

# Taxonomy of tomatoes in the Galápagos Islands: native and introduced species of *Solanum* section *Lycopersicon* (Solanaceae)

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**Abstract** The Galápagos Islands are of great conservation interest due to their high proportion of endemic species. The endemic tomatoes (*Solanum* section *Lycopersicon*) of the islands have long been of interest to plant breeders. We analyse the morphology of all the Galápagos tomatoes: two endemic species, *Solanum cheesmaniae* and *S. galapagense* (the latter described here as new) and two introduced species, *S. lycopersicum* and *S. pimpinellifolium*. Morphological characters were measured on greenhouse-grown plants raised from seeds obtained from the wild and seed-bank accessions. Species boundaries were examined by cluster analysis and principal component analysis. Although the four taxa are distinct and therefore regarded as bona fide species they exhibit considerable intraspecific variation. A taxonomic treatment of the tomatoes in the Galápagos is provided, with keys to all solanums in the islands, descriptions, listings of representative specimens examined and full exsiccatae. Field observations of plants in the wild in the Galápagos are also included in the species descriptions. We highlight the potential for genetic contamination of the endemic tomatoes by hybridization and introgression with the two introduced species.

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**Key words** Ecuador, endemism, invasive species, Galápagos Islands, morphology, new taxa, Solanaceae, *Solanum*, species delimitation, tomato

## Introduction

The flowering plant family Solanaceae contains many taxa of importance for humans, in agriculture (potatoes, tomatoes, peppers), medicine (mandrake, tobacco, deadly nightshade, henbane), and as ornamentals (*Solanum* spp., tobaccos, petunias). Members of the family occur worldwide, but the highest diversity, of both genera and species is found in the Neotropics. The largest genus in the family is *Solanum*, an estimated 1500–2000 species. This diversity places *Solanum* among the most species-rich genera of angiosperms. Species of *Solanum* exhibit an incredible range of morphological forms, ranging from tiny herbs to medium sized forest trees, and are found in all habitats worldwide. Species richness in *Solanum* (and in the family as a whole) is highest in the Neotropics, particularly in the Andes and associated valley systems.

Traditionally, several genera of economic importance have been segregated from *Solanum*, based largely on their use as human food plants. The tree tomatoes (*Cyphomandra* Sendtn.) and the tomatoes (*Lycopersicon* Mill.) have been shown to be deeply nested within a monophyletic larger *Solanum*, using both morphological (Child, 1990; Spooner *et al.*, 1993; Bohs, 1994, 1995) and molecular (Spooner *et al.*, 1993; Bohs & Olmstead, 1997, 1999; Peralta & Spooner, 2001) character sets.

As part of a larger study on the taxonomy and phylogeny of the wild tomatoes and their close relatives (Peralta *et al.*, in prep.) and broader studies of evolutionary genetics of the introduced and native tomatoes in the Galápagos (SD), we identified more variation between the Galápagos taxa than had been recognized previously (but see Lundgren *et al.*, 1985). This work is the result of field studies undertaken by SD, examination of herbarium specimens (see ‘Plant specimens’ and ‘Taxonomic treatment’) and morphometric analyses undertaken on greenhouse-grown accessions of all Galápagos tomato taxa. Our aims here are to document the variation found amongst and between Galápagos tomatoes, both native and introduced, to describe the species of tomatoes occurring in the islands and to provide tools for their identification that will be useful to those working with Galápagos plants.

## History of tomato classification

Linnaeus (1753) described three species of what are now recognized as tomatoes as members of the genus *Solanum* (*S. lycopersicum*, *S. peruvianum* L. and *S. pimpinellifolium*). Philip Miller (1754), a contemporary of Linnaeus, segregated the new genus *Lycopersicon* to accommodate *Solanum* species with multi-locular fruits, including the tomatoes, the potato (*S. tuberosum* L.) and several other species (Miller, 1754; Peralta *et al.*, in prep.).

Use of the generic name *Lycopersicon* settled upon the relatives of the cultivated tomato (*Solanum lycopersicum*), that

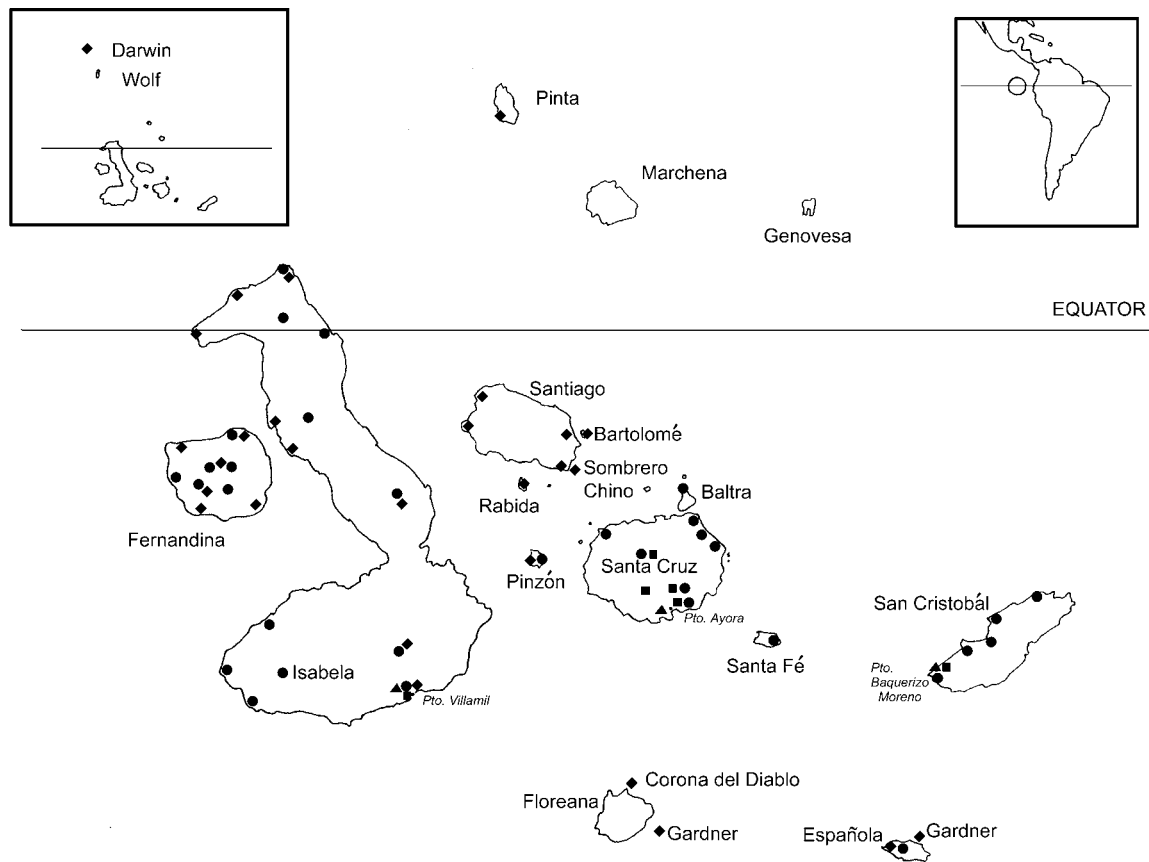
possessed yellow flowers, apparently longitudinal anther dehiscence and a long sterile appendage on the tips of the anthers (Peralta & Spooner, 2000). Some species in the group, however, are problematic with respect to this restricted generic definition. *Solanum pennellii* Correll, a species of the Peruvian and Chilean coastal deserts, has the requisite yellow flowers and apparently longitudinal dehiscence, but lacks the sterile anther appendage (Correll, 1962).

The classification of tomatoes as the genus *Lycopersicon* was maintained by several classical and modern botanists (Dunal, 1813, 1852; Müller, 1940; Luckwill, 1943; Correll, 1962; Symon, 1981; D’Arcy, 1991; Nee, 1999; Hunziker, 2001). Plant breeders have consistently maintained usage as *Lycopersicon* (Taylor, 1986; Rick, 1979, 1988; Rick *et al.*, 1990; C. M. Rick Tomato Genetics Resource Center. <http://tgrc.ucdavis.edu>). This treatment, however, has not been universal. In his original treatment of these species, Linnaeus (1753) included them as members of the genus *Solanum*, and many subsequent taxonomists have also recognized the tomatoes as belonging to *Solanum* rather than as the segregated *Lycopersicon* (Wettstein, 1891; Macbride, 1962; Seithe, 1962; Fosberg, 1987; Child, 1990).

Recent studies, firstly using morphological characters (Child, 1990) and then using molecular data from both the chloroplast and nuclear genomes (Spooner *et al.*, 1993; Bohs & Olmstead, 1997, 1999; Peralta & Spooner, 2001), have shown that the tomatoes are the sister group of the potatoes. If classifications are to be based on monophyletic groups (Judd *et al.*, 1999), the tomatoes and their relatives should be taxonomically treated as part of the genus *Solanum*. We are treating the Galápagos species examined here as species of *Solanum*, recognizing that the agronomy and plant breeding community might, for purely practical reasons, prefer to maintain familiar names of these taxa under the genus *Lycopersicon*. Nomenclatural issues arising from this will be treated in detail in an upcoming monograph of the wild tomatoes and their relatives (Peralta *et al.*, in prep.) and have also been examined previously (Spooner *et al.*, 1993).

## Introduction to the Galápagos

The Galápagos Islands are volcanic in origin and straddle the equator about 1000 km to the west of the coast of South America (Republic of Ecuador), the nearest landmass. The oldest islands towards the east of the archipelago are between 2–6.5 million years old (Geist, 1996). The younger, more western islands still have considerable volcanic activity; seven eruptions occurred on Fernandina between 1958 and 1998, and Volcán Cerro Azul on Isabela erupted in 1979 and 1998 (Stephenson, 2000). There are 13 large islands (over 10 km<sup>2</sup>) and over 40 officially named smaller islands, islets and emergent rocks (Fig. 1). The total landmass of the Galápagos is about 8000 km<sup>2</sup> (Jackson, 1993).



**Figure 1** Distribution map of tomatoes in the Galápagos Islands (island names follow Table 1). *Solanum cheesmaniae*, circles; *Solanum galapagense*, rhomboids; *Solanum pimpinellifolium*, squares; *Solanum lycopersicum*, triangles.

The fourth Bishop of Panamá, Fray Tomás de Berlanga, discovered the islands in 1535, when his ship was becalmed en route from Panamá to South America. Pre-conquest discovery of the islands remains in dispute, despite the presence of fragments of pre-Columbian pottery and legends of Incas visiting the islands in the 1400s (Perry, 1972).

In the sixteenth century the islands were only periodically visited by buccaneers and adventurers and by whaling ships in the seventeenth and eighteenth century. The Galápagos Islands were used as a source of fresh food and water – particularly giant tortoises, which were easily captured and stored live on ship for up to a year (Perry, 1972).

The first ‘proper’ Galápagos scientific collections were made at the end of the eighteenth century by Archibald Menzies, a surgeon–naturalist collecting plants for Sir Joseph Banks and the Royal Botanic Gardens at Kew. He collected ‘a few’ plant specimens, which later were accidentally mixed with plants collected from Hawaii. David Douglas (collecting for what is now the Royal Horticultural Society), John Scouler and James McRae visited the islands on their way to the western coast of the United States and Canada in the late 1820s. Hugh Cuming, an independent collector of natural history specimens resident in Chile, visited the Galápagos in 1829 as part of his general exploration of the western South America. Their plant collections, combined with those collected by Charles Darwin in 1835, when the *Beagle* visited the

islands, were the material of Joseph D. Hooker’s enumeration of Galápagos plants eventually published in 1847 (see note under *S. cheesmaniae* for discussion of dates of publication). The fact that the *Beagle* and Darwin visited the Galápagos at all was due to several factors. First, British naval captains had been interested in obtaining good navigational charts of the islands. Second, reports of the geology and unknown species to be found there sparked interest in further exploration and third, William J. Hooker, then Professor of Botany at Glasgow but later knighted and director of the Royal Botanic Gardens at Kew, specifically lobbied for more Galápagos collections (Larson, 2001). The voyage of the *Beagle*, including the collections and observations made in Galápagos, was a turning point in Charles Darwin’s career, and has made the islands a key locality not only for biodiversity, but for the history of science.

In 1832 the Galápagos Islands became a province of Ecuador, where they are officially known as the Archipiélago de Colón. The individual islands have been known by a wide variety of names, both English and Spanish. Table 1 summarizes the island synonyms relevant here. We use the official Ecuadorian island names (W. Tapia Aguilera, pers. comm., 2002) for discussion and in the specimen citations.

There are now five islands with permanent human habitations – Floreana, San Cristóbal, Isabela, Santa Cruz and Baltra. The first island to be settled was Floreana, in

Official island and islet names	Synonyms
Baltra	South Seymour
Bartolomé	Bartholomew
Corona del Diablo (near Floreana)	Devil's Crown; Onslow
Darwin	Culpepper
Española	Hood
Fernandina	Narborough
Floreana	Charles; Santa María
Gardner (near Española)	
Gardner (near Floreana)	
Isabela	Albemarle
Pinta	Abingdon
Pinzón	Duncan
Rabida	Jervis
San Cristóbal	Chatham
Santa Cruz	Indefatigable
Santa Fé	Barrington
Santiago	James; San Salvador
Sombrero Chino	
Wolf	Wenman

**Table 1** Galápagos Island names used in this study and synonyms (Slevin, 1959; W. Tapia Aguilera, pers. comm., 2002).

about 1807, by a marooned crew-member of a British ship (Slevin, 1959). In the late 1800s San Cristóbal and Isabela were settled, the latter with two villages established: Villamil on the south coast and San Tomás, to the north of Villamil. In 1926 Santa Cruz was settled by a group of Norwegian farmers, and finally Baltra in the 1940s became a US air-base (it is now an Ecuadorian Naval base) (Jackson, 1993). Santiago, in the past, had a settlement at Bahía James (Wiggins & Porter, 1971). The last published census in 1999 estimated a permanent resident population of just over 16 000 (<http://naturalist.net/news/Galápagoscensus.html>).

Most of the landmass and the waters surrounding the Galápagos are now officially protected. In 1959 the Ecuadorian government designated the uncolonized areas, approximately 90% of the landmass, as a Galápagos National Park. In the same year the Charles Darwin Foundation was set up dedicated to the conservation of the Galápagos ecosystems and a year later the Charles Darwin Research Station (CDRS) was established on Santa Cruz to conduct scientific research and environmental education (<http://www.darwinfoundation.org>). The islands were designated a UNESCO World Heritage Site in 1978. In 1986 the waters between the islands and 15 nautical miles (extended later to 40 nautical miles) surrounding the islands were designated as the Galápagos Marine Resources Reserve by INEFAN (Instituto Nacional Ecuatoriano de Fauna y Areas Naturales). In 2001 the Galápagos Marine Reserve was also designated a UNESCO World Heritage Site (<http://whc.unesco.org/nwhc/pages/sites/main.htm>).

Vegetation types vary within and between the islands and are dependent on several factors, including the age and size of the island, altitude and orientation. The younger islands have lava flows so recent that they have not fully been colonized by

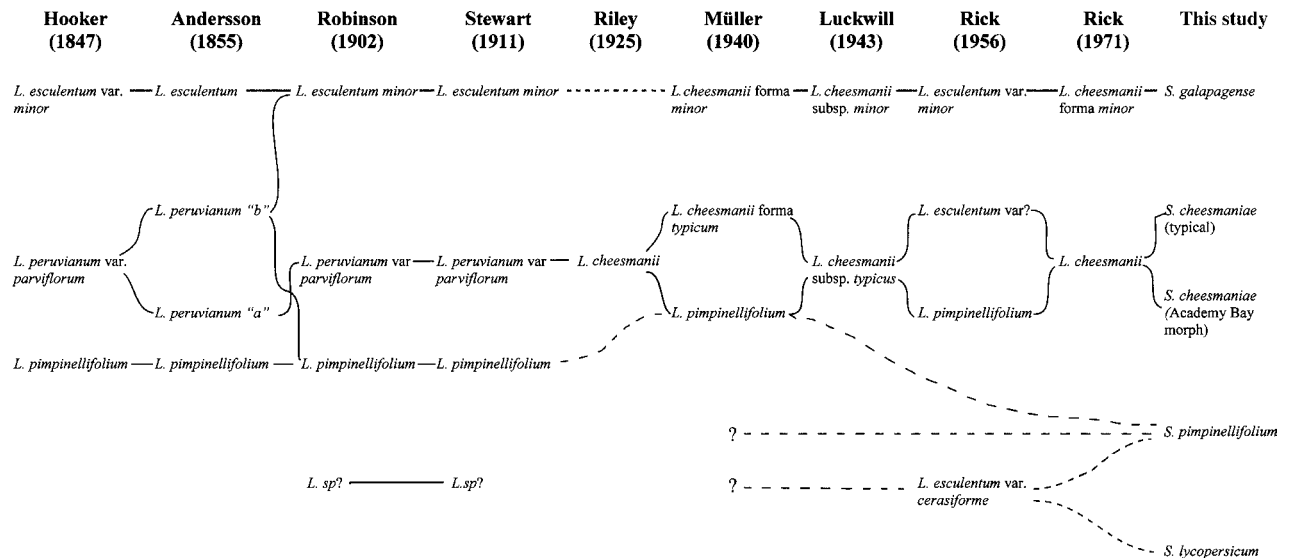
plants (Wiggins & Porter, 1971). The small low islands such as Baltra rarely receive much rain. Areas at higher elevations and on southern aspects receive precipitation from the prevailing southerly winds. On Santa Cruz, for example, the lowland arid zone receives between 0–300 mm of rain per annum; above this there is a moist zone receiving up to 1700 mm of rain per annum where cloud forest occurs between about 300–700 m altitude (Jackson, 1993).

Darwin wrote, soon after arriving in the Galápagos, 'I certainly recognize S. America in Ornithology. Would a botanist? 3/4 of the plants in flower' (quoted in Keynes, 1988). It is now documented that about 40% of the native flowering plant taxa are endemic to the islands (Wiggins & Porter, 1971). The total native vascular plant diversity in the Galápagos numbers approximately 596 taxa; with 372 natives and 224 endemics (Lawesson, 1990b). In common with other oceanic archipelagos, the Galápagos Islands suffer from the effects of introduced animals and plants (Loope *et al.*, 1988) brought in either accidentally or intentionally by humans. Fifteen years ago, the number of introduced plants in Galápagos was estimated to be approximately 260 (Lawesson, 1990a). More recent analyses show that the number of introduced plants is rising, currently it stands at over 500 taxa; 260 of these are naturalized in the islands (A. Tye, pers. comm. in prep., 2002).

## History of tomato classification in the Galápagos

The earliest collection of any of the endemic tomato species is that of John Scouler (*Solanum galapagense*, Scouler *s.n.*, E), collected in 1827. Both species of endemic Galápagos tomatoes were collected by Charles Darwin in 1835. Along with Darwin's other botanical collections they were described by Joseph D. Hooker, from specimens sent to him via John Stevens Henslow from the University of Cambridge (Porter, 1980). Hooker (1847) recognized three types of Galápagos tomatoes, all of them similar to specimens found in the mainland of South America: '*Lycopersicon pimpinellifolium* – Chatham Island' (San Cristóbal) ('precisely similar to the South American plant'), '*Lycopersicon esculentum* var. *minor* – James Island' (Santiago) (being 'smaller than the common state of the species') and '*L. peruvianum* var. *parviflorum* – Chatham Island' ('having smaller flowers than its mainland counterpart and no other difference seems to exist').

Andersson (1855) described the Galápagos tomatoes using both his own collections from the islands and Darwin's, but did not attempt to reconcile the already complex nomenclature of the Galápagos plants. He included three species in his treatment, '*Lycopersicum esculentum*', '*Lycopersicum pimpinellifolium*' and '*Lycopersicum peruvianum*', the latter with two informally named variants: '*a*' – 'a procumbent plant with irregularly toothed leaflet margins and subappressed pubescence' from Isabela and '*b*' – 'an erect plant with deeply divided leaf segments and long, divaricate hairs' from San Cristóbal. Robinson's (1902) *Flora of the Galápagos Islands* identified four taxa of '*Lycopersicum*', in general the same



**Figure 2** History of classification of tomatoes in the Galápagos.

as those recognized by Andersson, with the exception of an unnamed species from San Cristóbal which he identified as lacking the spreading pubescence of the other Galápagos tomatoes. Robinson (1902) recognized '*Lycopersicon esculentum* var. *minor*' as distinct, not relegating it to synonymy as had Andersson (1855). In the California Academy's botanical survey of the islands, Stewart (1911) followed Robinson (1902), maintaining the same four taxa of tomatoes in the Galápagos (Fig. 2).

Riley (1925) was the first to recognize the species-level distinctness of the Galápagos tomato and he described it as '*Lycopersicon cheesmanii*' (based on Evelyn Cheesman's specimen collected from Santa Cruz). Riley mentioned Andersson's collections and descriptions of the two variants of '*L. peruvianum*' from Galápagos, but stated that his new species differed from both.

In the 1940s, two herbarium taxonomists revised the tomatoes (as *Lycopersicon*) throughout their ranges. Müller's (1940) revision recognized three taxa occurring in the islands: '*L. cheesmanii* forma *minor*', '*L. cheesmanii* forma *typicum*' and '*L. pimpinellifolium*'. He placed all of the Galápagos tomatoes except those with larger leaves into a single species with two forms. The revision by Luckwill (1943) recognized only two tomato taxa from the Galápagos: '*L. cheesmanii* subspecies *typicus*' and 'subspecies *minor*'. Luckwill's (1943) circumscription of his '*L. pimpinellifolium*' did not include any of the specimens identified as that species occurring in Galápagos, but he indicated that its occurrence on the Galápagos needed confirmation. Both of these revisions were completed during the Second World War, a time difficult for the loan of specimens and for travel to the herbaria of Europe, where many of the previously collected specimens of these plants were held.

Since the 1950s, interest has increased in wild species as sources of genes for the improvement of the cultivated tomato. This interest was reflected in the increased collecting intensity for breeding purposes, with germplasm being kept for use

by all breeders in central localities. Collections of Galápagos tomatoes held in the C. M. Rick Tomato Genetics Resource Center (TGRC: <http://tgrc.ucdavis.edu>) seed bank, Department of Vegetable Crops, University of California, Davis, were described by Rick (1956), who collected extensively on the Galápagos Islands in the 1950s and 1960s. He recognized three taxa: '*L. pimpinellifolium*' (TGRC accession number LA166), '*Lycopersicon esculentum* var. *minor*' (TGRC accession number LA317), and '*L. esculentum* var. *cerasiforme*' (TGRC accession number LA292); the latter he later assumed had been introduced by human settlers (Rick, 1963). He also briefly mentioned another less widely distributed form of tomato as a variation of '*L. esculentum*' – we believe that he was referring to the 'typical' form of *Solanum cheesmaniae*, as exemplified by the type specimen Cheesman in Riley 403.

In the *Flora of the Galápagos Islands* (Wiggins & Porter, 1971), Rick (1971) recognized only two taxa of Galápagos tomatoes: '*Lycopersicon cheesmanii*' (combining the taxa previously recognized as '*L. pimpinellifolium*', '*L. cheesmanii* forma *typicum*' and the briefly mentioned variation of '*L. esculentum*') and '*L. cheesmanii* forma *minor*'. This circumscription of the Galápagos tomatoes has been maintained (Rick, 1983) and is the current nomenclature used at the TGRC and thus throughout the plant breeding community.

## Distribution and ecology of tomatoes in the Galápagos

Tomatoes occur on 19 different islands and islets throughout the archipelago (Fig. 1). On only two, Fernandina and Isabela, do the two endemic taxa appear to grow sympatrically in time as well as space. During the course of this research we found the two introduced tomatoes (*Solanum pimpinellifolium* and *S. lycopersicum*) on Santa Cruz, Isabela and San Cristóbal.

These three islands also support populations of endemic tomatoes, and the introduced tomatoes are now found in localities where the native tomatoes were collected in the past.

Both of the native Galápagos tomato species always develop yellow to orange ripe fruit; no native biotype has bright red fruit. This was also the opinion of the late Charles M. Rick, who considered all tomatoes with red fruit to be introduced taxa – either *Solanum pimpinellifolium* or *S. lycopersicum* (C. M. Rick, in litt., 1998). The specimen described by Hooker as '*L. pimpinellifolium*' based on Darwin's 1835 collections does not match the Linnaean type specimen and is clearly not the same species as the mainland *S. pimpinellifolium* with bright red fruit (Peralta *et al.*, in prep.; also see 'Taxonomic treatment'). To further complicate matters, genuine plants of *S. pimpinellifolium* and *S. lycopersicum* appear to have been introduced by human settlers from the mainland to Galápagos during the twentieth century.

The occurrence of putatively feral plants of *Solanum lycopersicum* (as *Lycopersicon esculentum* var. *cerasiforme*) on Isla San Cristóbal has been documented since the 1950s (Rick, 1956). *Solanum lycopersicum* was collected on San Cristóbal (Howell 8573) in 1932, from Santa Cruz in 1952 (TGRC LA 0292) and in 2000 on Isabela (*S. Darwin* 302). *Solanum pimpinellifolium* (as *L. pimpinellifolium*) has also been recorded in the archipelago (Rick, in litt., 1998). The earliest unequivocal collection was made in 1985 on Isabela (TGRC LA 2857). However it is possible that *S. pimpinellifolium* has occurred in the islands a lot longer. Müller (1940) cited several Galápagos specimens as *S. pimpinellifolium*; most belong to a variant of *S. cheesmaniae* informally recognized here as the 'Academy Bay' morph, save one (*Stewart* 3380). The leaf morphology of this specimen fits extremely well with the Linnaean type of *S. pimpinellifolium*. It is also similar to plants of *S. pimpinellifolium* currently found in the Galápagos, however, this specimen lacks mature fruit, precluding a firm identification (see 'Taxonomic treatment'). *Solanum pimpinellifolium* has been collected more recently in 2000 on Santa Cruz (*S. Darwin* 103) and San Cristóbal (*S. Darwin* 278).

Rick & Bowman (1961) found that the endemic tomatoes had severe seed dormancy broken by passage through the gut of the Galápagos giant tortoise (*Geochelone elephantopus*). Fewer than 1% of untreated seeds germinated (Rick & Bowman, 1961). However, populations of the endemic tomatoes occur in many areas within the archipelago that either no longer have, or possibly never had, resident populations of giant tortoises (Bartolomé, Sombrero Chino, Corona del Diablo and Darwin). The endemic tomatoes are known to be early colonizers of recent lava flows (Fosberg, 1987). Dispersal of seeds in salt water seems unlikely because exposure of seeds of the endemic tomatoes to even 20% salt water was shown to reduce seed viability (Kurth *et al.*, 1986). Rick & Bowman (1961) suggested that mockingbirds (*Nesomimus parvulus parvulus*), iguanas or feral goats were also potential seed dispersers of the endemic tomatoes. Dispersal mode and germination promoters of the Galápagos tomatoes in the wild have yet to be determined. Preliminary investigations (*S. Darwin*, unpubl. obs.) suggest that seed dormancy may be less strong than previously thought.

## Morphological analyses

### Plant specimens

In order to evaluate the morphological variation among species, we examined a large number of herbarium specimens from the Galápagos Islands (see Exsiccatae) and mainland South America, as well as plants that were grown from seed from wild and seed bank accessions and grown under greenhouse conditions. Valuable data about morphological variation among tomato populations and species in their natural habitats were obtained on Galápagos by SD. Tomatoes observed growing in the wild, greenhouse-grown plants and herbarium specimens were used to examine morphological variability and for the species descriptions but only greenhouse-grown plants were used for phenetic analysis. We have thereby examined a wider range of specimens than in any other previous treatment of these species.

Specimens examined were loaned by herbaria cited in the text, following the conventional abbreviations of Holmgren *et al.* (1990). The complete database of herbarium specimens of both wild and cultivated material examined is available from SK on request. Vouchers for all material grown are deposited at BM and CDS.

The comparative morphological study of 186 individuals from 84 accessions (on average two plants per accession) was performed using plants grown under heated greenhouse conditions at the Chelsea Physic Garden, London between November 2000 and March 2001. Plants were grown from both wild-collected seed accessions (SD in 2000) and from seed accessions kindly provided by Dr Charles Rick and Dr Roger Chetelat from the TGRC. The accessions included in this research represent much of the tomato diversity that exists throughout the archipelago.

Seed dormancy was broken using the method recommended by Rick & Borgnino ([http://tgrc.ucdavis.edu/seed\\_germ.htm](http://tgrc.ucdavis.edu/seed_germ.htm)). The dry seed weight was measured prior to treatment, and this character was included in the morphometric analyses. The seeds were soaked in 2.7% sodium hypochlorite for 30 minutes, then rinsed in fresh water and placed on moist blotting paper in numbered Petri dishes and stored in the dark. This treatment was repeated after 10 days to any un-germinated seeds. The seedlings were then transferred to 80 mm welled seed trays in John Innes loam (seven parts loam, three parts coir and two parts grit and bark). The trays were placed in a heated greenhouse. On average, seeds of *Solanum pimpinellifolium* germinated in approximately 11 days and those of the endemic species in approximately 20 days. As the experiments were conducted in the British winter, additional artificial lighting was provided between 10.00–12.00 h and between 16.00–18.00 h. Measurements were made on mature, reproductive plants.

### Characters used

For statistical and phenetic analyses, a total of 49 characters were assessed (45 quantitative and four qualitative). Characters were selected from Rick (1983), Peralta (2000) and from personal observations. The quantitative characters included 19 ratios that assessed shapes of different plant organs

(Table 2). Both original characters and ratios are presented in Table 2.

### Data analysis

The mean, range and standard deviation were estimated for each character within each putative species using SYSTAT (1999). ANOVA was performed (also in SYSTAT, 1999) on all continuous quantitative characters and all accessions to evaluate significant differences between taxa ( $P \leq 0.005$ ).

For the phenetic analysis we considered that the operational taxonomic unit (OTU) was the 'locality group' presented in Table 3. The 22 locality groups are based on the accession passport in the TGRC seed bank and from the collection notes made by SD in the Galápagos. Where the localities of the TGRC and the wild collections overlap they are considered as the same locality group (Table 3). Some locality groups are represented by only a single accession because many Galápagos populations are small, and can consist of only a single plant. We considered that the OTUs represented natural groups, for the clarity of the interpretation an average was therefore calculated to represent each OTU.

Cluster analyses were produced by NTSYS-pc<sup>R</sup> version 2.0 (Rohlf, 1992) using 33 characters, 23 continuous quantitative characters including 12 ratios, six discontinuous quantitative characters and three binary and one multistate qualitative character. The mean of each character was used for the phenetic analyses, and for that reason only the four qualitative characters can be assumed to be linear and thus treated as quantitative data (Abbott *et al.*, 1985). Averages for each character were standardized (STAND) and similarity matrices were generated, using average taxonomic distance (DIST), Manhattan distance (MANHAT) and Euclidean distance (EUCLID). Clustering was performed using the unweighted pair-group method (UPGMA) in SAHN. Cophenetic correlation coefficients (COPH and MXCOMP) were used to measure distortion between the similarity matrices and the resultant three phenograms (Rohlf & Sokal, 1981; Sokal, 1986). Principal component analyses (PCA) were performed on standardized data also using NTSYS. PCA makes no assumptions about group membership of OTUs under analysis, and effectively portrays the variation present in the data.

### Results and discussion

The phenetic analyses based on morphological characters support the circumscription of four distinct species of tomatoes currently occurring in the Galápagos Islands: *Solanum cheesmaniae* and *S. galapagense* (endemic) and *S. pimpinellifolium* and *S. lycopersicum* (introduced).

The ANOVA test showed significant differences among 30 characters or character ratios scored for all taxa (Table 2). For *Solanum galapagense*, leaf characters were found to be most distinctive and most strongly statistically supported (Table 4). Leaf structure in *S. galapagense* is more complex than in any other tomato species; the presence of more primary, secondary and interjected leaflets differentiate it from the other three species. *Solanum galapagense* usually also has tertiary leaflets and occasionally quaternary lobing

(very occasionally to leaflets), and this level of leaf division has not been observed in herbarium or cultivated accessions of the other three taxa during this research. Flower characters were significantly different for *S. pimpinellifolium* which has longer, more lanceolate corolla lobes than the other species.

Similar dendrograms were produced by DIST (Fig. 3A), EUCLID and MANHAT coefficients, and the OTUs clustered in four groups that correspond to the four previously recognized tomato entities from in the Galápagos, which we here recognize at the specific level. The cophenetic correlation is 0.77 when the first two coefficients were used, and 0.78 for the third. These values are good fits (almost good fits *sensu* Rohlf, 1992) to the cluster analysis.

Principal component analysis showed a similar relationship among OTUs as did the cluster analysis (Fig. 3B). The three principal components explained almost 70% of the variation found in the data set (first 37.6%, second 19.4% and third 11%). A further PCA performed in a subset of leaf characters (not illustrated) showed only plants of *S. galapagense* as distinct from the other taxa.

*Solanum galapagense* and *S. cheesmaniae* can readily be differentiated from *S. pimpinellifolium* and *S. lycopersicum* on fruit and seed characters and *S. pimpinellifolium* can be separated from the other three species by flower shape. *Solanum galapagense*, as has been recognized by most others studying Galápagos tomatoes (Fig. 2), is a markedly distinct taxon, which we recognize here at the specific level. The explicit morphological analyses on wild and cultivated plants, and complementary studies performed on herbarium specimens were very useful to show the relationships among taxa and to support our taxonomic treatment.

Studies of allozyme diversity in the Galápagos tomatoes support our species circumscription, revealing unique fixed allelic differences in several enzyme systems, particularly in *Solanum galapagense*. However, no fixed allelic differences between the different morphs within *S. cheesmaniae* were detected (Darwin *et al.*, in prep).

The origin of the Galápagos tomatoes remains unresolved. Phylogenetic analyses using DNA sequences of the nuclear gene *waxy* (GBSSI: granule-bound starch synthase), show that these four species discussed here are extremely closely related, suggesting recent origins and rapid morphological differentiation (Peralta & Spooner, 2001). Rick (1963) proposed that the closest relatives to the Galápagos tomatoes were *Solanum pimpinellifolium* and *S. habrochaites* S. Knapp & D.M. Spooner (as *Lycopersicon hirsutum* Dunal). Allozyme electrophoresis (Rick & Fobes, 1975) suggested that the populations of *S. pimpinellifolium* most closely related to the Galápagos tomatoes were from coastal Perú and that the most similar morphologically were populations from the region of Motupe-Olmos in the northern Peruvian department of Lambayeque (c. 6°S latitude). The Humboldt Current flows from here to the Galápagos at certain times of year giving support to this suggestion (Rick & Fobes, 1975).

Observations of the distribution and cover of the two introduced tomatoes were made in the field on Santa Cruz and Isabela to enable a classification of their status as alien plants.

Characters	Descriptions
<b>Leaves</b>	
1. <b>Petiole length (mm)*</b>	
2. <b>Leaf length (mm)*</b>	
3. Leaf axis length (mm)*	
4. Length from widest to leaf apex (mm)*	
5. Leaf width (mm)*	
6. Terminal leaflet length (mm)	
7. <b>Number of primary leaflets</b>	
8. <b>Number of secondary leaflets</b>	
9. <b>Number of tertiary leaflets</b>	
10. <b>Number of interjected leaflets</b>	
11. <b>Leaf length/petiole length ratio*</b>	
12. Leaf length/leaf axis length ratio*	
13. <b>Leaf length/length from widest to leaf apex ratio*</b>	
14. <b>Leaf length/leaf width ratio*</b>	
15. <b>Leaf length/terminal leaflet length ratio*</b>	
16. Leaf axis length/petiole ratio*	
17. Leaf axis length/terminal leaflet length ratio*	
18. Length from widest to leaf apex/petiole ratio*	
19. Leaf width/leaf axis length ratio*	
20. <b>Leaf width/terminal leaflet length ratio*</b>	
21. <b>Terminal leaflet length/petiole ratio*</b>	
22. Terminal leaflet length/length from widest point to leaf apex ratio*	
<b>Inflorescence</b>	
23. Inflorescence axis length (mm)	
24. <b>Number of flowers per axis</b>	
25. <b>Number of branches</b>	
26. <b>Bract-like leaflets</b>	
27. <b>Bracteole-like leaflets</b>	
28. <b>Inflorescence axis length/number of flowers per axis ratio</b>	

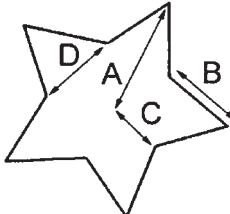

**Table 2** Characters measured for morphometric analysis. Characters used in the multivariate analysis are in bold, characters significantly different ( $P \leq 0.005$ ) using the ANOVA test are marked with an asterisk.

*Solanum lycopersicum* was found in rubbish dumps and by roadsides extending a maximum of about 20m away from human habitation. We would currently classify this species as a casual alien (*sensu* Richardson *et al.*, 2000). *Solanum pimpinellifolium* was also found in disturbed areas, rubbish dumps, roadsides and quarries, but it often occurs up to several km away from human habitation; for example along the roadside at Los Gemelos on Santa Cruz. It was also found at El Chato on Santa Cruz in an area seemingly undisturbed except for a tourist track and a population of giant tortoises. In this area the population of *S. pimpinellifolium* was so dense in places that it was virtually the only vascular plant present. We therefore classify *S. pimpinellifolium* preliminarily as an invasive plant (*sensu* Richardson *et al.*, 2000), and one which warrants further investigation to establish whether or not it is causing

a negative impact on native species. Invasive plants can have many negative effects on native biodiversity. Many important food crops hybridize with their wild relatives in areas of sympatry (Ellstrand *et al.*, 1999) and there is a real potential in Galápagos for these introduced tomatoes to threaten the genetic integrity of the endemic tomatoes through hybridization and introgression.

There seem to be no barriers to hybridization of the different species of tomatoes in Galápagos (also see below). In the field, variously exerted styles were found in individuals of all four species, enabling pollen from another flower to be received on the stigma. The endemic carpenter bee (*Xylocopa darwini*) was observed (S. C. Darwin, unpubl. obs.) visiting flowers of *Solanum cheesmaniae*, *S. galapagense* and *S. pimpinellifolium* (in allopatry). Rick & Fobes (1975) found



<b>Flowers</b>	
29. Length from centre of the corolla to apex of the corolla lobe (mm) <b>A*</b>	
30. Length of the corolla lobe from apex to the corolla lobe junction (mm) <b>B</b>	
31. Length from centre of the corolla to the corolla lobe junction (mm) <b>C*</b>	
32. Corolla lobe width (mm) <b>D*</b>	
33. Total anther length (mm) *	
34. Anther appendage length (mm) *	
35. Style length (mm) *	
36. Style exertion length (mm) *	
37. Pedicel length (mm)	
38. Pedicel articulation to axis length (mm)	
39. Sepal length (mm)*	
40. Sepal width (mm)	
41. Anthocyanin pigmentation on sepals	
42. Sepal angle on fruit	
43. Length from centre of the corolla to apex of the corolla lobe/length from centre of the corolla to the corolla lobe junction ratio*	 <b>appressed</b> <b>straight</b> <b>reflexed</b>
44. Length from centre of the corolla to apex of the corolla lobe/corolla lobe width ratio (A/C)*	
45. Length of the corolla lobe from apex to the corolla lobe junction/length from centre of the corolla to the corolla lobe junction ratio (A/D)*	
46. Length of the corolla lobe from apex to the corolla lobe junction/corolla lobe width ratio (B/C)*	
47. Total anther length/anther appendage length ratio (B/D)*	
48. Sepal length/sepal width ratio*	
49. Mean seed weight (mg)*	

**Table 2** Continued.

that there was ‘little or no’ insect activity and that the floral structure of the Galápagos tomatoes was adapted to automatic self-pollination (i.e. the styles were included within the staminal column). This is not consistent with our observations. In addition the discovery of sympatric populations of the endemic and the introduced species of tomatoes on Isabela highlight these concerns. The threat of hybridization between endemic and introduced tomatoes had already been suggested by A. Tye (in litt., 1999). In crossing experiments, Rick (1963) found that all four tomato species concerned here were fully intercompatible. Thus, hybridization and introgression could and might already be taking place between the four species.

## Species concepts

In previous taxonomic treatments of the tomatoes (publications of C.M. Rick, TGRC), species circumscription largely followed the biological species concept (i.e. species being groups of interbreeding populations that are unable to interbreed with other such groups; Briggs & Walters, 1997). Rick (1963) found no barriers to crossing between the endemic Galápagos tomatoes; in fact, most species of tomatoes experience some degree of interpopulational gene flow, especially self-compatible populations (see Rick, 1979). Rick (1971) also observed individual plants on both Isabela and Fernandina that he considered to be morphological intermediates between

Island and locality names	OTU	<i>che</i>	<i>gal</i>	<i>pim</i>	<i>lyc</i>
Santa Cruz	5				
Punta Carrion	5a	X+ (1)			
Between Cerro Colorado and Punta Carrion	5b	X+ (13)			
North of Cerro Colorado	5c	X+ (4)			
New basura and quarry	5d			X+ (3)	
Los Gemelos	5e			X+ (7)	
El Chato Tortoise Reserve	5f			X+ (11)	
Academy Bay	5h	X* (5)		X*+ (3)	
Bella Vista and roadside	5g			X+ (1)	
Isabela	2				
Cabo Tortuga	2a		X* (2)		
Tagus Cove	2b		X* (1)		
Volcán Alcedo	2c		X* (1)		
San Tomás and basura	2d	X* (2)			X+ (6)
Road from Villamil to San Tomás	2e		X*+ (3)		
San Cristóbal	7				
Puerto Baquerizo Moreno	7a				X+ (2)
Santiago	3				
Bartolomé	3a		X*+ (11)		
Fernandina	1				
North side, low elevations	1a	X* (1)			
'Low elevations'	1b	X* (1)			
Volcán	1c	X* (3)			
Pinzón	4a		X* (1)		
Corona del Diablo	6a		X* (2)		

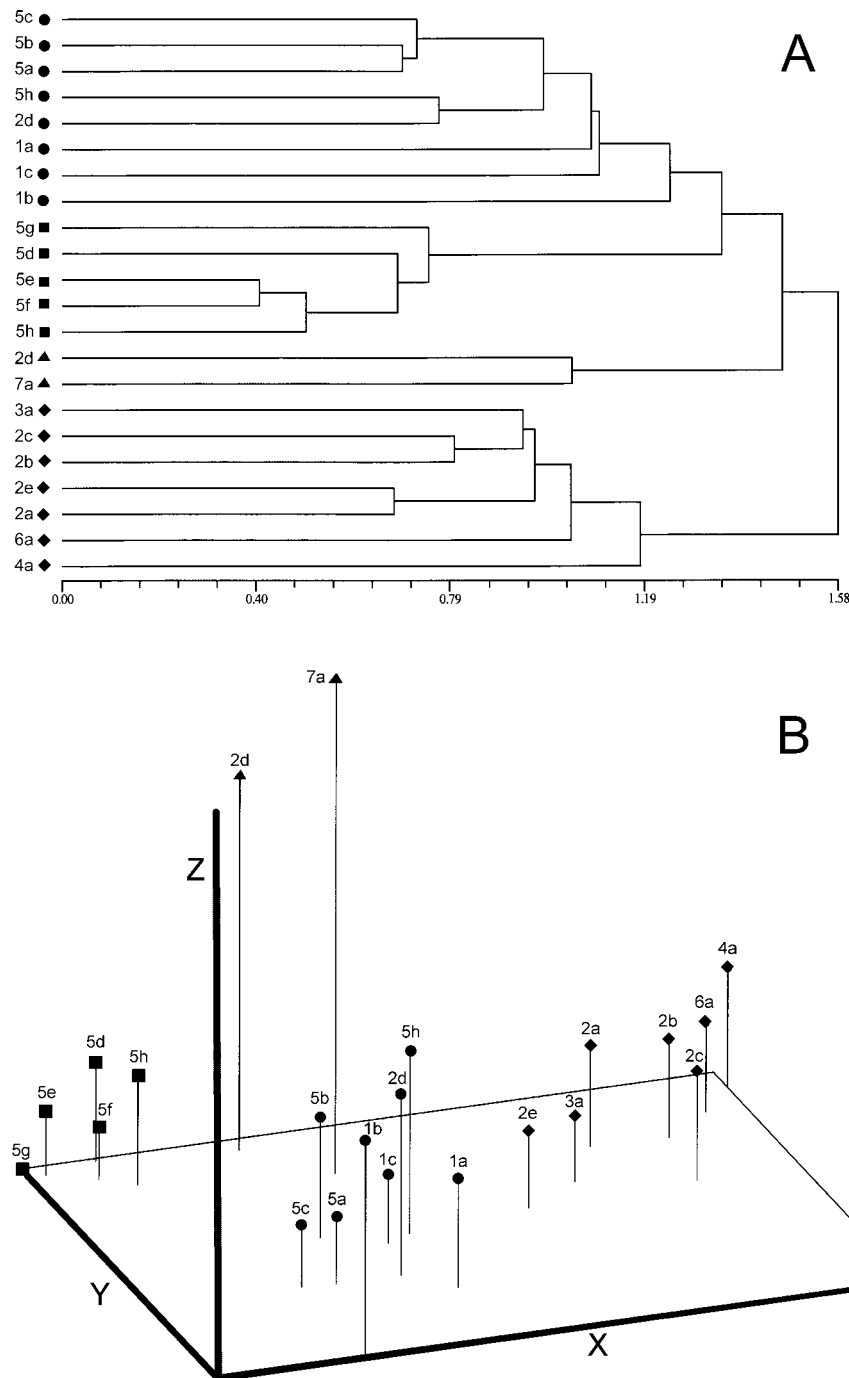
**Table 3** Locality groups as OTUs for the accessions used in cluster and principal component analyses. A total of 186 plants were measured representing 84 accessions. \* denotes TGRC collection, + denotes wild collection (SD 2000), numbers in parentheses denote number of accessions used. *che* – *S. cheesmaniae*, *gal* – *S. galapagense*, *pim* – *S. pimpinellifolium* and *lyc* – *S. lycopersicum*.

Character number	Character description	<i>che</i>	<i>gal</i>	<i>pim</i>	<i>lyc</i>
12	Leaf length:leaf axis length ratio	1.808 a	1.455 b	2.064 c	2.012 ac
13	Leaf length:length from widest to leaf apex ratio	1.317 a	1.495 b	1.312 a	1.359 a
14	Leaf length:leaf width ratio	1.199 a	1.292 b	1.121 a	1.179 a
15	Leaf length:terminal leaflet length ratio	2.422 a	3.495 b	2.031 a	2.098 a
16	Leaf axis length:petiole length ratio	2.231 a	3.764 b	2.725 a	2.338 a
17	Leaf axis length:terminal leaflet length ratio	1.422 a	2.495 b	1.031 a	1.098 a
18	Length from widest to leaf apex ratio:petiole length ratio	2.929 a	3.666 b	4.268 b	3.464 a
19	Leaf width:leaf axis length ratio	1.350 a	1.000 b	1.586 c	1.533 a
20	Leaf width:terminal leaflet length ratio	2.007 a	2.749 b	1.827 a	1.819 a
21	Terminal leaflet length:petiole length ratio	1.668 a	1.618 a	2.891 b	2.209 b
22	Terminal leaflet:length from widest to leaf apex ratio	0.565 a	0.447 b	0.661 a	0.673 a

**Table 4** Means of leaf characters ratios that were found to be statistically significantly different ( $P \leq 0.005$ ) between the taxa, and are indicated with a unique letter. The boxed regions indicate the characters that statistically support *Solanum galapagense* (see Table 2 for character descriptions). *che* – *S. cheesmaniae*, *gal* – *S. galapagense*, *pim* – *S. pimpinellifolium*, *lyc* – *S. lycopersicum*.

*Solanum cheesmaniae* and *S. galapagense* (also see discussion of *S. cheesmaniae*, p. 41). He concluded that the two endemic Galápagos tomato taxa should be recognized as two forms of one species due to their ability to interbreed (Rick, 1971).

In contrast, our views on species delimitation basically follow what is known as the 'morphological cluster' species concept (Mallet, 1995): i.e. 'assemblages of individuals with morphological features in common and separate from other such assemblages by correlated morphological discontinuities



**Figure 3** Results of the morphological analyses. A. Average taxonomic distance coefficient dendrogram. B. Principal component analysis ( $x = 1^\circ$ ,  $y = 2^\circ$ ,  $z = 3^\circ$ ): *Solanum cheesmaniae*, circles; *Solanum galapagense*, rhomboids; *Solanum pimpinellifolium*, squares; *Solanum lycopersicum*, triangles. See text for details.

in a number of features' (Davis & Heywood, 1963). Biological (Mayr, 1982), phylogenetic (Cracraft, 1989) and the host of other finely defined species concepts (see Mallet, 1995) are almost impossible to apply in practice when dealing with complex, highly variable groups and are therefore of little utility in a practical sense. It is important however to clearly state the criteria for the delimitation of species, rather than dogmatically follow particular ideological lines (see Luckow, 1995; Davis, 1997). We have been conservative in our approach, recognizing as distinct entities those population systems (sets

of specimens) that differ in several morphological characteristics or in combinations of these characteristics. We have not formally recognized subspecific categories, although we have described and documented the variation where it occurs. *Solanum cheesmaniae* includes two marked variants, which we here describe as morphs of a variable entity. The patterns of variation and the presence of intermediates between these two entities are such that no reliable units can be extracted, and we prefer to not encumber the literature with excess names at present. We have described the variation, realizing that other

taxonomists may wish to interpret it differently; future study of this variation is underway (see p. 41).

## Taxonomic treatment

**Solanum** section **Lycopersicon** (Mill.) Wettst. in Engl. & Prantl, *Natürlichen Pflanzenfamilien* IV, 3b (65): 24 (1891).

*Lycopersicon* Mill., *Gard. Dict.* ed. 4, abr. (1754). Lectotype species (designated by D'Arcy, 1972): *Lycopersicon esculentum* Mill. (1768). (= *Solanum lycopersicum* L.)

*Amatula* Medik., *Malvenfam.* 106 (1787). Type: *Amatula flava* Medik. (= *Solanum lycopersicum* L.).

**Solanum** section *Lycopersicon* (Tourn.) Bitter, *Botanische Jahrbücher* 54: 500 (1917). Lectotype species (designated by D'Arcy, 1972): *Lycopersicon esculentum* Mill. (1768). (= *Solanum lycopersicum* L.)

**Solanum** subgenus *Lycopersicon* (Tourn.) Seithe, *Botanische Jahrbücher* 81: 204 (1962). Lectotype species (designated by D'Arcy, 1972): *Lycopersicon esculentum* Mill. (1768). (= *Solanum lycopersicum* L.)

Perennial, biennial or annual herbs; branches usually sprawling or vining, robust to slender. Stems glabrous to variably pubescent, the trichomes always simple and usually uniseriate. Sympodial units di- or trifoliate (in Galápagos trifoliate only). Leaves interrupted imparipinnate, sometime with secondary and tertiary leaflet formation; estipulate, but occasionally with well-developed pseudostipules; leaflets variously lobed, the margins entire to coarsely dentate; petiole usually shorter than the leaf blade. Inflorescences simple to several 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, the lobes deltate to lanceolate; stamens 5, usually coherent in a tube with or without an apical sterile tip; anthers with variously developed papillae 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 coloured red, yellow or orange, usually 2-locular, but in cultivated species variously multi-locular; calyx in fruit accrescent, the lobes shorter than or longer than the mature fruit; seeds lenticular, appearing densely hairy due to the elongate testa cell walls.

Species descriptions of the introduced species of tomatoes are here taken only from Galápagos collected specimens. Synonymy for these species is also confined to that used in previous treatments of tomatoes in the Galápagos; the synonymy of these cultivated species is extremely complex and has been made more so by the description of many garden-generated hybrids and a superfluity of *nomina nuda*. Complete synonymy of these species will be presented in Peralta *et al.* (in prep.)

Leaves of *Solanum* vary from simple to deeply to completely compoundly dissected. The leaves of tomatoes and their close relatives the potatoes have often been characterized

as pinnate, but the presence of a minute wing of leaf tissue along the rachis connecting all dissections makes this distinction difficult to maintain in practice. We prefer to characterize the leaves of tomatoes as compoundly dissected following prevalent terminology in the current leaf development literature (Bharathan *et al.*, 2002; Gleissberg, 2002; Tsiantis *et al.*, 2002; but see Kessler *et al.*, 2001), although the species occurring in the Galápagos have nearly completely divided leaves that appear compoundly pinnate. We have followed common practice in using the term leaflet to mean a complete petiole division of the blade. In the species descriptions leaf length excludes the petiole and interjected leaflets were defined as all leaflets along the rachis that are under half the length of the primary leaflets. Flower measurements were taken from live and dried plants, and seed weights represent dry seed weight. Terminology used in the descriptions follows that in Table 2. Detailed distributions for the introduced species are given for the Galápagos only, as both are widely cultivated all over the world.

Herbaria are cited using the acronyms in *Index herbariorum* (Holmgren *et al.*, 1990). Types seen are indicated by an exclamation mark (!), and we have seen all cited specimens and those in the exsiccatae unless otherwise indicated. Specimens examined are cited using the current accepted names for the islands of the Galápagos (Table 1).

### Key to solanums in the Galápagos (the list of *Solanum* species currently occurring in the Galápagos Islands was obtained from the CDRS working database 2002)

- 1a. Plant with spines and stellate trichomes on at least some parts . . . . . 2
- 1b. Plants without spines, if stellate trichomes present, then the inflorescence many-branched . . . . . 4
- 2a. Leaves markedly bicoloured, white beneath; flowers white . . . . . **S. marginatum** L.f. (probably present, no herbarium specimen)
- 2b. Leaves not markedly bicoloured; flowers white or purple . . . . . 3
- 3a. Leaves large and repand, densely pubescent and the trichomes flushed with purple; fruit orange with green flesh when ripe; flowers white . . . . . **S. quitoense** Lam. (escaped)
- 3b. Leaves not repand, the trichomes white or translucent; fruit purple or white when ripe, the flesh cream; flowers purple . . . . . **S. melongena** L. (cultivated)
- 4a. Leaves deeply pinnatifid and divided, with interjected leaflets . . . . . 5
- 4b. Leaves simple, if pinnatifid, without interjected leaflets . . . . . 6
- 5a. Flowers white or purple; plants with underground tubers; ripe fruits green . . . . . **S. tuberosum** L. (escaped)
- 5b. Flowers yellow; plants without underground tubers; fruit brightly coloured red, orange or yellow when ripe . . . . . **Solanum** section **Lycopersicon** (see key below)
- 6a. Shrubs or small trees; inflorescences usually branched; flowers greater than 1 cm in diameter . . . . . 7

- 6b. Herbs; inflorescences usually simple; flowers smaller than 1 cm in diameter . . . . . 8
- 7a. Leaves densely pubescent with stellate trichomes, the plant appearing woolly; leaf base acute; fruit c. 1 cm in diameter, globose, yellowish green when ripe . . . . .  
. . . . . **S. erianthum** D. Don (naturalized)
- 7b. Leaves glabrous; leaf base cordate; fruit larger than 1 cm in diameter, ellipsoid, red, orangish red or pinkish when ripe . . . . . **S. betaceum** Cav. (cultivated)
- 8a. Leaves simple, the margins sinuate, entire or dentate; inflorescence umbelliform; plant glabrous or with simple non-glandular trichomes . . . . . **S. americanum** L.
- 8b. Leaves shallowly pinnatifid; inflorescence cymose; plant sticky with glandular trichomes . . . . .  
. . . . . **S. edmonstonei** Hook.f. (endemic)

## Keys to the tomatoes in the Galápagos

### Artificial dichotomous key

- 1a. Leaflet margins lobed . . . . . 2
- 1b. Leaflet margins more or less entire . . . . . 5
- 2a. Tertiary lobing present, often tertiary leaflets with quaternary lobing; secondary leaflets per leaf more than five (usually more than ten); sepal length often exceeding fruit diameter when ripe; plants often densely hairy with glandular trichomes; plants often found on coastal lava . . . . . 2. **S. galapagense**
- 2b. Tertiary lobing absent; secondary leaflets, if present, fewer than 15 per leaf; sepal length not exceeding fruit diameter when ripe; plants found in a variety of habitats . . . . . 3
- 3a. Ripe fruit yellow to deep orange, sometimes hairy; staminal column 4–7 mm long; bract-like leaves sometimes present in inflorescence; inflorescence sometimes branched; sepals usually appressed on to fruit; plants sometimes found on coastal lava . . . . . 1. **S. cheesmaniae**
- 3b. Ripe fruit bright red, glabrous; staminal column 6–9 mm long; bract-like leaves not present in inflorescence; inflorescence not branched; sepals on fruit reflexed; plants of disturbed areas, not from coastal lava beds . . . . . 4
- 4a. Leaflet margins shallowly lobed mainly towards the base; foliage when crushed with citrus odour; fruit less than 20 mm in diameter when ripe; corolla deeply stellate, the lobes divided almost to the base; stems slender with occasional long trichomes up to 2.2 mm . . . . . 4. **S. pimpinellifolium**
- 4b. Leaflet margins deeply lobed along whole margin; foliage when crushed without citrus odour; ripe fruit over 20 mm in diameter; corolla shallowly stellate, the lobes divided 1/3 to 1/2 way to base; stems robust with occasional long trichomes up to 3 mm . . . . . 3. **S. lycopersicum**
- 5a. Plants found on coastal lava at 0–5 m elevation; leaves fleshy and sticky to touch . . . . . 1. **S. cheesmaniae**
- 5b. Plants found above 5 m elevation; leaves membranous or fleshy, not markedly sticky to the touch . . . . . 6
- 6a. Ripe fruit yellow to deep orange, sometimes pubescent; sepals partially fused at base, free to only 2/3 of the way to the base, appressed on to fruit (not always apparent

- in herbarium specimens); seed weight 0.4–0.8 mg; staminal column 4–7 mm long; bract-like leaflets sometimes present in inflorescence . . . . . 1. **S. cheesmaniae**
- 6b. Ripe fruit bright red, glabrous; sepals stellate, free almost to the base, markedly reflexed along their entire length in fruit; seed weight greater than 0.8 mg; staminal column 6–8 mm long; bract-like leaflets not present in inflorescence . . . . . 4. **S. pimpinellifolium**

### Synoptic key

#### Habitat and habit

- Plants found within 5 m of the high tide mark: che, gal
- Plants found in the highlands: che, pim, lyc, gal
- Stems with dense short pubescence: che, gal
- Stems with sparse elongate uniseriate, multicellular trichomes 2–3 mm: pim, lyc
- Stems more or less glabrous: che, pim
- Foliage with strong citrus odour: che, gal, pim

#### Leaves

- Leaflets margins entire: che, pim
- Leaves fleshy: che, gal
- Leaves sticky: che, gal
- Leaves membranous: che ('Academy Bay' morph), pim, lyc
- Leaves with tertiary lobes/leaflets: gal
- Leaves with 10 or more secondary lobes/leaflets: gal

#### Flowers

- Corolla lobes narrowly lanceolate, narrower than 1/3 the length of lobe from tip to flower centre, the corolla stellate: pim
- Corolla lobes deltate, wider than 1/3 the length of lobe from tip to flower centre, the corolla more pentagonal: che, gal, lyc

#### Fruit

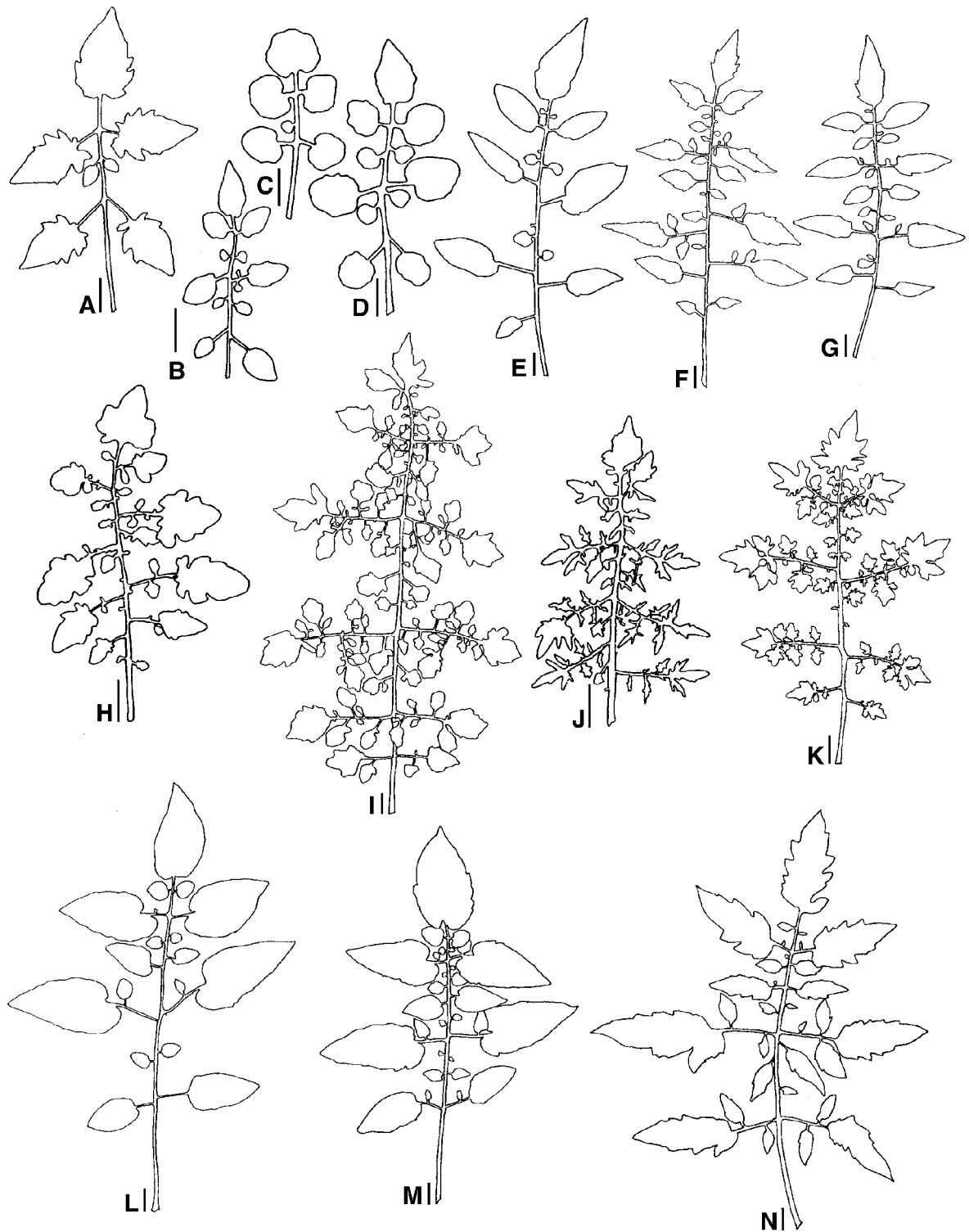
- Fruit yellow when ripe: che
- Fruit orange when ripe: che, gal
- Fruit bright red when ripe: pim, lyc
- Sepal lobes strongly reflexed in fruit: pim, lyc
- Sepal lobes appressed on to fruit (not always apparent in herbarium specimens): che, gal
- Sepals in fruit longer than berry: gal

1. **Solanum cheesmaniae** (L. Riley) Fosberg, *Phytologia* **62**: 181 (1987). *Lycopersicon cheesmaniae* L. Riley (as *cheesmanii*), *Kew Bull.* **1925**: 227 (1925). Type: Ecuador. Galápagos. Santa Cruz: 'Indefatigable, among lava rock in grassy patches', 28 July 1924, *Cheesman in Riley* 403 (K!-holotype).

*Lycopersicon peruvianum* (L.) Mill. var. *parviflorum* Hook.f., *Trans. Linn. Soc. London* **20**: 202 (1847) ('1851'). as '*L. peruanum*' Type: Ecuador. Galápagos. San Cristóbal: 'Chatham Island', end of September 1835, *Darwin s.n.* (K!-holotype).

Figs 4A–G; 6A, B.

**Perennial** herbs, undergoing secondary growth at the base; branches somewhat robust to slender and erect to vining,



**Figure 4** Leaf morphology variation in the Galápagos tomatoes. Scale bars all equal 1 cm. (h) – herbarium specimen, (g) – greenhouse grown plant. A–D. *Solanum cheesmaniae*, typical morph, A – North coast of Santa Cruz, *S. Darwin et al.* 236.1 (g); B – North coast of Santa Cruz, *S. Darwin et al.* 236 (h); C – North coast of Baltra, *S. Darwin et al.* 202, immature leaf (h); D – North coast of Baltra, *S. Darwin et al.* 202, mature leaf (h). E–G. *Solanum cheesmaniae*, ‘Academy Bay’ morph, E – El Lagoon del Manzanillo, *S. Darwin & Rosero* 366 (h); F – Academy Bay, Santa Cruz, *Howell* 9096 (h); G – Academy Bay, Santa Cruz, *Bentley* 342 (h). H–K. *Solanum galapagense*, H – Bartolomé, *S. Darwin & Schultz* 183.3 (g); I – El Lagoon del Manzanillo, *S. Darwin & Rosero* 364 (h); J – Rabida, *Day* 287 (g); K – Pinzón TGRC LA-0532 (g). L–M. *Solanum pimpinellifolium*, L – El Chato, Santa Cruz, *S. Darwin et al.* 403 (h); M – Los Gemelos, Santa Cruz, *S. Darwin et al.* 196 (h). N – *Solanum lycopersicum*, Villamil, Isabela, *S. Darwin* 289 (h).

extending up to 2 m from centre. **Stem** erect initially, later procumbent or decumbent, variously pubescent, coastal populations more glandular; trichomes of several types, the longer *c.* 1 mm, simple, uniseriate, patent, amongst uniseriate, 1–2-celled slender trichomes and shorter glandular, simple, 1–2-cellular trichomes, the glands unicellular or multicellular, the plant with a strong citrus-like scent. **Sympodial units** trifoliate. **Internodes** 1.5–5(–8) cm. **Leaves** interrupted imparipinnate, 3.5–14 × 1.5–8.5 cm, sparsely pubescent to glabrescent ('Academy Bay') adaxially, densely pubescent with uniseriate uni- or multicellular downy trichomes abaxially, lime green to dark green; primary leaflets 2–3(–4) pairs, opposite, subopposite or alternate, 0.8–6 × 0.4–2 cm, ovate or orbicular, the base asymmetric, rounded to cordate, the margins entire to irregularly lobed; terminal primary leaflet usually larger than the laterals, about half as long as the leaf rachis; secondary leaflets present mainly basiscopically, 0–5(–8) per leaf; tertiary leaflets absent; interjected leaflets usually present, 4–8(–14), opposite, subopposite or alternate, sessile to short-petiolate; rachis 1.0–9.5 cm. **Petiole** 0.5–30(–35) cm, sparsely pubescent; pseudostipules absent. **Inflorescences** simple or sometimes 2–3-branched, to 7.5 cm, to 11-flowered, bract and bracteole-like leaflets sometimes present on the axis; peduncle 1–3.3 cm; rachis pubescent like the stems; pedicels 0.6–2 cm, articulate in the upper 1/3, occasionally without an articulation (from Academy Bay, see Rick, 1967). **Calyx** *c.* 0.6–1.2 cm in diameter, pubescent with long and short simple uniseriate trichomes; tube 0.5–1 mm; lobes 3–5 × *c.* 1 mm, linear, the apex acute. **Corolla** 1.8–2.8 cm in diameter, yellow; tube to 0.2 cm long; lobes 0.9–1.4 × 0.25–0.4 cm, narrowly deltate, reflexed at anthesis. **Staminal column** 4–7 mm, narrowly cone-shaped; filaments 1–2(–2.5) mm; anthers 3–5 mm, the sterile tip 1–3 mm. **Ovary** conical, minutely glandular villous; style 3–6(–8) mm, usually included in the staminal column, but exerted to 1(–2) mm in some specimens; stigma minute. **Fruits** 0.6–1.4(–2.5) cm in diameter, globose and 2-locular, glabrescent and becoming yellow or orange at maturity; calyx lobes in fruit accrescent, to 0.45–1.3 × 0.5–0.3 cm, tightly appressed or spreading. **Seeds** (5–)20(–45) per fruit, *c.* 1.5–2.2 × 1 mm, with a pronounced beak; testa appearing hairy over entire surface with the elongate lateral cell walls; dry seed weight *c.* 0.6 mg.

**DISTRIBUTION.** Endemic to the Galápagos Islands, found both on coastal lava 1 m above sea level within the range of sea spray and at higher altitudes (Fig. 1).

**COMMON NAMES.** Tomatillo, Galápagos tomato.

**USES.** Putatively edible, although rather sharp to taste (SD, pers. obs.). Germplasm has been used to enhance cultivated tomatoes for the joint-less pedicel character found in some plants in Academy Bay, Santa Cruz (Rick, 1967).

**REPRESENTATIVE SPECIMENS EXAMINED.** (\* indicates specimens of the 'Academy Bay' morph.)

**ECUADOR. Galápagos. Baltra:** N. coast, coastal lava, 3 m, 00°24'86''S, 90°17'23''W, 3 July 2000, *Darwin, S. et al.* 203 (BM, CDS); N. coast, coastal lava, 3 m, 00°24'86''S, 90°17'23''W, 3 July 2000, *Darwin, S. et al.* 205 (BM, CDS); N.

coast, coastal lava, 3 m, 00°24'86''S, 90°17'23''W, 3 July 2000, *Darwin, S. et al.* 209 (QCA, QCNE). **Española:** sin. loc., 8–20 July 1983, *Touc s.n.* (CDS). **Fernandina:** alluvial fan near W. coast, periodically flooded *Bursera* forest, 25 m, 19 September 1974, *Adersen & Adersen 903\** (C, CDS); SE slope, approx. 2.5–3.5 km below the rim of the caldera, 740 m, 22 January 1972, *Hamann & Hamann 213\** (C); en la cumbre al oeste de la caldera, en pequeñas manchas densas dentro del 'bosque' de *Scalesia*, 1300 m, 00°20'S, 91°31'W, 7 December 1984, *Huttel 495\** (CDS, QCA). **Isabela:** Volcán Darwin, Isote Crater Beagle 2, entre las rocas, 11 June 1994, *Aldaz 350* (CDS); sin. loc., 1853, *Andersson s.n.* (S); Volcán Alcedo, from sea level nearly to the top, 18 August 1963, *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, 16 m, 00°55'85''S, 90°58'68''W, 25 July 2000, *Darwin, S. & Rosero 365\** (BM, CDS, QCNE); 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, 16 m, 00°55'85''S, 90°58'68''W, 25 July 2000, *Darwin, S. & Rosero 366\** (BM, CDS, QCNE); Caleta Black, sea shore, 0–10 m, 3 June 1959, *Eliasson & Eliasson 2207* (S); Volcán Alcedo, W. slope of caldera, 500 m, 14 July 1972, *Hamann & Hamann 1801\** (C); *Harling 5288* (S); Volcán Wolf, E. side, 1170 m, 21 May 1967, Iguana Cove, 21 May 1932, *Howell 9427\** (CAS); 5 miles N. of Webb Cove, 22 May 1932, *Howell 9447* (CAS); 3 miles S. of the equator, E. side of island, 30 May 1932, *Howell 9617* (CAS); Volcán Wolf, 11 April 1986, *Lawesson 3017\** (CDS); Volcán Darwin, 13 April 1986, *Lawesson 3080\** (CDS); Iguana Cove, abundant on side of cliff above the cove, 20 March 1905–1906, *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 'union de dos caminos'), rocky, dry thorn-scrub, *Prosopis juliflora*, *Croton scouleri*, 18 April 1975, *Clark & Clark 344* (WIS). **San Cristóbal:** sin. loc., end September 1835, *Darwin, C. s.n.* (K); sin. loc., end September 1835, *Darwin, C. s.n.\** (CGE); sin. loc., end September 1835, *Darwin, C. s.n.* (CGE); champ de laves récentes au NE de Cerro Brujo, préférence pour laves acoriacées, 75 m, 6 December 1988, *Huttel 1597* (CDS, QCA); Sappho Cove, occasional on recent lava, 18 February 1905–1906, *Stewart 3374* (CAS, GH). **Santa Cruz:** Charles Darwin Research Station, along path running between town station road and tortoise-rearing house, in sunny area, 2 May 1983, *Bentley 342\** (CDS, K, QCA, US); Academy Bay, collected on edge of 'barranco' at Puerto Ayora, 20 m, 13 April 1953, *Bowman 119\** (CAS, UC); 1.5 miles N. Academy Bay, 20 m, 20 April 1953, *Bowman 120\** (CAS, UC); 1 km NW of Cerro Colorado, coastal lava, 20 m, 00°33'95''S, 90°10'54''W, 5 July 2000, *Darwin, S. et al.* 214 (BM, CDS); *c.* 5 km NW of Cerro Colorado, coastal lava, < 15 m, 00°32'63''S, 90°12'50''W, 5 July 2000, *Darwin, S. et al.* 236 (BM); *c.* 5 km NW of Cerro Colorado, coastal lava, < 15 m, 00°32'63''S, 90°12'50''W, 5 July 2000, *Darwin, S. et al.* 239 (BM); Punta Carrion, coastal lava, 4 m, 00°28'91''S, 90°15'06''W, 5 July 2000, *Darwin, S. et al.* 272 (BM, CDS); Academy Bay, 0–10 m, 4 October 1966,

*Eliasson & Eliasson 201\** (MO, S); N. slope, c. 100 m from road between Santa Rosa and canal, dry seasonal deciduous steppe forest, 130 m, 17 March 1981, *Hamann & Seberg 1771* (C); Academy Bay, 4 May 1932, *Howell 9096\** (CAS); Academy Bay, semi-open habitat, lava (Halboffen, lavagelaende), 10 m, 25 June 1932, *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, without date, *Huttel 2735* (CDS); N. side, common among rocks, 75 m, 24 November 1905–1906, *Stewart 3376* (CAS, GH). **Santa Fé:** stony barranca, 100 m, 16–17 June 1959, *Harling 5371* (S); rocky shore, 15 m, 16–17 June 1959, *Harling 5476* (S); W. part of island, highest plateau, 280 m, 16 February 1972, *Hamann & Hamann 444* (C); sin. loc., 14 September 1973, *de Vries 1227* (CDS).

In the morphological analyses, plants of *Solanum cheesmaniae* form a cohesive group despite considerable variation, and we identify two extreme morphs showing differences in leaflet shape, margin, leaf division and pubescence (Fig. 4A–G). The type specimen represents the ‘typical’ morph, and has very small leaves and leaflets, with entire to regularly dentate margins (Fig. 4A–D) and dense pubescence in all parts of the plant with short glandular trichomes on the adaxial surface of the leaflet. These characters are consistently present on specimens collected from the north coast of Santa Cruz and Baltra, San Cristóbal, Santa Fé, Pinzón and coastal Isabela. The other extreme morph in *S. cheesmaniae*, which we here call the ‘Academy Bay’ morph, has leaves up to three times the size of the ‘typical’ morph, irregularly dentate leaflet margins (Fig. 4F–G), and the plants are altogether less pubescent; the lack of trichomes 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 with the two extremes (Fig. 4E). These plants have a velvety pubescence due to short trichomes of similar length; this pubescence is more apparent on the abaxial face of the leaflets. These intermediates have been collected from 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 (the areas where there is 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 Darwin (Fig. 2). We found that one of these specimens documented as having been collected from San Cristóbal, and identify by Hooker as ‘*L. pimpinellifolium*’, belongs to the ‘Academy Bay’ morph (Fig. 2). Some of the specimens cited by Müller (1940), as ‘*Lycopersicon pimpinellifolium*’ are also identified here as *S. cheesmaniae* ‘Academy Bay’ morph. Rick (1956, 1963) referred to three different tomatoes in Galápagos including a Galápagos ‘*L. pimpinellifolium* type’ (TGRC accession number LA166), which had orange fruit but flowers with corolla divided two thirds the way to the base (for

illustration see Rick, 1956). In his later work, Rick (1971) re-classified the Galápagos accessions of ‘*L. pimpinellifolium*’ with orange fruits under ‘*L. cheesmanii*’. He considered the red-fruited tomatoes in Galápagos to be introduced species (Rick in litt., 1998). The leaf morphology of some specimens of *S. cheesmaniae* ‘Academy Bay’ morph from Isabela is similar to individuals of *S. pimpinellifolium* found in Galápagos and on mainland South America (coastal Perú and Ecuador).

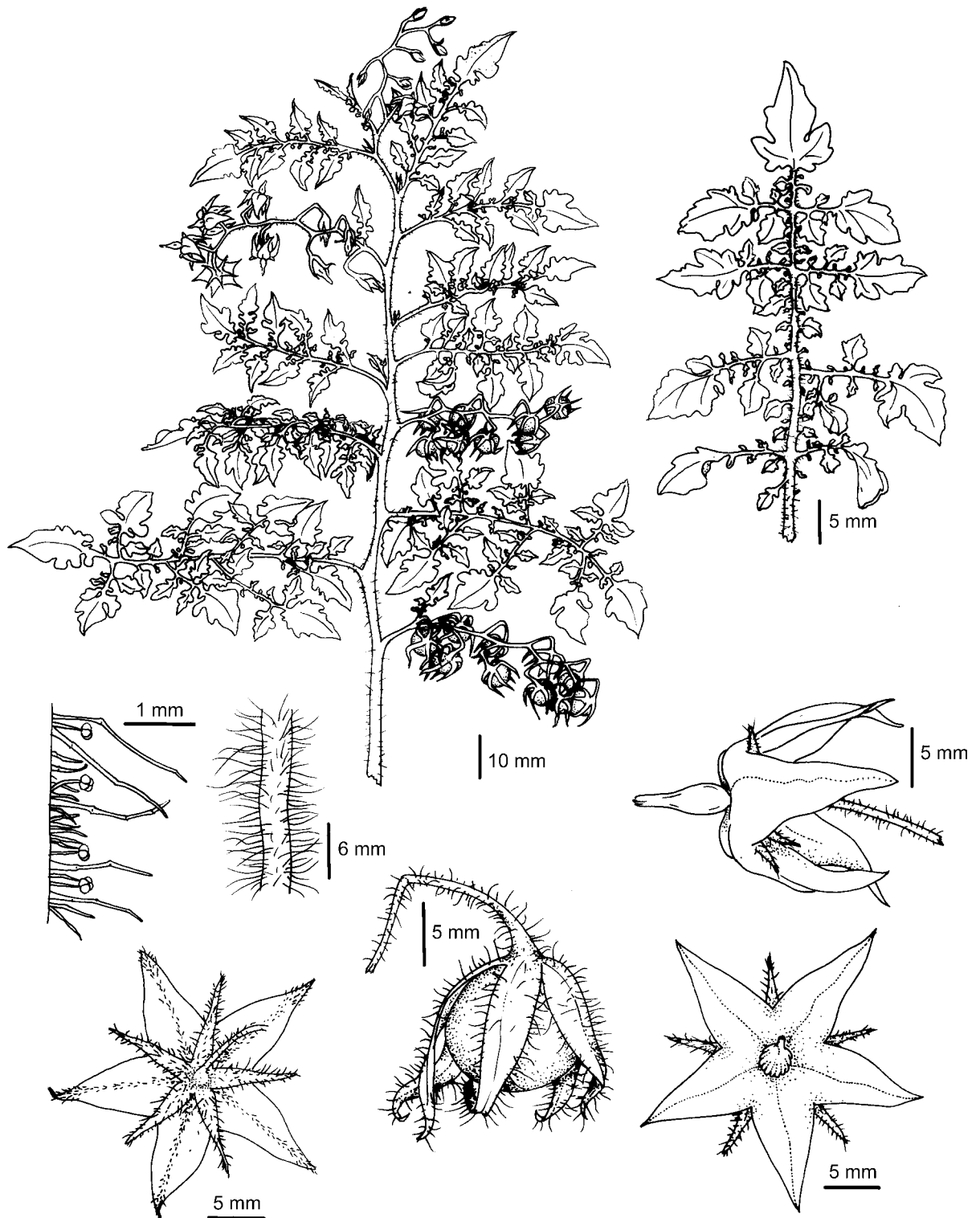
The morphological variation in this species is indeed complex. Rick (1963) also recognized this and pointed out that *S. cheesmaniae* from the northern side of Santa Cruz was intermediate in terms of pubescence density between *S. galapagense* and what we here define as the ‘Academy Bay’ morph of *S. cheesmaniae*. He also observed that ‘typical’ *S. cheesmaniae* shared morphological similarities with the ‘Academy Bay’ morph (Fig. 4E–G) but resembled *S. galapagense* (Fig. 5) with respect to its shorter internodes. Rick (1963) felt that the typical *S. cheesmaniae* had leaves that were less divided than two other forms and with orbicular lateral segments (Fig. 4A–D). Our observations are consistent with these morphological differences noted by Rick (1963).

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 (Fig. 4A, B). Size difference, however, did not wholly account for the differences between the typical *S. cheesmaniae* and the ‘Academy Bay’ morphs (Fig. 4A–G). Further investigations are being undertaken to resolve the relationships and taxonomic status of the ‘Academy Bay’ morph and to establish the reasons for these different morphologies found within *S. cheesmaniae*. Variation in *S. cheesmaniae* is potentially due to a variety factors. These include: (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.

The spelling of the specific epithet has been corrected from *cheesmanii* to *cheesmaniae*, as Evelyn Cheesman, the collector of the type and in whose honour the species was named, was a woman (see Fosberg, 1987; Spooner *et al.*, 1993; Greuter *et al.*, 2000). Although Fosberg (1987) pointed this out, usage has not changed in the plant breeding literature, but floristic studies have consistently used the correct spelling (Jørgensen & León-Yáñez, 1999).

The publication date of Hooker’s *Enumeration of Galapagos Plants*, in which he described both *Lycopersicon peruanum* var. *parviflorum* (= *Solanum cheesmaniae*) and *Lycopersicon esculentum* var. *minor* (= *Solanum galapagense*) is given on the frontispiece 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*. This accounts for considerable confusion over the dates of publication of these





**Figure 5** *Solanum galapagense* S. Darwin & Peralta (based on S. Darwin & Schultz 190, BM).

epithets and is further complicated by the publication, in 1846, of a summary of the reading of Hooker's enumeration. This publication, issued in the *Proceedings of the Linnean Society of London*, included some new generic descriptions (Hooker, 1846). No tomato taxa were mentioned in this 1846 work.

2. ***Solanum galapagense*** S. Darwin & Peralta, **sp. nov.** Type: Ecuador. Galápagos: Isla Bartolomé, E. of the saddle beach, c. 6 m, 0°17'01"S, 90°33'30"W, 28 June 2000, S. Darwin & Schultz 184 (CDS!-holotype; BM!-isotype).



**Figure 6** *Solanum* section *Lycopersicon* in the Galápagos. A. *Solanum cheesmaniae*, typical morph, B. *Solanum cheesmaniae*, 'Academy Bay' morph, C. *Solanum pimpinellifolium*, D. *Solanum lycopersicum*.

*Lycopersicon esculentum* Mill. var. *minor* Hook.f., *Trans. Linn. Soc. London* **20**: 202 (1847) ('1851'). *Lycopersicon cheesmaniae* L. Riley forma *minor* (Hook.f.) C.H. Müll, *U.S. Dept. Agric. Misc. Publ.* **382**: 21 (1940). *Lycopersicon cheesmaniae* L. Riley var. *minor* (Hook.f.) D.M. Porter, *Madroño* **25**: 58 (1978). Type: Ecuador. Galápagos. Santiago: 'James Island', October 1835, Darwin *s.n.* (CGE!-holotype).

Figs 4H–K, 5.

Species *S. cheesmaniae* baccibus aurantiacis similis, foliis valde divisis foliolis tri-dissectis, sepalis in fructo bacca longiori differt.

**Perennial** herbs, undergoing secondary growth at the base; branches somewhat robust to slender, erect to vining, extending up to 2 m from centre. **Stem** erect initially, later procumbent

or decumbent, densely pubescent; trichomes of several lengths, the longest 0.5–2 × *c.* 0.1 mm, simple, uniseriate, 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** trifoliolate. **Internodes** 1.5–3.5(–6) cm. **Leaves** interrupted imparipinnate, 5–25 × 2–17 cm, densely pubescent with uniseriate glandular trichomes *c.* 0.5 mm and shorter unicellular trichomes on both surfaces, denser abaxially, lime green; primary leaflets 2–4 pairs, subopposite or alternate, 2–7 × 1–4.5 cm, ovate or obovate, the base asymmetric, cuneate to cordate, the margins deeply lobed, forming secondary, tertiary and occasionally quaternary leaflets of varying sizes; terminal primary leaflet scarcely larger than the laterals; secondary leaflets present, always more than (6–)10–30 per leaf; tertiary leaflets usually present; interjected leaflets usually present, (3–)5–22(–30), subopposite or alternate, sessile to short-petiolate; rachis 12–18.5 cm. **Petiole** 0.6–4 cm, sparsely pubescent; pseudostipules absent. **Inflorescences** simple or occasionally 2–3-branched, to 10 cm, to 12-flowered, bract and bracteole-like leaflets occasionally present in some populations; peduncle 1–3.5 cm; rachis pubescent like the stems; pedicels 0.5–1.8 cm, articulate just below the middle. **Calyx** 0.6–1.2 cm in diameter, pubescent with long and short simple uniseriate trichomes; tube 0.5–1 mm; lobes 3–6 mm, linear, the apex acute. **Corolla** 1.6–3.2 cm in diameter, yellow, occasionally somewhat bilaterally symmetric due to fusion of adjacent lobes; tube 0.5–0.7 cm long; lobes 0.7–1.3 × 0.3–0.7 cm, deltate to narrowly deltate, reflexed at anthesis. **Staminal column** 3–7 mm, narrowly cone-shaped; filaments 1–2.75 mm; anthers 3–4.5 mm, the sterile tip 1–2(–4) mm. **Ovary** conical, minutely glandular-villous; style 4–8 mm, usually included in the staminal column, rarely exerted to less than 0.5 mm; stigma minute. **Fruits** 0.6–1.1 cm in diameter, globose and 2-locular, glabrescent to densely pubescent with simple uniseriate patent trichomes becoming pale to deep orange at maturity; calyx lobes in fruit accrescent, *c.* 1.4 × 0.1–0.3 cm, longer than fruit, basal half of sepals tightly appressed to berry base, the pedicels in fruit curving towards the axis. **Seeds** (5–) *c.* 30(–50) per fruit, *c.* 2 × 1 mm, usually beaked; testa appearing hairy over entire surface with the elongate lateral cell walls; dry seed weight *c.* 0.5 mg.

**DISTRIBUTION.** Endemic to the Galápagos Islands, particularly the western and southern islands, mostly occurring on coastal lava (see cover photograph) to within 1 m of high tide mark within range of sea spray (strongly salt tolerant) but also occasionally inland, for example on Isabela and Fernandina (Fig. 1).

**COMMON NAMES.** Tomatillo, Galápagos tomato.

**USES.** Putatively edible, although rather sharp to taste (SD, pers. obs.). Germplasm has been used to enhance salt tolerance in cultivated tomatoes (Tal & Shannon, 1983) and high fruit content of soluble solids (Garvey & Hewitt, 1991; Triano & St Clair, 1995).

#### REPRESENTATIVE SPECIMENS EXAMINED

**ECUADOR. Galápagos.** Sin. loc., 1827, *Scouler s.n.* (E). **Bartolomé:** to right of summit landing site, coastal lava, 2 m, 00°14'72"S, 90°33'12"W, 28 June 2000, *Darwin, S. & Schultz 181* (CDS, QCNE); coastal lava, 2 m, 00°14'72"S, 90°33'12"W, 28 June 2000, *Darwin, S. & Schultz 182* (BM, CDS); E. of the saddle beach, coastal lava, 6 m, 00°17'01"S, 90°33'30"W, 28 June 2000, *Darwin, S. & Schultz 189* (CDS); E. of the saddle beach, coastal lava, 6 m, 00°17'01"S, 90°33'30"W, 28 June 2000, *Darwin, S. & Schultz 190* (BM); rocas o lava, muy comun en las zona arida de la isla, 50 m, 00°16'41.6"S, 90°32'53.6"W, 19 July 1997, *Jaramillo 1052* (CDS); sin. loc., *Fagerlind & Wibon 3464* (S); on barren lava and in cinder patches among lava blocks and flows, 10–30 m, 3 February 1967, *Wiggins & Porter 296* (CAS, GH, SGO); barren lava along E. side of lava ridge *c.* 2 km from W. end of Isla San Bartolomé, 50 m, 3 February 1967, *Wiggins & Porter 314* (CAS, USN). **Corona del Diablo:** sin. loc., 10 m, 23 November 1966, *Eliasson & Eliasson 656* (S). **Darwin:** sin. loc., October 1983, *Touc s.n.* (CDS). **Española:** sin. loc., May 1899, *Snodgrass & Heller 741* (DS, GH); sin. loc., 8–26 July 1983, *Touc s.n.* (CDS). **Fernandina:** NW of rim, on 1968 ash deposit, 1300 m, 1974, *Adersen & Adersen 921* (C, CDS); green strip on SW slope, large clumps growing at edge of *Scalesia* zone on deep ash sand near crater rim, 1460 m, 4 February 1964, *Cavagnero 25* (MO); SW corner of island, Cabo Hammond, 27 April, *Reeder s.n.* (WIS); NW slope, 700–1200 m, September 1972, *Schmidt & Schmidt 2528* (C). **Gardner (nr. Española):** sin. loc., 3 October 1905–1906, *Stewart 3373* (CAS); **Gardner (nr. Floreana):** sin. loc., 16–19 August 1983, *Touc s.n.* (CDS). **Isabela:** fumarole on E. saddle, lava, 380 m, 12 November 1974, *Adersen & Adersen 1165* (C); El Lagoon del Manzanillo, growing next to gravel pit formed due to extraction of gravel for airport built in 1996, 16 m, 00°55'85"S, 90°58'68"W, 21 July 2000, *Darwin, S. et al. 291* (BM, CDS, QCA, QCNE); El Lagoon del Manzanillo, growing next to gravel pit formed due to extraction of gravel for airport built in 1996, 16 m, 00°55'85"S, 90°58'68"W, 21 July 2000, *Darwin, S. et al. 294* (CDS); just outside Villamil, by El Lagoon del Manzanillo, growing next to gravel pit formed due to extraction of gravel for airport built in 1996, 16 m, 00°55'85"S, 90°58'68"W, 25 July 2000, *Darwin, S. & Rosero 364* (BM, CDS, QCA, QCNE); Volcán Darwin, beach N. of Tagus Mountain, coastal, 0–5 m, 12 July 1972, *Hamman & Hamman 1729* (C); Punta Albemarle, 29 June 1961, *Lévêque 163* (MO); Sierra Negra, 10 km N. of Villamil, 75–80 m, 1 October 1972, *Hamann & Hamann 2483* (C); Tagus Cove, 120 m, 25 June 1963, *Snow s.n.* (CDS). **Pinta:** sin. loc., 460 m, 21 May 1964, *Castro s.n.* (CDS); sin. loc., 460 m, 21 May 1964, *Snow 591* (K); sin. loc., 200–500 m, 19 September 1905, *Stewart 3370* (CAS); nr fumarole, 12 October 1973, *de Vries s.n.* (CDS); SE – slope, 300 m, June 1975, *van der Werff 2129* (U); **Pinzón:** growing between rocks, 10 m, 7 February 1958, *Castro s.n.* (CAS). **Rábida:** among lava boulders on upper slopes of main volcanic peak, 22 March 1967, *DeRoy & DeRoy 11* (DS); sin. loc.,

6 June 1932, *Howell 9753* (CAS); barranca, N. slope, 300 m, 30 September 1975, *Reeder & Chapy s.n.* (WIS). **Santiago:** Caleta Bucanero, steep cleft, 10 m, 1 June 1977, *Adersen & Adersen 1771* (C, CDS); Sullivan Bay, 13 June 1932, *Howell 10012* (B, CAS, K); sin. loc., 1853, *Andersson s.n.* (BR); Crab Point (S. of James Bay–W. side of Island), coastal, in place inaccessible to goats, 16–20 August 1957, *Castro s.n.* (CAS); sin. loc., beginning October 1835, *Darwin, C. s.n.* (CGE); sin. loc., 5 June 1932, *Howell 9701* (CAS); sin. loc., June 1899, *Snodgrass & Heller 399* (GH); James Bay, 700–1600 m, 19 September 1905–1906, *Stewart 3369* (CAS); James Bay, 300 m, 6 August 1905–1906, *Stewart 3378* (BM, CAS, MO, NY, USN). **Sombrero Chino:** NE side of the islet, lava, 20 m, 00°22'15"S, 90°34'93"W, 28 June 2000, *Darwin, S. & Schultz 138* (QCA, QCNE); NE side of islet, lava, 20 m, 00°22'15"S, 90°34'93"W, 28 June 2000, *Darwin, S. & Schultz 139* (BM, CDS); NE side of islet, lava, 20 m, 00°22'15"S, 90°34'93"W, 28 June 2000, *Darwin, S. & Schultz 145* (QCNE); NE side of islet, lava, 20 m, 00°22'15"S, 90°34'93"W, 28 June 2000, *Darwin, S. & Schultz 149* (CDS); NE side of islet, lava, 20 m, 00°22'15"S, 90°34'93"W, 28 June 2000, *Darwin, S. & Schultz 157* (BM); sin. loc., 21 December 1993, *Snell 109* (CDS).

*Solanum galapagense* can be clearly differentiated from the other three taxa 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 the presence of branched inflorescences. These morphological characters were found at a lower frequency in *S. cheesmaniae*, only rarely in *S. lycopersicum* and *S. pimpinellifolium*. Note that the presence of appressed sepals is not always apparent in herbarium specimens as sepals apparently curl upwards as they dry and can become reflexed.

Throughout the numerous different Galápagos tomato classifications there has been little doubt that *S. galapagense* is distinct; indeed, this is the only taxon that remains consistently separated throughout all the different treatments of tomatoes in the Galápagos (see Fig. 2). The morphological analysis indicates that *S. galapagense* is more distinct from the other three taxa than *S. pimpinellifolium* and *S. lycopersicum* are from each other.

Orange fruit colour is only found in *Solanum cheesmaniae* and *S. galapagense*. This character is derived in these two species (Peralta & Spooner, 2001) and morphologically separates them from *S. pimpinellifolium* and *S. lycopersicum* which in the Galápagos have unequivocally bright red fruit. Fruit colour was described by Rick (1971) as a 'dependable key character' with which to differentiate the Galápagos tomatoes from all others.

**3. *Solanum lycopersicum* L., *Sp. Pl.* 185 (1753). *Lycopersicon esculentum* Mill., *Gard. Dict.* ed. 8, *Lycopersicon* No. 2 (1768). Type: Cultivated in Uppsala, *Anon.* (LINN 248.16!-lectotype, designated by Knapp & Jarvis, 1990 [BH neg. 6803: BH!, GH!, UC!, WIS!]).**

Figs 4N, 6D.

**Annual or biennial** herbs, undergoing secondary growth at the base; branches relatively robust and vining, extending up

to 1 m from centre. **Stem** erect initially, later procumbent or decumbent, pubescent and usually villous towards the apex; trichomes of two types, numerous simple unicellular trichomes and sparse simple, uniseriate trichomes up to 3 mm and composed of up to 10 cells, these usually denser at the nodes, the plant with a strong tomato scent. **Sympodial units** trifoliate. **Internodes** 1–4 cm, but very few specimens available. **Leaves** interrupted imparipinnate, 20–30 × 10–23 cm, sparsely pubescent like the stems on both surfaces or glabrescent, dark green; primary leaflets 2–3 pairs, opposite, subopposite or alternate, 3.5–8.5 × 1.3–3 cm, ovate or elliptic, the base asymmetric, truncate to cordate, the margins dentate or crenate mainly near the base, rarely deeply dentate or lobulate; terminal primary leaflet usually larger than the laterals; secondary leaflets fewer than 15 to absent, present mainly basiscopically; interjected leaflets usually present, 5–12 per leaf, subopposite or alternate, short-petiolate; rachis 1.9–14.5 cm. **Petiole** 1.2–4.2 cm, sparsely pubescent; pseudostipules absent. **Inflorescences** usually simple, rarely with 2 branches, to 5 cm, 5–8-flowered, shorter than the stems and growing leaves; peduncle 1–3.5 cm; rachis pubescent like the stems; pedicels 0.6–1.8 cm, articulate just above or just below the middle. **Calyx** to 1.8 cm in diameter, pubescent with long and short simple uniseriate trichomes; tube very short, less than 1 mm; lobes to 5–9 × 1 mm, linear, the apex acute. **Corolla** 2–3 cm in diameter, bright yellow; tube to 0.6 cm long; lobes 0.8–1.3 × 0.35–0.5 cm, narrowly lanceolate, spreading to somewhat reflexed at anthesis. **Staminal column** 6.5–8.5 mm, narrowly cone-shaped; filaments 1–3 mm; anthers 4–6.5 mm, the sterile tip less than half the total column length. **Ovary** conical, minutely glandular-villous; style 6.5–10 mm, usually included in the staminal column, but exerted in facultatively allogamous populations; stigma minute. **Fruits** (2–)2.2–4(–10 in some cultivars not known from Galápagos) cm in diameter, usually globose and 2-locular, but often of varying shape and multilocular, glabrescent and becoming red at maturity; calyx lobes in fruit accrescent, 0.75–1.6 cm, somewhat reflexed, never exceeding the length of the fruit. **Seeds** 25–85 per fruit, *c.* 3.5 × 2.5 mm, beaked; testa appearing hairy over entire surface with the elongate lateral cell walls; dry seed weight *c.* 1.5 mg.

**DISTRIBUTION.** Native distribution of the cultivated tomato is not known; in the Galápagos it is often found in rubbish dumps or near human habitation on Santa Cruz, Isabela and San Cristóbal. Probably introduced before 1932.

**COMMON NAMES.** Tomato, garden tomato, cherry tomato, cultivated tomato.

**USES.** Edible; widely used as a vegetable throughout the world. **SPECIMENS EXAMINED.**

**ECUADOR. Galápagos. Isabela:** Villamil, roadside, <10 m, 21 July 2000, *Darwin, S. 289* (BM); Villamil village, roadside, 10 m, 22 July 2000, *Darwin, S. 304* (CDS); San Tomas near Villamil, waste land, 330 m, 00°51'25"S, 90°01'54"W, 22 July 2000, *Darwin, S. et al. 302* (BM, CDS); Villamil, active rubbish dump, 133 m, 00°52'66"S, 90°00'42"W, 25 July 2000, *Darwin, S. & Rosero 354* (CDS); road from Villamil to San

Tomas, active rubbish dump, 133 m, 00°52'66"S, 90°00'42"W, 25 July 2000, *Darwin, S. & Rosero 358* (BM, CDS, QCA); road from Villamil to San Tomas, active rubbish dump, 133 m, 00°52'66"S, 90°00'42"W, 25 July 2000, *Darwin, S. & Rosero 360* (BM, CDS); Villamil, by ECCD office, roadside, 10 m, 25 July 2000, *Darwin, S. & Rosero 376* (CDS). **San Cristóbal:** Wreck Bay, 17 April 1932, *Howell 8573* (B, CAS). **Santa Cruz:** between Puerto Ayora and Bella Vista, trackside, 1953, *TGRC accession LA0292* (TGRC seed bank).

The cultivated tomato *S. lycopersicum* is grown wherever people establish towns and villages, and it is a quick-growing adventive weed in many parts of the world. The date of its introduction to the Galápagos is uncertain, as settlement on the islands was explosive in the last century. Rick (1963) mentions '*Lycopersicon esculentum* var. *cerasiforme*' (TGRC accession LA292 (SCD 067)) collected in 1952, as occurring as a garden escape between Puerto Ayora (Academy Bay) and Bella Vista on Santa Cruz. The earliest herbarium specimen for *S. lycopersicum* is *Howell 8573*, collected in 1932 from San Cristóbal.

4. ***Solanum pimpinellifolium*** L., *Cent.* 8 (1755). *Lycopersicon pimpinellifolium* (L.) Mill., *Gard. Dict.* ed. 8, *Lycopersicon* No. 4 (1768). Type: Cultivated in Uppsala, Anon. (LINN 248.15!-lectotype, designated by Knapp & Jarvis, 1990 [BH neg. 6802: GH!, UC!, WIS!]).

Figs 4L–M, 6C.

**Annual or biennial** herbs, undergoing secondary growth at the base; branches extremely slender and vining, extending up to 3 m from centre. **Stem** erect initially, later procumbent or decumbent, sparsely pubescent or nearly glabrous; trichomes of two types, the longer sparse to extremely sparse and occasionally absent, to 2.2 mm, simple, uniseriate, to 6-celled, amongst sparse shorter, unicellular non-glandular and glandular trichomes, the glands usually multicellular, the plant with a citrus scent. **Symphodial units** trifoliate. **Internodes** 1.5–6.5(–7.5) cm. **Leaves** interrupted imparipinnate, 5–20 × 2.5–15 cm, sparsely pubescent like the stems on both surfaces, less pubescent adaxially, dark green, often with purplish cast abaxially; primary leaflets 2–3 pairs, opposite, subopposite or alternate, 3–7 × 1–4 cm, ovate, the base asymmetric, cuneate to cordate, the margins entire or irregularly lobed mainly near the base; terminal primary leaflet usually larger than the laterals, approximately equal in length to the leaf axis; secondary leaflets fewer than 6, often absent; tertiary leaflets absent; interjected leaflets usually present, 2–12(–15), subopposite or alternate, short-petiolate; rachis 2.0–15 cm. **Petiole** 0.4–3.0(–5.5) cm, glabrous or with a few uniseriate trichomes; pseudostipules absent. **Inflorescences** simple, very rarely once-branched, elongate, to 9 cm, 5–6-flowered, shorter than the stems and growing leaves, bract and bracteole-like leaflets absent; peduncle 1–2.5 cm; rachis glabrous to sparsely pubescent like the stems; pedicels 0.7–1.5 cm, articulate in the lower half, with small glandular trichomes. **Calyx** 0.4–1.0 cm in diameter, pubescent with long and short, simple, uniseriate trichomes; tube less than 0.5 mm; lobes to 5 mm, linear, the apex acute. **Corolla** 1.6–

3 cm in diameter, bright yellow; tube minute, the corolla often divided almost to the base; lobes 0.7–1.2 × 0.2–0.5 cm, four times as long as wide, narrowly lanceolate, strongly reflexed at anthesis. **Staminal column** 6–8 mm, narrowly cone-shaped; filaments 1–2.5 mm; anthers 3.5–5 mm, the sterile tip approximately half the total anther length. **Ovary** conical, minutely glandular-villous; style 7–10 mm, usually exerted from the staminal column; stigma minute. **Fruits** (0.8–)1.1–1.6 cm in diameter, globose and 2-locular, glabrescent and becoming bright red at maturity; calyx lobes in fruit accrescent, 0.6–1.3 × 0.15–0.25 cm, strongly reflexed. **Seeds** (15–)50 (–80) per fruit, *c.* 2–3 × 1–1.5 mm, beaked; testa appearing hairy over entire surface and winged with the elongate lateral cell walls; dry seed weight *c.* 1 mg.

**DISTRIBUTION.** Coastal South America from Ecuador to Chile at low elevations; in the Galápagos mostly in disturbed areas on Santa Cruz, Isabela and San Cristóbal.

**COMMON NAMES.** Tomatillo, current tomato.

**USES.** Edible and sweet to taste. Cultivated and used by plant breeders to improve commercial cultivars of *Solanum lycopersicum*.

**REPRESENTATIVE SPECIMENS EXAMINED.**

**ECUADOR. Galápagos. Isabela:** Villamil, 1985, *TGRC accession LA2857* (TGRC seed bank); just outside Villamil, by El Lagoon del Manzanillo, 16 m, 00°55'85"S, 90°58'68"W, 25 July 2000 *Darwin, S. & Rosero 371* (BM). **San Cristóbal:** Puerto Baquerizo Moreno, E. side of town by Bethel School, roadside, 40 m, 00°54'37"S, 89°36'38"W, 5 August 2000, *Darwin, S. & Carrera 379* (BM, CDS), Puerto Baquerizo Moreno, E. side of town by Bethel School, roadside, 40 m, 00°54'37"S, 89°36'38"W, 5 August 2000, *Darwin, S. & Carrera 380* (BM, CDS). **Santa Cruz:** Bella Vista village, road S./SE of village, roadside lava, 200 m, 00°41'70"S, 90°19'43"W, 21 June 2000, *Darwin, S. 103* (BM, CDS, QCA, QCNE); between Puerto Ayora and Bella Vista, W. of main road, old basura site, disused rubbish dump, 125 m, 00°43'09"S, 90°19'81"W, 22 June 2000, *Darwin, S. et al. 104* (BM, CDS, QCNE); between Puerto Ayora and Bella Vista, W. of main road, old basura site, disused rubbish dump, 125 m, 00°43'09"S, 90°19'81"W, 22 June 2000, *Darwin, S. et al. 109* (BM, CDS, QCNE); between Los Gemelos and Canal, W. side of main road, the 'new' basura, disturbed ground around refuse area, 314 m, 00°35'04"S, 90°21'37"W, 22 June 2000, *Darwin, S. et al. 114* (BM, CDS, QCA, QCNE); between Los Gemelos and Canal, W. side of main road, the 'new' basura, disturbed ground around refuse area, 314 m, 00°35'04"S, 90°21'37"W, 22 June 2000, *Darwin, S. et al. 125* (CDS); Puerto Ayora, roadside, 40 m, 9 July 2000, *Darwin, S. 277* (BM, CDS); Puerto Ayora, roadside, 40 m, 9 July 2000, *Darwin, S. 278* (BM, CDS); El Chato Tortoise Reserve, by the lake, 200 m, 00°40'38"S, 90°26'32"W, 7 August 2000, *Darwin, S. et al. 400* (QCNE); El Chato Tortoise Reserve, by lake, 200 m, 00°40'38"S, 90°26'32"W, 7 August 2000, *Darwin, S. et al. 401* (BM); El Chato Tortoise Reserve, by lake, 200 m, 00°40'38"S, 90°26'32"W, *Darwin, S. et al. 402* (BM, CDS); El Chato Tortoise Reserve, by lake, 200 m, 00°40'38"S,

90°26'32"W, 7 August 2000, Darwin, S. et al. 403 (QCNE); Mino Granilla Roja, 565 m, 0°36'56.6"S, 90°21'53.9"W, 26 July 2001, Pozo & Herrera 2 (CDS).

*Solanum pimpinellifolium* can be distinguished from the other three species examined here by its markedly stellate flowers with narrowly lanceolate corolla lobes; the other three taxa have much more deltate lobes with longer corolla tubes (e.g. corolla divided approximately halfway rather than almost all the way to the base). The leaf margins are more entire than any of the other species and the bright red fruit are much smaller than those of *S. lycopersicum*. The dry seeds of *S. pimpinellifolium* are about double the weight of either of the two endemic tomatoes and about half the weight of *S. lycopersicum*.

It is not clear from the literature when the 'true' red-fruited *S. pimpinellifolium* and *S. lycopersicum* were first introduced to the Galápagos. The situation is made all the more complicated by earlier authors recognizing the native Galápagos taxa as varieties of *S. pimpinellifolium* and *S. lycopersicum*.

Müller (1940) cited several Galápagos specimens as *S. pimpinellifolium*; most are of the 'Academy Bay' morph of *S. cheesmaniae*, save one (Stewart 3380). The leaf morphology of this specimen fits extremely well with the Linnaean type of *S. pimpinellifolium*. It is also similar to plants of *S. pimpinellifolium* currently found in the Galápagos. This specimen, however, is enigmatic in that it has deltate corolla lobes and is more glabrous than Galápagos plants of *S. pimpinellifolium*, suggesting it belongs to the 'Academy Bay' morph of *S. cheesmaniae*. Stewart 3380 lacks mature fruit, precluding firm conclusions.

The distribution of *S. pimpinellifolium* in Galápagos to date is largely in disturbed areas, but is documented in detail to enable spread to be monitored. On Santa Cruz the species is found in Puerto Ayora (Academy Bay), Bella Vista, Los Gemelos on the borders of the cloud forest and the El Chato Tortoise Reserve. It is also found along roadsides throughout the island, quarries and rubbish dumps. In some areas, for example in the El Chato Tortoise Reserve, it covers large areas of ground to the exclusion of other plants. On Isabela *S. pimpinellifolium* occurs near Villamil and along the road towards San Tomás and at El Lagoon del Manzanillo. On San Cristóbal the species has been collected only near the town of Puerto Baquerizo Moreno. The first unequivocal record of *S. pimpinellifolium* in Galápagos is a TGRC accession (LA2857) from Villamil collected in 1985 (Chetelat in litt., 2002); however, the species may have been introduced to the islands before 1905 if Stewart 3380 is indeed from a plant of *S. pimpinellifolium*. Specimens collected by S. Darwin from Santa Cruz are therefore the earliest herbarium specimens that we can confirm as *S. pimpinellifolium*.

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- Castro, M.* s.n. (galapagense); s.n. (galapagense); s.n. (cheesmaniae); s.n. (galapagense); s.n. (galapagense).
- Cavagnero, D.* 25 (galapagense).
- Cheesman, L.E.* in Riley 403 (cheesmaniae).
- Clark, D.A. & Clark, D.B.* 344 (cheesmaniae).
- D'Arcy, W.G.* 17754 (galapagense).
- Darwin, C.* s.n. (galapagense); s.n. (cheesmaniae); s.n. (cheesmaniae); s.n. (cheesmaniae\*).
- Darwin, S.* 100 (pimpinellifolium); 101 (pimpinellifolium); 103 (pimpinellifolium); 276 (pimpinellifolium); 277 (pimpinellifolium); 278 (pimpinellifolium); 289 (lycopersicum); 304 (lycopersicum); 305 (lycopersicum).
- Darwin, S. & Carrera, P.* 378 (pimpinellifolium); 379 (pimpinellifolium); 380 (pimpinellifolium); 381 (lycopersicum); 384 (pimpinellifolium); 386 (pimpinellifolium).
- Darwin, S., Chavez, J., Gardener, M. & Rejmanek, M.* 290 (cheesmaniae\*); 291 (galapagense); 292 (galapagense); 293 (galapagense); 294 (galapagense); 295 (galapagense); 296 (galapagense); 298 (galapagense); 299 (galapagense); 302 (lycopersicum); 303 (lycopersicum).
- Darwin, S., Fitter, D. & Fitter, T.* 195 (pimpinellifolium); 196 (pimpinellifolium); 197 (pimpinellifolium); 200 (pimpinellifolium); 201 (cheesmaniae); 202 (cheesmaniae); 203 (cheesmaniae); 204 (cheesmaniae); 205 (cheesmaniae); 206 (cheesmaniae); 207 (cheesmaniae); 208 (cheesmaniae); 209 (cheesmaniae); 210 (cheesmaniae); 211 (cheesmaniae); 280 (pimpinellifolium); 282 (pimpinellifolium); 283 (pimpinellifolium); 284 (pimpinellifolium); 285 (pimpinellifolium); 286 (pimpinellifolium).
- Darwin, S., Fitter, D., Fitter, T. & Appleton, G.* 212 (cheesmaniae); 213 (cheesmaniae); 214 (cheesmaniae); 215 (cheesmaniae); 216 (cheesmaniae); 217 (cheesmaniae); 218 (cheesmaniae); 219 (cheesmaniae); 220 (cheesmaniae); 221 (cheesmaniae); 222 (cheesmaniae); 223 (cheesmaniae); 224 (cheesmaniae); 225 (cheesmaniae); 226 (cheesmaniae); 227 (cheesmaniae); 228 (cheesmaniae); 229 (cheesmaniae); 230 (cheesmaniae); 231 (cheesmaniae); 232 (cheesmaniae); 233 (cheesmaniae); 234 (cheesmaniae); 235 (cheesmaniae); 236 (cheesmaniae); 238 (cheesmaniae); 239 (cheesmaniae); 240 (cheesmaniae); 241 (cheesmaniae); 243 (cheesmaniae); 244 (cheesmaniae); 245 (cheesmaniae); 246 (cheesmaniae); 247 (cheesmaniae); 248 (cheesmaniae); 249 (cheesmaniae); 250 (cheesmaniae); 251 (cheesmaniae); 252 (cheesmaniae); 253 (cheesmaniae); 254 (cheesmaniae); 255 (cheesmaniae); 256 (cheesmaniae); 257 (cheesmaniae); 258 (cheesmaniae); 259 (cheesmaniae); 261 (cheesmaniae); 262 (cheesmaniae); 263 (cheesmaniae); 264 (cheesmaniae); 265 (cheesmaniae); 266 (cheesmaniae); 267 (cheesmaniae); 268 (cheesmaniae); 269 (cheesmaniae); 270 (cheesmaniae); 271 (cheesmaniae); 272 (cheesmaniae); 273 (cheesmaniae); 274 (cheesmaniae); 260 (cheesmaniae).

## Exsiccatae

Alphabetical by collector, all specimens examined.

- Adersen, A. & Adersen, H.* 201 (cheesmaniae); 464 (cheesmaniae\*); 465 (galapagense); 891 (galapagense); 903 (cheesmaniae\*); 919 (cheesmaniae\*); 921 (galapagense); 1165 (galapagense); 1771 (galapagense).
- Aldaz, I.* s.n. (cheesmaniae); 350 (cheesmaniae).
- Andersson, N.J.* s.n. (cheesmaniae); s.n. (galapagense).
- Baur, G.* s.n. (galapagense); 189 (galapagense).
- Belt, R.L.* s.n. (galapagense).
- Bentley, P.S.* 342 (cheesmaniae\*).



- Darwin, S., Gardener, M. & Callebaut, J.* 388 (pimpinellifolium); 389 (pimpinellifolium); 390 (pimpinellifolium); 391 (pimpinellifolium); 392 (pimpinellifolium); 393 (pimpinellifolium); 394 (pimpinellifolium); 395 (pimpinellifolium); 396 (pimpinellifolium); 397 (pimpinellifolium); 398 (pimpinellifolium); 399 (pimpinellifolium); 400 (pimpinellifolium); 401 (pimpinellifolium); 402 (pimpinellifolium); 403 (pimpinellifolium); 405 (pimpinellifolium); 407 (pimpinellifolium); 410 (pimpinellifolium); 411 (pimpinellifolium); 412 (pimpinellifolium); 413 (pimpinellifolium); 414 (pimpinellifolium); 415 (pimpinellifolium); 416 (pimpinellifolium); 417 (pimpinellifolium); 418 (pimpinellifolium); 419 (pimpinellifolium); 421 (pimpinellifolium); 422 (pimpinellifolium); 423 (pimpinellifolium); 424 (pimpinellifolium); 425 (pimpinellifolium); 426 (pimpinellifolium); 427 (pimpinellifolium).
- Darwin, S. & Robayo, J.* 377 (pimpinellifolium).
- Darwin, S. & Rosero, P.* 354 (lycopersicum); 355 (lycopersicum); 356 (lycopersicum); 357 (lycopersicum); 358 (lycopersicum); 359 (lycopersicum); 360 (lycopersicum); 364 (galapagense); 365 (cheesmaniae\*); 366 (cheesmaniae\*); 367 (galapagense); 372 (galapagense); 373 (galapagense); 374 (galapagense); 375 (galapagense); 376 (lycopersicum).
- Darwin, S. & Schultz, A.* 127 (galapagense); 132 (galapagense); 133 (galapagense); 134 (galapagense); 135 (galapagense); 138 (galapagense); 139 (galapagense); 140 (galapagense); 141 (galapagense); 142 (galapagense); 143 (galapagense); 144 (galapagense); 145 (galapagense); 146 (galapagense); 147 (galapagense); 148 (galapagense); 149 (galapagense); 150 (galapagense); 151 (galapagense); 152 (galapagense); 153 (galapagense); 154 (galapagense); 155 (galapagense); 156 (galapagense); 157 (galapagense); 158 (galapagense); 159 (galapagense); 160 (galapagense); 161 (galapagense); 162 (galapagense); 163 (galapagense); 164 (galapagense); 165 (galapagense); 166 (galapagense); 167 (galapagense); 168 (galapagense); 169 (galapagense); 170 (galapagense); 171 (galapagense); 173 (galapagense); 174 (galapagense); 175 (galapagense); 176 (galapagense); 177 (galapagense); 179 (galapagense); 180 (galapagense); 181 (galapagense); 182 (galapagense); 183 (galapagense); 184 (galapagense); 185 (galapagense); 186 (galapagense); 187 (galapagense); 188 (galapagense); 189 (galapagense); 190 (galapagense); 191 (galapagense); 192 (galapagense); 193 (galapagense); 194 (galapagense).
- Darwin, S., Tye, A., Jäger, H., Callebaut, J. & Schultz, A.* 104 (pimpinellifolium); 105 (pimpinellifolium); 106 (pimpinellifolium); 108 (pimpinellifolium); 109 (pimpinellifolium); 110 (pimpinellifolium); 111 (pimpinellifolium); 112 (pimpinellifolium); 113 (pimpinellifolium); 114 (pimpinellifolium); 124 (pimpinellifolium); 125 (pimpinellifolium); 126 (pimpinellifolium).
- Day, D.* 287 (galapagense).
- de Vries, T.* s.n. (galapagense); 1227 (cheesmaniae).
- DeRoy, A. & DeRoy, J.* 11 (galapagense).
- Eliasson, U. & Eliasson, I.* 201 (cheesmaniae\*); 656 (galapagense); 1106 (galapagense); 1643 (cheesmaniae\*); 2207 (cheesmaniae\*).
- Fagerlind, F. & Wibom, G.* 3070 (cheesmaniae\*); 3110 (cheesmaniae\*); 3464 (galapagense); 3471 (galapagense).
- Fosberg, F.R.* 45012 (cheesmaniae\*).
- Hamann, M. & Hamann, O.* 193 (cheesmaniae\* (sheet at C), mixed collection with galapagense (sheet at CDS)); 194 (galapagense); 213 (cheesmaniae\*); 267 (cheesmaniae\*); 269 (cheesmaniae\*); 444 (cheesmaniae); 1698 (cheesmaniae\*); 1729 (galapagense); 1801 (cheesmaniae\*); 2483 (galapagense).
- Hamann, O. & Seberg, O.* 1771 (cheesmaniae).
- Harling, G.* 5288 (cheesmaniae); 5371 (cheesmaniae); 5476 (cheesmaniae).
- Herndactmes, C.* s.n. (cheesmaniae).
- Howell, J.T.* 10012 (galapagense); 8573 (lycopersicum); 9096 (cheesmaniae\*); 9427 (cheesmaniae\*); 9447 (cheesmaniae); 9617 (cheesmaniae); 9701 (galapagense); 9753 (galapagense).
- Huttel, C.* 495 (cheesmaniae\*); 1597 (cheesmaniae); 2735 (cheesmaniae).
- Jaeger, H. & Leuchten, S.* 9068 (galapagense).
- Jaramillo, P.* 1052 (galapagense).
- Lawesson, J.E.* 3017 (cheesmaniae\*); 3080 (cheesmaniae\*); 2638 (galapagense); 3234 (galapagense).
- Lévêque, R.* 163 (galapagense).
- Müller & Müller* 2500 (cheesmaniae\*).
- Porter, D.M.* s.n. (galapagense).
- Pozo, P. & Herrera, H.* 2 (pimpinellifolium).
- Reeder, L.R.* s.n. (galapagense).
- Reeder ?? & Chapy* s.n. (galapagense).
- Reeder, Wm. G.* s.n. (galapagense).
- Schimpff, H.J.F.* 12 (cheesmaniae\*).
- Schmidt, A. & Schmidt, P.* 2528 (galapagense).
- Scouler, J.* s.n. (galapagense).
- Snell, H.* 109 (galapagense).
- Snodgrass, R.E. & Heller, E.* 305 (galapagense); 399 (galapagense); 741 (galapagense); 843 (galapagense); 911 (galapagense); 928 (cheesmaniae).
- Snow, A.W.* s.n. (cheesmaniae); s.n. (galapagense); 297 (galapagense); 498 (cheesmaniae); 591 (galapagense).
- Stewart, A.* s.n. (galapagense); 3369 (galapagense); 3370 (galapagense); 3372 (galapagense); 3373 (galapagense); 3374 (cheesmaniae); 3375 (cheesmaniae); 3376 (cheesmaniae); 3377 (galapagense); 3378 (galapagense); 3379 (cheesmaniae).
- Svenson, H.K.* 281 (cheesmaniae\*).
- Touc, L.T.* s.n. (galapagense); s.n. (cheesmaniae\*); s.n. (galapagense); s.n. (cheesmaniae); s.n. (cheesmaniae); s.n. (galapagense); s.n. (galapagense).
- van der Werff, H.H.* 1265 (cheesmaniae); 2129 (galapagense).
- Verdugo, A.* 15 (galapagense).
- Werner, D.* 2541 (cheesmaniae\*); 2552 (cheesmaniae).
- Wiggins, I.L. & Porter, D.M.* 296 (galapagense); 314 (galapagense); 604 (cheesmaniae\*).