*, and *Neolycopersicon*. The first two series correspond to the subgenera *Eulycopersicon* and *Eriopersicon* used by Müller (1940a) and Luckwill (1943a). In Child's sense series *Lycopersicon* included herbs with few or no pseudostipules, ebracteate inflorescences, and fruits with carotenoid pigments. Series *Eriopersicon* includes herbs to subshrubs with pseudostipules, bracteate inflorescences, and fruits with much lower concentrations of orange and red carotenoid pigments (fruits pure green or greenish white, dark green to purple-striped). Series *Neolycopersicon* only includes *S. pennellii* (Correll 1958), a species with curved, loosely coherent anthers of markedly unequal length and without sterile appendages. Child (1990) also suggested that *Solanum* sect. *Lycopersicon* (including his subsect. *Lycopersicoides*) and sect. *Juglandifolia* (as sect. *Juglandifolium*) were closely related.

The different criteria used in classification, morphology and crossability, therefore, have led to recognition of a large number of subgeneric groupings, species, subspecies, varieties, and forms of differing circumscriptions, as well as conflicting hypotheses of interspecific relationships. The treatments mentioned above have become outdated as recent collecting activity has increased considerably the number of recognized species and races from South America (Rick 1971, 1991; Holle et al. 1978, 1979; Taylor 1986). Within the last few years, three additional species were described: an orange-fruited species, *Solanum galapagense* (Darwin et al. 2003), based on studies of historical and recent collections from the Galápagos Islands, and two new green-fruited species from Peru, *S. arcanum* and *S. huaylasense* (Peralta et al. 2005), formerly included in *S. peruvianum*.

DOMESTICATION OF THE CULTIVATED TOMATO

Two competing hypotheses have been advanced for the original place of domestication of the cultivated tomato, one suggesting an origin in Peru, and another an origin in Mexico. Candolle (1886) advanced the Peruvian domestication hypothesis based on botanical (Bauhin 1623; Ruiz & Pavón 1797), linguistic (Roxburgh 1832), and historical (Hernández 1651) evidence and concluded: 1) there were no unambiguous natural records of tomato outside of the Americas before the arrival of European explorers, 2) Bauhin (1623) referred to tomato as "mala peruviana" and "pomi del Peru," which suggested initial domestication and transport of tomato from Peru to Europe, 3) its origin was from the wild cherry tomato (*S. lycopersicum*, "var. *cerasiforme*" of prior authors), which by Candolle's time was known from coastal Peru, and in Mexico and the southwestern U.S.A. (California), 4) the distribution of cultivated tomato and its progenitor outside of Peru originated by garden escapes, and 5) the plant was domesticated only just before the discovery of the Americas by Europeans. Candolle's hypothesis of Peruvian origin was later supported by other authors (Moore 1935; Müller 1940a, b; Luckwill 1943a, b), but recent genetic investigations have shown that the plants known as "cerasiforme" are an admixture of wild and cultivated tomatoes rather than "ancestral" to the cultivars (Nesbitt & Tanksley 2002).

Jenkins (1948) advanced the Mexican domestication hypothesis. He pointed out that the first reference to tomato in Europe was Matthioli's short description (1544, later amplified and named "pomi d'oro," and "mala aurea" in subsequent editions both during and after Matthioli's lifetime, see Pre-Linnaean Concepts). Despite the acknowledgment that

the plant was a recent introduction to Europe in his time, there was no reference to its geographical origin in any of Matthioli's works or in any other of the early 16th century herbals, such as Fuchs (see Pre-Linnaean Concepts). Anguillara (1561) first used the name "pomi del Peru," along with the name "pomi d'oro," but his reference is ambiguous as to whether he was referring to the same plant. Jenkins argued that "pomi del Peru" was used by early botanists to refer to other solanaceous plants, such as *Datura stramonium* L., and had nothing to do with tomato, thus weakening Candolle's linguistic evidence for a Peruvian domestication. Jenkins's second argument was that there was no evidence for pre-Columbian domestication of tomatoes in South America, yet there was what he considered good evidence for early domestication in Mexico. Guilandini (1572) referred to tomato as "tumatle ex Themistitan," using an indigenous Mexican name for tomato. Jenkins (1948) interpreted the name "Themistitan" as a variant spelling of "Temixtitan," which in turn is a corruption of "Tenochtitlan" the Aztec name for what is now Mexico City. He therefore concluded that tomatoes came from Mexico. During the seventeenth century the Nahuatl name "tomatl" was often mentioned by botanists, and variants of this name are used in different languages at present (tomate in Spanish, tomato in English, etc). The early Italian name "pomi d'oro" (=pomodoro) is still used in Italy. According to Jenkins (1948), evidence for early Mexican domestication also came from Hernández (1651), who documented early cultivation of tomato in Mexico at least before 1578 (the year of Hernández's death) and possibly from Acosta (1590), although Acosta could have been referring to Mexico or Peru. Nevertheless, Yakovleff and Herrera (1935) felt that Acosta's work documented the uses of tomatoes in ancient Peru, not Mexico. Jenkins's third argument was that there was considerably more variation of the landrace cultivars in Mexico than in Peru. Following ideas of Vavilov (1926), Jenkins argued that *S. lycopersicum* was introduced into Mexico in pre-Columbian times and that it was domesticated there at a secondary center of diversity. Jenkins agreed with Candolle (1886) that *S. lycopersicum* was originally native to South America, but disagreed with Candolle's suggestion that the place of domestication was in Peru; he thought a Mexican domestication was the more likely possibility.

Peralta and Spooner (2006) consider the question of the original site of domestication of cultivated tomato to be unanswered. Like Candolle (1886), we consider linguistic evidence to be a weak source of data, and the existing linguistic sources for tomato are scant, ambiguous, and subject to various interpretations. Contrary to Jenkins's (1948) statements that there are no indigenous Peruvian names for tomato, Horkheimer (1973) documented a Quechua name for tomato (pirca), and Yakovleff and Herrera (1935) cited another Quechua name (pescoco-tomate) possibly referring to *S. lycopersicum*. The historical evidence also is sparse and ambiguous with reference to tomatoes in the Andes. From the analysis of the original description by Hernández (1651), it is not clear that the plant cited as "tomatl" from Mexico referred to the true tomatoes or a native *Physalis* species ("jiltomate" is the common name for *Physalis philadelphica* Lam., the husk tomato, see Heiser 1969). Unless some new document is uncovered that clearly identifies introductions of tomato to Europe from a particular area (see McCue, 1952, for a comprehensive summary of historical references), the origin of tomatoes first introduced into cultivation in Europe will remain unknown. Yet, even such a clear reference would not determine a first site of domestication in Mexico vs. Peru. As well, Jenkins's (1948) Vavilovian argument of more diversity of cultivars in Mexico is not supported by comparative data from South America (Ecuador, Peru, and Chile) (Villand et al. 1998). Tomatoes from Europe and North America share similar isozymes with those from Mexico and Central America,

suggesting the tomato was introduced to Europe and North America from Mexico or Central America (Rick & Fobes 1975a). Nevertheless, comparisons among genetic variability of primitive tomato cultivars found in Mexico, Central America, and Peru and modern varieties have neither substantiated nor disproved the hypothesis that Mexico was the center of domestication (Rick et al. 1974; Rick & Fobes 1975a; Rick & Holle 1990). Rick and Holle (1990) provided an isozyme study of different accessions of *S. lycopersicum* from South America, but they did not include cultivars or landraces from Mexico. The only comparative molecular studies (RAPDs and/or nuclear RFLPs) of diversity of landrace cultivars (Williams & St. Clair 1993; Villand et al. 1998) of tomato have not specifically addressed the Peruvian/Mexican domestication hypotheses.

Any molecular study to investigate the origin of tomato domestication would be complicated by relative lack of variation within *S. lycopersicum* (including landraces), and by the difficulty in identifying existing landraces from Mexico and Peru as truly native in those regions today. The only putative archaeological evidence of tomato is found in decorated functional ceramics (“spindle whorls”) produced by the native Quimbaya culture (500–1000 AD) of Colombia (McMeekin 1992). Our examination of the figures in this publication does not convince us that these representations are unequivocally tomato flowers, but could be of other *Solanum* flowers (possibly potato or pepino). Like Rick and Holle (1990), we conclude that none of the evidence is conclusive regarding either a Mexican or a Peruvian initial site of domestication, and that tomatoes may have been domesticated independently in both areas, once the tomato had reached Mexico from South America.

INTRODUCTION AND SPREAD OF TOMATOES

What were the first morphotypes of cultivated tomatoes exported from the Americas and where did they come from? Jenkins (1948) and McCue (1952) both examined these questions through an extensive search of the literature, herbarium specimens, and early drawings. Despite this extensive search, we still know very little. The first European contact with Mexico was in 1519 (the taking of Mexico City) and with Peru in 1531 (beginning of the Peruvian conquest). Botanists at that time were mainly interested in the general medicinal and culinary properties of plants and had little interest or knowledge of distribution or origin of cultivars. The first tomato references mentioned above were from sixteenth-century herbalists, who were mainly interested with the medicinal values or ‘virtues’ of plants, but they knew them only from exchange among European botanical gardens.

From Matthioli’s description of the tomato (1544) all that is clear is that the earliest described tomato in Europe had yellow fruits and had the Italian name “pomi d’oro.” In a later edition of his work, Matthioli (1554) cited both yellow and red fruits, and mentioned both the Italian name for the tomato “pomi d’oro” and its Latin equivalent “mala aurea” or golden apple. Another early common name for tomato is “poma amoris,” or “love apples,” because during the sixteenth century it was believed that the fruits had aphrodisiacal properties. It could also be that “poma amoris” is a corruption of “pomi d’oro.” All these names persisted well into the nineteenth century (Moore 1935).

Georg Oelinger, a pharmacist in the German city of Nuremberg, was an avid plant collector in the mid-sixteenth century (Lutze & Retzlaff 1949). He cultivated tomatoes in his garden, probably as a curiosity or for their medicinal value. An edition of unpublished

paintings from Oelinger's herbarium (Lutze & Retzlaff 1949) contains a drawing of a tomato plant with both red and yellow fruits; the flowers are mixed 5- and 6-parted and all the fruits are deeply furrowed (fasciated). It is clear from early illustrations that the flowers of tomatoes grown in sixteenth and seventeenth century Europe had duplications of sepals and petals (6–7-parted), and exserted styles. Dodoens (1554, 1563) listed the Latin ("Mala Aurea"), German ("Goldtapfel"), Flemish ("Guldapel") and French ("Pome d'amour") names for the fruit along with an illustration of the entire plant (see Fig. 1), but did not mention uses. His later publications (Dodoens 1574, 1583) illustrated round fruits with furrows, flowers with 7–8 petals, and two of the flowers with exserted styles. The illustrations in L'Obel (1576) and Tabernaemontanus (1591) were similar to those of Dodoens (1554, 1563). Gesner (1561) mentioned that the tomato was easily grown in Germany, matured early, and had fruits varying in color from gold, red, and white, and in shape from round to lumpy. It is also clear from the Fuchs description and illustration in the 'Vienna Codex' (frontispiece; Meyer et al. 1999) that by the second half of the sixteenth century tomato plants yielding red, orange, yellow, and white fruits were cultivated, which varied in shape from small and spherical to highly fasciated and lobed.

The English herbalist John Gerard (1597) described tomato fruits (as "of Apples of Love") as "chamfered, vneeven [uneven], and bunched out in manie places; of a bright shining red color and the bignes of a Goose egg or a large pepin [cucumber]." His woodcut (Fig. 9) is the same as that used in Bauhin's (1598) edition of Matthioli's book (see Fig. 4) and is of a plant with 6–8-parted flowers and highly fasciated fruit; he also described a yellow-fruited variety that was identical to the red-fruited sort. Gerard (1597) received seeds from Spain and Italy, and carefully described the cultivation of tomatoes in England ("It is sowne in the beginning of April in a bed of hot horse dung after the maner of muske Melons and such like cold fruits"). He also described the use of tomato fruits by the Spanish and Italians as boiled and in sauces, but indicated his disregard for their nutritional properties—"but they yeelde very little nourishment to the bodie, and the same naught and corrupt" (Gerard 1597: 276).

Sabine (1820) speculated, based on descriptions from Bauhin (1623), that the cherry tomato was introduced into Europe at the same time as the large-fruited cultivars. The Fuchs illustration from the mid-sixteenth century shows a variety of fruit morphologies and colors including small fruits, supporting Sabine's hypothesis. In his *Hortus Eystettensis*, Besler (1613) illustrated two types of tomatoes, a red-fruited type "*Poma amoris fructu rubro. Mala peruviana. Lycopersicum*" and a yellowish orange fruited type "*Poma amoris fructu luteo. Mala aurea Dodon. Solanum*" of almost identical morphology, which Besler thought inferior to the red-fruited variety. Both types are shown with large, heavily ribbed and lobed fruits. In northern Europe, tomatoes initially were cultivated mainly as ornamental plants in gardens, and they were considered by some to be inedible or poisonous because they were similar to the poisonous European members of the Solanaceae, such as mandrake (*Mandragora officinarum*), henbane (*Hyoscyamus niger* L.) or belladonna (*Atropa belladonna* L.) (Esquinas-Alcázar & Nuez 1995)

In southern Europe, however, tomatoes were widely used as food (Ray 1673; Miller 1752; Walters 1792; reviewed in Esquinas-Alcázar & Nuez 1995) during the seventeenth and eighteenth centuries, and their use as food had been noted earlier by Matthioli (1544) and other sixteenth century herbalists. Filippo (1811) reported three varieties in Italy and gave instructions for their cultivation. Sabine (1820) reported four varieties of red tomatoes and two of yellow tomatoes that were cultivated in Europe; he also discussed the condition for cultivation in England based on the experience of gardeners. Alefeld (1866)

Poma Amoris. Tab. 765. Ic. 2.
Apples of Loue.



FIG. 9. Illustration of the tomato from John Gerard's *Herball* (1597). Reproduced with permission of the Natural History Museum Botany Library.

mentioned seven varieties in Germany, giving them varietal names based on fruit color and shape (see synonymy of *S. lycopersicum*).

Introduction and cultivation of tomatoes quickly spread from Europe as the Spanish and Portuguese colonized the New World; it is amazing how quickly the cultivated tomato became a common foodstuff far from its origins in South America. Tomato cultivation was not difficult even in the temperate climates of Europe and North America, where the plants were and still are grown as annuals, and the crop gained economic importance worldwide by the end of the nineteenth century and the beginning of the twentieth century, when tomato breeding programs were initiated (Lehmann 1955; Brezhnev 1964; Rick 1978, 1995).

Hans Sloane (1707) recorded tomatoes from Jamaica, but was uncertain whether they were native: "This [the tomato] grows in several places about the Town of St. Jago de la Vega, and in Guanaboa, near Mrs. Guy's house, in her Plantation, but I cannot be positive that 'tis wild. It grows likewise in the Caribes. . . . They are eaten by some here, are thought to be very naughty, and yielding little Nourishment, through they are eaten either boil'd or in a sauce by the Spaniards." In the Sloane herbarium held at BM, collected during Sloane's stay in Jamaica from 1687–1689, there is specimen of *S. lycopersicum* labeled "Solanum secundum racemosum cerasorum forma: vel cerasa amoris racemosa rubra. C. B." in Sloane's hand (BM000589946, see <http://internt.nhm.ac.uk/jdsml/research-curation/projects/sloane-herbarium/>). Hughes (1750) states that tomatoes were brought to Barbados "by his Excellency Governor Worsley, from Portugal." In English settlements in the present-day area of the Carolinas tomatoes were in cultivation by 1710 (Salmon 1710 in McCue 1952). The tomato was also mentioned by the collector and gardener John Bartram in 1766 (Harper 1942) as growing in the Carolinas: "ye 2 nights frost. . . . It killed ye pumpkin vines & many of ye leaves of ye carolina peas but did not hurt ye tomatis." By the end of the eighteenth century, tomatoes were commonly grown for consumption by French settlers in North America but often only for ornament by the English (McCue 1952), although Thomas Jefferson grew them for food in his gardens at Monticello (Jefferson 1800).

Along the coast of Africa, tomatoes were encountered by seventeenth century explorers along the Barbary Coast, North Africa—at the time they were still rare in Europe. The Rev. Lancelot Addison (1671), writing about his time as a chaplain in Tangiers, stated: "they have one sort rarely to be met with in Europe which they call by a word sound Spanish *Tomatés*. This grows in the common fields and when ripe is plucked and eaten with oil; it is pleasant, but apt to cloy." In the mid-eighteenth century Abbé Proyart (quoted in McCue 1952) recorded local people of what is today Zambia eating tomatoes "the size of a cherry" in soups and stews, and by the mid-nineteenth century the famous Scottish explorer David Livingstone (1857) listed tomatoes as among the plants commonly cultivated along the Zambesi River: in "kitchen gardens, in which the common European vegetables, as potatoes, peas, cabbages, onions, tomatoes, etc., etc., grow." Specimens collected by F. M. J. Welwitsch (see <http://www.nhm.ac.uk/solanaceasource/>) in Angola record the tomato as "wild but not indigenous" (*Welwitsch 6046*, BM).

In Southeast Asia tomatoes were documented from Malaysia with the common name "tomatte" in 1650 (Esquinas-Alcázar & Nuez 1995). Tomatoes were recorded as used for food on Ambon Island (Indonesia) by Rumphius (Rumpf 1747), and by the mid-nineteenth century, Roxburgh in his *Flora Indica* (1832) stated that, "Although this [the tomato] is now very common in India, I suspect it is as little a native as the common potato [*Solanum tuberosum*] which is now very generally cultivated over India, even by the

natives for their own use.” The use of tomatoes as a medicinal was recorded in the Philippines in the late seventeenth century by the Spanish herbalist Ignacio de Mercado (García-Paris 1991). It is clear that it did not take long for the tomato to become cultivated worldwide.

Even very early forms of tomatoes cultivated in Europe had a variety of fruit shapes. In addition, Rick (1995) suggested that domestication and subsequent improvement of tomato fruit production was accompanied by dramatic changes in the position of stigma in the anther tube. The closely related colored-fruited wild species and older Latin American cultivars tend to have well exerted stigmas. Rick (1995) emphasized that in the absence of appropriate pollinators, flowers with exerted stigmas diminished the percentage of fruit set. Strong artificial selection for less exerted stigmas must have occurred after the tomato was first introduced to Europe, and even more selection under greenhouse culture. As a result, the style of most cultivars is shortened, and the stigma is positioned at the mouth of the anther tube or even completely included in the anther tube. This shortening reduced outcrossing and increased fruit yield in the modern varieties but also narrowed the genetic variation of the crop.

ECONOMIC AND NUTRITIONAL VALUE OF THE CULTIVATED TOMATO

The tomato is one of the world’s most important vegetables in terms of both income generation and dietary and nutritional value (Esquinas-Alcázar & Nuez 1995). In 2000, over 126 million metric tons were produced; the 15 leading countries (listed in descending order) are China, U.S.A., India, Turkey, Egypt, Italy, Spain, Brazil, Islamic Republic of Iran, Mexico, Greece, Russian Federation, Ukraine, Chile, and Uzbekistan. There has been an increase in tomato production over the last ten years. Northern European countries, as well as Canada and New Zealand, produce most of their tomatoes under controlled greenhouse conditions and have higher yields than countries growing tomatoes in the field. Tomatoes supply a mean of 17.7 kg consumption per capita per year, but tomato consumption is higher in Mediterranean and Arab countries (usually between 40–60 kg/cap/yr). Tomatoes are highly popular in Egypt, Italy, Israel, Lebanon, Turkey, and United Arab Emirates (60–70 kg/cap/yr), but Greece and Libya have the highest tomato consumption, the residents eating more than 100 kg of tomatoes per capita per year. Tomatoes are also a popular food in Latin and North America (Peralta & Spooner 2006).

Tomatoes rank second among the leading vegetables of the U.S.A. (Ensminger et al. 1995), with a production of 11 million metric tons in 2000. Much of the U.S.A. production is processed; major products are canned tomatoes, ketchup, chili sauce, juice, paste, powder, puree, salad dressings, sauces, soups, and vegetable and juice cocktails. The U.S.A. farm gate (point of first sale) value of tomatoes in 2001 was \$1.12 billion for fresh tomatoes and \$0.54 billion for processed tomatoes (\$1.66 billion total) (USDA National Statistics Service 2002a). California and Florida clearly dominate the U.S.A. market, with Florida accounting for 40.3% of the fresh U.S.A. market, and California accounting for 24.1% of the fresh market and 90.7% of the processed market (USDA National Statistics Service 2002b). Tomato consumption has greatly increased in the U.S.A. since the beginning of the last century. While per capita consumption was only 8.2 kg per year in 1920, by 1978 it had increased to 25.5 kg per year (Rick 1978). Due to use of tomatoes in preserved forms, current consumption in the U.S.A has reached 40.5 kg per year (FAO 2004).

Tomatoes are a rich source of nutrients (Ensminger et al. 1995). Both raw and processed tomatoes are good sources of vitamins A and C, but unfortified tomato juice has only about 2/3 the vitamin C content of raw, ripe (red) tomatoes. Similarly, canned tomatoes contain only about 3/4 the vitamin C content of fresh ripe tomatoes. Ripe tomatoes contain 3–4 times as much vitamin A as mature green tomatoes, but otherwise red and green tomatoes are about equal in nutritional value. Tomato puree and plain types of tomato sauce (without added ingredients, such as meat or mushrooms) have about twice the solids content and about double the nutritional value of fresh tomatoes and tomato juice. Tomato paste, which has about four times the solids content of fresh tomatoes, is a concentrated source of nutrients, making it a valuable contribution when used in preparation of pastas, pizzas, and other foods. Ketchup and chili sauce are about equal in nutritional value, since each item is made with similar ingredients and contains about 32% solids (about 5 times the content of fresh tomatoes and tomato juice); however, the nutrients per calorie of these products are significantly less than those furnished by tomato paste, because the solids content and caloric values are boosted by added salt and sugar. Tomato popularity and its high level of consumption make this vegetable one of the major sources of vitamins and minerals in the current human diet (Peralta & Spooner 2006).

MORPHOLOGY

HABIT. Members of sect. *Lycopersicon* are herbaceous plants, although they can also undergo secondary growth at the base of the stems and the main root. In their natural habitats some wild tomatoes behave as annuals, probably because frost or drought kills the plants after the first growing season (Müller 1940a). In biennial and perennial forms, the main root and stem base can become quite woody by the end of the first growing season, and at the beginning of the following season several new shoots arise from buds on the lignified base or crown. These new stems are considerably smaller in diameter than the base.

The plant's life span is related to its capacity for developing secondary growth in roots and basal stems. In all species the shoots are initially erect, but later, due to the weight of the branches, the plants become decumbent or prostrate and can develop adventitious roots from basal nodes. In tomato cultivation it is a common cultural practice to heap soil at the base of the plant to insure a well-developed adventitious root system. Maldonado et al. (2002) found that *S. chilense* reproduces asexually by adventitious roots in Chilean desert habitats. Some species (*S. lycopersicum*, *S. habrochaites*, *S. chilense*, *S. huaylasense*) are robust and can maintain the erect habit until they reach 80–100 cm in height, or more in *S. habrochaites*. All species are spreading and can produce long branches, to 3–4 m in *S. lycopersicum*, *S. pimpinellifolium*, *S. cheesmaniae*, and *S. galapagense*, and to 6 m in *S. habrochaites*. Wild tomatoes have indeterminate development, but some forms of the cultivated *S. lycopersicum* have a semi-determinate or determinate growth habit, and are more compact with numerous short branches.

Members of sect. *Juglandifolia* are perennial woody vines or lianas, scandent or clambering into vegetation to 8–10 m or higher, while both members of sect. *Lycopersicoides* are coarse herbs or woody shrubs, erect to somewhat sprawling, with stems to 0.5–2.5 m in length.

STEMS. The main axis of the plant is a typical *Solanum* sympodium formed by a succession of lateral axes with alternate leaves arranged in a 1/3 phyllotaxic spiral, and inflorescences are terminal at the end of each sympodial unit (Luckwill 1943a; Danert 1958). In some species, inflorescences are formed at every second instead of every third node, and therefore the phyllotaxis of the shoot is 1/2, instead of 1/3 of a spiral. In the species of sections *Juglandifolia* and *Lycopersicoides* the inflorescences are formed at every five or more nodes.

Danert (1958, 1967, 1970) and Child and Lester (1991) documented sympodial units and anthoclades (patterns of foliar lateral branches and associated inflorescences) in the Solanaceae. The inflorescences of wild tomatoes, as in most members of Solanaceae, are terminal with a subtending lateral bud. The inflorescence occupies a position between leaf nodes. It is axillary when first formed, but the subtending leaf is extended away from the inflorescence by axillary growth. The first leaf above each inflorescence usually lacks axillary branches, whereas the others have axillary growth. Occasionally the leaf subtending the inflorescence remains opposite the inflorescence. The number of leaves per sympodium is very regular and of major taxonomic significance in the entire genus *Solanum* (see Knapp, 2001, for a further discussion).

LEAVES. (Plate 1). The leaves of tomatoes have often been characterized as pinnate, but the presence of a minute wing of leaf tissue along the main rachis connecting all the dissections has led some to suggest that tomato leaves are simple and merely highly dissected or deeply pinnatifid. We here characterize the leaves of tomatoes as pinnate following prevalent terminology in the current leaf development literature (Bharathan et al. 2002; Gleissberg 2002; Tsiantis et al. 2002; Piazza et al. 2005; but see Kessler et al. 2001), but recognize the continuum of leaf dissection that is involved in *Solanum*. During the growth of an individual plant it is possible to observe the gradual increase in leaf complexity. The first leaf is often simple, entire to lobed, or pinnate with only 1 or 2 leaflets; successive leaves become more dissected, and after 10 to 12 leaves, the mature leaf form is reached (Luckwill 1943a). Leaves of most species are imparipinnate (with 2–6 [7] opposite, subopposite, or alternate primary lateral leaflet pairs and a terminal leaflet), and the terminal leaflet is of equal size (Plate 1C) or larger than lateral leaflets (Plate 1B, I, L). Some leaves are interrupted imparipinnate (Plate 1A, I, K, L), meaning that the primary leaflets are alternatively small and large. The smaller leaflets are generally under half the length of the primary leaflets, and here referred to as interjected leaflets, but elsewhere called interstitial or intermediate leaflets. Smaller interjected leaflets also develop in the main leaf rachis, between the primary leaflets and interjected leaflets (Plate 1K). Some species have the primary lateral and terminal leaflets further divided, to form secondary to tertiary lateral leaflets (Plate 1A, H). In *S. galapagense* the tertiary leaflets are deeply lobed to form what we refer to as quaternary lobes (Plate 1D; see also Fig. 4 of Darwin et al. 2003). Holtan and Hake (2003), using introgression lines (IL lines) derived from *S. pennellii* (see http://zamir.sgn.cornell.edu/Qtl/il_story.htm and discussion of *S. pennellii*), found four major QTL types affecting leaf dissection in tomatoes. These classes of loci affected 1) numbers of primary and interstitial leaflets, 2) numbers of secondary and tertiary leaflets, 3) lobing (margins), and 4) all aspects of leaf morphology. Leaf morphology in the tomatoes and their relatives is complex, and governed by a complex set of interacting genes (Holtan & Hake 2003); this complexity can cause great variation, making identification difficult in some species. Leaflets are narrowly elliptic, elliptic to broadly elliptic, ovate or orbicular. The base is usually asymmetric, and varies from truncate or rounded,

to cordate; it is sometimes decurrent basiscopically. The apex (of leaves and leaflets) is rounded, acute, or acuminate. The margins are entire to regularly or irregularly crenate, serrate to dentate, to deeply lobed, and if lobed, the lobes are usually deeper at the leaflet base; the margins are straight or more commonly undulate. The primary leaflets can be sessile to petiolulate; the interjected, secondary and tertiary leaflets are usually sessile to subsessile.

PSEUDOSTIPULES. The pseudostipules in tomato appear to be morphologically identical to those in potato (*Solanum* sect. *Petota* Dumort, Spooner et al. 2004). The Solanaceae are considered to be exstipulate (Hunziker 2001), but tomatoes and potatoes possess stipule-like structures that traditionally have been referred to as pseudostipules (Correll 1962; Hawkes 1990; Child & Lester 1991; Hunziker 2001). They are not attached to the stem or petiole as many other stipules, but appear to be the first leaf pair (prophylls) of axillary shoots. Child and Lester (following Danert 1958, 1970) use the term pseudostipules because the vasculature of these structures arises one node below their emergence. Metcalfe and Chalk (1979) point out that stipules take many forms and have various points of attachment, including axillary attachment, and have various types of vasculature including origins from one node below, and argue that it is unresolved whether stipules are fundamentally part of the leaf or separate from it. Like the potatoes (*Solanum* sect. *Petota*), most pseudostipules in the tomatoes and relatives are paired, often clasping the stem, and lunate (e.g., Plate 1L) and they can be deeply lobed, especially in those species with deeply lobed leaves (Plate 1P). Similar outgrowths also sometimes develop at the base of the peduncle. Pseudostipules are entirely absent from the four species of sect. *Lycopersicon* (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) with carotenoid-pigmented fruits. In the remaining species of sect. *Lycopersicon* pseudostipules are present but in some species they are not present on all of the nodes or are small.

TRICHOMES AND VESTITURE. Trichome types and density are useful taxonomically. Wild tomatoes have a variety of uniseriate glandular and non-glandular trichomes (Fig. 10). The morphology and terminology of trichomes in *Solanum* has been reviewed by Seithe (1962), Gibson (1971), Roe (1971), and Seithe and Anderson (1982). Four types of glandular trichomes occur: 1) a short storied trichome ca. 10 μm long with a single basal cell, a unicellular stalk, and an 8-celled head (Fig. 10A), 2) a short-stalked trichome 10–60 μm long with a single basal cell, a larger unicellular stalk (sometimes 2–3 cells long), and a four-celled head containing a sticky substance enclosed by the cell walls and released by mechanical disruption (Fig. 10B), 3) a long unicellular trichome 15–80 μm long with a single basal cell and a small unicellular head (Fig. 10C), and 4) multicellular uniseriate trichomes with ovoid unicellular glands at the tip that produce a sticky exudate (Fig. 10D, E). Within this last glandular hair type are short slender hairs 20–80 μm long composed of 2–4 cells with a single basal cell (Fig. 10D), and longer hairs 200–2000 μm long with a basal pad composed of 4–6 cells (Fig. 10E). Our trichome types 2 (Fig. 10B) and 4 (Fig. 10D) are morphologically the same as those that Gibson (1971) described as a Type A and Type B glands in the species of sect. *Petota*. These glandular trichomes repel or entrap insects or otherwise inhibit their feeding and/or reproduction and are effective natural defenses. These glandular trichomes account for the distinctive smell of tomato leaves that varies considerably among species (Darwin et al. 2003).

Non-glandular trichomes include uniseriate multicellular types of many lengths without the glandular tip: 1) simple unicellular trichomes 5–10 μm long with a single basal

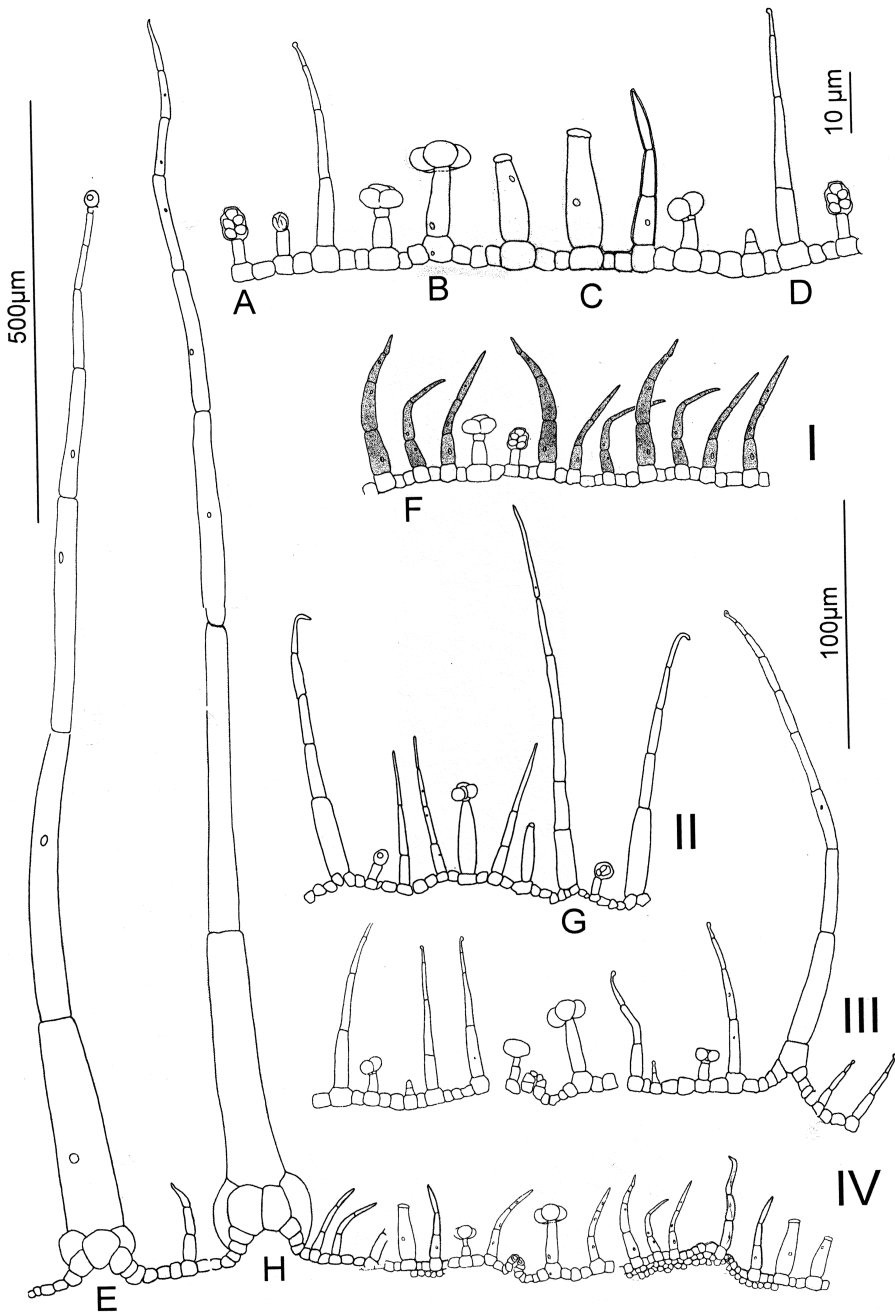


FIG. 10. Trichome types of *Solanum* sect. *Lycopersicon*, sect. *Juglandifolia*, and sect. *Lycopersicoides*. A. Short storied trichome with a single basal cell, a unicellular stalk, and a typical 8-celled head. B. Short-stalked trichome with a single basal cell, a larger unicellular stalk (sometimes 2-3 cells), and a four-celled glandular head. C. Long unicellular stalk with a single basal cell and a small unicellular head. D. Multicellular uniseriate trichome with an ovoid unicellular gland at the tip. E. Large multicellular uniseriate glandular trichome with 4-6 basal cells. F. Short 1-4-celled tapering trichomes with a single basal cell, often bent in the middle, with a typical pointed tip. G. Slender uniseriate 3-6-celled tapering trichome with a single basal cell. H. Uniseriate 2-5-celled tapering trichome with a multicellular base and pointed tip. I. Typical canescent vestiture of *S. peruvianum* (LA 2744). II. Villose surface in *S. habrochaites* (LA 1223). III. Mixture of glandular and non-glandular trichomes in *S. galapagense* (LA 317). IV. Mixture of glandular and non-glandular trichomes in *S. lycopersicum* (LA 1673).

cell; 2) short 1–4-celled tapering trichomes 15–60 μm long with a single basal cell and a typical pointed tip; these trichomes are often bent in the middle and under the microscope the cell walls are usually finely sculptured (Fig. 10F); 3) slender uniseriate 3–6-celled tapering trichomes 50–1000 μm long with a single basal cell and usually straight and pointed tip (Fig. 10G); 4) uniseriate 2–8-celled tapering trichomes 20–2500 μm long with a multicellular base and pointed tip (Fig. 10H), and sometimes with finely sculptured cell walls that make the trichomes more rigid. These multicellular tapering trichomes are often common on the veins and growing vegetative apex.

Glandular and non-glandular large trichomes (Fig. 10E, G, and H) produce the villos pubescence of different parts (stem, leaves, peduncles, pedicels, sepals, petals, and fruits) and often different types are combined (*S. lycopersicum*, *S. habrochaites*, *S. corneliomulleri*). The typical canescent surface of *S. chilense* and *S. peruvianum* (especially southern Peruvian and northern Chilean coastal populations) is produced by a dense development of short and bent tapering trichomes (Fig. 10F). Color of the plant parts is modified by the type, combination, and abundance of trichomes, and varies from bright green in subglabrous plants (*S. arcanum* and *S. huaylasense*) to grayish in canescent plants (*S. peruvianum* and *S. chilense*). The fruits of some species are typically pubescent early in development, but then lose the trichomes at maturity, e.g., the cultivated tomato (*S. lycopersicum*). Fruits of some species maintain the pubescence at maturity (Plate 3J, L, M).

INFLORESCENCES. The basic inflorescence in wild tomatoes, as in all other species of *Solanum*, is a scorpioid cyme with a variety of branching patterns. The inflorescences can be simple unbranched monochasia, as characteristic of the “*Lycopersicon*” and “*Arcanum*” species groups (see Species Relationships below). Dichasially branched cymes are present in sect. *Lycopersicon* in the “*Neolycopersicon*” and “*Eriopersicon*” species groups and sometimes can be branched more than once. Members of sect. *Lycopersicoides* have inflorescences that are 2–3 times dichotomously branched, and those of sect. *Juglandifolia* have inflorescences that are many times (4–5+) dichotomously branched. Inflorescences are usually bracteate in members of the “*Arcanum*,” “*Eriopersicon*,” and “*Neolycopersicon*” species groups, but in some species in these groups (*S. arcanum*, *S. chmielewskii*, *S. neorickii*, *S. chilense*, *S. huaylasense*) the bracts are occasionally absent or poorly developed. Bracts are entirely absent from the four species of the “*Lycopersicon*” species group, although bracteole-like leaflets sometimes occur in the inflorescences due to vegetative growth of axillary buds. The number of flowers and the arrangements of flowers on the inflorescence can be deduced by the scars left by the flower and fruit pedicels when they fall.

PEDICELS. Section *Lycopersicon* is distinguished by pedicel articulation above the middle or in the distal half, except for *S. pennellii*, where the pedicel is articulate at the base. In the two species of sect. *Juglandifolia*, the pedicels are articulated at about the middle, and the articulation is often swollen and conspicuous and darker in color. Pedicels are articulate in the distal 1/3–1/2 in members of sect. *Lycopersicoides*. In all the species the pedicel elongates with fruit development, and can be straight, slightly angled, or strongly angled at the articulation towards the inflorescence axis. When pollination of flowers fails, an abscission layer is developed around the articulation, the flower falls and leaves the basal part of the pedicel attached to the inflorescence rachis. Tomatoes and their wild relatives share the articulation of pedicels with members of sect. *Petota* (the

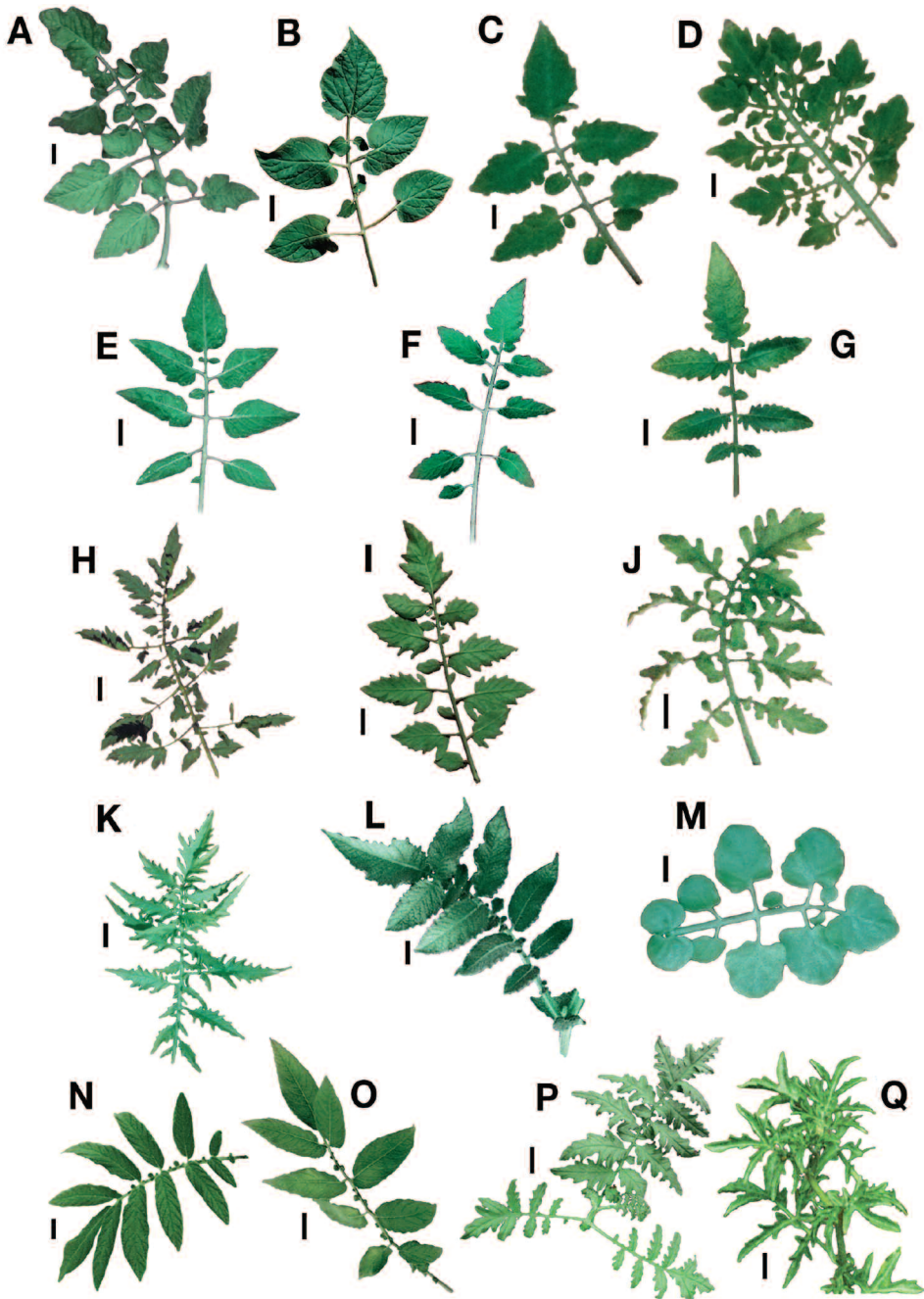


Plate 1. Leaves of *Solanum* sect. *Lycopersicon*, sect. *Juglandifolia*, and sect. *Lycopersicoides*. A. *S. lycopersicum* (LA1673). B. *S. pimpinellifolium* (LA2646). C. *S. cheesmaniae* (LA1450). D. *S. galapagense* (LA317). E. *S. neorickii* (LA247). F. *S. chmielewskii* (LA1306). G. *S. arcanum* (LA2152). H. *S. huaylasense* (LA2561). I. *S. peruvianum* (LA1947). J. *S. corneliomulleri* (LA1647). K. *S. chilense* (LA2884). L. *S. habrochaites* (LA1353). M. *S. pennellii* (LA1376). N. *S. ochranthum* (LA3650). O. *S. juglandifolium* (LA2134). P. *S. lycopersicoides* (LA2772). Q. *S. sitiens* (LA2876). Scale bars: A, B, E–K, M, P, Q, 2 cm; C, D, 1 cm; L, N, O, 3 cm. LA numbers from the C. M. Rick Tomato Genetic Resources Center.

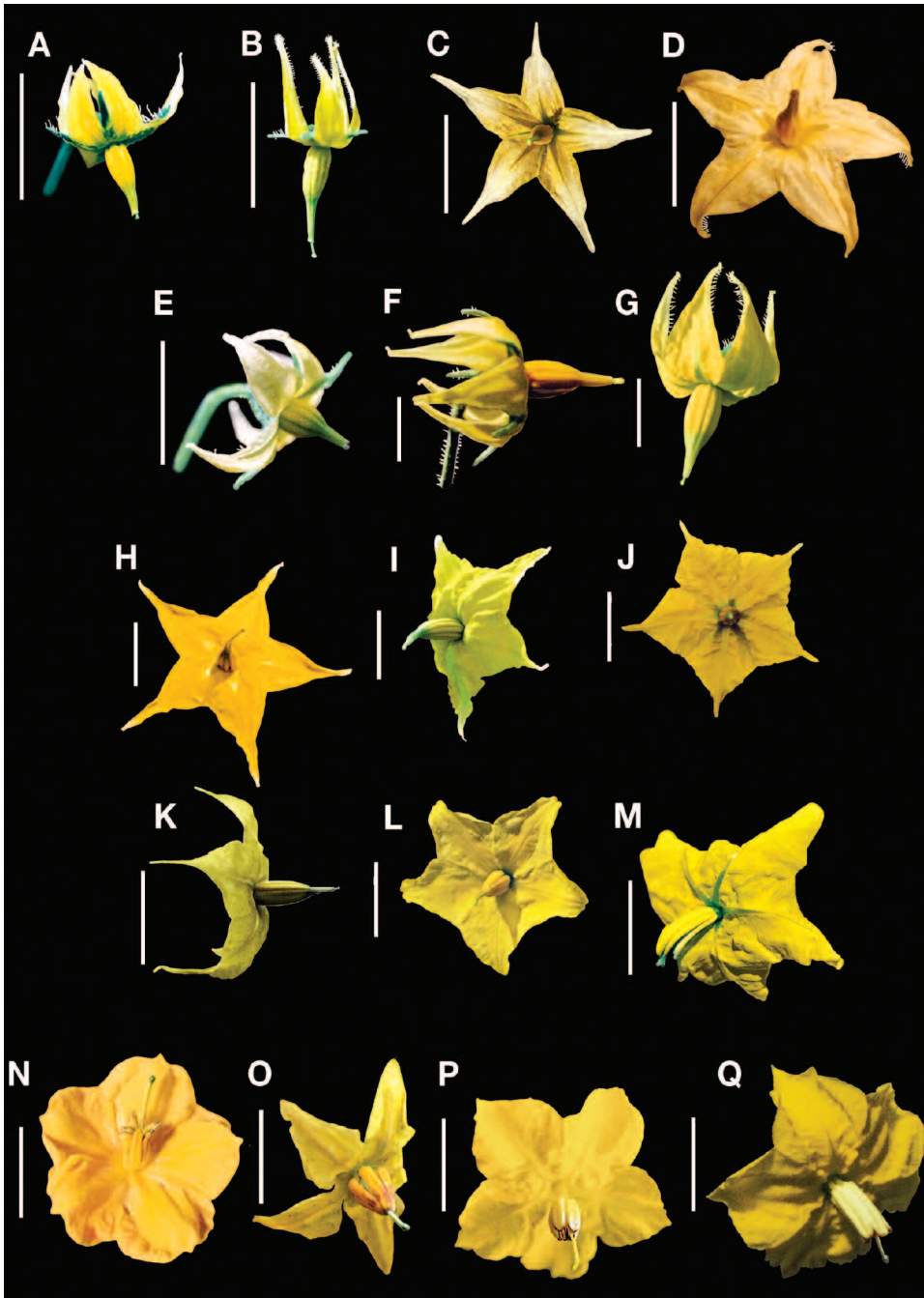


Plate 2. Flowers of *Solanum* sect. *Lycopersicon*, sect. *Juglandifolia*, and sect. *Lycopersicoides*. A. *S. lycopersicum* (LA1226). B. *S. pimpinellifolium* (LA1581). C. *S. cheesmaniae* (LA166). D. *S. galapagense* (LA317). E. *S. neorickii* (LA2200). F. *S. chmielewskii* (LA1306). G. *S. arcanum* (LA2328). H. *S. huaylasense* (LA2562). I. *S. peruvianum* (LA1954). J. *S. corneliomulleri* (LA1647). K. *S. chilense* (LA1930). L. *S. habrochaites* (LA1223). M. *S. pennellii* (LA1926). N. *S. ochranthum* (LA3650). O. *S. juglandifolium* (Spooner et al. 5088). P. *S. lycopersicoides* (LA2772). Q. *S. sitiens* (LA2876). Scale bars: A–D, H–Q, 1 cm; E–G, 0.5 cm. LA numbers from the C. M. Rick Tomato Genetic Resources Center.

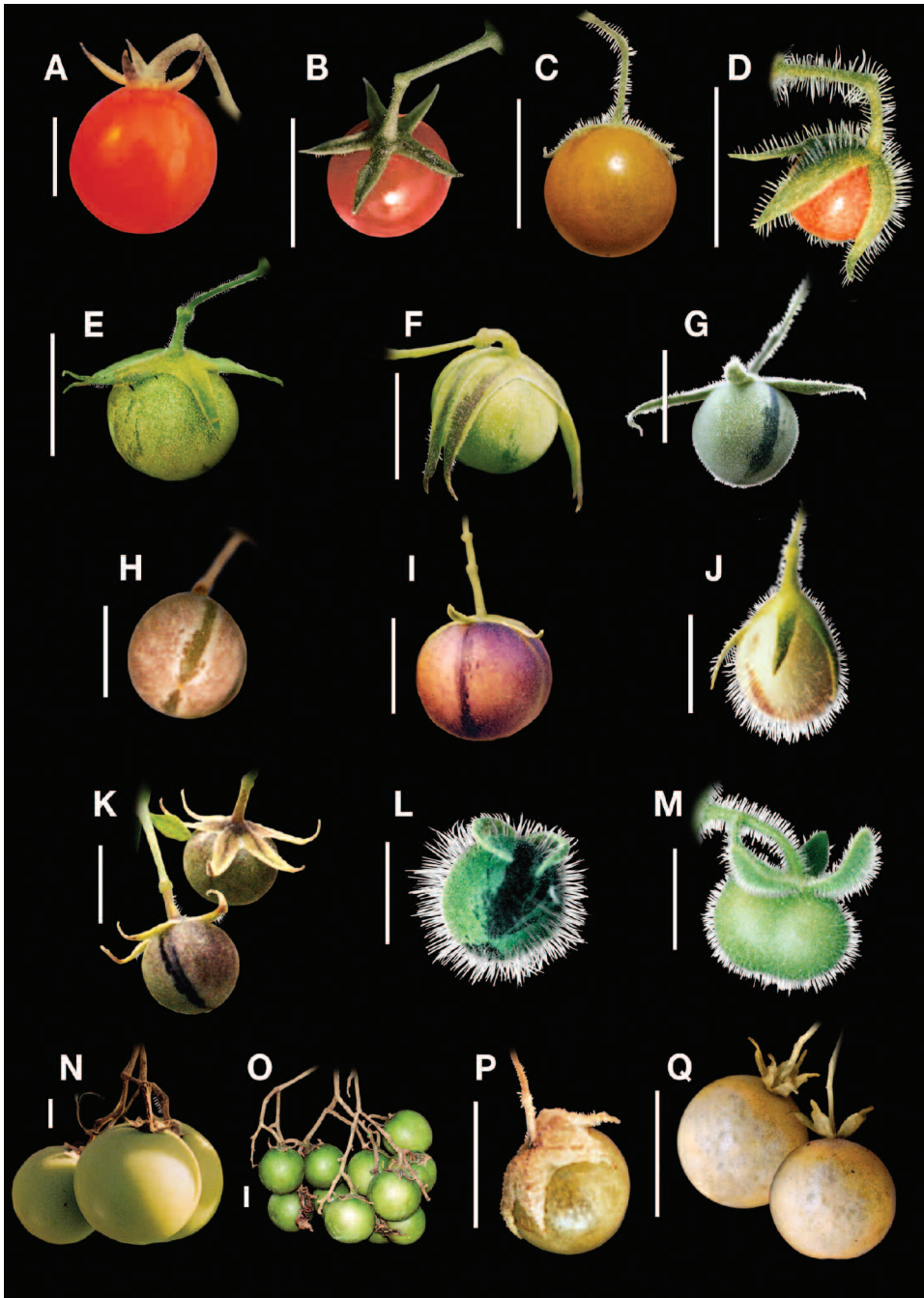


Plate 3. Fruits of *Solanum* sect. *Lycopersicon*, sect. *Juglandifolia*, and sect. *Lycopersicoides*. A. *S. lycopersicum* (LA1673). B. *S. pimpinellifolium* (LA1237). C. *S. cheesmaniae* (LA1450). D. *S. galapagense* (LA317). E. *S. neorickii* (LA2200). F. *S. chmielewskii* (LA2663). G. *S. arcanum* (LA2548). H. *S. huaylasense* (LA1365). I. *S. peruvianum* (LA153). J. *S. corneliomulleri* (LA1609). K. *S. chilense* (LA1930). L. *S. habrochaites* (LA1353). M. *S. pennellii* (LA716). N. *S. ochranthum* (Spooner et al. 5000). O. *S. juglandifolium* (Castillo et al. 1206). P. *S. lycopersicoides* (LA2772). Q. *S. sitiens* (LA2876). Scale bars = 1 cm. LA numbers from the C. M. Rick Tomato Genetic Resources Center.

potatoes) and their relatives; articulation above the base is a synapomorphy of this clade in *Solanum* (Bohs 2005).

CALYX. The calyx is typically sympetalous and 5-merous. The sepal primordia are initiated singly in a helical manner, followed by whorls of petals, stamens, and carpels in which primordia originated simultaneously (Chandra Sekhar & Sawhney 1984). The sepals later produce a minute 0.25–1 mm long calyx cup or tube by fusion of lobes at the basal regions, but several mutants of *S. lycopersicum* have extremely enlarged calyces (see Giovannoni 2001), caused by mutations in MADS box genes. The lobes are linear to lanceolate in all species of sect. *Lycopersicon*, except in *S. pennellii*, where they are spatulate and rounded at the apex (Plate 3M). The calyx lobes are somewhat more broadly deltate in sections *Lycopersicoides* (Plate 3P) and *Juglandifolia*. The calyx tissue is hyaline at the sinuses. The apex is acute, acuminate, or rounded. Tomato sepals are usually somewhat fleshy, and glabrous to sparsely to densely pubescent with trichomes like those of the inflorescence and leaflets. In all the species the calyx is accrescent during the development of the fruit. The lobes can be spreading (Plate 3K), somewhat to strongly reflexed with the lobe tips recurved (Plate 3A), to loosely investing the berry (Plate 3J) to tightly appressed to the fruit investing the berry like a cage (Plate 3D). The calyx lobes are usually shorter or of equal length than the fruit, but in *S. galapagense*, *S. habrochaites*, and in some populations of *S. corneliomulleri* from near Arequipa (Peru), the calyx lobes usually exceed and enclose the berry. In the two species of sect. *Juglandifolia* the calyx lobes are thickened and somewhat woody, slightly reflexed and usually break off at fruit maturity.

COROLLA. Corollas are typically light to golden-yellow, with little variation in color within species, and we found no consistent species-specific color traits in any of the three sections we recognize here. Shape varies from deeply stellate (Plate 2C) to rotate (Plate 2N), with intermediate shapes traditionally referred to as pentagonal (e.g., Plate 2L, M). Corollas are symmetric in all species, except *S. pennellii* (Plate 2M), where, due to differences in the sizes of corolla lobes, they are slightly bilaterally symmetric. Corolla diameter varies from 1 cm (*S. neorickii*) to 5 cm (*S. habrochaites*), but most species have corollas about 2 cm in diameter, and considerable variation within species exists. Self-compatible species (*S. cheesmaniae*, *S. chmielewskii*, *S. galapagense*, *S. lycopersicum*, *S. neorickii*, *S. pimpinellifolium*) tend to have smaller corollas than the self-incompatible species (Georgiady & Lord 2002). Corolla lobe shape can be useful at the specific level; for example, the narrowly triangular corolla lobes of *S. pimpinellifolium* are diagnostic. The dorsal surface of the petals is pubescent, and the trichomes can be observed in the flower bud before anthesis. When the flowers first open the petals are strongly reflexed (e.g., Plate 2A, B, E–G), and over a period of one or two days relax to a flat plane (e.g., Plate 2H–K); as they age the petals curve toward the anther tube (e.g., Plate 2C, L). The flowers dehisce and drop from the pedicel articulation if not pollinated.

ANDROECIUM. Anthers of species of sections *Juglandifolia* and *Lycopersicoides* conform to the typical poricidal morphology of all other species of *Solanum* (see Knapp 2001, 2002c). In these taxa, the pore usually “unzips” during anther dehiscence to form a teardrop shaped slit (Fig. 11A) from which pollen is shed during vibratile pollination (Buchmann 1986). Anthers of members of sect. *Juglandifolia* are loosely connivent, while those of sect. *Lycopersicoides* are not at all connivent but are loose and stand apart at anthesis.

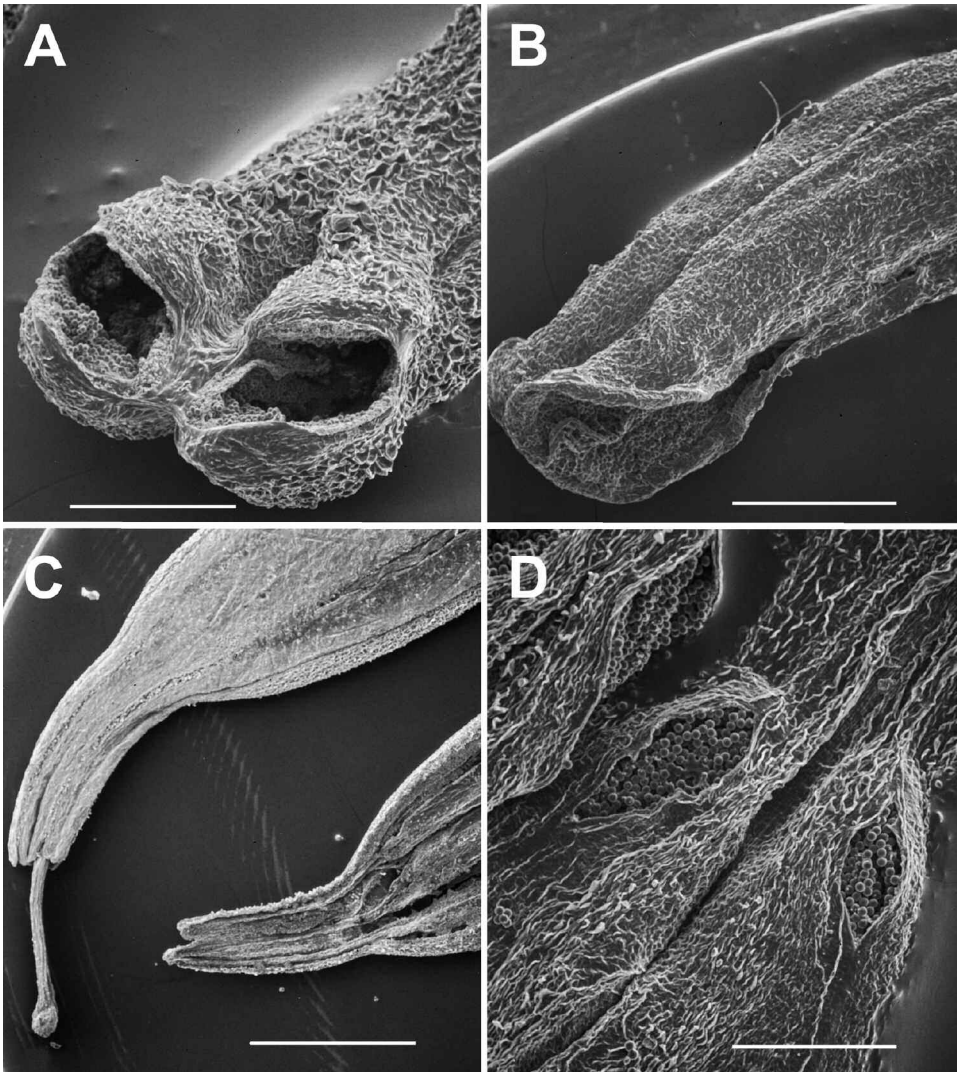


FIG. 11. Scanning electron micrographs of typical anthers of *Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, and sect. *Lycopersicon*. A. *S. juglandifolium* (sect. *Juglandifolia*), distal portion of anther showing typical *Solanum*-type poricidal anther dehiscence, the pore apical and the suture opening somewhat along the length of the anther. B. *S. lycopersicoides* (sect. *Lycopersicoides*), distal portion of anther showing the terminal pores elongating to slits as the anther dries at maturity. C. *S. corneliomulleri* (sect. *Lycopersicon*), distal portions of two anther tubes, one with exerted style; note the curvature typical of this species and the elongate sterile apical appendages. D. *S. arcanum* (sect. *Lycopersicon*), distal portion of anther showing poricidal dehiscence within the anther tube below the sterile apical appendage. Scale bars: A, 0.43 mm; B, 0.75 mm; C, 1.76 mm; D, 0.27 mm. (Based on: A, Nielsen 1126; B, Matthei & Rodríguez 250; C, Ferreyra 3480; D, Sánchez Vega 6084.)

The anthers of all members but one of sect. *Lycopersicon* are laterally connivent and form a tube; they have a sterile apical appendage and dehisce by introrse longitudinal slits that first appear as small oblong pores and then develop basipetally (Fig. 11D). Only *S. pennellii* has anthers without sterile apical appendages, which dehisce by apical pores (Fig. 11A) and later by introrse slits opening just part way down the anther at maturity, as in most other species of *Solanum* (Barboza & Hunziker 1991; Knapp 2001).

Adjoining anthers are connected by lateral and adaxial rows of hairs that produce a complex interweaving structure comparable to a zipper. The hairs initiate in the central region of the anther and progress acropetally and basipetally when the stamens reach two-thirds of their final size (Chandra Sekhar & Sawhney 1984). Anther and carpel sizes also affect lateral hair growth and thus anther connivance (Chandra Sekhar & Sawhney 1987). The anther tube varies in size and shape among the species of tomatoes, and typically takes the form of a bottle, with the sterile apical appendages forming the narrow neck. Anthers of members of sect. *Lycopersicon* (including *S. pennellii*) are tightly connivent owing to interlocking hairs, creating a “pepper-pot” type morphology. The development of this morphology is governed by very few genes (Glover et al. 2004). The anthers are usually of equal length and straight, but in some species (*S. corneliomulleri*, *S. huaylasense*, *S. peruvianum*, and *S. pennellii*) they are slightly to strongly curved, caused by the unequal growth of the three upper (distal) anthers that develop more than the lower (proximal) anthers. The curved anthers produce a pattern of bilateral symmetry (zygomorphy) of the flowers (Knapp 2002b).

Pollen of all members of the three sections treated here is similar in size and shape to that of other species of *Solanum* (Buchmann 1986; Carrizo García 2003); it is tricolporate with a relatively smooth exine and held in yellow “pollen shamming” anthers. Nitrogen and protein content is the same as for other species of *Solanum* (Buchmann 1986) and is typical for a buzz-pollinated plant.

GYNOECIUM. The gynoecium is typically bicarpellate (multicarpellate in many cultivars of *S. lycopersicum*). The carpels are fused in a superior ovary that has as many locules as carpels and axillary placentation. The ovary is usually globose or slightly elliptic in wild species, but can be a wide variety of different shapes in cultigens (see below). The ovary is subglabrous to pubescent; the trichomes often enlarge during fruit development (e.g., *S. corneliomulleri*). All tomato flowers lack nectaries, as do most other species of *Solanum*. The style is simple, straight or curved (especially in species with bilaterally symmetric flowers, e.g., *S. pennellii*, *S. corneliomulleri*), usually pubescent in the proximal half, and is included (Plate 2E) or exerted beyond the anther tube (Plate 2B). The stigma is capitate (e.g., *S. juglandifolium*, *S. pimpinellifolium*) to clavate and bilobed (e.g., *S. lycopersicoides*, *S. sitiens*). The ovules number 20–50 per locule, and are anatropous and non-arillate.

FRUITS. Fruits of all species of sections *Juglandifolia*, *Lycopersicoides*, and *Lycopersicon* are globose, bilocular berries, with the exception of few wild populations and many cultivated forms of *S. lycopersicum*, which are multilocular and can occur in many unusual shapes (e.g., van der Knaap & Tanksley 2003). Fruit shapes in wild species vary from subglobose, globose (e.g., Plate 3A), to elliptic globose-depressed to ovoid to pyriform (e.g., Plate 3J). In cross section the fruits are round or slightly flattened parallel to the septum. Color and pubescence of the fruits are useful characters for differentiating species and species groups. The color of the fruits is a result of a combination of pigments

present in the epicarp and that of the underlying flesh. Within sect. *Lycopersicon* members of the “*Lycopersicon*” species group have carotenoid pigments (red, orange, yellow) and are evenly colored throughout. Bright red is the typical fruit color of *S. lycopersicum* and *S. pimpinellifolium*, produced by the accumulation of the red pigment lycopene at the “breaker” stage of fruit ripening (Bramley 2002). In the species with orange to yellow fruits endemic to the Galápagos, *S. galapagense*, lycopene is not accumulated and the carotenoid biosynthetic pathway proceeds to produce orange carotenoids (β -carotene or δ -carotene), as in various mutants of *S. lycopersicum* (e.g., Ronen et al. 2000). When the epicarp lacks pigments and overlays a yellow flesh, the fruit appears pale yellow or white, and if the flesh is red the fruit appears pinkish. The cultivated tomato has been a model for the understanding of the carotenoid biosynthetic pathway in plants, and since the tomato fruit is almost the sole dietary source of lycopene for humans, its formation and control has been the subject of considerable interest for biotechnology (Bramley 2002). Members of the “*Lycopersicon*” species group have fruits that are often pubescent when young, but become glabrous and shining at maturity. This loss of fruit trichomes is also common in other cultivated *Solanum* species, such as the naranjilla (*S. quitoense*) and its relatives in sect. *Lasiocarpa* (Dunal) D’Arcy (Whalen et al. 1981).

The cultivated tomato has a wide variety of unusual fruit shapes, from small and round to large and lobed to pepper-shaped (‘Yellow Stuffer’) to extremely elongate (‘Long John’). These cultivar differences in gynoecium morphology occur at a variety of developmental stages, after the floral meristem has committed itself to ovary formation (Frary et al. 2000), and/or during fruit development (Van der Knaap & Tanksley 2001). Shape appears to be controlled by only a few genes, distributed on several chromosomes (Grandillo et al. 1996, 1999; Frary et al. 2000; Van der Knaap et al. 2004); many of these genes have strong epistatic interactions (see van der Knaap et al. 2002).

All other species groups of sect. *Lycopersicon* and all members of sections *Lycopersicoides* and *Juglandifolia* have green fruits owing to the presence of chlorophyll in the outer layers of the pericarp. Carotenoid and xanthophyll pigments are also present in these green fruits, at concentrations similar to those found in leaves; yellow is overlain by the green of chlorophyll. Color ranges from greenish white to light green (e.g., Plate 3E–G) to medium green (e.g., Plate 3N, O) to occasionally purple (e.g., Plate 3I). Purplish coloration is due to the presence of anthocyanin pigments distributed discontinuously under the epicarp, and the fruit appears mottled with areas of green and purple. A green, dark green, or purple stripe is typically present in fruits of members of the “*Arcanum*” species group (*S. arcanum*, *S. chmielewskii*, *S. neorickii*), and the “*Eriopersicon*” species group (*S. corneliomulleri*, *S. chilense*, *S. habrochaites*, *S. huaylasense*, *S. peruvianum*) (see Plate 3E–L). The colored fruit stripe is produced by a concentration of pigments in the parenchyma tissue along the septum, and indicates the number of carpels and locules in the fruit. These green fruits retain their pubescence at maturity, and vary from glabrescent to puberulent to long-pubescent to villous. Green fruits contain higher levels of starch at maturity than do the red fruits of *S. lycopersicum* or *S. pimpinellifolium* and differ significantly in a variety of metabolites of potential ecological significance (e.g., nicotimates); all green-fruited species show higher variation in fruit than leaf metabolites (Schauer et al. 2005).

Members of sect. *Juglandifolia* have green globose fruits more than 15 mm in diameter, with a thick, hard pericarp, and lack darker green stripes (Plate 3N, O). Members of sect. *Lycopersicoides* also have globose but smaller fruits 10–15 mm in diameter, with thin and leathery pericarp, and lack darker green or purplish stripes; the fruits are green-

yellow when young and become dark at maturity. The fruits of *S. sitiens* dry out at maturity to become papery and brittle (Plate 3Q).

SEEDS. Seed morphology has proved of great utility in *Solanum* taxonomy. Enzymatic digestion of the outer testal walls reveals great variety in the morphology and structure of the lateral testal cell walls, varying both among and within groups (Whalen 1979; Lester & Durrands 1984; Knapp & Helgason 1997). Souèges (1907) provided an early study of tomato seeds. He described the development of the integument and recognized outer and inner layers of the seeds. Tomato seeds are oval, obovate, or orbicular in outline and flattened laterally. The cells of the outer epidermal layer develop radial wall thickenings that form as “hair-like outgrowths” or “pseudohairs” in mature seeds (Lester & Durrands 1984; Lester 1991). These hair-like outgrowths often greatly enlarge the outer layer of the integument, and the seed coat appears pubescent. While still in the ovary during seed development, the placental tissue surrounds the external tangential walls of the outer coat cells and makes the seeds mucilaginous. In mature seeds the pseudohairs are translucent, connate or fused laterally to each other, and tightly adpressed to the epidermis giving a silky appearance to the seed surface, or, if they stand separate, produce a hairy and shaggy seed surface. These hair-like outgrowths are united laterally and form a short wing at the margin of the seeds that may be extended around the seed border or more typically are confined to the apex. Enzymatic digestion reveals a reticulate or honeycomb pattern of testal cells (see figures in Lester 1991). The cell outlines at the basal portions are deeply sinuous and irregular (*S. cheesmaniae*, *S. lycopersicum*, *S. pimpinellifolium*), straight-angular (*S. pennellii*) or somewhat intermediate (i.e., sinuous at the very base and angular at the base of the “pseudohairs,” *S. chilense*, *S. ochranthum*; Lester 1991); they are thickest at the angles from which the “pseudohairs” arise. The inner epidermal layer is highly pigmented, giving color to the mature seed. Seed size varies from 3 mm long and 2.5 mm wide in the majority of the species and to 5 mm long and 3.5 mm wide in cultivated tomatoes and in sections *Juglandifolia* and *Lycopersicoides*. Color varies from yellow or pale brown to dark brown. Seeds of members of sections *Juglandifolia* and *Lycopersicoides* have a short wing-like expansion of the integument around the entire seed margin.

HABITATS AND DISTRIBUTION

Wild tomatoes and their relatives are plants of western South America (Fig. 12). In general, wild tomatoes and their relatives are plants of dry areas, with the exception of the members of sect. *Juglandifolia*. *Solanum juglandifolium* and *S. ochranthum* both occur in cloud forests, although they are usually found in open areas, such as tree falls, or along streams or roads where light intensity is greatest. *Solanum habrochaites* also occurs in cloud forest habitats to elevations of 3600 m, but is found as well in coastal areas and in dry forests on the western Andean slopes. The species of sections *Lycopersicoides* and *Lycopersicon* are dry habitat plants, occurring in the inter-Andean valleys subject to severe rain shadows (e.g., *S. arcanum* in the Valley of the Río Marañón, *S. huaylasense* in the Valley of the Río Santa, *S. chmielewskii* in the upper Apurímac Valley of Peru and the Sorata Valley of Bolivia, *S. neorickii* in dry valleys from Ecuador to southern Peru), in the extremely dry high-elevation deserts of the western Andean slope (*S. lycopersicoides*, *S. sitiens*, *S. pennellii*, *S. corneliomulleri*, *S. chilense*), and in the unique lomas habitat

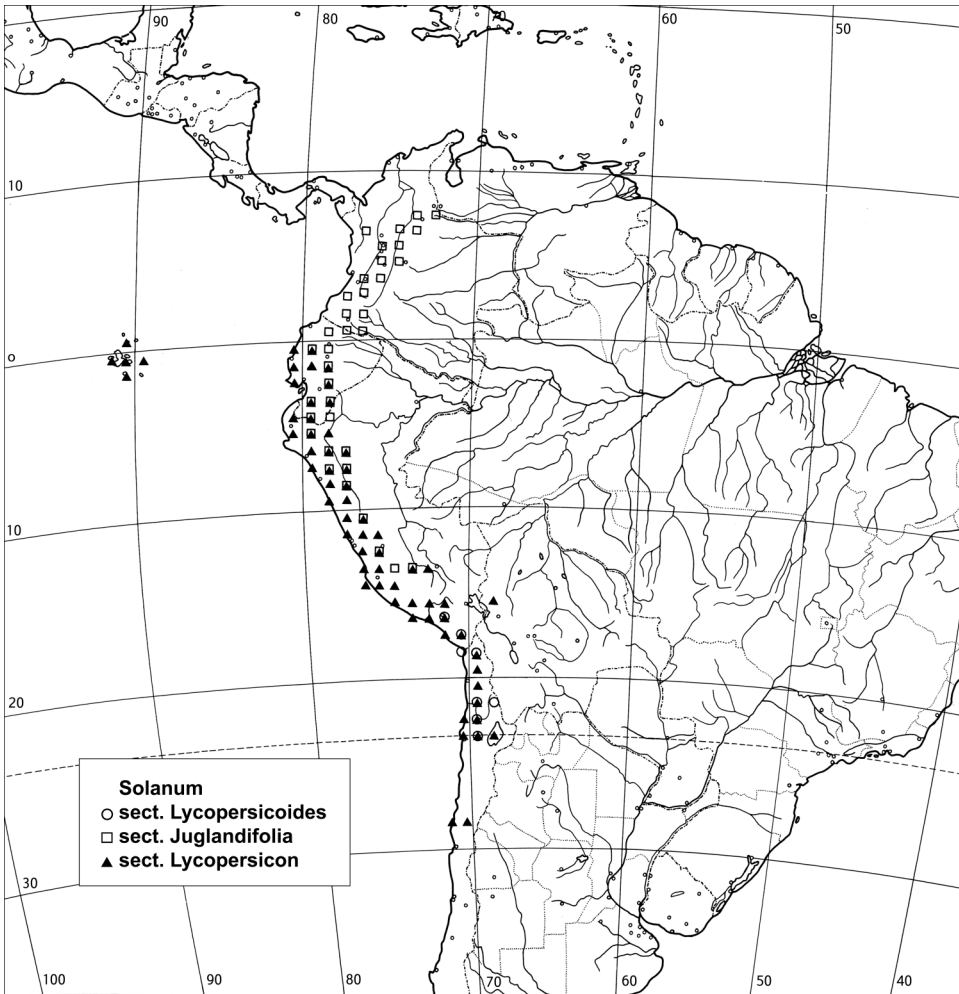


FIG. 12. Distribution of *Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, and sect. *Lycopersicon*.

along the Pacific coast of Peru and northern Chile (*S. chilense*, *S. habrochaites*, *S. pennellii*, *S. peruvianum*, and some populations of *S. arcanum*).

The lomas formation occurs within the Atacama and Peruvian desert hyper-arid belt that stretches for approximately 3500 km along the western coast of South America, from approximately 5°–30° S latitude. The lomas formations are small areas of vegetation occurring as islands in a sea of hyper-arid desert; they consist of highly endemic plant communities that form in near-shore localities where fog arising from the ocean provides sufficient moisture for vegetation (Rundel et al. 1991; Dillon 1997, 2005). Over 100 lomas localities have been identified in Peru and Chile (see Fig. 1 in Dillon 2005: 133), most of which include tomato species; Dillon (2005) lists five species (*S. chilense*, *S. habrochaites*, *S. pennellii*, *S. peruvianum*, *S. pimpinellifolium*). The lomas formation is caused by a variety of factors, among them the rain shadow of the Andes, the influence of cold sea surface temperatures associated with the Humboldt Current, and the positionally

stable subtropical anticyclone (Dillon 2005). Seasonal fogs form from September through December, which greatly increase moisture and hence flowering in these habitats at that time.

In addition to seasonal fogs, the vegetation of the lomas is also affected by periodic and recurring ENSO (El Niño Southern Oscillation) events, when the normally cold waters off the coast are displaced by warmer water from the Pacific, stimulating brief periods of heavy rainfall and high temperatures. Major El Niño events occur every 30–50 years and minor events approximately 3.5–7 years (Allan et al. 1996; see Quinn & Neal 1992 for a list of El Niño dates), and due to the high rainfall, mass flowering events often occur in El Niño years. In general, tomato specimens collected during these periods of high rainfall have larger leaves and are more robust, owing to better growing conditions, than those gathered at other times (Darwin et al. 2003). The island nature of the lomas formation, coupled with the periodicity of El Niño events, has certainly had a profound effect on tomato evolution and biogeography. High-rainfall El Niño events also affect inland tomato populations. For example, during a particularly strong El Niño event during 1997–1998, Sifres et al. (2006) documented a vast increase in the size of *S. pimpinellifolium* populations in northern Peru, where floods facilitated seed dispersal.

Some of the higher-elevation species also sporadically occur on the coast, usually on the edges of huaycos (avalanches of stone and mud that come from higher elevations), which occur after Andean rains. *Solanum pennellii* is often found in these extremely dry huayco sites (Holle et al. 1979), and some specimens of *S. corneliomulleri* occurring in lower elevations certainly arrived with mud from higher elevations (see specimens cited for *S. corneliomulleri*). In general, most of the tomato species will occur wherever moisture is found, and they have been characterized as weedy (Holle et al. 1978, 1979).

Solanum pimpinellifolium is also found in coastal habitats, but rather than as a strictly specialized lomas species, it occurs in river valleys where there is seasonal moisture from the higher Andean slopes (Caicedo & Schaal 2004a). Populations of *S. pimpinellifolium* are quite distinct in terms of haplotypes, indicating low gene flow in this fragmented and somewhat ephemeral habitat. In the Galápagos Islands, *S. cheesmaniae* occurs from sea level to the volcanic peaks in dry rocky areas, while *S. galapagense* tends to inhabit lower elevation habitats, often on lava flows in the sea spray. All of these desert species respond to the increased moisture available in El Niño years by growing more robustly and flowering more copiously.

The cultivated tomato, *S. lycopersicum*, is more moisture-dependent than its wild relatives and occurs in disturbed habitats all over the world, from the tropics to the temperate zone. Populations of feral tomatoes are common (see discussion of *S. lycopersicum*), but rarely persist for many generations in the absence of cultivation.

POLLINATION BIOLOGY

Like the flowers of all other species of *Solanum*, those of tomatoes are buzz-pollinated by bees, which, in vibrating their indirect flight muscles, set up a resonance that causes pollen to exit through the poricidal anthers (Buchmann et al. 1977; Michener 1978; Buchmann 1986). Pollen is the only reward for pollinators; no nectar is produced in any of these species, and pollen is used for larval nutrition and is the most important protein source for many of the bees that pollinate these plants (Buchmann 1983). Nitrogen and protein levels in the pollen are high (Buchmann 1986) and in line with those found in other

species of *Solanum*. Bees in the subfamily Apoidea are pollinators of some *Solanum* species (see Knapp 1986, 2002c), but honeybees (*Apis mellifera*) cannot vibrate the indirect flight muscles in order to extract pollen from the anthers of solanums; honeybees visit tomato flowers, but cut the anther tube and remove pollen by theft (Cribb et al. 1993, for *S. lycopersicum*; Teppner 2005, for *S. peruvianum* in cultivation). Both solitary and eusocial bees can buzz *Solanum* flowers (see Knapp, 2002c, for a discussion). Bumblebees (*Bombus* spp., Apidae) are well-known pollinators of tomatoes in cultivation, and in California mud bees (*Anthophora*, Anthophoridae) are also known to buzz flowers. Detailed studies of pollination of cultivated plants of *S. pimpinellifolium* (exserted style morph) and various cultivars of *S. lycopersicum* (Teppner 1993, 2005) in Austria showed that a wide variety of bees visit and pollinate tomatoes. Teppner (2005) observed bumblebees (three species of *Bombus*), halictine bees (Halictidae; five species of *Lasioglossum*), colletid bees (Colletidae; *Hylaeus gibbus*), and leafcutter bees (Megachilidae; *Megachile willughbiella*) all buzzing the flowers and effecting pollination. Bumblebees were the most efficient, but *Megachile* also visited many flowers and was large enough to achieve pollination in all flowers visited. Another species of *Megachile* visited the flowers of *S. chmielewskii* cultivated in a botanic garden, but vibration was not recorded (Teppner 2005). Hoverflies (Diptera: Syrphidae) also visited tomato flowers, inserting their proboscis into the anther tube in an apparent search for nectar; pollination was thought to be improbable (Teppner 2005). Teppner (1993) listed all previous records for pollinators of tomatoes and their relatives, which included 17 species of bees from four families (Colletidae, Halictidae, Anthophoridae, and Apidae). Rick (1950) observed bees visiting flowers of several species of tomatoes at multiple sites in the Rimac Valley, Depto. Lima, Peru: *S. lycopersicum* was mostly visited by *Augochlora nigromarginata* (Halictidae), but also received visits from *Exomalopsis bruesii* (Anthophoridae); *S. pimpinellifolium* was visited by *Augochlora nigromarginata* (Halictidae); *S. corneliomulleri* was visited by *Augochlora matucanensis*, *Thygater albiceps* (both Halictidae), and *Bombus funebris* (Apidae); *S. habrochaites* was visited by a species of *Lonchopria* (Colletidae), *Augochlora nigromaculata* and *A. matucanensis* (Halictidae), *Xylocopa brasiliatorum*, and *Centris surinamensis* (both Anthophoridae); and *S. peruvianum* was visited by the widest variety of bees, with *Augochlora nigropunctata* (Halictidae), *Anthophora tricincta*, *Exomalopsis bruesii*, *Thygater albiceps*, and *Xylocopa brasiliatorum* (all Anthophoridae) all recorded. In general, the same species of bee visited plants in different locations (Rick 1950), but in *S. pimpinellifolium* (and probably also in other species) a single bee species accounted for more than 90% of actual pollination events (Rick et al. 1978). More recent observations of pollination of tomatoes and relatives in their native habitats are very rare and usually confined to label data or to unpublished observations. In the Galápagos Islands, *Xylocopa darwini* (Anthophoridae) has been observed visiting the flowers of both *S. cheesmaniae* and *S. pimpinellifolium* (Darwin et al. 2003). Studies of tomato pollinators in native habitats should be a priority for field study.

HERBIVORES AND DISEASES

Data on herbivory on tomatoes comes mainly from observations on *Solanum lycopersicum* in cultivation in the temperate zone. Records of Lepidoptera feeding on species of tomatoes are presented in Table 2; only 5 of the 332 records (from the HOSTS database <http://internt.nhm.ac.uk/jdsml/research-curation/projects/hostplants/index.dsml>) are

TABLE 2. Records of Lepidopteran larvae feeding on members of sections *Lycopersicoides*, *Juglandifolia*, and *Lycopersicon* (data from HOSTS database, <http://www.nhm.ac.uk/research-curation/projects/hostplants/>)

LEPIDOPTERAN FAMILY	SPECIES OF SOLANUM
Arctiidae	<i>S. lycopersicum</i>
Gelechiidae	<i>S. lycopersicum</i> , <i>S. habrochaites</i>
Geometridae	<i>S. lycopersicum</i>
Hepialidae	<i>S. lycopersicum</i>
Lycaenidae	<i>S. lycopersicum</i>
Noctuidae	<i>S. lycopersicum</i> , <i>S. habrochaites</i> , <i>S. pennellii</i>
Nymphalidae (Ithomiinae)	<i>S. lycopersicum</i>
Psychidae	<i>S. lycopersicum</i>
Pterophoridae	<i>S. lycopersicum</i>
Pyalidae	<i>S. lycopersicum</i>
Sesiidae	<i>S. lycopersicum</i>
Sphingidae	<i>S. lycopersicum</i>
Tortricidae	<i>S. lycopersicum</i>

from the native range of tomatoes and their relatives. In Ecuador, *S. lycopersicum* is fed upon by the Solanaceae specialist herbivore *Mechanitis* spp. (Nymphalidae: Ithomiinae). The enormous literature on diseases of tomatoes is based on the cultivated species, *S. lycopersicum*, with a few notable exceptions (Huang et al. 2000; Van der Hoorn et al. 2001; Bai et al. 2003, 2004; Caicedo & Schaal 2004a, 2004b). Studies on disease in tomatoes are generally focused on the identification of alleles or genes conferring resistance that can be introduced into cultivated populations, and usually use gene bank accessions (see Van der Hoorn et al., 2001, as an example) rather than on naturally occurring populations of wild species (but see Soler et al. 2002; Caicedo & Schaal 2004a, 2004b). Tomatoes are susceptible to various fungal (*Phytophthora*, *Cladosporium*, and other blights), bacterial (tomato wilt, fusarium wilt), and viral (Pepino mosaic virus, tobacco mosaic virus) diseases, as well as attacks by nematodes and other pests. Resistance to powdery mildews has been identified in accessions of *S. arcanum* (Bai et al. 2004), *S. neorickii* (Bai et al. 2003), and *S. habrochaites* (Huang et al. 2000), and to *Cladosporium* and other fungal diseases in *S. pimpinellifolium* (Van der Hoorn et al. 2001; Caicedo & Schaal 2004a, 2004b). Little is known about the occurrence of disease in wild populations or in any of the wild species. Field observations on herbivores and diseases of tomatoes in their native habitats should be, like observations of pollinators, a priority for research.

BREEDING SYSTEMS AND INTERSPECIFIC HYBRIDIZATION

Mating systems in wild tomato species vary from allogamous self-incompatible to facultative allogamous and self-compatible, to autogamous and self-compatible (Rick 1963, 1979, 1982b, 1986b; Table 1). The self-incompatibility system in tomatoes is gametophytic and controlled by a single, multiallelic S locus (Tanksley & Loaliza-Figueroa 1985).

The self-incompatibility system has shown strong relationships with the degree of outcrossing, allelic diversity, floral display, and degree of stigma exertion in wild tomatoes. Rick (1982b) investigated the genetic bases of self-compatibility, self-incompatibility, and flower characters by studying interspecific hybrids between the self-compatible (SC) *S. pimpinellifolium*, used as recurrent parent, and the two self-incompatible (SI)

species *S. habrochaites* and *S. pennellii*. He postulated that three independent genetic phases, most probably regulated by different unlinked genes or gene complexes, are essential for successful functioning of the self-incompatibility system. These genes are operating on: 1) prevention of self-fertilization, 2) changes in the flower structures to ensure cross-pollination, and 3) development of secondary flower characters to attract pollinators. He concluded that the evolution of the mating system in wild tomatoes proceeded from self-incompatibility, as the ancestral condition, to self-compatibility, and probably never reversed to self-incompatibility. Changes from self-incompatibility to self-compatibility are expected to arise frequently and independently (Rick 1982b). This trend has been found in *S. habrochaites* and *S. pennellii*; both species have self-incompatible and self-compatible populations. The self-incompatible populations occupy the center of their species geographic distributions, and have higher genetic variation, larger flower parts, and exerted stigmas. Self-compatible populations occur toward the northern and southern edges of the ranges of *S. habrochaites* and *S. pennellii*, have less genetic variation, smaller flower parts, and little or no stigma exertion (Rick et al. 1979; Rick & Tanksley 1981). The change from self-incompatibility to self-compatibility has been reported in only one population of *S. peruvianum* (Rick 1986b).

In the self-compatible species, the extent of outcrossing and genetic variation is also related to floral display and degree of stigma exertion. Within *S. pimpinellifolium*, the most northern and southern populations at the margins of the species range are highly autogamous with little or no genetic variation, have small flower parts, and little or no stigma exertion, while the centrally located facultative allogamous populations have higher genetic variation, larger corollas, and marked stigma exertion (Rick et al. 1977). A comparison of different genotypes of *S. pimpinellifolium* in experimental plots in Peru showed that different outcrossing rates could be largely attributed to differences in floral characters, especially the level of stigma exertion, rather than to differences in numbers and types of pollinators (Rick et al. 1978). Smaller flower size in selfing forms of *S. pimpinellifolium* is due largely to variations in the growing time of individual flowers, with the larger outcrossed flowers growing (i.e., remaining open) for longer time periods than the smaller, selfing flowers (Georgiady & Lord 2002). Four QTLs (total anther length, anther sterile apical appendage length, style length, and flowers per inflorescence) cause major phenotypic variance (Georgiady et al. 2002). Early floral stages showed no significant differences; thus, the difference in size in these flower size transitions can be attributed to a simple heterochronic change in growth (Georgiady & Lord 2002). Chen and Tanksley (2004) have suggested that a locus on chromosome 2 is largely responsible for stigma length, and that the tightly linked genes in this compound locus represent a co-adapted gene complex controlling mating behavior.

Two self-compatible sister species, *S. chmielewskii* and *S. neorickii*, illustrate another example of changes in flower characters associated with outcrossing and genetic variation. *Solanum neorickii* is exclusively autogamous, has low intra-population genetic variation, small flowers, and stigmas included in the anther tube. In contrast, the facultative allogamous *S. chmielewskii* exhibits higher levels of heterozygosity, larger flower parts, and exerted stigmas. Rick et al. (1976) postulated that *S. neorickii* evolved from *S. chmielewskii*. All populations of *S. chilense* are self-incompatible. The species in the outgroup sections *S. lycopersicoides*, *S. sitiens*, *S. ochranthum*, and *S. juglandifolium*, are exclusively self-incompatible.

The Endosperm Balance Number (EBN) crossability phenomenon was analyzed for Rick's two wild tomato complexes by Ehlenfeldt and Hanneman (1992). The EBN

hypothesis (Johnston et al. 1980; Ortiz & Ehlenfeldt 1992; Hanneman 1994) postulates that in the absence of stylar barriers, the success or failure of a cross is determined primarily by a 2:1 maternal to paternal balance in the endosperm, independent of ploidy. The EBN data supported the hypothesis of two intra-fertile groups as proposed by Rick (1979). Rick's "Esculentum" complex showed uniformity of EBN values, which can be compared to the $2\times(1EBN)$ species in potato. On the other hand, the "Peruvianum" complex showed variable values for EBN, but most comparable to $2\times(2EBN)$ potato species (Ehlenfeldt & Hanneman 1992). These authors hypothesized that Rick's "Esculentum" and "Peruvianum" complexes are separated by a system analogous to the $2\times(1EBN)$ *S. commersonii* Dunal and $2\times(2EBN)$ *S. chacoense* Bitter crossability groups. This putative isolating mechanism may restrict or suppress gene flow among sympatric populations (Ehlenfeldt & Hanneman 1992), and may play a role in the reproductive isolation in tomatoes, such as the *S. arcanum* assemblages in northern Peru.

GENETIC STUDIES

Studies of tomato systematics and diversity have been greatly aided by the ready availability of germplasm collections of all of the wild species from across their ranges. These collections have been widely used in breeding programs as sources of disease resistances and agronomic traits (Esquinas-Alcázar 1981; Rick 1982a, 1986b; Stevens & Rick 1986; Rick et al. 1987; Laterrot 1989). Ross (1998) cited 62,832 accessions of *Solanum* sect. *Lycopersicon* maintained in gene banks around the world, although most of these accessions are various cultivars of *S. lycopersicum*. Villand et al. (1998) evaluated the genetic variation among *S. lycopersicum* accessions at the Asian Research and Development Center (one of the largest collections of cultivated tomato germplasm) with Random Amplified Polymorphic DNA (RAPDs). RAPD diversity was greater in accessions from the primary distribution center (Ecuador, Peru, Chile), and for breeding purposes variation can be obtained at a faster rate by sampling accessions from this area than from other geographic regions. Large collections of wild and cultivated species exist at the C. M. Rick Tomato Genetics Resources Center (TGRC, University of California, Davis, <http://tgrc.ucdavis.edu>), the USDA genebank (Geneva, New York), the National Plant Genetic Resources Laboratory (Laguna, The Philippines), the Institute of Plant Genetics and Crop Plant Research (Gatersleben, Germany), the N. I. Vavilov All Russian Institute of Plant Industry (St. Petersburg, Russia, see Spooner 1999), and at various other European genebanks (Daunay et al. 2003).

The tomato also serves as a model organism for understanding the basic genetics of diploid plants. Features that enhance the usefulness of tomatoes for genetic studies are: the naturally occurring variability in the species, self-pollination that leads to the expression of recessive mutations, the possibility of controlled hybridization within and among species, the lack of gene duplication, and ease with which each of the 12 chromosomes can be identified (Rick 1978).

Crosses among different tomato species allow the production of genetic linkage maps that indicate all species share the same basic genome structure, consistent with evidence from chromosome pairing in interspecific hybrids, and that speciation must therefore have been accomplished by gene mutation rather than genome rearrangement (Chetelat & Ji 2006). New methodological approaches, like molecular mapping of important agronomical characters, have provided powerful tools for the improvement of the tomato crop

(Tanksley & McCouch 1997). The genetic base of tomato has been expanded by hybridization and recombination with related species *S. lycopersicoides* and *S. sitiens*, which possess a paracentric inversion on chromosome 10L that appears to be ancestral in the tomato clade (sect. *Lycopersicon* as defined here). Recently synthesized introgression lines with wild species provide powerful tools for genome analysis and breeding (Fridman et al. 2004; Chetelat & Ji 2006). The relatively small genome of tomato is now well delineated with high resolution molecular linkage maps, providing a framework for comparative genetic analysis of tomatoes and related *Solanum* species (Y. Wang, unpubl.) and also identifying regions of microcolinearity between tomato and *Arabidopsis*, based on conserved ortholog set (COS) markers (Chetelat & Ji 2006; Wu et al. 2006).

Bioinformatic resources make these data widely available to the community through the Solanaceae Genomics Network website, SGN (<http://sgn.cornell.edu>). SGN currently houses map and marker data for Solanaceae species, a large expressed sequence tag collection with computationally derived unigene sets, an extensive database of phenotypic information for a mutagenized tomato population, and associated tools, such as real-time quantitative trait loci. The establishment of the International Solanaceae Project (SOL; <http://www.sgn.cornell.edu/>) began with the sequencing of the tomato genome. The genome is currently being sequenced by an international consortium of 10 countries (see Mueller et al. 2005a). The ordered BAC approach being taken (Mueller et al. 2005b) will result in high quality sequence that can be compared not only to wild tomatoes, but across the Solanaceae and to other related groups. Coupled with data from natural variation (available in monographs such as this and on the Solanaceae Source website, <http://www.nhm.ac.uk/solanaceaesource>), the tomato genome sequence will be a powerful tool for aiding broad scale comparative biology that spans datasets from gene sequences and unigene sets to natural variation in the wild.

SPECIES RELATIONSHIPS

As reviewed in Taxonomic History, Müller (1940a) and Luckwill (1943a) treated tomatoes as the genus *Lycopersicon* and recognized the two subgenera based on morphology: subg. *Eulycopersicon* and subg. *Eriopersicon* (Fig. 5). Luckwill (1943a) hypothesized that the two subgenera might have evolved from an ancestral simple form characterized by imparipinnate leaves with 5 to 7 entire leaflets, few interjected leaflets, probably no secondary leaflets, unbranched inflorescences, and undeveloped pseudostipules. He suggested that two lineages diverged from the ancestral forms, one characterized by fruits with carotenoid pigments and the other by green fruits with anthocyanin pigments.

Rick (1979), on the other hand, recognized two “complexes” based on crossing relationships, the “Esculentum complex” and “Peruvianum complex” (Figs. 5, 7). The most widespread and variable species was *L. peruvianum*, and crosses of northern and southern populations of *L. peruvianum* allowed Rick (1986a) to identify four groups of races that were isolated by reproductive barriers: three groups in northern Peru (the Chamaya-Cuvita group of races, the Marañón group, and the Chotano-*humifusum* group), and a fourth group from south-central Peru and northern Chile (see Fig. 8). He found crossing barriers between the northern and southern *L. peruvianum* races, and showed that some of the northern races could be crossed to a limited degree with southern races and with species from both his “Esculentum” and “Peruvianum” complexes. Rick (1986a) hypothesized

that the races of *L. peruvianum* found in the Río Marañón drainage in northern Peru were ancestral to all other wild tomatoes, and that speciation and differentiation took place with migration to the south. Rick (1963) suggested earlier that the pattern of *L. peruvianum* distribution signified a single origin of his broadly defined *L. peruvianum* with subsequent spread before or during the uplift of the central Andes.

Recent cladistic and phenetic studies of species boundaries and relationships have used a combination of molecular and morphological data. Our discussion above and in Taxonomic History used the names in *Lycopersicon* or *Solanum* according to their usage by the authors cited; all further discussion uses *Solanum* names as recognized in this monograph (Table 1). Figure 13 shows abstracted summary trees based on chloroplast DNA (cpDNA) restriction sites (Palmer & Zamir 1982; Fig. 13A; and Spooner et al. 1993; Fig. 13D), mitochondrial DNA (mtDNA) restriction sites (McClellan & Hanson 1986; Fig. 13B), nuclear RFLPs (Miller & Tanksley 1990; Fig. 13C), isozymes (Breto et al. 1993; Fig. 13E), internal transcribed spacer region of nuclear ribosomal DNA (ITS) gene sequences (Marshall et al. 2001; Fig. 13F), nuclear DNA microsatellites (Alvarez et al. 2001; Fig. 13G), and morphology-based cladistics (Peralta & Spooner 2005; Fig. 13H). We show the previously published trees (modified using our currently recognized names in *Solanum* for tomatoes and relatives) for the studies using GBSSI (Peralta & Spooner 2001) and companion AFLP (Spooner et al. 2005) and morphological phenetics (Peralta & Spooner 2005) studies as noted below. The results of these later studies are more complete than prior studies in that they are based on three or more accessions per species, with a concentration on the highly polymorphic and most widespread species *S. peruvianum* s.l. The present discussion highlights the studies based on data from chloroplast DNA, ITS, GBSSI, morphology, and AFLPs in more detail, because an analysis by Spooner et al. (2005) used them for combined data analyses.

The name *S. peruvianum* is used in three ways in this discussion. First, the name *S. peruvianum* s.l. refers to the broadly circumscribed species complex prior to our recognition of four species within it (Peralta et al. 2005). Second, *S. peruvianum* “north” and “south” refer to the geographic partitioning of *S. peruvianum* s.l. into two groups with the use of GBSSI (Peralta & Spooner 2001), morphological (Peralta & Spooner 2005), and AFLP (Spooner et al. 2005) data (Fig. 17). Third, in our current treatment, based on the results of these three investigations and our examination of hundreds of additional herbarium specimens, we divide *S. peruvianum* “north” into *S. arcanum* and *S. huaylasense*, and *S. peruvianum* “south” into *S. corneliomulleri* and *S. peruvianum* s.str. (Peralta et al. 2005). In addition, we recognize subsect. *Lycopersicoides* of Child (1990) at the sectional rank and sect. *Juglandifolia*; we modify the previously published graphics of our GBSSI (Peralta & Spooner 2001), AFLP (Spooner et al. 2005) and morphological (Peralta & Spooner 2005) studies to incorporate these new names.

CHLOROPLAST DNA RESTRICTION SITE DATA. The cpDNA restriction site phylogenetic study of Palmer and Zamir (1982; Fig. 13A) was one of the first studies using this technique and stimulated the use of chloroplast DNA in scores of other plant groups. The technique was soon refined to the use of heterologous probes, rather than total chloroplast banding patterns, to assess polymorphisms more accurately. Palmer and Zamir’s (1982) study, using 25 restriction endonucleases, placed *S. lycopersicoides* (*Solanum* sect. *Lycopersicoides*) and *S. juglandifolium* (*Solanum* sect. *Juglandifolia*) as sister to tomatoes, and supported the monophyly of the red- to orange- to yellow-fruited species (*S. cheesmaniae*, *S. lycopersicum*, and *S. pimpinellifolium*). Palmer and Zamir’s (1982) study was

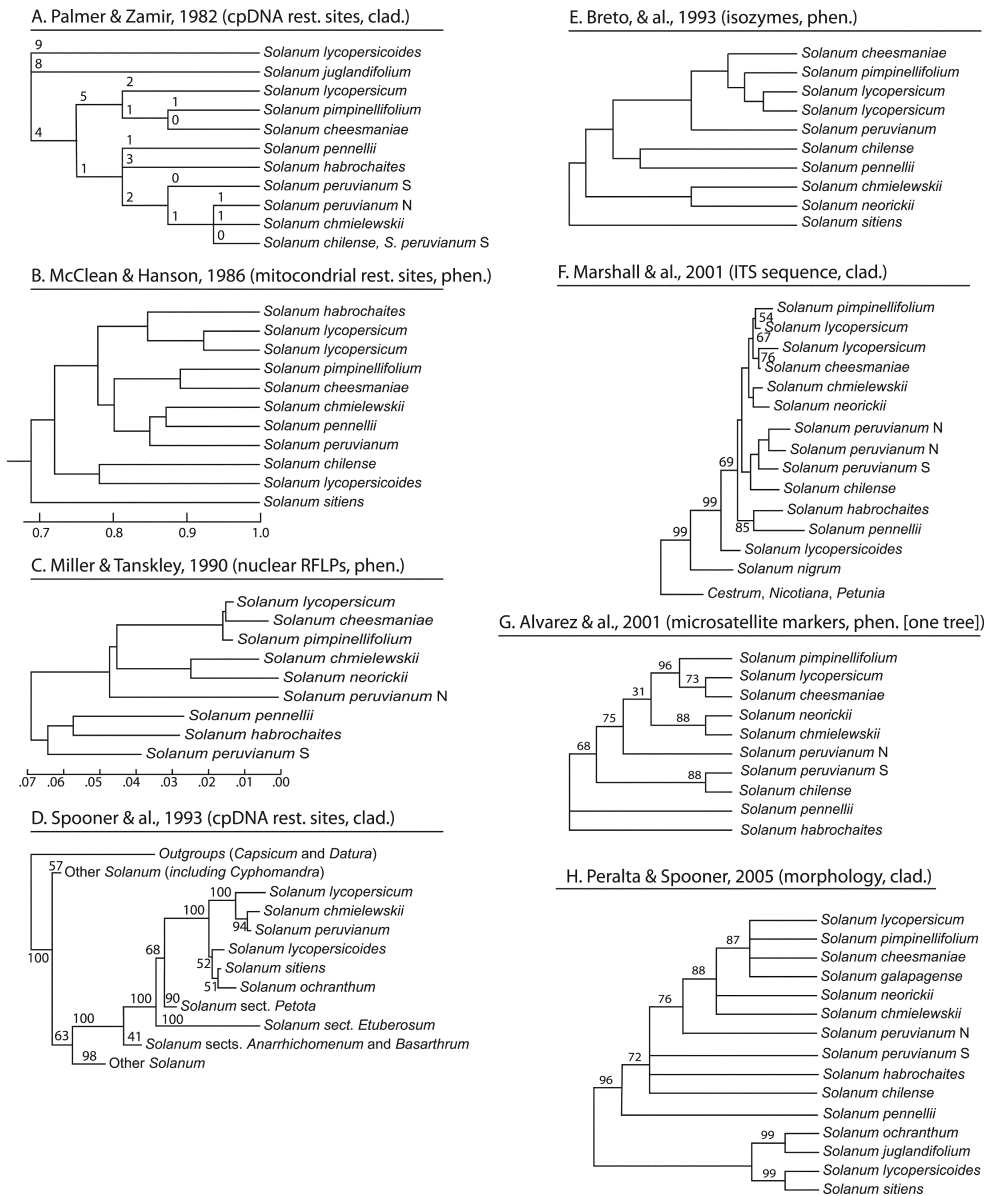


FIG. 13. An abstracted summary of cladistic (clad.) and phenetic (phen.) studies of tomatoes and outgroups using morphological, isozyme, and molecular data, including similarity coefficients (lines below Trees, B, C) restriction sites supporting each branch (A), or bootstrap values over 50% (D, F, G, H); the study in E showed no statistical support for the tree. The trees are shortened when necessary to show summary results; see Table 1 for equivalent names in *Lycopersicon*. “N” and “S” following *S. peruvianum* indicate northern (N) and southern (S) accessions of that species corresponding to the companion GBSSI sequence study (Peralta & Spooner 2001), morphological study (Peralta & Spooner 2005), and AFLP study (Spooner et al. 2005) of tomatoes and outgroups. Reproduced with permission from *Taxon* 54: 46, fig. 2, 2005.

not able to place into separate clades the northern and southern populations of *S. peruvianum*, or to resolve the relationships of *S. chilense* and *S. chmielewskii*.

Spooner et al. (1993; Fig. 13D) examined cpDNA polymorphism of representatives of tomato, potato, other species of *Solanum*, and outgroups in *Capsicum* L. and *Datura* L. with a focus on examining outgroup relationships of tomato and potato. Their study showed tomatoes and their immediate outgroups in *Solanum* sect. *Lycopersicoides* and sect. *Juglandifolia* to form a sister clade to potatoes (sect. *Petota*), with *Solanum* sect. *Etuberosum* (Buk. & Kameraz) Child as the sister to all the above. These results stimulated the taxonomic recognition of all tomatoes in *Solanum*, which was also supported by other chloroplast DNA restriction site and sequence data (Bohs & Olmstead 1997, 1999; Olmstead & Palmer 1997; Olmstead et al. 1999; Bohs 2005). These multiple data sets from a variety of genes unambiguously established tomatoes to be deeply nested in *Solanum*, and Spooner et al. (1993) proposed the necessary nomenclatural transfers. Assigning tomatoes to *Solanum* is now accepted by the majority of taxonomists as well as by most plant breeders and other users (Caicedo & Schaal 2004a, b; Fridman et al. 2004; Schauer et al. 2005; also see <http://tgrc.ucdavis.edu/dukey.html>).

GBSSI SEQUENCE DATA. Peralta and Spooner (2001) provided a GBSSI gene sequence phylogeny of 79 accessions of tomatoes and outgroups, concentrating on the most geographically widespread and polymorphic species *S. peruvianum* (Fig. 14). These results supported sect. *Juglandifolia* as sister to tomatoes; sect. *Lycopersicoides* as sister to tomatoes + sect. *Juglandifolia*; potatoes (sect. *Petota*) as sister to tomatoes + sect. *Juglandifolia* + sect. *Lycopersicoides*; and sect. *Etuberosum* as sister to tomatoes + sect. *Juglandifolia* + sect. *Lycopersicoides* + sect. *Petota*. Within sect. *Lycopersicon*, there was a polytomy composed of *S. chilense*, *S. habrochaites*, and *S. pennellii*, and the central-southern Peruvian to northern Chilean populations of *S. peruvianum*. A sister clade contained the northern Peruvian populations of *S. chmielewskii*, *S. neorickii*, and *S. peruvianum*, and a monophyletic group composed of the self-compatible and brightly colored (red- to orange- to yellow-fruited) species *S. cheesmaniae* (including accessions now recognized as *S. galapagense*), *S. lycopersicum*, and *S. pimpinellifolium*.

INTERNAL TRANSCRIBED SPACER REGION OF NUCLEAR RIBOSOMAL DNA (ITS) GENE SEQUENCES. Marshall et al. (2001) analyzed phylogenetic relationships of wild tomatoes with DNA sequences of the internal transcribed spacer region of nuclear ribosomal DNA (ITS) (Fig. 13F). *Solanum lycopersicoides* was supported as sister to tomatoes (members of sect. *Juglandifolia* were not included in this study). *Solanum chilense* and *S. habrochaites* were supported as sister to all other tomatoes. *Solanum chilense* and northern and southern populations of *S. peruvianum* formed a clade sister to *S. chilense* and *S. habrochaites*. *Solanum chmielewskii* and *S. neorickii* formed the next clade, followed by a clade of brightly colored-fruited species.

MORPHOLOGICAL PHENETICS. The phenetic morphological study of Peralta and Spooner (2005) used many of the same accessions as the GBSSI study. In total, 66 characters (50 quantitative and 16 qualitative) were measured for six individuals of 66 accessions, and averages of all six plants were taken as representative of the accession. Sixty-one of these 66 characters were found to be significantly different between at least two species and were used for phenetic analyses. Most of these 61 characters overlapped in

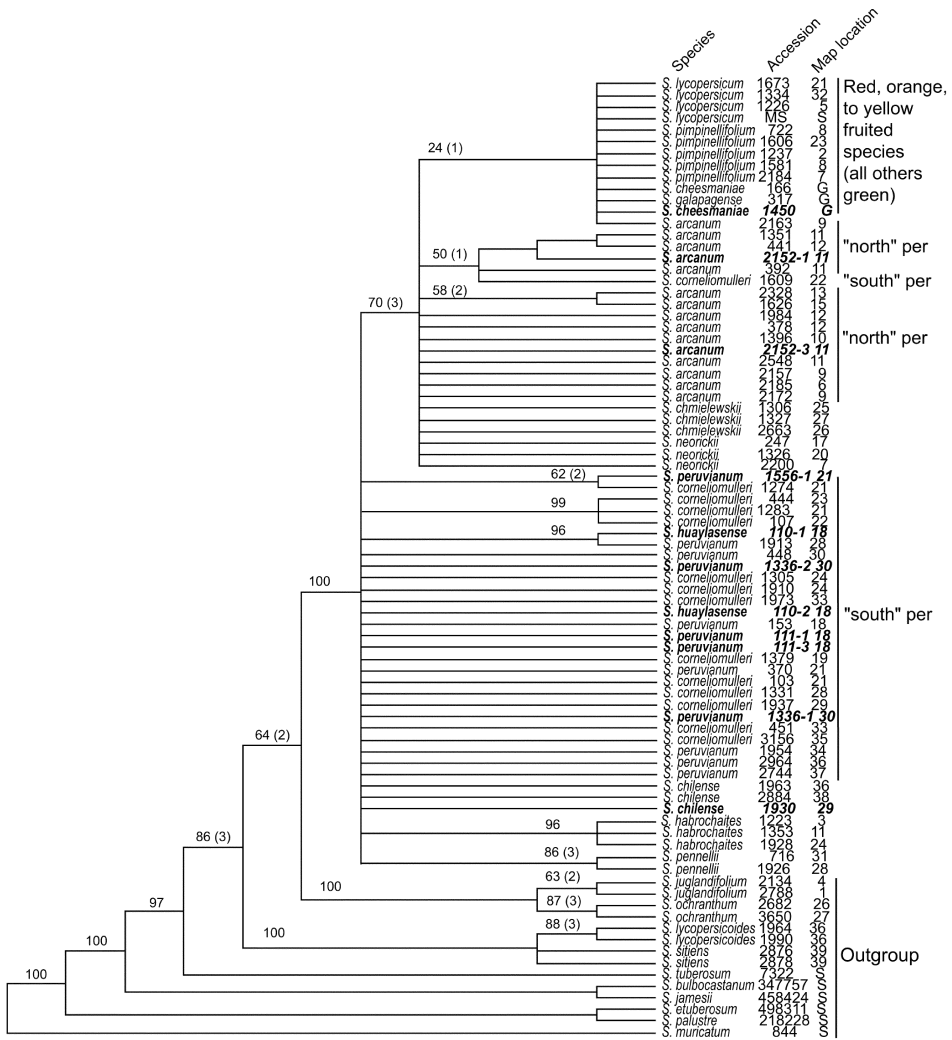


FIG. 14. Strict consensus tree of 15,000 most-parsimonious trees (including insertion-deletion characters) based on GBSSI (waxy) gene sequences, with overlaid bootstrap and decay values (in parentheses). The accessions in bold italics are distinct GBSSI sequence types from different clones obtained from the same single individual plant. Accession numbers are LA numbers from the C. M. Rick Tomato Genetic Resources Center. Map localities are given as in Spooner et al. (2005); "G" refers to accessions from the Galápagos Islands, "S" refers to unmapped continental accessions, "north" and "south" refer to northern and southern populations of *S. peruvianum* s.l. as distinguished by a line drawn at about 10°S. Modified from Spooner and Peralta (2001) with the designation of species as recognized here.

range among species, but 24 showed discrete breaks to differentiate species that were useful for additional morphological cladistic analyses (see below).

Similarity matrices for these 61 characters were generated with various algorithms, and dendrograms were constructed with the unweighted pair group method (UPGMA); we present here the distance and correlation methods with UPGMA results from Peralta

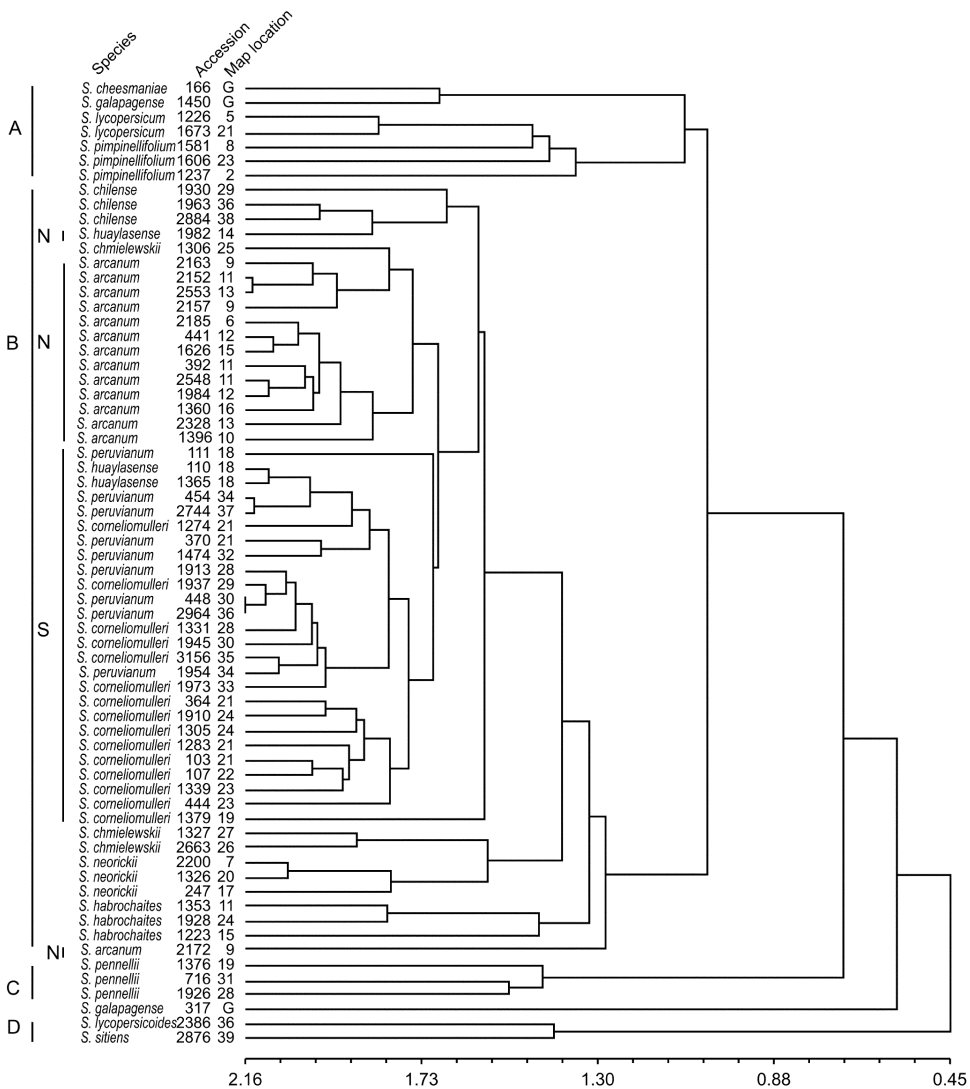


FIG. 15. UPGMA dendrogram (distance option) based on 61 morphological characters. Accession numbers are LA numbers from the C. M. Rick Tomato Genetic Resources Center. Map localities are given as in Spooner et al. (2005); "G" refers to accessions from the Galápagos Islands, "N" and "S" refer to northern and southern populations of *S. peruvianum* s.l. as distinguished by a line drawn at about 10°S. Groups A–D are discussed in the text. Modified from Peralta and Spooner (2005) with the designation of species as recognized in this monograph.

and Spooner (2005). The morphological distance phenogram (Fig. 15) has the best fit of the similarity matrix to the tree as determined by a cophenetic correlation coefficient (0.93), while the correlation matrix had a lower value (0.75). The distance phenogram defines four main groups (Fig. 15A–D). The outgroups, *S. lycopersicoides* and *S. siliens*, cluster as the external branch (group D), followed by *S. galapagense*, and then a group of all three accessions of *S. pennellii* (group C). The self-compatible, red- to orange- to yellow-fruited species (*S. lycopersicum*, *S. cheesmaniae*, and *S. pimpinellifolium*) form a

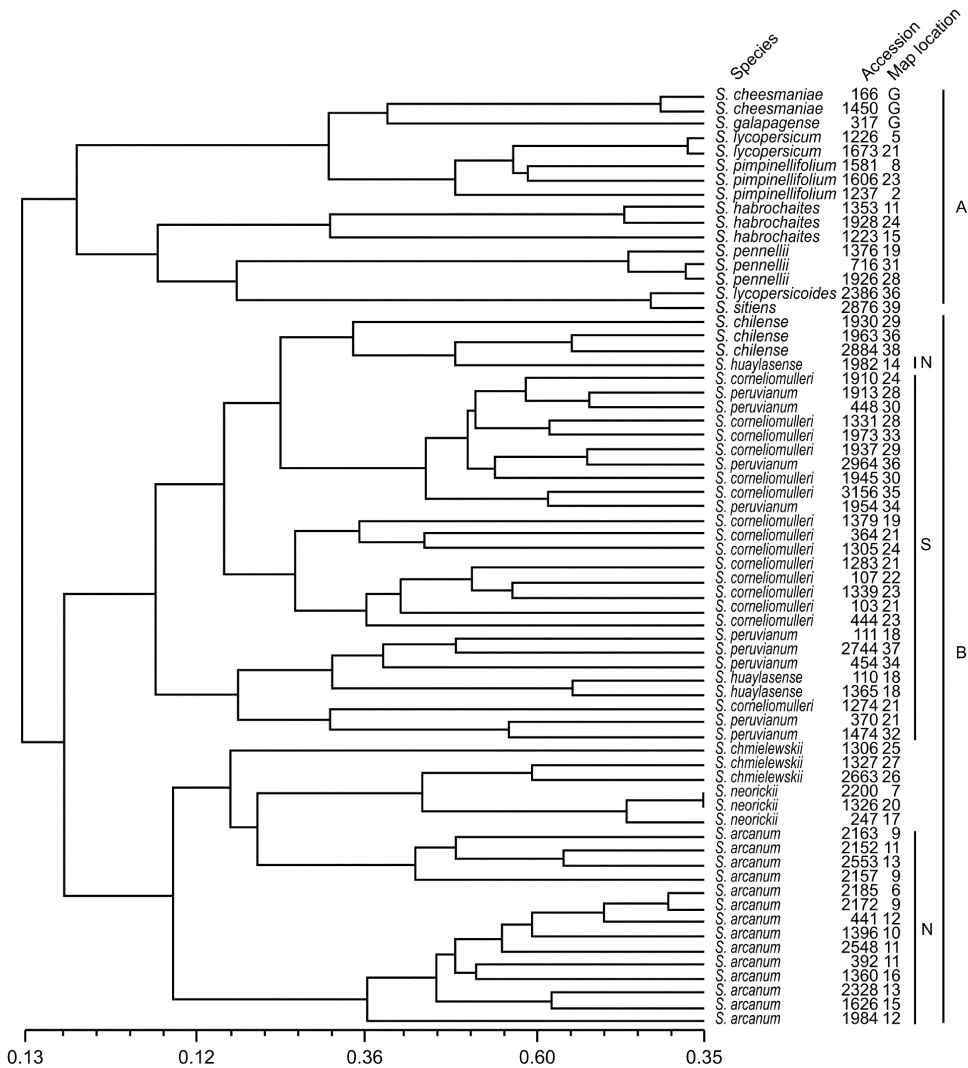


FIG. 16. UPGMA dendrogram (correlation option) based on 61 morphological characters. Accession numbers are LA numbers from the C. M. Rick Tomato Genetic Resources Center. Map localities are given as in Spooner et al. (2005); "G" refers to accessions from the Galápagos Islands, "N" and "S" refer to northern and southern populations of *S. peruvianum* s.l. as distinguished by a line drawn at about 10°S. Groups A and B are discussed in the text. Modified from Peralta and Spooner (2005) with the designation of species as recognized in this monograph.

third cluster (group A), but with the exclusion of the distinctive *S. galapagensis*. The fourth group (B) includes the remaining species. Within group B, *S. neorickii* and two accessions of *S. chmielewskii* cluster together, to the exclusion of one accession of *S. chmielewskii* (LA1306) that grouped with all accessions of *S. arcanum*. All accessions of *S. chilense* formed a group that also contained one accession of *S. huaylasense* (LA1982). The three accessions of *S. habrochaites* formed a separate group. Two major groups were recognized within former *S. peruvianum*: "north" and "south." Our current treatment now

recognizes the “northern” *S. peruvianum* as *S. arcanum* and *S. huaylasense*, and the “southern” group as *S. peruvianum* s. str. and *S. corneliomulleri*.

The correlation UPGMA dendrogram (Fig. 16) has a lower cophenetic correlation (0.75; vs. distance, 0.93), but it places *S. galapagense* with the other self-compatible, red- to orange- to yellow-fruited species, and better groups the former north and south populations of *S. peruvianum*. Unlike the distance phenogram, it places the two outgroups, *S. lycopersicoides* and *S. sitiens*, as an internal branch with one of two main clusters (A). The three accessions of *S. habrochaites* formed a separate group, and also the three *S. pennellii* accessions clustered together. The other main branch (B) includes *S. arcanum*, *S. chilense*, *S. chmielewskii*, *S. corneliomulleri*, *S. huaylasense*, *S. neorickii*, and *S. peruvianum* s. str. This dendrogram, unlike the distance phenogram, shows better clustering of the former northern and southern *S. peruvianum* groups. Like the distance phenogram, *S. huaylasense* clustered with *S. chilense*, as part of a larger cluster that includes *S. corneliomulleri* and *S. peruvianum*. *Solanum arcanum*, *S. chmielewskii*, and *S. neorickii* cluster together.

MORPHOLOGICAL CLADISTICS. Peralta and Spooner (2005) found that 24 of the 66 morphological characters could be scored as discrete for use in cladistic studies. A cladistic analysis of these characters in tomato and outgroups in sect. *Juglandifolia* and sect. *Lycopersicoides* supported *S. pennellii* as sister to all tomato species (see Fig. 8 in Peralta & Spooner 2005). The relationships among the self-incompatible species *S. chilense*, *S. habrochaites*, and *S. peruvianum* “south” were not resolved. *Solanum peruvianum* “north” appeared as sister to *S. chmielewskii* and *S. neorickii*. *Solanum chmielewskii* and *S. neorickii* always were sister to each other and these two sister to the monophyletic group formed by *S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, and *S. pimpinellifolium*.

AFLP CLADISTICS. Spooner et al. (2005) used four AFLP primer combinations to study the phylogenetic relationships of 65 accessions of tomato and outgroups, including most of the accessions corresponding to the GBSSI (Peralta & Spooner 2001) and morphological studies (Peralta & Spooner 2005) described above. A strict consensus tree of these 296 AFLP trees (Fig. 17) supports tomatoes (*Solanum* sect. *Lycopersicon*) and their immediate outgroup relatives in sect. *Juglandifolia* and sect. *Lycopersicoides* to form a sister clade to potatoes (sect. *Petota*) and further outgroups in sect. *Etuberosum*. *Solanum pennellii* and *S. habrochaites* are part of a polytomy in sect. *Lycopersicon*. All brightly colored-fruited, self-compatible species (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) form a well-supported clade. *Solanum chmielewskii*, *S. neorickii*, and four accessions of the self-incompatible *S. arcanum* from the Río Marañón drainage form a clade. AFLPs, like the GBSSI and morphological data, show a clear separation of the northern and southern groups of *S. peruvianum* s.l., which includes *S. corneliomulleri* and *S. peruvianum* s.str. Only one accession from northern Peru (LA1984) grouped with the southern *S. peruvianum*. Interestingly, Rick (1986a) thought that this accession represented a “crossing bridge” between northern and southern populations of *S. peruvianum*. AFLP data, unlike morphological data, grouped *S. arcanum* with *S. huaylasense* instead of *S. chilense*.

CONGRUENCE TESTS AMONG AFLP, cpDNA, GBSSI, ITS, AND MORPHOLOGICAL STUDIES. Spooner et al. (2005) tested congruence among AFLP, cpDNA (Palmer & Zamir 1982), GBSSI (Peralta & Spooner 2001), ITS (Marshall et al. 2001) and morphology

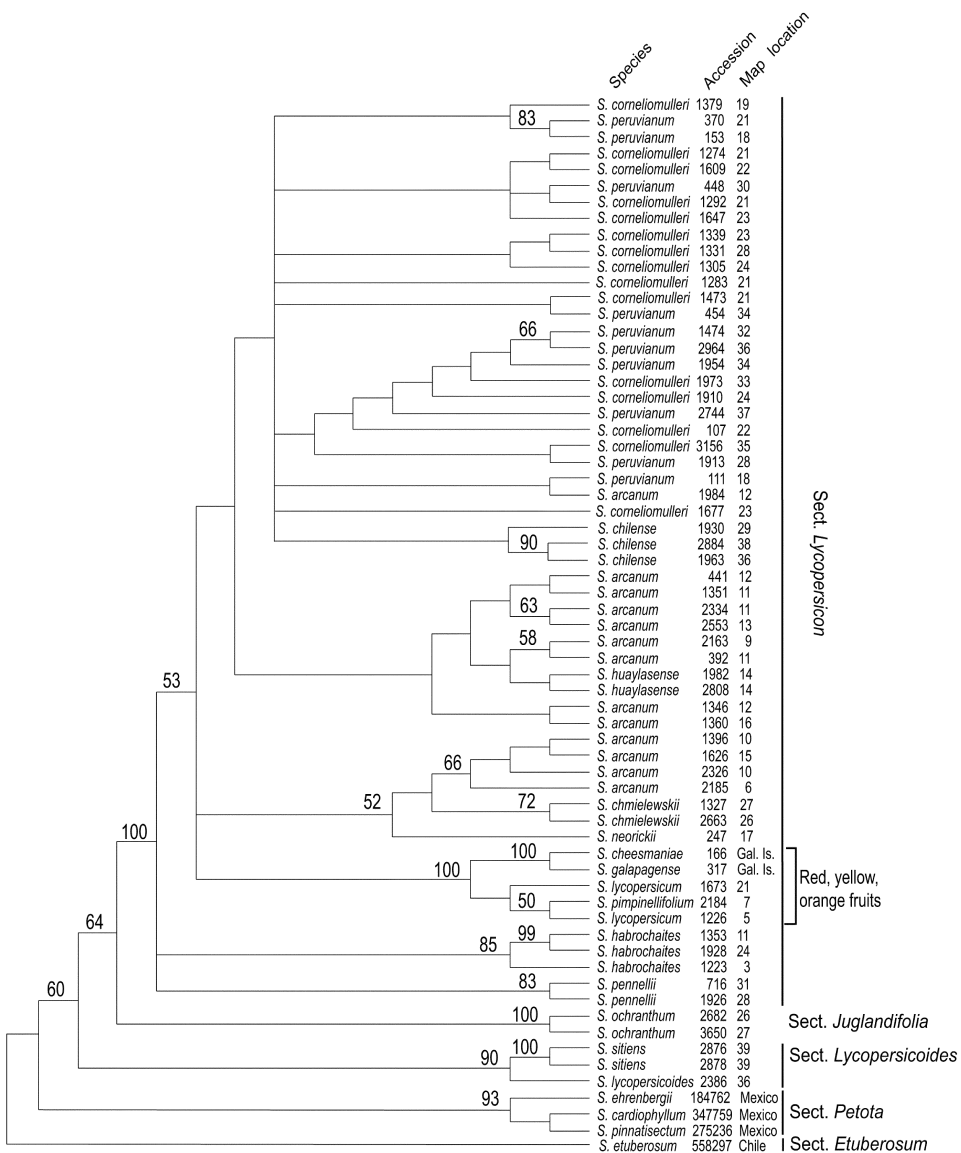


FIG. 17. Strict consensus cladogram of the 296 most parsimonious 1174-step Fitch trees from AFLP data. Accession numbers are LA numbers from the C. M. Rick Tomato Genetic Resources Center and map localities are as in Spooner et al. (2005). The numbers above each branch represent bootstrap values over 50%. Modified from Spooner et al. (2005) with the designation of species as recognized in this monograph.

(Peralta & Spooner 2005) datasets through three methods: 1) distance matrix-based comparisons (the Mantel test), 2) character-based comparisons (the incongruence length difference test (ILD), also called the partition homogeneity test of data partition congruence, of Farris et al. 1995), and 3) visual qualitative comparison of trees. Two comparative datasets were used: 1) a larger comparative dataset contained 47 identical tomato accessions from our AFLP and GBSSI studies and contained one additional accession of

S. etuberosum Lindl., as outgroup; and 2) the smaller comparative dataset contained only 10 accessions that were common to all studies cited above (all tomato species were included, except *S. neorickii*, which was lacking from the cpDNA dataset; the northern and southern accessions of *S. peruvianum* were included as separate taxa; and *S. lycopersicoides* was the common outgroup).

The distance-matrix test showed that all pairs of compared matrices were statistically correlated at $\alpha = 0.05$ except for GBSSI/ITS, GBSSI/morphology phenetics, and ITS/cpDNA. The matrix correlation coefficients of all comparisons varied greatly with AFLP/GBSSI the highest, and ITS/cpDNA the lowest. The character-based test showed the ITS/cpDNA, AFLP/GBSSI (both 10 and 48 taxon comparisons), the GBSSI/morphology, AFLP/ITS, GBSSI/ITS, AFLP/cpDNA, ITS/morphology, and AFLP/morphology data sets to be congruent. The other comparisons (cpDNA/morphology, cpDNA/GBSSI) proved to be incongruent.

Studies supported the close outgroup relationships of tomatoes to *Solanum* sect. *Juglandifolia* and sect. *Lycopersicoides* (Spooner et al. 2005). Both GBSSI and AFLP results supported *Solanum* sect. *Juglandifolia* as the sister group to tomatoes. Only two studies of eight that include *S. habrochaites* and *S. pennellii* support their grouping. Five of the seven studies including northern and southern accessions of *S. peruvianum* s.l. separated them into different groups. Two of the six studies that included northern and southern populations of *S. peruvianum* s.l. and *S. chilense* supported the grouping of the latter with the southern populations of *S. peruvianum* s.l. Four of the seven studies grouped *S. chmielewskii* and *S. neorickii*. Eight of the nine studies grouped all the species with brightly colored fruits. Four of the seven studies grouped the brightly colored-fruited species exclusively with *S. chmielewskii* and *S. neorickii*.

TOTAL EVIDENCE ANALYSIS OF CHLOROPLAST DNA, ITS, AFLP, AND GBSSI. A combined AFLP and GBSSI Fitch tree (Spooner et al. 2005), consisting of 48 taxa and constructed with 1652 characters, produced 34 most parsimonious 994-step trees with a consistency index of 0.35 and a retention index of 0.56. A strict consensus tree of these 34 trees (not shown) presented a topology very similar to that of the AFLP strict consensus tree (Fig. 17), including showing the relationship *S. chmielewskii*, *S. neorickii*, and four accessions of the self-incompatible northern *S. peruvianum* (now recognized as *S. arcanum*). A combined AFLP, GBSSI, cpDNA, ITS tree, and morphology analysis (10 taxa; 2301 characters of which 148 were parsimony informative) produced two most-parsimonious 577-step trees with a consistency index of 0.816 and a retention index of 0.603. A strict consensus tree of these two trees (Fig. 18) showed: 1) the brightly colored-fruited species as monophyletic, 2) *S. chmielewskii* and a northern population of *S. peruvianum* (now recognized as *S. arcanum*) to be a sister clade to the above, 3) *S. chilense* and a southern population of *S. peruvianum* (now recognized as *S. peruvianum* s.str. and *S. corneliomulleri*) to be a sister clade of the species above, 4) *S. habrochaites* and *S. pennellii* to be a well-supported clade forming a polytomy with the rest. *Solanum lycopersicoides* is sister to tomatoes.

OUR CONCLUSIONS ON RELATIONSHIPS. A summary of the morphological and molecular datasets shows (see also Fig. 18):

1) The tomatoes s.l. (sections *Lycopersicoides*, *Juglandifolia* and *Lycopersicon*) are clearly monophyletic and sister to the potatoes (sect. *Petota*), with sect. *Etuberosum* clearly monophyletic and sister to potatoes + tomatoes s.l.

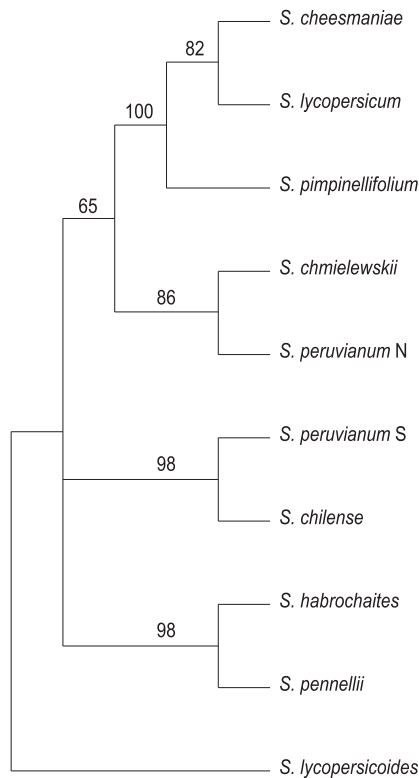


FIG. 18. The single combined AFLP, GBSSI, cpDNA, and ITS 530-step Fitch tree (10 taxa; 2275 characters). The numbers above each branch represent bootstrap values over 50% (from Spooner et al. 2005).

2) Section *Lycopersicoides* (formerly recognized as a subsection of sect. *Lycopersicon*) is clearly monophyletic and sister to sect. *Juglandifolia* + sect. *Lycopersicon*.

3) Section *Juglandifolia* is clearly monophyletic and sister to sect. *Lycopersicon*.

4) Within sect. *Lycopersicon*, *S. pennellii* in most cases appears at the base of the trees as a polytomy with *S. habrochaites*, or sometimes forms a clade with this species. We consider this relationship unresolved, but the morphological data suggest that *S. pennellii* is sister to the rest of the tomatoes s.str. (sect. *Lycopersicon*); it is the only species in that group lacking the sterile anther appendage, which is a morphological synapomorphy of *S. habrochaites* and the rest of the clade.

5) *Solanum chilense*, *S. corneliomulleri*, *S. habrochaites*, *S. huaylasense*, and *S. peruvianum* appear as a polytomy in the GBSSI tree, but the first four clustered with morphological characters. There is a conflict with the AFLP and morphological data regarding the relationships of *S. huaylasense* (only one accession of *S. huaylasense* was examined with GBSSI). AFLPs place *S. huaylasense* with *S. arcanum*, but with bootstrap values below 50%; morphological phenetics places one accession of *S. huaylasense* with *S. chilense*, and two accessions with *S. peruvianum* and *S. corneliomulleri*.

6) The self-compatible green-fruited species *S. chmielewskii* and *S. neorickii* are related to *S. arcanum* (northern *S. peruvianum* s.l.) and constitute a monophyletic group supported in almost all datasets.

7) The four species with red- to orange-colored fruits (*S. cheesmaniae*, *S. galapagense*, *S. lycopersicum*, *S. pimpinellifolium*) unambiguously form a closely related monophyletic group.

These results lead us to propose a formal classification at the sectional level, but without subdividing sect. *Lycopersicon*. We outline our ideas of relationships as informal species groups, as shown in Fig. 5, and our taxonomic treatment. Such informal group systems of classification have been widely applied to *Solanum* for similar reasons by Whalen (1984), Bohs (1994, 2005), Knapp (1991, 2000), and Spooner et al. (2004). They are not intended to represent formal classifications and are provisional groupings representing our best ideas of relationships that are still unresolved. They should not be confused with “cultivar groups,” which are formal taxonomic names for groups of cultivars, as recognized by the *International Code of Nomenclature of Cultivated Plants* (Spooner et al. 2003; Brickell et al. 2004). We group *S. huaylasense* (a “northern” segregate of *S. peruvianum* s.l.) with *S. chilense*, *S. habrochaites*, *S. corneliomulleri* (a segregate of “southern *S. peruvianum* s.l.”), and *S. peruvianum* s.str. in the “Eriopersicon” species group (see key). The self-compatible green-fruited species *S. chmielewskii* and *S. neorickii* are related to *S. arcanum* (another northern segregate of *S. peruvianum* s.l.), as supported in almost all datasets. We arrange these three species in the “Arcanum” species group. The species with red to orange fruits could be recognized as a formal taxonomic group (as a series, for example), but we do not propose this formal classification because of ambiguity in the other species groups in sect. *Lycopersicon*. We place *S. pennellii* in its own “group,” despite the fact that it is the only species, because it likely is sister to the rest of sect. *Lycopersicon*.

SPECIES CONCEPTS

Our goal for this study is to apply a phylogenetic concept and classification to sections and series, and a more pragmatic, practical concept incorporating a wide variety of data to species. Sections *Lycopersicon*, *Lycopersicoides*, and *Juglandifolia*, and the informal “Lycopersicon” species group are unambiguously monophyletic. The “Arcanum,” “Eriopersicon,” and “Neolycopersicon” species groups may be monophyletic, but there are ambiguities in various data sets regarding these.

Ultimately, all large-scale monographs rely on morphological characters to provide identifications for the many specimens needing determinations, but species concepts may also be influenced by molecular, ecological, and crossing relationships, despite inherent potential conflicts between biological and phylogenetic concepts. Our decisions relied on clear morphological discontinuities to define the easily distinguished species *S. habrochaites*, *S. lycopersicoides*, *S. pennellii*, and *S. sitiens*. The following closely related species are generally easy to distinguish but sometimes intergrade: 1) *S. lycopersicum*, *S. pimpinellifolium*, 2) *S. cheesmaniae*, *S. galapagense* (sometimes also with introduced *S. pimpinellifolium*), 3) *S. arcanum*, *S. chmielewskii*, *S. neorickii*, 4) *S. corneliomulleri*, *S. peruvianum*, 5) *S. chilense*, *S. huaylasense*. Specific characters used for recognition are detailed with each species description and in the keys. Potential reasons for variability and intergradation are recent divergence and hybridization. Despite the variability in tomato species, our decision to recognize the four segregants of *S. peruvianum* s.l. (Peralta et al. 2005) is based on a pragmatic combination of phylogeny and morphology, and reflects evolving, recognizable entities within the complex.

We do not recognize taxa below the species level, most notably the small-fruited

tomatoes known to many as “var. *cerasiforme*.” The name “*cerasiforme*” has been used to refer to putatively wild forms of *S. lycopersicum* that have been regarded as progenitors of the cultivated tomato (although see Frary et al., 2000, and Nesbitt & Tanksley, 2002). It is impossible to distinguish wild from cultivated forms using herbarium specimens, and we regard many specimens labeled as “var. *cerasiforme*” to be possible revertants from cultivation (i.e., feral plants) or possible hybrids of wild and weedy taxa. Many cultivar names have been proposed (often not validly published, see Appendix 1) as formal taxa following the principles laid out in the *International Code of Botanical Nomenclature* (McNeill et al. 2006, and earlier editions), but cultivars would be more usefully named using *The International Code of Nomenclature of Cultivated Plants* (Spooner et al. 2003; Brickell et al. 2004). In addition to species groups, we distinguish four weakly defined morphotypes within *S. arcanum* that show discrete geographic ranges but exhibit so much overlap of character states, especially in leaf morphology, that consistent assignment of any given specimen to a morphotype can be difficult in the absence of geographical data.

TAXONOMY

***Solanum* L.**, Sp. pl. 184. 1753.—LECTOTYPE, designated by Henderson, 1974: *Solanum nigrum* L. [We accept the generic synonymy proposed by D’Arcy (1972, 1974) with the addition of *Lycopersicon* and *Amatula* (see p. 77), and *Triguera* Cavanilles and *Cyphomandra* Martius ex Sendtner.

Herbs, shrubs, trees, or vines, with or without prickles, 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, but sometimes with “pseudostipules.” 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, equal or unequal, blunt or tapered toward apex, opening by terminal pores, sometimes expanding into longitudinal slits, or introrsely longitudinally dehiscent with age in sect. *Lycopersicon*; ovary 2-carpellate; ovules many; style articulated at base or above the base, usually slender; stigma capitate to elongate-clavate. Fruit a berry, usually fleshy but occasionally dry, usually many-seeded, the seeds often flattened; embryo curved, embedded in abundant endosperm. Chromosome number: $n = 12, 23, 24$.

The generic description applies to *Solanum* including all those genera traditionally segregated from it: *Cyphomandra* Mart. ex Sendtn. (Bohs 1995), *Lycopersicon* Mill. (Spooner et al. 1993), *Normania* Lowe, and *Triguera* Cav. (Bohs & Olmstead 2001). Data from chloroplast DNA sequences strongly support the inclusion of these segregates in a monophyletic *Solanum* (Bohs 2005). Some workers (e.g., Hunziker 2001) maintain these taxa as distinct genera.

The tomatoes and their close relatives are easily distinguished from any other group of *Solanum* species by their bright yellow flowers and pinnatifid, non-spiny leaves; the only other species in the genus with bright yellow flowers is *S. rostratum* Dunal, a member of sect. *Androceras* (Nutt.) Whalen (Whalen 1979). The tomatoes are most closely related to the potatoes and form a distinct clade (the Potato clade, sensu Bohs 2005) with

relatively high (80%) bootstrap support (Bohs 2005). This group includes most of the non-spiny species of *Solanum* with pinnately compound leaves, including sections *Anarrhicomenum* Bitter, *Herpystichum* Bitter, and *Pteroidea* Dunal (Knapp & Helgason 1997), as well as the groups traditionally thought of as related to the potatoes, e.g., sections *Basarthrum* (Bitter) Bitter and *Etuberosum* (Bukasov & Kameraz) A. Child.

We cite only wild-collected specimens in our treatment here. Many of the wild taxa are cultivated in botanical gardens and agricultural stations, but specimens are rarely prepared. When a species has been cultivated, we have listed the countries from which we have seen cultivated specimens in the species discussion, but this is a minimum rather than a maximum cultivated distribution. For *S. lycopersicum*, the cultivated tomato, countries from which herbarium specimens have been collected are listed in Appendix 3. Complete citations for all cultivated and wild specimens we studied can be found on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>). Citations of chromosome numbers for all species are taken from the data available from the TGRC (<http://www.tgrc.davis.edu>). To access these data, go to the TGRC website and search on the LA accession number cited in each species treatment here.

KEY TO THE SPECIES OF SOLANUM SECT. LYCOPERSICOIDES,
SECT. JUGLANDIFOLIA, AND SECT. LYCOPERSICON

1. Perennials, shrubs, or climbing vines; sympodial units plurifoliate with usually more than 3 leaves per sympodium; inflorescences with usually more than 4–5 dichotomous branches; corolla symmetric; anthers straight, of equal length, separate or moderately connivent, lacking an apical sterile appendage, initially dehiscent by apical pores and later by introrse slits to the anther base.
 2. Shrubs or subshrubs, to 2.5 m tall, or herbs with secondary growth mainly at stem base and to 0.5 m tall; leaves interrupted imparipinnate to pinnatifid, primary, secondary, and interjected leaflets with deeply divided margins; inflorescences bracteate; pedicels articulated just below the calyx; anthers pale yellow to almost white; fruits 1–1.3 cm in diameter, with a thin, leathery pericarp.
 - I. *Solanum* sect. *Lycopersicoides*
 3. Plants to 2.5 m tall; primary leaflets 4–5 pairs, the leaflet margins serrate to lobed no more than halfway to the leaflet rachis; fruits dark purple to black at maturity. 1. *S. lycopersicoides*
 3. Plants to 0.7 m tall; primary leaflets 3–4 pairs, the leaflet margins deeply lobed halfway or more to the leaflet rachis; fruits brown and dry at maturity. 2. *S. sitiens*
 2. Woody vines, to 5 m or longer; leaves imparipinnate to interrupted imparipinnate, primary and interjected leaflets with entire margins; inflorescences ebracteate; pedicels articulated at about the middle or just above the middle (rarely just below the calyx); anthers yellow; fruits 1.5–5 (+) cm in diameter, with a thick, hard pericarp.
 - II. *Solanum* sect. *Juglandifolia*
 4. Leaflets rough to the touch adaxially (with raised trichome bases), not markedly paler abaxially than adaxially; corolla stellate; calyx lobes long-acuminate; fruit 1.5–2 cm in diameter. 3. *S. juglandifolium*
 4. Leaflets smooth abaxially, the trichome bases not raised, markedly paler abaxially than adaxially; corolla rotate to rotate-stellate; calyx lobes acute; fruit 2–5 (+) cm in diameter. 4. *S. ochranthum*
 1. Annuals or biennials to herbaceous perennials arising from a woody base, sometimes trailing vines; sympodial units with 2–3 leaves per sympodium; inflorescence 1–2-branched (rarely 3–4-branched); corolla symmetric or asymmetric (*S. pennellii*), anthers strongly coalescent by interlocking lateral hairs and forming a tube with an apical sterile appendage and dehiscent by longitudinal introrse slits along their entire length (except *S. pennellii* with separate to slightly connivent anthers and without apical sterile appendage).
 - III. *Solanum* sect. *Lycopersicon*
 5. Primary leaflets broadly elliptic to orbicular, thick and fleshy; flower pedicels articulate at the base; corolla slightly zygomorphic; anthers without apical sterile appendage, dehiscent by introrse pores and later by introrse slits; “*Neolycopersicon*” group. 5. *S. pennellii*

5. Primary leaflets elliptic or ovate to lanceolate, membranous; flower pedicels articulate above the middle; corolla symmetric; anthers with apical sterile appendages, dehiscent by long introrse slits.
6. Fruits with carotenoid pigments (red, orange, yellow) and evenly colored throughout; pseudostipules absent; inflorescence ebracteate; "Lycopersicon" group.
7. Mature fruit red; continental South America (or cultivated).
 8. Plants usually sparsely pubescent or subglabrous (rarely dense-velvety pubescent), the longer trichomes up to 1 mm long; leaflet margin generally entire or slightly dentate or crenate; inflorescence generally with more than 12 flowers per inflorescence branch; corolla stellate (divided almost to the base); fruits usually ca. 1 cm in diameter. 14. *S. pimpinellifolium*
 8. Plants pubescent, the longer trichomes to 3 mm long; leaflet margin generally dentate, especially at the base, sometimes lobulate and with secondary leaflets; inflorescence generally with fewer than 12 flowers per inflorescence branch; corolla pentagonal (divided 1/3–1/2 to base); fruits usually more than 1.5 cm in diameter. 15. *S. lycopersicum*
7. Mature fruit yellow to orange; Galápagos Islands.
 9. Tertiary leaflets absent; calyx lobes not exceeding fruit diameter of mature fruit. 16. *S. cheesmaniae*
 9. Tertiary leaflets present, these often lobed; calyx lobes often exceeding fruit diameter of mature fruit. 17. *S. galapagense*
6. Fruits green or with purple anthocyanin pigments, mottled and/or with a dark green to purple stripe; pseudostipules present, or if absent, then the leaflets narrowly lanceolate; inflorescence bracteate.
10. Inflorescence usually unbranched, rarely 2-branched; staminal column always straight, style and stigma included in the tube or slightly exerted to 1 mm; "Arcanum" group.
 11. Corolla 1.6–2 cm in diameter; staminal column 0.8–1.1 cm long, anthers 0.4–0.7 cm long.
 12. Stem, leaves, and inflorescences green, glabrous to variously pubescent, with glandular and eglandular trichomes, the longest up to 1 mm long; usually more than 7 flowers per inflorescence (5–20 flowers per inflorescence). 11. *S. arcanum*
 12. Stem, leaves, and inflorescences pale grayish green, densely soft-velvety and short-pubescent, the longest trichomes up to 0.2 mm long; usually fewer than 7 flowers per inflorescence. 12. *S. chmielewskii*
 11. Corolla 1–1.2 cm in diameter; staminal column 0.4–0.6 cm long, anthers 0.25–0.3 cm long. 13. *S. neorickii*
10. Inflorescence usually with 2 or more branches; staminal column straight or curved; style and stigma generally exerted beyond 1 mm; "Eriopersicon" group.
 13. Sympodial units 3-foliolate; large sprawling viny plants to 6 m long. 6. *S. habrochaites*
 13. Sympodial units 2-foliolate (rarely 3-foliolate in *S. chilense* and *S. huaylasense*); plants erect and later decumbent, less than 3 m long.
 14. Inflorescence peduncle generally longer than the inflorescence branches; staminal column straight (curved in Río Fortaleza populations of *S. huaylasense*).
 15. Stem and leaves densely grayish pubescent; typically green-grey-canescenscent; coastal southern Peru and northern Chile. 7. *S. chilense*
 15. Stem and leaves sparsely pubescent, bright green; Ancash, Peru. 8. *S. huaylasense*
 14. Inflorescence peduncle generally equal or shorter than the inflorescence branches; staminal column curved.
 16. Plants with scattered short glandular hairs and short uniformly velvety non-glandular pubescence, pale grayish green; leaves imparipinnate; leaflet margin entire or slightly dentate or crenate to lobed. 9. *S. peruvianum*
 16. Plants with dense long glandular pubescence as well as non-glandular pubescence, green; leaves interrupted imparipinnate or bipinnatisect; leaflet margin usually dentate to crenate to lobed, sometimes deeply divided. 10. *S. corneliomulleri*

I. *Solanum* section *Lycopersicoides* (A. Child) Peralta, comb. et stat. nov. *Solanum* section *Lycopersicum* subsection *Lycopersicoides* A. Child, Feddes Repert. 101: 224. 1990.—TYPE: *Solanum lycopersicoides* Dunal.

Erect to somewhat sprawling perennial herbs, woody at the base, or shrubs with erect or tortuously ascending woody branches. Stems bright green to green-purple, glabrous, sparsely to densely pubescent with a mixture of simple uniseriate glandular and eglandular trichomes, glabrescent in age. Sympodial units 5-foliolate. Leaves interrupted imparipinnate to asymmetrically pinnatifid, foliolules rarely shortly petiolulate or most commonly sessile to decurrent on the rachis and therefore the divisions not clear cut, green, glabrous, sparsely to densely pubescent like the stems with a mixture of simple uniseriate glandular and eglandular trichomes, adaxially sparsely pubescent, abaxially densely pubescent with the longer trichomes more abundant along the veins, glabrescent in age; pseudostipules well developed; primary leaflets irregularly lobulate or coarsely crenate to serrate-dentate; sometimes with interjected leaflets. Inflorescences 2–3- or more branched, commonly bracteate; peduncle present, pedicels articulated just below the calyx. Flowers actinomorphic; calyx 5-parted, usually glabrescent to pubescent; corolla bright yellow, pentagonal to rotate, 5-parted, lobed about halfway to the base, the lobes deltate to short-triangular; stamens 5, staminal column absent, anthers pale yellow to almost white, straight, of equal length, separate or moderately connivent, lacking an apical sterile appendage, initially dehiscent by apical pores and later by introrse slits just part way down the anther; ovary globose-conical, glabrous; style minutely white-pubescent in the basal half, recurved, exerted 2–4 mm beyond the anthers; stigma elongate-clavate. Fruit a globose berry, yellowish to black when ripe, glabrous and shiny, with a thin and leathery pericarp when ripe; persistent calyx lobes shorter than the mature fruit, spreading, fruiting pedicels usually straight. Seeds obovate, lenticular, winged along the border.

Solanum lycopersicoides and *S. sitiens* are clearly sister taxa (Correll 1962; Child 1990; Peralta & Spooner 2001). Using a variety of crossing methods with *S. lycopersicoides* in a *S. lycopersicum* genetic background, Ji et al. (2001) found that chromosome pairing rates between these species were extremely low, although still some pairing did occur. They used these chromosome pairing differences, combined with data from ecology and other traits, to support the placement of *S. lycopersicoides* and *S. lycopersicum* in different genera (i.e., the maintenance of the genus *Lycopersicon*, see discussion of Species Relationships above).

Solanum sitiens and *S. lycopersicoides* are endemics of the western Andean deserts of Peru and Chile, and adapted to extremely arid conditions. Current knowledge of distribution patterns and awareness of habitat destruction resulting from livestock ranching indicate that both species should be considered vulnerable and given priority for *in situ* conservation.

1. *Solanum lycopersicoides* Dunal in A. DC., Prodr. 13(1): 38. 1852. *Lycopersicon lycopersicoides* (Dunal) A. Child ex J. M. H. Shaw, New Plantsman 5: 109. 1998.—TYPE: BOLIVIA [CHILE]. Without locality, *d'Orbigny 291* (holotype: P! [LL neg. 530: LL! UC!; UC neg. s.n.: UC!]; isotypes: MPU-fragment! P! [LL neg. 531: LL! UC!]).

Coarse herbs or small woody shrubs, 0.5–2.5 m tall, to 1 m or more in diameter, strong smelling (of XYLEDECOR fide Weigend & Förther 97/801). Stems 8–10 mm in

diameter at base, sparsely to densely pubescent with a mixture of glandular and eglandular trichomes; trichomes all simple and uniseriate with a uni- or multicellular base, of 4 principal types: 4–5-celled trichomes 1–1.5 mm long, either eglandular or with a single-celled gland at the tip; shorter, soft, white 1–3-celled trichomes 0.1–0.2 mm long, of varying abundance; unicellular trichomes with a 4-celled glandular tip; and occasionally shorter uniseriate trichomes with an ellipsoid 8-celled glandular tip in more densely pubescent populations. Sympodial units 5-plurifoliate; internodes 1–5 cm long. Leaves interrupted imparipinnate to pinnatifid, foliolules sessile and therefore the divisions not clear cut, 2.5–12 cm long, 1.2–6 cm wide, green, sparsely to densely pubescent like the stems with a mixture of simple uniseriate 2–3-celled trichomes with a multicellular base and various sorts of glandular trichomes, adaxially sparsely pubescent with the longer trichomes more abundant along the veins, abaxially densely pubescent, the eglandular trichomes tangled and weak-walled; primary leaflets 4–5 pairs, not clearly differentiated from the rachis, elliptic, deeply and irregularly lobed, apex acute to obtuse, base decurrent, margin irregularly lobed and the lobes irregularly serrate; terminal leaflet (0.5–) 1–3.5 cm long, (0.3–) 0.5–2.6 cm wide, decurrent on the rachis; lateral leaflets 1.2–3.5 cm long, 0.5–2 cm wide, decurrent on the rachis; secondary leaflets absent, the lobing of the leaflets never reaching the secondary axis; tertiary leaflets absent; interjected leaflets 0–6, 0.3–0.9 cm long, 0.2–0.5 cm wide, sessile and decurrent on the rachis; petiole (0.2–) 0.5–1.2 cm long; pseudostipules 0.5–1 cm long, 0.4–0.7 cm wide. Inflorescences 7–15 cm long, 2–3-times branched, with 30–50 (–75) flowers, bracteate in the proximal nodes, bracts 0.3–0.5 (–1) cm long, 0.2–0.5 (–0.7) cm wide; peduncle 3.5–7 (–10) cm long, pubescent like the stems and leaves. Pedicels 1.2–1.8 cm long, articulated in the distal 1/3. Buds 0.7–0.8 cm long, 0.4–0.5 cm wide, obovoid, the corolla halfway exerted beyond the calyx just before anthesis, the style often exerted from the bud before anthesis. Flowers with the calyx tube 0.5–1.5 mm long, lobes 3.5–4 mm long, 1–1.5 mm wide, deltate, sparsely white-pubescent with simple uniseriate trichomes, apex acute, sinus hyaline; corolla 1.6–2 cm in diameter, broadly rotate, bright yellow, tube 0.5–0.9 cm long, lobes 0.8–0.9 cm long, ca. 1 cm wide, densely papillate on the tips and distal margins, spreading or campanulate at anthesis; staminal column absent, stamens free, straight, filaments 1–1.5 (–2) mm long, anthers 0.35–0.5 cm long, equal, without a sterile apical appendage; ovary conical, glabrous; style 0.9–1.1 cm long, ca. 0.5 mm in diameter, minutely white-pubescent in the basal half, curved and exerted 2–4 mm beyond the anthers; stigma bifid, green (occasionally appearing elongate, clavate in dry material). Fruit 1–1.2 cm in diameter, globose, 2-locular, purple to black when ripe, glabrous and shiny; fruiting pedicels 1.1–1.6 cm, straight; calyx lobes in fruit 3–5 mm long, ca. 2 mm wide, not markedly elongating, spreading. Seeds 2.3–2.9 mm long, 1.8–2.3 mm wide, 0.5–0.7 mm thick, obovate, brown, pubescent with hair-like outgrowths of the lateral testa walls giving a silky appearance to the surface, narrowly winged along the entire border. Chromosome number: $n = 12$ ($2n = 24$, Correll 1962: 114). Plate 1P, Plate 2P, Plate 3P; Fig. 19.

Phenology. Flowers sporadically, but with a pronounced peak between February and May (Smith & Peralta 2002).

Distribution (Fig. 20). Southern Peru to northern Chile on the western slopes of the Andes; dry rocky hillsides; 1500–3700 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** AREQUIPA: without locality, 1862, *Isern 2063* (F).—TACNA: near Candarave, *Metcalf 30382* (A, G, US); Tarata Prov., on east shore of Lake Aricota, *Metcalf 30404* (G, MO, US); Prov. Tacna, Causiri, a un km más arriba de Palca y a 45 km de la ciudad de Tacna, *Ochoa 2035* (GH, US,

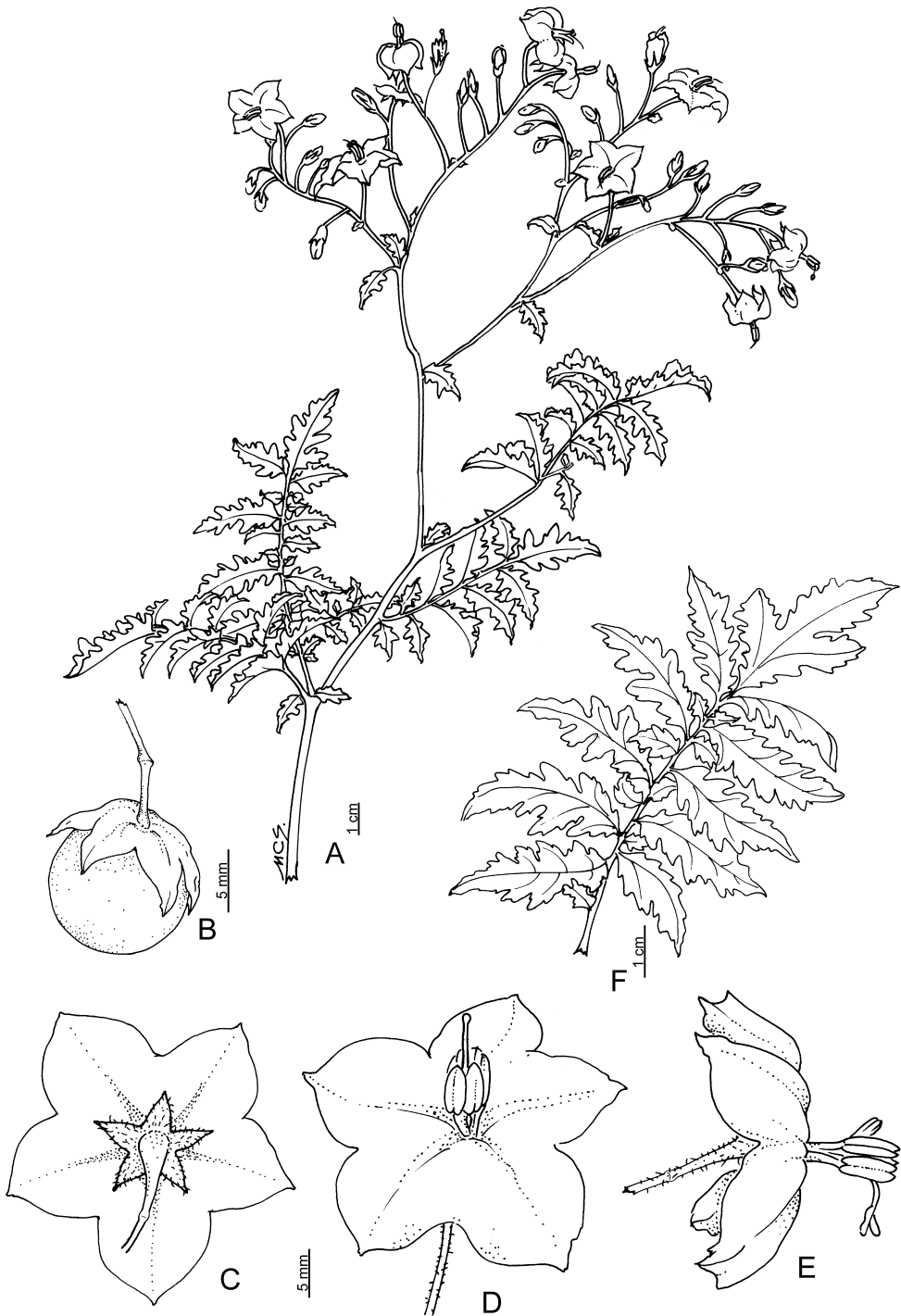


FIG. 19. *Solanum lycopersoides*. A. Branch. B. Fruit. C. Abaxial view of flower. D. Adaxial view of flower with young style erect and the stigma still closed. E. Side view of flower with the style reflexed and the stigma bifid. F. Leaf.

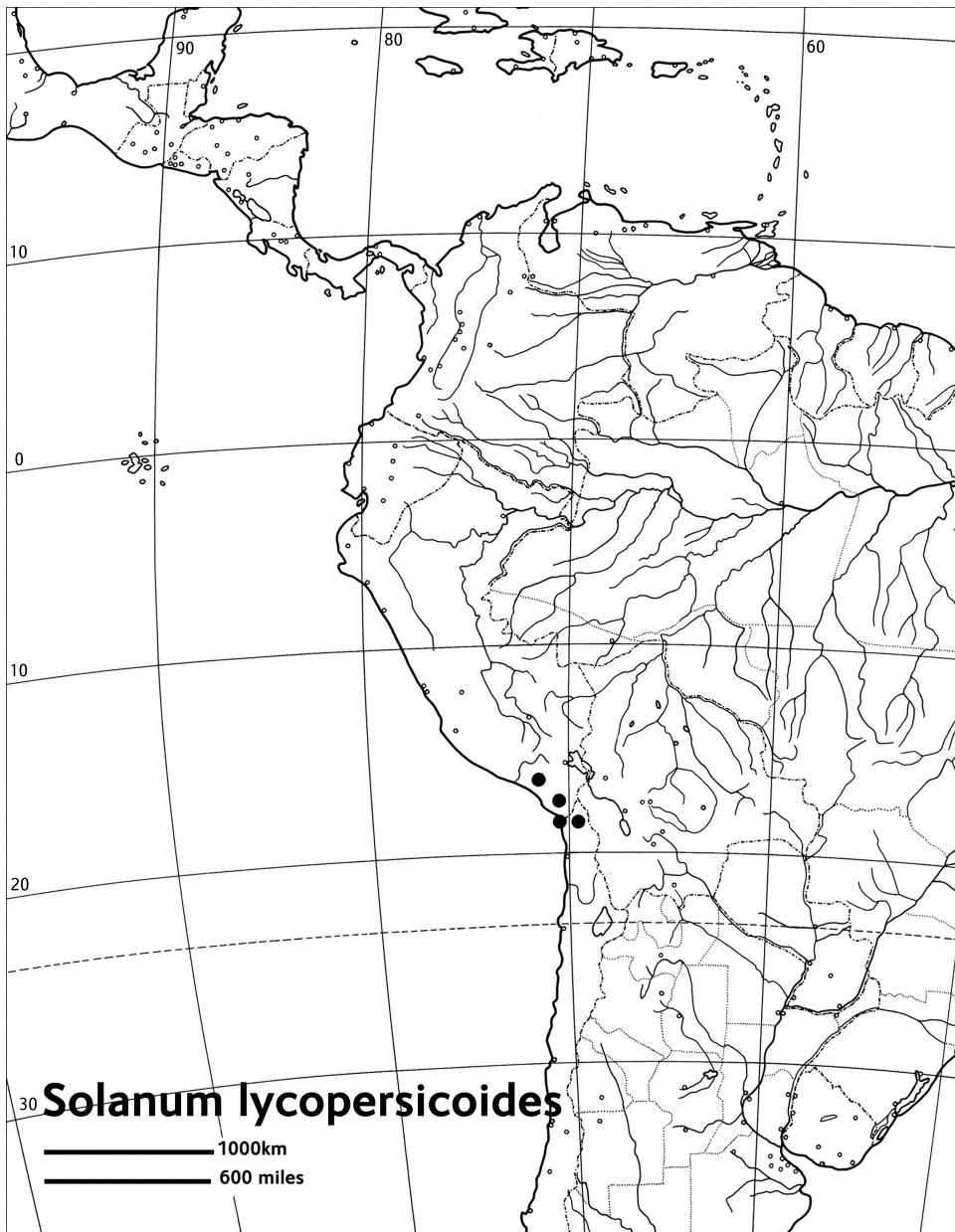


FIG. 20. Distribution of *Solanum lycopersicoides*.

USM); on the road from Tacna to Charaña, Bolivia, 38 km from Tacna, 7 km W of Palca, *Rick SAL-215* (LL); Quebrada de Palca, *Tschudi s.n.* (W); Prov. Tarata, 10 km S Candarave on road to Tarata (213 km W of Ilave), *Weigend & Förther 97/801* (F, M, USM). **Chile.** REGION I (TARAPACÁ): Quebrada Río Putre, *Armesto et al. 1150* (CONC); Prov. Parinacota, Camino Zapahuira a Putre, *Belmonte 88118* (CONC); Copaquilla, *Belmonte 98136* (CONC); Tarapacá, Parinacota, Putre, *Billiet & Jadin 5451* (MO); Arica, Quebrada Cardones–Río Lluta, Km 100, *Jiles C. 5613* (CONC); Putre, *Mathei & Rodríguez 250* (CONC, MA); desvío hacia Putre en la carretera Arica–Tambo Quemado, *Landero et al. 11* (CONC), *Landero et al. 62* (CONC).

Solanum lycopersicoides is sister to *S. sitiens* and morphologically very similar. The two species are easily distinguished by the degree of leaf dissection; leaves of *S. lycopersicoides* are more finely dissected and in general have more pairs of leaflets. The two species also differ in mature fruit color; the fruit of *S. lycopersicoides* is blackish green or purple and still fleshy at maturity, whereas that of *S. sitiens* is yellowish and becomes dry and papery. The flowers of both species are very similar in overall morphology (non-coherent anthers, clavate stigmas) to those of members of *Solanum* sect. *Regmandra* (Dunal) Ugent (e.g., *S. montanum* L.) occurring in similar dry western Andean habitats. Section *Regmandra*, however, is not closely related to the tomatoes (Bohs 2005); perhaps the convergent anther morphology in members of sect. *Regmandra* and these taxa reflects a similar pollination syndrome in these desert plants. Anthers are usually white in *S. lycopersicoides*, and dehiscence begins with the opening of two large apical pores that change to long introrse slits. In late anthesis the free anthers hang loosely on long filaments and are completely longitudinally dehiscent. Both *S. lycopersicoides* and *S. sitiens* have a strong chemical odor, according to notes on herbarium specimen labels. *Solanum lycopersicoides* and *S. sitiens* occur allopatrically at approximately the same elevation and may also be reproductively isolated by flowering time (Smith & Peralta 2002).

One TGRC accession of *S. lycopersicoides* (LA2951) has been important in the development of introgression lines with the *S. lycopersicum* cultivar VF36 (see <http://tgrc.ucdavis.edu/>). These lines have been useful in the production of genetic maps, and to the understanding of cold, pest, and pathogen resistances.

We examined specimens of *S. lycopersicoides* prepared from plants cultivated in the U.S.A.; full details are available on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>), and collectors and numbers are listed in the Index to Numbered Collections Examined.

2. *Solanum sitiens* I. M. Johnston, *Revista Chilena Hist. Nat.* 33: 25. 1930. *Lycopersicon sitiens* (I. M. Johnston) J. M. H. Shaw, *New Plantsman* 5: 109. 1998.—TYPE: CHILE. Antofagasta: near Calama, ca. 3300 m, 7 Sep 1919, *Moore & Abbott s.n.* (holotype: US-1038130!).

Solanum rickii Correll, *Wrightia* 2: 177. 1961.—TYPE: CHILE. Antofagasta: in shallow ravines of hills 1/2 km N of village of Chuquicamata, ca. 3000 m, 8 Jan 1957, *Rick SAL-224* (holotype: LL! [LL neg. 453: F! GH! UC!]; isotype: UC! [LL neg. 454: F! LL! UC!; LL neg. 455: F! GH! LL! UC!]).

Erect to somewhat sprawling shrubs, woody at the base, to 0.7 m tall, 30–40 cm diameter at base, pleasant smelling (fide *Moore & Abbott s.n.*). Stems 7–10 mm diameter at the base, bright green, glabrous to moderately pubescent with simple uniseriate glandular trichomes with 4-celled heads and sparser simple uniseriate eglandular 4–6-celled trichomes to 0.5 mm long, glabrescent in age. Sympodial units 5-plurifoliate; internodes (1–) 2–4 cm long. Leaves interrupted imparipinnate or pinnatifid, the divisions not clear-cut, 1.9–7 cm long, 1–5 cm wide, thick and fleshy, bright green, pubescent like the stems with sparse simple uniseriate trichomes, occasionally almost completely glabrous, glabrescent in age, the adaxial surface glandular to glabrous with a few simple uniseriate trichomes, the abaxial surface pubescent, especially along the veins; primary leaflets 3–4 pairs, not well differentiated from the axis, narrowly elliptic, apex acute, base decurrent, margin deeply once-lobed halfway to the rachis; terminal leaflet usually sessile and not well differentiated from the most distal lateral leaflets, 0.5–2.5 cm long, 0.3–2 cm wide,

base decurrent onto the rest of the leaf; secondary leaflets absent; tertiary leaflets absent; interjected leaflets 0–2 (–5), small lobes along the spaces between the lateral leaflets, orbicular, 0.1–0.3 cm in diameter; petiole 0.2–1 cm long; pseudostipules present, 0.5–0.9 cm long, 0.3–0.6 cm wide. Inflorescences 3.5–9 cm long, 2–3 times branched, with 10–50 flowers, bracteate, bracts 0.3–0.5 cm long, 0.2–0.4 cm wide, smaller towards the tip of the inflorescence; peduncle 1–5 cm long, glabrous to sparsely pubescent like the stems. Pedicels 0.7–1.1 cm long, articulated in the distal 1/3–1/2. Buds ca. 1 cm long, 0.4–0.5 cm wide, ellipsoid, the corolla halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube ca. 2.5 mm long, lobes 4–5 mm long, 1–1.5 mm wide, narrowly deltate, apex acuminate, sparsely pubescent with simple uniseriate trichomes and minute glandular trichomes like those of the stems; corolla 1.8–2.1 cm in diameter, rotate, yellow, finely pubescent abaxially, the trichomes more abundant at the tips, the tube 0.6–0.7 cm long, lobes 0.5–0.6 cm long, 0.5–0.7 (–0.9) cm wide, spreading at anthesis; staminal column not present, stamens free, straight, filaments 0.5–0.6 mm long, anthers 0.45–0.5 cm long, equal, sterile apical appendage absent; ovary conical, glabrous; style 1–1.2 cm long, ca. 0.5 mm in diameter, densely fine white-pubescent in the proximal half, curved and exerted 2–3 mm beyond the anthers; stigma bifid, green (occasionally appearing large-capitate to clavate in dry material). Fruit 1.1–1.3 cm in diameter, globose, 2-locular, pale yellow when ripe, shiny and glabrous, becoming dry and papery with age; fruiting pedicels 1–1.7 cm long, straight; calyx lobes in fruit 4–5 mm long, 1–1.5 (–2.5) mm wide, not markedly elongating, spreading. Seeds 2.2–2.8 mm long, 1.7–2.3 mm wide, 0.5–0.7 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged at apex, acute at base. Chromosome number: $n = 12$ ($2n = 24$, fide Rick in Correll 1962: 112). Plate 1Q, Plate 2Q, Plate 3Q; Fig. 21.

Phenology. Apparently with two flowering peaks, one between January and May and the other in November (Smith & Peralta 2002), but few specimens have been collected.

Distribution (Fig. 22). On the western Andean slopes in northern Chile; rocky hillsides and dry quebradas; 2350–3500 m.

ADDITIONAL SPECIMENS EXAMINED. **Chile**. REGION II (ANTOFAGASTA): Quebrada de Paqui, Arroyo *et al.* 97666 (CONC); Cerro Platero, lado O de la Quebrada de Paqui, Arroyo *et al.* 97672 (CONC); Cerro Bayo, Arroyo *et al.* 97677 (CONC); camino de Conchi a Chuquicamata, Cerro Platero, Arroyo *et al.* 97660 (CONC); cerca del camino entre Chuquicamata y María Elena (ruta 23), Baumann 257 (CONC); Prov. Antofagasta, Taracoles, Biese 2203 (B, C, SGO); Prov. El Loa, 20 km al SE de Aguada Limón Verde, Biese 2457 (SGO); Chuquicamata, Jovey 4377 (CONC); camino de Chuquicamata a Oyahue, Km 22, Marticorena *et al.* 390 (CONC); Prov. Tocopilla, camino de Tocopilla a Chuquicamata, 25 km antes de Chuquicamata, Matthei 460 (CONC); camino al Cerro del Quimal, Moreira *et al.* 192 (SGO); Cerro Agua Dulce, Moreira *et al.* 197 (SGO); entre Chuquicamata y Conchi, Ricardi *et al.* 440 (CONC); Chuquicamata, in shallow ravines of hills 1/2 km N of village, Rick SAL-124 (LL); camino de Augusta Victoria a La Escondida, Rodríguez & Ruiz 3548 (CONC); El Boquete, Rudolph *s.n.* (CONC); camino Calama–Conchi Viejo, quebrada al W de El Abra, Teillier 3691 (SGO).

Solanum sitiens is sister to *S. lycopersicoides*; differences between them are noted in the key and in the discussion of *S. lycopersicoides* (no. 1). *Solanum sitiens* has less dissected leaves than *S. lycopersicoides* and a yellowish brown rather than purple or black fruit. *Solanum sitiens* is a small shrub, which apparently retains its fruits for a long time; eventually they turn dry and papery. Flowering in *S. sitiens* appears to peak in November with a minor flowering episode in January to May, but the number of specimens collected is few, and this bimodality may be merely a collecting artifact.

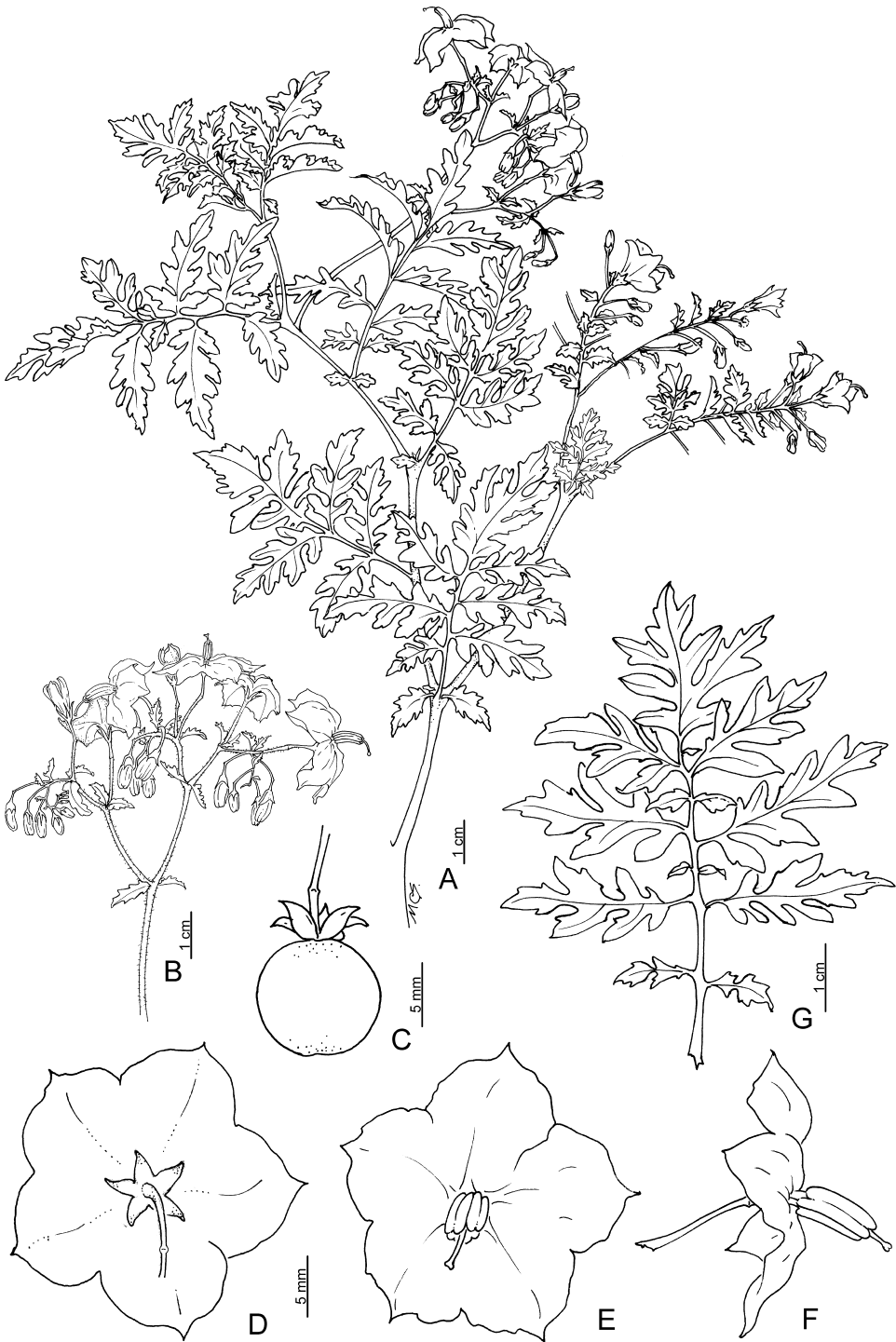
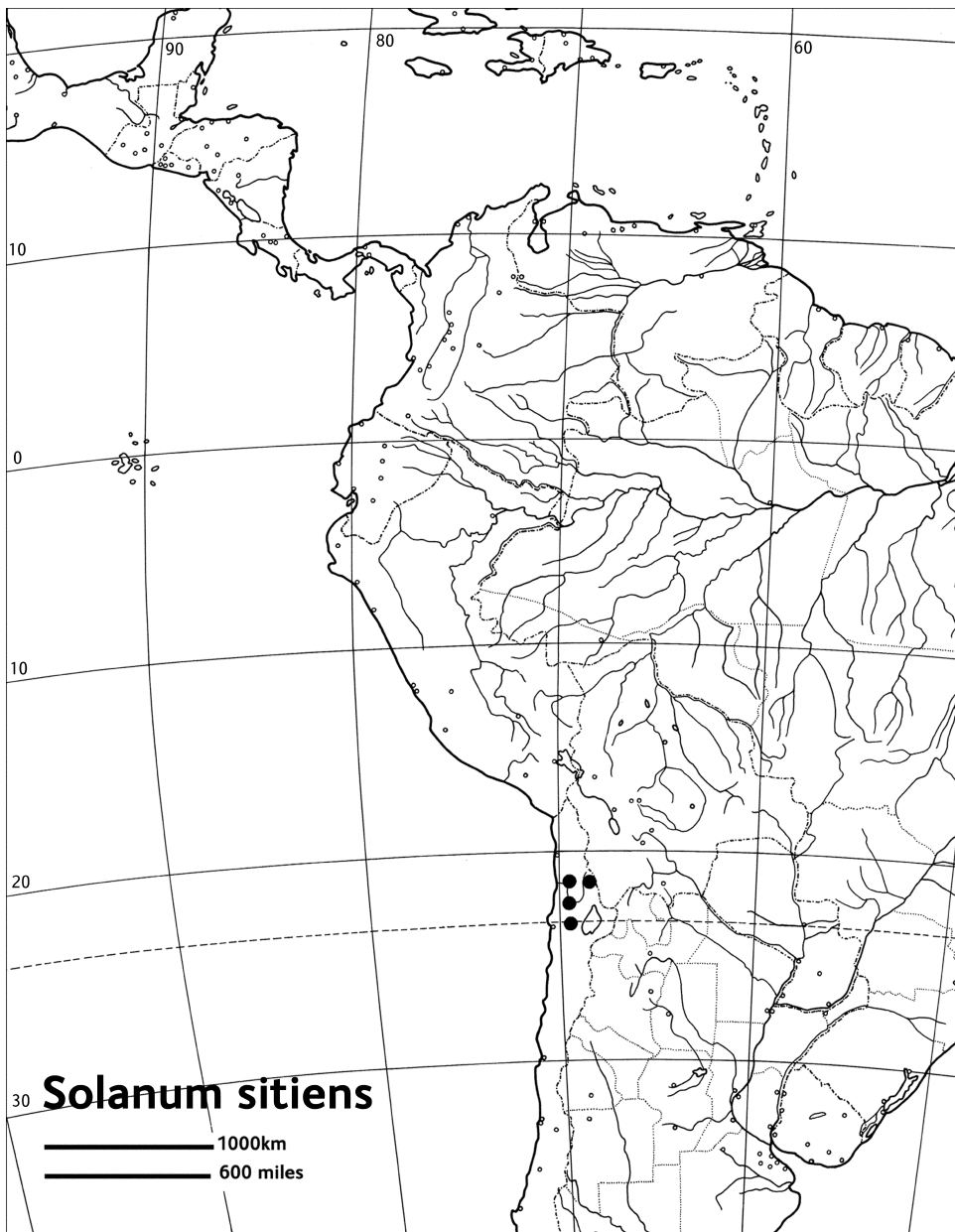


FIG. 21. *Solanum sitiens*. A. Branch. B. Inflorescence. C. Fruit. D. Abaxial view of flower. E. Adaxial view of flower. D. Side view of flower. G. Leaf.

FIG. 22. Distribution of *Solanum sitiens*.

II. *Solanum* section *Juglandifolia* (Rydberg) A. Child, Feddes Repert. 101: 220. 1990.
Solanum section *Tuberarium* (Dunal) Bitter series *Juglandifolia* Rydberg, Bull.
 Torrey Bot. Club 51: 146. 1924.—LECTOTYPE, designated by D'Arcy, 1972:
Solanum juglandifolium Dunal.

Large woody vines or lianas, scandent or clambering into vegetation. Stems green, pale greenish brown, to brown in branches with secondary growth, pubescent to densely pubescent with a mixture of simple uniseriate glandular and eglandular trichomes, the stems glabrescent in age. Sympodial units 5-plurifoliate. Leaves imparipinnate to interrupted imparipinnate, leaflets petiolulate, shortly petiolulate or sometimes sessile to decurrent on the rachis, dark green adaxially, paler abaxially, pubescent with simple uniseriate glandular and eglandular trichomes with a unicellular or multicellular broad base, adaxially sparsely to moderately pubescent, abaxially smooth or rugose and prominently reticulated-veined; pseudostipules present; primary leaflets entire; interjected leaflets absent, or if present entire, sessile and decurrent onto the rachis. Inflorescences many times branched, ebracteate; peduncle large; pedicels articulated at about the middle or just above the middle, the articulation conspicuous. Flowers actinomorphic; calyx 5-parted, usually glabrescent to pubescent; corolla bright yellow, yellowish, or creamy white, fragrant, stellate, pentagonal to rotate, 5-parted, lobed about 1/2 or 1/3 to the base, lobes deltate to short-triangular; stamens 5, staminal column absent, anthers yellow, straight, of equal length, separate or moderately connivent, lacking an apical sterile appendage, initially dehiscent by apical pores and later by introrse slits along the entire anther length; ovary globose-conical, glabrous; style white-pubescent in the basal half, recurved, exerted 2–4 mm beyond the anthers; stigma elongate-clavate to somewhat 2-lobed. Fruit a globose berry, green, glabrous, pericarp thick and hard when ripe; calyx lobes shorter than the mature fruit, thick and woody, spreading, slightly reflexed and breaking off in the mature fruit; fruiting pedicels usually straight, thickened and woody. Seeds obovate, lenticular, winged around the margin.

Members of sect. *Juglandifolia*, unlike members of sections *Lycopersicon* and *Lycopersicoides*, are large, thick-stemmed perennial vines sometimes growing into the forest canopy. Child (1990) published the sectional name as *Juglandifolium*, correcting what he thought was Rydberg's mistake in gender, but Rydberg's original (1924) spelling is correct, because the name of a section or series is to be a plural adjective or a genitive plural.

3. *Solanum juglandifolium* Dunal, Solan. Synopsis 6. 1816. *Lycopersicon juglandifolium* (Dunal) J. M. H. Shaw, New Plantsman 5: 109. 1998.—TYPE: COLOMBIA. "in umbrosis provinciae de las Pastas" *Humboldt & Bonpland s.n.* (holotype: P-Bonpl.! [F neg. 38997: F!]; isotype: MPU-fragment!).
Solanum lehmannianum Bitter, Repert. Spec. Nov. Regni Veg. 10: 532. 1912.
Solanum juglandifolium var. *lehmannianum* (Bitter) Bitter, Repert. Spec. Nov. Regni Veg. 11: 461. 1912.—TYPE: COLOMBIA. Cauca: Popayán, 1000–1500 m, March, *Lehmann 6982* (holotype: B, destroyed; lectotype, here designated: K! [LL neg. 209: F! GH! LL! UC!]; isotypes: F [LL neg. 532: F! LL! UC!], GH [LL neg. 534: F! LL! UC!], PH [LL neg. 533: F! LL! UC!], S [LL neg. 796: F! GH! LL! UC!], US! [LL neg. 535: F! LL! UC!]).
Solanum juglandifolium var. *oerstedii* Bitter, Repert. Spec. Nov. Regni Veg. 11: 461. 1912.—TYPE: "America Centralis?" *Oersted 1465* (holotype: C! [F neg. 22897: GH! MO!; LL neg. 208: LL! UC!]).

Solanum juglandifolium var. *suprascaberrimum* Bitter, Repert. Spec. Nov. Regni Veg. 11: 462. 1912.—TYPE: ECUADOR. Pichincha: Guatusi, Andes of Quito, Chanchán, Sep 1859, *Spruce 6067* (holotype: W! [F neg. 4: F!; LL neg. 798: F! LL! UC!]; isotypes: BM! K! [LL neg. 210: F! LL! UC!]).

Solanum juglandifolium subsp. *cundinamarcae* Bitter, Repert. Spec. Nov. Regni Veg. 12: 58. 1912.—TYPE: COLOMBIA. Cundinamarca: “in silvis non condensis supra Sibaté,” ca. 3000 m, 3 Feb 1803, *Lehmann 2504* (holotype: G! [LL neg. 797: F! LL!]; isotype: K!).

Solanum rhytidophyllum Gilli, Feddes Repert. 94: 322. 1983.—TYPE: ECUADOR. Pichincha: Baeza, 1960 m, 6 Jul 1975, *Gilli 328* (holotype: W!).

Woody vines or lianas, scandent or clambering into vegetation, to 10 m or more tall. Stems 50–80 mm at base, upper stems green, pubescent to densely pubescent with a mixture of simple uniseriate trichomes, short 1–2-celled glandular trichomes with 4-celled heads (the glandular trichomes more abundant near the growing tip), very sparse 1–2-celled white eglandular trichomes, and long transparent 8–10-celled trichomes 2–3.5 mm long, from stiff multicellular bases or the bases sometimes unicellular, these long trichomes breaking off and leaving the bases as protuberances from the stem, the stems glabrescent in age. Sympodial units 5-plurifoliate; internodes 4–15 (+) cm long, elongating as the plant grows. Leaves imparipinnate to interrupted imparipinnate, (5–) 9–35 cm long, (3–) 5–22 cm wide, dark green adaxially, occasionally slightly paler abaxially, adaxially the lamina sparsely to densely pubescent with conical 1–3-celled trichomes ca. 1 mm long, the basal cell much enlarged, base multicellular, these trichomes deciduous but leaving the stiff multicellular bases as bullate protuberances and the leaf surface rough and sandpapery to the touch, the veins and rachis densely pubescent with simple uniseriate trichomes 1–2 mm long from unicellular bases, abaxially the lamina, rachis, and veins densely pubescent with simple uniseriate transparent 2–7-celled trichomes 1–2 mm long from unicellular bases, these more abundant along the veins, more sparsely pubescent with small glandular trichomes less than 0.5 mm long with 4-celled heads, these densest along the rachis; primary leaflets 3–4 pairs, the basal pair sometimes, but not consistently smaller than the rest even on a single stem, elliptic to broadly elliptic, apex acute, base truncate, somewhat oblique and the lamina extended basiscopically, margin entire; terminal leaflet (3–) 5–10 cm long, (1.5–) 2.5–4.5 cm wide, the petiolule 0.4–1.1 cm long; lateral leaflets 4–11.5 cm long, 1.6–4.5 cm wide, the petiolule 0.3–0.8 cm long; secondary leaflets absent; tertiary leaflets absent; interjected leaflets usually absent, if present 0–6 (–9) per leaf, 0.2–0.8 (–1.5) cm long, 0.2–0.4 (–0.6) cm wide, usually sessile or sometimes with a short petiolule less than 0.05 cm long; petiole 2–7 cm long; pseudostipules usually absent, or poorly developed and deciduous. Inflorescences 9–30 (+) cm, many times (4–5+) dichotomously branched, with 20 to more than 100 flowers, ebracteate, peduncle 5–15 cm long, densely pubescent like the stems, in addition with a more abundant pubescence of short 1–2-celled uniseriate trichomes ca. 0.5 mm long. Pedicels 1–1.5 cm long, articulated near the middle, the articulation often darker in color. Buds 0.8–1 cm long, 0.4–0.5 cm wide, elliptic, the corolla halfway or less exerted beyond the calyx just before anthesis. Flowers with the calyx tube 3–4 mm long, lobes 4.5–5.5 mm long, 2.5–3 mm wide, deltate to long-acuminate, densely pubescent with long simple uniseriate trichomes 1–2 mm long, and much shorter glandular trichomes with 4-celled heads; corolla 1.8–3.3 cm in diameter, stellate, yellow, the tube 0.3–0.6 cm long, lobes 0.7–1.5 cm long, 0.6–0.9 cm wide, densely white-pubescent abaxially with simple



FIG. 23. *Solanum juglandifolium*. A. Branch. B. Fruit. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower.

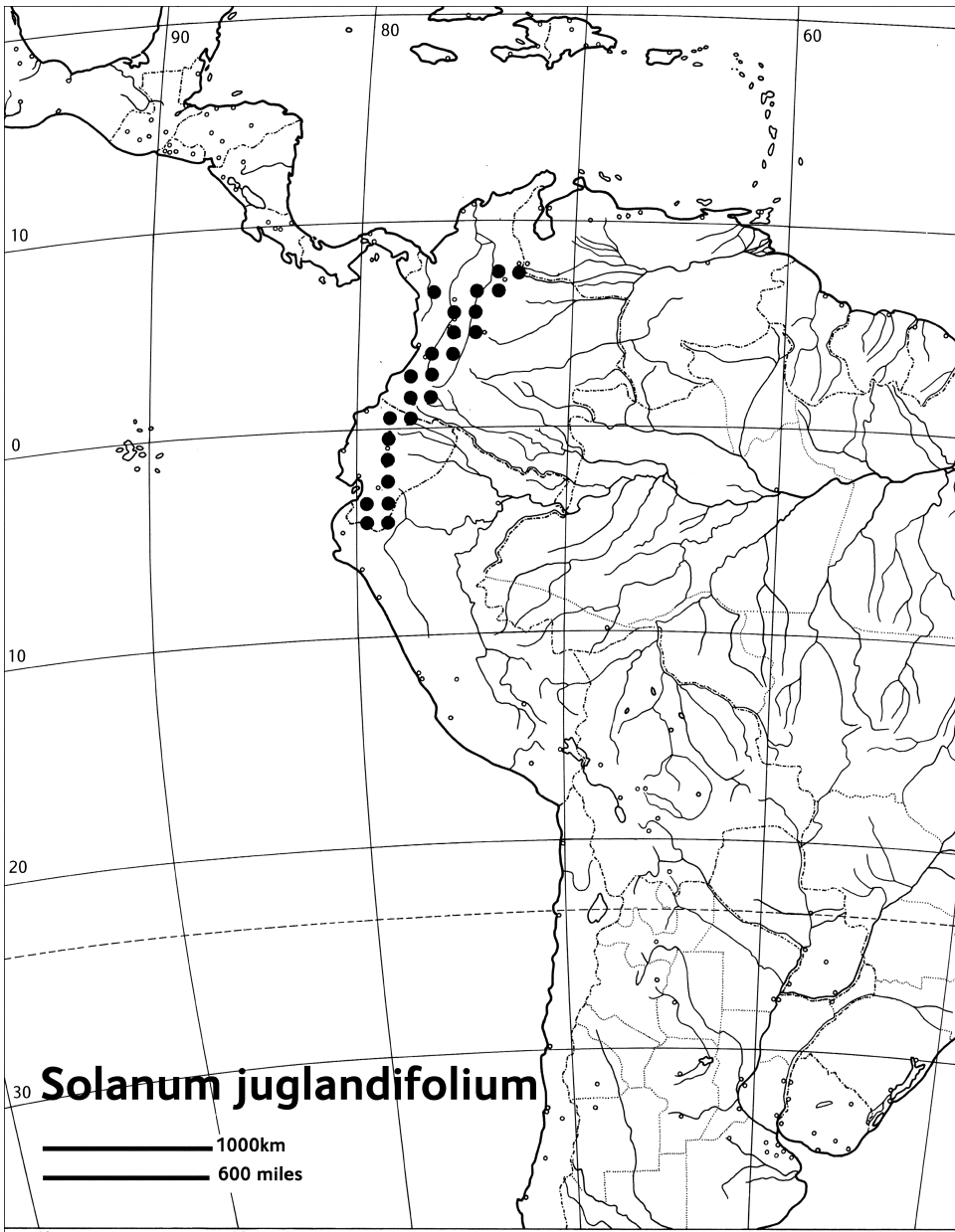


FIG. 24. Distribution of *Solanum juglandifolium*.

uniseriate trichomes ca. 0.5 mm long, and shorter glandular trichomes with 1-celled heads, these more abundant on the midveins, densely eglandular-papillate at the tips, reflexed at anthesis; staminal column absent, stamens free, straight, filaments 0.05–0.2 cm long, glabrous or minutely white-pubescent, anthers 0.4–0.65 cm long, equal, sterile apical appendage absent; ovary conical, glabrous; style 0.8–1.3 cm long, 0.8–1 mm in diameter, sparsely white-pubescent in the basal half, exserted 1–3 mm beyond the anthers;

stigma capitate, green. Fruit 1.5–2 cm in diameter, globose, 2-locular, green, glabrous; fruiting pedicels 2–3 cm long, thickened and woody, straight; calyx lobes in fruit 4–6 mm long, 2–3 mm wide, woody and breaking off, spreading at base of berry. Seeds 2.8–3.0 mm long, 1.7–2.1 mm wide, 0.6–0.8 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, winged (0.3–0.5 mm wide) along the entire seed border. Chromosome number: $n = 12$ ($2n = 24$, Correll 1962: 105; LA2788, <http://tgrc.ucdavis.edu>). Plate 10, Plate 20, Plate 30; Fig. 23.

Phenology. Flowers and fruits throughout the year, but with a peak of flowering between July and September (Smith & Peralta 2002).

Distribution (Fig. 24). Northeastern Colombia (Santander) in all three Cordilleras to southern Ecuador; open areas and roadsides or the edges of forest clearings, sometimes occurring in páramo in southern Ecuador; 1200–3100 m.

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** Without locality, *Dawe 857* (US); *Hawkes 185* (US); 1760, *Mutis 2001* (US).—ANTIOQUIA: Mpio. Sta. Bárbara, Alto de Minas, *Acosta-Arteaga 719A* (COL); La Sierra near Medellín, *Archer 1144* (US); Santa Elena, *Archer 1293* (US); Mpio. Caramanta, vereda Barroblanco, 5–10 km de Caramanta a Barroblanco, *Cordillera Central, Betancur et al. 1003* (F, NY); Mpio. Jardín, vía Jardín–Riosucio, 4–5 km de Jardín, Vereda Quebrada Bonita, *Callejas et al. 3788* (NY); Mpio. Rionegro, Vereda Yarumales, 20–30 km SE de Medellín en la vía a Rionegro, *Callejas et al. 9626* (NY); Cerro de la Vieja, *Bro. Daniel 1715* (US); Abajorral, *Bro. Daniel 2223* (US); Mpio. Salgar, camino de ascenso a Cerro Plateado, Quebrada La Liboriana, *Franco et al. 2293* (NY); Piedras Blancas, municipal water reserve 7 km NE of Medellín, *Hatheway 1573* (B); carretera de Medellín a Santa Elena, ca. 5–7 km de Medellín, *Hawkes 495* (COL); Mpio. Jardín, Vereda Ventanas, Jardín–Ventanas–Riosucio road, 12–19 km SSE of Jardín, *Luteyn & Escobar 12721* (NY); alrededores de Envigado, *Molina 25* (US); Mpio. Medellín & Guarne, Parque Ecológico Piedras Blancas, orilla Quebrada Piedras Blancas, *Roldán et al. 2217* (COL); Mpio. Medellín, along road to Cerro de Padre Amaya, 2.3 km from main Medellín–Santa Fe de Antioquia road, *Zarucchi & Escobar 6882* (NY); Mpio. Salgar, Km 13 of road Salgar–El Duero (Chocó), *Zarucchi et al. 6091* (NY).—CALDAS: Los Alpes, *Dryander 2789* (F); Acimaipa, Nacimiento, *Dryander 2789 a* (F); Ternates, Nacimiento, *Dryander 2789 b* (F); Manzales, Puente Olivares, carretera al N, 1 km al N del puente, *Hawkes 387* (US); carretera a Salento, 1 km distante de la carretera de Pereira a Armenia, *Hawkes 409* (COL, US); Salento, above Salento, *Pennell 8900* (GH, US); Pereira, *Sandeman 5675* (K, MA).—CAUCA: Munchique, *Alston 8291* (BM, COL, US); above Quebrada Puente de Tierra, above Argelia, *Core 1236* (US); Munchique, camino a Mina Tapada, poco antes de llegar a la primer casa, *Hawkes 185* (COL, US); La Gallera, Micay Valley, near Río San Joaquín, *Killip 7839* (NY, US); Parque Nacional Munchique, El Tambo, vereda La Romelia, La Gallera, *Velayos et al. 7001* (COL).—CHOCÓ: Mpio. El Carmen de Atrato, carretera a Urrao, ca. 15 km al NW de al cabecera municipal, *Galeano et al. 807* (COL, NY).—CUNDINAMARCA: W of Bogotá on road to El Colegio, ca. 1.5 km W of Salto de Tequendama near Km 8, *Barclay et al. 3310* (US); San Miguel, S of Sibate on road to Fusagasugá, between Km 34 and 35, *Barclay et al. 3416* (US); Albán, carretera entre Saisama y Cambao, *García-Barriga 21075* (MA); El Salto de Tequendama, al pie de la catarata, *García-Barriga 13350* (COL, US); road from La Mosquera to La Mesa, Km 18, *Gentry & Fallen 17058* (COL, MO, NY); Tequendama, *Haught 6497* (US); carretera entre Facatativa y Anolaima, ca. 54 km de Bogotá, en un vallecito arriba de la carretera, *Hawkes 628* (US); S de Usme, entre La Regedera y El Hato, Estación Agrícola Experimental Usme, *Idrobo et al. 380* (COL); Salto de Tequendama, *Foster et al. 1911* (A, COL); Salto de Tequendama, 25 km WSW of Bogotá, W margin Cordillera Oriental, *Smith & Idrobo 1085* (UC); barranca del Río Bogotá, los alrededores del Salto de Tequendama, *Schultes et al. 4059* (GH, US); vicinity of Salto de Tequendama, road past falls leading downhill to El Colegio, *Smith 1264* (WIS); entre el Salto de Tequendama y El Arracachal, *Uribe-Uribe 2200* (U); orilla de la carretera entre Mosquera y La Mesa, *Uribe-Uribe 3729* (NY); arriba de Granada en la carretera a Silvanía, *Uribe-Uribe 6130* (COL); road Facatativá–Albán, left side of road, 11 km after passing Alto de la Tribuna, *Wijnanga 587* (NY, U).—HUILA: forest around Merenberg, road from Popoyán, *D’Arcy et al. 15610* (CUVC, MO), *D’Arcy et al. 15658* (CUVC, MO); Mpio. La Argentina, finca Merenberg, derecha de la casa principal de la finca, *Orozco & Mayorga 2624* (COL); Belén, finca de Merenberg, *Rangel 2474* (NY).—NARIÑO: Mpio. Ricaurte, camino Chucunes–La Planada, *Benavides 340* (NY); Mpio. Ricaurte, trayecto San Isidro–La Planada, *Benavides 9312* (NY); ca. 1 km W of San Jorge, E of La Victoria, *Castillo et al. 1227* (COL); Río Chingual at San José, below La Victoria, Cordillera Oriental, *Ewan*

16208 (US); Mpio. Ricaurte, trayecto La Planada–San Isidro, *Ramírez P. 4264* (NY); Rionegrto, 14 km antes de Nariño, Fondo de Santa Elena, *Sonsón (Gutiérrez et al.) 1* (LL); Mpio. Nariño, Km 18 of road Nariño–Sonsón, 18 km from Sonsón and 3 km from fork in road to Argelia, *Zarucchi & Bedoya 4576* (COL).—PUTUMAYO: Valle de Sibundoy, Balsayaco, *Bristol 647* (GH, US); alto de la Cordillera en La Cabaña, carretera de Sibundoy a Urcusique, *Cuatrecasas 11532* (F, US); Valle de Sibundoy, cerca de San Francisco, arriba del puente sobre el Río Putumayo en la carretera para Mocoa, *Hawkes 608* (COL, US).—QUINDIO: 0.7 km E of road from Armenia to Pereira, on road to Salento, on N side of road, *Castillo et al. 1206* (COL); 5.4 km S of Salento, ascending Cordillera Cental on road to Toche, *Castillo et al. 1208* (COL); Palmilla, fôrets de Quindio, *Triana s.n.* (G-DC, P).—RISARALDA: Santa Rosa, alrededores del Hotel Termale, declive a la izquierda de la quebrada del hotel, Cordillera Central, Vertiente Occidental, *Idrobo et al. 9865* (U); Mpio. Santuario, estribación oriental de la Cordillera Occidental, transecto de las Colonias, Alto de Tigre, *Torres et al. 1365* (COL).—SANTANDER: vicinity of La Baja, *Killip & Smith 18318* (A, GH, NY, US).—VALLE: Cordillera Occidental, vertiente oriental, hoya del Río Cali, vertiente derecha, La Tulia, *Cuatrecasas 18582* (F, US); Cordillera Occidental, vertiente oriental, entre Las Brisas y La Carbonera, *Cuatrecasas 22707* (F, US, USM); Cordillera Occidental, vertiente occidental cerca del filo divisoria entre Depto. El Valle y Intendencia del Chocó, N de Albán, *Dugand & Jaramillo 3043* (COL); Peñas Blancas, cuenca del Río Pichindí, *Lozano et al. 8* (CUVC); Las Delicias, NW of Restrepo, *Robinson 204* (US); Mpio. El Cairo, Las Amarillas, carretera El Cairo–Río Blanco, a 1 hora en jeep de El Cairo, frontera Valle/Chocó cerca de base de Cerro del Inglés, Cordillera Occidental, Serranía de los Paraguas, *Silverstone Sopkin et al. 3879* (CUVC, NY).—VALLE/RISARALDA: Cordillera Occidental, cuenca del Río Cali, cercanías de Peñas Blancas, *López Figueiras 8216* (US). **Ecuador.** Without locality, *Gilmartin 29* (GH).—AZUAY: 1 km N of Sevilla de Oro, *Clemants 2314* (NY); San José de Huigra, alrededores, *Cornejo & Bonifaz 3902* (NY).—BOLÍVAR: Parroquia Chillanes, Lamirán, *Acosta Solís 6775* (F); carretera de San Pablo de Atenas–Chillanes, en la Loma de Peresán, *Zak & Jaramillo 2639* (F, NY); carretera Chillanes–Tambillo–Trigoloma, entre Bola de Oro y Panecillo, *Zak & Jaramillo 2759* (F, NY).—CARCHI: ca. 6 km above Maldonado, just below Puente de Palo, *Boyle & Bradford 1862* (NY); Maldonado, Quebrada Naranjo, near the waterfall, first quebrada W of the market in Maldonado, *Dorr & Barnett 6087* (NY); Valle de Maldonado, Km 60 on road Tulcán–Maldonado, *Holm-Nielsen et al. 5755* (NY); Valle de Maldonado, Km 71 on road Tulcán–Maldonado, *Holm-Nielsen et al. 6010* (NY); Cantón Mira, El Carmen, Cerro Golondrina, *Tirado et al. 1214* (NY); above Maldonado, *van der Werff & Gudiño 10844* (G, NY); Maldonado–Tulcán road Km 30, *Werling & Leth-Nissen 254* (NY); carretera Tulcán–Tufiño–Maldonado, sector La Pradera, *Zak 1386* (NY, QCA).—CHIMBORAZO: Sibambe, Alausí, *Acosta Solís 5581* (F); Cantón Pallatanga, comunidad Jesús del Gran Poder, from Pana Redonda on main hwy, 2 km S on cobble road, ca. 4 km NE of Pallatanga, *Clark et al. 1411* (NY); western Cordillera, between Chimbo River and village of Balsapampa, *Rimbach 363* (F); vicinity of Huigra, mostly on Hacienda de Licay, *Rose & Rose 22505* (NY, US); 4.4 km N of San Isidro de Yungilla on dirt road to Río Chimbo, at Pretoria, 36.5 km N of San Juan de Trigoloma, *Spooner et al. 5076* (QCA, WIS); carretera partidero Pallatanga–San Juna–Llimbe, *Zak 1774* (F, NY).—COTOPAXI: Cantón Pilalo, borde de Río Pilalo, *Cerón & Villavicencio 2772* (NY); 20 km W of Pilalo, *Gilmartin 807* (US); Pilalo, 2 km N of village, *Gilmartin 790* (US); around Pilalo, *Holm-Nielsen & Jeppesen 1126* (C); road Pilalo–Quevedo, between Pilalo and Macuchi, *Holm-Nielsen & Quintana 24719* (NY).—IMBABURA: vicinity of Apuela, *Madison & Coleman 2308* (GH); Cantón Cotocachi, Parroquia Plaza Gutiérrez, Tabla Chupa, arriba de Apuela, *Tipaz et al. 928* (MO); carretera Cotocachi–Cuicocha–Apuela–San Luis de la Delicia, sector San Luis de la Delicia, *Zak 1473* (F, NY).—MORONA-SANTIAGO: Lomipueero, road Gualaceo–Limón, *Holm-Nielsen et al. 20381* (AAU, NY).—NAPO: Sierra Azul (Agrícola Industrial Río Aragón), campamento Aragón, orillas de Río Colorado, *Alvarez et al. 215* (NY); Cantón Quijos, Reserva Ecológica Antisana, Río Aliso, 8 km SW de Cosanga, *Alvarez & Proaño 253* (NY); Sierra Azul (Agrícola Industrial Río Aragón), campamento Aragón, *Alvarez et al. 586* (NY); Baeza, SW of the village, *Balslev & Madson 10308* (AAU, NY); 7 km E of Cosango, *Bese et al. s.n.* (QCA); Cosanga, hillside N of town, *Boeke & McElroy 402* (GH, NY, W); cerca del Río Aragón, en el camino del Aliso, hacia el finca del Ing. Mora, *Freire-Fierro & Yánez 2687* (NY); above Baeza on road to Papallacta, *Plowman et al. 3891* (GH); Cantón Tena, Parque Nacional Llanganates, via Salcedo–Tena, margen derecha del Río Mulatos, *Vargas et al. 2334* (NY); Cantón Quijos, Reserva Ecológica Antisana, Río Aliso, 8 km SW de Cosanga, *Vargas et al. 2937* (NY); carretera Julio Andrade–San Francisco–Sta. Bárbara–La Alegría, *Zak 1583* (F, NY, QCA).—PICHINCHA: Saloya, descenso W de la Cordillera Occidental, *Acosta Solís 5633* (F); valley of Río Saloya, El Cuello, *Asplund 7317* (LL, US); Parroquia Chiriboga, cerca a Río Saloya, *Cerón et al. 6823* (NY); along hwy between Aloag and Santo Domingo de los Colorados, 25 km W of main Quito–Latacunga junction, 55 km E of Alluriquín, *Croat 56940* (NY); road from Calacalí to Tandayapa, at Km 23.7, W of junction into town of Calacalí, *Croat & Whitehill 82715* (BM); road from Quito to Santo Domingo de los Colorados, ca. 46 km E of Santo Domingo, *Gentry 9504* (NY); 11 km W of Tandapi, trail along Chicto River, tributary to Río Pilatón, *Gentry et al. 12078* (NY); Nono–Tandayapa, 28 Jan 1982, *Harling et al. 19991* (NY); Chiriboga on Quito–Santo Domingo road, *Haught 3200* (F, US);

carretera de Quito a Santo Domingo, entre Km 33 y 34 de Quito, *Hawkes 640* (COL, US); road Nono–Pacto–Río Yacuambi, 5–10 km above Nanegalito, *Holm-Nielsen et al. 24450* (QCA); road Santo Domingo de los Colorados–Quito, above Tandapi (Cornejo Astorga), *Holm-Nielsen et al. 7136* (NY); via San Juan–Chiriboga, *Jaramillo & Escobar 1101* (QCA); Reserva Florística-Ecológica Río Guajalito, Km 59 de la carretera antigua Quito–Santo Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, *Jaramillo & Zak 567* (NY, QCA); just N of town of Tandapi on Quito–Santo Domingo road, across Río Toachi, *Knapp et al. 6273* (BH, QCNE, US); old road Quito–Santo Domingo de los Colorados, 6–11 km W of San Juan de Chiriboga, *Luteyn et al. 8480* (COL, F, NY, QCA); old road Quito–Santo Domingo, 12–15 km NE of turnoff to old road from junction with new road near Alluriquín, *Luteyn et al. 8753* (F, NY, QCA); new road from Quito to Santo Domingo de los Colorados, ca. 2 km W of Tandapi to ca. 20 km E of Alluriquin and La Cumbre, *Smith 1917* (US, WIS); along S side of new road from Quito–Santo Domingo de los Colorados, 1.5 km E of Río Silante, 6.4 km E of La Virgen de Mercedes, *Spooner et al. 5027* (QCA, WIS); 9.1 km S of Chiriboga, *Spooner et al. 5124* (QCA, WIS); between Km 37–50 along Río Saloya, between Volcán Atacaso and Volcán Pichincha, *Steyermark 52556* (F, LL); side-track to right of Quito–Santo Domingo road, *Stock 19* (E, F); along road Nanegal–Nanegalito, *van der Werff et al. 12268* (NY); near Hacienda El Carmen, Maquipucuna Reserve, *Webster et al. 27076* (TEX, WIS); Parroquia Nanegal, Maquipucuna area, Cerro Sta. Lucía (Cerro Campana), ca. 6 km airline E of Nanegal, *Webster & Castro 28318* (QCA); along Río Alambí, 7.5 km by road SE of Tandayapa, *Webster et al. 28663* (TEX); Parroquia Nanegalito, W slopes of Cerro Negro, 2.5–3 km NE of Nanegalito, *Webster et al. 30496* (TEX); Reserva Florística-Ecológica Río Guajalito, Km 59 de la carretera antigua Quito–Santo Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, *Zak 1114* (F, NY, QCA); carretera Quito–Aloag–Santo Domingo de los Colorados, Km 94, 10 km al S de la carretera, estribaciones W del Volcán Corazón, *Zak 1501* (NY); Carretera Lloa–Mindo, entre Km 30–34, *Zak & Jaramillo 2119* (NY); carretera Quito–Chiriboga–El Empalme, entre Km 75–85, *Zak & Jaramillo 2313* (NY, US); along new road from Quito to Santo Domingo de los Colorados, *Zarucchi & Ramos 2290* (QCA).—ZAMORA–CHINCHIPE: banks of the Río Zamora, ca. 25 km E of Loja on the new road to Zamora, *Dorr & Valdespino 6601* (NY, QCA); road Loja–Zamora, ca. 13 km E of pass, just before junction with old road, *Øllgaard et al. 90849* (BM); Cantón Chinchipe, Parque Nacional Podocarpus, La Esmeralda (Cooperative San Francisco de Numbala Alto), *Palacios & Tirado 13038* (NY); Cantón Zamora, Parque Nacional Podocarpus, carretera Loja–Zamora, San Francisco, *Palacios & Tirado 13454* (NY); 27.6 km from Iglesia San Juan Bautista del Valle, on E side of Loja, on new road to Zamora, by bridge crossing over river in Quebrada Navidades, just S of Quebrada Zurita, 8.1 km W of Sabanillas, *Spooner et al. 5038* (QCA); trail between Mirador and Pailas, *Steyermark 54286* (F, LL).

Solanum juglandifolium is easily distinguished from *S. ochranthum* by its leaves, which are adaxially rough to the touch and abaxially not markedly paler, the fewer interjected leaflets, and the flowers with long-acuminate calyx lobes and a stellate corolla. The laminar roughness, resulting from the trichome-topped protuberances on the adaxial surface, feels like sandpaper in both live plants and herbarium specimens. Although *S. ochranthum* occasionally has slightly rough leaf surfaces, the trichome bases are never as large and well developed as in *S. juglandifolium*.

Correll (1962) in his key of the two taxa, reversed the number and character of interstitial leaflets; he indicated that *S. juglandifolium* has leaves usually with various-sized interstitial leaflets and *S. ochranthum* leaves without or with very few small orbicular interstitial leaflets. This error has led to considerable confusion in herbarium determinations made with the use of Correll's key. In fact, *S. juglandifolium* has fewer leaflets than does *S. ochranthum*, as well as fewer interjected interstitial leaflets, although some specimens can be difficult to determine in the absence of flowers or fruit. In *S. juglandifolium* pseudostipules are poorly developed, deciduous, and usually absent, while in *S. ochranthum* pseudostipules are usually present and well developed at all nodes.

Several varieties of *S. juglandifolium* have been described mainly based on leaflet size, differences in pubescence, and degree of roughness of the lamina. These infraspecific variations are not consistent with habitat preference or geographical distribution, and we do not consider them taxonomically significant.

The Central American locality for the type of var. *oerstedii* is almost certainly in error; Bitter did indicate it was questionable in the protologue (see above), although the number falls within Oersted's Costa Rican number series. The Danish collector A. S. Oersted did much collecting in Costa Rica, but he also traveled to other countries in South America, most notably Ecuador, from where we suggest the type of var. *oerstedii* comes. The numbering of collections in the 19th century did not always reflect the order in which they were gathered; numbers were often assigned upon return to the home herbarium, rather than in the field, and the label on the type specimen of var. *oerstedii* was certainly affixed in Copenhagen, not by Oersted himself.

- 4. *Solanum ochranthum*** Dunal, Solan. Synopsis 6. 1816. *Lycopersicon ochranthum* (Dunal) J. M. H. Shaw, New Plantsman 5: 109. 1998.—TYPE: ECUADOR. "in regno Quitense," *Humboldt & Bonpland s.n.* (lectotype, here designated: P! [P00136308, Morton neg. 8721: F! LL!]; isolectotypes: P! [P00136307, Morton neg. 8272: F! LL!], P! [P00136306, LL neg. 519: F! LL!], possible isolectotype: P! P00136309, LL neg. 514: F! K! LL!; Cibachrome: K!).
- Solanum caldasii* Dunal, Solan. Synopsis 6. 1816.—TYPE: ECUADOR. "in regno Quitense," *Humboldt & Bonpland s.n.* (lectotype, here designated: P! [P00136305, F neg. 38993: F!; LL neg. 518: F! K! LL!; Cibachrome: K!]; isolectotype: MPU-fragment!).
- Solanum fuscatum* Roemer & Schultes, Syst. veg. 4: 664. 1819 (as "*fuscatum*" in index, p. 872).—TYPE: "In Americ. merid.," *Humboldt & Bonpland s.n.* (holotype: B-W, microfiche: IDC 7440: 4356!).
- Solanum ochranthum* var. *connascens* Bitter, Repert. Spec. Nov. Regni Veg. 11: 465. 1912.—TYPE: ECUADOR. Without locality, *Jameson s.n.* (holotype: W! [LL neg. 789: F! K!]).
- Solanum ochranthum* var. *endopogon* Bitter, Repert. Spec. Nov. Regni Veg. 11: 464. 1912.—TYPE: ECUADOR. Pichincha: "prope Quito, Chillo" *Sodiolo 114/5* (holotype: B, destroyed).
- Solanum ochranthum* var. *glabrifilamentum* Bitter, Repert. Spec. Nov. Regni Veg. 11: 466. 1912.—TYPE: PERU. Apurímac: Río Pampa, Hacienda Catahuacho, 2600–2700 m, *Weberbauer 5097* (holotype: B, destroyed; lectotype, here designated: GH! [LL neg. 521: F! K! LL!]; isotypes: F! [LL neg. 522: F! K! LL!], US! [LL neg. 516: F! K! LL!]).
- Solanum ochranthum* var. *septemjugum* Bitter, Repert. Spec. Nov. Regni Veg. 11: 465. 1912.—TYPE: COLOMBIA. "prov. de Mariquita: Quindio, La Palmilla," 2200 m, *Triana s.n.* (holotype: W! [F neg. 2: F!; LL neg. 790: K! LL!]; isotypes: FI [LL neg. 791: F! K! LL!], P! [P00213204, LL neg. 513: F! K! LL!]).
- Solanum ochranthum* var. *quinquejugum* Hawkes, Bull. Imp. Pl. Breed. Genet., Cambridge 12: 112. 1944.—TYPE: ECUADOR. Carchi: San Gabriel, Guaca, 11,500 ft, 6 Aug 1939, *Balls & Hawkes 7345* (holotype: CPC [LL neg. 511: K! LL!]; isotypes: CPC [LL neg. 510: F! K! LL!], K! US! [LL neg. 512: K! LL!]).

Woody vines, to 8–10 m tall, clambering over vegetation. Stems 60–80 mm at base, younger stems green, pithy, 4–5 mm at base, pale greenish brown, densely white-pubescent with simple uniseriate trichomes, the longest 4–6-celled, 1.5–2.5 mm long, from multicellular bases, mixed with shorter white trichomes ca. 0.5 mm long, usually with unicellular bases, and glandular trichomes ca. 0.05 mm long, with a 4-celled glandular head.

Sympodial units 5-plurifoliate; internodes 2–10 cm long, or longer on older stems (not usually found on herbarium specimens). Leaves interrupted imparipinnate, 13–35 cm long, 11–20 cm wide, green, markedly paler abaxially, densely pubescent with simple uniseriate trichomes, adaxially sparsely to moderately pubescent with transparent patent trichomes 0.5–2 mm long, with multicellular bases, the trichomes breaking off and leaving the base as a projection from the lamina causing the surface to be slightly rough to the touch, tiny 1-celled trichomes with a large 1-celled glandular head also present, abaxially the pubescence dense and soft, of weaker-walled and tangled 8–10-celled trichomes with unicellular bases, these densest along the veins, the glandular trichomes like those of the adaxial surface but sparser, the lamina surface pale abaxially with dark venation in dry specimens; primary leaflets 3–5 pairs, the basal pair much smaller than the rest, elliptic to oblanceolate, apex acute to acuminate, base truncate to completely decurrent on the rachis, oblique basiscopically, margin entire; terminal leaflet usually larger than the laterals, 6–11 cm long, 2–4 cm wide, the petiolule 0.6–1.1 cm long; lateral leaflets 7.5–10 cm long, 2–3.5 cm wide, decurrent basiscopically to the rachis or with a tiny petiolule to 0.2 cm long; secondary leaflets absent; tertiary leaflets absent; interjected leaflets 7–16, opposite to subopposite, 0.1–0.5 cm long, 0.1–0.4 cm wide, in sets of 2 or 3 between the primary leaflets, completely decurrent onto the leaf rachis; petiole 2–4 cm long; pseudostipules usually present and well developed at all nodes, 0.5–1.5 cm long, 0.4–1.5 cm wide, pubescent like the leaves. Inflorescences 8–20 (–30) cm long, many times (to 4–5 times) branched, with 2–60 (+) flowers, ebracteate, peduncle 3.5–12 cm long, densely pubescent like the stems, the pubescence more abundant at the apices of the branches. Pedicels 1–1.5 cm long, articulated at the middle, the articulation often swollen and conspicuous. Buds ca. 1 cm long, 0.5 cm wide, elliptic, straight, the corolla more than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube 2.5–4 mm long, lobes 2–5 mm long, 2–3 mm wide, deltate and irregularly splitting, the tips acute, densely white-pubescent with 1–2-celled trichomes to 0.5 mm long, from unicellular bases; corolla 2.4–3.5 cm in diameter, rotate to rotate-stellate, bright golden-yellow, the tube 0.8–1.1 cm long, lobes 0.5–1 cm long, 0.5–1 cm wide, abaxially densely pubescent with simple uniseriate trichomes over entire surface, these more abundant and tangled at the tips and along the midveins, lobes spreading at anthesis; staminal column absent, stamens free, straight, filaments 1.5–2 mm long, glabrous or densely white-pubescent, anthers 0.5–0.6 cm long, equal, sterile apical appendage absent; ovary conical, glabrous or with a few white uniseriate trichomes to 0.5 mm long at the apex; style 1–1.3 cm long, pubescent 1/2–3/4 of its length, more densely pubescent basally, 0.5–0.7 mm in diameter, exerted 1–3 mm beyond the anthers; stigma capitate, occasionally somewhat 2-lobed, green. Fruit 2–5 cm in diameter (or sometimes larger), the walls thick and woody, 2–3-locular, green, glabrous; fruiting pedicels 1.5–2.5 cm long, thickened and woody, to 0.5 cm in diameter, straight or slightly bent at the articulation; calyx lobes in fruit 2–3 mm long, 2–3 mm wide, thickened and woody, slightly reflexed and breaking off. Seeds 4.3–5.0 mm long, 3.0–3.5 mm wide, 0.8–1.0 mm thick, obovate to orbicular, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, winged (0.7–0.8 mm wide) along the entire seed border. Chromosome number: $n = 12$ ($2n = 24$, Correll 1962: 108; LA2682, <http://tgrc.ucdavis.edu>). Plate 1N, Plate 2N, Plate 3N; Fig. 25.

Phenology. Flowers and fruits throughout the year, but with a marked flowering peak in June (Smith & Peralta 2002).

Distribution (Fig. 26). Central Colombia (Cordillera Central and Occidental) to southern Peru (Depto. Apurímac); montane forests, 1900–4100 m.

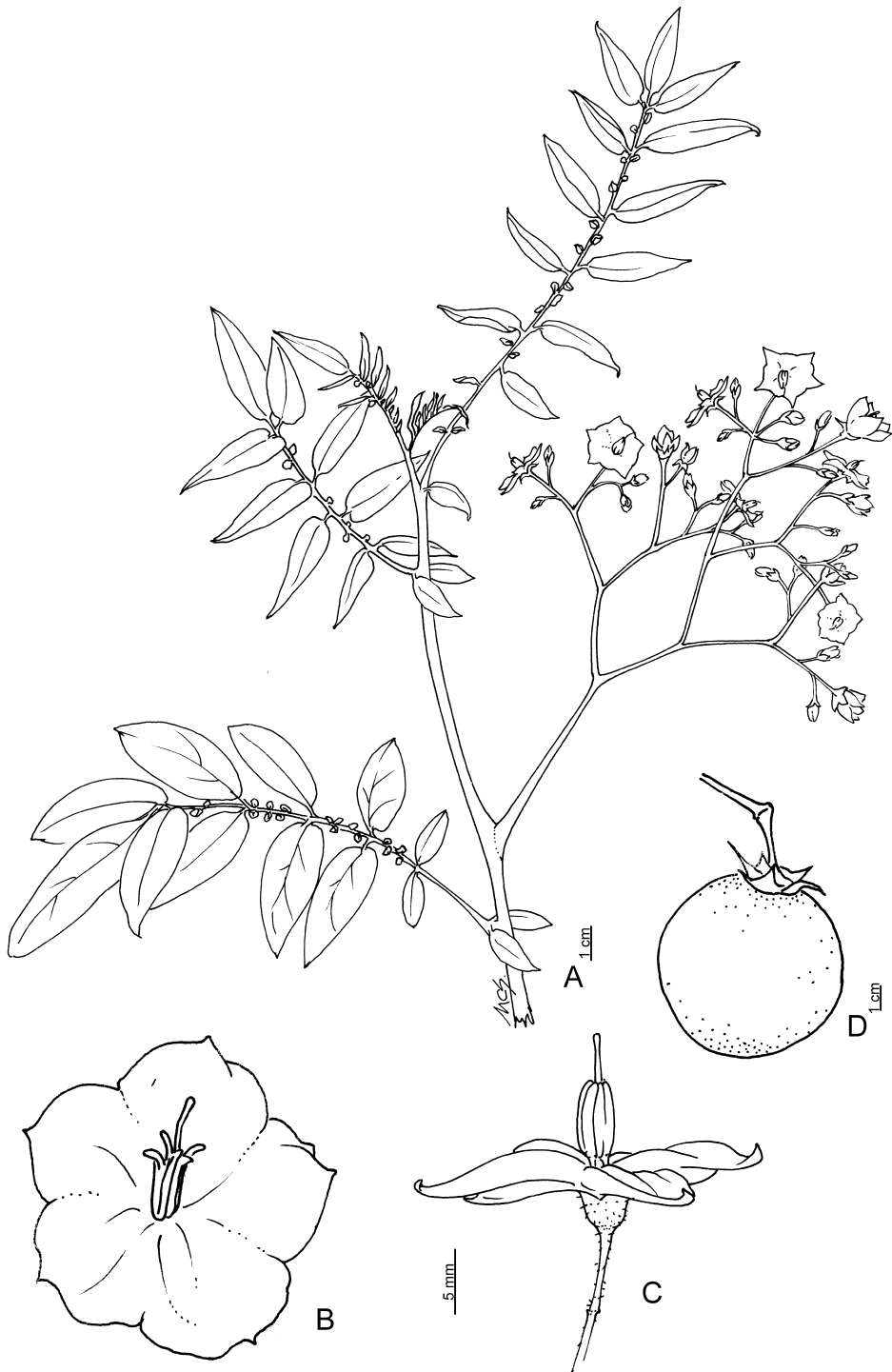


FIG. 25. *Solanum ochranthum*. A. Branch. B. Adaxial view of flower, C. Side view of flower. D. Fruit.

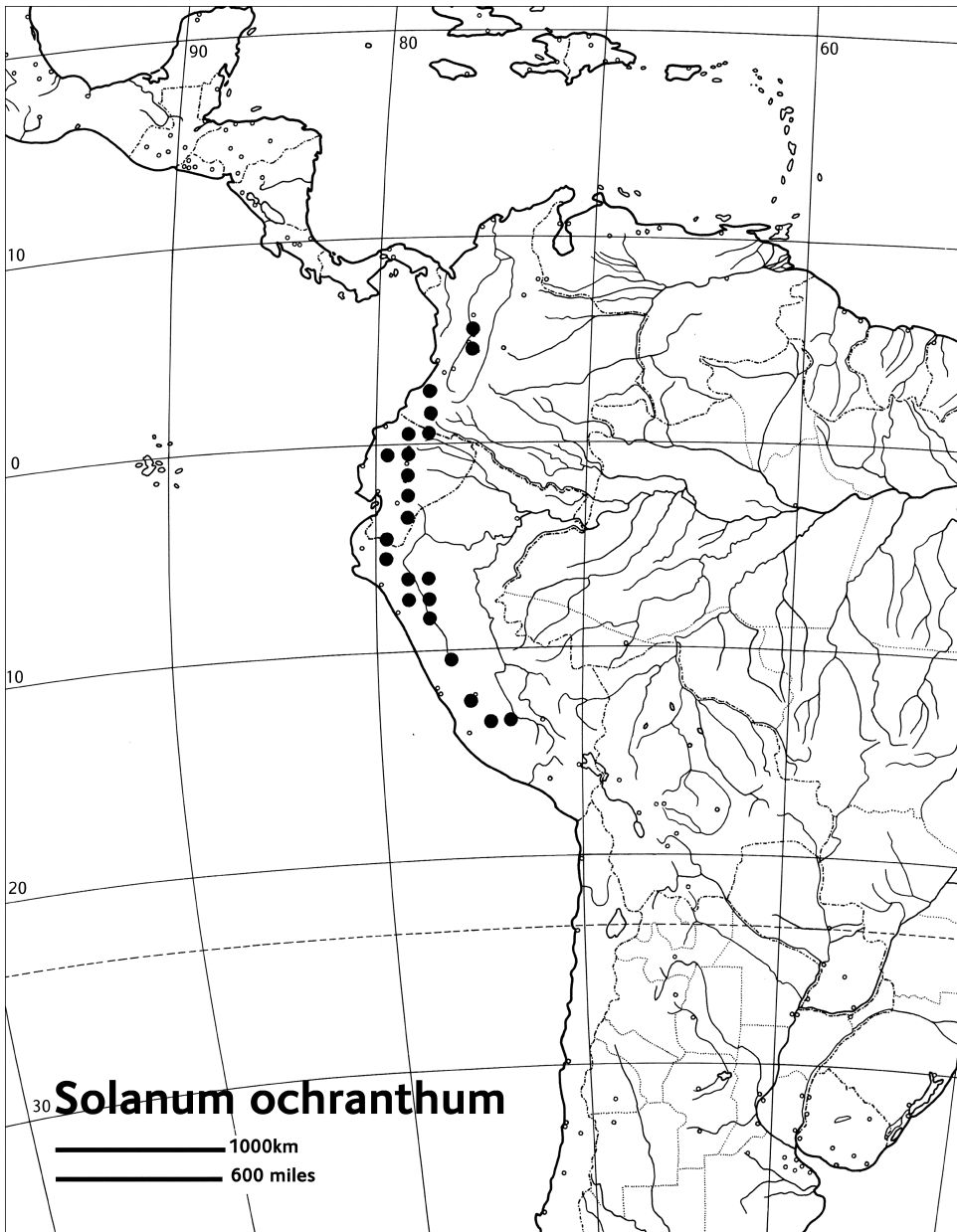


FIG. 26. Distribution of *Solanum ochranthum*.

ADDITIONAL SPECIMENS EXAMINED. **Colombia.** Without locality, *Goudot s.n.* (K); La Palmilla, *Goudot s.n.* (P); Pasto, *Karsten s.n.* (W).—CALDAS: camino de salento a Romerales, Quebrada de Cárdenas, *Hawkes 411* (COL).—NARIÑO: Meneses, W slope of Pasto Andes, *André 2873* (NY); Mpio. de la Cruz, Tajumbina, *Benavides 7399* (NY); just below Ipiales, 1 km SW walking from first gas station on road to Rumichaca to the limit between Colombia and Ecuador, *Castillo et al. 1216* (COL); Mpio. Ipiales, cerca de Paramillo, Voladero, *Hawkes 615* (COL).—PUTUMAYO: Corregimiento El Encano, Laguna de la "Cocha," páramo El Tábano, *García-Barriga 7821* (COL).—QUINDIO: El Chorro, ad flumen Tuluam, *Holton s.n.* (NY).—TOLIMA: camino de Toche a Cajamarca, ca. 3 km de Toche, Las Lajas, *Hawkes 467* (COL).—VALLE: Cordillera Central, vertiente occidental, hoya del Río Bugalagrande, Loma de Barragán, entre la población y Albania, *Cuatrecasas 20902* (F).

Ecuador. Without locality, *Jameson s.n.* (W).—AZUAY: Nudo de Portete, pass between headwaters of the Ríos Tarqui (Atlantic) and Girón (Pacific), Pacific side of pass, *Camp E-2155* (NY, WIS); near Laguna Zurrú Cuchu, *Prescott 784* (NY); sector El Chorro, *Verdugo et al. 239* (HA).—CARCHI: Hcda. Ishpingo, on El Ángel-Tulcán road, Km 1, turnoff towards E, *Jørgensen et al. 92245* (QCA); Cantón Espejo, near Ángel, *Mexia 7543* (F); El Ángel and vicinity, *Zarucchi 2343* (QCA).—IMBABURA: Shanshipamba, *Acosta Solís 14261* (F); Pimampiro Cantón, Carretera Mariano Acosta-Aloburo-Ibarra, 9 km desde Mariano Acosta, remanente de bosque andino en Tigri Rumi, Quebrada Pilcacho, *Cerón et al. 35482* (QCA); carretera de Ibarra a Cayambe, pasando Angochagua, *Hawkes 637* (COL); Hacienda Pimán, between Ibarra and Chota on the abandoned Pan-American Hwy, *Holm-Nielsen et al. 6533* (NY); Cantón Pimampiro, San Francisco de Sigsipamba, sector San Vicente, *Tipaz et al. 1632* (NY).—LOJA: steep ravine slopes near San Lucas, *Correll & Alborno E-380* (LL); carretera Yangana-Toledo, *Jaramillo 8757* (NY, QCA); Cerro Uritusinga, Loja-La Palma Km 18–20, *Jørgensen et al. 1041* (NY); on new road Loja-Cuenca, 7.8 km N of bridge in Santiago, *Spooner et al. 5042* (QCA, WIS); Sevilán, al lado de Río Curiyacu, *Vanden Eynden & Cueva 351* (NY).—PICHINCHA: Nono, below the village, *Asplund 7471* (S, US); 20 km S of Quito on road to Latacunga, *Correll & Alborno E-300* (LL, NY); Quitensian Andes, *Couthouy s.n.* (GH); Guápulo, *Heilborn 176* (G); E edge of Quito along river valley about 1 km N of the addition La Vicentina, *Humbles 6142* (F, NY); environs of Quito, *Jameson 829* (BM, NY, US, W); near Quito, *Lehmann 511* (G); Cantón Quito, Hacienda La Campiña near Nono, *Mexia 7663* (B, GH, NY); 2 km by road N and then turning S of Calicali, near Finca Yacucucho, *Spooner et al. 5000* (QCA, WIS); in Barrio Santa Rosa de Singuna, where road from Quito-Nono crosses Quebrada Singuna, just W of Quito, *Spooner & López 5008* (QCA, WIS); experimental plots of PRONATEC (Productos Naturales Ecuatorianos), Tumbaco, *Whalen & Velasco 829* (BH, NY).

Peru. AMAZONAS: Prov. Chachapoyas, Leimebamba, road to Chachapoyas, *Boeke 1968* (NY, WIS); Leimebamba, along river banks and in gorge of the Río Utcubamba, *Hutchison & Wright 5468* (F, M, NY, US, USM); Chilingote, cerca de Leimebamba, *Ochoa 1695* (US); Prov. Bongara, El Ingenio-Pomacochas, *Sagástegui 5966* (US); along roadside 20 km NE of Pedro Ruiz on road to Pomacochas, *Wasshausen & Encarnación 944* (NY, US, USM); jalca zone along Shipasbamba-Pomacocha trail, *Wurdack 1118* (NY, US, USM).—APURÍMAC: Prov. Abancay, cerca al río en Abancay, *Vargas C. 460* (F, WIS); Prov. Abancay, Cachora, *Vargas C. 9135* (W).—CAJAMARCA: cerca a Cutervo, *Ferreya & Acleto 15372* (US, USM); Prov. Chota, a 4 km de Querocoto, entre Llama y Huambos, *Leiva et al. 1367* (F, NY); Yatum, Socota, *Ochoa 11673* (US); Prov. Cutervo, Dist. Sócota, a 22 km sobre la carretera Cutervo-Sócota, *Sánchez Vega 2298* (US); arriba de Socota, siguiendo la ruta a San Andres, *Sánchez Vega et al. 5900* (NY); Huambos, *Soukup 4452* (US).—CUZCO: between Ollantaytambo and Torontoy, *Cook & Gilbert 829* (US); Prov. Urubamba, Cedrobamba, *Herb. Marin 1745* (F); Santuario Histórico Machu Picchu, camino Inca por puente Ruinas, *Núñez & Pyrke 9215* (NY); Prov. Anta, bajada de Wallpachaca, *Vargas C. 20553* (MA); Urubamba Valley, near Cedrobamba, *West 6461* (GH, UC).—HUANCAVELICA: Mantacra, Anco, *Hjerting 1063* (USM); entre las Haciendas Tocas y Pilcos, cerca de Colcabamba, *Ochoa 973* (GH, US); Salcabamba, *Stork & Horton 10276* (F, G); Uchuymarca, entre Mejorada y Anco, *Tovar 3319* (USM); Prov. Tayacaja, Andaimarca, entre Colcabamba y Surcubamba, *Tovar 1834* (USM).—JUNÍN: Calabazas, camino a Satipo, *Soukup 2874* (F).—PIURA: Shumbe, camino a Salalá-Las Huaringas, *Ferreya & Chanco 20429* (USM); Prov. Huancabamba, Sopalache a Jalca Chinguela, *Sagástegui et al. 10164* (NY).

Solanum ochranthum differs from *S. juglandifolium* in its markedly paler undersurfaces of the leaves, the more numerous interjected leaflets, the usually rotate, golden-yellow corollas, and the acute calyx lobes. The paler appearance of the abaxial leaf surface results from the dense pubescence as well as a paler lamina. Some specimens of *S. ochranthum* have slightly coarse adaxial leaf surfaces, but they are never as rough as in *S. juglandifolium*. Close examination with a dissecting microscope should allow the two taxa to be easily distinguished. For a discussion of the equivocal nature of the key in

Correll (1962), see *S. juglandifolium* (no. 3). *Solanum ochranthum* occurs at slightly higher elevations than does *S. juglandifolium*, particularly where the two taxa are sympatric.

Solanum ochranthum has large fruits (to more than 5 cm in diameter, see Plate 3N) with markedly woody walls at maturity, a character state unusual in *Solanum* in general, although *S. abitaguense* S. Knapp and *S. cucullatum* S. Knapp of section *Geminata* (G. Don) Walp. and *S. lycocarpon* Lam. (a prickly species from the cerrados of southern South America) also have very large fruits (Knapp 2002a).

The many varieties of *S. ochranthum* described by Bitter reflect the variability in leaf size and number of leaflets in the species, and the variability in pubescence throughout the range. Some populations are more pubescent than others, but the difference is only one of degree, and the character varies randomly throughout the distributional range of *S. ochranthum*.

Specimens of *S. ochranthum* labeled as *Jameson 829* at BM, NY, US, W [LL neg. 788: F] have been annotated as isotype material of *S. ochranthum* var. *connascens* by J. G. Hawkes, possibly due to their overall morphological similarity to the holotype at W. *Solanum ochranthum* is, however, remarkably uniform in the Ecuadorian Andes, so these sheets are possibly from another gathering made by William Jameson, a British ornithologist collecting in the Quito area in the 19th century. Jameson's localities are not consistent even within a single numbered collection; the holotype in W shows no locality data, whereas sheets of *Jameson 829* are labeled "Andes of Quito." These are very similar to the holotype of var. *connascens* and may be isotypes, but there is no specific evidence that specimens labeled *Jameson 829* were part of the same gathering as the type.

III. *Solanum* section *Lycopersicon* (Miller) Wettstein in Engler & Prantl, Nat. Pflanzenfam. IV, 3b: 24. 1891 [combination also proposed by Bitter, Bot. Jahrb. Syst. 54: 500. 1917]. *Lycopersicon* Miller, Gard. Dict. Abr. ed. 4, 1754. *Solanum* subgenus *Lycopersicon* (Miller) Seithe, Bot. Jahrb. Syst. 81: 204. 1962.—LECTOTYPE, designated by Britton and Brown, 1913: *Lycopersicon lycopersicum* (L.) H. Karsten [= *Solanum lycopersicum* L.]
Amatula Medikus, Malvenfam. 106. 1787.—TYPE: *Amatula flava* Medikus [= *Solanum lycopersicum* L.].
Lycopersicon subgenus *Eriopersicon* C. H. Müller, USDA Misc. Publ. 382: 16. 1940. *Solanum* series *Eriopersicon* (C. H. Müller) A. Child, Feddes Repert. 101: 223. 1990.—TYPE: *Lycopersicon peruvianum* (L.) Miller [= *Solanum peruvianum* L.].
Solanum section *Neolycopersicon* Correll, Contr. Texas Res. Found., Bot. Stud. 4: 39. 1962. *Lycopersicon* section *Neolycopersicon* (Correll) D'Arcy, Phytologia 51: 240. 1982. *Solanum* series *Neolycopersicon* (Correll) A. Child, Feddes Repert. 101: 224. 1990.—TYPE: *Solanum pennellii* Correll.

Perennial, biennial, or annual herbs or vines; branches usually sprawling or vining, robust to slender. Stems glabrous to variously pubescent, the trichomes always simple and usually uniseriate. Sympodial units di- or trifoliate (in the Galápagos trifoliate only). Leaves interrupted imparipinnate, sometimes with secondary and tertiary leaflet formation; estipulate, but occasionally with well-developed pseudostipules; leaflet margins entire to crenate to dentate to simply or doubly serrate to regularly or irregularly slightly or deeply lobed, forming secondary, tertiary, and occasionally quaternary leaflets (in *S. galapagense*); petiole usually shorter than the leaf blade. Inflorescences simple to 1–2- (3–4-) branched, bracteate or ebracteate; peduncle present, the flowers never basal. Flowers

actinomorphic or somewhat zygomorphic; calyx 5-parted, usually pubescent; corolla yellow, 5-parted, lobed to the base to about halfway to the base, lobes deltate to lanceolate; stamens 5, usually coherent in a tube with or without (*S. pennellii*) an apical sterile appendage, initially dehiscent by a small apical aperture and later by long introrse longitudinal slits that develop basipetally, or by an apical pore and later only slightly basipetally (*S. pennellii*); anthers yellow, with variously developed hairs laterally; ovary minutely glandular-villous to densely pubescent; style as long as or longer than the staminal column, exerted or included; stigma minute to capitate. Fruit a globose berry, green to whitish or brightly colored (red, yellow, or orange), usually 2-locular, but in cultivated species variously multilocular; calyx in fruit accrescent, lobes shorter than or longer than the mature fruit; seeds lenticular, appearing densely hairy owing to the elongate testal cell walls.

Many species originally described in the genus *Lycopersicon* used the Latinized variant spelling of the generic name *Lycopersicum*. This variant spelling is to be corrected to *Lycopersicon*; the Greek root of the name makes the *-on* ending originally used by Miller correct (see Article 60.1, McNeill et al. 2006). We have indicated original generic spellings, but many names were incorrectly listed in *Index kewensis* as *Lycopersicum*, and those wanting to use computerized indices are advised to search under both spellings. The two spelling variants are used somewhat randomly throughout the agricultural literature, but use of *Lycopersicum* does not constitute the coining of a new name.

Tournefort's *Lycopersicon* (1694) is a pre-Linnaean name and thus cannot serve as a basionym; the use of "*Lycopersicon* Tournefort" in "combinations" is incorrect.

"NEOLYCOPERSICON" GROUP

5. *Solanum pennellii* Correll, Madroño 14: 233. 1958. *Lycopersicon pennellii* (Correll) D'Arcy, Phytologia 5: 240. 1982.—TYPE: PERU. Lima: Quive, open rocky slope, 800–1000 m, 9 Jun 1925, *Pennell 14304* (holotype: PH-642829 [LL neg. 491: F! LL! UC!]).

Solanum pennellii var. *puberulum* Correll, Wrightia 2: 197. 1961. *Lycopersicon pennellii* var. *puberulum* (Correll) D'Arcy, Phytologia 5: 240. 1982.—TYPE: PERU. Ica: prov. Nazca, dry riverbed between Nazca and Palpa, 500–600 m, 21 Dec 1959, *Ferreya 14028* (holotype: LL! [LL neg. 854: LL! UC!]; isotypes: MO! UC! [LL neg. 484: F! GH! LL! UC!], USM!). (Specimens of plants cultivated from seeds of the type distributed under UC Davis No. 60 698-3: LL! [LL neg. 483: F! LL! UC!], UC! [LL neg., 485: F! GH! LL! UC!].)

Solanum pennellii var. *elachistus* C. Marticorena & M. Quezada, Gayana, Bot. 48: 125. 1991.—TYPE: CHILE. Región I (Tarapacá): Prov. Parinacota, camino de Arica a Zapahuira, Pampa Los Angeles, 1500 m, 18°29'S, 69°54'W, May 1989, *Hoffmann 89-13* (holotype: CONC!).

Spreading perennial herb, woody at the base, to 1 m tall, to 0.4–0.5 m in diameter. Stems 9–12 mm in diameter at base, although with some pith even in larger stems, brittle, yellowish green, sparsely to densely pubescent, the plants usually glutinous-viscous, the glandular trichomes always present, most frequently simple uniseriate 1–2-celled trichomes with a multicellular glandular head, sparsely to densely pubescent with 6–8-celled uniseriate simple trichomes 1.5–2.5 mm long, these with a unicellular glandular head in some populations, both laminar surfaces with an underlying velvety pubescence of

uniseriate simple trichomes to 0.1 mm long. Sympodial units 2-foliate; internodes 1–6 cm long. Leaves interrupted imparipinnate to imparipinnate, (1.5–) 3.5–13 cm long, (1.2–) 2.2–7.5 cm wide, yellowish green, pubescent like the stems, adaxially almost glabrous in some populations, the trichomes only on the veins and margins, abaxially the pubescence more abundant but usually the same as that of the adaxial face; primary leaflets 2–4 pairs, broadly elliptical to orbicular, apex rounded, base cordate, not markedly oblique, margin irregularly crenate to occasionally almost entire; terminal leaflet usually wider than long, 0.8–3 cm long, 0.8–4 cm wide, the petiolule 0.4–1.5 cm long; lateral leaflets 0.5–5 cm long, 0.4–4.5 cm wide, the petiolule 0.15–1 cm long; secondary leaflets absent; tertiary leaflets absent; interjected leaflets few but usually absent; petiole 0.5–4 cm long; pseudostipules present and well developed on all nodes, 0.5–1 cm long, 0.7–1.5 cm wide, orbicular, margins crenate. Inflorescences 4–11 cm long, simple or once-branched, with 6–15 flowers, bracteate at all nodes, bracts 0.2–1.5 cm long, 0.2–1.5 cm wide, margins crenate, peduncle 1–4 (–7) cm long, pubescent like the stems and leaves. Pedicels 1–2 cm long, articulated at the base. Buds 0.8–1 cm long, 0.4–0.5 cm wide, elongate-ellipsoidal, strongly curved, the corolla exerted more than halfway beyond the calyx just before anthesis. Flowers with the calyx tube ca. 5 mm long, lobes 4–5 mm long, 1–1.5 mm wide, triangular to spatulate, pubescent like the rest of the inflorescence, apex rounded; corolla 2–2.1 cm in diameter, pentagonal and slightly zygomorphic with the upper petal longer, golden-yellow, the tube 0.7–0.8 cm long, lobes 0.6–0.7 (–1) cm long, 0.5–0.6 (–0.9) cm wide, densely pubescent abaxially with weak uniseriate trichomes, these more abundant on the midveins and lobe tips, lobes slightly reflexed at anthesis; staminal column absent or only partially coherent with lateral papillae, strongly curved, filaments less than 0.5 mm long, united into a tube ca. 1 mm long, anthers 0.6–0.8 (–1) cm long, the upper two usually larger and the anther tube curved, sterile apical appendage absent, the tips of the anthers with a minute deltate appendage distal to the introrse pores; ovary globose, glabrous; style 0.9–1 cm long, ca. 0.5 mm in diameter, curved, finely pubescent in the basal 3/4, exerted 2–3 mm beyond the anthers; stigma capitate or slightly bifid, green. Fruit 1–1.3 cm in diameter, globose, 2-locular, green, sparsely to moderately pubescent with uniseriate simple trichomes with 4-celled and 1-celled glandular tips and eglandular trichomes ca. 0.5 mm long; fruiting pedicels 2–2.5 cm long, straight or slightly bent at the articulation; calyx lobes in fruit 9–10 mm long, 2–5 mm wide, spreading. Seeds 1.4–2.4 mm long, 0.7–1.2 mm wide, 0.5–0.6 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged (0.2 mm wide) at the apex and acute at the base. Chromosome number: $n = 12$ (LA0716, <http://tgrc.ucdavis.edu>). Plate 1M, Plate 2M, Plate 3M; Fig. 27.

Phenology. Flowers and fruits sporadically throughout the year in response to moisture, but with a flowering peak in October–November, during the wet, foggy season on the coast.

Distribution (Fig. 28). Northern Peru (Piura) to northern Chile (Tarapacá); dry rocky hillsides and sandy areas; sea level to 3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** Without locality, *Hutchison 3305* (MO, USM); without locality, 1909, *Weberbauer 5315* (F).—ANCASH: Prov. Casma, Km 249 Panamericana Norte, *Cerrate 5161* (USM); Prov. Santa, 6 mi oeste de Jimbe, *Rick SAL-440* (USM).—AREQUIPA: 20 km W of Caravelí, 5 km W of pass, *Erlenberg 8258* (MO); along Panamerican highway near sea level, between Chala and Atico, *Correll & Smith P-173* (LL); Prov. Caravelí, lomas de Capac, cerca a Chala, *Ferreyra 11532* (USM).—CAJAMARCA: El Portachuelo, between Ascope–Algarrobal, *Dillon & Sagástegui 6055* (F); El Balconcito (Ascope–San Benito), *Sagástegui et al. 9240* (F, MO); Prov. Contumazá, Algarrobal–San Benito, *Sagástegui & López M. 10493*

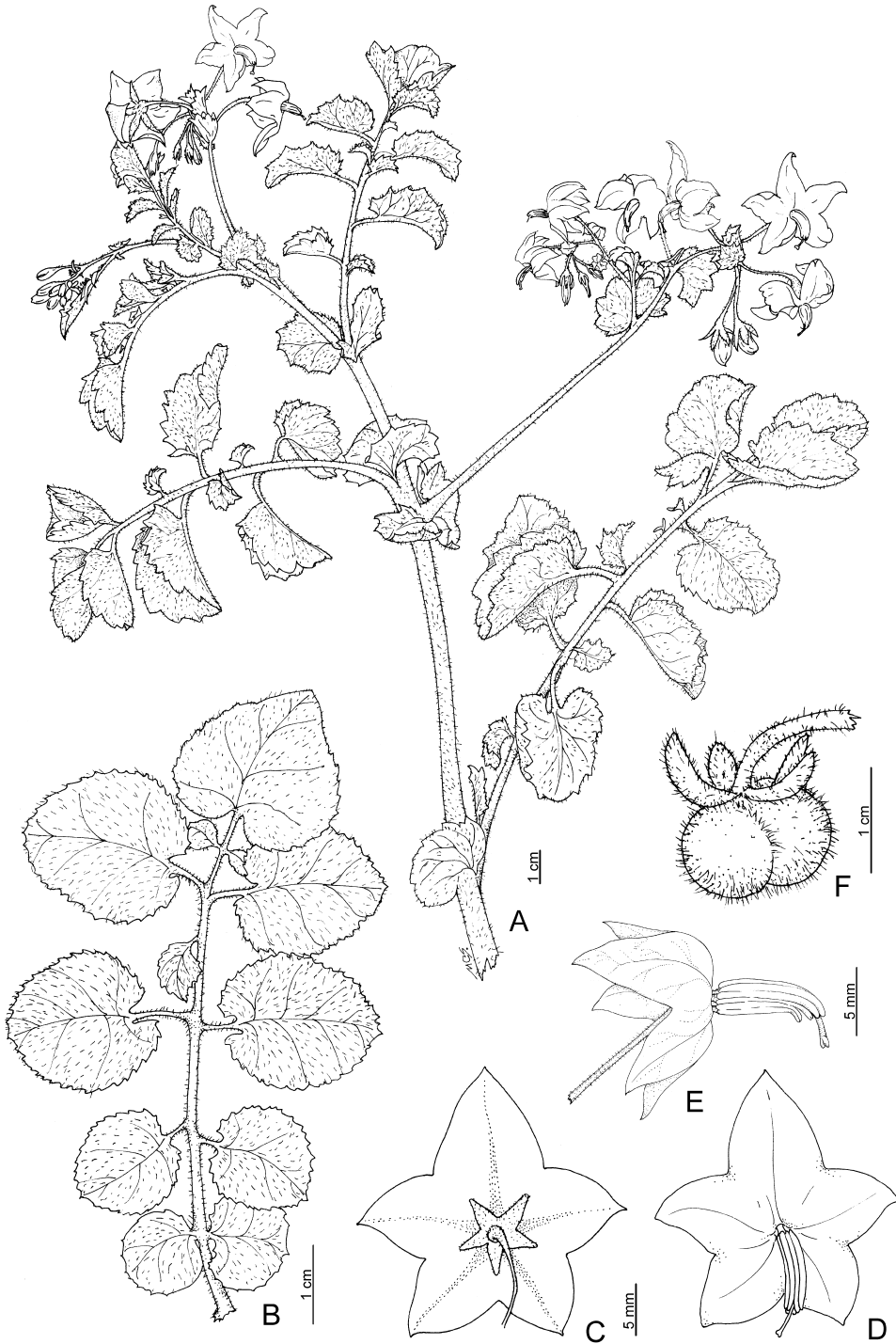


FIG. 27. *Solanum pennellii*. A. Branch. B. Leaf. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Fruit.

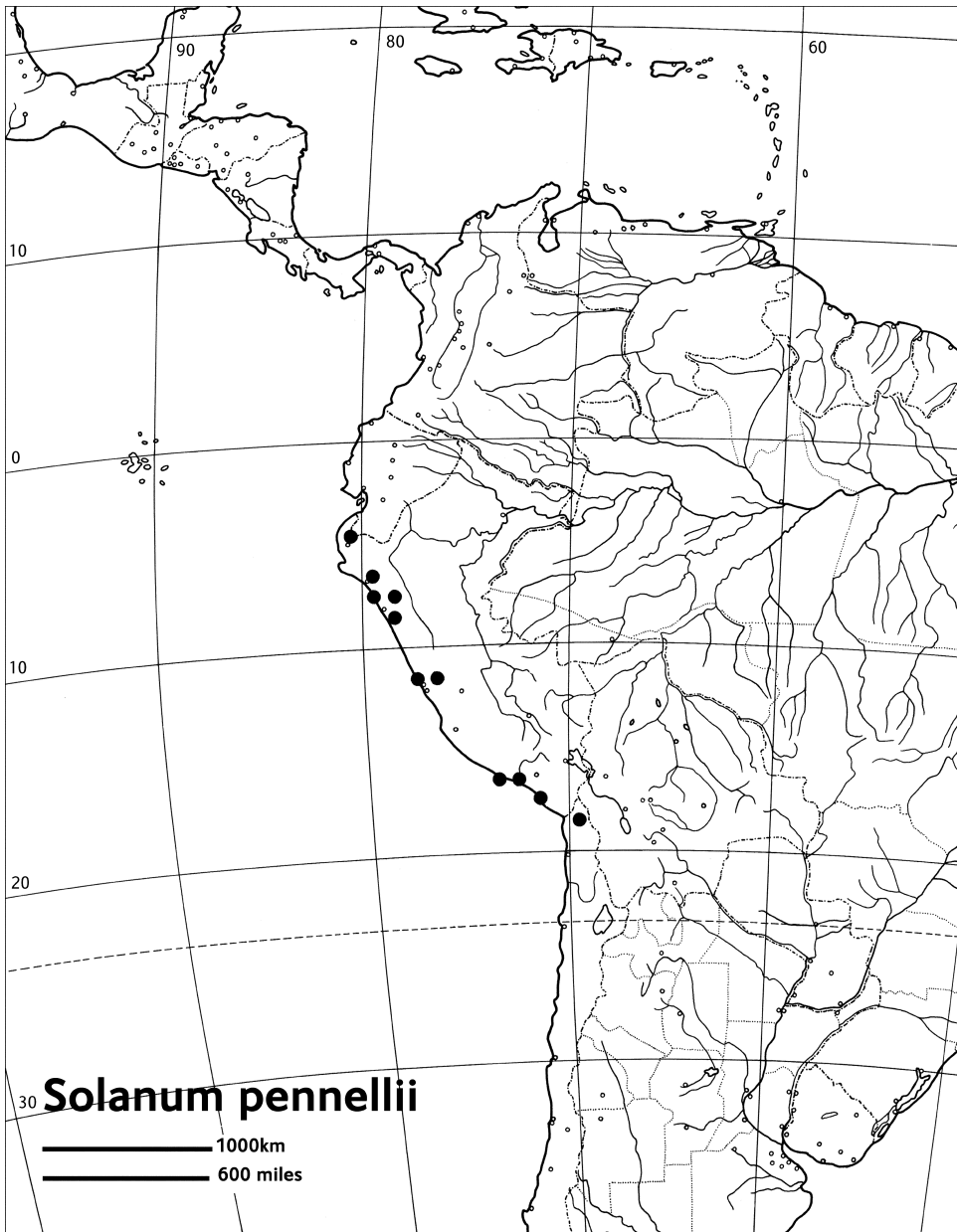


FIG. 28. Distribution of *Solanum pennellii*.

(F, MO); Ascope–Algarrobal, *Sagástegui & Mostacero 11338* (MO).—ICA: Km 14.2, Nazca–Puquio, *Baldeón Malpartida 899* (USM); cauce seco entre Nazca y Palpa, *Ferreya 14028* (MO); Quita Sol, on road to Castrovirreyña 30 mi from junction with Panamericana, *Rick et al. SAL-386* (USM); on road to Castrovirreyña 56 mi from junction with Panamericana, *Rick et al. SAL-387* (USM); Prov. Nazca, Panamericana Km 432, *Weigend & Förther 97/629* (HUT, M, USM).—LA LIBERTAD: alrededor de Shiran, *Leiva S. 768* (F, NY); Km 580, Cerro Cabezón, al norte de Trujillo, *Leiva S. et al. 2157* (F, HUT, M, NY); Prov. Virú, ruta canal de irrigación Chavimochic–Bocatoma, *Leiva S. et al. 2193* (F, MO); carretera Ascope–San Benito (Ascope), *López & Sagástegui 2539* (F); Prov. Trujillo, Barraza, *Sagástegui 7873* (F, GH, LL, MO); Pedregal, *Sagástegui 15290* (F, NY).—LAMBAYEQUE: Prov. Chiclayo, Cerro Reque, *Llatas Q. 762* (BM, MO); Cerro Roque, *Llatas Q. & Salazar 762* (USM).—LIMA: along road above Canta, *Correll et al. P-287* (LL 3 sheets); Chosica, cerca a Tiro al Blanco, *Ferreya 6107* (USM); cerca a Santa Rosa de Quives, *Ferreya 9007* (USM); Km 56, carretera Lima–Oroya, *Ferreya 9153* (USM); Prov. Huarochirí, Km 49–50, carretera central, Lima–Oroya, *Ferreya 10514* (USM); Chosica, *Ferreya 11088* (USM); Prov. Chancay, cerca a las Lomas de Chancayllo, entre Chancay y Lachay, *Ferreya 14235* (USM); entre Lurín y San Bartolo, *Ferreya 17961* (USM); carretera Panamericana, desvío a Punta Negra, *Ferreya 18053 A* (USM); road from Trapiche to Quilca, at ca. 6 km from Trapiche, *Hawkes et al. 4104* (C); Prov. Lima, 7 km NE of Trapiche, Canta Valley, *Hutchison 1013* (K, M, NY, S, US, USM); Loma de Pachacamac, *Lourteig 3267* (US); Km 71 from Lima to Canta, *Petersen & Hjerting 1154* (C); Had. Pisiquilla (family Pisiquera) 50 km E of Chancay along road to Pacaibamba, *Rick et al. SAL-354* (USM); 1 km al oeste de Espíritu Santo, Lima a 43 millas, *Rick & Rick SAL-366* (USM); 2 km E of Santa Rosa de Quives on roadside, on road to Canta, *Rick & Rick SAL-383* (USM); entre Capillucas y Pacarán, *Rick SAL-424* (USM); 1.1 mi al E de Santa Eulalia, *Rick SAL-451* (USM); 17.6 mi NE de Sayán, *Rick SAL-460* (USM); above Chosica, 42 km NE of Lima on the Carretera Central, *Ugent & Ugent 5266* (MO); Valle Chillón, *Velarde Núñez 872* (US); Prov. Canta, Quives, cerca al Santuario de Sta. Rosa, *Vilcapoma 282* (G); cerros al norte de Chosica, *Weberbauer s.n.* (USM); Prov. Yauyos, road from Pacarán to Yauyos, Km 34.2 after Pacarán, *Weigend et al. 7205* (BM); San Bartolo, *Zerpa 052* (USM).—MOQUEGUA: Prov. Mariscal Nieto, Quebrada Huaracane, norte de Moquegua, *Arakaki 181* (USM).—PIURA: Prov. Paita, Caleta Yacila, *Fernández et al. s.n.* (F, GH, HUT, LL, MO).

Solanum pennellii is easy to distinguish from all other tomato relatives by its compound leaves with almost orbicular leaflets and by the anther tube, composed of anthers connected by lateral hairs and lacking a sterile apical appendage. Carrizo García (2003) recognized *S. pennellii* in the genus *Solanum* but the other species of sect. *Lycopersicon* (all with a beaked staminal column) in the genus *Lycopersicon*. In contrast, D'Arcy (1982) placed *S. pennellii* in *Lycopersicon*. The spatulate calyx lobes and slightly zygomorphic flowers are also unique (among the tomatoes) in *S. pennellii*. Despite these distinctive characteristics, specimens of *S. pennellii* can be confused with *S. corneliomulleri*, especially when sterile or in fruit. *Solanum pennellii* never has the long glandular trichomes characteristic of *S. corneliomulleri*, but instead has a shorter, stickier pubescence. Pubescence morphs in *S. pennellii* have been described as subspecific taxa, but the differences are not consistent either geographically or in terms of habitat, suggesting the trait is of little taxonomic importance. Interestingly, in more densely pubescent individuals of *S. pennellii*, this increase in pubescence extends to the anthers (interlocking hairs) and may be of interest in further investigations of anther morphology in the groups (see Glover et al. 2004).

Solanum pennellii is an important component of the lomas vegetation (see Habitats and Distribution above), but also occurs in dry valleys along the western Andean slope. Blooming times of populations in the lomas and in other habitats appear to differ; the lomas populations bloom from September to November, coinciding with the foggy season on the Peruvian coast.

One TGRC accession of *S. pennellii* (LA716) has been important in the development introgression lines with *S. lycopersicum* cultivar M82 (see Eshed & Zamir 1994, 1995; http://zamir.sgn.cornell.edu/Qtl/il_story.htm). This resource has been critical to the

understanding of yield parameters (Eshed et al. 1996; Fridman et al. 2004) and of leaf dissection (Holtan & Hake 2003).

The type specimen of var. *elachistus* (*Hoffman 89-13*, CONC) is the only Chilean collection we have seen, but *S. pennellii* is certain to occur in more locations in Chile.

Cultivated accessions of *S. pennellii* from Colombia, Denmark, and the U.S.A. have been prepared as herbarium specimens; full details can be found on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>), and collectors and numbers are listed in the Index to Numbered Collections Examined.

“ERIOBERSICON” GROUP

6. *Solanum habrochaites* S. Knapp & D. M. Spooner, *Novon* 9: 375. 1999. *Lycopersicon hirsutum* Dunal, *Solan. Synopsis* 4. 1816, non *Solanum hirsutum* (Vahl) Dunal, 1813.—TYPE: ECUADOR. Loja: “hab. in agris Peruvianis prope Loxa,” *Humboldt & Bonpland s.n.* (holotype: P!; isolectotypes: F-fragment! MPU-fragment!).

Lycopersicon agrimoniifolium Dunal in A. DC., *Prodr.* 13(1): 24. 1852. *Lycopersicon hirsutum* var. *agrimoniifolium* (Dunal) Luckwill, *Univ. Aberdeen Studies* 120: 36. 1943. *Solanum agrimoniifolium* (Dunal) J. F. Macbride, *Field Mus. Nat. Hist. Bot. Ser.* 13: 159. 1962, non *Solanum agrimoniifolium* Rydberg, 1924.—TYPE: PERU. Without locality, *Ruiz & Pavón s.n.* (holotype: G!; isotypes: B [destroyed, F neg. 2595: GH! WIS!], F! MA! MPU-fragment!).

Lycopersicon hirsutum f. *glabratum* C. H. Müller, *U.S. Dept. Agric. Misc. Publ.* 382: 22. 1940 [name also proposed by C. M. Rick, Fobes & Tanksley, *Pl. Syst. Evol.* 132: 280. 1979]. *Lycopersicon hirsutum* var. *glabratum* (C. H. Müller) Luckwill, *Univ. Aberdeen Studies* 120: 36. 1943.—TYPE: ECUADOR. Chimborazo: 4 km W of Sibambe, in canyon, 5,800 ft, 20 Apr 1938, *Blood & Tremelling 638* (holotype: US-40278!).

Sprawling shrubs or vines, to 6 m long. Stems 2–5 (–10) mm in diameter, sparsely to densely pubescent, the less pubescent forms generally with sparser covering of the largest trichomes; trichomes of three types, the largest 2–4 mm long, 2–8-celled, uniseriate trichomes from a unicellular base, eglandular or with a minute glandular tip, the others 0.2–0.5 mm long, thin and weak-walled, with either a multicelled glandular tip or a minute glandular tip or eglandular, all trichomes with smooth, transparent cell walls. Sympodial units 3-foliolate; internodes 2–13 (+) cm long. Leaves interrupted imparipinnate, 7–30 (–36) cm long, 3–16 (–20) cm wide, sparsely to densely pubescent with a mixture of uniseriate trichomes, the longest 1–3 mm long, patent, 5–8-celled, arising from a stiff, multicellular base or from a unicellular base (primarily in the less-pubescent forms), eglandular or with a minute glandular tip, the rest 0.05–0.4 mm long, weak-walled and fragile, the tips either composed of a multicellular gland or a minute unicellular gland, or the trichomes eglandular, adaxial surface dark green, the long trichomes arising from the blade and the veins, abaxial surface paler, the long trichomes primarily from the veins, the veins dark abaxially in dry material; primary leaflets 3–5 pairs, decreasing in size towards the leaf base, narrowly elliptic to elliptic to sometimes ovate, apex acute to acuminate, base acute, oblique and extended basiscopically, margin regularly serrate to doubly serrate to occasionally almost entire; terminal leaflet 3–8.5 cm long, 1–5 cm wide, the petiolule 0.3–1 cm long; lateral leaflet 2–6.5 (–10) cm long, 0.7–2.5 (–7) cm wide, the petiolule 0.2–0.7

(–0.9) cm long, usually decurrent on the rachis basiscopically; secondary leaflets absent; tertiary leaflets absent; interjected leaflets 10–18, 0.5–1.2 cm long, 0.5–1.1 cm wide, sessile, opposite or subopposite to alternate, in sets of 2–4 between the primary leaflets; petiole (1–) 1.5–6 (–8) cm long; pseudostipules present and well developed at all nodes, 1–3 cm long, 1.4–4 cm wide, orbicular, margins serrate. Inflorescences 10–30 (–45) cm long, once-branched, with 20–30 flowers, bracteate, bracts ca. 1 cm long, 1 cm wide, decreasing in size towards the apex, the largest bract at the branching point, peduncle (2.5–) 6–15 cm long, pubescent like the stems, but with more glandular trichomes with multicellular heads. Pedicels (1–) 1.5–2 (–3) cm long, the articulation in the distal half. Buds 1.2–1.6 cm long, 0.5–0.6 cm wide, elongate conical, the corolla more than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube 1–1.5 mm long, lobes 7–12 mm long, 1.5–2 mm wide, narrowly elongate-triangular, densely pubescent with uniseriate trichomes like those of the inflorescence; corolla 2–4 (–5) cm in diameter, broadly rotate, deep golden-yellow, each lobe with a medial darker stripe, the tube (0.7–) 1–1.5 cm long, the free portion of the lobes 0.8–1 cm long, (0.5–) 1.2–1.5 cm wide at the base, the tips and midveins of the lobes densely pubescent with eglandular and glandular trichomes abaxially; staminal column 1–1.5 cm long, straight, filaments 0.5–1 mm long, anthers 0.75–1 cm long, equal, sterile apical appendage 0.3–0.5 cm long; ovary conical, densely to sparsely pubescent with uniseriate, patent trichomes 0.5–1 mm long; style 1.1–1.4 cm long, ca. 0.5 mm in diameter, glabrous in distal half, densely pubescent with trichomes like those of the ovary in the proximal half, usually exerted 1–5 mm (sometimes included in what are probably autogamous populations); stigma small, capitate, green. Fruit 1–1.5 cm in diameter, globose, 2-locular, pale green with a dark green stripe from apex to base, densely to sparsely pubescent with uniseriate, usually eglandular trichomes 1–3 mm long and shorter weak uniseriate trichomes ca. 0.4 mm long with a multicellular glandular tip; fruiting pedicels 1.1–2.4 cm long, strongly bent in towards the inflorescence axis at the pedicel articulation point; calyx lobes in fruit 17–25 mm long, 2–3 mm wide, enclosing the berry. Seeds 2.1–3.0 mm long, 1.0–1.6 mm wide, 0.5–0.7 mm thick, obovate, dark brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged (0.2 mm wide) at the apex and acute at the base. Chromosome number: $n = 12$ (LA1777, <http://tgrc.ucdavis.edu>). Plate 1L, Plate 2L, Plate 3L; Fig. 29.

Phenology. Flowers and fruits throughout the year; most flowering collections are from March, but this is almost certainly a collecting artifact.

Distribution (Fig. 30). Western slopes of the Andes from Central Ecuador to Central Peru, occasionally occurring in lomas formations in northern Peru; in a variety of forest types, from premontane forests to dry forests; 400–3600 m elevation.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** CHIMBORAZO: Alausí, *Asplund 6783* (S); Sibambe, *Balls B-7075* (E, F, K, UC, US); Naríz del Diablo, *Böcher et al. 161* (S); Cañón of the Río Chanchan near Huigra, *Camp 3060* (NY, S, US); on edge of Alausí, *Correll E-328* (NY); Alausí, *Gabinete de Botánica Universidad Central 2209* (M); Cubijes, *Fagerlind & Wibom 830* (NY, S); canyon of Río Sibambe, affluent of Río Chanchan, *Fosberg & Giler 22625* (NY, US); vicinity of Huigra, mostly on the hacienda de Licay, *Hitchcock 20337* (GH, NY, US); Huigra, about 1 km N of town, by the river, *Madsen 36840* (AAU, MO, NY); vicinity of Huigra, mostly on the hacienda de Licay, *Rose & Rose 22174* (NY, US); NW of Huigra, *Schimpff 448* (M, MO, Z); W of Riobamba, along Río Guano, *Schimpff 927* (Z).—GUAYAS: Cerro Azul, along ridge line N of Chongón, Km 22 Guayaquil–Salinas, N 10 km to crest the following crest to Km 16, *Dodson et al. 9672* (MO); Chongón, Hacienda Cerro Azul, *Harling et al. 9507* (MO); prope Guayaquil, *Mille 976* (F); Cantón Guayaquil, Bosque Protector Cerro Blanco, carretera a Salinas Km 15, *Rubio et al. 1768* (BM, MO, NY, QCNE); Bosque Protector Cerro Blanco, carretera Guayaquil–Salinas, Km 15, *Tipaz et al. 812* (MO).—LOJA: Loja, climbing in *Agave*

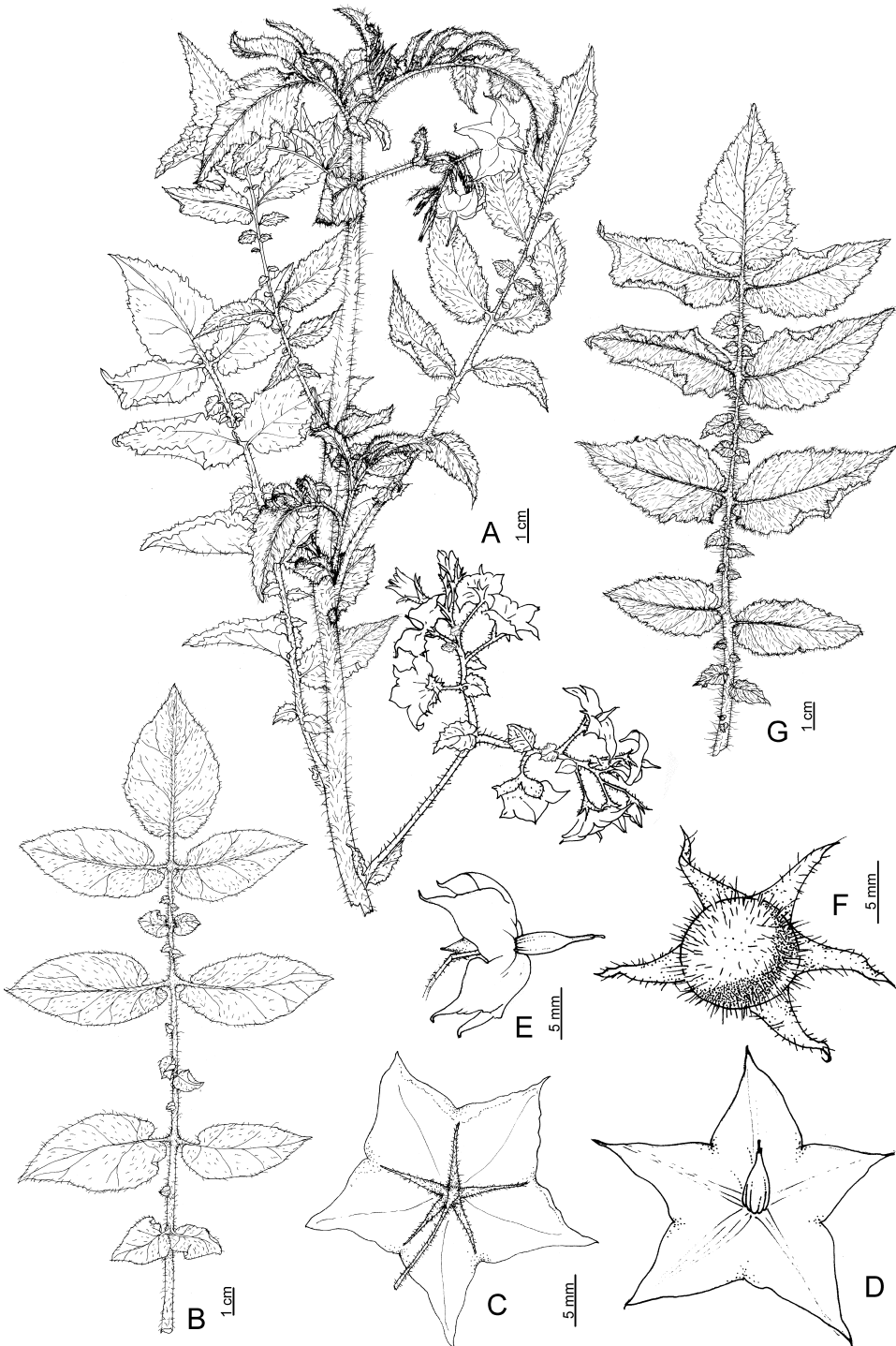


FIG. 29. *Solanum habrochaïtes*. A. Branch. B. Leaf from a "glabrous" population. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Fruit. G. Leaf from a "typical" populations.

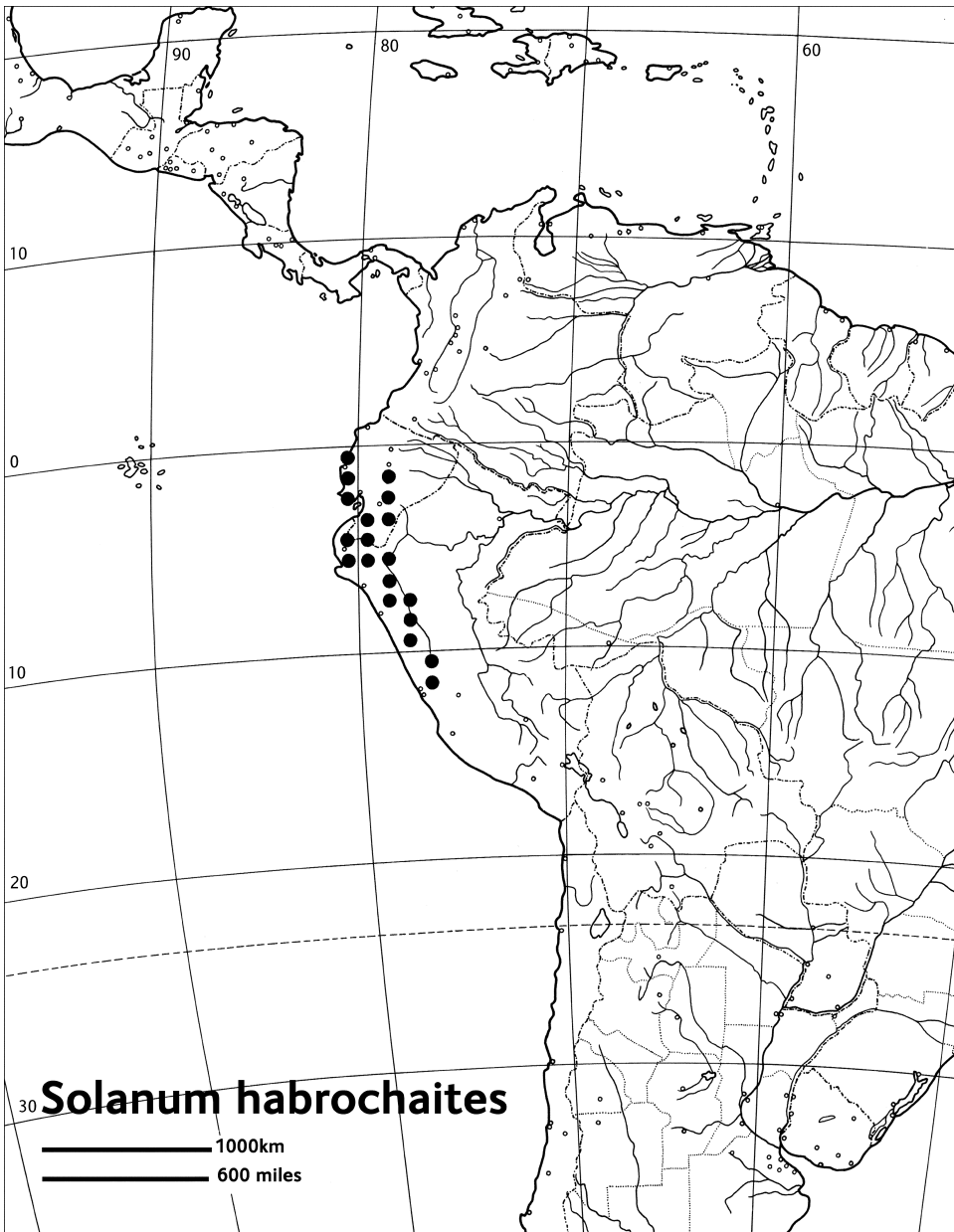


FIG. 30. Distribution of *Solanum habrochaites*.

hedge, *Asplund 17909* (B, K, NY, S); Valle Seco de Playas, Catacocha, *Acosta Solís 8000* (F); along road on Hacienda Colca, between Catamayo and Gonzanama, *Correll E-411* (NY); Loja, *Cornejo & Bonifaz 1912* (NY); near top of Loja Valley, *D'Arcy 16500* (MO); near top of Catamayo Valley on Portovelo side, *D'Arcy 16501* (MO); 10 km N of Saraguro, on Lugma Huaycu, *Ellemann 91705* (NY); Argelia, *Espinoza 378* (NY); camino Loja–Cuenca, apenas afueras de Loja, *Gavilanez et al. 374* (QCA); ca. 3 km above Macará, *Harling & Andersson 18294* (MO); Mollococha, ca. 10 km W of Vilcabamba, *Harling & Andersson 21780* (NY); at crest above Macará on road to Loja, *Harling & Andersson 22626* (NY); Celica–Alamor road, at crossing with Río Alamor, *Harling & Andersson 22212* (NY); ca. 30 km S of Catamayo on road to Cariamanga, *Knapp & Mallet 6253* (BH, K, QCA, QCNE, US); ca. 2 km N of Loja, *Knight 759* (WIS); around Loja, *Lehmann 7816* (US); road Loja–Catamayo, in the Catamayo Valley, *Øllgaard et al. 90672* (BM, NY); vicinity of Loja, *Penland & Summers 1129* (F, GH, US); La Merced, *Vanden Eynden 2* (QCA); Tambo Negro, *Vanden Eynden & Cueva 461* (NY).—MANABÍ: Cantón Jipipapa, Parque Nacional Machalilla (límites), 2–3 km E de Guale, orillas del Río Ayampe, *Yáñez et al. 1273* (QCA).—TUNGARAHUA: near Baños, *Blood & Tremelling 648* (GH, NY); “in Andibus Ecuadorensibus,” *Spruce 5169* (BM, E, F, G, GH, K 4 sheets, NY, OXF, W); Baños, *Spruce 5169* (K); Huataxi, *Spruce 5169* (K). **Peru.** About Purrucho, *Matthews 995* (BM, E 3 sheets, K); without locality, 1834, *Matthews 995* (BM); without locality, 1840, *Matthews 3245* (BM); without locality, *Raimondi 12662* (USM); without locality, *Soukup 1307* (F).—AMAZONAS: near Huamachuco, *Blood & Tremelling 112* (NY); encima de Leimebamba, *Ferreya 15470 A* (USM); encima de Leimebamba, *Ferreya 15519* (UC, US, USM); arriba de Balsas, hacia Calla-Calla, *Ferreya 20764* (USM); Tingo–Kuelap, *Kahn & Moussa 2771* (USM); Prov. Bongara, Leimebamba–Celendín, *Kahn & Moussa 2920* (USM); 8 km E of Chachapoyas, along road to Mendoza, *King & Bishop 9166* (K, MO, US); entre Chachapoyas y Jazán, *Sánchez Vega et al. 2241* (NY); Prov. Cajatambo, Baños de Churín, *Sandeman 5372* (K); between Samanaga and Leimebamba on Chachapoyas–Celendín road, *Smith & Cabanillas 7159* (MO, USM); Prov. Chachapoyas, Río Utcubamba, *Soukup 4904* (US).—ANCASH: Prov. Corongo, Mirasanta, *Cavero B. 129* (K); Prov. Yungay, Chilca, cerca de Llanganuco, *Cerrate 7770* (USM); on bank just above Pariacoto, *Correll & Smith P-944* (F, LL, NY); on banks about 15 km above Pariacoto, *Correll & Smith P-946* (LL, NY, US); about 5 km below Jupash, *Correll & Smith P-948* (LL); Pampas Grande, camino entre San Juan y Huiñapajatum, *Díaz S. 1985* (F, MO, NY); cerca Punta Caillán entre Casma y Huaráz, *Ferreya 14399* (MO, USM); entre Huaylas y Callejón, *Ferreya 14593* (USM); road from Yungay to Parque Nacional Huascarán, ca. 1 km E of Yungay, *Gentry et al. 37375* (BM, MO, NY, USM); Chacchan, hacienda 24 mi W of Huaráz, *Macbride & Featherstone 2554* (F); Chacchan, 46 mi E de Casma, *Rick SAL-446* (USM); opuesto a Cajacay, 54 mi E de Pativilca camino a Conococha, *Rick SAL-450* (USM); Prov. Aija, Huaylán, *Ochoa 11691-A* (US); entre Paria y Toclla, *Proaño s.n.* (USM); Prov. Huaráz, Dist. Pariacoto, on Huaráz–Casma road, *Saunders 1340* (F, K); Prov. Huaylas, Huascarán National Park, Quebrada Santa Cruz between Lago Santa Cruz Chico and Cashapampa exit, *Smith et al. 9338* (F, MO, USM); entre Carhuas y Carás, *Vargas C. 10278* (WIS).—CAJAMARCA: fields E of Cajamarca, *Blood & Tremelling 135* (F); 29 km from Cajamarca on road to Chilette, *Correll & Smith P-847* (LL, NY); environs of Huancabamba, trail to Cataluco from Huancabamba, *Davis & Turner 680* (F); ca. 30 km S of Cajamarca and 7 km N of San Juan, *Dillon & Whalen 4067* (F); Prov. Santa Cruz, Distrito Catache, upper Río Zaña Valley, ca. 5 km above Monte Seco on path below campsite, *Dillon et al. 4442* (F, NY); cerros de Cajamarca, *Ferreya 3172* (US, USM); debajo de Cascas, *Ferreya 19915* (USM); 45 km E of bridge over Río Maichil, *Gentry et al. 61411* (F, MO, NY, USM); Prov. Hualgayoc, Hacienda Taulis, vicinity of the Casa Hacienda, *Hutchison & Bismarck 6326A* (BR, C, E, F, M, NY, S, TEX, UC, US, WIS); Platanar, arriba de Cascas, *Leiva 726* (F, NY); Prov. Chota, Cásupe (Chota), *Llatas Q. 695* (MO, NY); Cajamarca, *Matthews 4235* (K); Distrito Cascas, carretera Cascas–El Chorrillo, slopes along road, *Merello et al. 1057* (MO); entre San Pablo–San Miguel, *Mostacero L. et al. 2783* (HUT); Juke, *Ochoa 13962* (US); without locality, *Raimondi 3243* (USM); Nanchó, *Raimondi 3077* (USM); Monte de Nancho, *Raimondi 3186* (USM); Prov. Contumazá, Cascas, *Raimondi 7951-a* (USM); Prov. Contumazá, Cascas, *Raimondi 8250* (USM); cuesta entre Cascas y Contumazá, *Raimondi 1489* (USM); without locality, *Rick 135* (USM); Gavilán pass on road to Cajamarca, *Rick 137* (USM); 18 km de la Panamericana, vía a Jaén, *Rick 151* (USM); Rupe, 13.5 mi S of Chilette along road to Contumazá, *Rick & Rick SAL-436* (USM); Lllame, Cutervo, *Sandeman 4083* (K); Tronache, Cruz Grande–Contumazá, *Sagástegui et al. 8998* (F, MO, PMA); Prov. Contumazá, alrededores de Guzmango, *Sagástegui et al. 9776* (HUT, MO, NY); Rupe–Contumazá, *Sagástegui et al. 9814* (HUT); Prov. San Pablo, Dist. San Bernadino, abajo de Sangal, *Sánchez Vega & Zarpán Arias 621* (F); Dist. San Bernadino, San Pablo Quebrada el Chingo, *Sánchez Vega & Zarpán Arias 643* (F); Dist. San Pablo, sobre El Molino, *Sánchez Vega 673* (F); Cerro Huacarís, valle de Cajamarca, *Sánchez Vega et al. 715* (NY); Dist. San Juan, carretera San Juan–Huacraruco, *Sánchez Vega 720* (F); alrededores de San Juan, ruta a Pacasmayo, *Sánchez Vega 1962* (F, NY); entre Lllamo y Chongoyape, sobre carretera Chiclayo–Chota, *Sánchez Vega 2346* (F, US); terrenos de la Ciudad Universitaria, *Sánchez Vega et al. 4975* (F); ca. 3 km (por aire) ENE de Montesecco, *Santisteban &*

Guevara, B. 0131 (BM, F, NY); Monte Seco, *Soukup* 3880 (COL, F, US); Prov. Cajamarca, 2 km from Baños del Inca along road to Llacanora, *Stevens* 22019 (F, MO, NY, USM); Prov. Cutervo, Río Susce Valley, W of So-cota, *Stork & Horton* 10111 (F, US); 30 km SW of Cajamarca on road to Chilete, *Whalen & Dillon* 892 (BH, NY, USM); without locality, *Woytkowski* 5 (F, US, USM).—LA LIBERTAD: Cerro Campana, *Angulo* 1234 (F); Cerro de Campanas, *Boeke* 1748 (MO, NY, Z); loma of Cerro Campana, ca. 16 km N of Trujillo on Pan-American highway, *Dillon et al.* 4665 (F); Prov. Huamachuco, Río Marañón canyon, 5 km below Aricapampa, *Hutchison et al.* 6208 (F, K, M, MO, NY, UC, US, USM); Cerro Campana, *Raimondi* 2101 (USM); alrededores de Cascas, *Rick* 125 (USM); Prov. Contumazá, Chimbilas, entre Cascas y El Molino, *Ochoa & Salas* 16229 (US); arriba de Piedra Grande, ruta a Samne, *Leiva et al.* 755 (F, NY); Cerro Campana, *Leiva & Suárez* 1880 (F); Cerro Campana, *Leiva & Quipuscoa* 2075 (F, NY); Prov. Santiago de Chuco, Picomas, Cachicadán, *López M. & Sagástegui* 8426 (F, MO, NY, PMA); Cerro Campana, *Mostacero L.* 651 (HUT, MO, NY); Cerro Campana, *Mostacero L. et al.* 705 (F); Shiran, *Mostacero L. et al.* 729 (MO, NY); Cerro Cabezón, *Mostacero L. et al.* 756 (F); Prov. Trujillo, Barraza, *Sagástegui & López* 7846 (F, GH, LL, MO, NY); Prov. Otuzco, alrededores de Sinsicap, *Sagástegui et al.* 15695 (F, NY).—LAMBAYEQUE: about 22 km from Olmos on road to Jaén, *Correll & Smith P-798* (LL), *Correll & Smith P-833* (LL); a 16 km al Marañón, cerca al cruce, entre Olmos y Abra de Porculla, *Ferreyra* 9129 (USM); carretera al Marañón, Paso de Porculla, al 20 km del cruce, *Ferreyra* 9138 (MO, USM); Prov. Ferreñafe, subiendo a Incahuasi cerca a Moyán, *Ferreyra* 20890 (USM); road to Jaén, Km 28 E of Olmos, vicinity of the restaurant El Salvador, *Hutchison & Wright* 4428 (F, K, M, MO, NY, UC, US, USM); Prov. Lambayeque, Olmos, *Llatas Q. et al.* 634 (USM); Sapotal, Motupe, *Llatas Q.* 667 (HUT); cerca del Km 12 de la ruta Olmos–Porculla, *Ochoa* 14495 (F, NY, US); road from Olmos to Abra Porculla, *Plowman* 5514 (GH); 20 km al E de Chongoyape, *Rick* 148 (USM); Ñaupe, *Torres Arce* 5 (USM).—LIMA: W of Río Canta, *Blood & Tremelling* 20 (GH, NY); along Río Canta, *Blood & Tremelling* 21 (F, MO), *Blood & Tremelling* 22 (MO), *Blood & Tremelling* 23 (GH, NY); Prov. Yauyos, Atjsacki, cerro al E de Tupe, *Cerrate & Tovar* 1054 (USM); Capia, abajo de Tupe, *Cerrate* 1087 (USM); Prov. Huarochirí, Cornaya, abajo de Huarochirí, *Cerrate* 1780 (MO, USM); Huariquiña, *Cerrate et al.* 8857 (USM); along river in dense shubbery below Canta, *Correll et al. P-279* (LL, NY); along stone fence between Yaso and Canta, *Correll et al. P-281* (LL, NY); Prov. Huarochirí, Km 69–70 de la carretera central, cerca a Surco, *Ferreyra* 2031 (US); Prov. Huarochirí, Km 74 de la carretera central, cerca a Surco, *Ferreyra* 4075 (US, USM); cerca a Canta, *Ferreyra* 7266 (M, US, USM); Prov. Huarichirí, cerca a Matucana, carretera Lima–La Oroya, *Ferreyra* 7601 (US, USM); cerca a los baños de Churín, *Ferreyra* 8016 (USM); abajo de Canta, *Ferreyra* 8116 (G, USM); camino a Canta, *Ferreyra et al.* 8707 (USM); abajo de Florida, *Ferreyra* 18421 (MO, USM); entre Quives y Canta, *Ferreyra* 19099 (USM); along Río Chillón, below Obrajillo, *Pennell* 14431 (F, NY); Prov. Canta, Canta, *Petersen & Hjerting* 1189 (C); 1 km W of Espíritu Santo, in gravel washes of Río Lurio, *Rick & Rick SAL-368* (USM); 23.4 mi NE de Sayán, *Rick SAL-462* (USM); vicinity of Lima, *Rose & Rose* 18589 (NY); Prov. Canta, encima de Acos, margen izquierda del Río Chancay, *Ochoa & Salas* 14624 (F, US); Canta, *Soukup* 2826 (F, GH, US); Surco, *Soukup* 3707 (F); Canta, *Soukup* 3952 (S); Prov. Cajatambo, Ambar, *Stork* 11463 (GH, K, UC); Prov. Yauyos, Atjsacki, cerro al E de Tupe, *Tovar & Cerrate* 475 (USM); Prov. Huarochirí, Cornaya, abajo de Huarochirí, *Tovar & Cerrate* 1558 (USM); valle de Chillón, Santa Rosa de Quives, *Velarde Núñez* 876 (US); Canta, Obrajillo, *Velarde Núñez* 947 (US); arriba de Santa Rosa de Quives, *Vilcapoma* 88 (USM); Lachaqui, *Vilcapoma* 107 (G, USM); puente de Collo y Arahua, *Vilcapoma* 143 (USM); Prov. Lima, La Molina, *Vilcapoma* 525 (USM); Lima–La Oroya, Matucana, *Weberbauer* 79 (G); road from Pacarán to Yauyos, Km 62 after Pacarán, *Weigend et al.* 7230 (BM).—PIURA: caserío El Paisaje, Cerro Caballito, *Arakaki* 024 (USM); abajo de Canchaque, *Ferreyra* 3154 (MO, US, USM); entre Serrán y Canchaque, *Ferreyra* 10786 (USM); entre Palambra y Faique, *Ferreyra et al. s.n.* (USM); at Tres Acequias, 10 km N of Huancabamba, *Hutchison & Wright* 6600 (F, UC, US, USM); Palambra, Canchaque, *López M. et al.* 8794 (HUT); bajando de Ayabaca al Río Quiroz, *Ochoa s.n.* (DS); Prov. Huancabamba, Canchaque, *Ochoa* 11635 (NY, US); Cashacoto, Distrito Sondor, *Sagástegui et al.* 8171 (MO, NY, US); Palambra, *Soukup* 4288 (US).—TUMBES: Prov. Zarumilla, El Caucho, Dtto. Matapalo, *del Carpio* 778 (USM); Pampas de Hospital, entre el cruce al puesto de vigilancia Cabo Cotrina y El Caucho, *Díaz & Vásquez* 3113 (NY, USM); Cerros de Amotape, Quebrada Los Conejos and adjacent ridges, ca. 25 km SE of Cherrelrique, *Gentry & Díaz* 58304 (BM, NY); region below El Caucho, *Plowman* 5492 (GH, USM).

Solanum habrochaites is very easy to distinguish from all other wild tomatoes. The sterile apical appendage of the anthers is extremely long and thin, and the broadly rotate, shallowly lobed, golden-yellow corolla is distinctive. Pubescence in *S. habrochaites* is quite variable, and Müller's (1940a) forma *glabratum* includes plants that are not strictly glabrous, but only have fewer of the longest trichomes on all parts (Fig. 29). The

characteristic strong odor of *S. habrochaites* is caused by secretions from glandular trichomes with a 4-celled head.

Solanum habrochaites is part of a basal polytomy in the tomatoes, or, in some analyses (see Species Relationships above), is a member of a clade containing *S. chilense*, *S. peruvianum*, *S. huaylasense*, and *S. corneliomulleri*.

Solanum habrochaites grows at high elevations in the northern range of sect. *Lycopersicon* (only *S. pimpinellifolium* is found as far north); it also occurs in the coastal lomas habitats in northern Peru. Some plants (e.g., *Rubio et al. 1768* from southern coastal Ecuador) that are smaller than more typical specimens of *S. habrochaites* can be confused with *S. corneliomulleri*, but the straight anther tube with a long, narrow “beak” and largely non-glandular pubescence aid identification. These smaller flowered plants are likely to be self-compatible, because small flowers are correlated with self-compatibility in other species (Georgiady & Lord 2002). The breeding system of *S. habrochaites* is self-incompatible allogamous, with some self-compatible populations (probably those with smaller flowers) at the margin of the range (Rick et al. 1979).

One TGRC accession of *S. habrochaites* (LA1777) has been important in the development of introgression lines with *S. lycopersicum* cultivar E-6203 (LA4024) (see <http://tgrc.ucdavis.edu/>). These lines have been useful in the production of genetic maps, and to explore resistance to insects and the improvement of yield and quality.

Solanum habrochaites has been collected from plants cultivated in Colombia, Iraq, and the U.S.A.; these collections are cited in the Index to Numbered Collections Examined, and full details can be found on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>).

7. *Solanum chilense* (Dunal) Reiche, *Anales Univ. Santiago* 124: 742. 1909. *Lycopersicon chilense* Dunal in A. DC., *Prodr.* 13(1): 24. 1852.—TYPE: CHILE. Region II (Antofagasta): Cobija, 1839, *Gaudichaud s.n.* (holotype: G-DC! [F neg. 6761: F! GH! WIS!]); isotypes: B [destroyed, F neg. 2726: F! GH! WIS!], F-fragment! G! [F neg. 2726: F! GH! WIS!], MPU-fragment! P! WIR!).

Lycopersicon atacamense Philippi, *Fl. Atacam.* 42. 1860.—TYPE: CHILE. “Paposo, Diciembre 1853, Tilopozo,” *Philippi s.n.* (lectotype, here designated: SGO-055593! [Departamento de Investigaciones Agrícolas neg. s.n.: F! GH!]).

Lycopersicon bipinnatifidum Philippi, *Anales Mus. Nac. Santiago de Chile, Bot.* 1891: 63. 1891.—TYPE: CHILE. Region I (Tarapacá): Chacarillas, Mar 1885, *Rahmer s.n.* (lectotype, here designated: SGO-055599!; isolectotype: SGO-042822! Departamento de Investigaciones Agrícolas neg. s.n.: F! GH!]).

Lycopersicon puberulum Philippi, *Anales Mus. Nac. Santiago de Chile, Bot.* 1891: 64. 1891. *Lycopersicon peruvianum* subsp. *puberulum* (Philippi) Luckwill, *Univ. Aberdeen Studies* 120: 30. 1943.—TYPE: PERU. “Tacna e seminibus e P. Ortega communicat culta Santiago,” Dec 1887, *Philippi s.n.* (lectotype, here designated: SGO-042824!; isolectotype: WU!).

Robust perennial herbs, erect becoming decumbent, woody at the base, to 1 m tall, to 1 m in diameter, occasionally spreading in rocky habitats. Stems 8–12 mm in diameter at base, grayish, densely velvety-pubescent with simple uniseriate eglandular white trichomes to 0.5 mm long (with a unicellular base and bent at the tip), much more abundant on young stems, and scattered short, uniseriate glandular trichomes with 4-celled heads and 8-celled heads amongst the glandular trichomes. Sympodial units 2- (rarely 3-) foliate; internodes

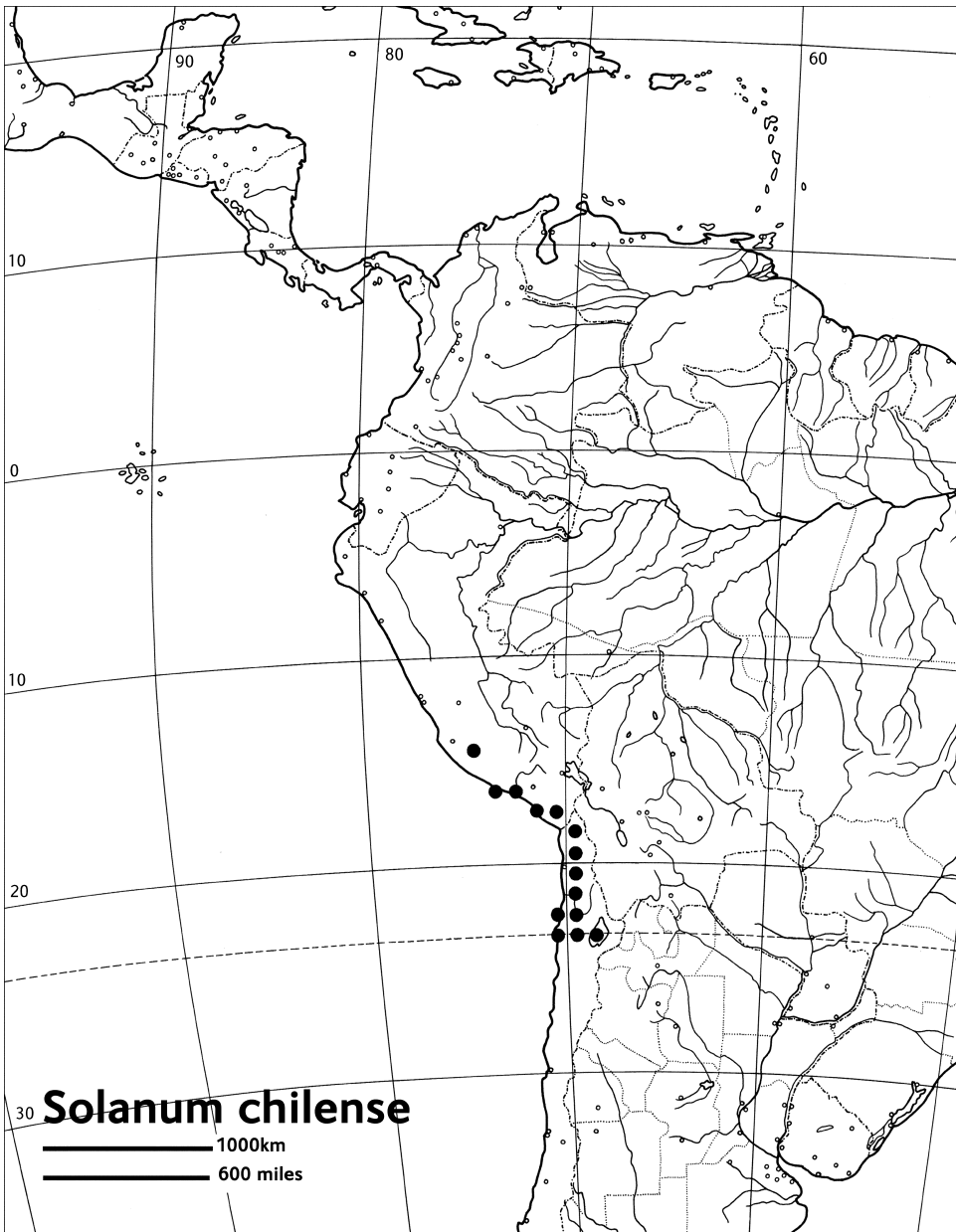
1–2 (–5) cm long. Leaves interrupted imparipinnate, (5–) 7–13 (–20) cm long, (2–) 2.5–6.5 (–10) cm wide, grayish green, densely white velvety-pubescent with simple uniseriate trichomes like those of the stems, the glandular trichomes fewer, abaxially more densely pubescent and paler; primary leaflets 5–7 pairs, not markedly decreasing in size towards the base, narrowly elliptic, apex broadly acute to acuminate, base decurrent on the rachis, oblique and the lamina broader basiscopically, the leaflets essentially sessile, margins irregularly crenate to deeply and irregularly lobed nearly to the leaflet rachis, especially basally; terminal leaflet narrower and larger than the laterals, 2–4 cm long, 0.7–2.5 cm wide, the petiolule absent, base decurrent along the rachis; lateral leaflets 1.2–3.5 cm long, 0.5–1.3 cm wide, the petiolule absent (or to 0.1 cm long in some specimens with especially large leaves); secondary leaflets often present acropically on the largest laterals, 0.2–0.4 cm long, 0.05–0.2 cm wide, decurrent on the leaflet rachis; tertiary leaflets absent; interjected leaflets 10–20, often 2 pairs between sets of lateral leaflets, 0.2–0.5 cm long, 0.1–0.3 cm wide, sessile and the base decurrent on the rachis, crowded between the lateral leaflets; petiole 0.5–2 cm long; pseudostipules present and well developed on most nodes, 0.5–0.9 cm long, 0.4–1.2 cm wide, margin irregularly crenate. Inflorescences 6–20 (–30) cm long, usually once-branched and regularly bifurcate, occasionally with additional bifurcations apically and the inflorescence to 3-branched, with (12–) 20–50 flowers, ebracteate or with most nodes bracteate, bracts 0.5–1.2 cm long, 0.2–0.5 cm wide, margins irregularly crenate, peduncle 4–15 cm long, densely white velvety-pubescent like the stems and leaves. Pedicels 1–1.6 cm long, articulate in the distal half. Buds 9–12 mm long, 3–4 mm wide, conical, straight, the corolla slightly less than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube 0.5–1 mm long, lobes 5–6 mm long, 1–2 mm wide, lanceolate, densely white velvety-pubescent on both surfaces; corolla 2–2.6 cm in diameter, rotate-stellate, bright yellow with medial darker midveins on each lobe, the tube 0.4–0.5 (–0.7) cm long, lobes 1–1.2 cm long, 0.5–0.6 (–0.7) cm wide, sparsely pubescent abaxially with simple white uniseriate trichomes to 0.25 mm long, these more abundant on the midveins, margins and tips, reflexed at anthesis; staminal column 0.9–1.3 cm long, straight, filaments less than 0.5 mm long, anthers 0.5–0.8 cm long, equal, sterile apical appendage 0.15–0.2 cm long; ovary globose, glabrous or minutely puberulent at the apex; style 1–1.4 cm long, ca. 0.5 mm in diameter, densely white-pubescent in the basal half, exerted 1.5–2 mm from the staminal column; stigma capitate, green. Fruit 1–1.5 cm in diameter, globose, 2–5-locular, greenish white with purple stripes at locule margins when ripe, sparsely to moderately pubescent with weak-walled, simple, white, uniseriate trichomes 0.5–0.7 mm long, these occasionally with unicellular glandular heads, the surface also occasionally with short uniseriate glandular trichomes with 4-celled heads, the fruit surface minutely papillate; fruiting pedicels 1.4–2.1 cm long, straight or slightly bent at the articulation; calyx lobes in fruit 12–16 mm long, 1.5–2 mm wide, narrowing at the base of the sinus, loosely investing the berry or spreading. Seeds 2.2–3.2 mm long, 1.2–1.6 mm wide, 0.5–0.7 mm thick, obovate, dark brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or sometimes shaggy, narrowly winged (ca. 0.2 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (LA1029, <http://tgrc.ucdavis.edu>). Plate 1K, Plate 2K, Plate 3K; Fig. 31.

Phenology. Flowers and fruits throughout the year, but with a distinct flowering peak in September and October.

Distribution (Fig. 32). On the western slopes of the Andes from the Department of



FIG. 31. *Solanum chilense*. A. Branch. B. Fruit. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Leaf.

FIG. 32. Distribution of *Solanum chilense*.

Tacna in southern Peru to northern Chile; in hyper-arid rocky plains and coastal deserts; sea level to 3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** AREQUIPA: Prov. Caraveli, Pan-American highway Km 648 S of Lima, 2 km S of Chala, Lomas de Capac, *Hutchison 1295* (F, G, M, MO, NY, S, UC, USM); without locality, *Isern 2063* (F); Prov. Camana, Río de Lomas, Acará, *Weberbauer 5736* (F, US).—AYACUCHO: along road between Nasca and Puquio, *Correll & Smith P-145* (LL).—MOQUEGUA: carretera Moquegua–Torata, *Arakaki 143* (USM); sitio arqueológico Camata, carretera a Omate, *Arakaki 172* (USM); Prov. Ilo, carretera Ilo–Toquepala, *Arakaki 332* (USM); 20 km W of (below) Moquegua, *Blood & Tremelling 514* (UC); E of Moquegua, *Blood & Tremelling 515* (GH); Prov. Mariscal Nieto, along road from Cuajone to Otorá, *Dillon et al. 3302* (F, NY, USM); 5 km Moquegua N to Río Osore, *Ellenberg 4173* (MO); cerca de Moquegua, *Ferreya et al. 19823 A* (USM); on the Pan-American highway, 2 km N of Río Moquegua, 7 km N of Moquegua, *Hutchison & Wright 7143* (C, E, F, G, GH, K, M, MO, NY, UC, WIS); Mt. Estuquiña, NW of Moquegua, *Weberbauer 7449* (F, US); Prov. Moquegua, Km 1126 Panamericana Sur, 14 km N of Moquegua turnoff, *Weigend & Förther 97/857* (F, M).—TACNA: Tacna 14 km hacia el mar, valle seco del Río Caplina, *Beck 2022* (F, LPB, NY); W of Tacna, *Blood & Tremelling 508* (GH), *Blood & Tremelling 509* (MO); Pampa Mogollo, ca. 18 km S of Tacna on Pan-American highway near Tacna airport, *Dillon et al. 4754* (BM, F, HUT, NY, USM); Prov. Tacna, Hacienda Puquio–Tacna, *Ferreya et al. 8609* (USM); cerca a Tacna, camino a Arica, *Ferreya 12528* (MO); on the road to Tarata, 35.5 km N of Tacna, *Hutchison & Wright 7160* (K, M, NY, UC, US); near Tacna on road to Calientes, *Metcalf 30349* (G, GH, US); Arica, *Née 731(345)* (MA); Prov. Tarata, NE of Tacna on Tarata road, *Tien Wei Yang 731295-1* (USM). **Chile.** Without locality, *Anon. s.n.* (BM); without locality, 2 Feb 1885, *Philippi s.n.* (SGO); without locality, *Philippi s.n.* (BM).—REGION I (TARAPACÁ): 8 km W de Chusmiza, inland from Iquique, *Aronson 7749* (CONC, MO); camino desde Cuesta de Cardones a Putre, *Arroyo 84–507* (CONC); Prov. Parinacota, Putre, *Belmonte 97033* (CONC); 87 km S of southern Pica junction, 109 km S of Parque del Tamarugal, 55 km N of Quilagua, *Dillon & Dillon 5702* (F); Prov. Iquique, 63 km from the Panamericana towards Mamiña, Quebrada Guataguata, small valley to the orographic left side of the road, *Egglie et al. 2734* (B, CONC, SGO, Z); Quebrada de Taltal, *Garaventa 4452* (CONC); Cuesta de Copaquilla, valle de Lluta, *Garaventa 5487* (CONC); Cuesta El Aguila, Valle de Lluta, *Garaventa 5575* (CONC); Putre, Cordillera de los Andes, CH11, road to Putre at Km 102, *Gardner & Knees 6258* (E); Arica, *Jaffuel 1647* (CONC); Arica, Camarones–Guamarane, *Kuschel s.n.* (SGO); Quebrada de Coscaya, *Larraín s.n.* (CONC); Mamiña, *Larraín 97667* (CONC); Putre, *Levi Heins s.n.* (CONC); Alarceca, *Levi Heins 144* (CONC); Putre, *Levi Heins 213* (CONC); Mamiña, *Lüerde Gunckel s.n.* (CONC); camino de Arica al Portazuelo de Chapiquiña, Km 50, *Martcorena et al. 5* (CONC); Azapa, *Martcorena et al. 279* (CONC); camino de Huara a Cancosa, Km 80, *Martcorena et al. 290* (CONC); camino entre Zapahuira y Arica, Quebrada Cardones, *Matthei & Rodríguez 337* (CONC, MA), *Montero O. 6191* (CONC, G 3 sheets); Iquique, Mamiña, *Montero O. 6342* (CONC); Iquique, Termes de Calamiña, *Montero O. 12048* (CONC); Arica, Poconchile, *Montero O. 12032* (CONC); Arica, valle de Azapa, *Montero O. 12059* (CONC); camino al Portezuelo de Chapiquiña, *Navarro s.n.* (CONC); región de Mamiña, camino de Mamiña a Macaya, *Niemeyer s.n.* (CONC); camino a Guatacondo, Km 22, *Ricardi & Parra 11* (CONC, G); salar de Llamara, 5 km antes de la junta camino a Guatacondo, *Ricardi et al. 22* (CONC); cerca de al cuesta de El Aguila, *Ricardi et al. 27* (CONC); camino al Portezuelo de Chapiquiña, a ca. 40 km arriba de Arica, *Ricardi et al. 28* (CONC); entre Guatacondo e Iguá, *Ricardi & Parra 35* (CONC); camino a Chapiquiña, quebrada frente a la Central Hidroeléctrica, *Ricardi et al. 289* (CONC); Pachica, *Ricardi et al. 353/1* (CONC), *Ricardi et al. 353/2* (CONC); camino entre Pachica y Poroma, *Ricardi et al. 372* (CONC); Termas de Mamiña, *Ricardi et al. 1357* (CONC); Arica, Quebrada Honda, Arica–La Paz, *Ricardi 3356* (CONC); FF.CC. de Arica–La Paz, Puquios, Km 108–106, *Ricardi 3527* (CONC); Iquique, Alto Hospicio, *Ricardi 3585* (CONC); Azapa, Prov. Tacna, Depto. Arica, *Ricardi & Martcorena 4692* (CONC); camino de Azapa a Chapiquiña, Km 43, *Ricardi & Martcorena 4719* (CONC); Codpa, *Ricardi & Martcorena 4774* (CONC); camino a Caritaya, Km 63, *Ricardi & Martcorena 4781a* (CONC); Azapa, *Pfister 9474* (CONC); Quebrada Vitor, Puente Chaca, *Rodríguez & Rivera 2* (CONC); Quebrada Cardones, *Schlegel 4849* (CONC); Tacna–Arica region, *Shepard 281* (CAS, F, GH, K, NY, US); Arica, Azapa Valley, *Skottsberg & Skottsberg 1072* (F, S); Cuesta de Ocsaya, near Arica, *Troll 3219* (B, M); entre Arica y Zapahuira, Quebrada Seca, *Villagrán et al. 1055* (CONC); trayecto entre Quebrada de Guasquiña y Chusmiza, *Villagrán et al. 9030* (CONC); trayecto entre Berengueta y Quebrada Camiña, *Villagrán et al. 9250* (CONC); Prov. Arica, Azapa, *Werdermann 706* (B, BM, CAS, CONC, E, F, G, GH, K, M, MO, NY, S, UC, US, Z); Valley of Azapa, *Zöllner 9610* (CONC, MO).—REGION II (ANTOFAGASTA): Lomas de Taltal, near road from Taltal to the Panamericana, *Ackermann 459* (BM); Socaire, *Anon. s.n.* (K); Peine, *Anon. s.n.* (SGO); camino de San Pedro de Atacama a Paso Jama, *Arroyo et al. 97127* (CONC), *Arroyo et al. 97159* (CONC), *Arroyo et al. 97168* (CONC); camino a Guaitiquina, Quebrada Honda, *Arroyo et al. 97788* (CONC); camino desde San Pedro de

Atacama hacia el Paso Jama, *Baeza et al.* 421 (CONC); Quebrada Paposo, 9 km de Paposo, *Biese* 398 (A); Prov. Loa, Opache, 8 km al SW de Calama, *Biese* 2241 (SGO); Río Loa, 18 km al W de Calama, *Biese* 2178 (SGO); Prov. Taltal, 15 km al N de Taltal, *Biese* 2472 (SGO); playa al 40 km al S de Paposo, *Biese* 2276 (B, SGO); Prov. Tocopilla, Cobija, Quebrada Agua Cañas, *Biese* 2797 (SGO); Quebrada Peralito, Paposo, Rte. 1, 50 km N of Taltal, *Billiet & Jadin* 5547 (BR, MO); Quebrada Bandurrias, Rte. 1, 30 km N of Taltal, *Billiet & Jadin* 5562 (BR); Quebrada los Peralitos, *Brinck s.n.* (SGO); near San Pedro de Atacama along Río Salado, trail of Llano de Pajonales, *Charpin et al.* 23534 (G); Cobija, Iquiqui et Arica “Peruviae meridionalis,” *Cuming* 935 (E, K); Quebrada San Ramón, ca. 6 km E of Taltal, *Dillon & Teillier* 5203 (F); ca. 20 km N of Taltal along road to Paposo, *Dillon & Tiellier* 5252 (F); Quebrada los Zanjones, 5 km SW on road (B-900) to Cifuncho, 15 km SW of Taltal, *Dillon et al.* 5495 A (F); Cerro Perales, ca. 5 km E of Taltal, *Dillon et al.* 5518 (F); Quebrada Paposo, ca. 5–12 km E of Caleta Paposo, *Dillon et al.* 5560 (F); quebrada 2–3 km N of Tocopilla, above old Caleta Duen-des just N of railway switchback, *Dillon & Dillon* 5710 (F); near Taltal, *Grandjot & Grandjot s.n.* (CONC); Quebrada San Ramón, al norte de Taltal, *Hoffmann* 208 (CONC); Antofagasta, Taltal, *Gardner & Matthews* 119 (E); Prov. Antofagasta, Salar de Atacama, Peine, *González & Böhme s.n.* (SGO); Prov. Antofagasta, 10 km N of Taltal, *Grau* 2138 (BM, M); Tocopilla, *Gülland s.n.* (CONC); Toconao on Laguna Lejía, *Hellwig* 5242 (G); 6 km al norte de Taltal, *Hartmann s.n.* (CONC); Quebrada Taltal, at junction of roads 2 km W of Breas and 18 km E of Taltal, *Hutchison* 391 (UC, US); Taltal, *Jaffuel & Pirion* 950 (CONC); Tocopilla, *Jaffuel* 1045 (GH); Tocopilla, *Jaffuel* 2252 (CONC); Quebrada de Carmelita, *Jiles* 5328 (CONC, G); Quebrada de Taltal, *Jiles* 5473 (CONC); vicinity of Paposo, Quebrada de Guanillo, above Posada (=Agua de Arriba), *Johnston* 5589 (GH); Cerro Perales (Cerro de Hueso Parado of Philippi), near Taltal, along trail to Caleta de Hueso Parado, *Johnston* 5607 (GH); Peine, *Klohn s.n.* (SGO); Quebrada de Paposo, *Léon* 22 (CONC); Tocopilla, *López M. s.n.* (CONC); Prov. Antofagasta, a 22 km al S de la Mina Santo Domingo, *Loyola* 94-3 (CONC); camino de Toconao a Tal-abre, Quebrada de Chiqueros, a 16 km de Toconao, *Matthei & Rodríguez* 199 (CONC); camino de Tocopilla a María Elena, a 2 km de Tocopilla, *Matthei* 477 (CONC); Taltal, Quebrada Taltal, *Montero O.* 2882 (CONC, G); Taltal, *Montero O.* 6302 (CONC); Taltal, *Montero O.* 11245 (CONC); Quebrada del Tucucaro, *Moreira et al.* 124 (SGO); Quebrada Río Seco, fondo quebrada lateral, *Moreira et al.* 211 (SGO); Quebrada Río Seco, *Moreira et al.* 229 (SGO); 5 km SE of Taltal, serpentine outcrops along the road in Quebrada Taltal, *Morrison* 17090 (G, GH, K, MO, UC); Socaire, *Munizaga A. s.n.* (CONC); Río Salado, Puente del Diablo, *Navas B.* 2049 (CONC); Quebrada Medano, Paposo Cota, *Niemeyer s.n.* (CONC); without locality, *Philippi s.n.* (US); Playa de la Victoria, 3 km al N del Puerto de Taltal, *Pisano V. & Bravo F.* 211 (SGO); Campamento entre Calama y San Pedro de Atacama, *Pisano V. & Venturelli E.* 1763 (SGO); Toconao, *Pisano V. & Venturelli E.* 1901 (SGO); Km 8.5 del camino al sur, *Prenafeta s.n.* (CONC); Quebrada Chapcase, 7 km al N de Tocopilla, *Quezada & Ruiz* 9 (CONC, G, M); camino a Mina Mantos de la Luna, faldeos escarpados a orillas del camino, *Quezada & Ruiz* 23 (CONC); frente a Chaleta Chinos, aluvión arrastrado desde Quebrada Tres Higueras, *Quezada & Ruiz* 39 (CONC); Quebrada Portezuelo, *Quezada & Ruiz* 223 (CONC, M); Quebrada Bandurrias, entre Taltal y Paposo, *Quezada & Ruiz* 226 (CONC, G); 19 km N of Taltal towards Paposo, *Rechinger & Rechinger* 63585 (W); Quebrada de San Ramón, *Ricardi & Parra* 7 (CONC); camino de Tocopilla a la Quebrada de Mamilla, *Ricardi et al.* 1064 (CONC, G); Taltal, *Ricardi et al.* 1088 (CONC); Taltal, Quebrada Anchuña, *Ricardi* 2556 (CONC); Taltal, Quebrada Changos, *Ricardi* 2571 (CONC); Quebrada Paposo, Agua Perales, *Ricardi* 2599 (CONC); Taltal, Quebrada El Nueve, *Ricardi* 2708 (CONC); Tocopilla, Cuesta Barriles, *Ricardi* 3026 (CONC); Quebrada de Camarones, *Ricardi* 3488 (CONC); Paposo, *Ricardi & Marticorena* 4637/1022 (CONC); Prov. El Loa, 14 km al N de Socaire, a los pies del cerro entrando al Salar de Atacama, *Rodríguez & Ruiz* 3748 (CONC); Paposo, *Ruelle* 361 (BR); Quebrada Mamilla, *Schlegel* 7705 (CONC); 11 km N of Taltal, *Smith* 24 (SGO); 4 km NE of Talabre, small slot canyon, *Smith* 26 (SGO); NE of Calama, along the road from near Chui Chui to Caspana, ca. 38–39 km from the Calama–Chui Chui road, *Taylor & Pool* 11539 (MO); Tocopilla, Cerro Mamilla, *Teillier* 429 (CONC, SGO); Cerro Perales, NE de Taltal, *Teillier* 599 (NY); Quebrada de Taltal, *Teillier et al.* 2634 (F); Quebrada los Yales, Paposo, *Torres s.n.* (SGO); trayecto desde el camino bifurcación a Talabre y el poblado de Talabre, *Villagrán et al.* 9301 (CONC); ca. 10 km E of Taltal road along R.R., quebrada to the N, *Worth & Morrison* 15812 (G, GH, K, UC); Toconao, Salar de San Pedro de Atacama, *Zöllner* 1354 (CONC).—REGION III (ATACAMA): hills S of Taltal, *Beetle* 26178 (G, K, MO, UC); en el lugar denominado “Casa de Válvulas” en el camino de Chui-Chui a San Pedro de Atacama, *Garaventa* 4281 (CONC).

Solanum chilense is remarkably uniform morphologically and relatively easy to distinguish from its close relatives (*S. huaylasense*, *S. peruvianum*, *S. corneliomulleri*) by its densely grayish pubescent stems and leaves, straight anther tubes, and long, erect peduncles. It is, however, extremely similar to *S. huaylasense* from Ancash in northern Peru,

with which it shares the elongate peduncle and branched inflorescence but not the densely canescent pubescence; in general, the flowers of *S. chilense* are larger than those of *S. huaylasense*.

Rick and Lamm (1955) undertook a broad series of crossing studies in order to test whether or not *S. chilense* deserved specific status. They concluded that *S. chilense* should be recognized as a distinct species, because it could not cross easily with other species, has a distinctive morphology, and occurs at the southern range of wild tomatoes.

B. Igc (pers. comm.) has discovered populations of *S. chilense* in the region of Tal-tal in northern Chile that are markedly different in some key genetic factors. Herbarium specimens, however, do not show substantial morphological differences from other populations throughout the range of the species and appear to be identical to *S. chilense* in all major respects. These populations merit further study.

Philippi (1860) cited two localities (Paposo and Tilopozo) in the protologue of his *Lycopersicon atacamense*. The only extant original material at SGO, here chosen as lectotype, is a single specimen with a label in Philippi's hand noting both localities. In the protologue of *Lycopersicon puberulum*, Philippi states only "in Peruvia australiore," but the sheet in SGO, designated here as lectotype, has more complete information, cited above.

We have examined a single specimen of *S. chilense* cultivated and collected in Germany; full details are available on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>).

8. *Solanum huaylasense* Peralta, Syst. Bot. 30: 429. 2005.—TYPE: PERU. Ancash: trail to cave across Río Santa from Mancos, 9 Apr 1970, *Smith & Blas 4889* (holotype: USM!; isotypes: F! US!).

Sprawling perennial herbs, woody at the base, to 1 m tall, to 1 m in diameter. Stem 7–10 mm in diameter at base, green, minutely puberulent with simple, uniseriate, stiff 1–2-celled trichomes with unicellular bases mixed with scattered simple uniseriate glandular trichomes with 4-celled heads, glabrescent in age, all trichomes less than 0.5 mm long. Sympodial units 2-foliolate (rarely 3-foliolate); internodes 2–6 cm long. Leaves interrupted imparipinnate, 3.5–13 (–16) cm long, 1–6 (–8) cm wide, bright green, minutely pubescent with stiff simple uniseriate trichomes like those of the stems, pubescence more abundant abaxially, especially along the veins; primary leaflets 3–7 pairs, gradually becoming smaller towards the base of the leaf, subopposite to alternate, narrowly elliptic, apex acute to acuminate, base truncate, more or less oblique basiscopically, margin deeply and irregularly lobed to occasionally almost entire in some leaflets; terminal leaflet 1.2–2.5 cm long, 0.4–1.5 cm wide, the petiolule 0.2–0.5 (–1) cm long, apex acute to acuminate; lateral leaflets 0.7–2.5 cm long, 0.3–1.2 cm wide, the petiolule 0–0.5 (–1) cm long, usually decurrent on the rachis basiscopically; secondary leaflets occasionally present in some leaflets, especially acroscopically, 0.3–0.5 cm long, 0.25–0.4 cm wide, sessile and decurrent on the leaflet rachis; tertiary leaflets absent; interjected leaflets (0–) 3–12 (–20), 0.2–0.5 cm long, 0.1–0.4 cm wide, sessile and decurrent on the main leaf rachis, often 2 sets of unpaired interjected leaflets between each set of primary lateral leaflets; petiole 1–4 (–6) cm long; pseudostipules present or absent, if present then present on most nodes, 0.3–0.4 cm long, 0.2–0.3 cm wide. Inflorescences (6–) 12–30 cm long, once-branched, usually regularly bifurcate, with 8–30 flowers, ebracteate or bracteate on most nodes from the base, bracts 0.2–0.6 cm long, 0.1–0.4 cm wide, the largest bract at the bifurcation and first nodes, peduncle 5–15 cm long, minutely pubescent like the stems,

with more prominent and numerous glandular trichomes especially at the apex. Pedicels 0.8–1.6 cm long, articulated in the distal half. Buds 1–1.2 cm long, 0.4–0.5 cm wide, narrowly conical, straight or curved at the very tip, the corolla more than half exerted beyond the calyx just before anthesis. Flowers with the calyx tube ca. 0.5–1 mm long, the sinuses often hyaline, the calyx lobes 2.5–5 mm long, 1–1.5 mm wide, lanceolate or in some populations (Río Fortaleza) the tips rounded, minutely pubescent like the rest of the inflorescence with short, simple uniseriate 1–2-celled white trichomes; corolla 1.8–2.5 cm in diameter, stellate, yellow, the tube 0.2–0.5 cm long, lobes 1–1.5 cm long, 0.3–0.7 cm wide, uniformly and sparsely pubescent abaxially with 1-celled uniseriate trichomes, these not more abundant along the midveins, the lobe tips elongate and acuminate, reflexed at anthesis; staminal column 1–1.2 cm long, straight or curved, filaments less than 0.5 mm long, anthers 0.4–0.6 cm long, equal, sterile apical appendage 0.15–0.4 cm long; ovary conical to globose, minutely and sparsely pubescent with simple trichomes at the apex; style 0.8–1.2 cm long, ca. 0.5 mm in diameter, sparsely pubescent in the basal half, exerted 0.5–1.7 mm beyond the staminal column; stigma capitate, green. Fruit 1–1.4 cm in diameter, globose, 2-locular, green with a dark green or purple stripe from apex to base at maturity, sparsely pubescent with weak-walled simple uniseriate trichomes to 0.5 mm long and occasionally also with minute glandular trichomes with 4-celled heads; fruiting pedicels 1–2 cm long, straight or slightly incurved towards the inflorescence axis; calyx lobes in fruit 11–16 mm long, 1.5–2 mm wide, spreading in some populations (Fortaleza) the lobe tips recurved. Seeds 2.4–3 mm long, 1.1–1.5 mm wide, 0.5–0.6 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged at the apex and acute at the base. Chromosome number: $n = 12$ (LA1982, <http://tgrc.ucdavis.edu>). Plate 1H, Plate 2H, Plate 3H; Fig. 33.

Phenology. Flowers from March to May; fruiting material has been collected from May to August.

Distribution (Fig. 34). Peru, on the rocky slopes around Callejón de Huaylas along the Río Santa in the Department of Ancash and in the adjacent Río Fortaleza drainage; 1700–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** ANCASH: Huallanca 5 km hacia Caraz, Callejón de Patos, *Beck 7906* (F, LPB, NY); near Km 290, on road from Conococha to coast, *Correll & Smith P-977* (F, LL); road from Pativilca to Conococha, *Gentry et al. 37473* (MO, USM); Prov. Recuay, Ditto. De Marca (Marahuay), *Gómez 134* (USM); Prov. Bolognesi, Valle de Fortaleza, *Ferreyra 16885* (USM); Prov. Corongo, Tres Cruces, desvío La Pampa–Sihuas, *Leiva et al. 843* (F); Prov. Huaylas, cerca de Shupluy, camino a Cueva Guitarrero, *León et al. 4874* (BM, USM); road from Huallanca to Yanac, near Yanac, *Weigend et al. 2001/185(5018)* (BM).

Solanum huaylasense is a member of a clade containing *S. chilense*, *S. corneliomulteri*, and *S. peruvianum* s.str. (+ in some analyses *S. habrochaites*). It is most similar to *S. chilense*, from which it differs in its less pubescent (green) leaves and slightly smaller flowers. The two species share an elongated peduncle and a bifid inflorescence. Populations from Río Fortaleza (in the Callejón de Huaylas) are slightly more pubescent than the others, and have curved buds and recurved calyx lobe tips in fruit. *Solanum huaylasense* grows on rocky cliff faces at the type locality (B. León, pers. comm.) and is generally a straggling, lanky plant in the wild. It is known from few collections in a narrowly circumscribed region and should be given priority in conservation efforts.

Solanum huaylasense was previously considered part of the broadly defined *S. peruvianum* s.l. Appendix 4 lists all the TGRC accessions (LA numbers) previously included

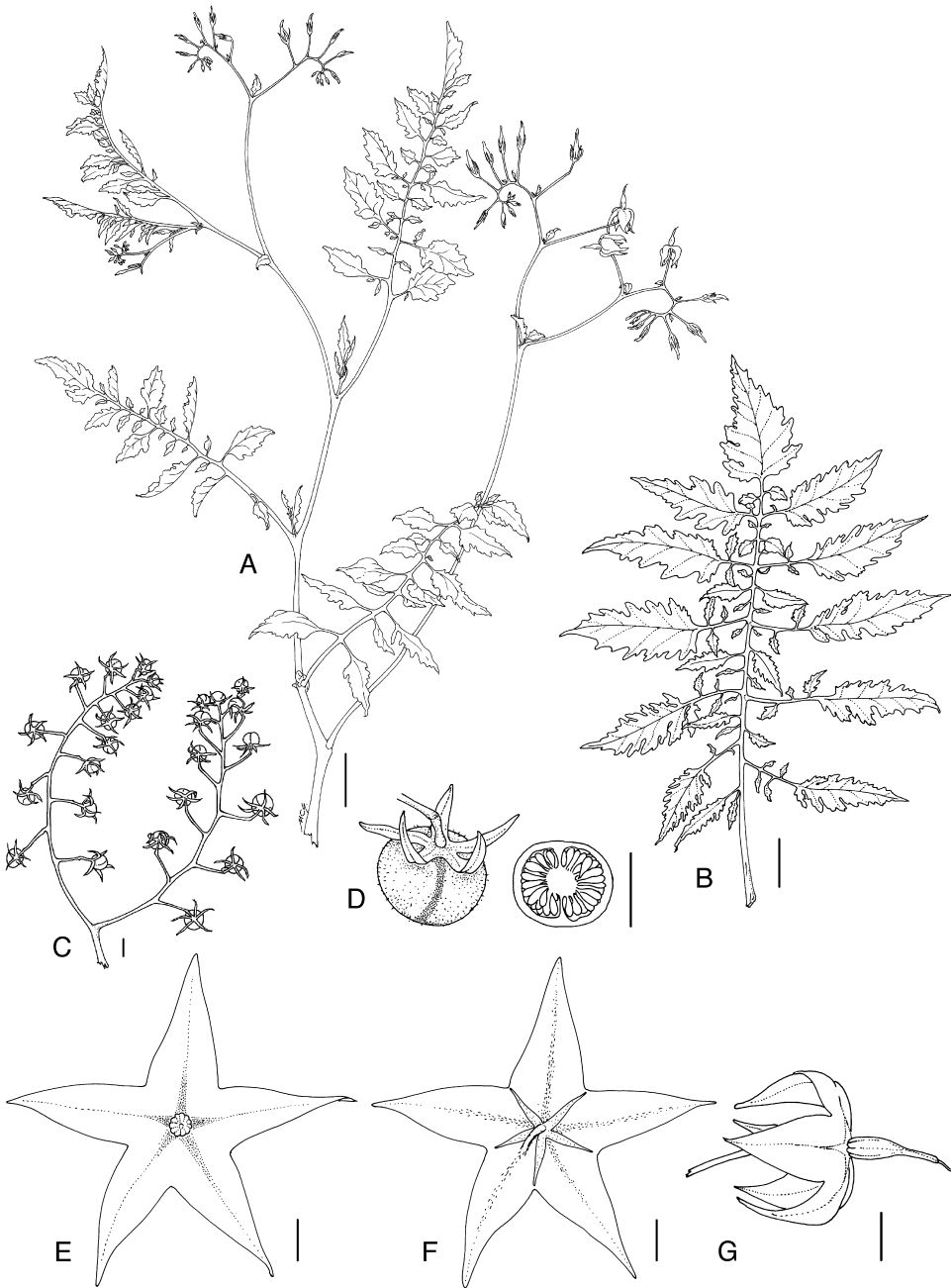
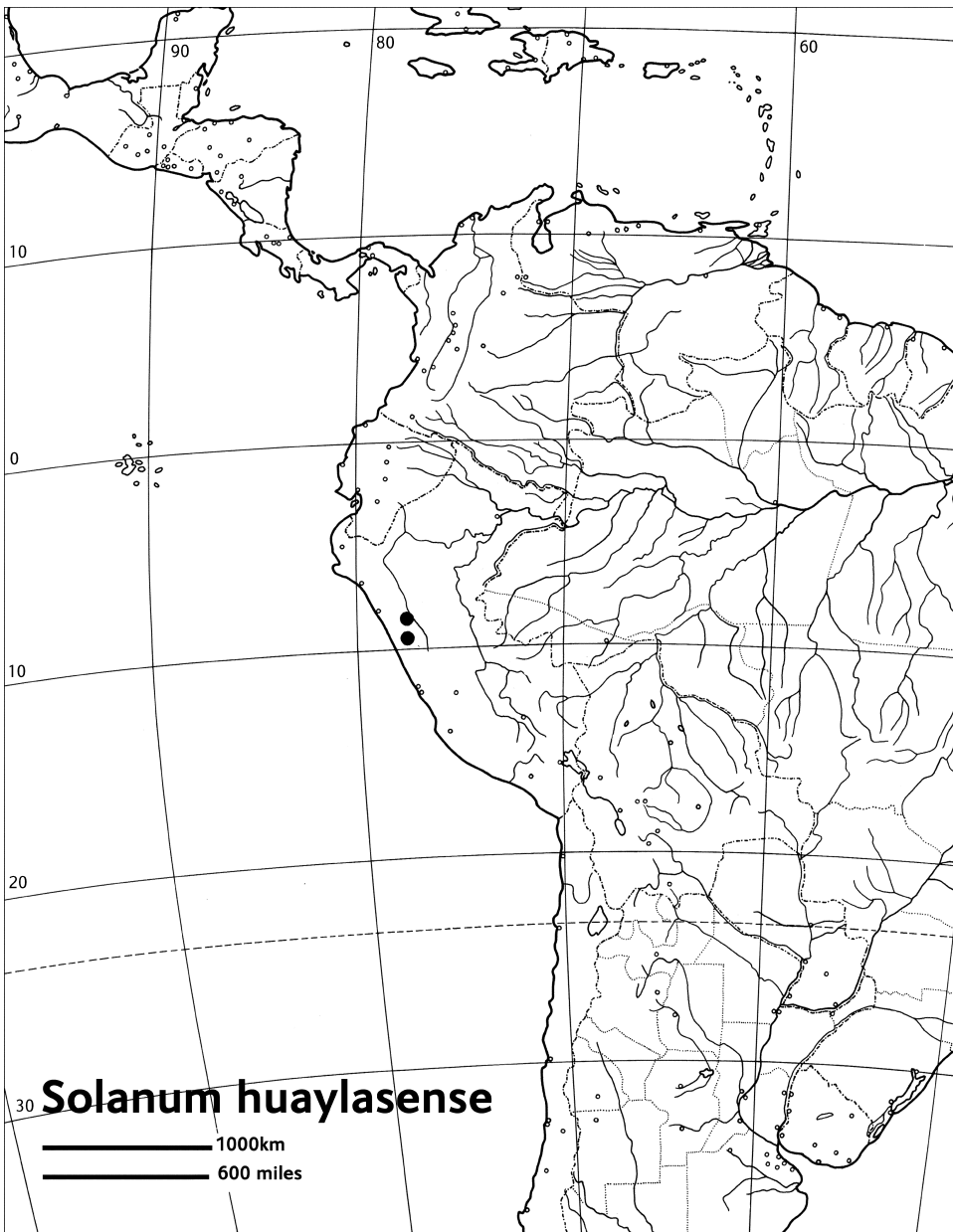


FIG. 33. *Solanum huaylasense*. A. Branch. B. Leaf. C. Early fruiting stage. D. Fruit (with cross section). E. Adaxial view of flower. F. Abaxial view of flower. G. Side view of flower. Reproduced with permission from *Systematic Botany* 30: 432, fig. 5. 2005.

FIG. 34. Distribution of *Solanum huaylasense*.

in Rick's broad definition of *S. peruvianum* with their current identifications according to this monograph.

Cultivated specimens of *S. huaylasense* are robust and erect plants during initial growth and later decumbent, with highly dissected leaves, very long peduncles, inflorescences typically two-branched but often three-branched. Stems, internodes, leaves, inflorescences, flowers, and fruits are usually larger in cultivation than in the wild, but maintain similar character proportions to those collected in the wild.

9. *Solanum peruvianum* L., Sp. pl. 186. 1753. *Lycopersicon peruvianum* (L.) Miller, Gard. Dict. ed. 8, *Lycopersicon* No. 5. 1759.—TYPE: Cultivated in Uppsala, from seeds said to have been sent to Jussieu from Peru, *Anon. s.n.* (lectotype, designated by Knapp & Jarvis 1990: LINN 248-17! [BH neg. 6804: BH! GH! UC-102331! US! WIS!]).

Solanum commutatum Sprengel, Pl. Min. Cogn. Pug. 1: 18. 1813. *Lycopersicon commutatum* (Sprengel) Roemer & Schultes, Syst. veg. 4: 569. 1819. *Lycopersicon peruvianum* var. *commutatum* (Sprengel) Link, Klotzsch & Otto, Icon. Pl. Rar. 1: 87. 1841. *Lycopersicon peruvianum* subsp. *commutatum* (Sprengel) Luckwill, Univ. Aberdeen Studies 120: 29. 1940.—TYPE: Cultivated from unknown source, *herb. Reichenbach fil. s.n.* (neotype, here designated: W-280088!).

Lycopersicon regulare Dunal, Solan. Synopsis 3. 1816. *Lycopersicon peruvianum* subsp. *typicum* Luckwill var. *regulare* (Dunal) Luckwill, Aberdeen Univ. Studies 120: 29. 1943.—TYPE: Cultivated, *Anon. s.n.* (holotype: G!).

Lycopersicon dentatum Dunal, Solan. Synopsis 4. 1816. *Lycopersicon peruvianum* var. *dentatum* (Dunal) Dunal in A. DC., Prodr. 13(1): 24. 1852. *Lycopersicon peruvianum* subsp. *dentatum* (Dunal) Luckwill, Univ. Aberdeen Studies 120: 30. 1943.—TYPE: Cultivated from unknown provenance, *herb. Thibaud* (holotype: G-DC!; probable isotype: MPU!).

Spreading to erect perennial herbs to small shrubs, woody at the base, to 0.5 m tall, to 1 m in diameter. Stems 3–5 mm in diameter at base, pale grayish green, densely and uniformly velvety-pubescent with white, simple, uniseriate eglandular trichomes less than 0.5 mm long and with a bent tip, and scattered glandular uniseriate trichomes with 1-celled, 4-celled, or 8-celled heads amongst and shorter than the eglandular trichomes, all trichomes with a unicellular base; the young stems more densely pubescent and sometimes more glandular. Sympodial units 2-foliate; internodes 1.5–5 (–10) cm long. Leaves interrupted imparipinnate, 4–10 (–19) cm long, 1.6–7 (–10) cm wide, grayish green adaxially and abaxially, densely velvety-pubescent like the stems with simple, uniseriate trichomes to 0.5 mm long, mixed with sparse scattered shorter glandular trichomes with 4-celled heads; primary leaflets 2–4 pairs, elliptic to almost orbicular in some populations (mostly in the southern part of the range), apex bluntly acute to rounded, base truncate, markedly oblique and decurrent basiscopically, margin entire to crenate to more or less deeply lobed ca. 1/4–1/3 of the way to the leaflet rachis; terminal leaflet usually markedly larger than the laterals, 1.5–3.5 (–6) cm long, 0.6–1.5 (–4) cm wide, the petiolule 0.2–0.8 cm long; lateral leaflets 0.8–3 cm long, 0.5–1.5 cm wide, sessile and the base decurrent or the petiolule to 0.5 cm long; secondary leaflets very occasionally present on the larger lower lateral leaflets, 0.1–0.3 cm long, 0.1–0.3 cm wide, sessile, often appearing as mere lobes at the base of the lateral leaflets; tertiary leaflets absent; interjected leaflets (0–) 2–9, 0.1–0.7 cm long, 0.15–0.9 cm wide, sessile or in extremely large leaves with a petiolule

of 0.1–0.5 cm long; petiole 1–3 cm long; pseudostipules present and developed in all nodes, 0.2–1 cm long, 0.3–1.1 cm wide, margins crenate or entire. Inflorescences (4–) 8–16 cm long, usually once-branched and bifurcate, occasionally more than once-branched, with 8–20 flowers, all nodes bracteate, bracts 0.1–1 (–1.5) cm long, 0.2–1.5 (–2) cm wide, cordate and surrounding the pedicels, the largest bract at the first inflorescence branch, peduncle (1.5–) 4–10 cm long, densely white velvety-pubescent like the stems and leaves. Pedicels 1–1.5 cm long, articulated in the proximal half or at the middle. Buds 0.8–1.2 cm long, 0.3–0.4 cm wide, elongate conical, strongly curved, the corolla more than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube minute, the calyx divided essentially to the base, lobes 5–7 mm long, 1.5–2 mm wide, lanceolate, densely white velvety-pubescent like the rest of the inflorescence on both surfaces; corolla 1.7–2.3 cm in diameter, rotate to slightly stellate, bright yellow with the midveins occasionally darker, the tube 0.6–0.8 cm long, lobes 0.8–0.9 cm long, 0.8–0.9 cm wide, densely white-pubescent on the tips and margins, reflexed at anthesis; staminal column 0.8–1.3 cm long, strongly curved, filaments completely united into a tube ca. 0.5 mm long, anthers 0.5–0.7 cm long, the upper two usually longer and curved, sterile apical appendage 0.3–0.4 cm long, often greenish; ovary conical, minutely puberulent at the apex or over entire surface; style 1–1.5 cm long, ca. 0.5 mm in diameter, curved, densely white-pubescent in the basal 2/3, exerted 0.5–1 mm beyond the staminal column; stigma capitate to slightly clavate. Fruit 1–1.5 cm in diameter, globose, green to greenish white and often flushed with purple, with a dark green or purple stripe from the apex to base at maturity, 2-locular, pubescent to densely pubescent with soft, weak-walled simple uniseriate trichomes to 0.5 mm long, the surface densely papillate; fruiting pedicels 1.5–2 cm long, usually straight or slightly bent at the articulation; calyx lobes in fruit 10–14 mm long, 2–2.5 mm wide, narrowing just distal to the sinus, loosely investing the berry or spreading. Seeds 1.8–3.0 mm long, 1.0–1.4 mm wide, 0.5–0.7 mm thick, obovate, dark brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or sometimes shaggy, narrowly winged (0.2 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (Luckwill 1943a; LA1944, <http://tgrc.ucdavis.edu>). Plate II, Plate 2I, Plate 3I; Fig. 35.

Phenology. Flowers and fruits throughout the year, but with an extended peak from September through December during the coastal foggy period.

Distribution (Fig. 36). In lomas formations and occasionally in coastal deserts from central Peru to northern Chile, occasionally occurring as a weed at field edges in coastal river valleys; sea level to 600 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** Without locality, *Mathews s.n.* (W); without locality, 1862, *Mathews 393* (NY); “Guayaquil,” without locality, *Née (Expedición Malaespina) s.n.* (MA); without locality, *Raimondi 10735* (USM), *Raimondi 11969* (USM); without locality, *Ruiz & Pavón s.n.* (F), *Ruiz & Pavón 379* (G).—ANCASH: Paramonga, *Blood & Tremelling 77* (GH); Km 249 Panamericana Norte, *Cerrate 5179* (USM); Lomas de Lupín, 31–32 km N of Paramonga, Km 239–241 N of Lima along Pan-American highway, *Dillon & Santisteban 4717* (F, USM); Prov. Santa, Lomas de Lupín, entre Barranca y Huarney, *Ferreya 13536* (USM); Lomas de Lupín, entre Barranca y Huarney, *Ferreya 13794* (USM); roadside at Punto Huarto, on main tarmac road from Lima to Huaráz, *Gibby & Barrett 6* (BM); Caranquillo, a 57 mi E de Pativilca, *Rick SAL-449* (USM); Prov. Casma, 46 km from Barranca on Panamerican highway, *Smith & Vásquez 3226* (MO, NY, USM); Los Zorros, 30 km S of Huarney, *Stork et al. 9194* (G, UC, US); Prov. Huarney, Panamericana Norte Km 589, *Weigend et al. 2000/656* (BM, HUT, M).—AREQUIPA: Lomas de Lluta, road from Arequipa to the coast, *Ackermann & Caceras 438* (BM), *Ackermann & Caceras 451* (BM); Km 694.5, just N of Atico, *Anderson et al. 7896* (F); between Km 594 and Km 595 N of Chala along Hwy 1 (Panamerican highway), *Anderson et al. 7975* (F); Km 705, small unnamed quebrada, *Anderson et al. 7905* (F); in collinis aridis “Lomas” nuncupatis, ditone Mollendo,

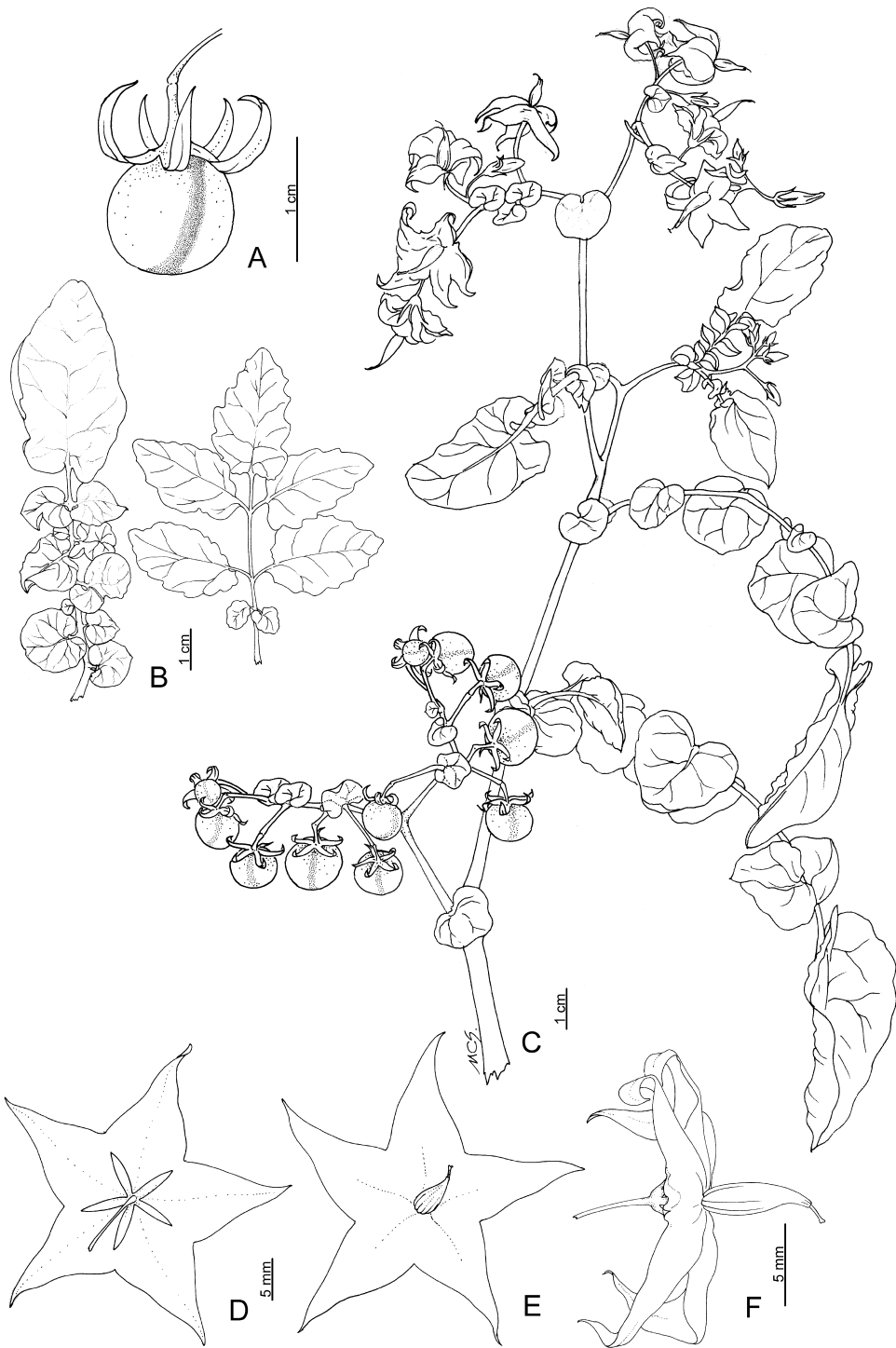


FIG. 35. *Solanum peruvianum*. A. Fruit. B. Two leaves. C. Branch. D. Abaxial view of flower. E. Adaxial view of flower. F. Side view of flower.

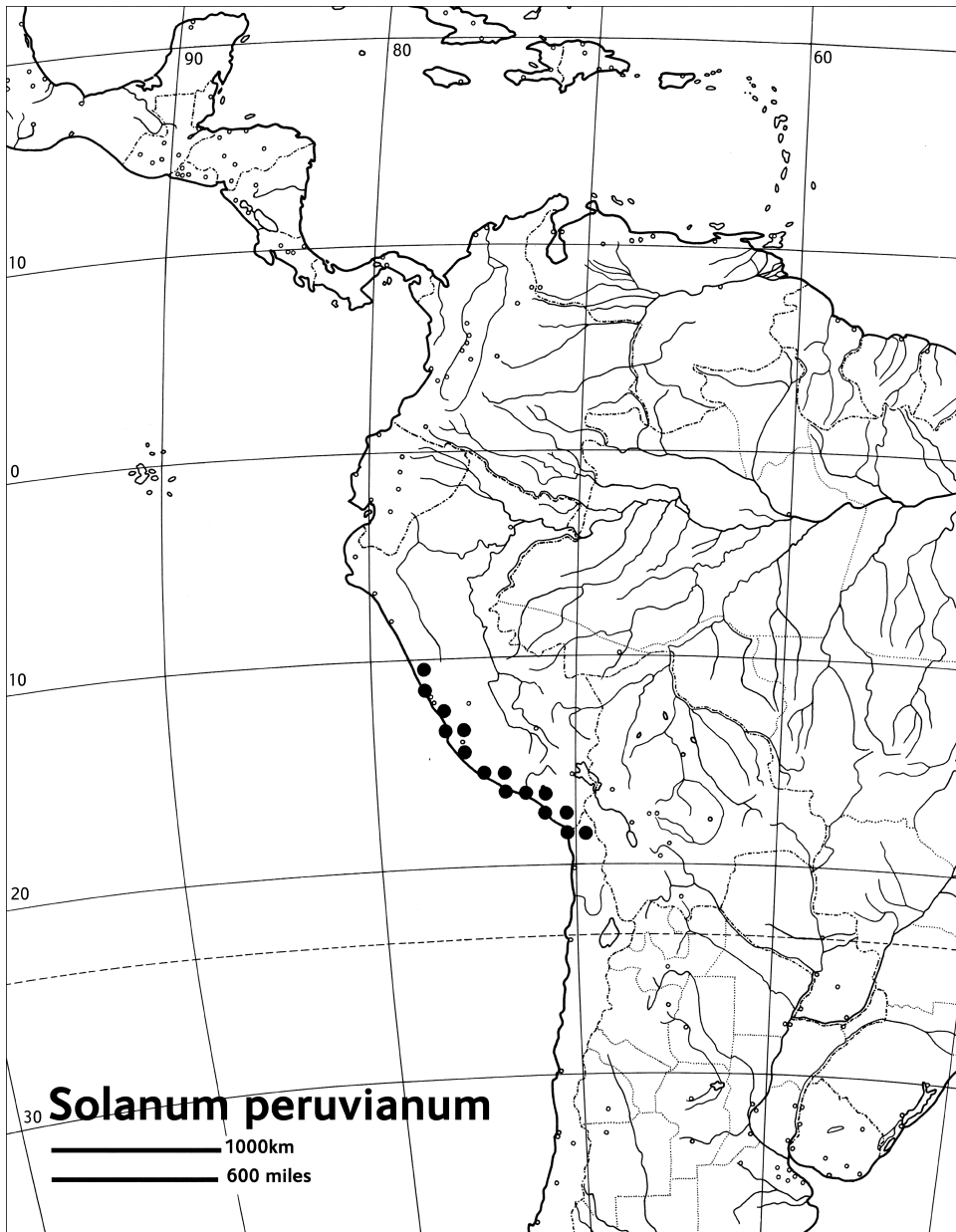


FIG. 36. Distribution of *Solanum peruvianum*.

Bernardi et al. 16915 (F, G); above Mollendo, *Blood & Tremelling* 161 (F, GH); E of Tambo, *Blood & Tremelling* 538 (MO, UC); near Matarani, *Böcher et al.* 419 (C, S); Lomas de Mollendo, *Bornas et al.* 34 (USM); Lomas de Atiquipa, *Cerrate et al.* 8631 (USM); Lomas de Camaná, Quebrada del Toro, *Chanco & Carrillo* 1194 (USM); near Atico, *Correll & Smith P-174* (F, LL, NY, US); Lomas of Atiquipa, ca. 10.5 km N of turnoff to Atiquipa, Km 584 S of Lima, *Dillon & Dillon* 3782 (F, USM); 12 km S Atico, Strassen Km 715, *Ellenberg* 8580 (MO); about 1 km SE of Mollendo, *Eyerdam* 25158 (K, UC); Lomas de Lluta, Mollendo–Matarani, *FLSP* 1477 (NY); Atiquipa, *Ferreyra* 1501 (USM); Prov. Caravelí, Lomas de Atico, entre Chala y Camaná, Km 747–749 de

la carretera Panamericana, *Ferreyra 2517* (US, USM); Lomas de Camaná, *Ferreyra 6434* (US, USM); Lomas de Capac, cerca a Chala, *Ferreyra 7227* (US, USM); Lomas de Camaná, Km 163–164 carretera Canamá–Arequipa, *Ferreyra 8831* (USM); Lomas de Atico, *Ferreyra 8886* (USM); Lomas de Camaná, *Ferreyra 11686* (USM); Lomas de Atico, entre Chala y Camaná, *Ferreyra 12021* (MO, USM); Lomas de Mollendo, *Ferreyra 12587* (USM); Lomas de Atico, *Ferreyra 13904* (USM); Lomas de Atico, entre Chala y Ocoña, *Ferreyra 18627* (USM); Prov. Islay, Mollendo, *Ferreyra 18645* (USM); Lomas de Atiquipa, cerca de Chala, *Ferreyra et al. 19836* (USM); Lomas de Camaná, *Ferreyra & Ono 20326* (USM); Lomas de Atiquipa, cerca a Chala, *Ferreyra & Ono 20339* (USM); Lomas de Atiquipa, cumbre detrás del pueblo, *Ferreyra 20717* (USM); Mollendo, *Günther 12306* (US); Mollendo, *Hitchcock 22362* (US); 15 km N of Chala, Lomas de Atiquipa, *Holt 163* (K); Pan Am highway at Km 748.5, ca. 15 km SE of Atico, *Iltis et al. 1558* (US, WIS); above Pacific Ocean at Km 621 of Pan Am highway, ca. 20 km NW of Puerto Chala, *Iltis et al. 1575* (WIS); 4 km from Caravelí on road to Atico, *Metcalf 30342* (MO); Quebrada de Guerrero, entre Mollendo y la variante de carretera Arequipa–Moquegua, *Ochoa 11255* (US); Lomas de Atico–Chala, *Ochoa 11756* (US); 160 km from Arequipa towards Camaná, *Petersen & Hjerting 1116* (C); Km 756 from Lima, between Atico and Puerto Chala, *Petersen & Hjerting 1129* (C); Lomas de Atiquipa, *Rick 200* (USM); en las lomas, 10 km S de Cahal, pampa de Capac, *Rick 202* (USM); Lomas de Camaná, *Rick 204* (USM); immediately S of Río Tambo, *Rick 208* (USM); Prov. Caravelí, Atico, *Tovar 2655* (USM); Lomas de Camaná, *Tovar 3448* (USM); Lomas de Atico, *Tovar 3466* (USM); Lomas de Tiquipa, *Vargas C. 10918* (WIS); hills of Mollendo, loma zone, *West 8239* (MO, UC); Prov. Camaná, 14 km S of Chala, small quebrada to the south, *Worth & Morrison 15678* (G, K, UC); 8 km S of Mollendo, *Worth & Morrison 15733* (F, G, MO, UC).—LA LIBERTAD: Culebras, near Trujillo, *Blood & Tremelling 98* (NY).—LIMA: Lima, *Andersson s.n.* (S); ad pedem montis Amancaes prope Lima, *André 4110* (F, K, NY); vicinity of Lima, San Agustín, *Asplund 13813* (S); Atocongo, *Baldeón et al. 87* (USM); in convalle fluminis Rimac, *Ball s.n.* (E); Amancaes, near Lima, *Balls B-7073* (E, F, US); Lomas de Lachay, *Bernardi 16395* (G, UC); Lomas de Manchay, valle de Lurín, *Biegman s.n.* (USM); between Miraflores & Barranco, near Lima, *Blood & Tremelling 5* (F, NY, UC); Pacasmayo, *Blood & Tremelling 85* (NY); Prov. Chancay, Lomas de Lachay, *Carrillo 1159* (USM); Prov. Chancay, Lomas de Lachay, *Cerrate 855* (USM); Lomas de Amancaes, *Cerrate 2761* (USM); Lomas de Pachacamac, *Cerrate et al. 8784* (USM), *Cerrate et al. 8798* (USM); Prov. Huaral, Iguanil, cerca de Huaral, *Cerrate 9159* (USM); near Km 94 between Chancay and Huacho, *Correll & Smith P-789* (LL, NY); Lomas de Iguanil, *del Carpio et al. 456* (USM); Prov. Barranca, Cerro Paccar, *del Carpio 503* (USM); Lomas de Atocongo, bei Lima, *Diers 1303* (S); Lomas de Lachay; ca. 105 km N of Lima on Panamerican Hwy, *Dillon et al. 3620* (F); Lomas de Granados (Iguanil), *Ferreyra 19510* (USM); Lomas de Lachay, cerca a Chancay, *Ferreyra 3844* (USM); Lomas de Chancayllo, *Ferreyra 16604* (USM); ruinas de Cajamarquilla, a 25 km al E de Lima, *Ferreyra 2836* (US); Lomas de Atocongo, 28 km a sur de Lima, *Ferreyra 3469* (USM); Chancay Prov., Lomas de Lachay, *Ferreyra 3844* (US); Lomas de Amancaes, cerca a Lima, *Ferreyra 3950* (USM); alrededores de San Juan, Surco (Barranco), *Ferreyra 4093* (USM); cerca a las ruinas de Cajamarquilla, *Ferreyra 16887* (USM); Prov. Chancay, Lomas de Lachay, *Ferreyra 17074* (USM); Lomas de Pachacamac, cerca a Lurín, *Ferreyra 17690* (USM); Lomas de Huaral, Iguanil, *Ferreyra 18576* (USM); Barranco, between Pacasmayo and railhead, *Forbes s.n.* (BM); Lomas de Pachacamac, 25 km S of Lima, hills back of coast, *Fosberg 56218* (F); Callao–Lima–San Lorenzo, *Gaudichaud s.n.* (G); Lomas de Amancaes, S of Lima near Pachacamac, *Gentry 16471* (BM, MO); Lomas de Lachay, 80 km N of Lima on Pan-American Highway, *Gentry et al. 74513* (MO); Amancaes, *Goodspeed 33137* (G, GH, MO, US, US); road from Trapiche to Quilca, at ca. 6 km from Trapiche, *Hawkes et al. 4102* (C); La Palma, Miraflores, *Maisch s.n.* (USM); Lomas de Iguanil o Granados, *Malpartida 487* (USM); Amancaes, *Matthews 393* (E); Lomas de Amancaes, cerca de Lima, Cerro de San Gerónimo, *Ochoa 595* (F); entre Cieneguilla y Santo Domingo, *Ochoa 13099* (US); Lomas del Cerro el Caraqueño, del desvío de Cajatambo hasta San Miguel y de aquí hasta Santa Rosa, antes La Enseñada, 30 km E de Panamericana, *Ochoa & Salas 14867* (F, NY, US); Barranco de Miraflores, *Raimondi 11970* (USM); Matucana, *Raimondi 12148* (USM); Barranco de Miraflores, *Raimondi 12392* (USM); lugares secos cerca de Lima, *Raimondi 12399* (USM); Barranco, *Raimondi 19987* (USM); Km 173 cerca a Supe, *Rick 116* (USM); Magdalena del Mar, cerca a Lima, *Ridoutt s.n.* (USM); Distrito de La Victoria, Lima, *Ridoutt s.n.* (USM); Lomas de Amancaes, *Ridoutt 12176* (USM); Lomas de Lachay, entre Lima y Huacho, *Ridoutt 14497* (USM); Lomas de Lachay, entre Chancay y Huacho, *Ridoutt 14508* (USM); vicinity of Lima, *Rose & Rose 18589* (US); without locality, 1778, *Ruiz & Pavón s.n.* (F); San Cristóbal, hill near Lima, *Sandeman s.n.* (BM); Cajamarquilla, Lima, *Sandeman s.n.* (BM); St. Cristóbal, hill near Lima, *Sandeman s.n.* (BM); Cajamarquilla, *Sandeman s.n.* (BM); Prov. Lima, 7 km inland from San Bartolo (coast), about 4–5 hr. S of Lima, *Saunders 146* (BM); Barranca, *Savatier 1519* (K); Barranca, *Sjöstedt 45* (S); Amancaes, *Soukup 155(?)* (S); without locality, *Soukup 1045* (F); Cerro Jerónimo, *Soukup 1616* (US); Cerro Agustinos, *Soukup 2554* (F, US); 1 km S of Supe, Km 167 N of Lima on the Panamerican highway, *Ugent & Ugent 5379* (WIS); Lomas de Atocongo, *Velarde Núñez 852* (US); without locality,

Weberbauer 2 (G); Lima, in the Rimac, *Wilkes s.n.* (US); Obrajillo, *Wilkes s.n.* (US).—MOQUEGUA: Chucarapi–Pampa Clemenés, *Ferreyra 11590* (USM).—TACNA: Prov. Tacna, Morro de Sama, *Müller & Charin 3563* (USM). **Chile.** REGION I (TARAPACÁ): Arica, valle de Azapa, *Ackermann 137* (BM); Valle de Arica, *Anon. 731* (MA); Quebrada de Lluta, *Anon. 32970* (CONC); Lluta Valley, between Lluta & Arica, *Blood & Tremelling 476* (NY); Azapa Valley, SE of Arica, *Blood & Tremelling 477* (GH); Arica, *Anon. s.n.* (GH); Arica, *Buchtien 4382* (US), *Buchtien s.n.* (GH); Cobija, Iquiqui et Arica “Peruviae meridionalis,” *Cuming 913* (K); Arica, Quebrada Azapa, 10 km E of Arica, *Eyerdam 24643* (K, UC); Prov. Arica, Arica, Quebrada de Azapa, 2 km E of Arica, *Gardner & Knees 6204* (E); Valle de Chaca, *Hartmann 29138* (CONC); Arica, *Jaffuel 1712* (US); Arica, *Jaffuel 3910* (GH), *Jaffuel 3913* (GH); Arica, near coast, *Jaffuel 25* (GH); ex Arica, *Née s.n.* (MA); Arica, valle de Azapa, cerca del pueblo, *Ricardi 3294* (CONC); Valle de Azapa, Azapa, *Ricardi 3347* (CONC); Quebrada Vitor, Chaca, *Ricardi 3444* (CONC), *Ricardi 3447* (CONC); Valle de Lluta, Arica, *Pfister 9487* (CONC); Valle de Azapa, Arica, *Pfister 9503* (CONC); Arica, Azapa Valley, *Skottsberg & Skottsberg 1072* (NY).

Solanum peruvianum is a member of the clade containing *S. corneliomulleri*, *S. chilense*, and *S. huaylasense* (+ in some analyses *S. habrochaites*). It is distinguished from its close relatives by the combination of uniform, dense, velvety pubescence with only scattered short glandular hairs (in contrast to the longer glandular hairs of *S. corneliomulleri*), usually strongly bracteate inflorescence, and curved anther tube. The peduncle in *S. peruvianum* usually is equal or shorter than the length of the inflorescence branches, and is consistently shorter than that of *S. chilense* and *S. huaylasense*. There is considerable variation in leaf morphology in populations of *S. peruvianum* along the Peruvian coast. More northerly populations around Lima and the Department of Ancash have leaflets that are crenate to deeply lobed to 1/4 of the way to the rachis and inflorescences that are sometimes almost ebracteate. The other populations of *S. peruvianum* from the southern part of the species range (e.g., Lomas de Atico, Department of Arequipa) have nearly entire leaflets and very large inflorescence bracts. *Solanum peruvianum* is a low-elevation coastal species, characteristic of the lomas vegetation (see Habitats and Distribution above). Appendix 4 lists all the TGRC accessions (LA numbers) previously included in Rick’s broad definition of *S. peruvianum* with their current identification according to this monograph.

Solanum peruvianum was one of the first wild tomatoes to be cultivated in European botanical gardens. Original introductions appear to have come from at least two different parts of the species range. The type specimen of *S. peruvianum* in the Linnaean herbarium (LINN, see <http://www.nhm.ac.uk/solanaceaesource>) and plants grown by Philip Miller in the Chelsea Physic Garden in the early 18th century match plants from the area around Lima, Peru, while many continental botanical gardens, such as those in Berlin, Vienna, and Hamburg (e.g., Sprengel’s *Solanum commutatum*) grew plants with a morphology more similar to that of plants collected in more southern Peruvian populations; we have selected the neotype for Sprengel’s name from amongst these latter specimens (Fig. 37). The sheet we have chosen includes a small tag bearing an annotation in what is an extremely close match to Sprengel’s handwriting. Heinrich Gustav Reichenbach (Reichenbach filius), the great German orchidologist, had specimens from Sprengel’s herbarium in his own collection, which was bequeathed to the Naturhistorisches Museum in Vienna (W). The specimen we selected as the neotype for *S. commutatum* matches the original description and is likely to have been prepared from plants grown in botanic gardens at the time Sprengel named *S. commutatum*.

It is probable that Linnaeus (1753) received the seeds from which he cultivated his specimen of *S. peruvianum* at Uppsala from Bernard de Jussieu (Knapp & Jarvis 1990); he indicated in the introduction to *Species plantarum* that he had received seeds from “B. Jussieu” and he cited “Jussieu” in the protologue of *S. peruvianum*. Bernard de Jussieu’s

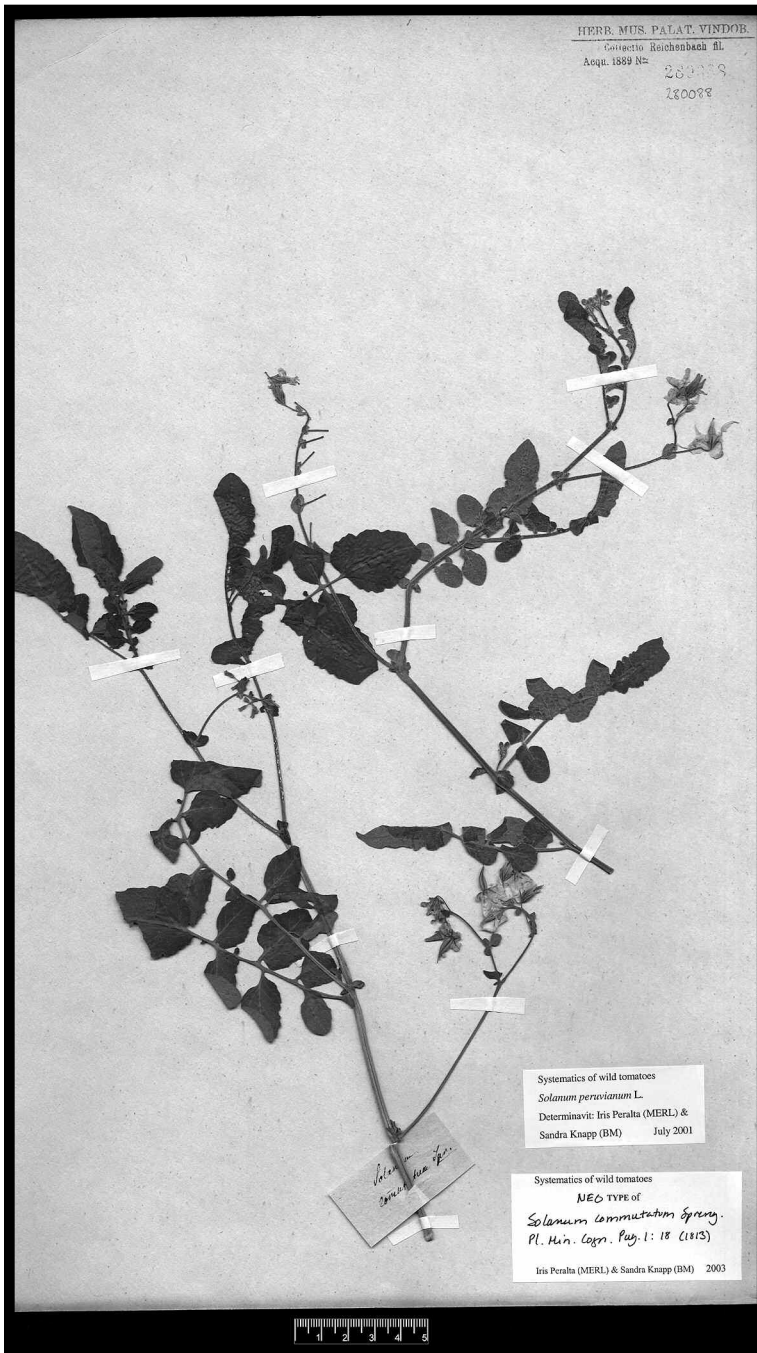


FIG. 37. Neotype of *Solanum commutatum* (unknown collector s.n., W).

younger brother Joseph was a member of the expedition of Charles-Marie de la Condamine (Staffeu 1971) to equatorial South America from 1735–1743, where he collected plants in Ecuador and afterwards in Peru and Chile (Jørgensen 1999). He certainly sent seeds back to his brother from the region; these may have been the source of the plant cultivated by Linnaeus in Uppsala.

In addition to the type, we saw specimens of *S. peruvianum* from cultivated plants from Austria, Belgium, Colombia, France, Germany, Iraq, Italy, the Russian Federation, Spain, the United Kingdom, and the U.S.A. A population of *S. peruvianum* apparently escaped from cultivation at the USDA horticultural station near Torrey Pines, California, and several specimens were collected (*Clark s.n.*, WIS; *Moran s.n.*, UC; *Fuller 16892*, CAS) in the late 1960s. It is possible that *S. peruvianum* established “wild” populations in this area, although no recent collections are known.

10. *Solanum corneliomulleri* J. F. Macbride, Publ. Field Mus. Nat. Hist., Bot. 13(5B, no. 1): 160. 1962. *Lycopersicon glandulosum* C. H. Müller, U.S. Dept. Agric. Misc. Publ. 382: 23. 1940, non *Solanum glandulosum* Ruiz & Pavón, 1799.—TYPE: PERU. Lima: between Yangos and Canta, Canta Valley, near Lima, 5,600–8,500 ft, 24 Nov 1937, *Blood & Tremelling 15* (holotype: US-2249637 [ex-40377]!; isotype: MO!).

Spreading, erect to decumbent perennial herbs, woody at the base, to 1 m tall, to 1 m in diameter. Stems 7–12 mm in diameter at base, green, densely velvety-pubescent with a mixture of simple uniseriate trichomes, the largest stout, patent 5–7-celled trichomes 1.5–2 mm long, with a unicellular or multicellular base, either eglandular or tipped with tiny 1-celled glands or occasionally larger 4-celled glandular heads, the abundance and density of these patent trichomes extremely variable, shorter velvety pubescence of more slender trichomes to 0.5 mm long, sparser and mixed with a variety of small glandular trichomes, the most common 1–2-celled with a 4-celled glandular head, in more glandular populations the head occasionally elliptical and 8-celled, 1-celled trichomes with tiny 1-celled glandular heads also present, but scattered amongst the more common, larger, glandular trichomes. Sympodial units 2-foliolate; internodes 2–9 cm long. Leaves interrupted imparipinnate, (2–) 3.5–13 cm long, (1–) 1.5–6.5 cm wide, green, densely pubescent like the stems, more glandular trichomes present, adaxially densely glandular-pubescent with stout patent trichomes to 1 mm long along the rachis and midveins, abaxially more densely velvety-pubescent, the stout trichomes more abundant along the veins, but also on the surface, in general trichomes of the laminar surface shorter than those of the veins or the stems; primary leaflets 3–5 pairs, the basal pair usually half the size of the rest, orbicular to broadly elliptic (elliptic in populations from around Arequipa), apex rounded or acute, base cordate to truncate, somewhat oblique and decurrent onto the rachis, margin crenate to dentate to irregularly lobed ca. halfway to the rachis or more, the lobing deeper near the leaflet base; terminal leaflet usually larger than the lateral leaflets, (0.4–) 1–3.5 cm long, (0.1–) 0.7–2 cm wide, the petiolule 0.05–1 cm long, apex usually more acuminate than that of the lateral leaflets; lateral leaflets (0.2–) 0.7–3 cm long, (0.1–) 0.7–2 cm wide, the petiolule to 1 cm long, or absent and the leaflets sessile and decurrent onto the rachis; secondary leaflets sometimes present on the larger lateral leaflets and on the terminal leaflet, (0.04–) 0.1–0.3 cm long, (0.02–) 0.1–0.3 cm wide, broadly decurrent on the leaflet rachis, more developed acroscopically; tertiary leaflets absent; interjected

leaflets (0–) 5–10, usually 2–4 between each primary leaflet, 0.1–0.6 cm long, 0.1–0.5 cm wide, sessile, occasionally with a short petiolule to 0.3 cm long; petiole 0.2–1 (–2) cm long; pseudostipules present but not developed at all nodes, 0.4–1 cm long, 0.5–1 cm wide, margins crenate, glandular-pubescent like the leaves. Inflorescences 4–12 cm long, simple or more often once-branched and bifurcate, with (5–) 8–16 flowers, usually bracteate, bracts 0.3–0.5 cm long, 0.3–0.5 cm wide, margins rounded crenate, peduncle 2.1–8 (–12) cm long, densely pubescent like the stems with a mixture of glandular and eglandular trichomes. Pedicels 0.7–1.5 cm long, articulated at the middle or in the distal half, often more densely pubescent with patent trichomes distal to the articulation. Buds 0.8–1.2 cm long, 0.4–0.6 cm wide, conical, strongly curved, the corolla more than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube to 0.5 mm long, lobes 3–6 mm long, 0.7–1.5 mm wide, lanceolate to narrowly deltate, the sinuses hyaline, densely pubescent with simple trichomes like those of the inflorescence to 0.5 mm long; corolla 1.5–2.4 (–3.2) cm in diameter, rotate-stellate, vivid yellow, the tube 0.3–0.8 cm long, lobes 0.6–0.9 (–1.2) cm long, 0.6–0.9 cm wide, abaxially sparsely pubescent with white uniseriate trichomes to 0.5 mm long, these more abundant along the margins, the tips densely papillate-pubescent, reflexed at anthesis and the margins irregularly undulate; staminal column 0.7–1 cm long, 0.3–0.4 cm wide, strongly curved, filaments 0.5 mm long, not forming a united tube, anthers 0.45–0.6 cm long, the upper two usually larger and curved, sterile apical appendage 0.25–0.4 cm long, often greenish; ovary globose, glabrous or with a few slender uniseriate trichomes at the apex; style 1.1–1.3 cm long, ca. 0.5 mm in diameter, curved, densely white-pubescent 1/2–3/4 of its length, exerted 1–2.5 mm beyond the staminal column; stigma capitate, green. Fruit 0.9–1.3 cm in diameter, globose, 2-locular, green to greenish white, with a dark green or purple stripe from apex to base and sometimes flushed with purple when ripe, sparsely to densely pubescent with a mixture of simple uniseriate trichomes, stout patent, 2–4-celled trichomes 1.5–2 mm long, eglandular or with 1-celled glandular heads, mixed with sparse to dense glandular 1-celled trichomes with 4-celled heads, the berries sometimes glabrescent when ripe, the trichomes apparently deciduous; fruiting pedicels 1.5–2.1 cm long, usually straight, occasionally somewhat angled at the articulation towards the infructescence axis; calyx lobes in fruit 9–17 mm long, 1.5–2 mm wide, investing the fruit like a cage, usually as long as or longer than the berry, in populations from near Arequipa always longer than the berry. Seeds 1.7–3.0 mm long, 1.2–1.6 mm wide, 0.5–0.8 mm thick, obovate, dark brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or sometimes shaggy, narrowly winged (0.2 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (Luckwill, 1943a; LA1473, <http://tgrc.ucdavis.edu>). Plate 1J, Plate 2J, Plate 3J; Fig. 38.

Phenology. Flowers and fruits sporadically throughout the year, but with a distinct flowering peak in March to April.

Distribution (Fig. 39). Middle to higher elevations on the western slope of the Andes from central (near Lima) to southern Peru; occasionally on lower slopes on the edges of landslides (huaycos) towards the southern part of the species range; (400–) 1000–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** Without locality, *Soukup 1216* (F).—AREQUIPA: road from Juliaca to Arequipa, after Pampas Arieras, *Ackermann 416* (BM); subida Estanquilla Ahogado, *Arenas P. 90* (USM); subida Estanquilla Ahogado, Chachani, *Arenas P. 91* (USM); Prov. Arequipa, Campo de Aviación–Zamácola, *Arenas P. 92* (USM); subida Estanquilla Ahogado, *Arenas P. 93* (USM); Yura, *Balfour Gourlay 116* (E,

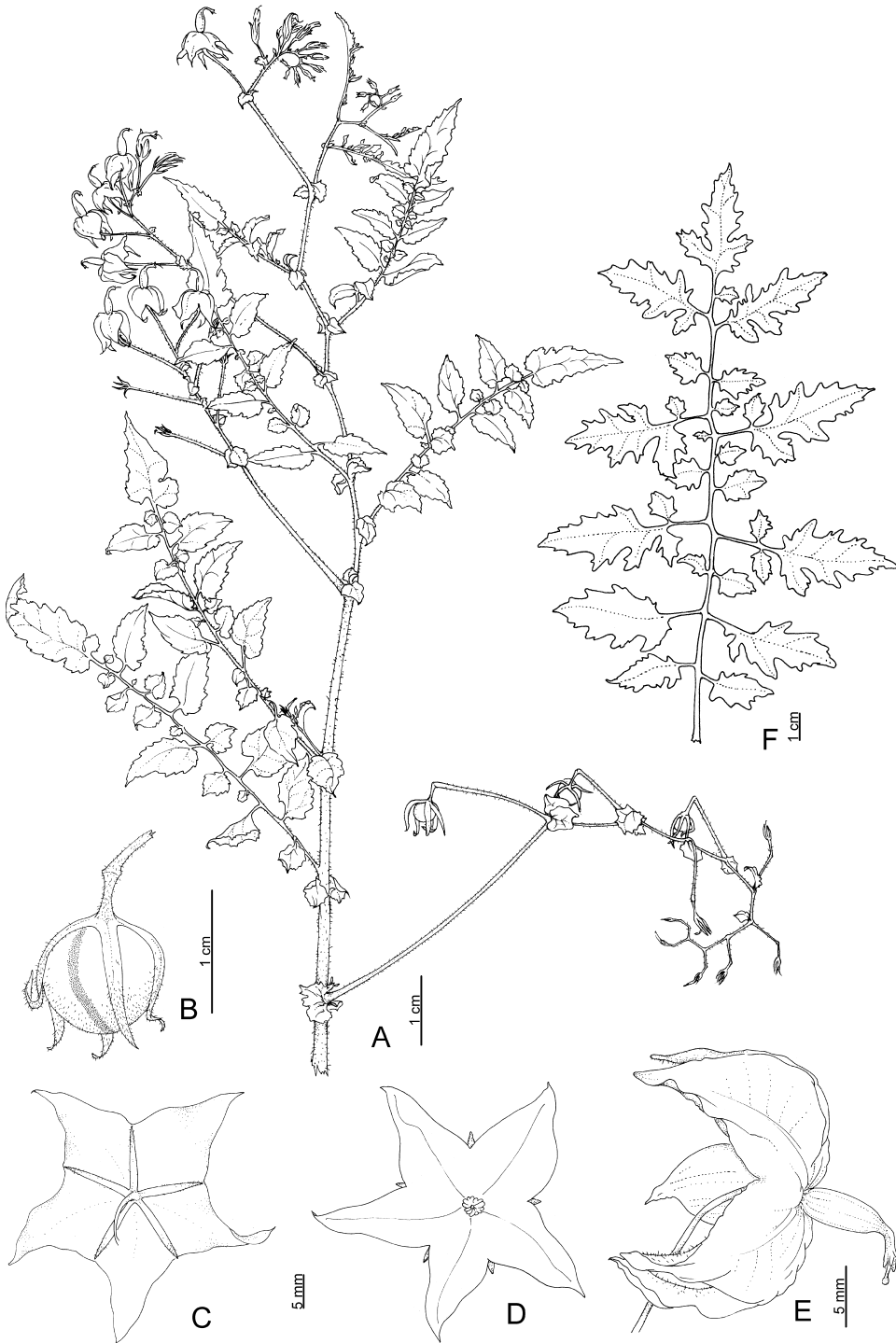


FIG. 38. *Solanum corneliomulleri*. A. Branch. B. Fruit. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Leaf.

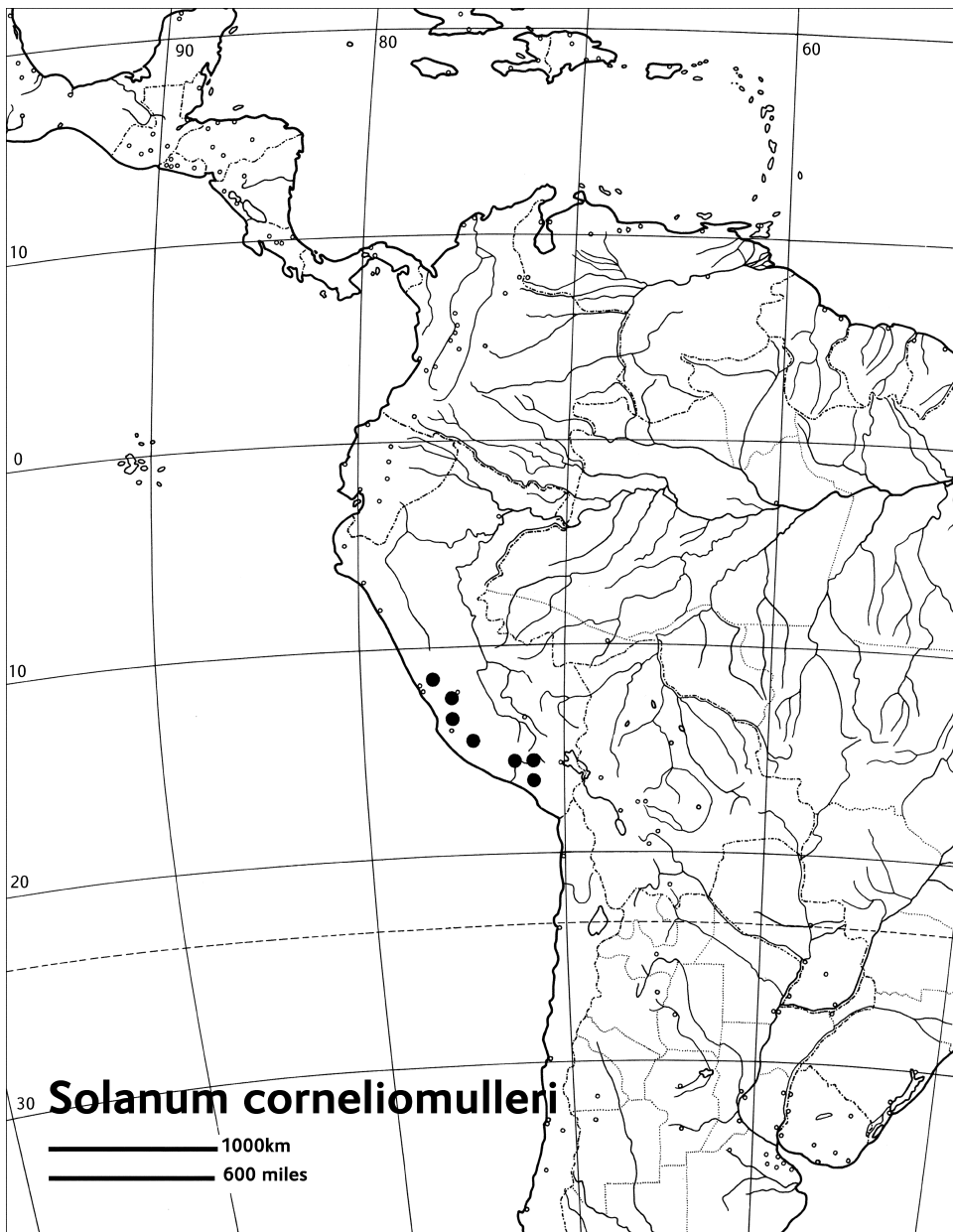


FIG. 39. Distribution of *Solanum corneliomulleri*.

NY); along terrace on outskirts of Arequipa, *Blood & Tremelling 168* (GH, MO, NY); Timago, near Arequipa, *Cockerell s.n.* (US); Chuquibamba, *Ellenberg 136* (U); Cerrillo Savandia (Lavancha?) near Laspinas 14 km N of Arequipa, *Eyerdam & Beetle 22150* (K, MO, UC); cerros de Arequipa, *Ferreyra 14265* (USM); faldas de Misti, *Guillen Cárdenas & Calienes Rodríguez 10* (F); S slopes of Chachani Mountain, N of Arequipa, *Hinkley & Hinkley 36* (NY, US); Km 23 SSW of Arequipa along Panamerican Hwy, ca. 15 km SSW of Arequipa, *Illis et al. 1512* (US, WIS); Cabanaconde, *López G. 352* (MO, WIS); town of Chilina, outside city of Arequipa, *Ozasky 42* (WIS); Tingo, *Pennell 13147* (F, GH, NY, S, US); Estancia Trabaya, near Río Chili, *Petersen & Hjerting 1114* (C); cerros entre Uchumayo y la Caldera, *Raimondi s.n.* (USM); Yura, a los lados de la carretera a 8 km al S de Yura, *Rick 206* (USM); Tingo, *Schmidt s.n.* (F); Km 18 on road between Arequipa and Yura, lower slopes of Nevado Chachani, *Solomon 2867* (USM); Chilinas, hills on SW side of Río Chili, ca. 4 km N of Arequipa, *Solomon 2769* (MO); Yura, hills to the E, *Solomon 2819* (MO); Morro Verde, 18 km above Yura by rail, *Straw 2381* (US, USM); about 2 km S of Yura toward Arequipa, *Straw 2260* (US, USM); Arequipa, *Williams 2525* (NY), *Williams 2566* (NY).—AYACUCHO: W slope of the Andes, on Nasca to Puquio road, *Correll & Smith P-147* (LL); Prov. Lucanas, entre Nazca y Puquio, *Ferreyra 5455* (US, USM); Ayacucho, *Monro et al. 3986* (BM).—HUANCAVELICA: Teciapo on road to Castrovirreyna, 82 mi from junction with Panamericana (Huancaquilla), *Rick et al. SAL-388* (USM); Prov. Huaytará, above Puerto Santa Ana, 0.5 km before Huaytará, Km 99.5 on road Pisco–Ayacucho, *Weigend & Förther 97/589* (F, HUT, M, USM).—ICA: Prov. Nasca, surroundings of Nasca, *Binder & Daxberger 1999/363* (HUT); Prov. Pisco, cerca a Pisco, *Cerrate 905* (USM); on Panamerican highway, Km 216 from Lima, ca. 12 km N of Pisco, *Illis et al. 412* (GH, NY, U, US, USM, WIS); between Pisco and Chinchá Alta, *Petersen & Hjerting 1149* (C); Prov. Chinchá, Chinchá, *Rick 199* (USM); 17 mi E de Nazca, *Rick SAL-415* (USM); Prov. Ica, Tambillo, *Rick SAL-3152* (USM); Prov. Nazca, Km 37 on road Nazca–Puquio, *Weigend & Förther 97/658* (F, HUT, M, USM).—ICA/AYACUCHO: 43 km E of Nazca on road to Puquio, *Gentry et al. 23255* (BM, MO).—JUNÍN: between La Merced and Tarma, *Blood & Tremelling 54* (F).—LIMA: without locality, *Acleto 607* (USM); above Paya, *Asplund 10827* (G, S, US); Prov. Huarochirí, Matucana, *Asplund 10990* (S); Sayan, cerca a ruina La Mina, *Beltrán 06* (USM); without locality, *Beigman s.n.* (USM); between Yangas and Canta, near Lima, *Blood & Tremelling 15* (MO, US); in Canta Valley, *Blood & Tremelling 16* (F, MO, NY); E of Matucana, *Blood & Tremelling 31* (NY); W of San Mateo, *Blood & Tremelling 75* (F, UC); near Lima, *Blood & Tremelling 78* (F); Pucusana, cerca al gruta, *Cerrate & Acleto 3489* (USM); Prov. Huarochirí, San Mateo, *Cerrate 4233* (USM); Km 72 Carretera Central, Pte. Quitasombbrero, *Cerrate 4890* (USM); Prov. Huarochirí, Chacahuaro, carretera central cerca a Surco, *Cerrate et al. 8818* (USM); Km 85 along Central Highway E of Matucana, *Correll & Smith P-717* (LL, NY); above Canta, *Correll et al. P-286* (LL); Central Highway ca. 26 km above Chosica, 18 km W of Matucana, *Edwin & Schunke V. 3789* (BM, F, GH, NY, S, US); Matucana, W towards Lima, *Diers 1043* (S); at Km 88 along road between Lima and San Mateo, *Duncan et al. 2706* (MO); between Quichas and Sayín in Churín mountains, *Ellenberg 8717* (MO); entre Chosica y San Mateo, valle del Rimac, *Ferreyra 1370* (USM); Km 69–70 carretera central entre Chosica y San Mateo, *Ferreyra 2031* (USM); Surco, entre Lima y La Oroya, valle del Rimac, *Ferreyra 3475* (USM); Km 70 carretera central entre Chosica y San Mateo, *Ferreyra 3480* (MO, US, USM); entre Oyón y Churín, *Ferreyra 3537* (USM); Oyón, *Ferreyra 3547* (US, USM); Surco, entre Lima y La Oroya, *Ferreyra 4082* (US, USM); Surco, *Ferreyra 4083* (US, USM); entre Matucana y San Mateo, *Ferreyra 5313* (US); entre Cocachacra y Surco, carretera central Lima–Oroya, Km 65–66, *Ferreyra 5438* (US, USM); Prov. Lima, Chosica, cerca a Tiro al Blanco, *Ferreyra 6115* (US, USM); abajo de San Mateo, carretera Lima–Huancayo, *Ferreyra 6966* (MO, US, USM); Tornamesa, entre Chosica y Surco, carretera Lima–Huancayo, *Ferreyra 7034* (MO, US, USM); entre San Mateo y Matucana, Km 93 carretera central, valle del Rimac, *Ferreyra 7694* (US, USM); Prov. Huarochirí, Matucana, entre Lima y Oroya, valle del Rimac, *Ferreyra 8300* (USM); ruinas de Cajamarquilla, cerca a Lima, *Ferreyra 8348* (MO, USM); cerca a Canta, *Ferreyra et al. 8681* (USM); camino a Canta, *Ferreyra et al. 8722* (USM); ruinas de Cajamarquilla, cerca a Lima, *Ferreyra 10403* (USM); Km 56 de la carretera central, entre Lima y La Oroya, valle del Rimac, *Ferreyra 10484* (USM); Km 56 entre Lima y Oroya, *Ferreyra 13591* (USM); Km 70 carretera Lima–Oroya, *Ferreyra 14869* (G); San Juan, valle de Chancay, *Ferreyra 18348* (G, USM); cerca a Trapiche, antiguo camino a Hualar, *Ferreyra & Ferreyra 19150* (USM); Santa Eulalia, 40 km E of Lima in Valley of Río Rimac, *Gentry et al. 19147* (MO, NY); above Chosica, on Lima–La Oroya road, *Gentry et al. 19909* (BM, USM); Santa Eulalia road, few km N of Chosica and S of Huinca, *Gentry & Smith 36094* (MO); along roadside Lima–Chosica, *Goodspeed 11312* (UC); valley of Río Rimac, near Lima–Oroya highway at Km 60 E of Lima, *Goodspeed & Metcalf 30223* (UC); valley of Río Rimac, near Lima–Oroya highway at Km 81 E of Lima, *Goodspeed & Metcalf 30234* (MO, US, US); Prov. Huarochirí, dry wash above Santa Eulalia, *Goodspeed 33147* (MO, UC); Prov. Huarochirí, 91 km before Lima on road from Huancayo, *Hawkes et al. 5249* (C); along road from La Oroya to Lima, 1 km after Matucana, *Hermann 47* (NY); Cordillera de Nizaugate, paso de Hualla-hualla, *Humbert 30841* (US); Prov. Huarochirí, canyon of the Río Rimac just above San Bartolomé, on trail to Zarate,

Hutchison & Wright 7077 (F, UC, US); Km 78 on the Carretera Central (Central Highway) at river crossing, *Illis et al. P-1* (WIS); San Mateo on road to la Oroya, *Landrum 4639* (MO, NY); Prov. Huarochirí, Ocotara, Matucana, *Llatas Q. et al. 3798* (USM); Matucana, *López G. 214* (WIS); Matucana, *Macbride & Featherstone 159* (F, G, US); Tornamesa, *Malca & Zelada 023* (USM); road Chosica Matucana, *Mexia 04077* (MO, UC); Pishicoto, route Cieneguilla, Sicicaya, *Ochoa 11763* (US); camino frente a la estación ferrocarril, Matucana, *Pacheco & Palomino 1350* (USM); Prov. Canta, Canta, *Petersen & Hjerting 1192* (C, MO); Km 70 from Lima, near Surco, *Petersen & Hjerting 1217* (C); Matucana, Escuela de Agricultura, *Petersen & Hjerting 1228* (C, MO), *Petersen & Hjerting 1230* (C, MO); Tambo de Viso, Km 87 on carretera Central, *Plowman & Davis 4625* (GH); Quebrada Pedregales, 2 km debajo de Chosica, *Rick 112* (USM); Prov. Cajatambo, 5 km arriba de Churín, camino a Oyón, *Rick 235* (USM); 1/2 km S of Pacaibamba, *Rick & Rick SAL-356* (USM); 1 km al oeste de Espiritu Santo, a 43 mi de Lima, *Rick & Rick SAL-367* (USM); Capillucas, 16 mi NE de Catahuasi, camino de Imperial–Yauyos, *Rick SAL-423* (USM); oeste del pueblo de San Gerónimo, *Rick SAL-453* (USM); 38.2 mi NE de Sayán, *Rick SAL-463* (USM); Hacienda Limatambo, *Ridoutt s.n.* (USM); alrededores de Viso, entre Lima y Oroya, *Ridoutt 15384* (USM); Km 91, inmediaciones de Viso, entre Matucana y Casapalca, *Ridoutt 15385* (USM); Chosica, W of Lima, *Rutten 922* (U); up the valley of the Rimac, Matucana, *Safford s.n.* (NY, US); San Mateo, Andrés, *Sandeman 257* (BM); Prov. Huarochirí, San Eulalia–San Juan de Iris road, *Smith & León 1354a* (MO, USM); Canta, *Soukup 2802* (S, US); Matucana, *Soukup 4620* (F, US); Matucana, near Lima highway, *Stork & Horton 9139* (UC); Prov. Huarochirí, S of Matucana along the Carretera Central, *Sullivan et al. 847* (MO, NY); road to Canta, Km 74 near Yasao to outside Canta, *Sullivan et al. 949* (MO, NY, USM); Valley of Río Rimac NW of Matucana, ca. 7 km W of San Mateo, *Teppner 79/424* (US); Yaso, *Tovar 1023* (USM); Chuichin–Churín, *Tovar 9394* (USM); below Surco, Km 61 on the central highway (Carretera Central), *Ugent & Ugent 5285* (US, WIS); 6 km ENE of Matucana, Km 84 of Carretera Central (Central Highway), above the Rimac River, *Ugent & Ugent 5294* (F, MO, US, WIS); Bosque Zárate (Chunaca), *Valencia 1375* (NY); Santa Rosa de Quives, Valle de Chillón, *Velarde Núñez 871* (US); Canta, Km 103, *Velarde Núñez 924* (US); Surco, *Velarde Núñez 3156* (US); Huarhuan, carretera Quives–Arahuay, *Vilcapoma 79* (USM); alrededores de Canta, *Vilcapoma 182* (USM); Prov. Chancay, alrededores de Ñaupay, *Vilcapoma et al. 261* (USM); cerros al N de Chosica, *Weberbauer s.n.* (USM); Prov. Huarochirí, Bosque de Zárate above San Bartolo, *Weigend & Förther 97/4* (F, M); Prov. Yauyos, road from Pacaran to Yauyos, Km 52 after Pacaran, *Weigend et al. 7218* (BM); road from Yauyos to Jauja, few km after Magdalena, *Weigend et al. 7232* (BM); Sta. Eulalia, above Chosica, *West 3600* (MO, UC); 1 km E of Matucana on road to La Oroya, Rimac Canyon, *Whalen 849* (BH, MO, NY, USM).—MOQUEGUA: Mt. Estuquiña, NW of Moquegua, *Weberbauer 7445* (BM, F, G, S, US); cerro between Puquina and Omate, last roadbends before descent to Omate, near Charjon, *Weigend et al. 7762* (BM).—TUMBES: Prov. Zarumilla, Puerto Pizarro, *Cerrate 4956* (USM, see note below).

Solanum corneliomulleri is a very distinctive species, with its strongly curved anther tube and copious glandular pubescence interspersed with very long uniseriate trichomes that are usually gland-tipped. Rick (1986a) included it in his broadly defined *S. peruvianum* (as *Lycopersicon peruvianum*), based on its ability to interbreed with *S. peruvianum* s.str. and *S. arcanum* as defined here. Appendix 4 lists all the TGRC accessions (LA numbers) previously included in Rick's broad definition of *S. peruvianum* with their current identification according to this monograph. Populations of *S. corneliomulleri* from the region of Volcán Misti (Yura and Tingo) in the Department of Arequipa (e.g., *Schmidt s.n.*, F) are distinct in having narrower leaflets, shorter pubescence, and extremely long calyx lobes in fruit that enclose the berry like a cage.

Our AFLP analyses (Spooner et al. 2005) suggest that *S. corneliomulleri* and *S. peruvianum* are hybridizing in the southern part of Peru, especially in the coastal parts of the Department of Arequipa. The two taxa do not form two monophyletic clades in the AFLP analysis (see Fig. 17) although morphologically easily distinguishable, which suggests genetic exchange in this region. This genetic mixing is perhaps due to the migration of people and animals from the Peruvian highlands to the coast during the wetter parts of the year, when highland farmers bring animals to the lomas for grazing, which may potentially disperse the fruits and seeds (B. León, pers. comm.). This practice is especially

common in the wet valleys of Pisco (Dept. Ica) and Nazca (Dept. Nazca), where cultivation of crops is extensive and adventive seeds may become established.

The locality of a single specimen of *S. corneliomulleri* from Puerto Pizarro, Department of Tumbes (*Cerrate 4956*, USM), is anomalous in being very far north from the rest of the species range and right on the coast. This specimen is a good match for others collected in populations near Matucana (Department of Lima, ca. 1500 m elevation) region; we suspect it is mislabeled and did not include this record on the distribution map for this species (Fig. 39). *Solanum corneliomulleri* has never been collected north of Lima, and we have seen no other specimens approaching this morphology from the Department of Tumbes.

Specimens of cultivated plants of *S. corneliomulleri* from Colombia and the U.S.A. were examined; full details are available on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>).

“ARCANUM” GROUP

11. *Solanum arcanum* Peralta, Syst. Bot. 30: 429. 2005.—TYPE: PERU. Amazonas: western base of the Cerros Calla Calla, 9 km E of Balsas on road to Leimebamba, 1340 m, 30 May 1964, *Hutchison et al. 5449* (holotype: USM!; isotypes: F! K! M! MICH, MO! NY! UC! US!).

Lycopersicon peruvianum var. *humifusum* C. H. Müller, U.S. Dept. Agric. Misc. Publ. 382: 19. 1940.—TYPE: PERU. Cajamarca: between San Juan and Magdalena, 23 Dec 1937, *Blood & Tremelling 142* (holotype: US-40370!).

Spreading, erect or often prostrate, perennial herbs, woody at the base, to 1 m tall, to 1 m or more in diameter. Stem 7–12 mm in diameter at base, green, glabrous to variously pubescent with a mixture of simple uniseriate trichomes, short trichomes to 0.5 mm long (these eglandular or with a 1-celled head), longer patent trichomes to ca. 1 mm long, from multicellular bases, short glandular trichomes with 1-celled or multicellular heads, some populations (Chota Valley) with very sparse short unicellular trichomes. Sympodial units 2-foliate; internodes 2–6 cm long. Leaves interrupted imparipinnate, (3–) 5–15 (–25) cm long, (1–) 2.5–7 (–10) cm wide, green to pale beneath, glabrous to sparsely short-pubescent to densely pubescent with a mixture of simple uniseriate trichomes, some populations lacking stout patent trichomes to 1 mm long on the leaves, adaxially nearly glabrous with a few scattered 1-celled trichomes to densely pubescent with short and long trichomes, abaxially the pubescence more abundant, with more stout trichomes to 1 mm long along the veins; primary leaflets 2–4 (–5) pairs, the basal pair half the size of the rest, elliptic to broadly elliptic, apex acute, base acute to truncate, oblique and decurrent basiscopically, margin almost entire (Jequetepeque) to regularly or irregularly crenate-serrate to lobed; terminal leaflet usually longer than the lateral leaflets, 1.2–5 cm long, 0.6–2 (–2.5) cm wide, the petiolule 0.5–1 cm long, apex long-acuminate in Marañón populations; lateral leaflets 0.7–3.5 (–5) cm long, 0.4–2 (–2.5) cm wide, the petiolule 0.2–1 cm long; secondary leaflets occasionally present acropically on the larger leaflets, 0.1–0.2 cm long, 0.1–0.2 cm wide, sessile; tertiary leaflets absent; interjected leaflets 0–8, 0.1–0.5 cm long, 0.1–0.4 cm wide, decurrent on the leaflet rachis; petiole 0.5–2.5 (–3.5) cm long; pseudostipules present but not developed at all nodes, 0.5–1 cm long, 0.5–1 cm wide, margin entire to irregularly crenate. Inflorescences 6–20 cm long, unbranched, with 5–20 flowers, ebracteate or nearly all the nodes bracteate, bracts 0.1–0.4 (1) cm long, 0.1–0.2 (–1) cm

wide, larger in the basal nodes, peduncle (1.5–) 3.5–10 cm long, glabrous and minutely glandular to densely velvety-pubescent with intermixed longer patent trichomes like those of the stems. Pedicels 1.1–1.7 cm long, articulated at the middle or in the distal half. Buds 0.8–1 cm long, 0.3–0.4 cm wide, conical, straight, the corolla approximately halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube minute, lobes 5–7 mm long, 1.5–2 mm wide, lanceolate, glabrous to pubescent like those of the inflorescence; corolla 1.8–2 cm in diameter, pentagonal, yellow, the tube 0.5–0.6 (–0.8) cm long, lobes 0.8–1 cm long, 0.8–1 cm wide, white-pubescent on the tips and margins, reflexed at anthesis; staminal column 0.8–0.9 cm long, straight, filaments 0.25–0.5 mm long, anthers 0.4–0.5 cm long, equal, sterile apical appendage 0.1–0.25 cm long; ovary globose, glabrous or with a few minute trichomes at the apex; style 0.8–1 cm long, ca. 0.5 mm in diameter, densely white-pubescent in the basal half, straight, scarcely exerted to exerted ca. 0.5 mm beyond the staminal column; stigma capitate, green. Fruit 1–1.4 cm in diameter, globose, 2-locular, green, from apex to base with a dark green stripe (sometimes becoming purple at maturity), glabrous to more or less densely pubescent with weak-walled simple uniseriate trichomes less than 0.5 mm long; fruiting pedicels 1.5–2.3 cm long, angled towards the inflorescence axis, occasionally straight; calyx lobes in fruit 9–10 mm long, 2–2.5 mm wide, spreading to loosely investing the berry. Seeds 2.2–3.2 mm long, 1.2–1.6 mm wide, 0.5–0.6 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged at the apex and acute at the base. Chromosome number: $n = 12$ (LA 1396, <http://tgrc.ucdavis.edu>). Plate 1G, Plate 2G, Plate 3G; Fig. 40.

Phenology. Flowers and fruits sporadically throughout the year; populations in the lomas formations appear to flower in the foggy season (September to November), but this varies with rainfall and El Niño events.

Distribution (Fig. 41). Coastal and inland Andean valleys in northern Peru; in lomas, dry valleys, and on dry rocky slopes; 100–2500 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** AMAZONAS: Prov. Bagua, Km 248 entre Milagro y Amojao, cerca a Pongo de Retema, *Ferreya 13674* (USM); Prov. Bongará, Pedro Ruiz–Chachapoyas, Km 35, *Kahn & Moussa 2882* (USM).—ANCASH: just above Pariacoto, *Correll & Smith P-943* (LL, NY), *Correll & Smith P-945* (F, LL, NY); Prov. Huaráz, abajo de Callán, entre La Punta y Casma, *Ferreya et al. 16510* (USM); hacienda 24 mi W of Huaráz, Chacchán, *Macbride & Featherstone 2554* (F, G); Prov. Casma, cerca Yaután, 28.1 mi E de Casma, *Rick SAL-442* (USM); Prov. Caraz (Carhuaz?), Distr. Pamparomas, road from Moro to Pamparomas, *Weigend et al. 2000/962* (BM).—CAJAMARCA: near Magdalena between Chilete and pass on road to Cajamarca, *Correll & Smith P-834* (F, LL, NY); 34 km from Cajamarca on road to Chilete, *Correll & Smith P-845* (F, LL, NY), *Correll & Smith P-846* (LL, NY); between San Marcos and Cajabamba, *Correll & Smith P-904* (LL, NY), *Correll & Smith P-905* (LL, NY), *Correll & Smith P-907* (LL); near Choropampa, ca. 11 km W of San Juan and 48 km SW of Cajamarca on road to San Pedro de Lloc, *Dillon & Whalen 4081* (BH, F, USM); arriba de Chilete, más o menos a 15 km de Chilete carretera a Cajamarca, *Ferreya 3336* (USM); San Antonio–Portachuelo (carretera Ascope–San Benito), *López M. & Sagástegui 7922* (NY), *López M. & Sagástegui 7931* (F, MO); El Balcón (Algarrobal–San Benito), *López M. & Sagástegui 8432* (HUT, NY); arriba de Rupe (Chilete–Cachicadán), *López M. et al. 9224* (BM, F, HUT, MO); Prov. San Pablo, Distr. San Pablo, Cunish, 26.1 km NE along road from Chilete, *Merello et al. 1088* (CAS, MO); Chiquidén, de San Juan a Cajamarca, *Ochoa 1976* (F); alrededores de Sascas, *Rick 126* (USM); a lo largo del Río Jequetepeque, camino a Cajamarca, *Rick 132* (USM); Magdalena, camino a Cajamarca, *Rick 139* (USM); Rupe, 9.2 mi S de Chilete, *Rick SAL-435* (USM); El Portachuelo (Ascope–San Benito), *Sagástegui et al. 9228* (F, MO, NY); Rupe–Contumazá, *Sagástegui et al. 9814* (BM, MO); El Platanar, arriba de Cascas, *Sagástegui et al. 14625* (F), *Sagástegui & Leiva 14795* (BM, F, HUT, NY); alrededor de Guzmango, *Sagástegui et al. 15473* (F); Distr. San Juan, carretera San Juan–Cajamarca, arriba de San Juan, *Sánchez Vega 733* (F); Distr. San Marcos, Chugur, Km 55 de la carretera Cajamarca–Cajabamba (cerca a San Marcos), *Sánchez Vega 2258* (F, MO); Prov. Chota, Distrito Cochabamba, a 1 km sobre la carretera Cochabamba–Cutervo, *Sánchez Vega 2291* (F, MO); Prov. San Miguel, al O de la localidad de Quinden, sobre

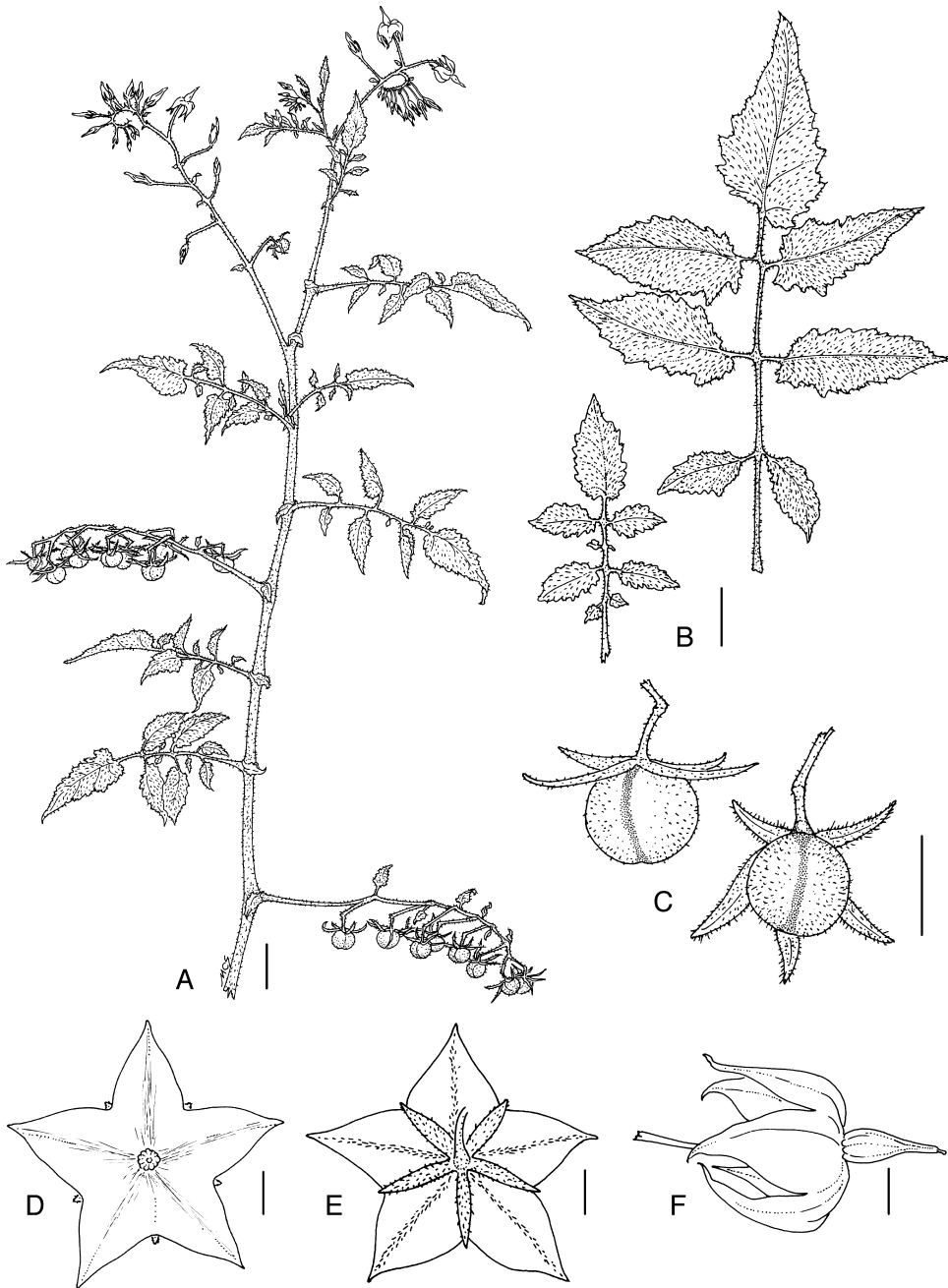


FIG. 40. *Solanum arcanum*. A. Branch. B. Two leaves. C. Two fruits. D. Adaxial view of flower. E. Abaxial view of flower. F. Side view of flower. Reproduced with permission from *Systematic Botany* 30: 427, fig. 1. 2005.

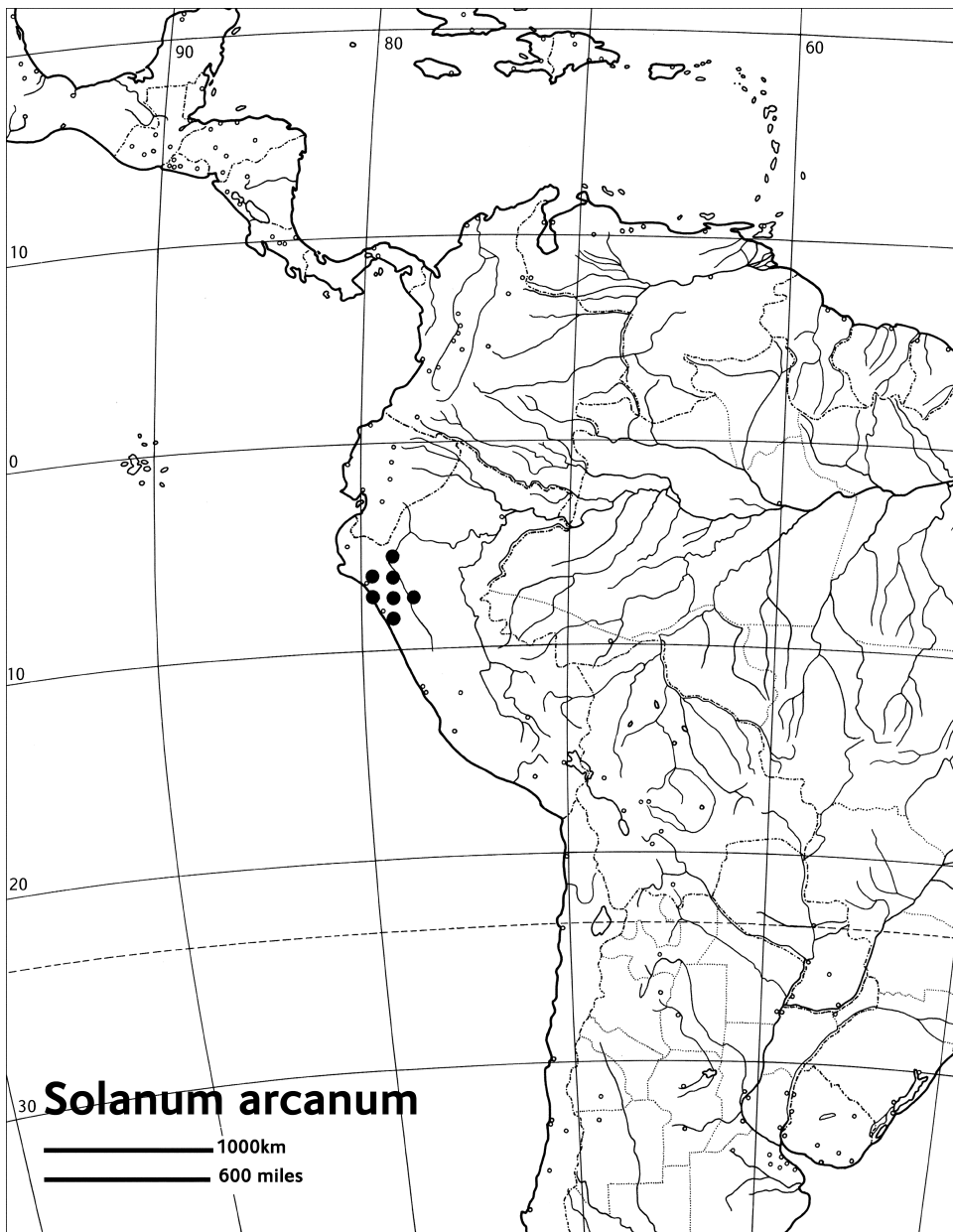


FIG. 41. Distribution of *Solanum arcanum*.

la carretera a Chapan, *Sánchez Vega et al. 3027* (F, NY); en la quebrada arriba de Choropampa, cerca al Puente Los Naranjos, sobre Km 128 de la carretera Cajamarca–Pacasmayo, *Sánchez Vega 3690* (F, NY); arriba de Cochabamba (a 2 km) siguiendo la ruta a Huambos, *Sánchez Vega 4573* (F); Lucmachucho, 1 km al NO de Cajamarca, sobre la ladera que converge al Río Ronquillo, *Sánchez Vega 6094* (F); Prov. Contumazá, 5 km W of Chilete, *Ugent & Ugent 5523* (F, MO, US, WIS); Prov. Cajamarca, 50 km SW of Cajamarca, between Magdalena and San Juan, *Ugent & Ugent 5388* (US, WIS); Prov. Santa Cruz, 9 km from Santa Cruz on road to Catache (FO1), *Weigend et al. 7541* (BM); 10 km W of San Juan on road to Chilete, Río Jequetepeque Valley, *Whalen & Dillon 896* (BH, MO, NY, USM).—LA LIBERTAD: Prov. Trujillo, Cerro Prieto, *Angulo 1018* (F); Cerro Campana, *Angulo 1236* (F); near Trujillo, *Blood & Tremelling 97* (GH), *Blood & Tremelling 111* (UC); Cerro Campana, *Boeke 1754* (MO, NY); Prov. Otuzco, Plaza-pampa, *Cevasco s.n.* (USM); E side of Cerro Campana, ca. 15 km N of Trujillo, *Dillon et al. 2703* (F, MO, NY, TEX, USM); Cerro Campana, *Ferreya 8610* (USM); encima de Samme, entre Trujillo y Otuzco, *Ferreya 14088* (USM); SE side of Cerro Campana, *Hutchison 1356* (UC); Prov. Huamachuco, Río Marañón Canyon, 1 km below Aricapampa, *Hutchison et al. 6203* (E, F, GH, K, MO, NY, S, UC, US, USM); abajo de José Balta (cerca de Agallpampa), *Leiva 952* (F, HUT); abajo de José Balta (ruta a Agallpampa), *Leiva 1015* (F); alrededores de El Platanar (oeste de Salpo), *Leiva 1019* (F, NY); abajo de José Balta (ruta a Agallpampa), *Leiva 1137* (F); alrededores de Huangabal (Simbal–La Cuesta), *Leiva & Salinas 1785* (F, M, NY); Cerro Campana, *Leiva & Quipuscoa 2077* (F, NY); Km 580 Cerro Cabezón, al N de Trujillo, *Leiva et al. 2159* (F, NY); Lomas de Virú, *López M. & Sagástegui 8418* (NY); Lomas de Virú, *Mostacero L. & Ramírez 678* (BM, HUT, MO); Lomas de Virú, *Mostacero L. et al. 1451* (F); alrededores de Otuzco, Cerro Chologday, *Mostacero L. & Quipuscoa 3163* (HUT); Prov. Bolívar, entre Pusac y Longotea, *Mostacero L. et al. 3566* (HUT); Lomas de Cerro Campana, *Rick 128* (USM); Cerro Campana, *Sagástegui 7821* (MO, NY); Cerro Campana, *Sagástegui & López M. 10414* (F, G, MO, NY); Cerro Campana, *Sagástegui 10939* (F); Cerro Cabezón, *Sagástegui & López M. 11017* (F); Cerro Chiputur, *Sagástegui & Mostacero 11035* (F); Lomas de Virú, *Sagástegui & Mostacero 11380* (BM, MO); Cerro Cabezón, cerca a Trujillo, *Weberbauer s.n.* (USM); Lomas de Virú, Cerro de las Lomas, *Weigend et al. 2000/696* (BM, M).—PIURA: Prov. Talara, 10 mi al E de Talara, *Haught 2* (USM).

Solanum arcanum is a member of a clade containing *S. neorickii* and *S. chmielewskii*, and is sister to them. It can be distinguished from them by its generally more finely crenate leaflets (leaflets of the other two species usually have more widely spaced crenations), larger inflorescences with more flowers, and the more complex mix of trichome types. *Solanum arcanum* and *S. neorickii* are sympatric in northern Peru, but *S. arcanum* is easily distinguished by its much larger corollas (1.8–2 cm in diameter vs. 1–1.2 cm in diameter) and greater number of flowers per inflorescence (10 vs. 7). Because accessions we now recognize as *S. arcanum* did not cross successfully with either *S. chmielewskii* or *S. neorickii* (Rick et al. 1976), Rick believed that they were not closely related. As we noted above, we do not feel crossability is a reliable indicator of relationship in the tomatoes and their relatives.

Solanum arcanum is an extremely variable species, comprising four weakly defined morphotypes (“assemblages”) with discrete geographic ranges. The complex overlapping variability, especially in leaf morphology, dissuades us from recognizing these as formal taxa. Appendix 4 lists all the TGRC accessions (LA numbers) previously included in Rick’s broad definition of *S. peruvianum* with their current identification according to this monograph. In this table we have also indicated the assemblages of *S. arcanum* to which individual accessions belong.

A. ‘MARAÑÓN’ ASSEMBLAGE. Robust erect plants, sometimes to 1 m tall, decumbent when mature; little to no velvety pubescence, with dense long patent trichomes, leaflets dentate or more deeply incised; growing in the Río Marañón Valley (includes the type of *S. arcanum*, *Hutchison et al. 5449*). This assemblage includes the Chamaya-Cuvita and the Marañón assemblages of races that Rick (1986 a) recognized as closely related based on their interfertility in experimental crosses.

B. 'HUMIFUSUM' ASSEMBLAGE. Slender prostrate plants; pubescence velvety; leaflets entire or with only a few marginal teeth, velvety-pubescent on the abaxial side, and dark green; inflorescence unbranched; growing in Pacific drainages (includes the type of *Lycopersicon peruvianum* var. *humifusum*, Blood & Tremelling 42).

C. 'CHOTANO' ASSEMBLAGE. Slender prostrate plants; almost completely glabrous; lateral leaflets deeply lobed; growing in the Río Chota Valley near Yamaluc in the Department of Cajamarca (e.g., *Sánchez Vega* 2291). The 'humifusum' and 'Chotano' assemblages also appear to be closely related based on data from interfertility experiments (Rick 1986a) and molecular analyses (Peralta & Spooner 2001), and differ mainly in pubescence.

D. 'LOMAS' ASSEMBLAGE. Slender prostrate to semi-erect plants; pubescence velvety; leaflets dentate or almost entire; inflorescences simple or sometimes branched; growing at the Lomas of Cerro Campana and Virú (e.g., *Dillon et al.* 2703). These populations are incredibly variable from year to year; specimens collected in El Niño years have very large leaves, while those collected in drier seasons have smaller, more pubescent leaves with fewer leaflets with less lobed margins. The 'Lomas' populations are also quite variable in other characters, such as the inflorescence branching pattern, and appear morphologically somewhat like southern populations of *S. peruvianum* s.str. (see that species, no. 9).

This variability and apparent morphological intermediacy led Rick to include populations now recognized as *S. arcanum* as part of a broadly constituted *S. peruvianum* (as *Lycopersicon peruvianum*). The northern populations of Rick's *L. peruvianum*, now recognized as *S. arcanum*, have complex crossing relationships with more southerly populations of *S. peruvianum* s.l. and with *S. chilense* (Rick 1963, 1986a). Because these northern populations could be crossed successfully with *S. chilense* but not with *S. peruvianum* s.str., Rick (1986a) suggested that they were ancestral to the rest of the "peruvianum complex," and that northern Peru was a major site of evolutionary development in the wild tomatoes.

Genes for resistance to powdery mildew have been identified in *S. arcanum* (LA2172, Bai et al. 2004). A list of TGRC accessions previously identified as *L. peruvianum* s.l. but now recognized as *S. arcanum* can be found in Peralta et al. (2005).

Individuals of *S. arcanum* grown in cultivation tend to be vigorous plants, with larger stems, internodes, leaves, inflorescences, flowers, and fruits than specimens collected from the wild, but they maintain similar characters found in wild specimens collected in similar geographic areas, and the cultivated accessions generally can also be assigned to the four assemblages mentioned above. Cultivated specimens of *S. arcanum* not cited here (but listed in Index to Numbered Collections Examined) have been examined from the U.S.A.; full details of these can be found on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>).

12. *Solanum chmielewskii* (C. M. Rick, Kesicki, Fobes & M. Holle) D. M. Spooner, G. J. Anderson & R. K. Jansen, *Amer. J. Bot.* 80: 683. 1993. *Lycopersicon chmielewskii* C. M. Rick, Kesicki, Fobes & Holle, *Theor. Appl. Genet.* 47: 58, figs. 2, 3. 1976.—TYPE: PERU. Apurímac: Prov. Abancay, Casinchihua, above Abancay, 21 Dec 1962, *Iltis et al.* 832 (holotype: WIS!; isotypes: GH! K! WIS! UC!).

Trailing or spreading perennial herbs, woody at the base, to 1 m tall, to 1 m or more in diameter. Stems 4–5 mm in diameter, pale grayish green, densely soft velvety-

pubescent with white, uniseriate trichomes to 0.2 mm long with a unicellular base, these interspersed with longer uniseriate 3–4-celled trichomes from multicellular bases and tiny glandular trichomes with 4-celled glands (sometimes 1- or 8-celled), the glandular trichomes more abundant on the young growth. Sympodial units 2-foliolate; internodes 3–8 cm long. Leaves interrupted imparipinnate, 5–12 cm long, 2–6 cm wide, dark green to pale green beneath, adaxially soft velvety-pubescent with simple, uniseriate eglandular trichomes like those of the stems, occasionally with longer more robust trichomes from a darker, multicellular base, abaxially the pubescence similar but denser, evenly spread on the veins and the lamina, the abaxial surface paler due to more abundant pubescence; primary leaflets 2–3 pairs, the basal pair usually smaller, narrowly elliptic to elliptic, apex acute, base truncate, very oblique and decurrent basiscopically, margin entire to deeply crenate, the crenations deeper near the base of the leaflets; terminal leaflet equal to or often larger than the lateral leaflets, (1.5–) 2–4.8 cm long, (0.5–) 0.6–1.8 cm wide, apex long-acuminate, the petiolule 0.2–1 cm long, apex acute; lateral leaflets (0.5–) 1–3.4 cm long, (0.3–) 0.4–1.5 cm wide, sessile or the petiolule to 0.5 cm long; secondary leaflets absent; tertiary leaflets absent; interjected leaflets 0–4, 0.1–0.9 cm long, 0.1–0.7 cm wide, sessile; petiole 1–3 cm long; pseudostipules present on some nodes, 0.5–1 cm long, 0.4–0.8 cm wide, margin entire to irregularly crenate. Inflorescences (2–) 3–9 cm, unbranched or sometimes once-branched, with 2–7 (–15) flowers, with bracts on the basal nodes, bracts 0.3–0.7 cm long, 0.4–0.5 cm wide, peduncle (1–) 2–4 (–11) cm long, pubescent like the stems. Pedicels 0.7–1 cm long, articulated in the distal half. Buds 1–1.2 cm long, ca. 0.5 cm wide, conical, the corolla halfway exerted beyond the calyx lobes just before anthesis. Flowers with the calyx tube 0.5–1 mm long, lobes 5–7 mm long, 1.5–2 mm wide, lanceolate, sparsely to densely pubescent with small simple, uniseriate trichomes and a few glandular trichomes like those of the inflorescence axis; corolla 1.6–2 cm in diameter, rotate-stellate, bright yellow, the tube 0.3–0.5 cm long, lobes 0.5–0.8 cm long, 0.5–0.6 cm wide, reflexed at anthesis; staminal column 0.9–1.1 cm long, straight, filaments ca. 0.5 mm long, anthers 0.6–0.7 cm long, equal, sterile apical appendage 0.15–0.2 cm long; ovary globose, or minutely papillate at the apex; style 0.8–0.9 cm long, ca. 0.5 mm in diameter, densely white-pubescent in the basal half, straight, exerted 0.5–1 mm beyond the anthers; stigma minutely capitate, green. Fruit 1–1.3 cm in diameter, globose, 2-locular, green, with a dark green stripe from apex to base, densely papillate and sparsely pubescent with extremely slender and weak simple uniseriate trichomes to 0.5 mm long; fruiting pedicels 1–1.3 cm long, straight or slightly angled at the articulation; calyx lobes in fruit 8–10 mm long, 2–3 mm wide, loosely investing the base of the berry to somewhat spreading. Seeds 2.2–3.2 mm long, 1.2–1.6 mm wide, 0.6–0.8 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged (0.2 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (LA1028, <http://tgrc.ucdavis.edu>). Plate 1F, Plate 2F, Plate 3F; Fig. 42.

Phenology. Flowers from December to April, but it is likely that flowering occurs sporadically throughout the year (Rick et al. 1976).

Distribution (Fig. 43). In high dry Andean valleys from the Department of Apurímac in southern Peru to Sorata in northern Bolivia; 2300–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Peru.** APURÍMAC: Prov. Abancay, above Río Pachacacha, W side, 1–2 km below Casinchiua, Hacienda Casinchiua in Río Pachacacha Valley, 33 km by air SW of Abancay, *Illis et al.* 833 (F, GH, K, NY, U, UC, US, WIS); N of Curahuasi, *Monro et al.* 3864 (BM); Prov. Andahuaylas, Km 234 from Abancay to Ayacucho, *Petersen & Hjerting* 1424 (C). **Bolivia.** LA PAZ: Prov. Larecaja, de Sorata

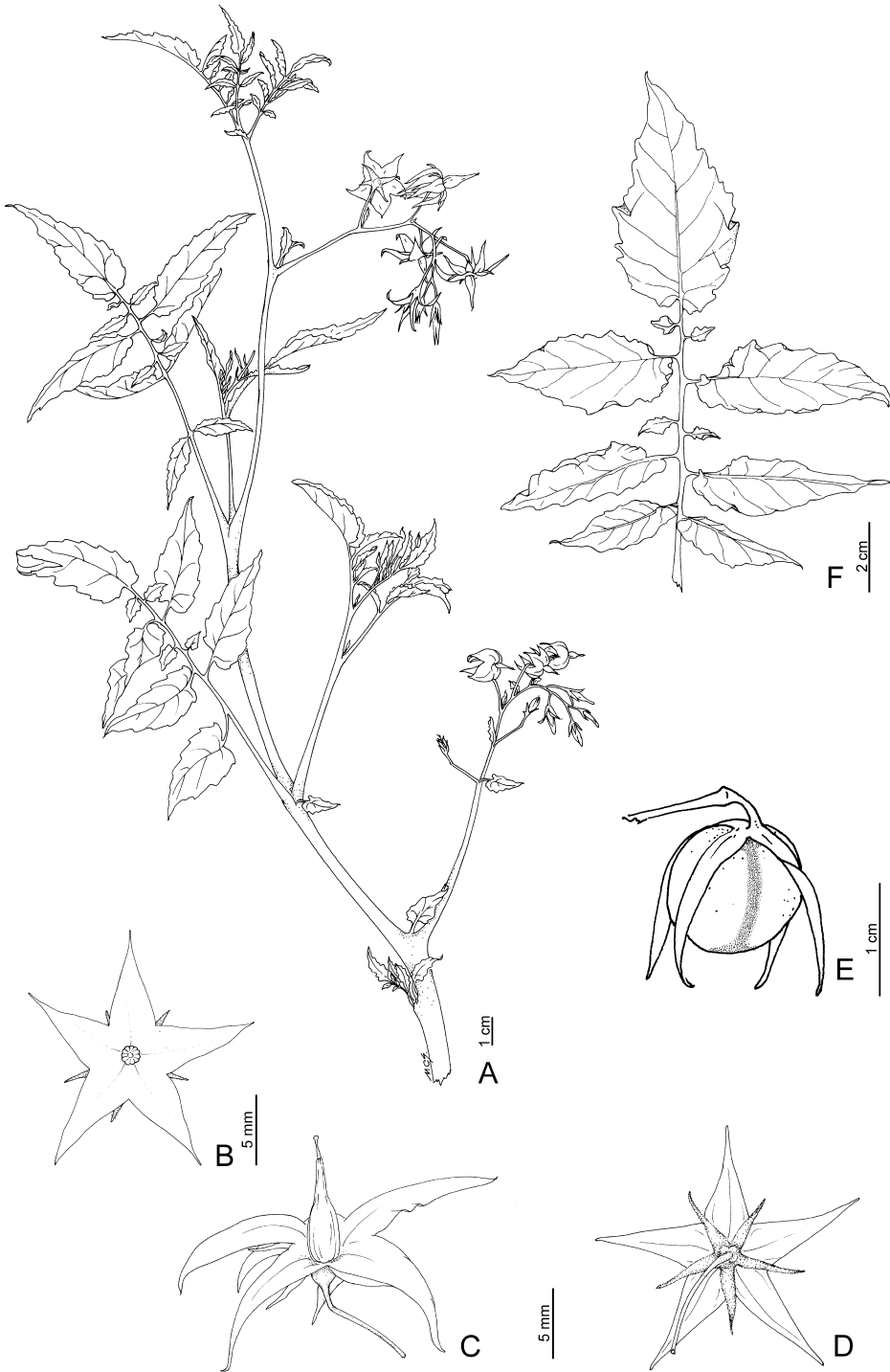


FIG. 42. *Solanum chmielewskii*. A. Branch. B. Adaxial view of flower. C. Side view of flower. D. Abaxial view of flower. E. Fruit. F. Leaf.

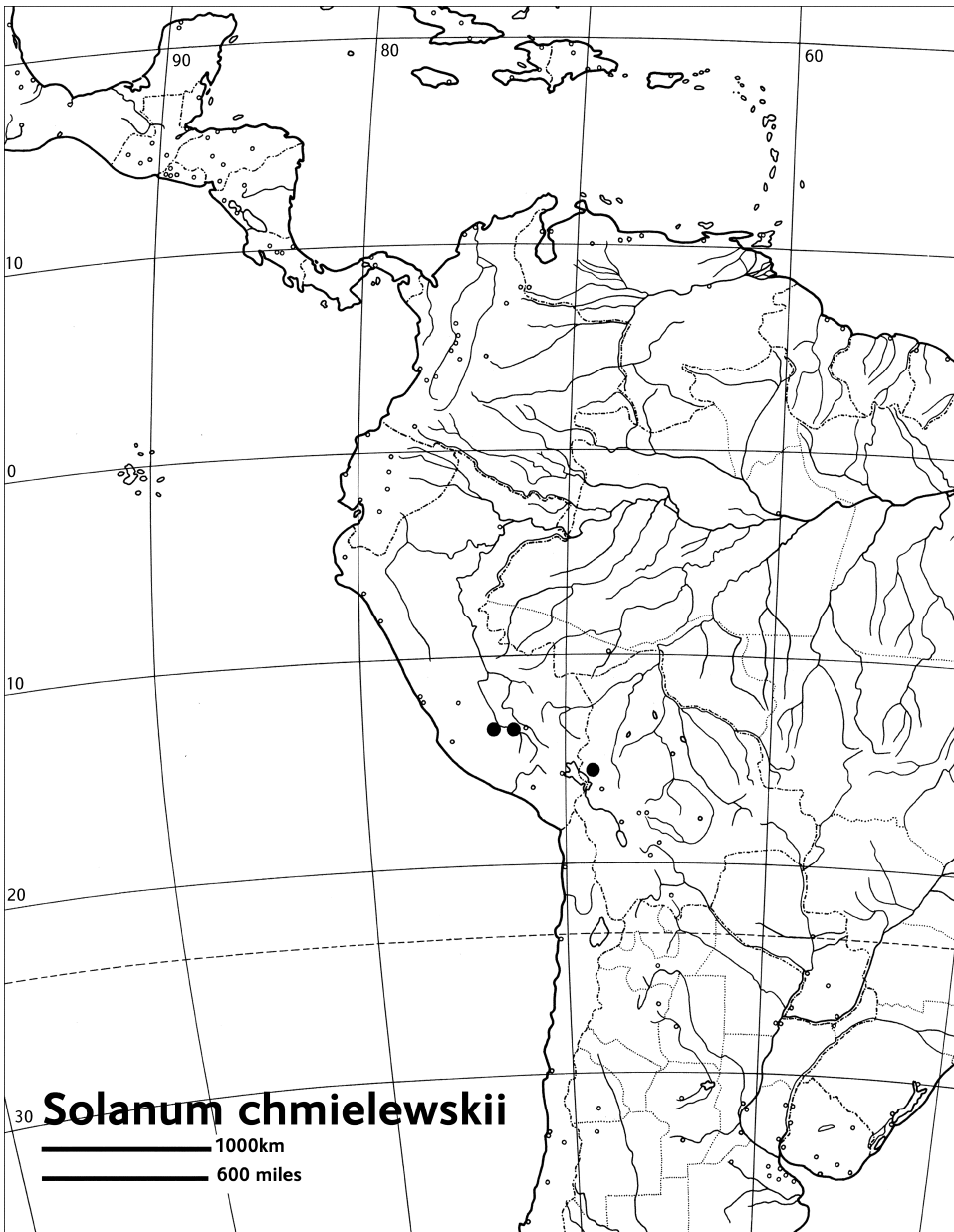


FIG. 43. Distribution of *Solanum chmielewskii*.

bajando el Río San Cristóbal, hasta la Gruta de San Pedro, Beck 18709 (LPB, NY); viciniis Sorata, San Pedro, Mandon 392 (BM, G, W).

Solanum chmielewskii is sister to *S. neorickii* and is difficult to distinguish from that species in the absence of flowers. Both species are related to *S. arcanum*, from northern Peru, rather than to *S. lycopersicum* and the other red-fruited species, as was suggested by

Rick et al. (1976). The flowers of *S. chmielewskii* are about twice the size of those of *S. neorickii*, and the stigma is always exerted from the anther cone. The corolla tube tends to be slightly larger in diameter, with a more pentagonal corolla outline. Both species have uniform, short whitish pubescence and small green fruits.

Rick et al. (1976) suggested that the outcrossing *S. chmielewskii* gave rise to the autogamous *S. neorickii* in their area of sympatry in southern Peru (Dept. Apurímac) near the type localities for both species. Crosses between the two species usually resulted in low seed set (Rick et al. 1976), suggesting they have developed reproductive isolation, at least in their area of sympatry. Hybrids obtained were intermediate in size between the two parents. *Solanum chmielewskii* prefers drier, better-drained habitats than *S. neorickii* (Rick et al. 1976) and is found at somewhat higher elevations. The only Bolivian collection is from the Sorata Valley (Mandon 392), which is drier than other Yungas valleys in Bolivia and is the southern limit for other species of Solanaceae of dry habitats, such as *Nicotiana glutinosa* L.

13. *Solanum neorickii* D. M. Spooner, G. J. Anderson & R. K. Jansen, Amer. J. Bot. 80: 683. 1993. *Lycopersicon parviflorum* C. M. Rick, Kesicki, Fobes & Holle, Theor. Appl. Genet. 47: 57, figs. 1, 3. 1976, non *Solanum parviflorum* Cavanilles, 1795.—TYPE: PERU. Huánuco: Prov. Dos de Mayo, Chavinillo, 2100 m, 18 Mar 1951, Ochoa 1071 (holotype: “herb. Ochoa” n.v.). [Type number corrected from Ochoa 1017 as cited in Rick et al. 1976, see below.]

Trailing perennial herbs, somewhat woody at the base, to 2 m long. Stems 2–2.5 (–5) mm in diameter, dark green, densely soft velvety-pubescent with mostly eglandular trichomes, the more abundant trichomes 1–2-celled, eglandular, white, uniseriate, 0.3–0.5 mm long, with a unicellular base, occasionally interspersed with sparse glandular trichomes with unicellular heads or multicellular heads, in northern populations with scattered robust patent uniseriate trichomes to 1 mm long with multicellular bases. Sympodial units 2-foliate; internodes (1–) 2–4.5 cm long. Leaves interrupted imparipinnate, (3–) 5–8 cm long, (1.5–) 3–5 cm wide, dark green to pale green beneath, adaxially sparsely pubescent with soft eglandular trichomes distributed evenly on the veins and lamina, abaxially densely pubescent with eglandular trichomes, the abaxial surface paler owing to the velvety pubescence; primary leaflets 2–4 pairs, the basal pair markedly smaller, narrowly elliptic to elliptic, apex acute to acuminate, base acute to truncate, usually decurrent basiscopically, margin crenate-serrate, the crenations deeper in the basal 1/3, occasionally the distal half of the leaflet margin entire; terminal leaflet usually larger than the laterals (1–) 2.5–3.5 cm long, (0.4–) 1–2 cm wide, usually long-acuminate, the petiolule 0.4–0.5 cm long, apex acute; lateral leaflets (0.5–) 1.2–2.5 cm long, (0.2–) 0.7–1.2 cm wide, the petiolule 0.2–0.5 cm long, or absent and the leaflets sessile; secondary leaflets absent; tertiary leaflets absent; interjected leaflets 0–4, 0.3–1 cm long, 0.3–0.5 cm wide, orbicular or elliptic, the petiolule ca. 0.1 cm long; petiole 0.5–1.5 cm long; pseudostipules present but not developed at all nodes. Inflorescences (2–) 5–14 cm long, simple, with 5–10 (–12) flowers, sometimes with 1–2 bracts 0.1–0.5 cm long, 0.1–0.5 cm wide, peduncle 1–4 cm long, pubescent like the stems, but with scattered glandular trichomes with multicellular heads and a few stout patent uniseriate 2–3-celled trichomes ca. 2 mm long, arising from multicellular bases along the axis. Pedicels 0.6–1 cm long, articulated in the distal half. Buds 0.4–0.5 cm long, 0.3–0.35 cm wide, broadly conical, the corolla more than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube ca. 1 mm long,

lobes 2.5–3 mm long, 1–1.5 cm wide, lanceolate, densely pubescent with uniseriate trichomes like the inflorescence axis; corolla 1–1.2 cm in diameter, pentagonal, golden-yellow, the tube (0.1–) 0.2–0.3 cm long, lobes 0.3–0.4 cm long, 0.3–0.4 cm wide, strongly reflexed at anthesis, margins irregularly undulate in living plants; staminal column 0.4–0.6 cm long, straight, filaments 0.5 mm long, anthers 0.25–0.3 cm long, equal, sterile apical appendage 0.1–0.15 cm long; ovary globose, glabrous; style 0.4–0.45 cm long, ca. 0.5 mm in diameter, densely pubescent in the proximal 2/3 with long, white uniseriate trichomes, just included in the staminal column or rarely exerted to 0.5 mm; stigma capitate, green. Fruit 1–1.1 cm in diameter, globose, 2-locular, green with a dark green stripe from apex to base, sparsely white velvety-pubescent when maturing, the trichomes all eglandular to 0.2 mm long, glabrescent when ripe; fruiting pedicels 1–1.5 cm long, straight or somewhat angled at the articulation; calyx lobes in fruit 9–12 mm long, 2–3 mm wide, not reflexed, loosely enclosing the berry but often spreading. Seeds 1.7–2.6 mm long, 1.0–1.3 mm wide, 0.4–0.6 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface, narrowly winged (0.2 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (LA0247, <http://tgrc.ucdavis.edu>). Plate 1E, Plate 2E, Plate 3E; Fig. 44.

Phenology. Flowers and fruits sporadically throughout the year.

Distribution (Fig. 45). Southern Peru (Department of Apurímac) to southern Ecuador (Department of Azuay); in dry inter-Andean valleys, often found trailing over rocky banks and roadsides; 1950–3000 m.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** AZUAY: above the Río León, *Camp E-278* (NY); Km 89 S of Cuenca on Panamerican Highway, *Holm-Nielsen et al. 4923* (NY, S). **Peru.** AMAZONAS: Prov. Bongará, entre Jazán y Pomacocha, *Ferreyra et al. 20595* (USM).—APURÍMAC: near first crossing of stream ca. 1 km E of Curahuasi on road to Apurímac River and Cuzco, *Ittis et al. 739* (USM, WIS); south of Abancay, *Monro et al. 3924* (BM); Prov. Abancay, Río Pachacacha, 20 km N of Abancay, *Stork et al. 10543* (F, UC).—CAJAMARCA: between San Marcos and Cajabamba, *Correll & Smith P-905* (LL), *Correll & Smith P-907* (LL).—CUZCO: Punta Cunyac, Valle de Apurímac, desde Ocha de Quilca alrededor de Limatambo, *Velarde Núñez 1406* (US).—HUÁNUCO: Prov. Ambo, Puente Huandobamba, *Ochoa 14548* (US).—PASCO: San Rafael, *Macbride 3141* (F, G, S); about 3.6 km N of San Rafael to about 4 km S of San Rafael, *Smith s.n.* (USM).

Solanum neorickii is sister to *S. chmielewskii* and, in the absence of flowers, difficult to distinguish from it (see that species, no. 12). In general *S. neorickii* has smaller inflorescences and somewhat less robust stature than *S. chmielewskii*. *Solanum neorickii* is autogamous and self-pollinating, which perhaps accounts for its much broader distribution compared to that of *S. chmielewskii* (throughout the inter-Andean valleys from southern Ecuador to southern Peru as opposed to southern Peru and adjacent northern Bolivia). Rick et al. (1976) suggested that *S. neorickii* was an example of “speciation via the simple device of autogamy,” although they did not observe pollination or reproduction in the wild. The species is remarkably uniform genotypically throughout its range in Peru, and all allelic diversity in *S. neorickii* is also found in *S. chmielewskii* (Rick et al. 1976).

The location of the type of *Solanum neorickii* is problematic. Although in the original publication of *Lycopersicon parviflorum* Rick et al. (1976) designated a specimen of *Ochoa 1017* as the type of their new species, that collection is actually a grass collected at “Km 40 on the road Carhuamayo–Paucartambo” in the Department of Pasco (C. Ochoa in litt., 25 April 2003). Ochoa’s collection (*Ochoa 1071*) from “Km 18 of Huánuco–Chavinillo road, department of Huánuco” (fide C. Ochoa in litt., 25 April 2003), is the type of *L. parviflorum*; this correct number is maintained in the TGRC database under



FIG. 44. *Solanum neorickii*. A. Branch. B. Fruit. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Leaf.

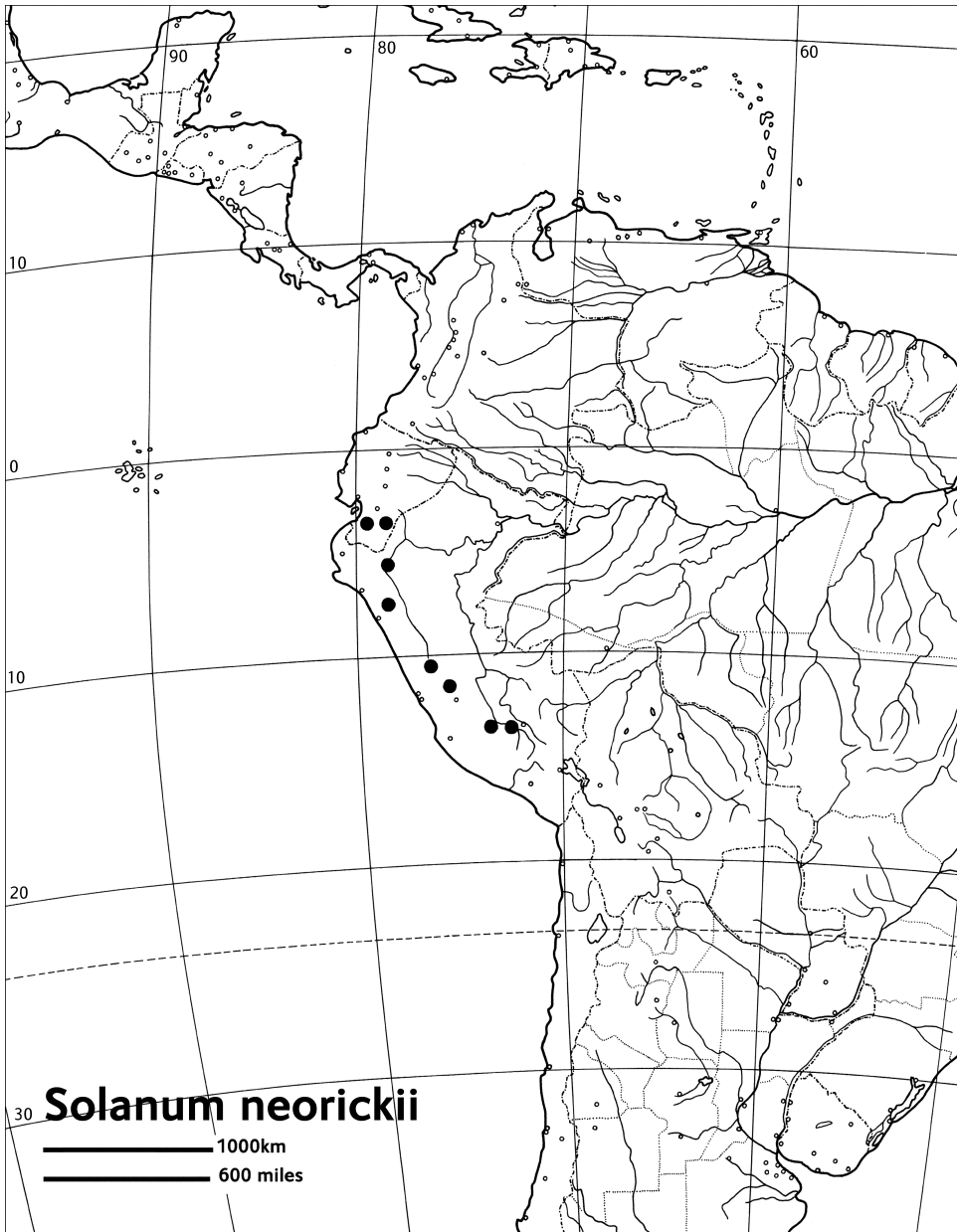


FIG. 45. Distribution of *Solanum neorickii*.

LA247. The whereabouts of the type specimen of this species is still unclear; Rick et al. (1976) cite it from “herb. Ochoa,” whereas Ochoa (C. Ochoa, in litt., 25 April 2003) suggests it is to be sought at DAV, F, or US. Dr. Ochoa’s personal herbarium has been widely dispersed (mostly at CUZ), and we were unable to find a specimen of either *Ochoa 1071* or *Ochoa 1017*. Searches at F and US were similarly fruitless. Many of Ochoa’s potato specimens have been donated to CUZ, but we have not had the opportunity to search there for this specimen. If the original specimen cannot be found at CUZ, a neotype should be designated from material grown from original seed of *Ochoa 1071* (LA247).

The unpublished name “*Lycopersicon minutum*” was written on herbarium sheets by Holle and occasionally by Rick, and was “applied to the whole complex” (Rick et al. 1976), i.e., *S. chmielewskii* and *S. neorickii* as recognized here. This herbarium name has no nomenclatural standing; specimens were “tentatively labeled” by the authors, who did not intend to propose a new name (Rick et al. 1976).

“LYCOPERSICON” GROUP

- 14. *Solanum pimpinellifolium* L.**, Cent. 8. 1755. *Lycopersicon pimpinellifolium* (L.) Miller, Gard. Dict. ed. 8, *Lycopersicon* No. 4. 1768. *Lycopersicon esculentum* subsp. *pimpinellifolium* (L.) Brehznev in Zhukovskii, Kult. Fl. SSSR 20: 64. 1958.—TYPE: Cultivated in Uppsala, *Anon. s.n.*. (lectotype, designated by Knapp & Jarvis, 1990: LINN 248.15! [BH neg. 6802: GH! UC! WIS!]).
- Lycopersicon pissisi* Philippi, Anales Univ. Chile 56. 1861. *Solanum pissisi* (Philippi) Reiche, Anales Univ. Chile Santiago 124: 743. 1909.—TYPE: CHILE. Region III (Atacama): Vallenar, 1850, *Volkman s.n.* (holotype: SGO-055601 [Departamento de Investigaciones Agrícolas neg. s.n.: F! GH!]).
- Lycopersicon racemigerum* Lange, Ind. Sem. Hort. Haun. 26. 1865. *Lycopersicon racemiforme* Lange, Bot. Tidsskr. 5: 189. 1872, nom. superfl. *Solanum racemigerum* (Lange) Zodda, Ann. Bot. Roma 2: 272. 1905. *Lycopersicon esculentum* subsp. *pimpinellifolium* var. *racemigerum* (Lange) Brezhnev in Zhukovskii, Kult. Fl. SSSR 20: 65. 1958.—TYPE: Specimen prepared from plants cultivated in Copenhagen from seeds originally sent from New York (lectotype, here designated: C!; isolectotype: C!).
- Solanum lycopersicum* var. *ribesioides* Voss, Vilm. Blumengärtn. ed. 3, 1: 721. 1894.—TYPE: unknown.
- Lycopersicon esculentum* subsp. *intermedium* Luckwill, Aberdeen Univ. Studies 120: 24. 1943. *Lycopersicon pimpinellifolium* var. *intermedium* (Luckwill) Prokhanov, Fl. USSR 22: 50. 1950.—TYPE: Specimen prepared from plants cultivated at John Innes Horticultural Institute, United Kingdom (holotype: unknown).

Annual, biennial, or sometimes perennial herbs, erect initially, later procumbent and viny with branches extending to 3 m from center. Stems 8–11 mm in diameter at base, green, usually sparsely (rarely densely velvety-) pubescent; trichomes of several types, the most common uniseriate, 1–2-celled, white and thin, ca. 0.5 mm long, with a unicellular base, also with sparsely scattered glandular trichomes with unicellular or multicellular heads, occasionally (in northern Peruvian populations) with larger, robust patent uniseriate trichomes to 1 mm long, with a multicellular base and eglandular or with a minute unicellular glandular head, and minute glandular trichomes with unicellular heads.

Sympodial units 3-foliolate; internodes 2–8 cm long. Leaves interrupted imparipinnate, 4–12 cm long, 1.5–8 cm wide, green, sparsely to densely pubescent with a mixture of uniseriate glandular and eglandular trichomes, pubescence velvety, denser along the veins and abaxially, in northern Peruvian populations with robust patent uniseriate trichomes like those of the stems along the veins abaxially; primary leaflets 2–4 pairs, slightly decreasing in size towards the leaf base, elliptic to broadly elliptic to ovate to broadly ovate, apex somewhat rounded or acute to acuminate, base cordate or occasionally truncate, oblique and extended basiscopically, margin entire or round-crenate or slightly dentate in the proximal third (more crenate in putatively hybrid populations in northern part of the species range); terminal leaflet 2.5–5 cm long, 1–3.5 cm wide, the petiolule 0.5–2 cm long; lateral leaflet (largest) 1.5–3.5 cm long, 1–2 cm wide, the petiolule 0.5–0.7 cm long, with the base usually decurrent basiscopically; secondary leaflets absent; tertiary leaflets absent; interjected leaflets usually few, 1–4 pairs, 0.5–1.2 cm long, 0.2–0.7 cm wide, sessile or with the petiolule to 0.2 cm long, the length between the lateral and interjected leaflets extremely variable, generally 0.5–2 cm long; petiole (0.8–) 1.5–5 cm long; pseudostipules absent. Inflorescences 4–25 cm long, usually simple, occasionally once-branched, with 7–30 flowers, ebracteate, peduncle 2–3 (–5) cm long, pubescent like the stems but with more glandular trichomes with multicellular heads. Pedicels 1–1.3 cm long, the articulation in the distal half. Buds 0.5–1.2 cm long, elongate conical, the corolla more than 2/3–3/4 of the way exerted beyond the calyx just before anthesis. Flowers with the calyx tube 0.5–1 mm long, lobes 2.5–5 mm long, 1–2.5 mm wide, lanceolate, densely pubescent with uniseriate trichomes like the rest of the inflorescence; corolla 1.2–3 cm in diameter, stellate, pale yellow to bright yellow, the tube 0.1–0.25 cm long, the free portion of the lobes 1–1.5 cm long, 0.2–0.4 cm wide, the tips and margins densely and minutely white-pubescent abaxially, lobes strongly reflexed at anthesis; staminal column 0.7–1 cm long, straight, filaments 0.5–1 mm long, anthers 0.5–0.7 cm long, equal, sterile apical appendage 0.3–0.4 cm long; ovary conical to globose, glabrous; style 0.7–1 cm long, ca. 0.5 mm in diameter, densely white-pubescent in the basal 1/3, straight, included to usually exerted 0.5–1 mm beyond the anthers; stigma capitate, green. Fruit to ca. 1 cm in diameter, globose, 2-locular, bright red when ripe, sparsely to densely glandular-pubescent with short uniseriate trichomes ca. 0.5 mm long, with multicellular and unicellular heads during maturation, glabrous when mature; fruiting pedicels 1.5–2 cm long, straight or bent in towards the rachis at the articulation point; calyx lobes in fruit 10–12 mm long, 2.5–4 mm wide, strongly reflexed and parallel with the fruiting pedicel. Seeds 2–3 mm long, 1–1.3 mm wide, 0.5–0.8 mm thick, obovate, narrowly winged at the apex and acute at the base, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or more often shaggy, narrowly winged (0.3–0.4 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (LA1280, <http://tgrc.ucdavis.edu>). Plate 1B, Plate 2B, Plate 3B; Fig. 46.

Phenology. Flowers and fruits throughout the year in response to moisture.

Distribution (Fig. 47). Apparently native to coastal areas from northern Peru to central Chile, although populations are found to central coastal Ecuador (but see below); in wet places and on the edges of cultivated fields throughout its native range; apparently escaped from cultivation in the Galápagos Islands (see Darwin et al. 2003); sea level to 500 m.

ADDITIONAL SPECIMENS EXAMINED: **Ecuador**. Without locality, *Fraser s.n.* (BM); without locality, *Jame-son s.n.* (W).—EL ORO: Pénjamo, *Albert de Escobar 835* (MO); Santa Rosa, *Blood & Tremelling 587* (NY);

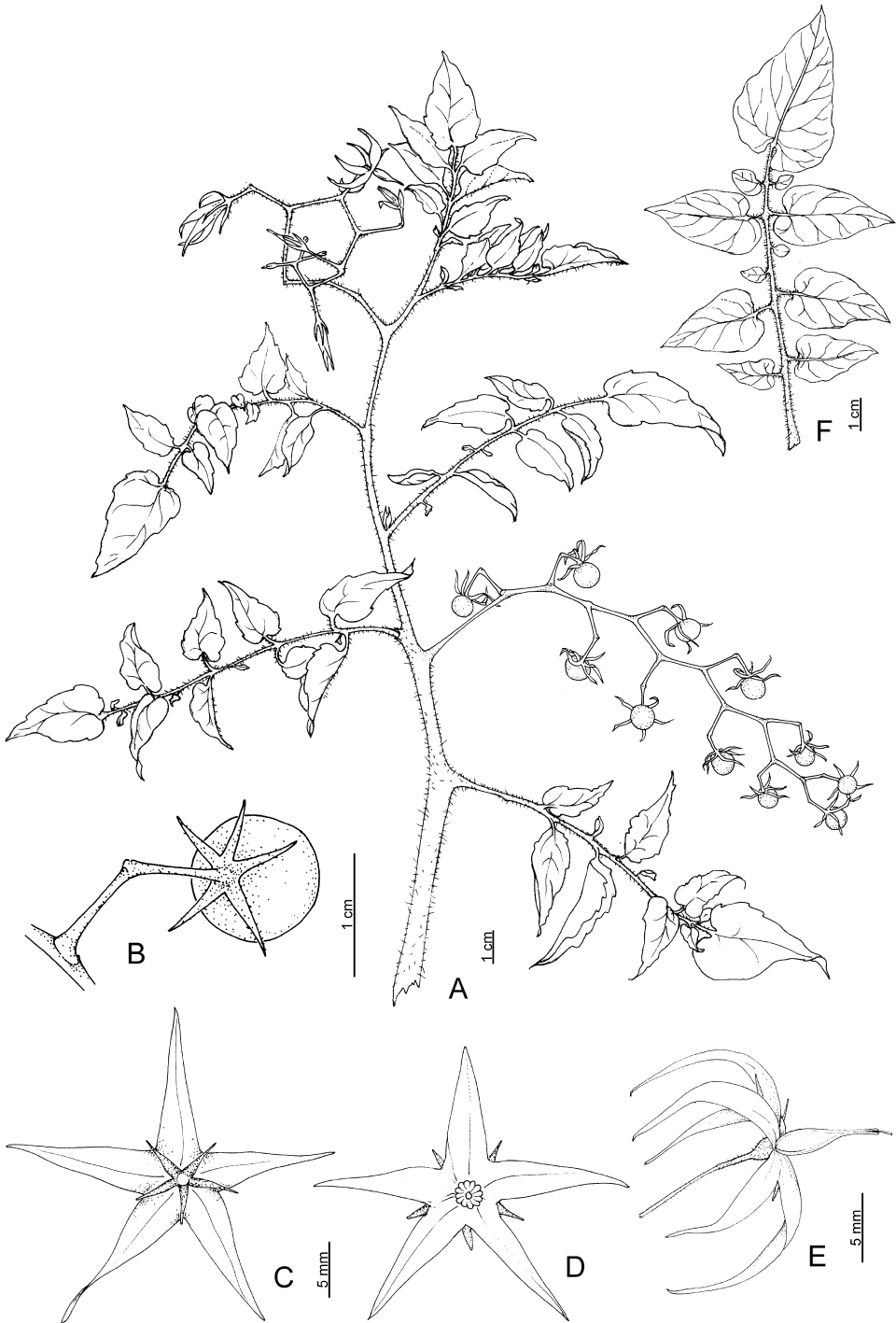
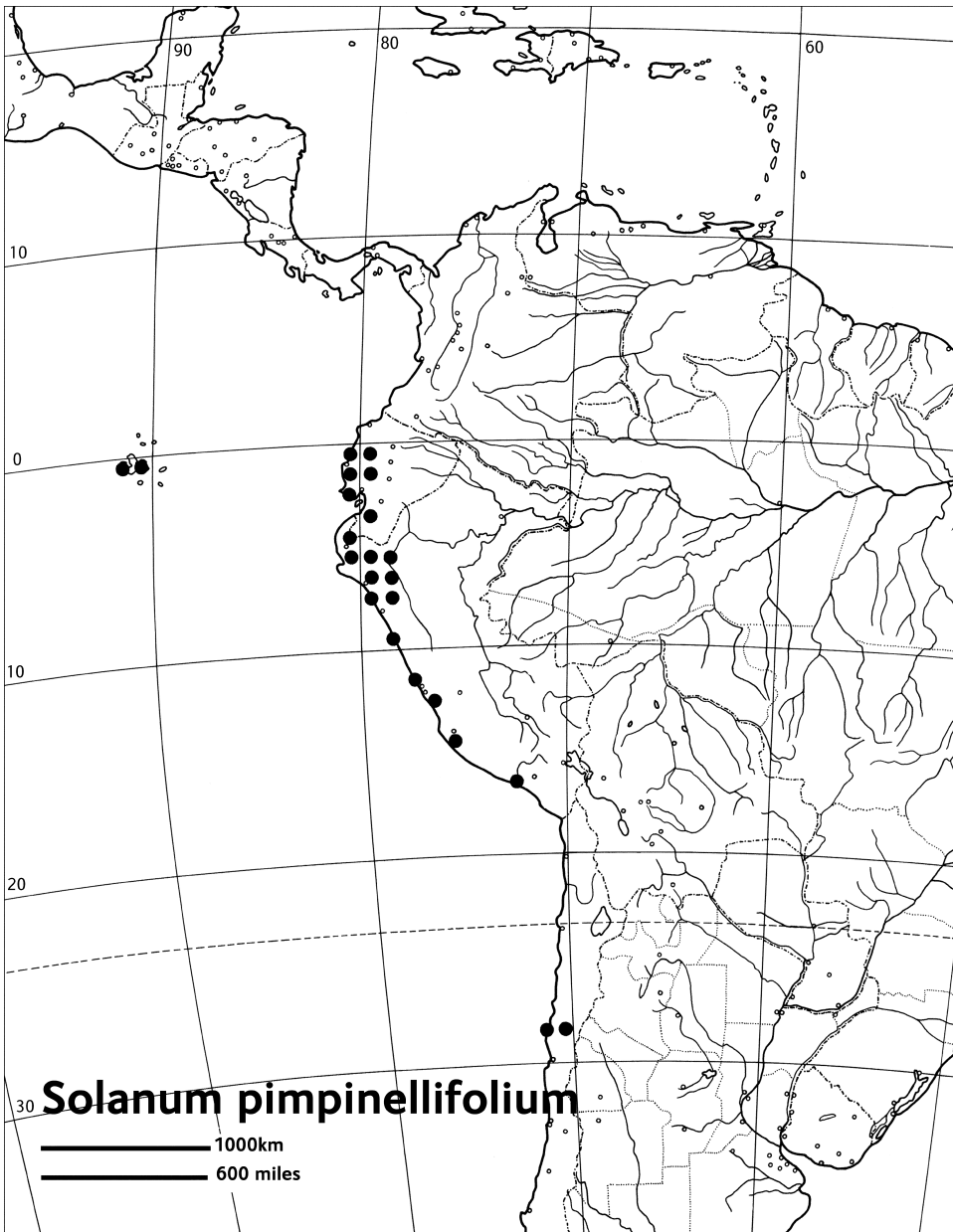


FIG. 46. *Solanum pimpinellifolium*. A. Branch. B. Fruit. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Leaf.

FIG. 47. Distribution of *Solanum pimpinellifolium*.

Pasaje, *Blood & Tremelling* 591 (GH); SW of Pasaje, *Blood & Tremelling* 604 (F, MO); 30 km SW of Santa Rosa on road to Piñas, *Dodson et al.* 8884 (MO); Recreo, *Eggers* 15809 (F); W of Babahoyo, *Schimpff* 303 (G, M, MO, Z); Chacras, Cantón Arenillas, *Van den Eynden & Cueva* 933 (QCA).—ESMERALDAS: environs of Lita, on the Ibarra–San Lorenzo R.R., *Madison et al.* 5291 (F); Quinindé, carretera vecinal Herrera–Los Monos, cabecera del Río Aguacatal, Finca de Francisco Cantos, *Palacios* 13695 (MO); Atacames beach, *Webster & Lockwood* 22806 (TEX).—GALÁPAGOS: Santa Cruz, Bella Vista village NW side of the play ground, *Darwin* 100 (BM), *Darwin* 101 (CDS); Santa Cruz, Bella Vista village, on road S/SE of the village, *Darwin* 103 (BM, CDS, QCA, QCNE), *Darwin et al.* 104 (BM, CDS, QCNE); Santa Cruz, between Puerto Ayora and Bella Vista, to the west of the main road, at the old basura site, *Darwin et al.* 109 (BM, CDS, QCNE); Santa Cruz, between Los Gemelos and the Canal, on the west side of the main road, the “new” basura, *Darwin et al.* 114 (BM, CDS, QCA, QCNE), *Darwin et al.* 125 (CDS); Santa Cruz, first hill N of Los Gemelos, *Darwin et al.* 195 (BM), *Darwin et al.* 196 (CDS); Santa Cruz, Puerto Ayora, *Darwin* 277 (BM, CDS); Santa Cruz, Puerto Ayora, *Darwin* 278 (BM, CDS); Isabela, 13 km N of Villamil, Las Merceditas near San Tomás, *Darwin et al.* 300 (BM, CDS); Isabela, just outside Villamil, by El Lagoon del Manzanillo, *Darwin & Rosero* 371 (BM); San Cristóbal, Puerto Baquerizo Moreno, E side of the town by Bethel School, *Darwin & Carrera* 379 (BM, CDS), *Darwin & Carrera* 380 (BM, CDS); Santa Cruz, El Chato Tortoise Reserve, by the lake, *Darwin et al.* 400 (QCNE), *Darwin et al.* 401 (BM), *Darwin et al.* 402 (BM, CDS), *Darwin et al.* 403 (QCNE); Santa Cruz, quarry between Los Gemelos and the Canal, *Darwin et al.* 426 (BM, CDS); Santa Cruz, Mina Granillo Roja, *Pozo & Herrera* 2 (CDS); Isabela, Villamil, *TGRC accession LA2857* (BM).—GUAYAS: 8 km E of Durán and highway between Guayaquil and Cuenca, Guayas River drainage, *Anderson* 2423 (MO); about 15 km W of Guayaquil, *Blood & Tremelling* 582 (UC); at tributary of Río Daule, *Böcher et al.* 30 (C, S); from Libertad (near Salinas) to 10 km W along coast, *D’Arcy* 13730 (MO); summit of Cerro Azul above Casas Viejas, 22 km NW of Guayaquil on road to Salinas, *Dodson & Dodson* 11947 (MO); road Guayaquil–Boca de los Sapos (El Triunfo), between Durán and Km 26, *Harling & Andersson* 16038 (MO); Guayaquil, 1841, *Hinds s.n.* (K); oil camp between Guayaquil and Salinas, *Hitchcock* 20119 (GH, NY, US); at Río Tenguel, near San Ignacio, *Holmgren & Heilborn* 13 (S); Punta Carnero, *Holm-Nielsen et al.* 2041 (F, MO, NY, S); 1 km N of Chanduy towards Atahualpa, *Holm-Nielsen et al.* 2134 (F, MO, NY, S); low mountain NE of Chanduy, *Holm-Nielsen et al.* 2206 (S); road Babahoyo–Guayaquil, near Yaguachi Nuevo, *Holm-Nielsen et al.* 27749 (K, NY); 100 mi N of Guayaquil, *Horn s.n.* (US); upper slopes and top of Cerro Carmen (big Christ statue) and saddle between it and Cerro Cemeterio, above main cemetery of Guayaquil, in center of old town, *Iltis & Iltis E-578* (WIS); 30.5 km S of Troncal on road to Naranjal, *MacBryde* 424 (MO, US); Tuna, Guayaquil, *Sinclair s.n.* (K).—LOJA: Agrotécnico, *Vivar C. E-20* (BM); Cantón Celica, Sabanilla, Los Higuerones, *Vanden Eynden et al.* 612 (QCA).—LOS RÍOS: Hacienda Clemenita on Río Pita, *Asplund* 5446 (US); Río Palenque Field Station, halfway between Santo Domingo de los Colorados and Quevedo, *Gentry* 10162 (MO, S); prop. Sto. Domingo, *Sodiño* 114/3 (Q); Prov. Santo Domingo de los Colorados, Sto. Domingo–Quevedo road Km 35, Hacienda Margarita, *Werling & Leth-Nissen* 597 (F, NY).—MANABÍ: Manta, *Asplund* 15961 (B, NY); Bahía de Caráquez, *Asplund* 16573 (NY, S); between Portoviejo and Montecristi, 5 km W of Montecristi, *Brandbyge* 42769 (BM); Bahía de Caráquez, *Harling et al.* 9459 (MO); above the bay of the side of Río Chone, just in back of Sitio Mauricio, along main road 4 km SSE of Bahía de Caráquez, *Iltis & Iltis E-175* (MO); road from Jipijapa to Pedro Carbo, ca. 12 km S of Jipijapa, *Plowman & Alcorn* 14357 (F, NY); Bahía de Caráquez, Leonidas Plaza, along the road between Co. Estación Naval and the sea, *Sparre* 19674 (A, S); Montecristo, above the town, *Sparre* 19862 (A, S); Cantón Jipijapa, Parque Nacional Machalilla, Isla de la Plata, 36 km NW of Puerto López, *Woodruff & Núñez* 583 (MO, QCNE); Parque Nacional Machalilla, Punta los Frailes, *Yáñez et al.* 1323 (QCA).—PICHINCHA: Cantón Quito, Parroquia Pacto, Saguangal, Montaña de La Conquista, *Quipuscoa et al.* 919 (F, M, MO, NY). **Peru.** DEPARTMENT UNKNOWN: Guadalupe, *Blood & Tremelling* 123 (MO); Tamboyeque, *Blood & Tremelling* 128 (GH); without locality, *Gay* 1773 (MO); without locality, 1838, *Wilkes s.n.* (NY).—AMAZONAS: between La Peca and Bagua Chica, *Barbour* 4253 (MO, USM); Prov. Bagua, Bagua Grande–Cajaruro, *Ferreyra et al.* 20588 (USM).—ANCASH: Huarney, *Blood & Tremelling* 95 (F); Km 249 Norte, *Cerrate et al.* 5157 (USM); Prov. Casma, Río Culebras, *Rick* 118 (USM); Prov. Chimbote, road from the Panamericana Norte to Nepeña, *Weigend et al.* 2000/676 (BM, M).—AREQUIPA: Prov. Camaná, Río Ocoña, *Petersen & Hjerting* 1127 (C); Pescadores, 51.4 mi al N de Camaná, *Rick & Rick SAL-419* (USM); Islay, Posco, *Vargas C.* 2016 (MO).—CAJAMARCA: entre Oyotum y Nanchoc, *Ferreyra* 20010 (USM); Prov. Jaén, Pucará on the Río Huancabamba, Km 127 E of Olmos, vicinity of town, Mesones–Muro highway between Olmos and Jaén, *Hutchison & Wright* 3563 (F, MO, NY, UC, US); Magdalena, along road to Cajamarca, *Rick* 140 (USM); Prov. Contumazá, Cascas, 1 km from Cascas on the road to Santa Ana, “La Cienaga” in Cascas Valley, *Simpson* 83-07-11-1 (TEX); Prov. San Pablo, Dist. San Bernardino, Maichil, carretera Chilete–San Pablo, *Sánchez Vega & Zárpán Arias* 604 (F).—ICA: Prov. Nasca, Pajonal Alto, Km 457 Panamericana Sur, *Cano et al.* 5798 (USM); Taruga, aproximadamente 10 km al E de San Luis Pajonal, *Cano et al.* 5810 (USM);

Prov. Ica, Laguna de Orovilca, al SE y a dos leguas y media de la capital, *Luna Campos* 23 (USM); Andahuasi, Huacho, *Sandeman* 4032 (F, K).—LA LIBERTAD: near Trujillo, *Blood & Tremelling* 93 (NY), *Blood & Tremelling* 94 (F), *Blood & Tremelling* 105 (NY), *Blood & Tremelling* 114 (F); La Taza–Plazapampa, *Cevasco s.n.* (USM); ca. 1 km S of San Pedro de Lloc on Panamerican Hwy, *Dillon & Whalen* 4017 (F); Río Chicama, margen izquierda, cerca puente, *Ferreyra* 19926 (USM); Chicama Valley, *Graywood Smyth* 8 (F, US); Salpo, Platanar, *Leiva & Leiva* 701 (MO); Prov. Ascope, Pampas de Ventura–El Algarrobal, *López M. et al.* 9318 (HUT); Prov. Trujillo, Huanchaco, Trujillo, *López M. & Fernández H.* 7973 (MO, NY), *López M. & Fernández H.* 7976 (C, F); Prov. Otuzco, Campiña de Moche, *Mostacero L. & Mejía C.* 3198 (HUT); entre Baños Chimú y Pinchaday, *Mostacero L. & Mejía C.* 3382 (HUT); valle de Río Chicama, Ascope, Laguna San Bartolo, *Müller & Krebs* 12122 (USM); Prov. Pacasmayo, 5 km S de San Pedro de Lloc, *Rick* 129 (USM); cañón de the Río Tablachaca, Perichugo, broad river terrace N of La Galgada, *Smith & Trujillo* 6075 (USM); S outskirts of San Pedro de Lloc, *Whalen & Dillon* 873 (BH, MO, NY); bridge near Trujillo, *Worth et al.* 8886 (G, K, UC).—LAMBAYEQUE: Lambayeque, *Blood & Tremelling* 127 (MO); entre Olmos y Motupe, *Cerrate* 4983 (USM); Km 636–637 entre Trujillo y Chiclayo, *Cerrate* 5191 (MO, USM); cerca del Portachuelo de Olmos, *Cerrate* 5228 (MO, USM); road from Saña to Oyotún, Km 15.5–14.5, *Dostert* 98/151 (F, M); Pampa de Olmos, Portachuelo, *Ferreyra* 12371 (USM), *Ferreyra* 17784 (USM), *Ferreyra* 17977 (USM), *Ferreyra* 18548 (USM); Mórrope, *Ferreyra & Chanco* 20198 (US, USM); Zaña, *Llatas Q.* 724 (MO); Cayaltí, *Llatas Q.* 725 (MO), *Llatas Q.* 726 (BM, MO, USM); Prov. Ferreñafe, Las Tres Tomás, *Llatas Q.* 734 (BM, MO); Prov. Ferreñafe, Pitipo, *Llatas Q.* 815 (USM); Prov. Lambayeque, Dist. Olmos, portachuelo de Olmos, *Llatas Q. et al.* 9066 (F, NY); El Cascajal, Olmos–Naupe, *López M.* 2477 (HUT); Prov. Chiclayo, 20 km al E de Chongoyape, *Rick* 149 (USM); Motupe, *Rick* 150 (USM); Cuculí, 26.5 mi al E de Chiclayo, *Rick & Rick SAL-433* (USM); Tumán–Chongoyape, *Sagástegui & Diestra Q.* 11470 (BM, HUT, MO, NY).—LIMA: Ins. San Lorenzo, extra Callao, collector unknown *s.n.* (S); Chacalío, *Balls B-5858* (K, UC, US); near Lima, *Blood & Tremelling* 6 (GH), *Blood & Tremelling* 7 (NY), *Blood & Tremelling* 8 (UC), *Blood & Tremelling* 9 (F), *Blood & Tremelling* 10 (MO); Pasamayo, *Blood & Tremelling* 84 (NY); 10 mi E of Lima, *Blood & Tremelling* 76 (UC); pantanos de Villa, *Cano* 2535 (F); alrededores de Laguna de Villa, *Cerrate* 818 (USM); Santa Ana, *Cook & Gilbert* 1405 (BM, CAS, F, GH, MO, NY, US), *Cook & Gilbert* 1702 (US); alrededores de Lima, *Cornejo s.n.* (USM); Lomas de Atocongo, 28 km al S de Lima, *Dreyfus s.n.* (USM); cerca de laguna de Villa, a 18 km al S de Lima, *Ferreyra* 2951 (US, USM); Prov. Lima, alrededores de San Juan, Surco (Barranco), *Ferreyra* 4098 (US, USM); Km 49–50 de la carretera central Lima–Oroya, valle de Rimac, *Ferreyra* 10512 (USM); Lurín al S de Lima, *Ferreyra* 11802 (USM); Lurín, Km 38 al S de Lima, *Ferreyra* 11805 (MO, USM); Prov. Chancay, entre Sayán y Churín, *Ferreyra, R.* 17927 (USM); Prov. Lima, Cascadas de Barranco, 10 km S of Lima, *Fosberg et al.* 28204 (A, B, F, K, NY, US); Santa Eulalia, 40 km E of Lima in Valley of Río Rimac, *Gentry et al.* 19159 (F, MO, NY); dry wash above Santa Eulalia, *Goodspeed* 33147 (UC); route from Trapiche to Quilca, a little above Quilca (route 34), *Hawkes et al.* 4105 (C); Estación Experimental de INIA, La Molina, *Hermann et al.* 502 (NY); Santa Eulalia, 55 km E of Lima, *Holt* 47 (K); Laguna de Villa, Chorrillos, *León* 257 (USM); 5 km NE of village of Pachacamac, *Mexia* 8328 (B, BM, F, GH, K, S, UC, US); Pishicoto, route Cieneguilla, Sicisaya, *Ochoa* 11762 (F, US); Prov. Yauyos (Chancay?), Quebrada de Lunahuamá, *Ochoa* 14874 (F, NY, US); Prov. Cañete, near Cañete, *Petersen & Hjerting* 1152 (C); Callao, *Savatiér* 1580 (K); Lima, *Seemann* 878 (K); Prov. Huarochirí, Santa Eulalia–San Juan de Iris road, *Smith & León* 1344 (MO, USM); Amancaes, *Soukup* 4184 (F, US); sea cliffs at Miraflores, *Tryon & Tryon* 5218 (USM); Prov. Canta, Licaahuasy, *Vilcapoma* 48 (USM); arriba de Quives, *Vilcapoma* 86 (USM); Ciudad Universitaria de San Marcos, *Vilcapoma* 369 (USM); without locality, *Wilkes s.n.* (US); San Gerónimo, *Wawra* 469 (W); La Molina, *Vilcapoma* 532 (USM); Magdalena, *Zúñiga s.n.* (USM).—PIURA: Miramar at Río Chira, *Böcher et al.* 274 (C); camino a Paita, *Cerrate* 4941 (USM); Sullana, *Cerrate* 4975 (USM); top of Talara Tablazo off old Panamerican Hwy between Lobitos and El Alto, *Chrostowski lot 2-3* (WIS); caserío Burgos, La Peñita, *Díaz S. & Baldeón* 2372 (F, MO, NY, USM); Olmos, *Ellenberg* 1226 (U); W of Piura, *Ellenberg* 1553 (U); Prov. Paita, Amotape Hills, near Talara, *Haught* 2 (US); Amotape Hills, about 10 mi E of Talara, *Haught s.n.* (F); in foothills E of La Brea, 25 km SE of Talara, *Horton* 11582 (F, G, GH, K, UC); Prov. Huancabamba, Buenos Aires, en ruta a Huancabamba, *Rick* 152 (USM); a 17 km al S de Piura, *Ferreyra* 5886 (USM); a 65 km S de Piura, *Ferreyra* 5919 (USM); Prov. Sullana, Hda. Mallares, cerca a Sullana, *Ferreyra* 6011 (US, USM); Had. Pabur, carretera a Huancabamba, *Ferreyra* 6027 (US, USM); despoblado de Piura, *Ferreyra* 9114 (USM); El Alto, cerca a Talara, *Ferreyra* 12357 (USM); Prov. Morropón, Had. Pabur, approx. 50 km al S de Piura, *Ferreyra* 16282 (G, USM); Prov. Piura, Laguna Ramón, desierto de Sechura, *Ferreyra* 18546 (USM); despoblado de Piura, *Ferreyra* 20024 (US, USM); without locality, *Townsend* 1395 (US).—TUMBES: alrededores de Tumbes, *Ferreyra et al.* 10742 (USM); cerca a Puerto Pizarro, *Ferreyra et al.* 12302 (USM); Prov. Contralmirante Villar, Cuesta de Animas, entre Zorritos y Casitas, *Ferreyra* 12242 (USM); Prov. Tumbes, Bocatoma, La Peña, *Ferreyra* 12331 (USM); entre Puerto Pizarro y est. militar El Bendito, *Ferreyra* 16236 (USM); Prov. Zarumilla, Agua Verde, near Zarumilla, on

Ecuador border, *Fosberg 27669* (MO, NY, US, WIS). **Chile.** REGION III (ATACAMA): Vallenar, *collector unknown 3520* (K); without locality, *Montero 7690* (CONC, G).

Solanum pimpinellifolium is very closely related to *S. lycopersicum* and hybridizes with it freely. It differs from cultivated plants of *S. lycopersicum* in a variety of genetic characteristics, and we feel maintenance of *S. pimpinellifolium* at the specific rank will better serve both nomenclatural stability and the plant breeding community, who have long used this species in studies of tomato genetics (Frery et al. 2000; van der Knaap & Tanksley 2001). Since the two taxa are so similar, and identification of individual specimens can be problematic owing to putative introgression we use a suite of characters to identify *S. pimpinellifolium*. Our rule of thumb for identifying individual specimens (especially those that we suspect are of hybrid origin) is to assign to *S. pimpinellifolium* any specimen that has a majority of these characters: 1) corollas stellate, deeply (>3/4) divided, the lobes narrowly lanceolate; 2) the sterile appendage of the staminal tube longer than the pollen-bearing portion, the buds thus long and thin in comparison to those of *S. lycopersicum*; 3) elongate inflorescence (longer than 3 cm) with many (>20) flowers; 4) very small fruits (<1 cm in diameter); 5) few interjected leaflets; 6) leaflets entire or only slightly crenate in proximal 1/3; 7) terminal leaflet base cordate. In addition, identification can be facilitated by noting the nature of the terminal leaflets, broadly elliptical in *S. pimpinellifolium* rather than narrowly ovate (*S. lycopersicum*), and the overall velvety pubescence of very short trichomes in *S. pimpinellifolium* and without long trichomes (except in putatively introgressed populations).

Populations in the northern part of the range of *S. pimpinellifolium* (coastal Ecuador) and occasionally in higher elevation valleys in northern Peru apparently are the result of introgression with *S. lycopersicum* and consequently have deeper crenate leaflets and often have a few stout, patent trichomes on the stems and inflorescences. There is great variation owing to introgression, which makes determinations difficult wherever the two species are in contact.

In the Galápagos Islands, *S. pimpinellifolium* has been introduced or has arrived only recently, and forms hybrids with the endemic Galápagos tomato *S. cheesmaniae*, where the two species occur in sympatry (Darwin et al. 2003; S. C. Darwin, unpubl.). Some plants identified by Nuez et al. (2004) as “*Lycopersicon esculentum* var. *cerasiforme*” we assign to *S. pimpinellifolium*.

Autogamous populations of *S. pimpinellifolium* have smaller flowers than outcrossing populations (Georgiady & Lord 2002), caused by heterochronic growth differences in the flower. A single QTL is responsible for four of six flower traits associated with autogamy (Georgiady et al. 2002), but much variation in all these traits exists in both sets of populations. Autogamy is associated with the margins of the range of *S. pimpinellifolium* (Rick et al. 1977), and studies of variation in nuclear gene sequences (*Vac* – fruit vacuolar invertase) in northern Peruvian populations (Caicedo & Schaal 2004a) show levels of outcrossing decreasing towards the south (towards the center of the species range). Caicedo and Schaal (2004a, 2004b) showed that genetic variation is high, and that there is no congruence between geographical distribution and genealogy in these populations. They suggest their data shows a northern Peruvian origin for *S. pimpinellifolium*, but they did not sample across the entire species range (into Chile). The more northerly populations in both their and Rick et al.’s (1977) study may have introgressed with *S. lycopersicum*.

Solanum pimpinellifolium has been of great importance to tomato breeding for the introduction of important agronomic traits, such as disease resistance, and for the

investigation of the genetic control of traits, such as fruit shape and size (e.g., van der Knaap et al. 2004). Crosses between *S. lycopersicum* and the TGRC accession *S. pimpinellifolium* accession LA1589 (an autogamous population from the lower Virú Valley in the Department of La Libertad, Peru) have been the mainstay of studies in fruit development in the tomato (see Morphology), and LA1589 has recently been used in metabolic profiling (Schauer et al. 2005). *Solanum pimpinellifolium* had the lowest fruit protein content of any of the species tested, but its leaf metabolite content is very close to that of *S. lycopersicum*, further underlining their close relationship (Schauer et al. 2005).

One TGRC accession of *S. pimpinellifolium* (LA1589) has been used to produce recombinant inbred lines with the cultivated tomato (see <http://tgrc.ucdavis.edu/>). These introgressed lines have been important in the production of genetic maps.

The type specimen of *S. pimpinellifolium* in the Linnaean herbarium in London (see Knapp & Jarvis 1990; <http://www.nhm.ac.uk/solanaceaesource>) is a close match for collections from the region of Lima (e.g., *Mexia* 8328) in central Peru. These populations comprise glabrous plants with entire leaflets with cordate bases, elongate inflorescences, and very narrow petals. Seed of the type specimen of *S. peruvianum* was sent to Linnaeus by Bernard de Jussieu (Knapp & Jarvis 1990), whose brother Joseph collected in the Lima area (see discussion under *S. peruvianum*). Linnaeus indicated no provenance for *S. pimpinellifolium*, but perhaps seeds were also sent by Jussieu along with those for *S. peruvianum*. Miller (1768) mentioned that he received seeds of both species from Bernard de Jussieu.

Luckwill (1943a) misunderstood *Lycopersicon pissisi* and equated it with *S. peruvianum*, possibly due to its habitat in coastal deserts. The protologue clearly states that the species has red fruit and lacks inflorescence bracts. Also, the type specimen has three leaves per sympodial unit and is unmistakably a member of the “*Lycopersicon*” species group.

Luckwill (1943a: 24) described his *L. esculentum* subsp. *intermedium* citing a “well-defined and pure breeding form . . . which has been under cultivation for scientific purposes at the John Innes Horticultural Institute, Merton, for a number of years and has been widely employed for research work under the name of *L. racemigerum* Lange.” From his description of this taxon and from several specimens cultivated in the United Kingdom and collected during that time (but none from the John Innes Institute found), we conclude Luckwill’s subspecies is a hybrid between *S. lycopersicum* and *S. pimpinellifolium*, as is the type of *L. racemigerum* itself. These hybrids apparently form easily in cultivation, and Brezhnev (1958) therefore recognized *S. pimpinellifolium* only at the subspecific rank (see synonymy above).

“*Lycopersicon pimpinellifolium* (L.) Mill. subsp. *intermedium* Luckwill” is a misprint in *Index kewensis* for *L. esculentum* subsp. *intermedium* Luckwill, but the subspecific epithet was indeed transferred to *L. pimpinellifolium* later (see synonymy above) by Prokhanov (1950) in the treatment of *Lycopersicon* for the *Flora of the USSR* (see also discussion under *S. lycopersicum*).

Specimens are cited above only within the native range of *S. pimpinellifolium*. Cultivated and possibly adventive specimens have been seen from Argentina, Austria, Belgium, Brazil, Denmark, France, Germany, Indonesia, Iraq, Mexico, Namibia, Sweden, Switzerland, the United Kingdom, and the U.S.A.; these are listed in the Index to Numbered Collections Examined, and complete data on these accessions is available on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>). *Solanum pimpinellifolium* is somewhat invasive where it is introduced (see Darwin et al. 2003).

- 15. *Solanum lycopersicum* L.**, Sp. pl. 185. 1753. *Lycopersicon esculentum* Miller, Gard. dict. ed. 8, *Lycopersicon* No. 2. 1768. *Lycopersicon pomumamoris* Moench, Meth. 515. 1794, nom. superfl. *Lycopersicon lycopersicum* (L.) H. Karsten, Deut. Fl. (Karsten) 966. 1882. *Solanum lycopersicum* var. *esculentum* (Miller) Voss, Vilm. Blumengärtn. ed. 3, 1: 721. 1894.—TYPE: Specimen prepared from plants cultivated in Uppsala (lectotype, designated by Knapp & Jarvis 1990: LINN 248.16! [BH neg. 6803: BH! GH! UC! WIS!]).
- Lycopersicon galenii* Miller, Gard. dict. ed. 8, *Lycopersicon* no. 1. 1768. *Lycopersicon cerasiforme* Dunal, Hist. Solanum 113. 1813, nom. superfl. *Lycopersicon esculentum* var. *cerasiforme* (Dunal) Alefeld, Landw. Fl. 135. 1866 [combination also proposed by A. Gray, Syn. Fl. N. Am., ed. 2, 2: 226. 1886]. *Solanum lycopersicum* var. *cerasiforme* (Dunal) Voss, Vilm. Blumengärtn. ed. 3, 1: 721. 1894 [combination also proposed by Fosberg, Phytologia 5: 290. 1955; D. M. Spooner, G. J. Anderson & R. K. Jansen, Amer. J. Bot. 80: 683. 1993]. *Lycopersicon esculentum* subsp. *galenii* (Miller) Luckwill, Aberdeen Univ. Studies 120: 23. 1943. *Lycopersicon lycopersicum* var. *cerasiforme* (Dunal) M. R. Almeida, Fl. Maharashtra 3B: 364. 2001.—TYPE: Specimen prepared from plants cultivated in the Chelsea Physic Garden (lectotype, here designated: BM!).
- Solanum pseudolyopersicum* Jacquin, Hort. bot. vindob. 1: 4, t. 11. 1770–1771. *Solanum spurium* J. F. Gmelin, Syst. nat. 384. 1791, nom. superfl. *Lycopersicon spurium* Link, Handb. 1: 556. 1824, nom. superfl. —TYPE: “in horto pertissimi Pharmacopaei Jacobi Wel vidi” [no specimens extant] (lectotype, here designated: Jacquin’s illustration, t. 11, accompanying the description).
- Solanum pomiferum* Cavanilles, Descr. 1: 112. 1802. *Lycopersicon pyriforme* Dunal, Hist. Solanum 112. 1813, nom. superfl. *Lycopersicon esculentum* var. *pyriforme* (Dunal) Alefeld, Landw. Fl. 135. 1866 [combination also proposed by L. H. Bailey, Standard cycl. hort. ed. 2, 1931. 1917]. *Solanum lycopersicum* var. *pyriforme* (Dunal) Voss, Vilm. Blumengärtn. ed. 3, 1: 721. 1894. *Lycopersicon esculentum* forma *pyriforme* (Dunal) C. H. Müller, U.S. Dept. Agric. Misc. Publ. 382: 12. 1940.—TYPE: Specimen prepared from plants cultivated in Madrid [“se cultivada en el Jardín del Rey”] (lectotype, designated by Knapp, 2007b: MA-308485!).
- Solanum humboldtii* Willdenow, Hort. berol. 1(3): 27. 1804. *Lycopersicon humboldtii* (Willdenow) Dunal, Hist. Solanum 112. 1813. *Lycopersicon esculentum* var. *humboldtii* (Willdenow) Alefeld, Landw. Fl. 135. 1866. *Lycopersicon esculentum* subsp. *humboldtii* (Willdenow) Luckwill, Aberdeen Univ. Stud. 120: 24. 1943. *Lycopersicon esculentum* subsp. *subspontaneum* Brezhnev var. *humboldtii* (Willdenow) Brezhnev in Zhukovskii, Kult. fl. SSSR 20: 73. 1958.—TYPE: “in American meridionali ad flumen nigrum Rio Negro dictum,” *Humboldt & Bonpland s.n.* (734?) (holotype: B-W! [microfiche IDC 7440:5360]).
- Lycopersicon cerasiforme* var. *leptophyllum* Dunal in A. DC., Prodr. 13(1): 26. 1852. *Lycopersicon esculentum* var. *leptophyllum* (Dunal) D’Arcy, Ann. Missouri Bot. Gard. 65: 771. 1978.—TYPE: NEPAL (?), *Wallich cat. 2611* (lectotype, designated by D’Arcy, 1978: G-DC!; isolectotypes: BM! K!).
- Lycopersicon philippinarum* Dunal in A. DC., Prodr. 13(1): 27. 1852.—TYPE: unknown (Dunal provided a name for a species described but misdetermined by Blanco as “*Solanum lycopersicum*” in Fl. Filip. 133. 1837).—THE PHILIPPINES. Luzon: Benguet subprovince, Bagaio, May 1914, *Merrill 14* (neotype, here designated: K!; isoneotypes: BM! ECON! F! MO! NY! US! W!). [See note below.]

- Lycopersicon macrophyllum* Gussone, Enum. pl. Inarim. 230. 1854, as “*Lycopersicum*.”—TYPE: ITALY: Campania (Napoli): Ischia, *Gussone s.n.* (lectotype, here designated: NAP!).
- Lycopersicon esculentum* var. *luteum* Alefeld, Landw. Fl. 135. 1866, as “*Lycopersicum*.”—TYPE: unknown.
- Lycopersicon esculentum* var. *vulgare* Alefeld, Landw. Fl. 135. 1866, as “*Lycopersicum*.”—TYPE: unknown.
- Lycopersicon esculentum* var. *cydonicum* Alefeld, Landw. Fl. 135. 1866, as “*Lycopersicum*.”—TYPE: unknown.
- Lycopersicon esculentum* var. *myrobalaneum* Alefeld, Landw. Fl. 135. 1866, as “*Lycopersicum*.”—TYPE: unknown.
- Solanum lycopersicum* var. *oviforme* Voss, Vilm. Blumengärtn. ed. 3, 1: 721. 1894.—Type: unknown.
- Solanum lycopersicum* var. *pruniforme* Voss, Vilm. Blumengärtn. ed. 3, 1: 721. 1894.—Type: unknown.
- Lycopersicon esculentum* var. *vulgare* L. H. Bailey, Stand. cycl. hort., ed. 2, 4: 1931. 1917, as “*Lycopersicum*.” *Lycopersicon esculentum* var. *commune* L. H. Bailey, Man. cult. pl. 656. 1924, as “*Lycopersicum*.” *Lycopersicon lycopersicum* var. *commune* (L. H. Bailey) Farwell, Amer. Midl. Nat. 10: 217. 1927.—TYPE: unknown.
- Lycopersicon esculentum* var. *grandifolium* L. H. Bailey, Stand. cycl. hort., ed. 2, 4: 1932, f. 2232. 1917, as “*Lycopersicum*.”—TYPE: unknown.
- Lycopersicon esculentum* var. *validum* L. H. Bailey, Stand. cycl. hort., ed. 2, 4: 1931, f. 2233. 1917, as “*Lycopersicum*.”—TYPE: unknown.
- Lycopersicon cerasiforme* var. *cognitum* Mazkevich, Trudy Prikl. Bot., suppl. 47: 283, 529. 1930.—TYPE: MEXICO. Chiapas: Tuxtla Gutiérrez, Cangrejós, *Bukasov s.n.* (holotype: WIR?).
- Lycopersicon cerasiforme* var. *rotundilobum* Mazkevich, Trudy Prikl. Bot., suppl. 47: 283, 529. 1930.—TYPE: MEXICO. Veracruz: without locality, *Bukasov s.n.* (holotype: WIR?).
- Lycopersicon esculentum* var. *bukasovii* Mazkevich, Trudy Prikl. Bot., suppl. 47: 285, 530. 1930.—TYPE: COLOMBIA. Valle: Barranquilla, *Bukasov K-378* (lectotype, here designated: WIR-1452!).
- Lycopersicon esculentum* var. *colombianum* Mazkevich, Trudy Prikl. Bot., suppl. 47: 285, 530. 1930.—TYPE: COLOMBIA. Cauca: Popayán, *Bukasov K-387* (lectotype, here designated: WIR-4612!).
- Lycopersicon esculentum* var. *macrocalyx* Mazkevich, Trudy Prikl. Bot., suppl. 47: 285, 530. 1930.—TYPE: MEXICO. “Cedral,” *Bukasov K-354* (lectotype, here designated: WIR-4702!).
- Lycopersicon esculentum* var. *umbertianum* Mazkevich, Trudy Prikl. Bot., suppl. 47: 286, 530. 1930.—TYPE: COLOMBIA. Santander: Barranca Bermeja, *Bukasov K-381* (lectotype, here designated: WIR-4578!).
- Lycopersicon esculentum* convar. *infiniens* C. O. Lehmann, Der Züchter, Sonderheft 3: 39. 1955 [“1954”]. *Lycopersicon esculentum* provar. *flammatum* C. O. Lehmann, Der Züchter, Sonderheft 3: 45. 1955 [“1954”], nom. superfl.—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Lukullus,’ von Benary, Erfurt, 1946 erhalten. Sortiment Gatersleben Nr. LYC 127” (holotype: GAT).

- Lycopersicon esculentum* convar. *fruticosum* C. O. Lehmann, Der Züchter, Sonderheft 3: 39. 1955 [“1954”]. *Lycopersicon esculentum* provar. *finiens* C. O. Lehmann, Der Züchter, Sonderheft 3: 58. 1955 [“1954”], nom. superfl.—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Bonita’ von Olson & Sons, Hammenshögs (Schweden), 1952 erhalten. Sortiment Gatersleben Nr. 4127/53” (holotype: GAT; current accession number: LYC 231).
- Lycopersicon esculentum* convar. *scopigerum* C. O. Lehmann, Der Züchter, Sonderheft 3: 39. 1955 [“1954”]. *Lycopersicon esculentum* var. *scopigerum* C. O. Lehmann, Der Züchter, Sonderheft 3: 60. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Blondköpfchen’ von Benary, Erfurt, 1946 erhalten. Sortiment Gatersleben Nr. LYC 31” (holotype: GAT).
- Lycopersicon esculentum* provar. *violaceum* C. O. Lehmann, Der Züchter, Sonderheft 3: 45. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Acme’ vom Sortenamnt für Nutzpflanzen in Vieselbach 1952 erhalten. Sortiment Gatersleben Nr. 4023/53” (holotype: GAT; current accession number: LYC291).
- Lycopersicon esculentum* provar. *densifolium* C. O. Lehmann, Der Züchter, Sonderheft 3: 48. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Immulen’ von Benary, Erfurt, 1947 erhalten. Sortiment Gatersleben Nr. LYC 224” (holotype: GAT).
- Lycopersicon esculentum* provar. *amplipinnatum* C. O. Lehmann, Der Züchter, Sonderheft 3: 49. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Deutscher Fleiss’ vom Sortenamnt für Nutzpflanzen in Vieselbach 1952 erhalten. Sortiment Gatersleben Nr. 4158/53” (holotype: GAT; current accession number: LYC327).
- Lycopersicon esculentum* provar. *subviride* C. O. Lehmann, Der Züchter, Sonderheft 3: 49. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Hellfrucht’ von Mohrenweiser, Altenweddingen, 1946 erhalten. Sortiment Gatersleben Nr. LYC 121” (holotype: GAT).
- Lycopersicon esculentum* provar. *mikadofolium* C. O. Lehmann, Der Züchter, Sonderheft 3: 54. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Belle Arlesienne’ von Benary, Erfurt, 1950 erhalten. Sortiment Gatersleben Nr. LYC 93” (holotype: GAT).
- Lycopersicon esculentum* provar. *pluriloculare* C. O. Lehmann, Der Züchter, Sonderheft 3: 55. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Super Sioux’ von Kornacke, Wehrden, 1951 erhalten. Sortiment Gatersleben Nr. LYC 273” (holotype: GAT).
- Lycopersicon esculentum* provar. *incarnatum* C. O. Lehmann, Der Züchter, Sonderheft 3: 55. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Berner Rosen’ von Haubensack, Basel, 1952 erhalten. Sortiment Gatersleben Nr. 4118/53” (holotype: GAT; current accession number: LYC 353).
- Lycopersicon esculentum* provar. *perspicuum* C. O. Lehmann, Der Züchter, Sonderheft 3: 56. 1955 [“1954”].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; “Sorte ‘Dwarf Champion’ von Chrestensen, Erfurt, 1952

erhalten. Sortiment Gatersleben Nr. 4126/53" (holotype: GAT; current accession number: LYC 355).

Lycopersicon esculentum provar. *cordiforme* C. O. Lehmann, Der Züchter, Sonderheft 3: 57. 1955 ["1954"].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; "Sorte 'Ochsenherz' von M. Herb, Neapel, 1952 erhalten. Sortiment Gatersleben Nr. 4117/53" (holotype: GAT; current accession number: LYC 356).

Lycopersicon esculentum provar. *persicoides* C. O. Lehmann, Der Züchter, Sonderheft 3: 57. 1955 ["1954"].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; "Sorte 'Pêche' von Vilmorin-Andrieux, Paris, 1952 erhalten. Sortiment Gatersleben Nr. 4156/53" (holotype: GAT; current accession number: LYC 357).

Lycopersicon esculentum provar. *pygmaeum* C. O. Lehmann, Der Züchter, Sonderheft 3: 58. 1955 ["1954"].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; "Sorte 'Heinemanns Jubilaeum' von Heinemann, Erfurt, 1948 erhalten. Sortiment Gatersleben Nr. LYC 221" (holotype: GAT).

Lycopersicon esculentum provar. *speciosum* C. O. Lehmann, Der Züchter, Sonderheft 3: 59. 1955 ["1954"].—TYPE: Specimen prepared from plants cultivated in Gatersleben, Germany; "Sorte 'Bounty' von W. A. Burpee & Co., Philadelphia (USA), 1951 erhalten. Sortiment Gatersleben Nr. LYC 195" (holotype: GAT).

Annual, biennial, or sometimes perennial herbs, erect initially, later procumbent and viny with branches extending to 4 m from centers. Stems 10–14 mm in diameter at base, green, pubescent and usually villous towards the apex; trichomes of two types: numerous simple unicellular trichomes to 0.5 mm long, and sparse uniseriate multicellular trichomes to 3 mm long and composed of up to 10 cells, some gland-tipped, particularly the longer ones, giving the plant a strong scent, and short sparse 1–2-celled glandular trichomes with 1-, 4-, or 8-celled heads. Sympodial units 3-foliolate, internodes 1–6(+) cm long. Leaves interrupted imparipinnate, (10–) 20–35 (+) cm long, (3–) 7–10 (+) cm wide, sparsely pubescent with a mixture of simple unicellular and simple uniseriate multicellular trichomes like those of the stems on both surfaces; primary leaflets 3–4 (–5) pairs, 3–7 cm long, 1–4 cm wide, ovate or elliptic, apex acute to attenuate, base oblique and basiscopically decurrent, truncate to cordate, margin dentate or crenate mainly near the base, rarely entire or deeply dentate or lobulate; terminal primary leaflet usually larger than the laterals, 3–5 cm long, 1.5–3 cm wide, the petiolule 0.5–1.5 cm long, apex usually attenuate; lateral leaflets 2–4.5 cm long, 0.8–2.5 cm wide, the petiolule 0.3–2 cm long; secondary leaflets present mainly acropically on basal leaflets, 0.2–0.8 cm long, 0.1–0.5 cm wide, sessile or with a short petiolule to 0.4 cm long; tertiary leaflets absent; interjected leaflets usually present, 6–10, 0.1–0.8 cm long, 0.1–0.6 cm wide, the petiolule 0.1–0.3 cm long; petiole 1.2–6 (+) cm long; pseudostipules absent. Inflorescences to 10 cm long, usually simple, rarely with 2 branches, with 5–15-flowers, peduncle less than 3 cm long, pubescent like the stems. Pedicels 1–1.2 cm long, articulated in the distal 1/3. Buds 0.5–0.8 cm long, 0.2–0.3 cm wide, conical, straight, the corolla about halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube minute, lobes to 5 mm long, linear, pubescent with long and short simple uniseriate trichomes, the apex acute; corolla 1–2 cm in diameter, pentagonal, bright yellow, often fasciated and with more than 5 lobes in some cultivars, the tube 0.2–0.4 cm long, lobes 0.5–2 cm long, 0.3–0.5 cm wide, narrowly lanceolate, sparsely pubescent with tangled uniseriate trichomes ca. 0.5 mm long on the tips and

margins, lobes spreading at anthesis; staminal column 0.6–0.8 cm long, 0.2–0.3 (–0.5) cm wide, straight, filaments minute to 0.5 mm long, anthers 0.4–0.5 cm long, equal, sterile apical appendage 0.2–0.3 mm long, always less than half the total anther length; ovary conical, minutely glandular-villous; style 0.6–1 cm long, <0.5 mm in diameter, usually included in the staminal column, but exerted in facultatively allogamous populations; stigma capitate, green. Fruits 1.5–2.5 cm (–10 cm in some cultivars) in diameter, usually globose, 2-locular, but often of varying shape and/or multilocular, glabrescent and becoming red, yellow, or deep orange at maturity; fruiting pedicels 1–3 cm long, straight or angled at the articulation toward the infructescence axis, thickening in large-fruited varieties; calyx lobes in fruit accrescent, ca. 8–10 mm long, 2–2.5 mm wide, somewhat to strongly reflexed. Seeds 2.5–3.3 mm long, 1.5–2.3 mm wide, 0.5–0.8 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or more often shaggy, narrowly winged (0.3–0.4 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (LA3475, <http://tgrc.ucdavis.edu>). Plate 1A, Plate 2A, Plate 3A; Fig. 48.

Phenology. Flowers and fruits throughout the year, but usually with only a single flowering and fruiting peak at any one locality (e.g., temperate summer).

Distribution. *Solanum lycopersicum* occurs worldwide, but is known only from cultivation; specimens collected from natural habitats may be feral escapes and do not represent wild populations.—We do not cite specimens examined for this widespread and weedy species here but refer the reader to the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>), where details of all the more than 2000 specimens of *S. lycopersicum* examined for this monograph are listed in full. See Appendix 3 for a list of countries in which *S. lycopersicum* has been collected.

Solanum lycopersicum can be distinguished from the wild tomatoes by its bright red or yellow ripe fruit, usually autogamous flowers with the styles always included in the staminal column, and its copious trichomes that are often more than 3 mm long. The only other tomato species with red, yellow, or orange fruits are *S. pimpinellifolium* (with much smaller fruit and stellate, rather than pentagonal corollas) and the Galápagos endemics *S. cheesmaniae* and *S. galapagense* (with orange fruit and foliage smelling of limes).

Solanum lycopersicum has been recorded on all continents, except Antarctica, and is a widespread escape wherever it is cultivated, although in temperate climates it rarely survives the freezing conditions of winter. The species originated from western South America, but whether or not it ever existed in the wild or instead was derived by human selection from the closely related *S. pimpinellifolium* will be impossible to ascertain, given its long use and wide dissemination all over the world. The observation (see above in discussion of *S. pimpinellifolium*) that the two species hybridize in northern Peru and southern Ecuador lends some support to Brezhnev's (1958, 1964) suggestion that the two are conspecific. Despite this possibility, we retain the two taxa as distinct species. Both names are widely used in the agricultural literature, and the two species are relatively easy to distinguish in the absence of hybridization. The use of fine mapping techniques is currently being developed for isolation of characters of breeding importance in elite breeding lines in the cultivated tomato as the genetic base has narrowed (Zamir 2001; Yang et al. 2004). These techniques may help to identify genes of potential utility in examining the history of cultivation and the relationships of these elite breeding lines to heritage and semi-feral cultivars.

Most previous workers in tomatoes have suggested that the cultivated tomato was derived from small-fruited forms called by many authors “var. *cerasiforme*” (see also

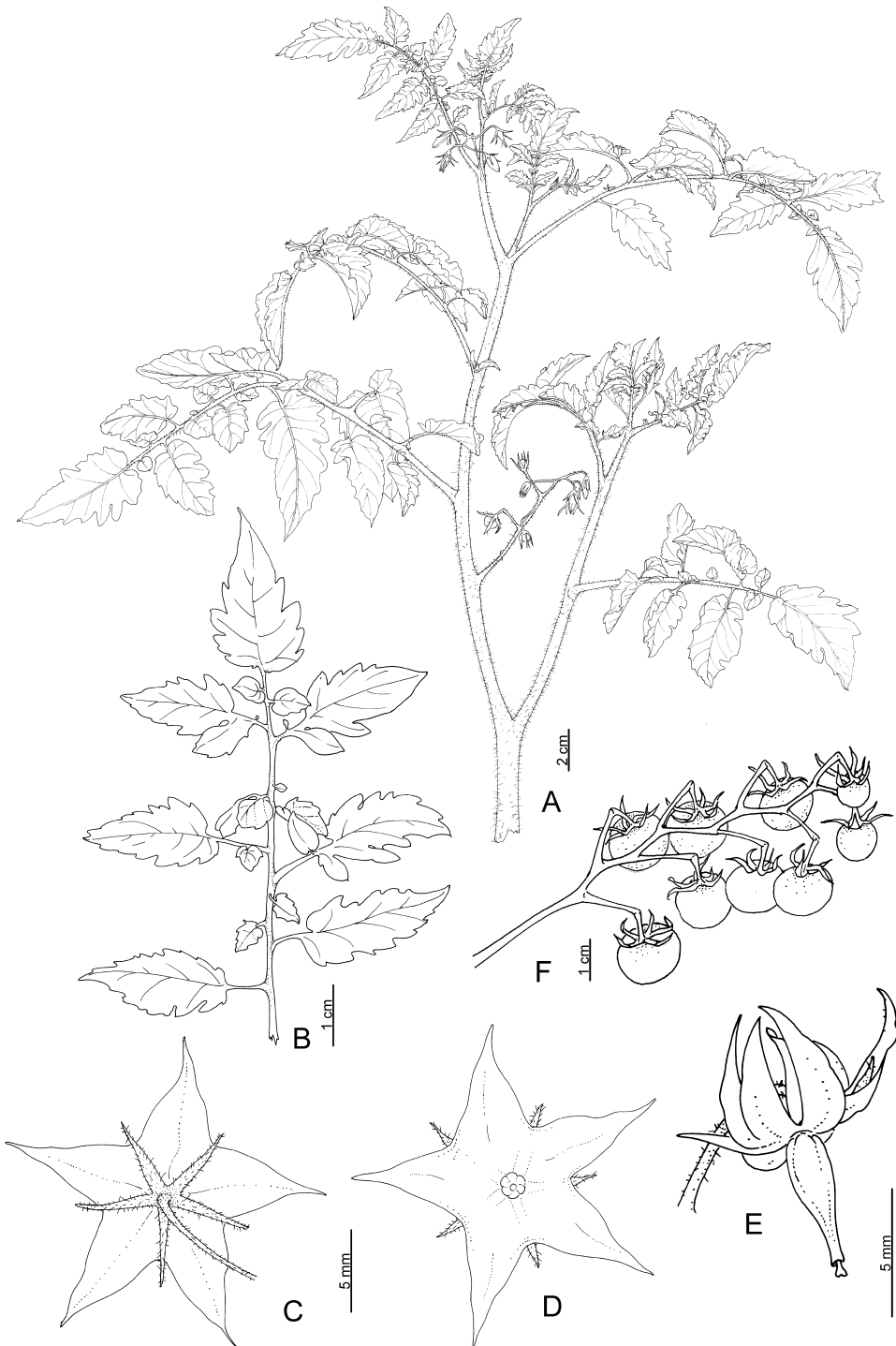


FIG. 48. *Solanum lycopersicum*. A. Branch. B. Leaf. C. Abaxial view of flower. D. Adaxial view of flower. E. Side view of flower. F. Inflorescence.

discussion under Morphology). Research into the genetic control of fruit shape and size in tomatoes has shown that the incredible variation in fruit shape seen in cultivars of *S. lycopersicum* is controlled by a very few tightly linked loci (e.g., van der Knaap et al. 2002, 2004), and that the small-fruited forms are not ancestral but instead a mixture of wild and cultivated forms (Nesbitt & Tanksley 2002). Fruit shape in *S. lycopersicum* is a very interesting character state with which to explore the effects of few genes on broadly divergent morphology and is being actively studied, especially using newly developed genomics tools.

Lehmann's (1954) names for infraspecific taxa in *S. lycopersicum* are all validly published, with a Latin description and a type designation (a specimen prepared from plants cultivated in Gatersleben). Herbarium specimens prepared from all these lines are held in GAT, and are here recognized as holotypes of Lehmann's names. In the synonymy for *S. lycopersicum* we indicate the current germplasm designation, if the numerical designation of the line cited by Lehmann has been superseded. Although the printed date of publication of the Sonderheft 3 of *Der Züchter* is 1955, the copy in the Gatersleben library was received already in 1954 (H. Knupffer, pers. comm, November 2007); therefore, the correct date of publication for Lehmann's names 1954.

Brezhnev's (1958, 1964) classification of *S. lycopersicum* [as *Lycopersicon esculentum*] is replete with subspecific taxa. Brezhnev attempted to describe all details of the cultivars known to him. He classified escaped plants with smallish fruits as "subsp. *spontaneum*" (a nomen nudum, see Appendix 1), reflecting his belief that these plants represented feral or less developed forms of the cultivated tomato. He named six varieties of this subspecies, varieties "*cerasiforme*," "*pyriforme*," "*pruniforme*," "*elongatum*," "*humboldtii*," and "*succenturiatum*," most of which are nomina nuda. These "varieties" were then seen to "rejoin" genetically to give rise to two geographical groups (Mexican and Peruvian). The large-fruited, highly morphologically aberrant forms were classified as "subsp. *cultum*" (again see Appendix 1), within which he recognized several units, each as "grex conculorum" and defined geographically ("*australioeuropium*," "*occidentaliuropium*," "*australirossicum*," "*mediirossicum*," "*borealirossicum*" and "*borealiamericanum*"). Each "grex conculorum" contained 3–7 cultivars with Russian common names (such as 'Comet' and 'Korol Gumbert'). As with "subsp. *spontaneum*," each "grex conculorum" was depicted in his diagram as derived from an amalgamation of all three varieties of "subsp. *cultum*." His classification was an attempt to bring order to the huge number of tomato cultivars then grown in the Soviet Union, linking them to their supposed places of origin. Although Brezhnev's work has been largely neglected by tomato workers in the U.S.A. and western Europe, it is essential for anyone interested in examining the identities of cultivars and heritage varieties from that time. Khrapalova (2001) gave a complicated series of varietal and subvarietal names to many of these variants, but none of her names was validly published (see Appendix 1).

In general, *S. lycopersicum* only persists as a feral plant in subtropical or tropical regions; frost kills the plants and the commonly cultivated forms behave as annuals, although they can persist for several years in the absence of frosts. Human transportation of plant material, both intentional and accidental, accounts for the wide distribution of *S. lycopersicum*. We are certain that the species occurs in many places from which we did not examine collections. We do not list in Appendix 3 the countries from which cultivated specimens have been seen, as we have for all other species; these can be found on Solanaceae Source (www.nhm.ac.uk/solanaceaesource).

Solanum pseudolycopersicum has sometimes been considered a synonym of *S. peruvianum* owing to Jacquin's description indicating it to have hairy, yellow fruits ("Baccae in eadam cerasi magnitudem raro superant; suntque globosae, villosae, flavescentes . . ."; Jacquin 1770–1771: 4), although Luckwill (1943: 23) recognized *S. pseudolycopersicum* as a synonym of *S. lycopersicum* (his *L. esculentum* subsp. *galenii*). The plate in *Hortus Vindobensis* (Jacquin 1770–1771), however, is clearly of *S. lycopersicum*; it shows ebracteate inflorescences and 3-foliate sympodia (Fig. 49), and we choose it as the lectotype of *S. pseudolycopersicum*.



FIG. 49. Lectotype of *Solanum pseudolycopersicum*, plate 11 from Jacquin's *Hortus vindobonensis* (1770). Reproduced with permission of the Natural History Museum Botany Library.

Lycopersicon spurium Link is perhaps a new combination based on Gmelin's (1791) superfluous name *Solanum spurium*. Link's protologue, however, makes no reference to Gmelin's work or to the name "*Solanum spurium*."

Dunal thought that Blanco (Fl. filip. 133. 1835) had misapplied the name *Solanum lycopersicum* L. to an undescribed species of tomatoes and supplied the name *Lycopersicon philippinarum*. He explicitly stated that *L. philippinarum* was not based on specimens seen by him and added the query "An *L. cerasiforme*?" We neotypify *L. philippinarum* with the Kew duplicate of *Merrill 14*, which bears a label with a detailed discussion of the identity of Blanco's concept of the tomato in the Philippines.

We do not designate neotypes for the varieties described by Alefeld (1866) based on fruit color and shape variation in cultivated plants. These names, although validly published, are better regarded as cultivar names and treated under the *International Code of Nomenclature of Cultivated Plants* (Brickell et al. 2004). Alefeld (1866) did not cite any specimens, nor did he specify the exact region where these particular cultivars grew.

Suitable type material for some of the subspecific names coined by Russian tomato taxonomists could not be found at WIR; we did not propose neotypes in the hopes that future work on the relationships of cultivars will bring suitable type specimens or illustrations to light.

The name "*Lycopersicon solanum* Medik." listed in IPNI and earlier in *Index kewensis* is a mistake in data entry. In Medikus's *Beobachtungen* (1783) the name occurs not on page 245, as indicated in IPNI, but on page 383 (as *Solanum lycopersicum*) and page 384 (as *S. lycopersicum*) with an attached figure of the anther cone (Fig. 38 of Medikus, 1783). Medikus did not coin a new name and did not write "*Lycopersicon solanum*."

16. *Solanum cheesmaniae* (L. Riley) Fosberg, *Phytologia* 62: 181. 1987, nom. cons. prop., non *Solanum cheesmanii* Gerasimenko, 1971. *Lycopersicon cheesmaniae* L. Riley, as '*cheesmanii*,' *Kew Bull.* 1925: 227. 1925.—TYPE: ECUADOR. Galápagos: [Isla Santa Cruz] Indefatigable Island, among lava rock in grassy patches, 28 Jul 1924, *Cheesman in Riley 403* (holotype: K!).

Lycopersicon peruvianum var. *parviflorum* J. D. Hooker, *Trans. Linn. Soc. London* 20: 202. 1847 ["1851"], as '*peruanum*'.—TYPE: ECUADOR. Galápagos: [Isla San Cristóbal] "Chatham Island, end of Sep 1835," *Darwin s.n.* (holotype: K!).

Perennial herbs, erect initially, later procumbent, slender to robust and viny, to 4 m in long. Stem 6–10 mm in diameter at base, green, variously pubescent, coastal populations more glandular, the pubescence composed of trichomes of several types: simple, uniseriate, patent trichomes ca. 1 mm long, with multicellular bases, mixed with uniseriate, 1-3-celled slender trichomes, 0.2–0.4 mm long, with unicellular bases, and shorter glandular, simple, 1–2-cellular trichomes, the glandular heads unicellular or multicellular, the plant with a strong citrus-like scent. Sympodial units 3-foliolate; internodes 1.5–5 (–8) cm long. Leaves interrupted imparipinnate, 3.5–14 cm long, 1.5–8.5 cm wide, lime green to dark green, sparsely pubescent to glabrescent ('Academy Bay') adaxially, densely velvety-pubescent with uniseriate uni- or multicellular velvety trichomes abaxially; primary leaflets 2–3 (–4) pairs, ovate or orbicular, apex acute, base asymmetric, rounded to cordate, margin entire to irregularly lobed; terminal leaflet 1–4 cm long, 1–3 cm long, usually larger than the laterals, about half as long as the leaf rachis, the petiolule 0.1–0.3 cm long; lateral leaflets 0.8–6 cm long, 0.4–2 cm wide, the petiolule 0.2–2 cm long; secondary leaflets if present, mainly on proximal leaflets and basiscopically, 0–5 (–8) per

leaf, ca. 0.2 cm long, sessile; tertiary leaflets absent; interjected leaflets usually present, 4–8 (–14), 0.1–0.2 cm long, 0.1–0.2 cm wide, sessile or with a short petiolule to 0.2 cm long; petiole 0.5–3.0 (–3.5) cm long; pseudostipules absent. Inflorescences to 7.5 cm long, simple or sometimes 2–3-branched, with up to 11 flowers, usually ebracteate but bract and bracteole-like leaflets sometimes present on the axis, peduncle 1–3.3 cm long, pubescent like the stems. Pedicels 0.6–2 cm long, articulated in the distal 1/3, occasionally without an articulation (“jointless,” see Rick 1967). Buds 0.7–0.8 cm long, 0.15–0.2 cm wide, narrowly conical, the corolla more than halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube 0.5–1 mm long, lobes 3–5 mm long, ca. 1 mm wide, linear, pubescent with long and short simple uniseriate trichomes, apex acute; corolla 1.8–2.8 cm in diameter, pentagonal, yellow, the tube 0.2–0.4 cm long, lobes 0.9–1.4 cm long, 0.25–0.4 cm wide, narrowly deltate, minutely to densely pubescent abaxially with tangled, transparent simple uniseriate trichomes, these more abundant along the margins, mixed with smaller and much sparser uniseriate glandular trichomes with 4-celled heads, lobes reflexed at anthesis; staminal column 0.4–0.7 cm long, narrowly cone-shaped, straight, filaments 1–2 (–2.5) mm long, anthers 0.3–0.5 cm long, equal, sterile apical appendage 0.1–0.3 cm long; ovary conical, minutely glandular-villous; style 0.3–0.6 (–0.8) cm long, < 0.5 mm in diameter, usually included in the staminal column, but exerted to 1 (–2) mm in some specimens, usually only just exerted from the staminal column; stigma minutely capitate, green. Fruits 0.6–1.4 (–2.5) cm in diameter, globose, 2-locular, yellow or orange at maturity, glabrescent; fruiting pedicels 0.9–1.5 cm long, more or less straight, sometimes angled at the articulation; calyx lobes in fruit accrescent, to 4.5–13 mm long, 5–3 mm wide, tightly appressed or spreading. Seeds 1.5–2.0 mm long, 0.8–1.2 mm wide, 0.4–0.5 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or sometimes shaggy, narrowly winged (0.2 mm) at the apex and acute at the base, with a pronounced beak; dry seed weight ca. 0.6 mg. Chromosome number: $n = 12$ (LA0749, <http://tgrc.ucdavis.edu>). Plate 1C, Plate 2C, Plate 3C; Fig. 50.

Phenology. Flowers and fruits throughout the year, but with a flowering peak from April to June.

Distribution (Fig. 51). Galápagos Islands, Ecuador; sea level to 1300 m.

ADDITIONAL SPECIMENS EXAMINED (* indicates specimens of the ‘Academy Bay’ morph). **Ecuador.** GALÁPAGOS. BALTRA: N coast, coastal lava, *Darwin et al. 203* (BM, CDS), *Darwin et al. 205* (BM, CDS), *Darwin et al. 209* (QCA, QCNE).—ESPAÑOLA: without locality, *Touc s.n.* (CDS).—FERNANDINA: alluvial fan near W-coast, periodically flooded *Bursera* forest, *Adrsersen & Adrsersen 903** (C, CDS); SE slope, approx. 2.5–3.5 km below the rim of the caldera, *Hamann & Hamann 213** (C); en la cumbre al oeste de la caldera, en pequeñas manchas densas dentro del bosque de *Scalesia*, *Huttel 495** (CDS, QCA).—ISABELA: Volcán Darwin, Islote Crater Beagle 2, *Aldaz 350* (CDS); without locality, 1853, *Andersson s.n.* (S); Volcán Alcedo, from sea level nearly to the top, *Castro s.n.* (CDS); just outside Villamil, by El Lagoon del Manzanillo, growing next to gravel pit formed due to the extraction of gravel for the airport built in 1996, *Darwin & Rosero 365** (BM, CDS, QCNE), *Darwin & Rosero 366** (BM, CDS, QCNE); Caleta Black, *Eliasson & Eliasson 2207* (S); Volcán Alcedo, W slope of caldera, *Hamann & Hamann 1801** (C); *Harling 5288* (S); Volcán Wolf, E side, Iguana Cove, *Howell 9427** (CAS); 5 mi N of Webb Cove, *Howell 9447* (CAS); 3 mi S of the equator, E side of island, *Howell 9617* (CAS); Volcán Wolf, *Lawesson 3017** (CDS); Volcán Darwin, *Lawesson 3080** (CDS); Iguana Cove, abundant on the side of the cliff above the cove, *Stewart 3379** (CAS, GH, US).—PINZÓN: NW slope of island, a square 5-ha area with its SE corner in MacFarland’s (Director CDRS) old camp, crossed by trails to crater and to W slope tortoise nesting zone (area includes “unión de dos caminos”), *Clark & Clark 344* (WIS).—SAN CRISTÓBAL: without locality, end of Sep 1835, *Darwin s.n.* (K); without locality, end Sep 1835, *Darwin s.n.** (CGE); without locality, end Sep 1835, *Darwin s.n.* (CGE); champ de laves récentes au NE de Cerro Brujo, préférence pour laves acoriacées, *Huttel 1597* (CDS, QCA); Sappho Cove, occasional on recent lava, *Stewart*

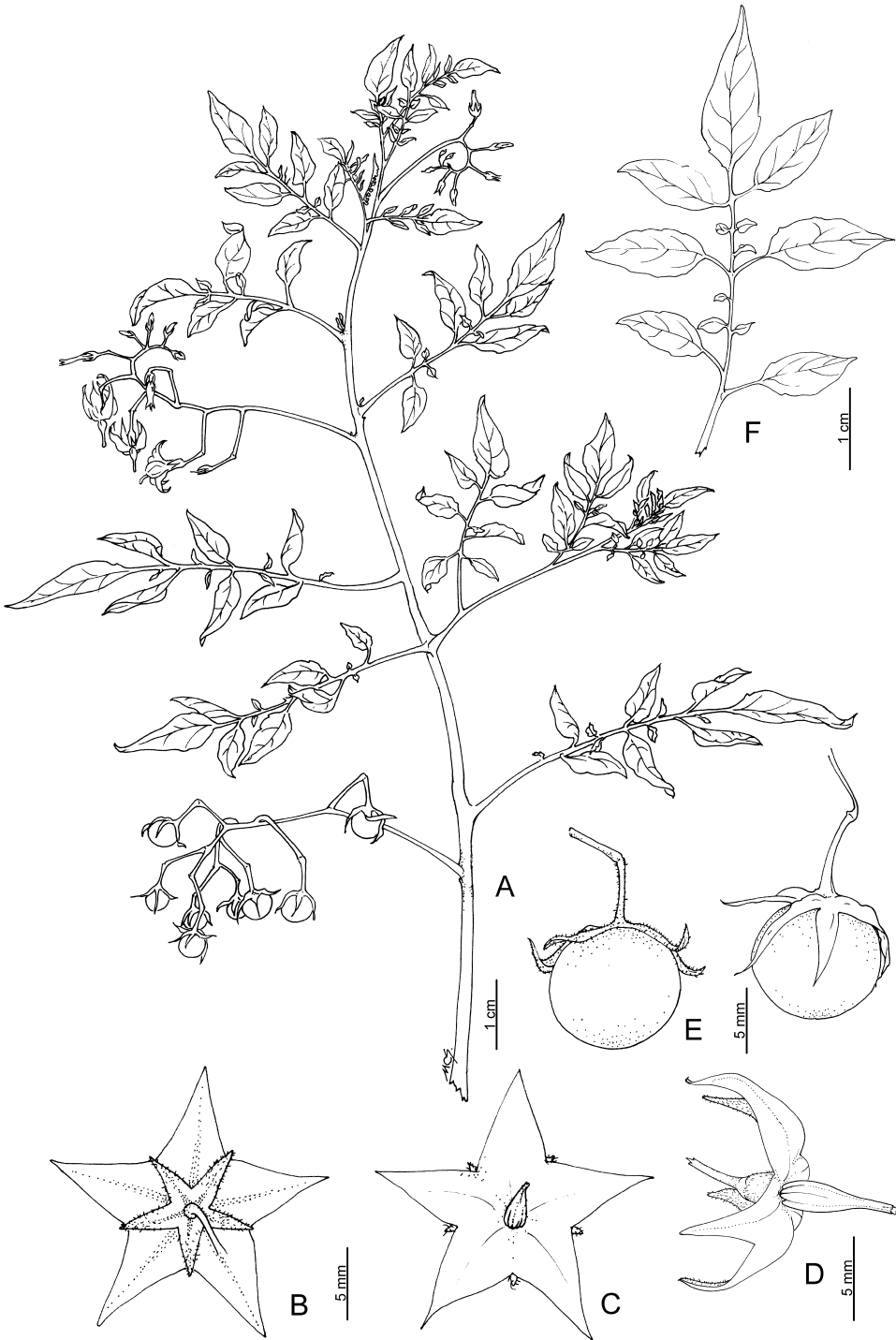


FIG. 50. *Solanum cheesmaniae*. A. Branch. B. Abaxial view of flower. C. Adaxial view of flower. D. Side view of flower. E. Two fruits. F. Leaf.

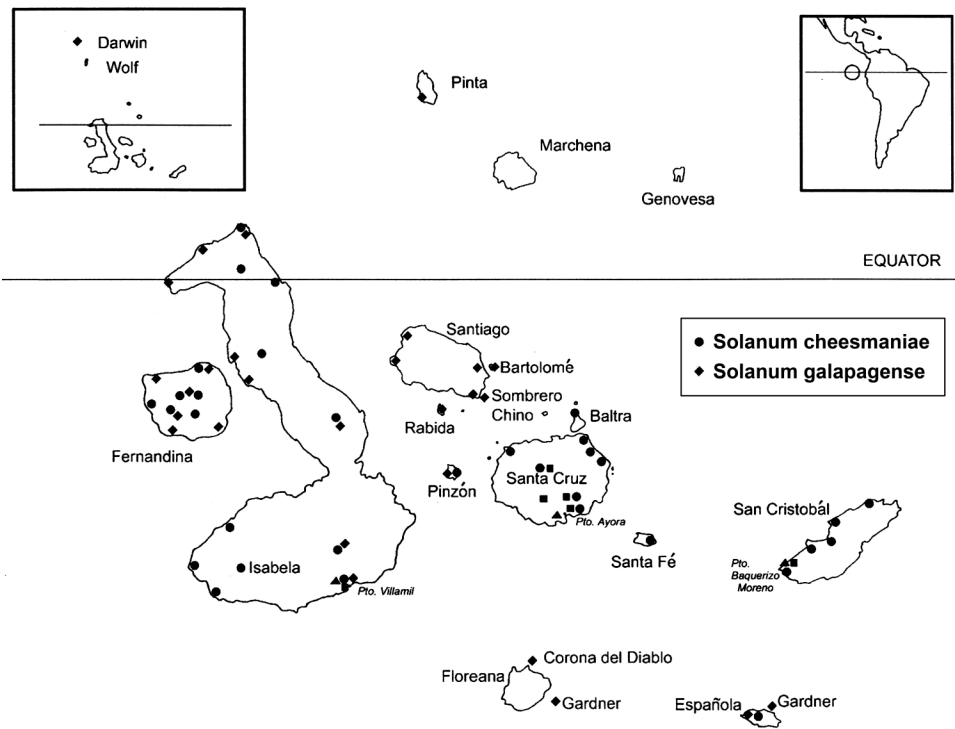


FIG. 51. Distribution of *Solanum cheesmaniae* and *S. galapagense*. Modified and reproduced with permission from *Systematics and Biodiversity* 1: 31, fig. 1. 2003.

3374 (CAS, GH).—SANTA CRUZ: Charles Darwin Research Station, along the path running between the town station road and the tortoise rearing house, growing in sunny area, *Bentley 342** (CDS, K, QCA, US); Academy Bay, collected on edge of ‘barranco’ at Puerto Ayora, *Bowman 119** (CAS, UC); 1.5 miles N Academy Bay, *Bowman 120** (CAS, UC); 1 km NW of Cerro Colorado, *Darwin et al. 214* (BM, CDS); about 5 km NW of Cerro Colorado, *Darwin et al. 236* (BM), *Darwin et al. 239* (BM); Punta Carrión, *Darwin et al. 272* (BM, CDS); Academy Bay, *Eliasson & Eliasson 201** (MO, S); on the N slope, approximately 100 m from the road between Santa Rosa and the canal, *Hamann & Seberg 1771* (C); Academy Bay, *Howell 9096** (CAS); Academy Bay, *Schimpff 12** (BM, CAS, G, M, MO, NY, S, U, Z); Punta Bowditch–Costa, en las pendientes de un pequeño crater entre la costa y el Cerro Montura, *Huttel 2735* (CDS); N side, *Stewart 3376* (CAS, GH).—SANTA FÉ: stoney barranca, *Harling 5371* (S); rocky shore, *Harling 5476* (S); W part of the island, the highest plateau, *Hamann & Hamann 444* (C); without locality, *de Vries 1227* (CDS).

Solanum cheesmaniae is morphologically quite variable, but can be distinguished from its sympatric close relative *S. galapagense* by its less divided leaves, fewer numerous interjected leaflets, and shorter calyx lobes, which do not enclose the ripe fruit. In the morphological analyses of Darwin et al. (2003) plants of *S. cheesmaniae* form a cohesive group despite considerable variation, but two extreme morphs show differences in leaflet shape, margin, leaf division, and pubescence. The type specimen of *S. cheesmaniae* represents the ‘typical’ morphology, and has very small leaves and leaflets, with entire to regularly dentate margins and dense pubescence in all parts of the plant, and bearing short glandular trichomes on the adaxial surface of the leaflets. These characters are consistently present in specimens collected from the north coast of Santa Cruz and Baltra, San

Cristóbal, Santa Fé, Pinzón, and coastal Isabela. The other extreme morph of *S. cheesmaniae*, called by Darwin et al. (2003) the 'Academy Bay' morph, has leaves to three times the size of the 'typical' morph, irregularly dentate leaflet margins (see Fig. 4 in Darwin et al. 2003), and the plants are altogether less pubescent; the sparse pubescence is especially notable on both leaflet faces. The 'Academy Bay' morph has been collected from near areas of human habitation on southern Santa Cruz (Academy Bay = Puerto Ayora). Other specimens that we here consider to fall within the 'Academy Bay' morph show intermediate leaf morphology compared to the two extremes. These plants have a velvety pubescence composed of short trichomes of similar length; this pubescence is more apparent on the abaxial face of the leaflets. These intermediates have been collected in Isabela, Fernandina, and Santa Cruz, and also possibly occur on San Cristóbal and Española. Specimens of the 'Academy Bay' morph have been collected mostly from the southern sides of the islands or at high altitudes (areas with maximum precipitation). Many of these specimens were collected during El Niño years (see Quinn & Neal, 1992, for a list of El Niño dates).

Hooker (1847) recognized three different species of tomatoes from the Galápagos, all based on the specimens collected by Charles Darwin. We found that one of these specimens, documented as having been collected from San Cristóbal and identified by Hooker as "*L. pimpinellifolium*," belongs to the 'Academy Bay' morph. Some of the specimens cited by Müller (1940) as "*Lycopersicon pimpinellifolium*" are also assigned here to the *S. cheesmaniae* 'Academy Bay' morph. Rick (1956, 1963) referred to three different tomato variants in Galápagos, including a Galápagos "*L. pimpinellifolium* type" (TGRC accession number LA166), which had orange fruit but flowers with the corolla divided 2/3 the way to the base (for illustration see Rick, 1956). In his later work, Rick (1971) reclassified the Galápagos accessions of "*L. pimpinellifolium*" with orange fruits under "*L. cheesmanii*." He considered the red-fruited tomatoes in Galápagos to be introduced species (C. M. Rick in litt. 1998). The leaf morphology of some specimens of the *S. cheesmaniae* 'Academy Bay' morph from Isabela is similar to that of individuals of *S. pimpinellifolium* found in Galápagos and on mainland South America (coastal Peru and Ecuador).

The morphological variation in *S. cheesmaniae* is indeed complex. Rick (1963) also recognized this and pointed out that populations from the type locality on the northern side of Santa Cruz are intermediate in terms of pubescence density between *S. galapagense* and what we here define as the 'Academy Bay' morph of *S. cheesmaniae*. He also observed that "typical" *S. cheesmaniae* shared morphological similarities with the 'Academy Bay' morph but resembled *S. galapagense* with respect to its shorter internodes. Rick (1963) felt that typical *S. cheesmaniae* had leaves that were less divided than in the two other forms and with orbicular lateral segments (see leaf variation in Figs. 4, 5 in Darwin et al. 2003). Our observations are consistent with these morphological differences noted by Rick (1963). Using AFLP polymorphisms, Nuez et al. (2004) identified Galápagos tomatoes as "*Lycopersicon cheesmanii*," and designated some of the TGRC accessions we identify as *S. cheesmaniae* 'Academy Bay' as "*L. esculentum*" and others as "*L. cheesmanii* long." Our AFLP data from the *S. peruvianum* complex (Spooner et al. 2005) indicate that if hybridization is occurring or has occurred, then AFLP polymorphisms are not useful for distinguishing species that may be hybridizing. We know that *S. cheesmaniae* and *S. pimpinellifolium* hybridize in the Galápagos (S. C. Darwin, unpubl.), complicating patterns of molecular relationships.

A comparison between herbarium specimens and greenhouse-grown progeny collected from the same plants showed that the greenhouse grown-plants had larger leaf

dimensions than their field-collected parents, as is common in wild tomatoes. Size difference, however, did not wholly account for the differences between the typical *S. cheesmaniae* and the ‘Academy Bay’ morphs. Further investigations being undertaken by S. C. Darwin may resolve the relationships and taxonomic status of the ‘Academy Bay’ morph, and may discern the causes for these different morphologies found within *S. cheesmaniae*. Variation in *S. cheesmaniae* is potentially due to: (1) plants here recognized as the ‘Academy Bay’ morph could be an ecotype of *S. cheesmaniae*, (2) plants are potentially of hybrid origin involving *S. pimpinellifolium*, or (3) plants could be morphologically aberrant due to increased soil humidity found in the southern parts of the islands and during El Niño years.

Results from allozyme electrophoresis (Rick & Fobes 1975a) suggested that the populations of *S. pimpinellifolium* from the coastal region of Motupe-Olmos (ca. 6°S latitude) in the northern Peruvian Department of Lambayeque were most closely related to the Galápagos tomatoes. They also suggested that the observation that the Humboldt Current flows from about 6°S latitude to the Galápagos at certain times of year also lent support to this origin for *S. pimpinellifolium* in the Galápagos (Rick & Fobes 1975b).

The publication date of Hooker’s “*Enumeration of Galápagos Plants*,” in which he described both *Lycopersicon peruvianum* var. *parviflorum* (= *S. cheesmaniae*) and *Lycopersicon esculentum* var. *minor* (= *S. galapagense*) is given on the title page of Volume 20 of the *Transactions of the Linnean Society of London* as 1851, but Part II, in which the paper appeared (read on 4 May, 6 May and 16 December 1845) was available as a separate on 11 December 1847 (Raphael 1970). Thus the correct date of publication of the names published therein is 1847, not 1851 as it appears in most bound library copies of the *Transactions*.

The spelling of the specific epithet has been corrected from *cheesmanii* to *cheesmaniae*; the species was named in honor of Lucy Evelyn Cheesman (1881–1969), who collected the type (see Fosberg 1987; Spooner et al. 1993; McNeill et al. 2006). Although Fosberg (1987) pointed this out, the spelling has not changed in the plant breeding literature, but floristic studies have consistently used the correct feminine ending (e.g., Jørgensen & León Yanez 1999).

The combination *Solanum cheesmaniae* (L. Riley) Fosberg (1987) postdates the name *Solanum cheesemanii* Gerasimenko (a synonym of *S. aviculare* G. Forst.), coined to honor the New Zealand botanist Thomas H. Cheesman. The two names are very similar, and the rejection of Gerasimenko’s name in favor of the commonly and widely used combination for this tomato species has been proposed (Knapp & Darwin 2006).

17. *Solanum galapagense* S. C. Darwin & Peralta, Syst. Biodiv. 1: 45. 2003.—TYPE: ECUADOR. Galápagos: Isla Bartolomé, E of the saddle beach, ca. 6 m, 0°17′01″S, 90°33′30″W, 28 Jun 2000, *Darwin & Schulz 184* (holotype: CDS!; isotype: BM!).

Lycopersicon esculentum var. *minor* J. D. Hooker, Trans. Linn. Soc. London 20: 202. 1847 [“1851”]. *Lycopersicon cheesmaniae* f. *minor* (J. D. Hooker) C. H. Müller, U.S. Dept. Agric. Misc. Publ. 382: 21. 1940. *Lycopersicon cheesmaniae* var. *minor* (J. D. Hooker) D. M. Porter, Madroño 25: 58. 1978.—TYPE: ECUADOR. Galápagos: [Isla Santiago] James Island, Oct 1835, *Darwin s.n.* (holotype: CGE!).

Perennial herbs, erect initially, later procumbent, slender to robust and viny, to 3 m long. Stems 10–12 mm in diameter at base, green, densely pubescent, the pubescence

composed of simple uniseriate trichomes of several lengths, the longest 0.5–2 cm long, ca. 0.1 mm wide, some gland-tipped, the longer ones with minute single-celled glands, among dense uniseriate 1–2-celled trichomes, some gland-tipped, the glands unicellular and minute or multicellular, the plant with a strong citrus scent, smaller trichomes unicellular, uniseriate, and usually gland-tipped. Sympodial units 3-foliolate; internodes 1.5–3.5 (–6) cm long. Leaves interrupted imparipinnate, 5–25 cm long, 2–17 cm wide, bright green, densely pubescent with uniseriate glandular trichomes ca. 0.5 mm long, and shorter unicellular trichomes on both surfaces, more abundant abaxially, lime green; primary leaflets 2–4 pairs, subopposite or alternate, ovate or obovate, apex acute to rounded, base oblique and decurrent basiscopically, cuneate to cordate, margin deeply lobed, forming secondary, tertiary, and occasionally quaternary leaflets of varying sizes; terminal leaflet scarcely larger than the laterals, often with secondary leaflets, 0.5–2 cm long, 0.4–1 cm wide, the petiolule 0.2–0.3 cm long; lateral leaflets 2–7 cm long, 1–4.5 cm wide, the petiolule 0.1–0.6 cm long; secondary leaflets present, always more than (6–) 10–30 per leaf, 0.3–1 cm long, 0.2–0.5 cm wide, sessile or with a petiolule to 0.4 cm long; tertiary leaflets usually present, ca. 0.1–0.2 cm long, 0.1–0.2 cm wide, sessile or with a minute petiolule; interjected leaflets usually present, (3–) 5–22 (–30), 0.1–0.5 cm long, 0.1–0.5 cm wide, sessile or with a short petiolule to 0.3 cm long; petiole 0.6–4 cm long; pseudostipules absent. Inflorescences to 10 cm long, simple or occasionally 2–3-branched, with up to 12 flowers, usually ebracteate, but bract and bracteole-like leaflets occasionally present in some populations, peduncle 1–3.5 cm long, pubescent like the stems. Pedicels 0.5–1.8 cm long, articulated just below the middle. Buds 0.7–1 cm long, 0.3–0.4 cm wide, conical, straight, the corolla about halfway exerted beyond the calyx just before anthesis. Flowers with the calyx tube 0.5–1 mm long, lobes 3–6 mm long, 1–1.5 mm wide, linear, pubescent with long and short simple uniseriate trichomes, apex acute; corolla 1.6–3.2 cm in diameter, pentagonal, occasionally somewhat bilaterally symmetric due to fusion of adjacent lobes, yellow, the tube 0.5–0.7 cm long, lobes 0.7–1.3 cm long, 0.3–0.7 cm wide, densely pubescent along the midveins with tangled transparent uniseriate trichomes ca. 0.5 mm long, reflexed at anthesis; staminal column 0.3–0.7 cm long, narrowly cone-shaped, straight, filaments 1–2.7 mm long, anthers 0.3–0.45 cm long, equal, sterile apical appendage 0.1–0.2 (–0.4) cm long; ovary conical, minutely glandular-villous; style 0.4–0.8 cm long, straight, <0.5 mm in diameter, usually included in the staminal column, rarely exerted to less than 0.5 mm long; stigma minute, green. Fruits 0.6–1.1 cm in diameter, globose, 2-locular, pale to deep orange at maturity, glabrescent to densely pubescent with weak eglandular simple uniseriate patent trichomes to 3 mm long, and smaller uniseriate glandular trichomes with 4-celled heads; fruiting pedicels 0.7–1.5 cm long, curving towards the axis; calyx lobes in fruit accrescent, to 14 mm long, 1–3 mm wide, often longer than fruit, basal half of calyx tightly appressed to berry base. Seeds (5–) ca. 30 (–50) per fruit, 1.5–2.0 mm long, 0.8–1.2 mm wide, 0.4–0.5 mm thick, obovate, pale brown, pubescent with hair-like outgrowths of the lateral testa cell walls giving a silky appearance to the surface or more often shaggy, narrowly winged (0.2 mm) at the apex and acute at the base. Chromosome number: $n = 12$ (LA0317, <http://tgrc.ucdavis.edu>). Plate 1D, Plate 2D, Plate 3D; Fig. 52.

Phenology. Flowers and fruits throughout the year in response to moisture.

Distribution (Fig. 51). Galápagos Islands, particularly the western and southern islands; mostly on coastal lava to within 1 m of high tide mark within range of sea spray (strongly salt-tolerant) but also occasionally inland, e.g., on volcanic slopes on Isabela and Fernandina; sea level to 50 m (exceptionally to 1500 m on volcanic slopes).

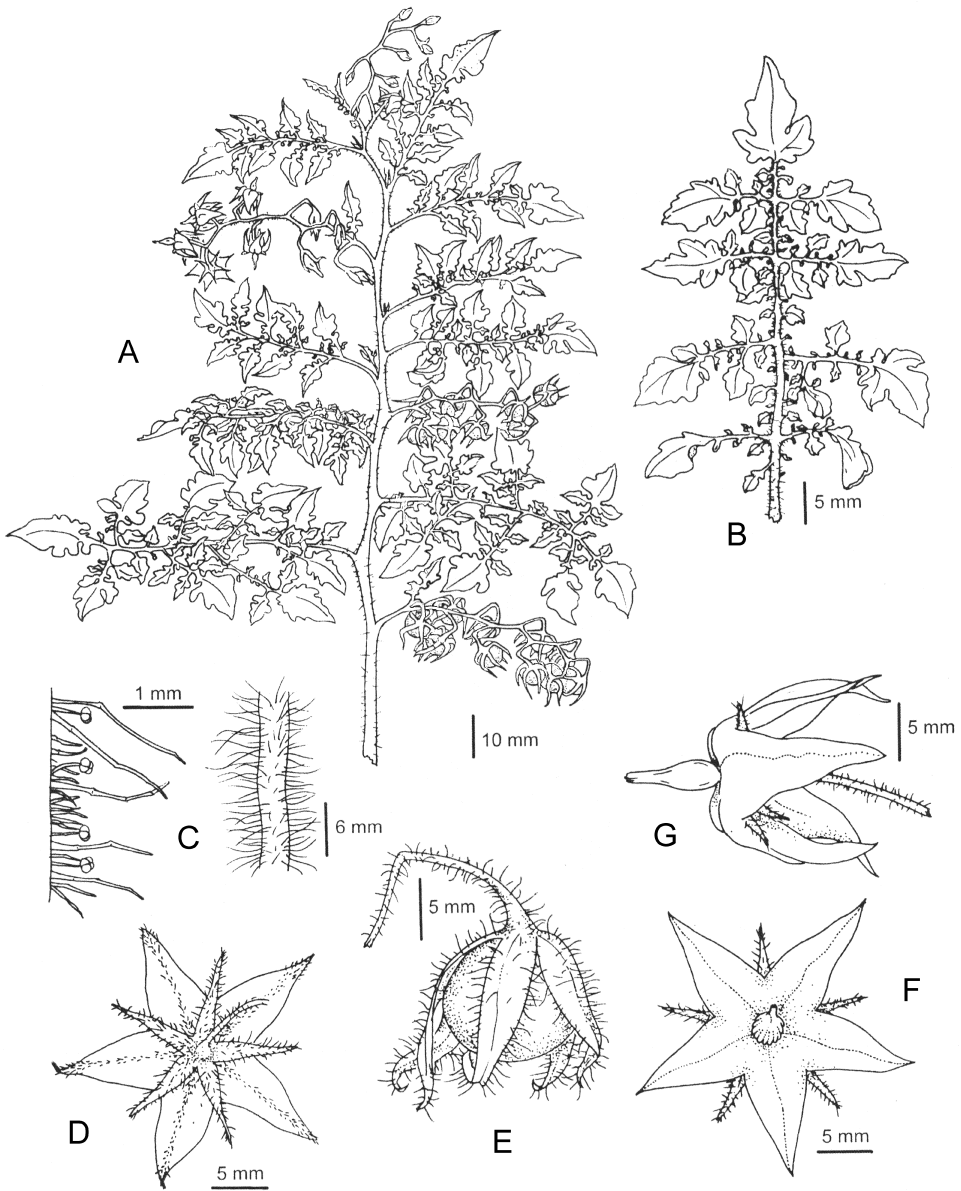


FIG. 52. *Solanum galapagense*. A. Branch. B. Leaf. C. Portion of stem and detail showing trichomes. D. Abaxial view of flower. E. Fruit. F. Adaxial view of flower. G. Side view of flower. Reproduced with permission from *Systematics and Biodiversity* 1: 45, fig. 5. 2003.

ADDITIONAL SPECIMENS EXAMINED. **Ecuador.** GALÁPAGOS. Without locality, *Scouler s.n.* (E).—BAROLOMÉ: to right of summit landing site, *Darwin & Schultz 181* (CDS, QCNE), *Darwin & Schultz 182* (BM, CDS); E of the saddle beach, *Darwin & Schultz 189* (CDS), *Darwin & Schultz 190* (BM); rocas o lava, *Jaramillo 1052* (CDS); without locality, *Fagerlind & Wibon 3464* (S); on barren lava and in cinder patches among lava blocks and flows, *Wiggins & Porter 296* (CAS, GH, SGO); on barren lava along E side of a lava ridge about 2 km from W end of Isla San Bartolomé, *Wiggins & Porter 314* (CAS, USN).—CORONA DEL DIABLO: without locality, *Eliasson & Eliasson 656* (S).—DARWIN: without locality, *Touc s.n.* (CDS).—ESPAÑOLA: without locality, *Snodgrass & Heller 741* (GH, DS), *Touc s.n.* (CDS).—FERNANDINA: NW of rim, on 1968 ash deposit, *Adersen & Adersen 921* (C, CDS); green strip on SW slope, large clumps growing at the edge of *Scalesia* zone on deep ash sand near crater rim, *Cavagnero 25* (MO); SW corner of island, Cabo Hammond, *Reeder s.n.* (WIS); NW slope, *Schmidt & Schmidt 2528* (C).—GARDNER (NR. ESPAÑOLA): without locality, *Stewart 3373* (CAS); GARDNER (NR. FLOREANA): without locality, *Touc s.n.* (CDS).—ISABELA: fumarole on E saddle, *Adersen & Adersen 1165* (C); El Lagoon del Manzanillo, growing next to gravel pit formed due to the extraction of gravel for the airport built in 1996, *Darwin et al. 291* (BM, CDS, QCA, QCNE), *Darwin et al. 294* (CDS), *Darwin & Rosero 364* (BM, CDS, QCA, QCNE); Volcán Darwin, beach N of Tagus Mountain, *Hamman & Hamman 1729* (C); Punta Albemarle, *Lévêque 163* (MO); Sierra Negra, 10 km N of Villamil, *Hamann & Hamann 2483* (C); Tagus Cove, *Snow s.n.* (CDS).—PINTA: without locality, *Castro s.n.* (CDS), *Snow 591* (K), *Stewart 3370* (CAS); nr. fumarole, *de Vries s.n.* (CDS); SE slope, *van der Werff 2129* (U).—PINZÓN: growing between rocks, *Castro s.n.* (CAS).—RÁBIDA: among lava boulders on upper slopes of main volcanic peak, *DeRoy & DeRoy 11* (DS); without locality, *Howell 9753* (CAS), *Menzies s.n.* (BM); barranca, N slope, *Reeder & Chapy s.n.* (WIS).—SANTIAGO: Caleta Bucanero, *Adersen & Adersen 1771* (C, CDS); without locality, *Andersson s.n.* (BR); Crab Point (S of James Bay-W side of Island), *Castro s.n.* (CAS); without locality, beginning Oct 1835, *Darwin s.n.* (CGE); without locality, *Howell 9701* (CAS); Sullivan Bay, *Howell 10012* (B, CAS, K); without locality, *Snodgrass & Heller 399* (GH); James Bay, *Stewart 3369* (CAS), *Stewart 3378* (BM, CAS, MO, NY, USN).—SOMBRERO CHINO: NE side of the islet, *Darwin & Schultz 138* (QCA, QCNE), *Darwin & Schultz 139* (BM, CDS), *Darwin & Schultz 145* (QCNE), *Darwin & Schultz 149* (CDS), *Darwin & Schultz 157* (BM); without locality, *Snell 109* (CDS).

Solanum galapagense can be clearly differentiated from the rest of the “Lycopersicon” species group on leaf morphology alone. Other discriminating characters included appressed sepals that exceed the ripe fruit diameter, the presence of bract-like leaflets on the inflorescence, and presence of branched inflorescences (sometimes 2–3-branched, very occasionally simple). These morphological characters were found at a lower frequency in *S. cheesmaniae*, and only rarely in *S. lycopersicum* and *S. pimpinellifolium*. Note that the presence of appressed sepals is not always apparent in herbarium specimens, because sepals apparently curl upwards as they dry and can become reflexed; in live plants they remain tightly appressed until fruit abscission.

Solanum galapagense has always been recognized as a distinct taxon (Darwin et al. 2003). Orange fruit color is found only in *S. cheesmaniae* and *S. galapagense*. This character is derived in these two species (Peralta & Spooner 2001) and separates them from *S. pimpinellifolium* and *S. lycopersicum*. Fruit color was described by Rick (1971) as a “dependable key character” with which to differentiate the Galápagos tomatoes from all others.

Solanum galapagense and *S. cheesmaniae* are both endemic to the Galápagos Islands. The introduction of cultivated tomatoes and evidence of natural introgression with wild tomatoes (see Darwin et al. 2003) generate concern about *in situ* conservation of natural populations. These two species can be considered vulnerable due to their narrow range, island endemism, and potential for genetic exchange with non-native species.

Darwin et al. (2003) identified *Scouler s.n.* (E), collected in 1826, as the oldest specimen of one of the Galápagos tomatoes. Since publication of that paper, we have discovered a specimen in BM collected by Archibald Menzies in 1791, probably from northern Isabela, where his ship (HMS *Discovery*) stopped very briefly on its way to the Pacific Northwest (Eric Groves, pers. comm.). The specimen was mislabelled as “Sandwich

Islands” (Hawa‘i) and thus remained unnoticed until databasing of herbarium specimens as part of the PBI *Solanum* project began (see Knapp et al. 2004).

Various misspellings of Hooker’s epithet *minor* as *minus* (“*Lycopersicon esculentum* var. *minus* Hook. f.” and “*Lycopersicon cheesmanii* L. E. Riley subsp. *minus* Hook. f.”) occur in some privately circulating lists, but are orthographic errors (*minor* is the comparative degree of the adjective *parvus*; *minus* is an adverb).

DOUBTFUL AND EXCLUDED NAMES

(see Appendix 1 for names not validly published)

Lycopersicon aethiopicum (L.) Miller, Gard. Dict., ed. 8, *Lycopersicon* 3. 1768. = *Solanum aethiopicum* L.; a member of the *Leptostemonum* clade (the spiny solanums) (Bohs 2005) related to *Solanum melongena* L.

Lycopersicon diadelphum Dunal in A. DC., Prodr. 13(1): 27. 1852.—TYPE: not located, probably destroyed.—Dunal provided this name for a specimen noted by Sendtner (in Martius, *Flora brasiliensis* 10: 125. 1846), who stated that he had found in the Berlin herbarium a specimen labeled “*Lycopersicon agrimonifolium*” in which two anthers were united and the rest free. In the absence of the type, the application of Dunal’s name remains unknown.

Lycopersicon dulcamara (L.) Medikus, Beobacht. 245. 1783. = *Solanum dulcamara* L.; a member of the *Dulcamara* clade (Bohs 2005).

Lycopersicon procumbens Miller, Gard. Dict., ed. 8, *Lycopersicon* no. 6. 1768.—TYPE: unknown; not at BM.—The name cannot be associated with any known species of *Solanum* and may not even apply to a species of Solanaceae. Miller based the name on plants raised from seeds of unknown provenance obtained “from Mr. James Gordon, Mile-End gardener” and characterized them follows: “This has the very weak, trailing smooth stalks, not more than a foot long, garnished with smooth leaves standing in pairs opposite; there are regularly cut on the sides nearly to the midrib, in the form of a winged leaf; and these segments are also indented on their edges and at their points. The flowers come out on the stalks singly; they are of a whitish yellow color, and have a pretty large spreading impalement which is deeply cut at the brim into many acute segments which spread open. The flowers are succeeded by small roundish berries a little compressed at the top, of a herbaceous yellow color when ripe.”

Lycopersicon tuberosum (L.) Miller, Gard. Dict., ed. 8, *Lycopersicon*. 7. 1768. = *Solanum tuberosum* L.; a member of *Solanum* sect. *Petota*.

ACKNOWLEDGMENTS

We are greatly indebted to the late Charles M. Rick, who provided invaluable advice in choosing and sending accessions from the C. M. Rick Tomato Genetic Resources Center for the GBSSI, morphological, and AFLP studies; he was an inspiration for all our studies in tomatoes. We also thank Roger Chetelat of TGRC and the staff of the US genebank in Geneva for help in obtaining accessions; Dani Zamir of the Hebrew University of

Jerusalem for his insights into the world of tomatoes; Mélica Muñoz Schick of the Herbario (SGO) at the Museo Nacional de Historia Natural in Santiago, Chile, for help with finding Philippi types; Sarah Darwin for useful discussion about the diversity and ecology of tomatoes in the Galápagos; Zara Frankiel (NHM Library) for help with Russian translation; The Natural History Museum Photographic Unit, especially Pat Hart and Kevin Webb, for the production of photographic figures and maps; Kandis Elliot, Dept. of Botany, University of Wisconsin-Madison, for preparation of the color plates; Cecilia Scoones from the Argentinean Institute of Arid Zone Research (IADIZA-CONICET) for the line drawings and Fig. 51; and the Natural History Museum Botany Library for permission to reproduce library materials in their care. Dan Nicholson (US), R. K. Brummitt (K), J. McNeill (E), and Charlie Jarvis (BM) provided essential nomenclatural advice. Christiane Anderson and Jaime Prohens provided detailed and insightful reviews. We especially thank the curators and staff of the following herbaria for providing access to the specimens in their care: A, AAU, B, BH, BM, BR, C, CAS, CICY, COL, CONC, CR, CUVV, DS, E, ECON, F, FCQ, G, GAT, G-DC, GH, HUT, INB, JBSD, K, LINN, LL, LPB, M, MA, MEXU, MO, NAP, NEBC, NY, OXF, P, PMA, S, SGO, SI, SP, TEX, U, UC, UCZ, US, USM, W, WIR, WIS, WU, Z. Peter Schäfer (MPU), Irina Khrpalova, Nadezha Zoteyeva, Tamara Swekalova, and Alexanian Sergei (WIR), Laurent Gautier (G), Philippe Morat (P), and Michael Daly and Simon Owens (K) were particularly helpful during Iris Peralta's travels in Europe. Iris Peralta also thanks Claudio Galmarini for his love and support. The Fulbright-LASPAU Program, the National Science Council of Argentina (CONICET), the National University of Cuyo (UNC), the USDA, and the NSF (DEB-0316614 'PBI *Solanum* - a worldwide treatment') funded research. The A. W. Mellon Foundation via the Kew Latin American Research Fellowships (KLARF) supported Iris Peralta's stay in London, and the Office of Economic Cooperation and Development and the USDA supported David Spooner's stay in London.

LITERATURE CITED

- Acosta, J. de. 1590. *Historia natural y moral de las Indias*. Seville.
- Addison, L. 1671. *West Barbary, or a short narrative of the revolutions of the kingdoms of Fex and Morocco*. London: Published by the author.
- Alefeld, F. G. C. 1866. *Landwirthschaftliche Flora*. Berlin: Wiegandt und Hempel.
- Allan, R., J. Lindsay, and D. Parker. 1996. *El Niño southern oscillation and climatic variability*. Sydney: CSIRO.
- Alvarez, A. E., C. C. M. van de Wiel, M. J. M. Smulders, and B. Vosman. 2001. Use of microsatellites to evaluate genetic diversity and species relationships in the genus *Lycopersicon*. *Theor. Appl. Genet.* 103: 1283–1292.
- Anguillara, L. 1561. *Semplici dell' eccellente M.L.A., Liquali in piu Pareri a diversi nobili huomini scritti appaiono, et Nouvamente da M. Giovanni Martinello mandati in luce*. Venice: V. Valgrisi.
- Arber, A. 1990. *Herbals: their origin and evolution*. (reprint of 3d ed). Cambridge: Cambridge University Press.
- Bai, Y., C. C. Huang, R. van der Hulst, F. Meijer-Dekens, G. Bonnema, and P. Lindhout. 2003. QTLs for powdery mildew resistance (*Oidium lycopersici*) in *Lycopersicon parviflorum* G1.1601 co-localize with two qualitative powdery mildew resistance genes. *Mol. Plant Microbe Interact.* 16: 169–176.
- Bai, Y., R. van der Hulst, C. C. Huang, L. Wei, P. Stam, and P. Lindhout. 2004. Mapping OI-4, a gene conferring resistance to *Oidium neolyopersici* and originating from *Lycopersicon peruvianum* LA2172, requires multi-allelic, single-locus markers. *Theor. Appl. Genet.* 109: 1215–1223.
- Barboza, G., and A. T. Hunziker. 1991. Estudios sobre Solanaceae XXXI. Peculiaridades del androceo de interés taxonómico en *Solanum*. *Kurtziana* 21: 185–194.
- Bharathan, G., T. E. Goliber, C. Moore, S. Kessler, T. Pham, and N. R. Sinha. 2002. Homologies in leaf form inferred from *KNOX1* gene expression during development. *Science* 296: 1858–1860.
- Bauhin, C. 1623. *Pinax theatri botanici*. Basel: Lucovici Regis.
- Bentham, G., and J. D. Hooker. 1873. Solanaceae. In *Genera plantarum* 2: 882–913. London: Reeve & Co.
- Besler, B. 1613. *Hortus eystettensis*. Nuremberg: published by the author.
- Bidwell, J. 2003. *Matthioli's herbal: a short account of its illustration with a print from an original woodblock*. New York: The Pierpoint Morgan Library.
- Blunt, W. 1971. *The compleat naturalist: a life of Linnaeus*. London: Collins.
- Bohs, L. 1994. *Cyphomandra* (Solanaceae). *Fl. Neotrop. Monogr.* 63: 1–175.
- . 1995. Transfer of *Cyphomandra* (Solanaceae) and its species to *Solanum*. *Taxon* 44: 583–587.
- . 2005. Major clades in *Solanum* based on *ndhF* sequences. In "A Festschrift for William G. D'Arcy: the legacy of a taxonomist," ed. R. C. Keating, V. C. Hollowell, and T. B. Croat. *Monogr. Syst. Bot. Missouri Bot. Gard.* 104: 27–49.

- 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.
- . 2001. A reassessment of *Normandia* and *Triguera* (Solanaceae). *Pl. Syst. Evol.* 228: 33–48.
- Börner, C. 1912. *Solanum* L. und *Solanopsis* gen. nov. *Abh. Naturwiss. Verein Bremen* 21: 282.
- Bramley, P. 2002. Regulation of carotenoid formation during tomato fruit ripening and development. *J. Exp. Bot.* 53: 2107–2113.
- Breto, M. P., M. J. Asins, and E. A. Carbonell. 1993. Genetic variability in *Lycopersicon* species and their genetic relationships. *Theor. Appl. Genet.* 86: 113–120.
- Brezhnev, D. D. 1958. Tomat. In “Ovoshchnye paslenovye (Tomat, Baklazhan, Chernyi Paslen, Dynnaia Grusha, Perets, Fizalis, Mandragora).” *Kul’turnaia Flora SSSR*, ed. P. M. Zhukovskii, 20: 7–278. Moscow, Leningrad: State Printing House.
- . 1964. *Tomaty* [Tomatoes], 2d ed. Leningrad: 12D-VO Kolos.
- Brickell, C. D., B. R. Baum, W. L. A. Hetterscheid, A. C. Leslie, J. McNeill, P. Trehane, F. Vrugtman, and J. H. Wiersma. 2004. International code of nomenclature of cultivated plants. *Acta Hort.* 647: 1–123.
- Britton, N.L., and A. Brown. 1913. Solanaceae. In *Illustrated flora of the northern United States, Canada and their British possessions*, 2d ed., 3: 154–171. New York: C. Scribner’s Sons.
- Buchmann, S. L. 1983. Buzz pollination in angiosperms. In *Handbook of experimental pollination biology*, ed. C. E. Jones and R. J. Little, 73–113. New York: Van Nostrand Reinhold Co.
- . 1986. Vibratile pollination in *Solanum* and *Lycopersicon*: a look at pollen chemistry. In *Solanaceae: biology and systematics*, ed. W. G. D’Arcy, 237–252. New York: Columbia University Press.
- Buchmann, S. L., C. E. Jones, and L. J. Colin. 1977. Vibratile pollination of *Solanum douglasii* and *S. xanti* (Solanaceae) in southern California. *Wassman J. Biol.* 35: 1–15.
- Caicedo, A. L., and B. A. Schaal. 2004a. Population structure and phylogeography of *Solanum pimpinellifolium* inferred from a nuclear gene. *Mol. Ecol.* 13: 1871–1882.
- . 2004b. Heterogenous evolutionary processes affect *R* gene diversity in natural populations of *Solanum pimpinellifolium*. *Proc. Nat. Acad. Sci., USA* 101: 17444–17449.
- Candolle, A. de. 1886. *Origin of cultivated plants*, 2d ed. New York: D. Appleton (1959 reprint; New York: Hafner Publishing Company).
- Carrizo García, C. 2003. Morfología comparada del androceo en tomates y especies afines (Solaneae, Solanaceae). *Kurtziana* 30: 27–39.
- Chandra Sekhar, K. N., and V. K. Sawhney. 1984. A scanning electron microscope study of the development and surface features of floral organs of tomato (*Lycopersicon esculentum*). *Can. J. Bot.* 62: 2403–2414.
- . 1987. Ontogenetic study of the fusion of floral organs in the normal and “solanifolia” mutant of tomato (*Lycopersicon esculentum*) *Can. J. Bot.* 65: 215–221.
- Chen, K.-Y., and S. D. Tanksley. 2004. High-resolution mapping and functional analysis of *se2.1*: a major stigma exertion quantitative trait locus associated with the evolution from allogamy to autogamy in the genus *Lycopersicon*. *Genetics* 168: 1563–1573.
- Chetelat, R. T., and Y. Ji. 2006. Cytogenetics and evolution. In *Genetic improvement of solanaceous crops, vol. 2: Tomato*, ed. M. K. Razdan and A. K. Mattoo, 77–112. Enfield, USA: Science Publishers.
- Child, A. 1990. A synopsis of *Solanum* subgenus *Potatoe* (G. Don) (D’Arcy) (*Tuberarium* (Dun.) Bitter (s.l.)). *Feddes Rept.* 101: 209–235.
- Child, A., and R. N. Lester. 1991. Life form and branching within the Solanaceae. In *Solanaceae III: taxonomy, chemistry, evolution*, ed. J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada, 151–159. Kew: Royal Botanic Gardens.
- Chmielewski, T., and C. M. Rick. 1962. *Lycopersicon minutum*. *Tomato Genet. Coop. Rep.* 12: 21–22.
- Correll, D. S. 1958. A new species and some nomenclatural changes in *Solanum* section *Tuberarium*. *Madroño* 14: 232–236.
- . 1962. The potato and its wild relatives. *Contr. Texas Res. Found., Bot. Stud.* 4: 1–606.
- Cribb, D. M., D. W. Hand, and R. N. Edmondson. 1993. A comparative study of the effects of using the honey-bee as a pollinating agent of glasshouse tomato. *J. Hort. Sci.* 68: 79–88.
- D’Arcy, W. G. 1972. Solanaceae studies II: typification of subdivisions of *Solanum*. *Ann. Missouri Bot. Gard.* 59: 262–278.
- . 1974 [“1973”]. Solanaceae. In “Flora of Panama,” *Ann. Missouri Bot. Gard.* 60: 573–780.
- . 1987. The circumscription of *Lycopersicon*. *Solanaceae Newslett.* 2: 60–61.

- . 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, 75–137. Kew: Royal Botanic Gardens.
- Danert, S. 1958. Die Verzweigung der Solanaceen im reproduktiven Bereich. *Abh. Deutsch. Akad. Wiss. Berlin, Kl. Chem.* 1957, 6: 1–183.
- . 1967. Die Verzweigung als infragenerisches Gruppenmerkmal in der Gattung *Solanum* L. *Kulturpflanze* 15: 275–293.
- . 1970. Infragenerische Taxa der Gattung *Solanum* L. *Kulturpflanze* 18: 253–297.
- Darwin, S. C., S. Knapp, and I. E. Peralta. 2003. Tomatoes in the Galápagos Islands: morphology of native and introduced species of *Solanum* section *Lycopersicon* (Solanaceae). *Syst. Biodiv.* 1: 29–54.
- Daunay, M. C., L. Maggioni, and E. Lippman. 2003. *Solanaceae genetic resources in Europe. Report of two meetings—21 September 2001, Nijmegen, The Netherlands/23 May 2003, Skierniewice, Poland*. Rome: International Plant Genetic Resources Institute.
- Dillon, M. O. 1997. *Lomas formations—Peru*. In *Centres of plant diversity: a guide and strategy for their conservation*, ed. S. D. Davis, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, 519–527. Oxford: WWF.
- . 2005. The Solanaceae of the lomas formations of coastal Peru and Chile. In “A Festschrift for William G. D’Arcy: the legacy of a taxonomist,” ed. R. C. Keating, V. C. Hollowell, and T. B. Croat. *Monogr. Syst. Bot. Missouri Bot. Gard.* 104: 27–49.
- Dodoens, R. 1554. *Trium priorum de stirpium historicis commentariorum imagines ad vivum expressae*. Antwerp: J. van der Loe.
- . 1557. *Histoire des plantes* (transl. by C. de L’Ecluse). Antwerp: J. van der Loe.
- . 1563. *Crujde Boeck*. Antwerp: J. van der Loe.
- . 1574. *Purgantium aliarumque eo facientium, tum et radicum, conuoluulorum ac deletriarum herbarum historiae, libri iiii*. Antwerp: C. Plantin.
- . 1583. *Stirpium historiae pemptades sex, sive libri XXX*. Antwerp: C. Plantin.
- Dunal, M. F. 1813. *Histoire naturelle, medicinale et économique des Solanum*. Paris: A. Koenig.
- . 1816. *Solanorum generumque affinium synopsis*. Montpellier: Renaud.
- . 1852. Solanaceae. In *Prodromus systematis naturalis regni vegetabilis*, ed. A. de Candolle, 13: 1–690. Paris: V. Masson.
- Ehrlenfeldt, M. K., and R. E. Hanneman, Jr. 1992. Endosperm dosage relationships among *Lycopersicon* species. *Theor. Appl. Genet.* 83: 397–372.
- Ensminger, A. H., M. E. Ensminger, J. E. Konlande, and J. R. K. Robson. 1995. *The concise encyclopedia of foods and nutrition*. Boca Raton, Florida: CRC Press.
- Eshed, Y., and D. Zamir. 1994. A genomic library of *Lycopersicon pennellii* in *L. esculentum*: a tool for fine mapping of genes. *Euphytica* 79:175–179.
- . 1995. An introgression line population of *Lycopersicon pennellii* in the cultivated tomato enables the identification and fine mapping of yield associated QTL. *Genetics* 141: 1147–1162.
- Eshed, Y., G. Gera, and D. Zamir. 1996. A genome-wide search for wild-species alleles that increase horticultural yield of processing tomatoes *Theor. Appl. Genet.* 93: 877–886.
- Esquinas-Alcázar, J. T. 1981. Genetic resources of tomatoes and wild relatives. *Rep. Internat. Board Plant Genet. Res. No. AGP. IBPGR-80-103*: 1–65.
- Esquinas-Alcázar, J., and F. Nuez. 1995. Situación taxonómica, domesticación y difusión del tomate. In *El cultivo del tomate*, ed. F. Nuez Viñals, 1–793. Madrid: Mundi-Prensa.
- FAO. 2004. On-line crop production statistics. <http://apps.fao.org/>. Rome: FAO.
- Farris, J. S., M. Källersjö, A. G. Kluge, and C. Bult. 1995. Testing significance of incongruence. *Cladistics* 10: 315–319.
- Filippo, R. 1811. *L’Ortolano*. Milan.
- Fosberg, F. R. 1987. New nomenclatural combinations for Galapagos plant species. *Phytologia* 62: 181–183.
- Frery, A., T. C. Nesbitt, A. Frery, S. Grandillo, E. van der Knaap, B. Cong, J. Liu, J. Meller, R. Elber, K. B. Alpert, and S. D. Tanksley. 2000. *fw2.2*: a quantitative trait locus key to the evolution of tomato fruit size. *Science* 289: 85–88.
- Fridman, E., F. Carrari, Y.-S. Liu, A. R. Fernie, and D. Zamir. 2004. Zooming in on a quantitative trait for tomato yield using interspecific introgressions. *Science* 305: 1786–1789.
- Fuchs, L. 1542. *De historia stirpium*. Basel: Isingrin.
- García-Paris, J. 1991. *Intercambio y difusión de plantas de consumo entre el nuevo y viejo mundo*. Madrid: M.A.P.A.

- Gerard, J. 1597. *The herball or generall historie of plants*. London: John Norton.
- Georgiady, M. S., and E. M. Lord. 2002. Evolution of the inbred flower form in the currant tomato, *Lycopersicon pimpinellifolium*. *Int. J. Pl. Sci.* 163: 531–541.
- Georgiady, M. S., R. W. Whitkus, and E. M. Lord. 2002. Genetic analysis of traits distinguishing outcrossing and self-pollinating forms of currant tomato, *Lycopersicon pimpinellifolium* (Jusl.) Mill. *Genetics* 161: 333–344.
- Gesner, C. 1561. *Horti germaniae*. Strasbourg: J. Rihel.
- Gibson, R. W. 1971. Glandular hairs providing resistance to aphids in certain wild potato species. *Ann. Appl. Biol.* 68: 113–119.
- Giovannoni, J. 2001. Molecular biology of fruit maturation and ripening. *Ann. Rev. Pl. Physiol. & Pl. Molec. Biol.* 52: 725–749.
- Gleissberg, S. 2002. Comparative developmental and molecular genetic aspects of leaf dissection. In *Developmental genetics and plant evolution*, ed. Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins, 404–417. London: Taylor & Francis.
- Glover, B. J., S. Bunnell, and C. Martin. 2004. Convergent evolution with the genus *Solanum*: the specialized anther cone develops through alternative pathways. *Gene* 331: 1–7.
- Grandillo, S., H. Ku, and S. D. Tanksley. 1996. Characterization of *fs8.1*, a major QTL influencing fruit shape in tomato. *Mol. Breed.* 2: 251–260.
- Grandillo, S., H. Ku, and S. D. Tanksley. 1999. Identifying the loci responsible for natural variation in fruit size and shape in the tomato. *Theor. Appl. Genet.* 99: 978–987.
- Guilandinus, M. 1572. *Papyrus hoc est commentarius in tria C. Plinii maioris de papyro capita*. Venice.
- Haider, S. N., M. S. Ramanna, E. Jacobsen, and R. Risser. 2000. Alien chromosome additions indicate taxonomic distance in Solanaceae. Abstracts of the Fifth International Solanaceae Conference, 27. Nijmegen: printed for the conference.
- Hanneman, R. E., Jr. 1994. Assignment of Endosperm Balance Numbers to the tuber-bearing Solanums and their close non-tuber-bearing relatives. *Euphytica* 74: 19–25.
- Harper, F. (ed.) 1942. [John Bartram] *Diary of a Journey through the Carolinas, Georgia, and Florida from July 1, 1765, to April 10, 1766*. *Trans. Amer. Phil. Soc., New Ser.* 33: 1–120.
- Hawkes, J. G. 1990. *The potato: evolution, biodiversity and genetic resources*. London: Belhaven Press.
- Heine, H. 1976. *Flora de la Nouvelle Calédonie*, vol. 7. Paris: Museum National d'Histoire Naturelle.
- Heiser, C. B. Jr. 1969. *Nightshades: the paradoxical plants*. San Francisco: W. H. Freeman and Company.
- Henderson, R. J. F. 1974. *Solanum nigrum* L. (Solanaceae) and related species in Australia. *Contr. Queensland Herb.* 16: 1–78.
- Hernández, F. 1651. *Nova plantarum animalium et mineralium Mexicanorum historia*. Rome.
- Holle, M., C. M. Rick, and D. G. Hunt. 1978. Catalog of collections of green-fruited *Lycopersicon* species and *Solanum pennellii* found in watersheds of Peru. Part 1. *Tomato Genet. Coop. Rep.* 28: 49–78.
- . 1979. Catalog of collections of green-fruited *Lycopersicon* species and *Solanum pennellii* found in watersheds of Peru. Part 2. *Tomato Genet. Coop. Rep.* 29: 63–91.
- Holmgren, P. K., N. H. Holmgren, and L. C. Barnett. 1990. *Index herbariorum*. Part. I: The herbaria of the world, 8th ed. *Regnum Veg.* 120: 1–693.
- Holtan, H. E. E., and S. Hake. 2003. Quantitative trait analysis of leaf dissection in tomato using *Lycopersicon pennellii* segmented introgression lines. *Genetics* 165: 1541–1550.
- Hooker, J. D. 1847 [“1851”]. An enumeration of the plants of the Galapagos Archipelago with descriptions of those which are new. *Trans. Linn. Soc., London* 20: 163–233.
- Horkheimer, H. 1973. *Alimentación y obtención de alimentos en el Perú prehispánico*. Lima: Universidad Nacional Mayor de San Marcos.
- Huang, C. C., P. M. Hoffs-Van De Putte, J. G. Haanstra-Van Der Meer, F. Meijer-Deken, and P. Lindhout. 2000. Characterization and mapping of resistance to *Oidium lycopersicum* in two *Lycopersicon hirsutum* accessions: evidence for close linkage of two O1-genes on chromosome 6 of tomato. *Heredity* 85: 511–520.
- Hughes, G. 1750. *The natural history of Barbados in ten books*. London: printed for the author.
- Hunziker, A. T. 1979. South American Solanaceae: a synoptic survey, In *The biology and taxonomy of Solanaceae*, ed. J. G. Hawkes, R. N. Lester, and A. D. Skelding, 49–85. London: Academic Press.
- Hunziker, A. T. 2001. *Genera Solanacearum, the genera of Solanaceae illustrated, arranged according to a new system*. Ruggell, Liechtenstein: A. R. G. Gantner Verlag.
- Jacquin, N. 1770–1771. *Hortus vindobonensis*, vol. 1. Vienna: L. J. Kaliwoda.
- Jefferson, T. 1800. *Jefferson's notes on the state of Virginia: with the appendixes. . . .* Baltimore: published by the author.

- Jenkins, J. A. 1948. The origin of the cultivated tomato. *Econ. Bot.* 2: 379–392.
- Ji, Y., Y. Du, and R. T. Chetelat. 2001. Pairing and recombination between *Solanum lycopersicoides* and *Lycopersicon esculentum* chromosomes: taxonomic implications and breeding prospects. In *Solanaceae V: advances in taxonomy and utilization*, ed. R. G. van den Berg, G. W. M. Barendse, G. M. van der Weerden, and C. Mariani, 217–224. Nijmegen: University of Nijmegen Press.
- Johnston, S. A., T. P. M. Den Nijs, S. J. Peloquin, and R. E. Hanneman, Jr. 1980. The significance of genetic balance to endosperm development in interspecific crosses. *Theor. Appl. Genet.* 53: 262–269.
- Jørgensen, P. M. 1999. History of collecting/Historia de las colecciones botánicas. In *Catalogue of the vascular plants of Ecuador/Catálogo de las plantas vasculares del Ecuador*, ed. P. M. Jørgensen, and S. León Yáñez. Monogr. Syst. Bot. Missouri Bot. Gard. 75: 25–70.
- Jørgensen, P. M., and León Yáñez, S. 1999. *Catalogue of the vascular plants of Ecuador/Catálogo de las plantas vasculares del Ecuador*. Monogr. Syst. Bot. Missouri Bot. Gard. 75: 1–1181.
- Jussieu, A. L. de. 1789. *Genera plantarum*. Paris: Herissant.
- Kessler, S., M. Kim, T. Pham, N. Weber, and N. R. Sinha. 2001. Mutations altering leaf morphology in tomato. *Int. J. Pl. Sci.* 162: 475–492.
- Khrapalova, I. A. 1999. The genus *Lycopersicon* (Tourn.) Mill. [in Russian] *Trudy Prikl. Bot.* 157: 24–55.
- . 2001. *Lycopersicon* (Tourn.) Mill. [in Russian]. In *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, ed. V. A. Dragavtsev, 3: 18–93. Saint Petersburg: Vavilov Institute.
- Knapp, S. 1986a. Reproductive biology of *Solanum* section *Geminata* in a Costa Rican cloud forest. In *Solanaceae: biology and systematics*, ed. W. G. D'Arcy, 253–263. New York: Columbia University Press.
- . 1991. A revision of *Solanum sessile* species group (section *Geminata* pro parte: Solanaceae). *Bot. J. Linn. Soc.* 105: 179–210.
- . 2000. A revision of *Solanum thelopodium* species group (section *Anthoresis* sensu Sheite, pro parte): Solanaceae. *Bull. Nat. Hist. Mus. London (Bot.)* 30: 13–30.
- . 2001. Is morphology dead in *Solanum* taxonomy? In *Solanaceae V: advances in taxonomy and utilization*, ed. R. G. Van den Berg, G. W. M. Barendse, G. M. van der Weerden, and C. Mariani, 23–38. Nijmegen: Nijmegen University Press.
- . 2002a. Tobacco to tomatoes: a phylogenetic perspective on fruit diversity in the Solanaceae. *J. Exp. Bot.* 53: 2001–2022.
- . 2002b. Floral diversity and evolution in the Solanaceae. In *Developmental genetics and plant evolution*, ed. Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins, 267–297. London: Taylor & Francis.
- . 2002c. *Solanum* section *Geminata* (G. Don) Walpers (Solanaceae). *Fl. Neotrop. Monogr.* 84: 1–405.
- . 2002d. Assessing patterns of plant endemism in Neotropical uplands. *Bot. Rev.* 68: 22–37.
- . 2007a. The description of *Solanum* and other Solanaceae collected by Humboldt and Bonpland: a case study of collaboration versus competition in 19th century taxonomy. *Bot. Jahrb. Syst.* 127: 117–132.
- . 2007b. Lectotypification of Cavanilles's names in *Solanum* (Solanaceae). *Anales Jard. Bot. Madrid* 64: 195–203.
- Knapp, S., and S. C. Darwin. 2006. (1736) Proposal to conserve the name *Solanum cheesmaniae* (L. Riley) Fosberg against *S. cheesmanii* Geras. (Solanaceae). *Taxon* 55: 806–807.
- Knapp, S., and T. Helgason. 1997. A revision of *Solanum* section *Pteroidea*: Solanaceae. *Bull. Nat. Hist. Mus., London (Bot.)* 27: 31–73.
- Knapp, S., and C. E. Jarvis. 1990. The typification of the names of New World *Solanum* species described by Linnaeus. *Bot. J. Linn. Soc.* 104: 325–367.
- Knapp, S., L. Bohs, M. Nee, and D. M. Spooner. 2004. Solanaceae: a model for linking genomics and biodiversity. *Compar. Funct. Genom.* 5: 285–291.
- L'Obel, M. de. 1576. *Plantarum seu stirpium historia*. Antwerp: C. Plantin.
- Laterrot, H. 1989. The tomato. Advantages and use of wild varieties for varietal creation. *Rev. Hort.* 295: 13–17.
- Lehmann, C. O. 1954 [“1955”]. Das morphologische System der Kulturtomaten (*Lycopersicon esculentum* Miller). *Züchter. Sonderheft* 3: 1–64.
- Lester, R. N. 1991. Evolutionary relationships of tomato, potato and pepino, and wild species of *Lycopersicon* and *Solanum*. In *Solanaceae III: taxonomy, chemistry, evolution*, ed. J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada, 283–301. Kew: Royal Botanic Gardens.
- 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.
- Linnaeus, C. 1753. *Species plantarum*. Stockholm: L. Salvius.
- Livingstone, D. 1857. *Missionary travels and researches in Africa*. London: Harper & Bros.

- Luckwill, L. C. 1943a. The genus *Lycopersicon*: an historical, biological, and taxonomical survey of the wild and cultivated tomatoes. *Aberdeen Univ. Stud.* 120: 1–44.
- . 1943b. The evolution of the cultivated tomato. *J. Royal Hort. Soc.* 68: 19–25.
- Lutze, E., and H. Retzlaff. 1949. *Pflanzenbuch des Apothekers Georg Oellinger zu Nürnberg (Herbarium des Georg Oellinger anno 1553 zu Nürnberg)*. Salzburg: Akademischer Gemeinschaftsverlag.
- MacBride, J. F. 1962. Solanaceae. In “Flora of Peru.” *Field Mus. Nat. Hist., Bot. Ser.* 13: 3–267.
- Maldonado, C., E. Pujado, and F. A. Squeo. 2002. El efecto de la disponibilidad de agua durante el crecimiento de *Lycopersicon chilense* sobre la capacidad de sus semillas para germinar a distintas temperaturas y concentraciones de manitol y NaCl. *Rev. Chilena Hist. Nat.* 75: 651–660.
- Marshall, J. A., S. Knapp, M. R. Davey, J. B. Power, E. C. Cocking, M. D. Bennett, and A. V. Cox. 2001. Molecular systematics of *Solanum* section *Lycopersicum* (*Lycopersicon*) using the nuclear ITS rDNA region. *Theor. Appl. Genet.* 103: 1216–1222.
- Matthioli, P. A. 1544. *Di Pedacio Dioscoride Anazarbeo libri cinque della historia, et materia medicinale trodotti in lingua uolgare Italiana*. Venice: N. de Bascariini.
- . 1554. *Commentarii, in libros sex Pedacci Dioscoricis Anazarbei, de medica materia*. Venice: V. Valgrisi.
- . 1562. *Herbarz*. Prague.
- . 1563. *New Kreüterbuch*. Prague: G. Melantrich.
- . 1565. *Commentarii, in sex libros Pedacci Dioscoricis Anazarbei, de medica materia*. Venice: V. Valgrisi.
- . [ed. M. J. des Moulins] 1572. *Les Commentaires de M. Pierre André Matthioli sur les six livres de Ped. Dioscoride*. Lyon: G. Roville.
- . [ed. J. Camerarius] 1586. *De plantis epitome utilissima Petri Andreae Matthioli*. Frankfurt.
- . [ed. C. Bauhin] 1598. *Commentarii in VI libros Pedacii Dioscoridis Anazabei de Medica materia*. Frankfurt: N. Basse.
- Mattiolo, O. 1899. *Illustrazione del primo volume dell'erbario di Ulisse Aldrovandi*. Genoa: A. Ciminago.
- McClellan, P. E., and M. R. Hanson. 1986. Mitochondrial DNA sequence divergence among *Lycopersicon* and related *Solanum* species. *Genetics* 112: 649–667.
- McCue, G. A. 1952. The history and use of the tomato: an annotated bibliography. *Ann. Missouri Bot. Gard.* 39: 289–348.
- McMeekin, D. 1992. Representations of pre-Columbian spindle whorls of the floral and fruit structure of economic plants. *Econ. Bot.* 46: 171–180.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. Wiersma, and N. J. Turland, eds. 2006. *International code of botanical nomenclature (Vienna Code)*. *Regnum Veg.* 146: 1–586.
- Medikus, F. K. 1783. *Botanische Beobachtungen des Jahres 1782–(1783)*, vol. 10. Mannheim.
- Metcalf, C. R., and L. Chalk. 1979. *Anatomy of dicotyledons*, vol. 1, 2d ed. Oxford: Clarendon Press.
- Meyer, F. G., E. E. Trueblood, and J. L. Heller. 1999. *The great herbal of Leonhart Fuchs: de historia stirpium commentarii insignes, 1542 (Notable commentaries on the history of plants)*, vol. 1, Commentary. Stanford: Stanford University Press.
- Michener, C. D., M. L. Winston, and R. Jander. 1978. Pollen manipulation and related activities and structures in bees of the family Apidae. *Univ. Kansas Sci. Bull.* 51: 575–601.
- Miller, J. C., and S. D. Tanksley. 1990. RFLP analysis of phylogenetic relationships and genetic variation in the genus *Lycopersicon*. *Theor. Appl. Genet.* 80: 437–448.
- Miller, P. 1731. *The gardeners dictionary*. London: printed for the author.
- . 1752. *The gardeners dictionary*, 6th ed. London: printed for the author.
- . 1754. *The gardeners dictionary abridged*, 4th ed. London: printed for the author.
- . 1768. *The gardeners dictionary*, 8th ed. London: printed for the author.
- . 1807. *The gardener's and botanist's dictionary*, posthumous edition, ed. Thomas Martyn. London: F. C. and J. Rivington.
- Moore, J. A. 1935. The early history of the tomato or loveapple. *Missouri Bot. Gard. Bull.* 23: 134–138.
- Müller, C. H. 1940a. A revision of the genus *Lycopersicon*. *U.S.D.A. Misc. Publ.* 382: 1–28, + 10 pl.
- . 1940b. The taxonomy and distribution of the genus *Lycopersicon*. *Nat. Hort. Mag.* 19: 157–160.
- Mueller, L. A., S. D. Tanksley, J. J. Giovannoni, J. van Eck, S. Stack, D. Choi, B. D. Kim, M. Chen, Z. Cheng, C. Li, H. Ling, Y. Xue, G. Seymour, G. Bishop, G. Bryan, R. Sharma, J. Khurana, A. Tyagi, D. Chatopadhyay, N. K. Singh, W. Stiekema, P. Lindhout, T. Jesse, R. K. Lankhorst, M. Bouzayen, D. Shibata, S. Tabata, A. Granell, M. A. Botella, G. Giuliano, L. Frusciante, M. Causse, and D. Zamir. 2005a. The

- Tomato Sequencing Project, the first cornerstone of the International Solanaceae Project (SOL). *Comp. Funct. Genom.* 6: 153–158.
- Mueller, L. A., T. H. Solow, N. Taylor, B. Skwarecki, R. Buels, J. Binns, C. Lin, M. H. Wright, R. Ahrens, Y. Wang, E. V. Herbst, E. R. Keyder, N. Menda, D. Zamir, and S. D. Tanksley. 2005b. The SOL genomics network. A comparative resource for Solanaceae biology and beyond. *Plant Physiol.* 138: 1310–1317.
- Nesbitt, T. C., and S. D. Tanksley. 2002. Comparative sequencing in the genus *Lycopersicon*: implications for the evolution of fruit size in the domestication of cultivated tomatoes. *Genetics* 162: 365–379.
- Nuez, F., J. Prohens, and J. M. Blanca. 2004. Relationships, origin, and diversity of Galápagos tomatoes: implications for the conservation of natural populations. *Amer. J. Bot.* 91: 86–99.
- Olmstead, R. G., and J. D. Palmer. 1997. Implications for 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.
- Ortiz, R., and M. K. Ehlenfeldt. 1992. The importance of Endosperm Balance Number in potato breeding and the evolution of tuber-bearing *Solanum* species. *Euphytica* 60: 105–113.
- Palmer, J. D., and D. Zamir. 1982. Chloroplast DNA evolution and phylogenetic relationships in *Lycopersicon*. *Proc. Natl. Acad. Sci. U.S.A.* 79: 5006–5010.
- Peralta, I. E., and D. M. Spooner. 2001. GBSSI gene phylogeny of wild tomatoes (*Solanum* L. section *Lycopersicon* [Mill.] Wettst. subsection *Lycopersicon*). *Amer. J. Bot.* 88: 1888–1902.
- . 2005. Morphological characterization and relationships of wild tomatoes (*Solanum* L. Section *Lycopersicon* [Mill.]). In “A Festschrift for William G. D’Arcy: the legacy of a taxonomist,” ed. R. C. Keating, V. C. Hollowell, and T. B. Croat. *Monogr. Syst. Bot. Missouri Bot. Gard.* 104: 227–257.
- . 2006. History, origin and early cultivation of tomato (Solanaceae). In *Genetic improvement of Solanaceous crops*, vol. 2: *Tomato*, ed. M. K. Razdan and A. K. Mattoo, 1–27. Enfield: Science Publishers.
- Peralta, I. E., S. Knapp, and D. M. Spooner. 2005. New species of wild tomatoes (*Solanum* section *Lycopersicon*: Solanaceae) from northern Peru. *Syst. Bot.* 30: 424–434.
- Philippi, R. A. 1860. *Florula Atacamensis*. Halle: E. Anton.
- Piazza, P., S. Sjiniski, and M. Tsiantis. 2005. Evolution of leaf developmental mechanisms. *New Phytol.* 167: 693–710.
- Prokhanov, J. I. 1950. *Lycopersicon* (Solanaceae) In *Flora SSSR*, ed. B. K. Shishchkin and E. G. Bobrov, 22: 36–50. Moscow and Leningrad: Izdatel’stvo Akademii Nauk SSSR. [in Russian]
- Quinn, W. H., and V. T. Neal. 1992. The historical record of El Niño events. *Climate since 1500*, ed. P. Bradley and P. Jones, 623–648. London: Routledge.
- Raphael, S. 1970. The publication dates of the Transactions of the Linnean Society of London, Series I, 1791–1875. *Biol. J. Linn. Soc.* 2: 61–76.
- Raphael, S. 1989. Matthioli’s herbal. In *The Matthioli woodblocks* (catalog without pagination). London: B. Quaritch Ltd.
- Ray, J. 1673. *Observations topographical, moral and physiological, made in a journey through part of the Low-Countries, Germany, Italy, and France*. London: J. Martyn.
- Rick, C. M. 1960. Hybridization between *Lycopersicon esculentum* and *Solanum pennellii*. Phylogenetic and cytogenetic significance. *Proc. Natl. Acad. Sci. U.S.A.* 46: 78–82.
- . 1950. Pollination relations of *Lycopersicon esculentum* in native and foreign regions. *Evolution* 4: 110–122.
- . 1963. Barriers to interbreeding in *Lycopersicon peruvianum*. *Evolution* 17: 216–232.
- . 1967. Fruit and pedicel characters derived from Galápagos tomatoes. *Econ. Bot.* 21: 171–184.
- . 1971. *Lycopersicon*. In *Flora of the Galapagos Islands*, ed. I. L. Wiggins and D. M. Porter, 468–471. Stanford: Stanford University Press.
- . 1978. The Tomato. *Sci. Amer.* 239: 76–87.
- . 1979. Biosystematic studies in *Lycopersicon* and closely related species of *Solanum*. In *The biology and taxonomy of Solanaceae*, ed. J. G. Hawkes, R. N. Lester, and A. D. Skelding, 667–677. New York: Academic Press.
- . 1982a. The potential of exotic germplasm for tomato improvement. In *Plant improvement and somatic cell genetics*, ed. I. K. Vasil, W. R. Scowcroft, and K. J. Frey, 1–28. New York: Academic Press.
- . 1982b. Genetic relationships between self-incompatibility and floral traits in the tomato species. *Biol. Zentralbl.* 101: 185–198.

- . 1986a. Reproductive isolation in the *Lycopersicon peruvianum* complex. In *Solanaceae, biology and systematics*, ed. W. G. D'Arcy, 477–495. New York: Columbia University Press.
- . 1986b. Germplasm resources in the wild tomato species. *Acta Hort.* 190: 39–47.
- . 1988. Tomato-like nightshades: affinities, autoecology, and breeders' opportunities. *Econ. Bot.* 42: 145–154.
- . 1991. Tomato resources of South America reveal many genetic treasures. *Diversity* 7: 54–56.
- . 1995. Tomato. *Lycopersicon esculentum* (Solanaceae). In *Evolution of crop plants*, 2d ed., ed. J. Smartt, and N. W. Simmonds, 452–457. Harlow, England: Longman Scientific and Technical.
- Rick, C. M., J. W. Deverna, R. T. Chetelat, and M. A. Stevens. 1987. Potential contributions of wide crosses to improvement of processing tomatoes. *Acta Hort.* 200: 45–55.
- Rick, C. M., and J. F. Fobes. 1975a. Allozyme variation in the cultivated tomato and closely related species. *Bull. Torrey Bot. Club* 102: 376–384.
- . 1975b. Allozymes of Galapagos tomatoes: polymorphism, geographic distribution and affinities. *Evolution* 29: 443–457.
- Rick, C. M., J. F. Fobes, and M. Holle. 1977. Genetic variation in *Lycopersicon pimpinellifolium*: evidence of evolutionary change in mating systems. *Pl. Syst. Evol.* 127: 139–170.
- Rick, C. M., M. Holle, and R. W. Thorp. 1978. Rates of cross-pollination in *Lycopersicon pimpinellifolium*: impact of genetic variation in floral characters. *Pl. Syst. Evol.* 129: 31–44.
- Rick, C. M., J. F. Fobes, and S. D. Tanksley. 1979. Evolution of mating systems in *Lycopersicon hirsutum* as deduced from genetic variation in electrophoretic and morphological characters. *Pl. Syst. Evol.* 132: 279–298.
- Rick, C. M., and M. Holle. 1990. Andean *Lycopersicon esculentum* var. *cerasiforme*: genetic variation and its evolutionary significance. *Econ. Bot.* 44: 69–78.
- Rick, C. M., M. Holle, and R. W. Thorp. 1978. Rates of cross-pollination in *Lycopersicon pimpinellifolium*: impact of genetic variation in floral characters. *Pl. Syst. Evol.* 129: 31–44.
- Rick, C. M., and R. Lamm. 1955. Biosystematic studies on the status of *Lycopersicon chilense*. *Amer. J. Bot.* 42: 663–675.
- Rick, C. M., and S. D. Tanksley. 1981. Genetic variation in *Solanum pennellii*: comparison with two other sympatric tomato species. *Pl. Syst. Evol.* 139: 11–45.
- Rick, C. M., H. Laterrot, and J. Philouze. 1990. A revised key for the *Lycopersicon* species. *Tomato Genet. Coop. Rep.* 40: 31.
- Rick, C. M., R. W. Zobel, and J. F. Fobes. 1974. Four peroxidase loci in red-fruited tomato species: genetics and geographic distribution. *Proc. Natl. Acad. Sci. U.S.A.* 71: 835–839.
- Rick, C. M., E. Kesicki, J. F. Fobes, and M. Holle. 1976. Genetic and biosystematic studies on two new sibling species of *Lycopersicon* from Interandean Perú. *Theor. Appl. Genet.* 47: 55–68.
- Roe, K. E. 1971. Terminology of hairs in the genus *Solanum*. *Taxon* 20: 501–508.
- Ronen, G., L. Carmel-Goren, D. Zamir, and J. Hirschberg. 2000. An alternative pathway to β -carotene formation in the plant chromoplast discovered by map-based cloning of beta and old-gold color mutations in tomato. *Proc. Nat. Acad. Sci., U.S.A.* 97: 11102–11107.
- Ross, R. J. 1998. Review paper: global genetic resources of vegetables. *Pl. Var. Seeds* 11: 39–60.
- Roxburgh, W. 1832. *Flora indica*, vols. 1, 2. Serampore: W. Thacker.
- Ruiz, H., and J. Pavón. 1797. *Florae peruviana, et chilensis prodromus, sive novorum generum plantarum peruvianarum, et chilensium descriptiones, et icones*, 2d ed. Rome.
- Rumpf, G. E. 1747. *Het amboinsch Kruid-Boek/Herbarium amboinense*, vol 5. Amsterdam: F. Changuon, J. Catuffe, and H. Uytwerf.
- Rundel, P. W., B. Palma, H. A. Mooney, S. L. Gulmon, and J. R. Ehrlinger. 1991. The phytogeography and ecology of the coastal Atacama and Peruvian Deserts. *Aliso* 13: 1–50.
- Sabine, J. 1820. On the love apple or tomato. *Trans. Roy. Hort. Soc., London* 3: 342–354.
- Schauer, N., D. Zamir, and A. R. Fernie. 2005. Metabolic profiling of leaves and fruits of wild species tomato: a survey of the *Solanum lycopersicum* complex. *J. Exp. Bot.* 56: 297–307.
- Seithe, A. 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Bot. Jahrb. Syst.* 81: 261–336.
- Seithe, A., and G. J. Anderson. 1982. Hair morphology and relationships of species in *Solanum* sect. *Basarthurum*. *Pl. Syst. Evol.* 139: 229–256.
- Sifres, A., B. Picó J., M. Blanca, R. De Frutos, and F. Nuez. 2006. Genetic structure of *Lycopersicon pimpinellifolium* (Solanaceae) populations collected after the ENSO event of 1997–1998. *Genet. Res. Crop Evol.* 54: 359–377.

- Sloane, H. 1707. *A Voyage to the Islands Madera [Madeira], Barbados, Nieves, S. Christophers and Jamaica, with the natural history of the Herbs and Trees, Four-footed Beasts, Fishes, Birds, Insects, Reptiles, &c. of the last of those islands, &c.*, vol. 1. London: published by the author.
- Smith, S., and I. E. Peralta. 2002. Ecogeographic surveys as tools for analyzing potential reproductive isolating mechanisms: an example using *Solanum juglandifolium* Dunal, *S. ochranthum* Dunal, *S. lycopersicoides* Dunal, and *S. sitiens* I. M. Johnston. *Taxon* 51: 341–349.
- Soler, S., J. Provens, M. J. Díez, and F. Nuez. 2002. Natural occurrence of *Pepino mosaic virus* in *Lycopersicon* species in central and southern Peru. *J. Phytopath.* 150: 49–53.
- Souèges, R. 1907. Développement et structure du tégument séminal chez les Solanacées. *Ann. Sci. Nat. Bot. Sér. 9, Botanique* 6: 1–124.
- Spooner, D. M. 1999. Plant Genetic Resources for Food and Agriculture in situ and ex situ: where are the genes of importance for food security likely to come from? In *Proceedings of an international workshop, interdependence and food security: which list of plant genetic resources for food and agriculture for the future multilateral system?*, October 1–3, 1998, 133–164. Florence: Ministero Affari Esteri, Istituto Agronomico per L'Oltremare.
- Spooner, D. M., G. J. Anderson, and R. K. Jansen. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (Solanaceae). *Amer. J. Bot.* 80: 676–688.
- Spooner, D. M., W. L. A. Hettterscheid, R. G. van den Berg, and W. Brandenburg. 2003. Plant nomenclature and taxonomy: an horticultural and agronomic perspective. *Hort. Rev.* 28: 1–60.
- Spooner, D. M., R. G. van den Berg, A. Rodríguez, J. Bamberg, R. J. Hijmans, and S. I. Lara Cabrera. 2004. Wild potatoes (*Solanum* section *Petota*; Solanaceae) of North and Central America. *Syst. Bot. Monogr.* 68: 1–209.
- Spooner, D. M., I. E. Peralta, and S. Knapp. 2005. Comparison of AFLPs to other markers for phylogenetic inference in wild tomatoes [*Solanum* L. section *Lycopersicon* (Mill.) Wettst.]. *Taxon* 54: 43–61.
- Stafleu, F. A. 1971. *Linnaeus and the Linnaeans: the spreading of their ideas in systematic botany, 1735–1789*. *Regnum Veg.* 79: 1–386.
- Stearn, W. T. 1957. An introduction to the *Species plantarum* and cognate botanical works of Carl Linnaeus. In *Species plantarum* by C. Linnaeus, facsimile edition, 1–169. London: Ray Society.
- Stevens, M. A., and C. M. Rick. 1986. Genetics and breeding. In *The tomato crop: a scientific basis for improvement*, ed. J. G. Atherton, and J. Rudich, 35–109. London: Chapman and Hall.
- Sturtevant, E. L. 1891. The history of garden vegetables (continued). *Amer. Nat.* 25: 694–706.
- Symon, D. E. 1981. The solanaceous genera *Browallia*, *Capsicum*, *Cestrum*, *Cyphomandra*, *Hyoscyamus*, *Lycopersicon*, *Nierembergia*, *Physalis*, *Petunia*, *Salpichroa*, *Withania*, naturalized in Australia. *J. Adelaide Bot. Gard.* 3: 133–166.
- . 1985. The *Solanaceae* of New Guinea. *J. Adelaide Bot. Gard.* 8: 1–177.
- . 1994. *Kangaroo apples: Solanum sect. Archaeosolanum*. Keswick, Australia: published by the author.
- Tabernaemontanus, J. T. 1591. *Neuw Kreuterbuch*. Frankfurt: N. Basse.
- Tanksley, S. D., and F. Loaiza-Figueroa. 1985. Gametophytic self incompatibility is controlled by a single locus on chromosome 1 in *Lycopersicon peruvianum*. *Proc. Natl. Acad. Sci. U.S.A.* 82: 5093–5096.
- Tanksley, S. D., and S. R. McCouch. 1997. Seed banks and molecular maps: unlocking genetic potential from the wild. *Science* 277: 1063–1066.
- Taylor, I. B. 1986. Biosystematics of the tomato. In *The tomato crop: a scientific basis for improvement*, ed. J. G. Atherton and J. Rudich, 1–34. London: Chapman and Hall.
- Teppner, H. 1993. Die Tomate: Verwandtschaft, Geschichte, Blütenökologie. *Kataloge des OÖ. Landesmuseums, Neue Folge* 61, S: 189–212.
- . 2005. Pollinators of tomato, *Solanum lycopersicum* (Solanaceae), in Central Europe. *Phyton* 45(2): 217–235.
- Tournefort, J. P. de. 1694. *Éléments de botanique*. Paris: l'Imprimerie royale.
- Tsiantis, M., A. Hay, N. Ori, H. Kaur, I. Henderson, H. Holtan, S. McCormick, and S. Hake. 2002. Developmental signals regulating leaf form. In *Developmental genetics and plant evolution*, ed. Q. C. B. Cronk, R. M. Bateman, and J. A. Hawkins, 418–430. London: Taylor & Francis.
- USDA, National Agricultural Statistics Service. 2002a. Crop Values. U.S. Dept. Agric. Nat. Agric. Stat. Serv., Publ. PR2(02).
- USDA, National Agricultural Statistics Service. 2002b. Vegetables, 2001 Summary. U.S. Dept. Agric. Nat. Agric. Stat. Serv., Publ. VG1(02).

- Van der Hoorn, R. A. L., M. Kruijt, R. Roth, B. F. Brandwagt, M. H. A. J. Joosten, and P. J. M. DeWit. 2001. Intragenic recombination generated two distinct *Cf* genes that mediate AVR9 recognition in the natural population of *Lycopersicon pimpinellifolium*. *Proc. Natl. Acad. Sci. U.S.A.* 98: 10493–10498.
- Van der Knaap, E., and S. D. Tanksley. 2001. Identification and characterization of a novel locus controlling early fruit development in tomato. *Theor. Appl. Genet.* 103: 353–358.
- . 2003. The making of a bell-pepper shaped tomato fruit: identification of loci controlling fruit morphology in Yellow Stuffer tomato. *Theor. Appl. Genet.* 107: 139–147.
- Van der Knaap, E., Z. B. Lippman, and S. D. Tanksley. 2002. Extremely elongated tomato fruit controlled by four quantitative trait loci with epistatic interactions. *Theor. Appl. Genet.* 104: 241–247.
- Van der Knaap, E., A. Sanyal, S. A. Jackson, and S. D. Tanksley. 2004. High-resolution fine mapping and fluorescence *in situ* hybridization analysis of *sun*, a locus controlling tomato fruit shape, reveals a region of the tomato genome prone to DNA rearrangements. *Genetics* 168: 2127–2140.
- Vavilov, N. I. 1926. Studies on the origin of cultivated plants. *Trudy. Prikl. Bot. Genek. Sel.* 26: 135–199.
- Villand, J., P. W. Skroch, T. Lai, P. Hanson, C. G. Kuo, and J. Nienhuis. 1998. Genetic variation among tomato accessions from primary and secondary centers of diversity. *Crop Sci.* 38: 1339–1347.
- Walters, J. I. 1792. *Gartenkunst*. Stuttgart.
- Warnock, S. J. 1988. A review of taxonomy and phylogeny of the genus *Lycopersicon*. *HortScience* 23: 669–673.
- Watson, W. P. 1989. The Matthioli woodblocks: a rare survival. In *The Matthioli woodblocks* (catalog without pagination). London: B. Quaritch Ltd.
- Wettstein, R. von. 1895. Solanaceae. In *Die natürlichen Pflanzenfamilien*, ed. A. Engler and K. Prantl, 4(3b): 4–38. Leipzig: Wilhelm Engelmann.
- Whalen, M. D. 1979. Taxonomy of *Solanum* section *Androceras*. *Gentes Herb.* 11: 359–426.
- . 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herb.* 12: 179–282.
- Whalen, M. D., D. E. Costich & C. B. Heiser, Jr. 1981. Taxonomy of *Solanum* section *Lasiocarpa*. *Gentes Herb.* 12: 41–129.
- Williams, C. E., and D. A. St. Clair. 1993. Phenetic relationships and levels of variability detected by restriction fragment length polymorphism and random amplified polymorphic DNA analysis of cultivated and wild accessions of *Lycopersicon esculentum*. *Genome* 36: 619–630.
- Wu, F., L. A. Mueller, D. Crouzillat, V. Petiard, and S. D. Tanksley. 2006. Combining bioinformatics and phylogenetics to identify large sets of single copy, orthologous genes (COSII) for comparative, evolutionary and systematics studies: a test case in the Euasterid plant clade. *Genetics* 174:1407–1420.
- Yakovlev, E., and F. L. Herrera. 1935. El mundo vegetal de los antiguos peruanos. *Rev. Mus. Nac. Lima, Bot. Etnol.* 4(1): 55.
- Yang, W., X. Bai, E. Kabelka, C. Eaton, S. Kamoun, E. van der Knapp, and D. Francis. 2004. Discovery of single nucleotide polymorphisms in *Lycopersicon esculentum* by computer aided analysis of expressed sequence tags. *Mol. Breeding* 14: 21–34.
- Zamir, D. 2001. Improving plant breeding with exotic genetic libraries. *Nat. Rev. Genetics* 2: 983–990.

APPENDIX 1

NAMES NOT VALIDLY PUBLISHED

Here we list nomina nuda and names published only in synonymy, as well as names not published in accordance with the rules of the *International Code of Botanical Nomenclature* (as defined in the pertinent edition of the Code). Many names circulating in lists or in the agricultural literature from past centuries are not validly published for a variety of reasons; see the current edition of the Code (McNeill et al. 2006) for criteria for valid publication. In some publications concerned largely with tomato breeding in the former Soviet Union (Brezhnev 1958; Khrapalova 2001) many new names for subspecific categories in the cultivated tomato, *Solanum lycopersicum*, were introduced but without regards for the rules in the Code. The protologues for a majority of these novelties lack a Latin diagnosis or description (ICBN, Article 36.1) and designation of a type (ICBN, Article 37.1); many of the new combinations are proposed without reference to the basionym (ICBN, Art. 33.3). We have endeavored to find all of these names and to ascertain their status, but there are names in the agricultural literature that we may have missed. We have noted names that were casually mentioned in the literature in the species discussions where they are relevant, as well as orthographic errors and incorrect entries in *Index*

kewensis. Erroneous listings found in *Index kewensis* are being corrected in the electronic International Plant Name Index (<http://www.ipni.org>).

Lycopersicon subgenus *Eulycopersicon* C. H. Müller, USDA Misc. Publ. 382: 10. 1940; not validly published (ICBN, Article 21.3).

Lycopersicon subgenus *Neolycopersicon* (Correll) Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 23. 2001; not validly published (ICBN, Article 33.4).

Lycopersicon agrimoniifolium Sendtner in Martius, *Fl. bras.* 10: 125. 1846, nomen nudum, non *Lycopersicon agrimoniifolium* Dunal in A. DC., *Prodr.* 13(1): 24. 1852. [See also *Lycopersicon diadelphum* Dunal under "Doubtful and Excluded Names.]

Lycopersicon cerasiforme var. *luteum* Sweet, *Hort. Brit.* 385. 1830, nomen nudum.

Lycopersicon cerasiforme var. *ruber* Sweet, *Hort. Brit.* 385. 1830, nomen nudum.

Lycopersicon cheesmaniae subsp. *typicum* Luckwill, *Aberdeen Univ. Studies* 120: 34. 1943, as "cheesmanii"; not validly published.

Lycopersicon esculentum subsp. *cultum* Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 87. 1958; not validly published.

Lycopersicon esculentum subsp. *cultum* var. *grandifolium* (L. H. Bailey) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 88. 1958; not validly published.

Lycopersicon esculentum subsp. *cultum* var. *validum* (L. H. Bailey) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 88. 1958; not validly published.

Lycopersicon esculentum subsp. *cultum* var. *vulgare* Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 88. 1958; not validly published.

Lycopersicon esculentum subsp. *pimpinellifolium* var. *eupimpinellifolium* Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 64. 1958; not validly published.

Lycopersicon esculentum subsp. *pimpinellifolium* var. *racemigerum* (Lange) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 65. 1958; not validly published.

Lycopersicon esculentum subsp. *subspontaneum* Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 68. 1958; not validly published.

Lycopersicon esculentum subsp. *subspontaneum* Brezhnev subvar. *flaviocarpum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 24. 2001; not validly published.

Lycopersicon esculentum subsp. *subspontaneum* Brezhnev subvar. *rosicarpum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 24. 2001; not validly published.

Lycopersicon esculentum subsp. *subspontaneum* var. *cerasiforme* (Dunal) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 68. 1958; not validly published.

Lycopersicon esculentum subsp. *subspontaneum* var. *elongatum* Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 72. 1958; not validly published.

Lycopersicon esculentum subsp. *subspontaneum* var. *humboldtii* subvar. *rubescens* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 24. 2001; not validly published.

- Lycopersicon esculentum* subsp. *subspontaneum* var. *humboldtii* subvar. *xanthocarpum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* subsp. *subspontaneum* var. *pruniforme* Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 71. 1958; not validly published.
- Lycopersicon esculentum* subsp. *subspontaneum* var. *pruniforme* subvar. *rhodocarpum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* subsp. *subspontaneum* var. *pruniforme* subvar. *luteocarpum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* subsp. *subspontaneum* var. *pyriforme* (C. H. Mull.) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 70. 1958; not validly published.
- Lycopersicon esculentum* subsp. *subspontaneum* var. *succenturianum* (Pasq.) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 74. 1958; not validly published.
- Lycopersicon esculentum* subsp. *subspontaneum* var. *succenturianum* subvar. *rubicundum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* subsp. *typicum* Luckwill, *J. Royal Hort. Soc.* 68: 22. 1943; Aberdeen Univ. *Studies* 120: 21. 1943, as “typicus”; not validly published (ICBN, Article 24.3).
- Lycopersicon esculentum* var. *chrysocarpum* Sweet, *Hort. Brit.* 385. 1830, nomen nudum.
- Lycopersicon esculentum* var. *erythrocarpum* Sweet, *Hort. Brit.* 385. 1830, nomen nudum.
- Lycopersicon esculentum* var. *leucocarpum* Sweet, *Hort. Brit.* 385. 1830, nomen nudum.
- Lycopersicon inodorum* Juss. ex Miller, *Gard. Dict.* ed. 8, *Lycopersicon* No. 4. 1768, pro syn.
- Lycopersicon peruvianum* subsp. *typicum* Luckwill, *Aberdeen Univ. Studies* 120: 28. 1943, as “typicus”; not validly published (ICBN, Article 24.3).
- Lycopersicon peruvianum* var. *dentatum* (Dunal) Brezhnev in Zhukovskii, *Kult. Fl. SSSR* 20: 25. 1958; not validly published.
- Lycopersicum rotundatum* Sturtevant, *Amer. Nat.* 25: 705. 1891.—This name is not validly published, because Sturtevant (1891) did not accept the name but stated, “I would not have it understood that at present I consider this group as forming a true species in the botanical sense.” (ICBN, Article 34.1).
- Lycopersicon solanumlycopersicon* Hill, *Hort. Kew* 148. 1768, as “*Lycopersicum solanum-lycopersicum*” = *Solanum lycopersicum* L.—This name is perhaps only an instance of Hill’s giving a binomial synonym for what he was calling *Lycopersicum*. In his *Hortus kewensis* Hill did use some binomials, but we are not convinced he was coining a new name here. Because the name is not associated with a description or diagnosis, it is not validly published.
- Solanum chrysobotrys* Walpers, *Repert. bot. syst.* 3: 100. 1844, pro syn.
- Solanum pimpinellifolium* Miller ex Dunal in A. DC., *Prodr.* 13 (1): 25. 1852.—Erroneous entry in *Index kewensis* and IPNI; Dunal was not publishing a name but merely citing an annotation on a specimen, now lost, in the Banks herbarium (BM).
- Solanum racemigerum* K. Koch, *Wochenschrift* 13: 181. 1870, nomen nudum, non *Lycopersicon racemigerum* Lange, 1865.

Solanum spurium Balbis, Cat. hort. taur. 60. 1810, nomen nudum, non *Solanum spurium* J. F. Gmelin, 1791.

The following set of names was published by Khrapolova (2001) for subordinate taxa of “convar. *esculentum*,” which was equivalently numbered (3.3.2) in her system with *Lycopersicon esculentum* subsp. *spontaneum* (3.3.1). These names are better regarded as cultivar names and treated under the *International Code of Nomenclature of Cultivated Plants* (Brickell et al. 2004).

Lycopersicon esculentum var. *aurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *detgrandifolioaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *detvalidoaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *detvulgareaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *indetgrandifolioaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *indetvalidoaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *indetvulgareaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *nanovalidoaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *aurantium* subvar. *nanovulgareaurantium* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *brunneorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 26. 2001; not validly published.

Lycopersicon esculentum var. *brunneorubrum* subvar. *indetvulgarebrunneorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 26. 2001; not validly published.

Lycopersicon esculentum var. *chlorocorallinum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 26. 2001; not validly published.

Lycopersicon esculentum var. *chlorocorallinum* subvar. *indetvulgarechlorocorallinum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 26. 2001; not validly published.

Lycopersicon esculentum var. *chlorosarcum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 26. 2001; not validly published.

Lycopersicon esculentum var. *chlorosarcum* subvar. *indetvulgarechlorosarcum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 26. 2001; not validly published.

Lycopersicon esculentum var. *citrinum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 24. 2001; not validly published.

Lycopersicon esculentum var. *citrinum* subvar. *detvalidocitreum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii*, Part 3, 24. 2001; not validly published.

- Lycopersicon esculentum* var. *citrinum* subvar. *detvulgarecitrium* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* var. *citrinum* subvar. *indetvulgarecitrium* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* var. *esculentum* subvar. *indetvulgarealbum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 24. 2001; not validly published.
- Lycopersicon esculentum* var. *luteum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *luteum* subvar. *detvalidoluteum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *luteum* subvar. *detvulgareluteum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *luteum* subvar. *indetgrandifolioluteum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *luteum* subvar. *indetvulgareluteum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *roseum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *roseum* subvar. *detgrandifolioroseum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 26. 2001; not validly published.
- Lycopersicon esculentum* var. *roseum* subvar. *detvulgareroseum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 26. 2001; not validly published.
- Lycopersicon esculentum* var. *roseum* subvar. *indetgrandifolioroseum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 26. 2001; not validly published.
- Lycopersicon esculentum* var. *roseum* subvar. *indetvulgareroseum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *roseum* subvar. *nanovulgareroseum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 26. 2001; not validly published.
- Lycopersicon esculentum* var. *rubrum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *rubrum* subvar. *detgrandifoliorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *rubrum* subvar. *detvalidorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *rubrum* subvar. *detvulgarerubrum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.
- Lycopersicon esculentum* var. *rubrum* subvar. *indetgrandifoliorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kolleksii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rubrum* subvar. *indetvalidorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rubrum* subvar. *indetvulgarerubrum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rubrum* subvar. *nanovalidorubrum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rubrum* subvar. *nanovulgarerubrum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rufum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rufum* subvar. *detvulgarerufum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *rufum* subvar. *indetvulgarerufum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *variegatum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *variegatum* subvar. *detvulgarevariegatum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *variegatum* subvar. *indetvalidovariegatum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

Lycopersicon esculentum var. *variegatum* subvar. *indetvulgarevariegatum* Khrapolova in Dragavetsev, *Geneticheskie Kollektzii Ovoshchnykh Rastenii'*, Part 3, 25. 2001; not validly published.

APPENDIX 2

NATIVE DISTRIBUTION OF SPECIES OF SOLANUM SECT. LYCOPERSICOIDES, SECT. JUGLANDIFOLIA, AND SECT. LYCOPERSICON

Asterisks indicate species endemic to the country listed. *Solanum lycopersicum* occurs in all these countries; its present distribution is the result of human intervention and dispersal, and it is no longer possible to state with certainty where it was once native, if indeed it ever was a wild plant.

Colombia: *S. juglandifolium*.

Ecuador: *S. juglandifolium*, *S. ochranthum*, *S. habrochaites*, *S. neorickii*, *S. pimpinellifolium*, *S. cheesmaniae**, *S. galapagense**.

Peru: *S. lycopersicoides*, *S. ochranthum*, *S. pennellii*, *S. habrochaites*, *S. chilense*, *S. huaylasense**, *S. peruvianum*, *S. corneliomulleri**, *S. arcanum**, *S. chmielewskii*, *S. neorickii*, *S. pimpinellifolium*.

Bolivia: *S. chmielewskii*.

Chile: *S. lycopersicoides*, *S. sitiense**, *S. chilense*, *S. peruvianum*, *S. pimpinellifolium*.

APPENDIX 3

DISTRIBUTION OF *SOLANUM LYCOPERSICUM*

The cultivated tomato occurs on all continents, except Antarctica, both as a cultivated plant and sometimes as a feral escape. Here we list countries and geographic units from which we have seen herbarium specimens. Data for these collections can be found on the Solanaceae Source website, established as part of the PBI: *Solanum* Planetary Biodiversity Inventory project (<http://www.nhm.ac.uk/solanaceaesource>).

Afghanistan	Germany	Norfolk Island
Angola	Greece	Northern Mariana Islands
Antigua and Barbuda	Guadeloupe	Pakistan
Argentina	Guam	Panama
Armenia	Guatemala	Papua New Guinea
Australia	Guyana	Peru
Austria	Haiti	Philippines
Bahamas	Honduras	Portugal
Barbados	Hungary	Puerto Rico
Belgium	India	Republic of the Congo
Belize	Indonesia	Republic of Yemen
Bhutan	Iran	Romania
Bolivia	Iraq	Russian Federation
Brazil	Israel	Samoa
British Virgin Islands	Italy	Senegal
Cambodia	Ivory Coast	Serbia and Montenegro
Cameroon	Jamaica	Sierra Leone
Canada	Japan	Sikkim
Cape Verde	Jordan	Slovakia
Central African Republic	Kenya	South Africa
Chile	Kiribati	Spain
China	Lebanon	St. Helena
Christmas Island	Leeward Islands	Surinam
Colombia	Liberia	Sweden
Cook Islands	Madagascar	Switzerland
Costa Rica	Malaysia	Syrian Arab Republic
Croatia	Mali	Taiwan
Cuba	Malta	Tanzania
Czech Republic	Marshall Islands	Thailand
Denmark	Martinique	Trinidad and Tobago
Dominica	Mascarene Islands	Tunisia
Dominican Republic	Mauritius	Turkey
Ecuador	Mexico	U.S.A.
Egypt	Myanmar	United Kingdom
El Salvador	Namibia	Vanuatu
Equatorial Guinea	Nepal	Venezuela
Eritrea	Netherlands	Vietnam
Ethiopia	New Caledonia	Virgin Islands
Fiji	New Zealand	Zaire
France	Nicaragua	Zimbabwe
French Guiana	Niger	
French Polynesia	Nigeria	

APPENDIX 4

CURRENT DETERMINATIONS FOR GERmplasm BANK ACCESSIONS

The accessions of tomatoes managed and provided by the TGRC (C. M. Rick Tomato Genetics Resource Center) are widely used in tomato breeding and in the genetics, physiology, and genomics community. Here we provide a list of the wild species accessions earlier attributed to *Solanum peruvianum* from the TGRC with their LA number (*Lycopersicon* accession) and the current determination in agreement with our species definitions. Delimitations of the other taxa of tomatoes and wild relatives are the same as those currently used by TGRC; names in both the *Solanum* and *Lycopersicon* for all accessions can be found on the TGRC website (<http://tgrc.ucdavis.edu/>) with the use of the search facilities for accessions of wild species. The majority of these accessions of *S. peruvianum* were studied in experimental fields in Wisconsin (U.S.A.) and Mendoza (Argentina). Accession numbers with asterisks were studied in crossability tests by Charles M. Rick. Accessions A3, 16, 93, 105, 108, 119, 124, 150, 364, 466, 447, 449, 450, 452, 465, 479 are inactive at present in the TGRC, but we indicate here the corresponding active accessions. Details of collecting localities for each of these accessions as well as other information on compatibility, etc., can be found using the database searches on the TGRC website (<http://tgrc.ucdavis.edu/>).

TGRC ACCESSION NUMBER	SPECIES IDENTITY AS RECOGNIZED IN THIS MONOGRAPH
LA A3*	<i>S. huaylasense</i>
LA 16*	<i>S. arcanum</i> ('humifusum' assemblage)
LA 93* (=1473)	<i>S. corneliomulleri</i>
LA 103	<i>S. corneliomulleri</i>
LA 104*	<i>S. corneliomulleri</i>
LA 105*	<i>S. peruvianum</i>
LA 107*	<i>S. corneliomulleri</i>
LA 108*	<i>S. corneliomulleri</i>
LA 110*	<i>S. huaylasense</i>
LA 111*	<i>S. peruvianum</i>
LA 119*	<i>S. peruvianum</i>
LA 124*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 150*	<i>S. peruvianum</i>
LA 153*	<i>S. peruvianum</i>
LA 366*(=364)	<i>S. corneliomulleri</i>
LA 370*	<i>S. peruvianum</i>
LA 374*	<i>S. peruvianum</i>
LA 378*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 382*	<i>S. arcanum</i> ('humifusum' assemblage)
LA 383*	<i>S. arcanum</i> ('humifusum' assemblage)
LA 385	<i>S. arcanum</i> ('humifusum' assemblage)
LA 389	<i>S. arcanum</i> ('humifusum' assemblage)
LA 392*	<i>S. arcanum</i> ('humifusum' assemblage)
LA 441*	<i>S. arcanum</i> ('lomas' assemblage)
LA 444*	<i>S. corneliomulleri</i>
LA 448*	<i>S. peruvianum</i>
LA 451*	<i>S. corneliomulleri</i>
LA 454*	<i>S. peruvianum</i>
LA 462*	<i>S. peruvianum</i>
LA 1032*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1133	<i>S. corneliomulleri</i>
LA 1271	<i>S. corneliomulleri</i>
LA 1274	<i>S. corneliomulleri</i>
LA 1281	<i>S. corneliomulleri</i>
LA 1283*	<i>S. corneliomulleri</i>
LA 1292	<i>S. corneliomulleri</i>
LA 1293	<i>S. corneliomulleri</i>

TGRC ACCESSION NUMBER	SPECIES IDENTITY AS RECOGNIZED IN THIS MONOGRAPH
LA 1294	<i>S. corneliomulleri</i>
LA 1304	<i>S. corneliomulleri</i>
LA 1305	<i>S. corneliomulleri</i>
LA 1331	<i>S. corneliomulleri</i>
LA 1333	<i>S. peruvianum</i>
LA 1336 (=449*)	<i>S. peruvianum</i>
LA 1339	<i>S. corneliomulleri</i>
LA 1346	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1351	<i>S. arcanum</i> ('humifusum' assemblage)
LA 1358	<i>S. huaylasense</i>
LA 1360	<i>S. arcanum</i> ('humifusum' assemblage)
LA 1364	<i>S. huaylasense</i>
LA 1365*	<i>S. huaylasense</i>
LA 1373*	<i>S. corneliomulleri</i>
LA 1377	<i>S. corneliomulleri</i>
LA 1379 (=479*)	<i>S. corneliomulleri</i>
LA 1394	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1395	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1396	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1473* (=367*)	<i>S. corneliomulleri</i>
LA 1474 (=450*)	<i>S. peruvianum</i>
LA 1513 (=466*-447*)	<i>S. peruvianum</i>
LA 1556 (=119)	<i>S. peruvianum</i>
LA 1551	<i>S. corneliomulleri</i>
LA 1552	<i>S. corneliomulleri</i>
LA 1554	<i>S. corneliomulleri</i>
LA 1609 (=108)	<i>S. corneliomulleri</i>
LA 1616	<i>S. peruvianum</i>
LA 1626*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1646	<i>S. corneliomulleri</i>
LA 1647	<i>S. corneliomulleri</i>
LA 1653	<i>S. corneliomulleri</i>
LA 1672	<i>S. corneliomulleri</i>
LA 1677	<i>S. corneliomulleri</i>
LA 1694	<i>S. corneliomulleri</i>
LA 1708*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1722	<i>S. corneliomulleri</i>
LA 1723	<i>S. corneliomulleri</i>
LA 1744	<i>S. corneliomulleri</i>
LA 1910	<i>S. corneliomulleri</i>
LA 1913	<i>S. peruvianum</i>
LA 1929	<i>S. peruvianum</i>
LA 1935	<i>S. peruvianum</i>
LA 1937	<i>S. corneliomulleri</i>
LA 1944	<i>S. corneliomulleri</i>
LA 1945	<i>S. corneliomulleri</i>
LA 1947	<i>S. peruvianum</i>
LA 1949*	<i>S. peruvianum</i>
LA 1951	<i>S. peruvianum</i>
LA 1955	<i>S. peruvianum</i>
LA 1954* (=105)	<i>S. peruvianum</i>
LA 1973 (=452*)	<i>S. corneliomulleri</i>
LA 1975	<i>S. peruvianum</i>
LA 1981	<i>S. huaylasense</i>
LA 1982	<i>S. huaylasense</i>

TGRC ACCESSION NUMBER	SPECIES IDENTITY AS RECOGNIZED IN THIS MONOGRAPH
LA 1983	<i>S. huaylasense</i>
LA 1984* (=124)	<i>S. arcanum</i> ('Marañón' assemblage)
LA 1985	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2068	<i>S. huaylasense</i>
LA 2150	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2151	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2152 (=16)	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2153	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2157*	<i>S. arcanum</i> ('Chotano' assemblage)
LA 2163*	<i>S. arcanum</i> ('Chotano' assemblage)
LA 2164	<i>S. arcanum</i> ('Chotano' assemblage)
LA 2172*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2185*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2326*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2327	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2328*	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2330	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2331	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2333	<i>S. arcanum</i> ('Marañón' assemblage)
LA 2334*	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2388	<i>S. arcanum</i> ('Chotano' assemblage)
LA 2548	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2550	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2553	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2555	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2561	<i>S. huaylasense</i>
LA 2562	<i>S. huaylasense</i>
LA 2563	<i>S. huaylasense</i>
LA 2565	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2566	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2575	<i>S. huaylasense</i>
LA 2581	<i>S. peruvianum</i>
LA 2582	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2583	<i>S. arcanum</i> ('humifusum' assemblage)
LA 2717	<i>S. corneliomulleri</i>
LA 2721	<i>S. corneliomulleri</i>
LA 2724	<i>S. corneliomulleri</i>
LA 2732	<i>S. peruvianum</i>
LA 2742	<i>S. peruvianum</i>
LA 2744 (=465*)	<i>S. peruvianum</i>
LA 2745	<i>S. peruvianum</i>
LA 2770	<i>S. peruvianum</i>
LA 2808	<i>S. huaylasense</i>
LA 2809	<i>S. huaylasense</i>
LA 2834	<i>S. peruvianum</i>
LA 2955	<i>S. peruvianum</i>
LA 2959	<i>S. peruvianum</i>
LA 2962	<i>S. corneliomulleri</i>
LA 2964	<i>S. peruvianum</i>
LA 2981B	<i>S. corneliomulleri</i>
LA 3154	<i>S. corneliomulleri</i>
LA 3156	<i>S. corneliomulleri</i>
LA 3218	<i>S. peruvianum</i>
LA 3219	<i>S. corneliomulleri</i>
LA 3220	<i>S. peruvianum</i>

TGRC ACCESSION NUMBER

SPECIES IDENTITY AS RECOGNIZED IN THIS MONOGRAPH

LA 3637	<i>S. corneliomulleri</i>
LA 3639	<i>S. corneliomulleri</i>
LA 3664	<i>S. corneliomulleri</i>
LA 3666	<i>S. corneliomulleri</i>

NUMERICAL LIST OF SPECIES

1. <i>S. lycopersicoides</i>	10. <i>S. corneliomulleri</i>
2. <i>S. sitiens</i>	11. <i>S. arcanum</i>
3. <i>S. juglandifolium</i>	12. <i>S. chmielewskii</i>
4. <i>S. ochranthum</i>	13. <i>S. neorickii</i>
5. <i>S. pennellii</i>	14. <i>S. pimpinellifolium</i>
6. <i>S. habrochaites</i>	15. <i>S. lycopersicum</i>
7. <i>S. chilense</i>	16. <i>S. cheesmaniae</i>
8. <i>S. huaylasense</i>	17. <i>S. galapagense</i>
9. <i>S. peruvianum</i>	

INDEX TO NUMBERED COLLECTIONS EXAMINED

The numbers in parentheses refer to the corresponding species in the text and in the Numerical List of Species above. The many collections by anonymous collectors without date or other identifying features are not listed here (ca. 1200 collections), but can be found on the Solanaceae Source website (<http://www.nhm.ac.uk/solanaceaesource>); most of these are *Solanum lycopersicum* and come from botanical gardens.

- Acevedo, R., & F. Vazquez 383 (15).
 Ackermann, M. 137 (9), 416 (10), 459 (7).
 Ackermann, M., & F. Caceras 438 (9), 451 (9).
 Acleto, C. 607 (10).
 Acosta-Arteaga, C. E. 719 A (3).
 Acosta-Solís, M. 5581 (3), 5633 (3), 6775 (3), 8000 (6), 10816 (15), 14261 (4).
 Acuña 16795 (15).
 Adams, C. D. 11204 (15).
 Adersen, H., & A. Adersen 201 (16), 464 (16), 465 (17), 891 (17), 903 (16), 919 (16), 921 (17), 1165 (17), 1771 (17).
 Aedo, C., & Anon. 4524 (15).
 Agostini, G. 678 (15).
 Aitchison, J. E. T. 483 (15).
 Al-Rawi, A. 13991 (14), 13992 (9), 13993 (6).
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 Aldaz, I. 350 (16).
 Alfaro, A. 32417 (15).
 Allard, H. A. 16260 (15).
 Alston, A. H. G. 8291 (3).
 Alvarez, A., & O. Proaño 253 (3).
 Alvarez, A., et al. 215 (3), 586 (3).
 Anderson, E. F. 2423 (14).
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 Andino, A. R. 176 (15).
 Andrade F., B. 5 (15).
 André, E. 2873 (4), 4110 (9).
 Angulo, N. 1018 (11), 1234 (6), 1236 (11).
 Antonio, T. 2346 (15).
 Arakaki, M. 143 (7), 172 (7), 181 (5), 332 (7).
 Arakaki, N. 024 (6), 99 (15).
 Arango, M. C., & A. Santiago A. 50 (15).
 Araquistain, M. 372 (15).
 Araquistain, M., & P. P. Moreno 2030 (15), 2395 (15).
 Archer, W. A. 1144 (3), 1293 (3), 1564 (15), 4070 (15).
 Arenas P., G. 90 (10), 91 (10), 92 (10), 93 (10).
 Ariza, C. 7 (15).
 Armesto et al. 1150 (1).
 Arockiasamy, D. I. 5067 (15).
 Aronson, J. 7749 (7).
 Arroyo, M. T. K. 84-507 (7).
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 Aymard, G., & N. Cuello. 7530 (15).
 Aznavour, G. V. 5186 (15).
 Bachmann, F. 1207 (15).
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- Bakhuizen van den Brink Jr., R. C. 4955 (15).
 Baldeón Malpartida, S. 899 (5).
 Baldeón, S., et al. 87 (9).
 Balfern, C. W. 14 (15).
 Balfour Gourlay, W. 116 (10).
 Balls, E. K. 7075 (6), 7345 (4), B-5858 (14), B-7073 (9), B-7075 (6).
 Balls, E. K., & J. G. Hawkes 7345 (4).
 Balslev, H. 4877 (15).
 Balslev, H., & D. Irvine 4619 (15).
 Balslev, H., & E. Madsen 10308 (3).
 Barbour, P. 4253 (14).
 Barclay, A. S., et al. 3310 (3), 3416 (3).
 Barkley, F. A. 14550 (15).
 Barkley, F. A., et al. 7658 (15).
 Barlow, F. D. 29/24 (15).
 Barnhart, J. H. 1256 (15).
 Bässler, H. C. 77 (15).
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 Baur, G. 189 (17).
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 Beckwith, F. 779 (15).
 Bedi, R. 674 (15).
 Beetle, A. A. 26178 (7).
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 Beltrán, H. 06 (10).
 Benavides, O. de 340 (3), 5226 (15), 7399 (4), 9312 (3).
 Benítez de Rojas, C. E. 96 (15), 2376 (15).
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 Bernardi, L., et al. 16915 (9).
 Betancur, J., et al. 1003 (3).
 Biese, W. 398 (7), 2178 (7), 2203 (2), 2241 (7), 2276 (7), 2457 (2), 2472 (7), 2797 (7).
 Billiet, F., & B. Jadin 5451 (1), 5547 (7), 5562 (7).
 Binder, M., & A. Daxberger 1999/ 363 (10).
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 Bourgeau, E. 933 (15).
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 Bowman, R. 40 (16), 119 (16), 120 (16), 121 (16).
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 Brand, F. F. 108 (15).
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 Breckon, G. J. 2119 (15).
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 Brenkle, J. F. 47-417 (15).
 Brett, J. 349 (15).
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 Burdet, E. 364 (15).
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 Bye, R. A. 2861 (15), 3590 (15), 3602 (15).
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