

Systematics and Taxonomy of
Solanum sections *Dunaliana* and *Irenosolanum* (Solanaceae).

By
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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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Abstract

Systematics and Taxonomy of

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by

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The monophyly and phylogenetic relationships of the *Solanum dunalianum* group have been the subject of controversy. The *S. dunalianum* group was investigated using fifty-eight morphological characters and DNA sequence data: molecular markers ITS, *trnT-trnF*, and *waxy*. The individual datasets, combined molecular dataset, and total evidence dataset were analyzed under the parsimony criterion. In all analyses, the *S. dunalianum* group was resolved as not monophyletic, necessitating taxonomic realignment. In the total evidence strict consensus, all species of the *Solanum dunalianum* group, except *S. tetrandrum*, fell into either of two clades, compatible with the previously proposed *Solanum* sections *Dunaliana* and *Irenosolanum*. *Solanum tetrandrum* was resolved with *S. melongena* indicating an affinity with species from tropical Asia. *Solanum* section *Dunaliana* was sister to New Guinean species of the *S. ferocissimum* group. *Solanum* section *Irenosolanum* was sister to a clade of Australian and New Guinean species of various groups. No unique synapomorphies support either section, but morphological trends exist. Taxonomic treatments for each section are presented. Both include a key to species, distribution maps, and images of type specimens. *Solanum* section *Dunaliana*, centered on New Guinea, is restricted to a morphologically coherent clade of six species including *S. labyrinthinum* named herein. It is characterized by a large shrub or small tree habit,

sparse, broad-based prickles, entire leaves with the blade unarmed, many-flowered inflorescence with all flowers fertile, corollas with poorly developed interpetalar tissue, and juicy, red fruit. A neotype is designated for *S. peekelii*; lectotypes are designated for *S. dunalianum* var. *inerme* and *S. torricellense*. *Solanum* section *Irenosolanum* is comprised of twenty-nine species, the following seven of which are named as new herein: *Solanum albertii*, *S. memaoyanum*, *S. nudatum*, *S. pseudopedunculatum*, *S. ratale*, *S. semisucculentum*, and *S. vanuatuense*. *Solanum* section *Irenosolanum* is morphologically diverse; tendencies include: paucity or absence of prickles, spreading (non-connivent) anthers, white corollas, and horizontal presentation of flowers. The section is restricted to the islands of the Pacific; all native species of *Solanum* subgenus *Leptostemonum* from the Pacific belong to section *Irenosolanum* except *S. lasiocarpum* and *S. repandum* of section *Lasiocarpa*. Thirty taxa including *Solanum* section *Irenosolanum* are typified.

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This work is not intended as valid publication of the new species discussed herein.

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Chapter 1
A phylogenetic analysis of the
***Solanum dunalianum* group (Solanaceae)**
based on DNA sequence and morphological data

Abstract

The monophyly and phylogenetic relationships of the *Solanum dunalianum* group have been the subject of controversy in the taxonomic literature. The *S. dunalianum* group, consisting of thirty-one species, was investigated using DNA sequence data and morphological data. Three molecular markers, ITS, *trnT-trnF*, and *waxy*, and fifty-eight morphological characters were used for phylogenetic analyses. Each molecular dataset was analyzed separately as was the morphological dataset. The combined molecular data were analyzed and the morphological dataset and combined molecular dataset were evaluated together for a total evidence analysis. The results of all analyses were more or less congruent. In all analyses, the *S. dunalianum* group was resolved as not monophyletic, necessitating taxonomic realignment. The previously proposed *Solanum* section *Dunaliana* is herein applied to the morphologically coherent clade of predominately New Guinean species of the *Solanum dunalianum* group. Likewise, *Solanum* section *Irenosolanum* is applied to the morphologically diverse clade of species from the Pacific Islands including the *S. sandwicense* group. *Solanum* section *Dunaliana* is resolved as sister to New Guinean species of the *S. ferocissimum* group. *Solanum* section *Irenosolanum* is resolved as sister to a clade consisting of Australian and New Guinean species of previously recognized groups. No unique synapomorphies support either section. However, general morphological trends exist in both sections.

Introduction

Solanum L. (Solanaceae) is a species-rich, economically important, and widely distributed genus. It is one of the ten largest genera of plants and is one of only nineteen with more than 1000 species (Frodin, 2004). *Solanum* includes the familiar crops tomato (*S. lycopersicum* L.), potato (*S. tuberosum* L.), and eggplant (*S. melongena* L.) as well as many lesser known edible species like the scarlet eggplant (*S. aethiopicum* L.), naranjilla or lulo (*S. quitoense* Lam.), and pepino (*S. muricatum* Ait.). *Solanum* has a cosmopolitan distribution absent only from Antarctica; it is most species rich in South America (D'Arcy, 1991) and likely originated there. *Solanum* has considerable infrageneric structure and several genus-wide phylogenetic investigations have evaluated the monophyly of the various infrageneric taxa (Bohs & Olmstead, 1997; Olmstead & Palmer, 1997; Bohs, 2005; and Weese and Bohs, 2007). Currently *Solanum* is divided into three subgenera, *Solanum* L., *Bassovia* (Aubl.) Bitter, and *Leptostemonum* (Dunal) Bitter, and numerous sections (Nee, 1999).

Subgenus *Leptostemonum* includes between 350 and 450 species, nearly a third of *Solanum* (Levin *et al.*, 2006). It has a cosmopolitan distribution, like *Solanum*, and is most species rich in Latin America, Africa, and Australia (Levin, *et al.*, 2006). The subgenus is characterized by a suite of three characters: presence of prickles on the stems, leaves, inflorescences, and/or calyces; stellate hairs on above ground organs; and attenuate anthers. However, one or more of these characters may be missing in a few species of subgenus *Leptostemonum*, and several of the characters can be found in species outside subgenus *Leptostemonum*. For example *S. rugosum* Dunal in subgenus *Solanum* section *Brevantherum* Seithe has stellate hairs.

Whalen (1984) wrote a conspectus on *Solanum* subgenus *Leptostemonum* where he divided the subgenus into unranked groups. One of these groups was the *Solanum dunalianum* group composed of twenty species from New Guinea, Northern Australia, the Philippines, and the South Pacific (see Appendix I). The *S. dunalianum* group, including *Solanum* [unranked] *Dunaliana* Bitter, was assigned the rank of section by Symon (1985) and many of the other species treated by Whalen (1984) in various groups have been assigned to formal ranks. However, to preserve clarity, Whalen's (1984) group names are consistently used herein; all species group discussed below are from Whalen (1984). Whalen (1984) characterized the *S. dunalianum* group as 2–6 m tall shrubs having a paucity of broad-based prickles, entire leaves that are typically glabrate adaxially with closely spaced brochidodromous lateral veins, inflorescences with tightly spaced hermaphroditic flowers which tend towards being tetramerous, and juicy red berries. He also proposed relationships between the *S. dunalianum* group and his *S. giganteum* group, *S. sandwicense* group, and *S. macoorai* group (Whalen, 1984). The *S. dunalianum* group as circumscribed by Whalen (1984) was essentially a combination of *Solanum* [unranked] *Dunaliana* Bitter and *Solanum* section *Irenosolanum* (Bitter) Bitter with a few additional species. Whalen's (1984) concept of a united *S. dunalianum* group differed from Bitter's concepts of his two taxa as Bitter (1919, 1921, 1922) did not indicate any relationships between them. The hypothesized close relationship of the *S. dunalianum* group with the *Solanum giganteum* group, which Whalen (1984) likely based on D'Arcy (1972), also contradicted Bitter's (1919, 1921, 1922) ideas concerning the taxa; when Bitter (1922) elevated *Solanum* series *Irenosolanum* Bitter to the sectional level, he stated that with its paucity of prickles *Solanum* section *Irenosolanum* was different from all other taxa of *Leptostemonum sensu* Dunal (1952).

Whalen's (1984) circumscription of the *S. dunalianum* group proved controversial. Symon (1985) and Bean (2004) accepted the inclusion of some species of *Solanum* section *Irenosolanum* within the *S. dunalianum* group but doubted the inclusion of some of the New Caledonian endemics. Instead, Symon (1985) and Bean (2004) believed these species to be more closely related to the *S. ferocissimum* group based on their morphology.

To date, two species of the *S. dunalianum* group have been included in phylogenetic analyses. *Solanum pancheri* was included in the molecular phylogenetic analysis of Levin *et al.* (2006) where it was resolved as sister to the two species sampled from the *S. sandwicense* group. The *S. pancheri* plus *S. sandwicense* group clade was nested in an unresolved clade of Australian species of the *S. ellipticum* group, *S. ferocissimum* group, *S. hystrix* group, and *S. macoorai* group. This clade was, in turn, nested in the poorly resolved Old World *Solanum* subgenus *Leptostemonum* clade, including the two species sampled from the *S. giganteum* group (Levin *et al.*, 2006). The analysis by Levin *et al.* (2006) provided information regarding the phylogenetic placement of *S. pancheri*, but the placement of the *S. dunalianum* group was not definitively resolved as the type species of the group, *S. dunalianum* Gaudich., was not included. *Solanum dunalianum* was included in a morphological cladistic analysis (Lepschi & Symon, 1999). In that study, *S. dunalianum* fell into the totally unresolved *Solanum* subgenus *Leptostemonum* clade, returning no more than subgeneric placement.

In light of the controversy concerning the unity, circumscription, and phylogenetic relationships of the *S. dunalianum* group, and the limited representation of the section in analyses, a phylogenetic study focused on the *S. dunalianum* group was conducted. This investigation focuses on: assessing the monophyly of the *S. dunalianum* group, revealing the phylogenetic affiliations of the section to other sections of subgenus *Leptostemonum*,

determining the relationships of the species within the section, and understanding the biogeographic history of subgenus *Leptostemonum* in Oceania.

Materials and Methods

An in-depth review of the taxonomic and floristic literature relevant to the *S. dunalianum* group was conducted. This review added three species, *S. incanoalabastrum* Symon, *S. bauerianum* Endl., and *S. peekelii* Bitter, which fall within the morphological circumscription of the *S. dunalianum* group. *Solanum incanoalabastrum*, named in 1985, was placed in the *S. dunalianum* group by Symon (1985). Whalen (1984) made no mention of either *S. bauerianum* Endl. or *S. peekelii* Bitter. However, *S. peekelii* was part of the *Solanum* großart *dunalianum* of Bitter (1919) and is quite similar to *S. dunalianum* morphologically. Likewise, *S. bauerianum* is morphologically similar to *S. viride* a relationship between the two had been proposed in the previously (Seemann, 1863).

A taxonomic investigation was also conducted to define species limits. Species were circumscribed using a morphological species concept similar to that of Nixon & Wheeler (1990), in which the least diagnosable units were recognized. Approximately 2,200 herbarium specimens including digital images constituting about 950 collections of the *S. dunalianum* group from the following herbaria were studied: A, AD, B, BH, BISH, BM, BRI, C, CAHUP, CANB, CAS, CBG, DS, E, ECON, F, G, GH, GOET, HAM, K, L, M, MEL, MICH, MO, MU, NLUH, NOU, NSW, NY, P, PNH, PTBG, RSA, S, SING, U, UC, US, UZH, VT, W, and WU (Theirs [continuously updated]). Protologues and type material were seen for all species of the *S. dunalianum* group to insure the accurate application of names and to evaluate the status of

synonyms. This taxonomic study led to the resurrection of four species placed under synonymy by Whalen (1984) and the identification of eight new species described in chapters 2 & 3. It also led to the exclusion of two species, *S. athroanthum* Dunal and *S. retrorsum* Elmer (as *S. luzoniense* Merrill in Whalen (1984)), from the *S. dunalianum* group. With the addition of fourteen species and the exclusion of two, the total number of species in the *S. dunalianum* group was thirty-one.

The practice of excluding species from a group prior to a phylogenetic analysis may seem questionable, however the case for doing so here is strong. Scant herbarium material exists for both *S. athroanthum* and *S. retrorsum*, and it is likely that Whalen was poorly acquainted with the species. Close examination of all available collections of these species reveal that they do not fall within Whalen's (1984) morphological characterization of the *S. dunalianum* group. Furthermore, excluding these species was justifiable as Whalen (1984) indicated that his species list for the *S. dunalianum* group was tentative, clearly leaving room for such minor adjustments. *Solanum athroanthum* differs from the *S. dunalianum* group by its deeply lobed juvenile leaves, prickles on the primary and secondary veins of the leaves, and anisandry, the androecium having three long anthers and two short ones per flower. Except for a single example of the second, these characters are not found in any members of the *S. dunalianum* group. *Solanum retrorsum* differs most strikingly from the *S. dunalianum* group by its often very dense armament of the stem with acicular prickles. And, both *S. athroanthum* from Bali and Java, Indonesia, and *S. retrorsum* from northern Luzon, the Philippines, are also geographic outliers, growing in different floristic regions. The two species were not included in the analyses presented here even “for good measure” as the scant herbarium material made coding morphological characters difficult and unreliable, a much larger group of Old World solanums would have been needed for the

morphological dataset, and all collections of these species were old and not well enough preserved for reliable DNA extraction. DNA extraction was unsuccessful for *S. retrorsum*. Consequently, DNA extraction was not attempted for *S. athroanthum* due the extreme scarcity of specimens.

Taxon sampling – For the morphological dataset, all thirty-one species of the *S. dunalianum* group were sampled. Sampling for the molecular dataset was restricted by the availability of silica dried material and modern specimens. For the most part, species known from one or a few herbarium specimens were not sampled because of the limited material. Likewise, species known only from very old specimens were not sampled, as reliable amplification of DNA was not expected due to several failed attempts on similar material. Isolation of DNA from herbarium specimens of several species was difficult or unsuccessful. In all, seventeen species of the *S. dunalianum* group were sampled. This included the type species of the *S. dunalianum* group, species from across the geographic range of the group, and species that Symon (1985) and Bean (2004) doubted belong in the *S. dunalianum* group. See Appendix II for a complete list and voucher information.

Outgroups – Some of the outgroup taxa were selected from other species groups that Whalen (1984) and Symon (1985) hypothesized were related to the *S. dunalianum* group but not included in it. These taxa were used to test the monophyly of the *S. dunalianum* group and included species of the *Solanum giganteum*, *S. macoorai*, *S. sandwicense*, and *S. ferocissimum* groups. Other more distantly related species that had not been hypothesized as close relatives to the *S. dunalianum* group were also included. These species included representatives from the Australian *S. ellipticum* and *S. hystrix* groups, the Asian and African *S. incanum* group, and the predominately New World *S. torvum* group (one Old World species and one New World species

were included), as well as the unplaced species *S. nienkui* Merrill & Chun. Most of the Australian species of the *S. ferocissimum*, *S. macoorai*, *S. hystrix*, and *S. ellipticum* groups were selected based on the availability of the DNA sequences produced by Levin *et al.* (2006). Additional species of the *S. ferocissimum* group from New Guinea were selected in order to include representatives of that group that were sympatric with the *S. dunalianum* group. Although these species were not treated by Whalen (1984), Symon (1985) placed them in *Solanum* section *Gracilliflora sensu* Symon (1981) equivalent to the *S. ferocissimum* group. The distantly related species *Solanum dulcamara* of *Solanum* subgenus *Solanum* (Weese & Bohs, 2007) was selected to root the molecular and total evidence trees. The Australia species *S. prinophyllum* of the *S. hystrix* group (not previously hypothesized as closely related to the *S. dunalianum* group) was selected to root the morphological tree. See Appendix II for species group representatives and voucher information.

DNA extraction and amplification – Genomic DNA was extracted from silica-dried samples and herbarium specimens using the Qiagen DNeasy plant mini kit following the manufacturer's protocol, a modification of the protocol of Alexander *et al.* (2007) replacing the reciprocating saw with a FastPrep™ FP120 and the chrome steel beads with ceramic bead and ca. 0.5 ml of garnet sand, or a modification of the CTAB protocol of Doyle & Doyle (1987) using a FastPrep™ FP120, ceramic bead, and garnet sand to grind samples rather than a mortar and pestle and incubating the samples for 24 hours in a Fisher Scientific Isotemp with the addition of 33 µL of β-mercaptoethanol per sample before the extraction with 24:1 chloroform to isoamyl alcohol.

Three regions were amplified: the entire internal transcribed spacer (ITS) region, the nuclear granule-bound starch synthase (GBSSI or *waxy*) gene from the 3' end of exon 1 to the 3'

end of exon 10, and the entire plastid *trnT-trnF* region. These regions have been shown to be useful for phylogenetic investigation of *Solanum* (Anderson *et al.*, 2006; Levin *et al.*, 2005, 2006; Weese & Bohs, 2007). Additionally, use of the same regions as previous workers allowed for a broader sample of outgroups and provided new compatible data for future studies. The reaction mixture for all PCRs was 14.3 μL of autoclaved ion-exchanged H_2O , 2.5 μL 10x PCR buffer [200 mM Tris pH 8.8, 100 mM KCl, 100 mM $(\text{NH}_4)_2\text{SO}_4$, 20 mM $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 1 % (v/v) Triton X-100, 50 % (w/v) sucrose, 0.25 % (w/v) cresol red], 2.5 μL dNTP's (2.5 mM stock of each dNTP), 2.5 μL bovine serum albumin (BSA; 0.25 $\mu\text{g } \mu\text{L}^{-1}$ stock), 1.0 μL F primer (10 mM stock), 1.0 μL R primer (10 mM stock), and 0.2 μL *Taq* polymerase with 1 μL DNA. For all amplification either a BIORAD DNAEngine[®] Peltier Thermo Cycler or a GeneAmp PCR[®] System 9700 thermocycler was used. PCR products were sequenced using the Big Dye terminator sequencing kit version 3.1 (Applied Biosystems, Carlsbad, CA) with an ABI 3700 sequencer (at the High Throughput Genomics Unit, University of Washington, Seattle, WA).

ITS was amplified whole using primers ITSleu1 (Vargas *et al.* 1998) and ITS4 (White *et al.*, 1990), or ITS 1 and ITS 2 were amplified separately using the internal primers ITS 2C58S (Suh, *et al.*, 1993) and ITS 5HP (Hershkovitz and Zimmer, 1996). For all ITS amplifications the following thermocycler program was used: 4 minutes at 94°; 30 cycles of 94° for 45 seconds 50° for 1 minute 72° for 1 minute; 72° for 7 minutes.

Waxy was amplified in two pieces. The primers 1171R (Walsh and Hoot (2001)) and 181F (Levin *et al.* (2005) modified from Walsh & Hoot (2001)) were used for amplifying the 5' end. The primers 1058f (Levin *et al.* (2006)) and 2R (Levin *et al.* (2005) modified from Miller *et al.* (1999)) were used for amplifying the 3' end. For all *waxy* amplifications the following thermocycler program was used: 94° for 4 minutes; 2 cycles of 94° for 30 seconds, 55° for 1

minute 72° for 2 minutes; 2 cycles of 94° for 30 seconds, 45° for 1 minute 72° for 2 minutes; 94° for 30 seconds, 53° for 1 minute 72° for 2 minutes; 94° for 30 seconds, 52° for 1 minute 72° for 2 minutes; 94° for 30 seconds, 51° for 1 minute 72° for 2 minutes; 30 cycles of 94° for 30 seconds, 50° for 1 minute 72° for 2 minutes; 72° for 10 minutes.

The region *trnT-trnF* was amplified in two pieces. The primers Tab a and Tab b (Taberlet et al. 1991) were used to amplify *trnT-trnL*; *trnL-trnF* was amplified using primers Tab c & Tab f (Taberlet et al. 1991). For all these amplifications the following thermocycler program was used: 95° for 2 minutes and 30 seconds; 34 cycles of 95° for 30 seconds; 48° for 30 seconds; 72° for 1 minute; 72° for 10 minutes.

Sequence alignment – Contigs were assembled using the sequence analysis software Sequencher version 4.9 (Gene Codes Corporation, Ann Arbor, MI USA). DNA sequences were initially aligned using the program Multiple Sequence Comparison by Log- Expectation (MUSCLE) (Edgar, 2004) accessed through the website: www.ebi.ac.uk/Tools/msa/muscle/. The resulting alignments were reviewed using Sequencher version 4.9 and, when necessary, indel edges were manually realigned to eliminate obvious inconsistencies; the least potentially phylogenetically informative alignments were always selected. Indels were coded using simple indel coding with the program FastGap v. 1.0.8 (Borchsenius, 2007).

Morphological data – Character states were assessed through a combination of field observations of living plants, observations of herbarium material, and consultation of the literature. For some species most of the characters were scored from living material while for others, no living material was seen. Due to the morphological plasticity of *Solanum* the capability to have a character state sometimes replaced strict presence/absence designations. For example, some species in the *S. dunalianum* group are capable of producing prickles though on

an individual collection prickles may be lacking. Other species are incapable of producing prickles as they are never present regardless of the growth phase or environmental conditions. In this situation the former species were coded as “prickles present” while the latter were coded as “prickles absent.”

The following fifty-eight characters were used in the analysis. All but one were potentially phylogenetically informative. Two multistate characters, numbers 16 and 17, were coded as additive; the remaining multistate characters were coded as non-additive. (See Appendix III for the morphological matrix.)

1. Stature: shrub (0); small tree (1). Solanums are rarely large trees and many of the larger species are described as shrubs or small trees. However, many species of subgenus *Leptostemonum* are strictly shrubs and could never be described as small trees. Here the shrubs and trees are coded as separate character states to account for this distinction. Species that can be small trees (several meters tall) even if reported as “shrubs or small trees” are coded as trees.

2. Erectness: erect (0); prostrate to semi-erect (1). This character distinguishes between species that are erect and freestanding and those that are lax and sprawling, scandent and depending or surrounding vegetation for support, or prostrate.

3. Type of non-erect habit: sprawling (lax) (0); scandent (1); prostrate (2). This character compliments character 2 by segregating different non-erect states. It is not potentially informative for the taxa sampled here. This character was coded as inapplicable for erect taxa.

4. Rhizomatous habit: absent (0); present (1). Some species of *Solanum* spread through the production of rhizomes to form clusters or colonies while other species do not. Such growth forms yield important differences in adaptive capabilities. Bean (2004) listed some species of the *S. dunalianum* group from Australia as rhizomatous; however, Lepschi & Symon (1999) coded

these species as not rhizomatous in their morphological matrix. No indication has been found in herbarium material suggesting a rhizomatous habit in the species listed as such by Bean (2004). Therefore, in agreement with Lepschi & Symon (1999), they are treated as not rhizomatous here.

5. Short shoots: absent (0); present (1). Most species of *Solanum* do not produce dimorphic shoots. However, several species from New Caledonia produce short lateral shoots that bear the leaves and inflorescences after the primary leaves of the long shoots have fallen off.

6. Branch robustness: robust (0); gracile (1). The branches of several species from New Caledonia are quite thin (ca. 1 mm in diameter). These branches differ strikingly from those of typical solanums.

7. Transparent sloughing epidermis on the mature stems: absent (0); present (1). Several species from New Caledonia and one from Fiji produce a thickened epidermis on young shoots. This unusual, transparent layer sloughs off as the stems mature.

8. Prickles on the stem: absent (0); present (1). Presence of prickles is a synapomorphy for subgenus *Leptostemonum*. However, many species of subgenus *Leptostemonum* from the Pacific do not have prickles at all. Except for *Solanum abollatum*, all species of subgenus *Leptostemonum* from the Pacific that are capable of producing prickles at any point during development or under certain environmental conditions produce them at least on their stems. Therefore, this character also acts as a surrogate for a prickle presence/absence character, which is not coded to prevent over-emphasis.

9. Prickle type: broad-based (0); aciculate (1). Many groups of subgenus *Leptostemonum* produce either broad-based or aciculate prickles, thus prickle type can be phylogenetically important. For all species that never produce prickles, this character and the other prickle characters hereafter are inapplicable.

10. Curvature of the prickles on the stem: straight (0); retrorse (1). Prickle shape can provide different adaptive advantages. Retrorse prickles aid scandent species to cling to surrounding vegetation rather than simply acting as a defense against herbivory.

11. Leaf size: reduced (0); normal (1). Like other characteristics of the leaves, size is variable within limits in subgenus *Leptostemonum*. However, some species consistently produce small leaves, only a few centimeters long, and are incapable of producing larger more typically sized leaves.

12. Leaf arrangement: solitary (0); geminate (1). *Solanum* exhibits sympodial branching. Some species have all sympodial units \pm equal in length resulting in the leaves being solitary along the stem. Other species have unequal sympodial units alternating between long and condensed. In these species, the leaf of the condensed unit is borne adjacent to the leaf of the long unit below resulting in geminate clusters of leaves along the stem.

13. Leaf texture: chartaceous (0); subcoriaceous (1); semisucculent (2). The leaves of most species of *Solanum* are chartaceous. The leaves can also be thick, though truly leathery leaves are lacking. Species with thick leaves are assigned the character state subcoriaceous to distinguish them from thin leaved species. A few species in New Caledonia have unusually thick leaves that are somewhat succulent. The leaves of living material have almost a rubbery feel, and in herbarium specimens the leaves have a characteristic wrinkled surface from the drying process.

14. Lobes on immature leaves: absent (0); present (1). In *Solanum*, the lobing of the leaves often differs between juvenile and mature growth. Typically, juvenile leaves are more lobed than mature leaves. This phenotypic plasticity can lead to drastically different leaf morphologies on a single individual or between different individuals of the same species. However, some species of

Solanum never have lobed leaves. Lobing of immature leaves was only coded as absent for those species that never have lobed juvenile leaves.

15. Lobes on mature leaves: absent (0); present (1). Some species of *Solanum* have lobed mature leaves while others have entire mature leaves. For a species to be assigned the character state of absent, the mature leaves are never lobed.

16. Prickles on the adaxial surface of the leaves: absent (0); on the primary vein only (1); on the primary and secondary veins (2); on the primary, secondary, and tertiary veins (3) (additive). This character and character 17 are additive. When prickles are present on the leaves of subgenus *Leptostemonum* they are always produced on a vein. Prickles are not present on the secondary veins without being present on the primary vein; likewise, prickles are not present on the tertiary veins without also being on the secondary veins and the primary vein. Therefore, the character was coded as additive. Presence of prickles can differ between the adaxial and abaxial surfaces of the leaves. Presence of prickles on the abaxial surface of the leaves is coded in character 17.

17. Prickles on the abaxial surface of the leaves: absent (0); on the primary vein only (1); on the primary and secondary veins (2); on the primary, secondary, and tertiary veins (3) (additive).

18. Multangulate hairs type C of Roe (1967) on the adaxial surface of the leaves: absent (0); present (1).

19. Multangulate hairs type B of Roe (1967) on the adaxial surface of the leaves: absent (0); present (1).

20. Simple hairs on the adaxial surface of the leaves: absent (0); present (1).

21. Longevity of the stellate indumentum on the abaxial surface of the leaves: deciduous (0); persistent (1). The longevity of the stellate pubescence can differ between the abaxial and adaxial surfaces of the leaves. For example, in some species both surfaces are pubescent when the leaves

are young, but the adaxial surface is glabrescent while the hairs of the adaxial surface are persistent. Therefore, longevity of the stellate indumentum is coded separately as character 22.

22. Longevity of the stellate indumentum on the adaxial surface of the leaves: deciduous (0); persistent (1).

23. Prickles on the petioles: absent (0); present (1). Even though the midvein of the leaf is essentially an extension of the petiole, prickles can be present on the petiole but absent from the midvein. Therefore, this character was coded separately from characters 16 and 17.

24. Orientation of the lateral veins: craspedodromous (0); semicraspedodromous (1); brochidodromous (2); joining a pseudointermarginal vein (3). Character state 3 is an extreme form of brochidodromous venation where the proximal and distal portions of the lateral veins have distinctly different orientations, the proximal section being \pm perpendicular to the midvein while the distal portion lies parallel to the margin of the leaf.

25. Position of the inflorescence on the stem on mature growth: appearing terminal and not soon overtopped (0); appearing lateral, overtopped by the lateral branch (1). The inflorescences of *Solanum* are developmentally terminal. Typically, however, they appear lateral due to the growth of the subtending lateral meristem. Additionally, they are often concaulescent with the hypopodium or mesopodium of the subtending lateral meristem resulting in an extra-axillary position. In some species in New Caledonia, the inflorescences appear terminal on short lateral shoots and are not soon overtopped.

26. Rachis of the inflorescence length: greatly reduced and nearly absent or absent (0); well-developed (1). Typically solanums have inflorescences with well-developed rachices and are many-flowered, but some have sessile or sub-sessile inflorescences with solitary or few flowers.

27. Peduncle: absent (0); pseudo-peduncle present (1); true peduncle present (2). *Solanums* can have or lack a peduncle. Some species produce a pseudo-peduncle with a single flower at the base of the inflorescence with a section of the inflorescence rachis free of flowers directly above. The remaining flowers of the inflorescence are produced on the distal portion of the rachis.

28. Prickles on the axis of the inflorescence: absent (0); present (1).

29. Inflorescence branching: unbranched (0); branching (1). The ability to produce branching inflorescences varies. Some species never have branching inflorescences while others are capable of producing many-branched ones. To be assigned the character state “unbranched,” the inflorescences of a species are never branched. Species capable of having branching inflorescence are assigned the state “branching” even if unbranched inflorescences are sometimes produced.

30. Infructescence attitude: fruit held erect (0); fruit inverted (1). The angle at which the fruits are presented to potential dispersers differs. Some fruits are held erect with the apex of the fruit uppermost. Others are inverted with the apex directed towards the ground.

31. Pedicel rigidity: rigid (0); limp (1). While the pedicels of most species of subgenus *Leptostemonum* are rigid, holding the flowers or fruit at a particular angle, the pedicels of some species are limp, allowing the flowers and/or fruits to dangle freely from the inflorescence.

32. Prickles on the pedicel: absent (0); present (1).

33. Terminal pedicel bulge: absent (0); present (1). In fruit, a bulge is present at the distal end of the pedicels immediately below the calyx of some species of *Solanum* (see Figure 1). In some species, the bulge is accentuated below each calyx lobe, while in others it is more uniform. The function of this bulge is unknown.

34. Pedicel bent below the calyx in flower: not bent (0); bent to $\pm 90^\circ$ (1). The pedicels of some species are abruptly bent below the calyx at anthesis (see Figure 1). This reorients the flower, often directing it towards the ground. The bend can straighten out after anthesis or persist as the fruit ripens.

35. Pedicel diameter in flower and fruit: \pm uniform along the length of the pedicel (0); distinctly enlarged distally (1).

36. Change in the diameter of the pedicel in flower and fruit: evenly increasing from the base to the calyx (0); only the distal 1/2–2/3 increasing in diameter to the calyx (1).

37. Flower sex: imperfect flowers present or potentially so (0); all flowers perfect (1). Some species of subgenus *Leptostemonum* are andromonoecious or functionally dioecious (Anderson & Symon, 1989) while others have all flowers perfect. The former are coded as character state 0 while the latter are coded as character state 1.

38. Prickles on the calyx: absent (0); present (1).

39. Opacity of the intersepal tissue: translucent when dry (0); opaque when dry (1). This character was always scored from herbarium material.

40. Accrescence of the calyx in fruit: not accrescent (0); accrescent (1).

41. Outline of the corolla in bud: globose (0); elongate (1) (see Figure 1).

42. Surface of the corolla of the mature flower bud: smooth (0); ridged along the margins of the midribs of the petals (1). The surface of the corolla of most species of *Solanum* is smooth until anthesis. The surface of the corolla of several species however becomes ridged along the margins of the midribs just before anthesis (see Figure 1).

43. Corolla shape: \pm flat (0); campanulate (1).

44. Outline of the corolla: stellate (0); stellate-rotate (1).

45. Development of the interpetalar tissue: poorly-developed (0); well-developed (1). The interpetalar tissue of the corolla can be variously developed. Some species have little interpetalar tissue resulting in relatively large corolla lobes. Other species have well-developed interpetalar tissue and thus shorter corolla lobes. The stellate-rotate corollas of some species have exceedingly well-developed interpetalar tissue altering the general outline of the corolla. Species with the corolla tube less than 1/3 the length of the corolla are coded as poorly-developed, while those with the corolla tube over half the length of the corolla are coded as well-developed. Fortunately, intermediates were not encountered here.

46. Color of the laminar tissue of the corolla: white (0); purple, various shades (1). *Solanums* typically have either white or purple flowers though yellow, off-white, and greenish flowers occur as well. Some species can have either white or purple flowers depending on environmental conditions while other species are restricted to either white or purple flowers. In purple-flowered species, the shade can be affected by environmental conditions; shades of purple extend from pale lilac to dark violet. Here all shades of purple are coded as one character. This accounts for environmental factors as well as differences in the perception of shades by collectors. A few species produce flowers with white laminar tissue and purple primary or primary and secondary veins. This character is restricted to the laminar tissue and excludes the veins, therefore these species are coded as white.

47. Color pattern of the corolla: concolorous (0); bicolorous (1). Several species in the Hawaiian Islands have bicolorous petals where the primary or primary and secondary veins of the petals are purple while the laminar tissue is white.

48. Anther curvature: straight or nearly so (0); arcuate (1). The anthers of most species of *Solanum* are straight or slightly inwardly curved. As these two conditions differ only slightly

they are coded together. A few species from Hawaii have very strongly incurved anthers. These are coded as arcuate (see Figure 1).

49. Degree of attenuation of the anthers: markedly attenuate (0); scarcely or not attenuate (1). A synapomorphy for subgenus *Leptostemonum* is attenuate anthers. However, several species from the Pacific have oblong anthers or only very slightly attenuate anthers. Species with oblong anthers and those with the anthers nearly oblong are assigned the character state 1.

50. Anther dehiscence: poricidally dehiscent (0); longitudinally dehiscent (1). *Solanum* is typified by poricidally dehiscent anthers. However, a few species from the Pacific have longitudinally dehiscent anthers where the lateral sutures of the anthers split most of the way to the base to release the pollen.

51. Anther position at anthesis: spreading (0); connivent (1). Whether the anthers are connivent forming a cone and functioning as a single unit or spread apart and functioning independently affects the pollination of the species. If the anthers are held apart and could not be reasonably grasped by a pollinator as one unit, the species is coded as character state 0.

52. Style shape: straight (0); curved or hooked towards the tip (1); sigmoid (2).

53. Emergence of the style from the stamens: between the apices of the anthers (0); between the side of two adjacent stamens (1). This character and character 52 are independent. For example, some species of *Solanum* section *Archosolanum* (Bitter ex Marzell) Danert have straight styles that emerge between the sides of the anthers as they are flexed at the base. However, this character and character 52 are correlated in the species sampled here.

54. Relative lengths of the styles: homostylous (0); heterostylous (1). Most species of *Solanum* are homostylous. Some species are heterostylous due to the presence of functionally unisexual flowers; however, here character state 1 is applied only to fertile flowers.

55. Position of the pubescence on the ovary: evenly distributed (0); restricted to the base (1); restricted to the apex (2). The pubescence for this character can be stellae, simple glandular hairs, or minute glandular hairs. The hair types present on an individual ovary can vary within a species especially when only a few hairs are present, however the position does not. In this analysis, only the position of the hairs on the ovary is scored. The limited availability of herbarium material for many species made accurate assessment of hair types on the ovary unreliable.

56. Coloration of immature fruit: evenly green (0); striped or mottled with light and dark green (1). This character was scored from living material, photographs, and the literature. Many collectors do not note any patterns of green marking on immature fruit and the character is usually lost in herbarium material. The difficulty in accurately assessing this character for species not seen living led to a large percentage of missing data for this character.

57. Mature fruit color: red or orange (0); black (1); yellow (2); brown (4); green (5); purple (6). For species not seen living by me, the literature and herbarium specimen labels were used to assess this character. Subtle shades were not used as many collectors record colors with differently. Several species of *Solanum* have fruits that are green at maturity. However, as immature fruits of *Solanum* are also green, extra attention was paid to the scoring of this character state.

58. Moistness of the fruit at maturity: juicy (0); dry (1). Most species of *Solanum* have juicy berries, while comparatively few have fruits that are dry at maturity. For species not seen living, this character was scored from the literature and from herbarium material where the two states were easily discernible.

Phylogenetic analyses – Six separate parsimony analyses were conducted. Each molecular region was analyzed individually, and an analysis was performed on the combined molecular dataset. The morphological dataset was analyzed alone and with the combined molecular dataset for a total evidence analysis. For all six parsimony analyses the program “Tree analysis using New Technology” (TNT) (Goloboff *et al.*, 2008) was used; to help insure that all most parsimonious trees were found, all datasets were analyzed with the Ratchet (Nixon, 1999) (2000 iterations), Drift (50 iterations), Tree fusing (10 iterations), and Random Sectorial Search algorithms. Except for the number of iterations, the default settings were used for all algorithms. Branch support was assessed with jackknife support values based on 1000 iterations with 100 search replicates, 1 starting tree per replicate, and tree bisection-reconnection (TBR) branch swapping to 100 trees maximum, saving the consensus tree.

Results

Sequence alignment and molecular phylogenetic analyses – The aligned *trnT-trnF* dataset was 2104 base pairs long and contained 42 (2.0%) potentially informative characters. The aligned dataset contained 44 indels of which 10 (22.7%) were potentially informative. The analysis of *trnT-trnF* produced 1002 MPTs with a length of 73, CI of 0.73, and RI of 0.84., and the strict consensus of the MPTs was very poorly resolved. All species of the *S. dunalianum* group except *Solanum tetrandrum* fell into a single poorly resolved clade with most of the Australian and all of the New Guinean and Hawaiian outgroup taxa (see Figure 2).

The aligned ITS dataset was 770 base pairs long of which 83 (10.7%) were potentially informative. The aligned dataset contained 47 indels of which 24 (51.1%) were potentially

informative. The analysis of ITS yielded 279 most parsimonious trees (MPTs) with a length of 299, CI of 0.44, and RI of 0.61. In the strict consensus of the MPTs, all species of the *S. dunalianum* group, except *Solanum tetrandrum* fell into a large poorly resolved clade including almost all of the Australian, New Guinean, and Hawaiian outgroup taxa. The subclades within this clade were primarily species pairs; however, the eight species of the *S. dunalianum* group sampled from New Caledonia formed a partially resolved clade (see Figure 3).

The aligned *waxy* dataset was 1851 base pairs long of which 66 (3.6%) were potentially informative. The aligned dataset contained 31 indels of which 8 (25.8%) were potentially informative. The analysis of *waxy* returned 343 MPTs with a length of 99, CI of 0.82, and RI of 0.90. The strict consensus of the MPTs contained a clade with all species of the *S. dunalianum* group, except *Solanum tetrandrum*, and the Australian and New Guinean outgroup taxa of the *S. ferocissimum*. This clade was more resolved than the equivalent clade in the ITS and *trnT-trnF* strict consensus trees. In the *waxy* strict consensus tree, the *S. dunalianum* group was not monophyletic. The species from New Guinea and the Solomon Islands formed a clade with a New Guinean outgroup species of the *S. ferocissimum* group. This clade was nested in a clade with Australian species of the *S. ferocissimum* group. The remainder of the *S. dunalianum* group, except *S. tetrandrum*, formed a poorly resolved clade with *S. trichostylum*, another species of the *S. ferocissimum* group from New Guinea, and the species of the *S. sandwicense* group (see Figure 4).

The combined molecular dataset was 4861 characters long with 233 (4.8%) potentially informative, including coded indels. The analysis of the combined molecular dataset resulted in 90 MPTs with a length of 538, CI of 0.58, and RI of 0.69. The strict consensus reflected the topologies of the individual analyses and was relatively well resolved with twenty-five nodes

maintained; eleven nodes collapsed. In the strict consensus, the *S. dunalianum* group was resolved as polyphyletic. All the species except *Solanum tetrandrum* fell into either of two clades; as in the individual analyses, *S. tetrandrum* formed a clade with *S. melongena* L. The two main clades containing the *S. dunalianum* group were similar to those of the *waxy* strict consensus tree. They differed primarily in that *S. trichostylum*, an outgroup species from New Guinea, fell with the other New Guinean species (see Figure 5).

Morphological analysis – The cladistic analysis of the morphological dataset yielded 144 MPTs with a length of 217, CI of 0.32, and RI of 0.71. In the strict consensus, the *S. dunalianum* group, including *Solanum tetrandrum*, was resolved as paraphyletic with the *S. sandwicense* group nested within it. The entire *S. dunalianum* group plus the *S. sandwicense* group clade was sister to a clade of New Guinean species of the *S. ferocissimum* group. This larger clade was in turn sister to Australian species of the *S. ferocissimum* group. A clade composed of species from the *S. dunalianum* group from New Guinea, northern Australia, and the Solomon Islands was recovered, as in the combined molecular analysis. Likewise the remainder of the *S. dunalianum* group from various Pacific islands formed a second clade with species of the *S. sandwicense* group (see Figures 6 and 7). The paraphyletic rather than polyphyletic grouping of the *S. dunalianum* group in this analysis was to some extent an artifact of rooting of the tree.

Total evidence – The total evidence dataset consisted of 4919 characters of which 290 (5.9%) were informative. The analysis of this dataset resulted in 35 MPTs with a length of 737, CI of 0.45, and RI of 0.68. In the well resolved strict consensus, the *S. dunalianum* group was not resolved as monophyletic. As in the other analyses, *Solanum tetrandrum* fell well away from the other species of the *S. dunalianum* group forming a clade with *S. melongena*. The remaining species of the *S. dunalianum* group were distributed between two clades equal to *Solanum*

sections *Dunaliana* and *Irenosolanum*. *Solanum* section *Dunaliana*, from New Guinea, Queensland, Australia, and the Solomon Islands, was sister to a clade of New Guinean species of the *S. ferocissimum* group. The *Solanum* section *Dunaliana* plus the New Guinean *S. ferocissimum* clade was sister to a clade composed of all the Australian outgroup species of various groups. *Solanum* section *Irenosolanum* from various Pacific islands formed a clade sister to the Australian/New Guinean clade (see Figure 8).

Discussion

Monophyly and taxonomy – In this study, the *Solanum dunalianum* group was resolved as not monophyletic in all the analyses. In light of these findings, taxonomic realignment is necessary. The taxonomic changes proposed herein are based on the strict consensus of the total evidence analysis. In that tree all but one of the species of the *S. dunalianum* group fell into either of two distinct clades (see Figure 8). These clades correspond to *Solanum* section *Dunaliana sensu* Bitter (1919) and *Solanum* section *Irenosolanum sensu* Bitter (1921, 1922), which includes the *Solanum sandwicense* group. Therefore, *Solanum* section *Dunaliana* is herein restricted to the clade containing six species, including *S. dunalianum*, from New Guinea, Queensland, Australia, and the Solomon Islands, and *Solanum* section *Irenosolanum* (Bitter) Bitter is applied to the clade containing the species from Fiji, New Caledonia, Lord Howe and Norfolk Islands, Polynesia (except New Zealand), and the Marianas Islands. *Solanum tetrandrum*, which fell outside the *Solanum* section *Dunaliana* and *Solanum* section *Irenosolanum* clades, formed a clade with *S. melongena*. Sampling of more species from Southeast Asia is needed to place *S. tetrandrum* with more precision, but the affinity of *S.*

tetrandrum with Asian species of *Solanum* is not altogether a surprise given the proximity of the Lesser Sunda Islands to the northern end of the Northern Territory, Australia, where *S. tetrandrum* occurs.

Sectional relationships – Whalen (1984) proposed relationships between the *Solanum dunalianum* group and several other groups. He hypothesized that the *S. dunalianum* group was closely related to the *S. giganteum* group and perhaps not meaningfully distinct. This hypothesis was also propounded by Symon (1985); however, both the present study and Levin *et al.* (2006) reject it. Whalen (1984) also proposed a distant relationship between the *S. dunalianum* group and the *S. macoorai* group, which is supported for *Solanum* section *Dunaliana* by the combined molecular and total evidence analyses of this study; likewise, he proposed a probable, though old, relationship between the *S. sandwicense* group and the *S. dunalianum* group of the western Pacific, i.e. *Solanum* section *Irenosolanum*. In fact, the *S. sandwicense* group is nested within *Solanum* section *Irenosolanum* in the combined molecular, morphological, and total evidence analyses. Symon (1985) and Bean (2004) doubted Whalen's (1984) inclusion in the *S. dunalianum* group of New Caledonian species with reduced leaves and inflorescences believing them to be more closely related to the *S. ferocissimum* group than other to species of the *S. dunalianum* group. The results presented here support the distinctness of these species; however, it is *Solanum* section *Dunaliana* that is resolved as closely related to the *S. ferocissimum* group in New Guinea. The New Caledonian species in question are instead related to the remaining New Caledonian species and species of the other Pacific islands. The phylogenetic placement of *S. pancheri* does not differ between this study and that of Levin *et al.* (2006), but, due to the taxonomic realignment herein, the conclusions about the relationship of *Solanum* section *Dunaliana* and the *S. sandwicense* group do.

Solanum section *Dunaliana* – *Solanum* section *Dunaliana* consists of six morphologically coherent species. However, no unique synapomorphies for *Solanum* section *Dunaliana* were found in this analysis. The *Solanum* section *Dunaliana* clade was supported by five characters in both the total evidence analysis (characters 21, 22, 29, 30, and 39) and the morphological analysis (characters 1, 21, 22, 29, and 39), but all these characters also occur in species of other groups (see Figures 6, 7, and 9). Nonetheless, *Solanum* section *Dunaliana* can be characterized by the following: small trees with glabrescent stems and a general paucity of prickles; leaves typically glabrescent and never lobed; inflorescences branching and many-flowered; berries juicy and red at maturity. The geographic distribution of *Solanum* section *Dunaliana* is centered on the island of New Guinea where the section most likely originated given its sister relationship to other New Guinean species (see Figure 8). Within *Solanum* section *Dunaliana*, resolution is poor and more data is needed to determine the relationships among the species.

Solanum section *Irenosolanum* – *Solanum* section *Irenosolanum* consists of twenty-nine morphologically dissimilar species. These species range from small bushes to small trees. They can be prostrate, scandent, or erect, glabrous or densely pubescent, and armed or more typically unarmed. The leaves can be lobed or entire, and the inflorescences can be large and many-flowered or reduced to a single or a few flowers. The section is distributed across the islands of the Pacific with centers of diversity in New Caledonia, Fiji, and Hawaii. *Solanum* section *Irenosolanum* is composed of two main clades with distinct geographic distributions. All the species from New Caledonia and Vanuatu, with the addition of a single species from Fiji, form one of these clades while the remaining species from across the Pacific form the second clade (see Figure 8). Based on the analyses presented here, *Solanum* section *Irenosolanum* originated in the western Pacific though its exact center of origin is unclear. Likely, it is derived from an

Australian group, but broader sampling of Australian species is needed to adequately resolve this question. However, it is clear from the total evidence analysis that *Solanum* section *Irenosolanum* colonized the Pacific islands from west to east with the species in the Hawaiian Islands being the most derived. The Marianas Islands, Lord Howe and Norfolk Islands, and Tonga each have a single endemic species from the section. For the three island groups with more than one endemic species, two had a single introduction while the third had two introductions. A single introduction accounts for all fourteen species in the region composed of New Caledonia and Vanuatu. Likewise, a single introduction into the Hawaiian Islands accounts for the six endemic species there. Two introductions of *Solanum* section *Irenosolanum* gave rise to the five endemic species in the Fijian Islands. Of these species, one is derived from the New Caledonia and Vanuatu clade while the remaining four belong to the widely dispersed clade.

Like *Solanum* section *Dunaliana*, no unique synapomorphies for *Solanum* section *Irenosolanum* were found in this analysis. *Solanum* section *Irenosolanum* is supported by the presence of white laminar tissue (character 46) in the total evidence analysis and the morphological analysis. In the morphological analysis, the clade was also supported by having leaves borne individually instead of in geminate clusters (character 12), though both character states are represented in *Solanum* section *Irenosolanum*. One phenomenon found across *Solanum* section *Irenosolanum* is the orientation of the flowers towards the ground at anthesis. This orientation is a result of either the pedicels being limp and hanging freely or the pedicels being bent to $\pm 90^\circ$ just below the calyx. This phenomenon was not included in the analysis as the statement of homology could be questionable. Perhaps with more field study a transition series might be found.

Relationships within *Solanum* section *Irenosolanum* are well resolved, with several synapomorphies supporting subclades in both the morphological and total evidence analyses (See Figures 6, 7, and 9). Of these, some have a single origin and are of particular interest. The presence of arcuate anthers (character 48) supports the *S. sandwicense*, *S. nelsonii*, and *S. caumii* clade from Hawaii, and these highly incurved anthers are unique within *Solanum*. The clade consisting of *S. viride* and the former *S. sandwicense* group is supported by the presence of a terminal bulge on the peduncle (character 33) and a ridged surface of the corolla in mature bud (character 42) (see Figure 1). The presence of heterostyly (character 54) supports the clade consisting of *S. inamoenum*, *S. viride*, and the former *S. sandwicense* group. These four characters all have a single origin in this analysis. A globose corolla in bud (character 41) supports the clade consisting of *S. albertii*, *S. pseudopedunculatum*, *S. ratale*, *S. bauerianum*, *S. inamoenum*, *S. viride* and the former *S. sandwicense* group, but is also found in *S. nudatum*. In New Caledonia, the clade composed of *S. hugonis*, *S. vaccinioides*, *S. actephilum*, and *S. camptostylum* is supported by a semi-erect habit (character 2), presence of retrorse prickles (character 10), sigmoid styles (character 52), and emergence of the styles between the sides of the anthers rather than from between their tips (character 53). In these species, the semi-erect habit and retrorse prickles are not altogether independent from each other as they are scandent shrubs, using the prickles to cling to surrounding vegetation. Nonetheless, this represents a single origin of the scandent habit in *Solanum* section *Irenosolanum*. Characters 52 and 53 are also present in *S. vanuatuense* but are otherwise unique in *Solanum* section *Irenosolanum*. A larger clade including the New Caledonian clade discussed above and *S. insulae-pinorum*, *S. pancheri*, and *S. pseuderanthemoides* also from New Caledonia is supported by the presence of short shoots (character 5), gracile branches (character 6), and terminal inflorescences not soon

overtopped (character 25). These characters are all unique to this clade in this analysis. This larger clade with the addition of *S. nudatum* from Fiji is also supported by the presence of reduced leaves.

Three morphologically similar species from New Caledonia, *S. semisucculentum*, *S. memaoyanum*, and *S. leratii* have unusual semisucculent leaves (character 13); however, this character failed to unite these species in the strict consensus trees. Longitudinally dehiscent anthers, an extremely uncommon condition in *Solanum*, are present in three species of *Solanum* section *Irenosolanum*. These species do not form a clade and represent three independent origins of this unusual adaptation.

Future directions – Although all thirty-five species of *Solanum* section *Dunaliana* and *Solanum* section *Irenosolanum* were sampled for the morphological dataset, only twenty were sampled for the molecular dataset. Five of the six species of *Solanum* section *Dunaliana* were represented in the molecular dataset, but not all regions were successfully amplified from herbarium specimens (no silica-dried material was available for these species). Molecular markers were successfully amplified for only fifteen of the twenty-nine species of *Solanum* section *Irenosolanum* though again the dataset was not complete. Though not possible for the few extinct (or probably extinct) species of *Solanum* section *Irenosolanum*, collection of and amplification of molecular markers from silica-dried samples of the remaining species would provide a more complete phylogeny. Likewise, the development of more informative (i.e. variable) molecular markers is desirable for constructing a more robust phylogeny.

Expanded outgroup sampling would provide more detailed hypotheses of intersectional relationships and biogeographic histories of *Solanum* sections *Irenosolanum* and *Dunaliana*. Inclusion of a broader sample of *Solanum* section *Graciliflorum* from New Guinea would

determine the specific relationship of *Solanum* section *Dunaliana*. And, expanded sampling from the Sunda Islands, Lesser Sunda Islands, and Southeast Asia would clarify the placement of the native sections of *Solanum* subgenus *Leptostemonum* of Australia, New Guinea, and the Pacific in the broader context of subgenus *Leptostemonum* in the Old World. Unfortunately, the species of these areas are poorly known and much more work is needed to accomplish this end. All this notwithstanding, the preliminary results provided here represent another step towards understanding the diversity and history of *Solanum* subgenus *Leptostemonum*.

Additional notes – *Solanum nienkui* Merrill & Chun, from China and not previously sampled in a phylogenetic analysis, falls in the main clade of Old World species of subgenus *Leptostemonum* found by Levin *et al.* (2006). This species is anisandrous like *S. athroanthum*, having three long anthers and two short ones per flower. As the two species share this unusual character, they may be phylogenetically close. *Solanum inaequilaterale*, from the island of Luzon in the Philippines and also not previously sampled, formed a clade with the New World *S. torvum*. Whalen (1984) placed *S. inaequilaterale* in the *S. torvum* group a placement that has been the subject of some informal skepticism. The results herein, however, support Whalen's (1984) grouping and would indicate an additional introduction of subgenus *Leptostemonum* to the Old World.



Figure 1. Illustration of selected character states. A. *Solanum sandwicense* open flower and flower buds showing arcuate anthers (character 48) and globose corollas in bud (character 41); B. Immature fruit of *S. sandwicense* showing the terminal bulge on the pedicel (character 33). C. Inflorescence of *S. nelsonii* showing flexion of the pedicel below the calyx at anthesis (character 34). D. Flower bud of *S. viride* showing ridged corolla of mature flower bud (character 42).

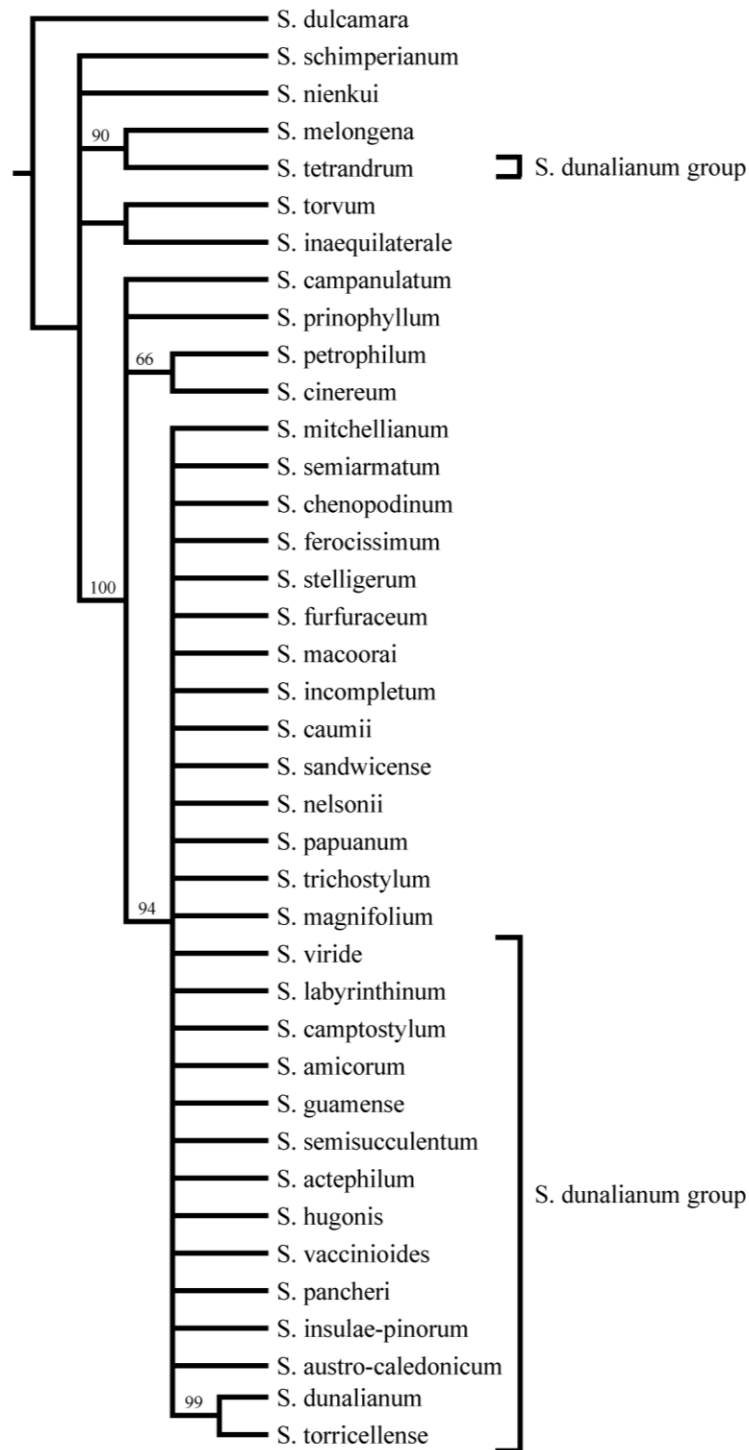


Figure 2. Strict consensus of 1002 most parsimonious trees resulting from the analysis of *trnT-trnF* sequence data. Jackknife values over 50% are given above the nodes.

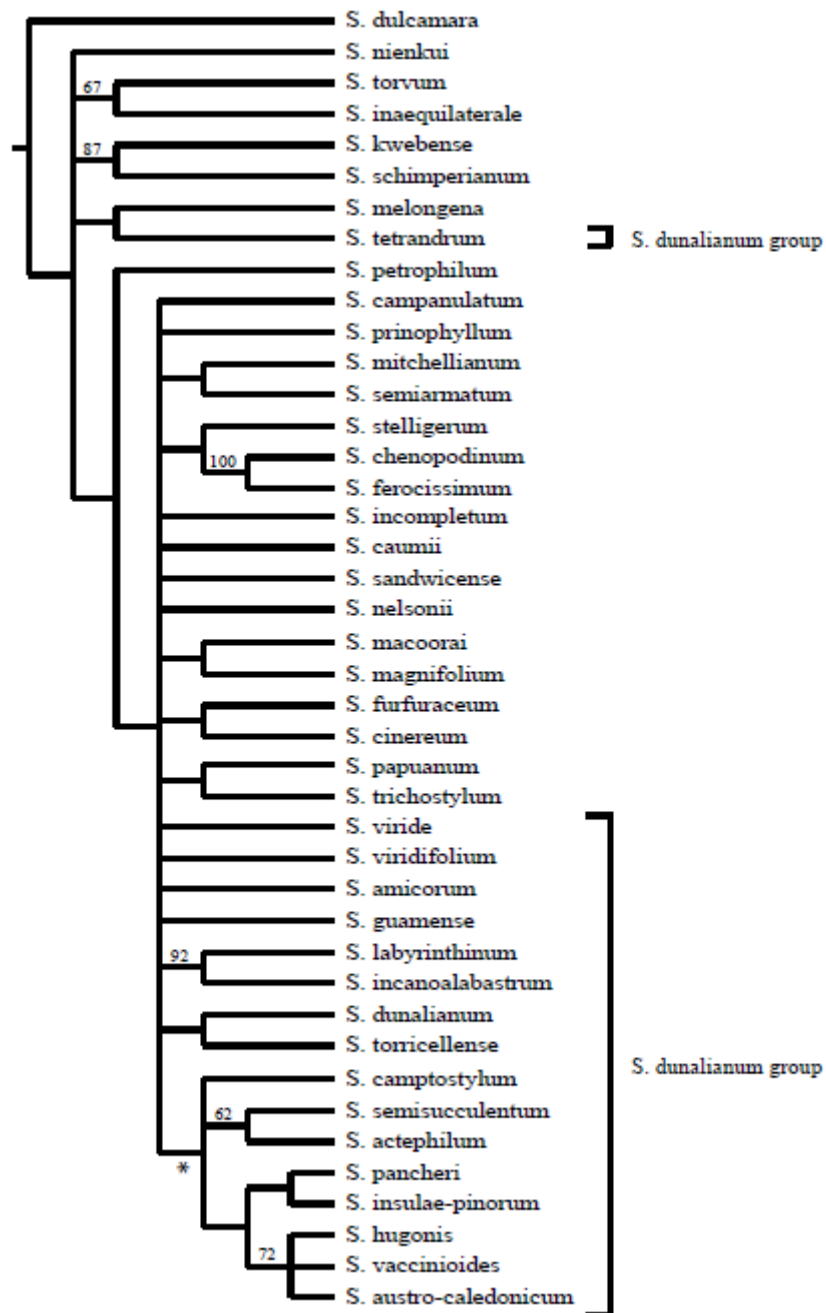


Figure 3. Strict consensus of 279 most parsimonious trees resulting from the analysis of ITS sequence data. Jackknife values over 50% are given above the nodes. The clade indicated by an asterisk is composed of New Caledonian species.

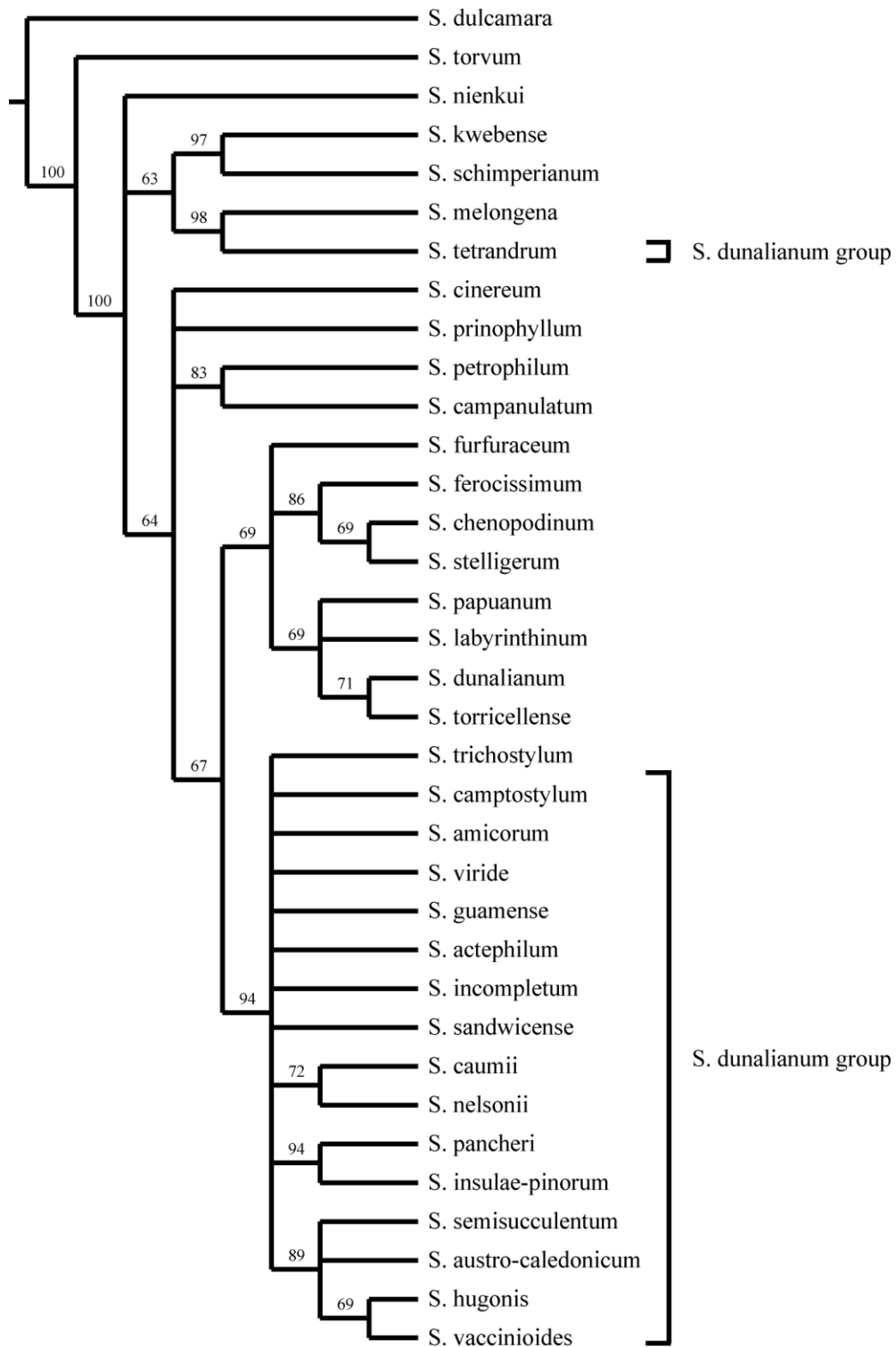


Figure 4. Strict consensus of 343 most parsimonious trees resulting from the analysis of *waxy* sequence data. Jackknife values over 50% are given above the nodes.

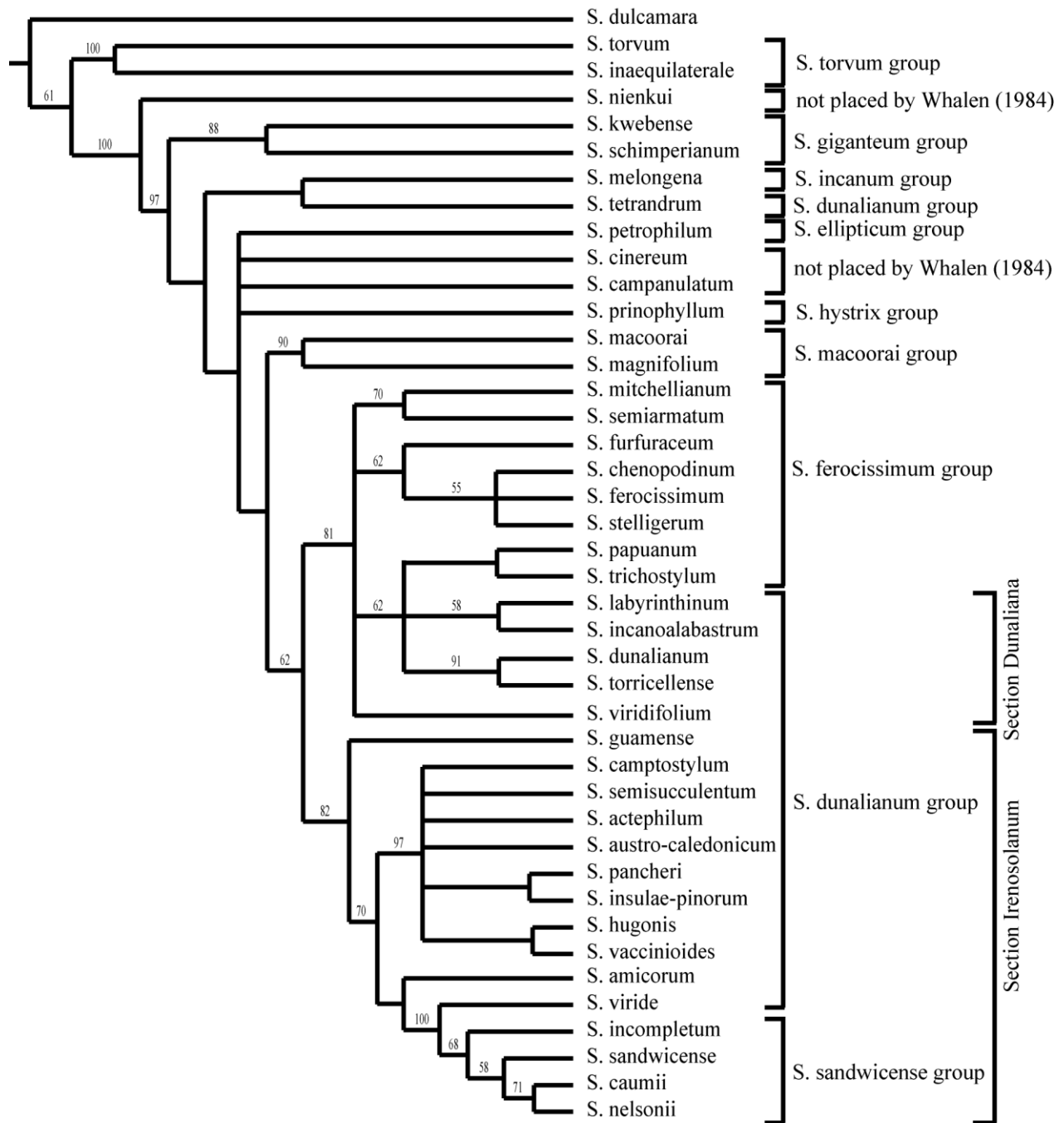


Figure 5. Strict consensus of 90 most parsimonious trees resulting from the analysis of the combined ITS, *trnT-trnF*, and *waxy* sequence data. Jackknife values over 50% are given above the nodes.

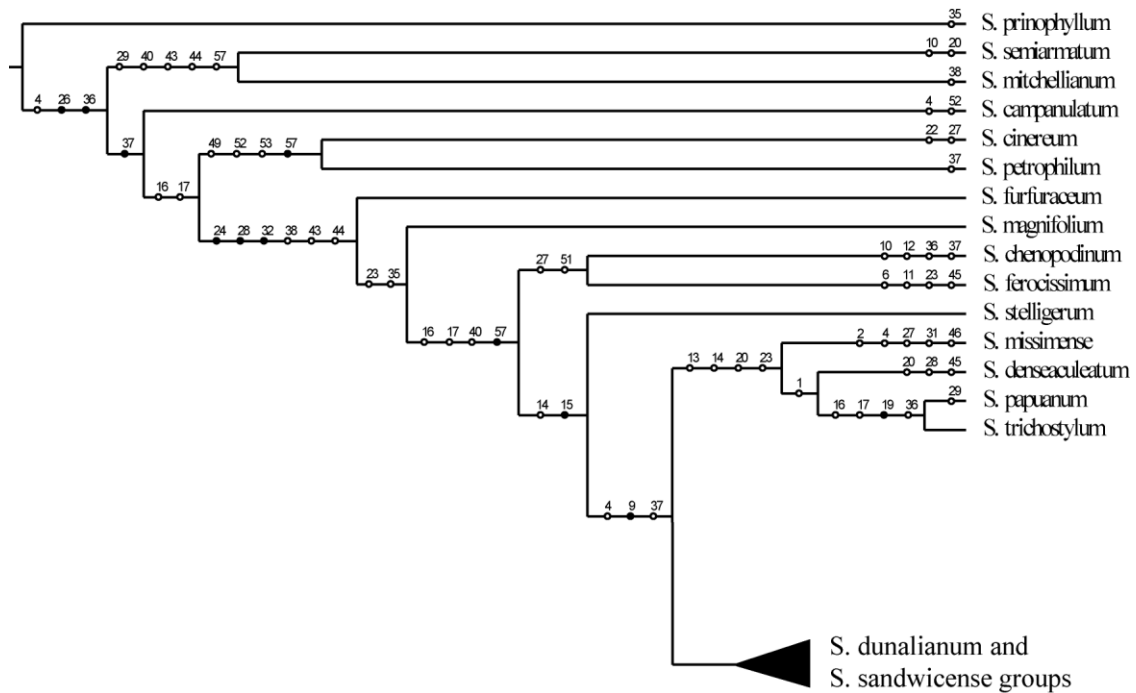


Figure 6. One of the 144 most parsimonious trees from the analysis of the morphological dataset. Characters are optimized using accelerated transformation. The character numbers shown above the dots correspond to the character numbers in Appendix II. Open dots represent homoplasious characters while closed dots represent unique synapomorphies.

Solanum dunalianum and S. sandwicense groups

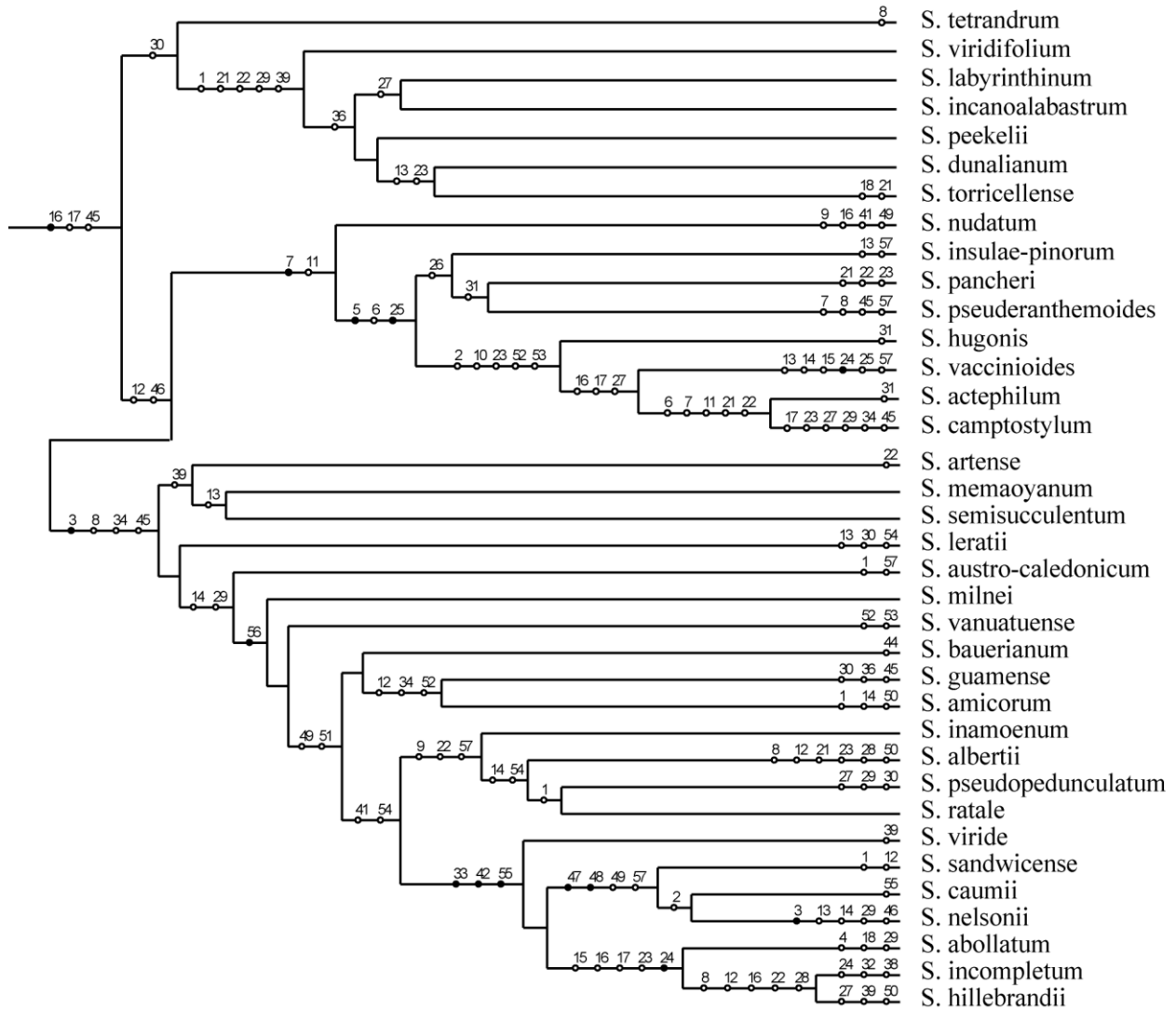


Figure 7. The *Solanum dunalianum* group and *S. sandwicense* group clade from the same most parsimonious tree as Figure 6. Characters are depicted as in that figure.

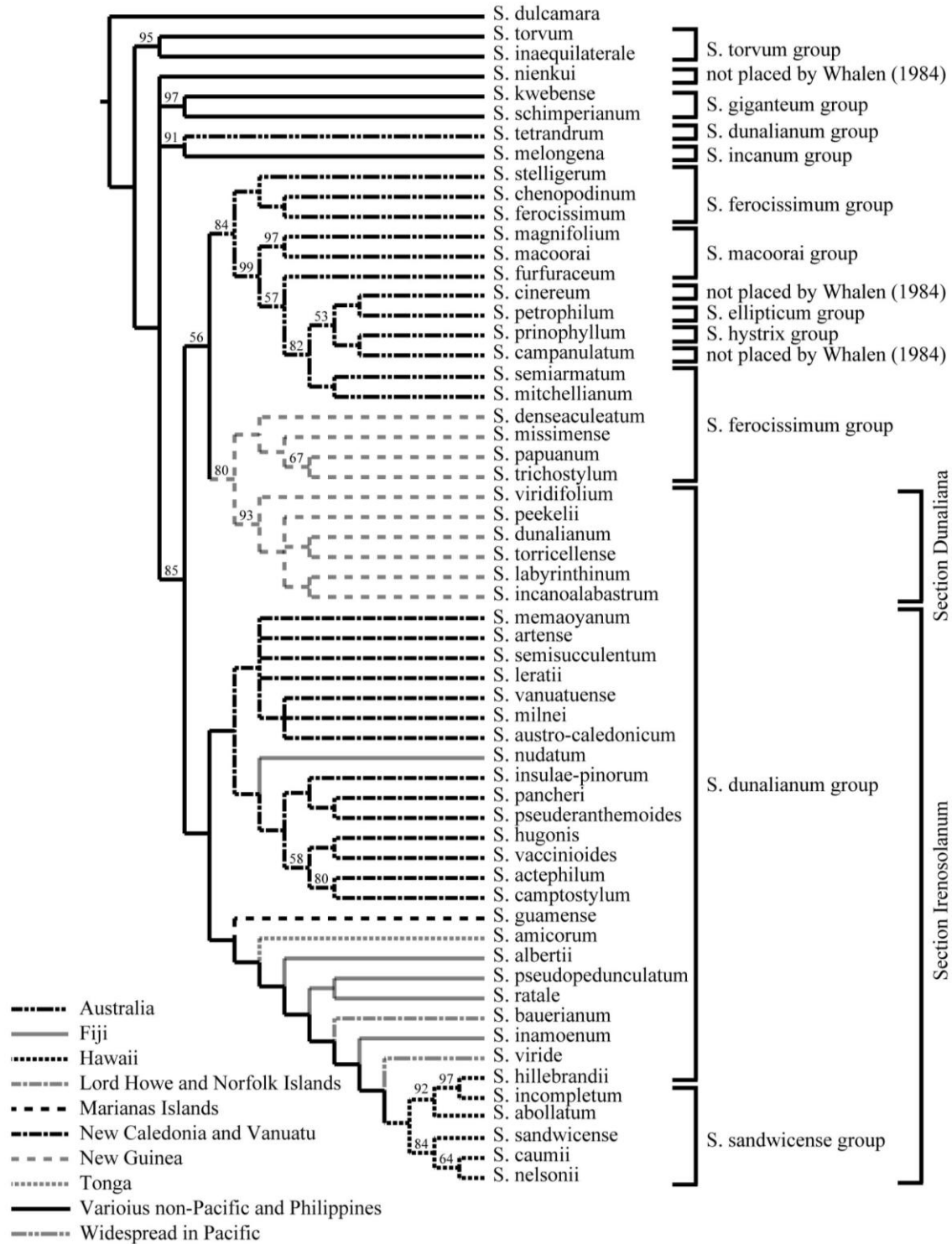


Figure 8. Strict consensus of 35 most parsimonious trees resulting from the total evidence analysis. Jackknife values over 50% are given above the nodes. General geographic distributions are indicated.

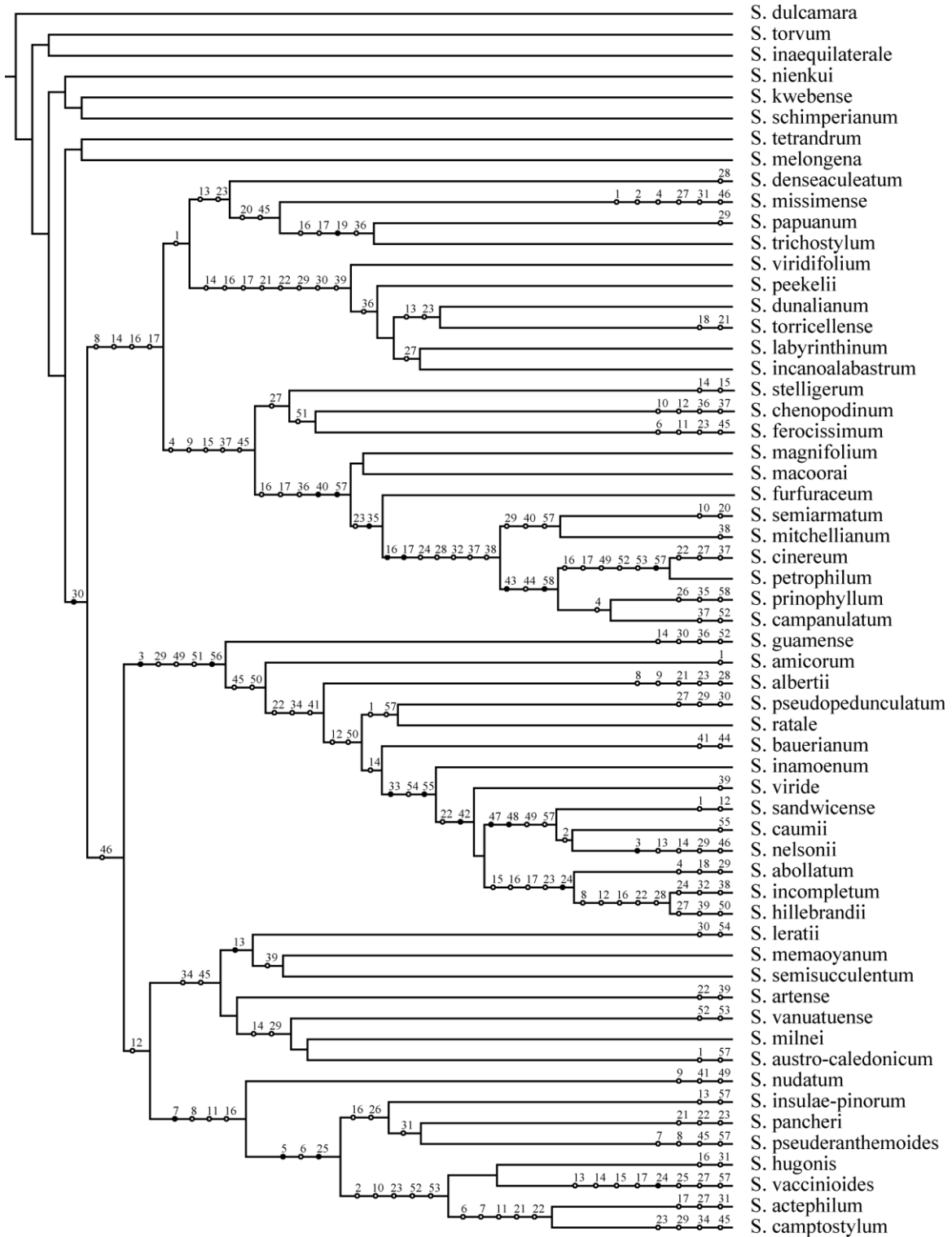


Figure 9. One of the 35 most parsimonious trees resulting from the total evidence analysis. Characters are optimized using accelerated transformation. The character numbers shown above the dots correspond to the character numbers in Appendix II. Open dots represent homoplasious characters while closed dots represent unique synapomorphies.

Literature Cited

- Alexander, P. J., R Govindarajalu, C. D. Bacon, and C. D. Bailey.** 2007. Recovery of plant DNA using a reciprocating saw and silica-based columns. *Molecular Ecology Notes* 7: 5–9.
- Anderson G. D. & A. E. Symon.** 1989. Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43: 204–219.
- Anderson G. J., G. Bernardello, L. Bohs, T Weese, & A. Santos-Guerra.** 2006. Phylogeny and biogeography of the Canarian *Solanum vespertilio* and *S. lidii* (Solanaceae). *Anales del Jardín Botánico de Madrid* 63: 159–167.
- Bean, A.R.** 2004. The taxonomy and ecology of *Solanum* subg. *Leptostemonum* (Dunal) Bitter (Solanaceae) in Queensland and far north-eastern New South Wales, Australia. *Austrobaileya* 6: 639–816.
- Bitter, G.** 1919. Dei papuasischen Arten von *Solanum*. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 55: 59–113.
- Bitter, G.** 1921. *Solanum*. Pp. 221–228. *In:* F. Sarasin and J. Roux (eds.), *Nova Caledonia B. Botanik von Hans Schinz & A. Guillaumin Vol I Livr. III*, Berlin und Viesbaden, C. W. Kreidels Verlang.
- Bitter, G.** 1922. *Solana africana*. III. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*. Leipzig. 57: 248–286.
- Borchsenius, F.** 2007. FastGap 1.0.8. Department of Biological Sciences, University of Aarhus, Aarhus, Denmark. (http://192.38.46.42/aubot/fb/FastGap_home.htm)
- Bohs, L. & R. G. Olmstead.** 1997. Phylogenetic relationships in *Solanum* (Solanaceae) base on *ndhF* sequences. *Systematic Botany* 22: 5–17.
- Bohs, L.** 2005. Major Clades in *Solanum* based on *ndhF* Sequence Data. Pp. 27–49. *In:* T. B. Croat, V. C. Hollowell, and R. C. Keating (eds.), *A Festschrift for Willian G. D’Arcy The Legacy of a Taxonomist*. Missouri Botanical Garden Press, St. Louis.
- D’Arcy, W. G.** 1991. The Solanaceae since 1976, with a review of its biogeography. Pp 75–137. *In:* J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada-R. Richmond, (eds.), *Solanaceae III: taxonomy, chemistry, evolution*. Royal Botanic Gardens, Kew.
- Doyle, J. J., & J. L. Doyle.** 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemistry Bulletin*. 19: 11–15.
- Dunal, F. M.** 1852. Solanaceae. *In:* A. De Candolle (ed.), *Prodromus Systematics Naturalis Regni Vegetabilis* 13: 1–690.
- Edgar, R. C.** 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- Goloboff, P., S. Farris, & K. Nixon.** 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Hershkovitz, M., & E. Zimmer.** 1996. Conservation patterns in angiosperm rDNA ITS2 sequences. *Nucleic Acids Research* 24: 2857–2867.
- Lepschi, B. J. & D. E. Symon.** 1999. A preliminary cladistic analysis of Australian *Solanum* and *Lycianthes*. Pp. 161–170. *In:* M. Nee, D. E. Symon, R. N. Lester, & J. P. Jessop (eds.), *Solanaceae IV*.
- Levin, R. A., K. Watson, & L. Bohs.** 2005. A four-gene study of evolutionary relationships in *Solanum* section *Acanthophora*. *American Journal of Botany* 92: 603–612.

- Levin, R., N. Myers, & L. Bohs.** 2006. Phylogenetic relationships among the “Spiny Solanums” (*Solanum* subgenus *Leptostemonum*, Solanaceae). *American Journal of Botany* 93: 157–169.
- Miller, R. E., M. D. Rauscher, & P. S. Manos.** 1999. Phylogenetic systematics of *Ipomoea* (Convolvulaceae) based on ITS and *waxy*. *Systematic Botany* 24: 209–227.
- Nixon, K. C. & Q. D. Wheeler.** 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.
- Nixon, K. C.** 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.
- Olmstead, R. G. & J. D. Palmer.** 1997. Implications for the phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. *Systematic Botany* 22: 19–29.
- Roe, K. E.** 1967. A revision of *Solanum* sect. *Brevantherum* (Solanaceae) in North and Central America. *Brittonia* 19: 353–373.
- Suh, Y., L. B. Thein, H. E. Reeve, & E. A. Zimmer.** 1993. Molecular evolution and phylogenetic implications of internal transcribed spacer sequences of ribosomal DNA in Winteraceae. *American Journal of Botany* 80: 1042–1055.
- Symon, D. E.** 1981. A revision of the genus *Solanum* in Australia. *Journal of the Adelaide Botanic Garden*. 4: 1–367.
- Symon, D. E.** 1985. The Solanaceae of New Guinea. *Journal of the Adelaide Botanic Gardens* 8: 1–171.
- Taberlet, P., L. Gielly, G. Pautou, & J. Bouvet.** 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109.
- Thiers, B. [continuously updated].** Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
- Vargas, P., B. G. Baldwin, L. Constance.** 1998. Nuclear ribosomal DNA evidence for a western North American origin of Hawaiian and South American species of *Sanicula* (Apiaceae). *Proc. Natl. Acad. Sci. USA* 95, 235–240.
- Walsh, B. M., & S. B. Hoot.** 2001. Phylogenetic relationships of *Capsicum* (Solanaceae) using DNA sequences from two noncoding regions: the chloroplast *atpB-rbcL* spacer region and nuclear *waxy* introns. *International Journal of Plant Sciences* 162: 1409–1418.
- Weese T. & Bohs L.** 2007. A Three-Gene Phylogeny of the Genus *Solanum* (Solanaceae). *Systematic Botany* 32: 445–463.
- Whalen, M.** 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12: 179–282.
- White, T., T. Bruns, S. Lee, & J. Taylor.** 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In M. Innis, D. Gelfand, J. Sninsky, and T. White (eds.), *PCR protocols: a guide to methods and applications*, 315–322. Academic Press, San Diego, California, USA.

Appendix I. The species of the *Solanum dunalianum* group and *S. sandwicense* group and their new subgeneric placement.

Species	Treatment by Whalen (1984)	Current subgeneric classification
<i>Solanum abollatum</i> H. St. John	not treated	Section <i>Irenosolanum</i>
<i>S. actephilum</i> Guillaumin	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. albertii</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. amicorum</i> Benth.	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. artense</i> Montr.	<i>S. dunalianum</i> group <i>in syn.</i>	Section <i>Irenosolanum</i>
<i>S. athroanthum</i> Dunal	<i>S. dunalianum</i> group	not placed
<i>S. austro-caledonicum</i> Seem.	<i>S. dunalianum</i> group <i>in syn.</i>	Section <i>Irenosolanum</i>
<i>S. bauerianum</i> Endl.	not treated	Section <i>Irenosolanum</i>
<i>S. camptostylum</i> Bitter	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. caumii</i> stat. nov.	<i>S. sandwicense</i> group as <i>S. nelsonii</i> Dunal	Section <i>Irenosolanum</i>
<i>S. dunalianum</i> Gaudich.	<i>S. dunalianum</i> group	Section <i>Dunaliana</i>
<i>S. guamense</i> Merr.	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. hillebrandii</i> H. St. John	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. hugonis</i> Heine	not treated	Section <i>Irenosolanum</i>
<i>S. inamoenum</i> Benth.	<i>S. dunalianum</i> group <i>in syn.</i>	Section <i>Irenosolanum</i>
<i>S. incanoalabastrum</i> Symon	not treated	Section <i>Dunaliana</i>
<i>S. incompletum</i> Dunal	<i>S. sandwicense</i> group	Section <i>Irenosolanum</i>
<i>S. insulae-pinorum</i> Heine	not treated	Section <i>Irenosolanum</i>
<i>S. labyrinthinum</i> sp. nov.	not treated	Section <i>Dunaliana</i>
<i>S. leratii</i> Schltr.	<i>S. dunalianum</i> group <i>in syn.</i>	Section <i>Irenosolanum</i>
<i>S. memaoyanum</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. milnei</i> Seem.	<i>S. dunalianum</i> group <i>in syn.</i>	Section <i>Irenosolanum</i>
<i>S. nelsonii</i> Dunal	<i>S. sandwicense</i> group	Section <i>Irenosolanum</i>
<i>S. nudatum</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. pancheri</i> Guillaumin	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. peekelii</i> Bitter	not treated	Section <i>Dunaliana</i>
<i>S. pseuderanthemoides</i> Schltr.	not treated	Section <i>Irenosolanum</i>
<i>S. pseudopedunculatum</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. ratale</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. retrorsum</i> Elmer	<i>S. dunalianum</i> group as <i>S. luzoniense</i> Merr.	not placed
<i>S. sandwicense</i> Hook & Arn.	<i>S. sandwicense</i> group	Section <i>Irenosolanum</i>
<i>S. semisucculentum</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. tetrandrum</i> R. Br.	<i>S. dunalianum</i> group	not placed
<i>S. torricellense</i> Bitter	<i>S. dunalianum</i> group	Section <i>Dunaliana</i>
<i>S. vaccinioides</i> Schltr.	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. vanuatuense</i> sp. nov.	not treated	Section <i>Irenosolanum</i>
<i>S. viride</i> Sprengel	<i>S. dunalianum</i> group	Section <i>Irenosolanum</i>
<i>S. viridifolium</i> Dunal	<i>S. dunalianum</i> group	Section <i>Dunaliana</i>

Appendix II. Voucher information for species sampled and GenBank accessions for molecular markers used in this study.

Taxon	Voucher	GenBank Accession ITS	GenBank Accession <i>trnT-trnF</i>	GenBank Accession <i>waxy</i>
<i>Solanum acetophilum</i> Guillaumin	McKee 21989			
<i>S. amnicorum</i> Benth.	Buelow 2677			
<i>S. austro-caledonicum</i> Seem.	McClelland 550			
<i>S. campanulatum</i> R. Br.	Olmstead S-78	AY996488	DQ180395	AY996388
<i>S. campostyllum</i> Bitter	McPherson 5720			
<i>S. caunii</i> stat. nov.	McClelland 452			
<i>S. chenopodium</i> F. Muell.	no voucher	AY996492	DQ180396	AY996393
<i>S. cinereum</i> R. Br.	Bohs 2852	AY996493	DQ180397	AY996394
<i>S. dulcamara</i> L.	no voucher	AF244742	AY266231	AY996410
<i>S. dunalianum</i> Gaudich.	Takeuchi 9323			
<i>S. ferocissimum</i> Lindl.	Olmstead S-83	AY996510	DQ180400	AY996415
<i>S. furfuraceum</i> R. Br.	Olmstead S-84	AY996417	DQ180401	AY996417
<i>S. guamense</i> Merr.	Wood & Perlman 3329			
<i>S. hugonis</i> Heine	Yeillon 7843			
<i>S. inaequilaterale</i> Merr.	McClelland 467			
<i>S. incanoalabastrum</i> Symon	Schodde 1599			
<i>S. incompletum</i> Dunal	McClelland 451			
<i>S. kvebenese</i> N.E.Br. ex C.H. Wright	Bohs 2849	AY996522	AY996430	AY998429
<i>S. labrinthinum</i> sp. nov.	Brass 25460			
<i>S. macoorai</i> F. M. Bailey	Bohs 3585	GQ163606	GQ163537	GQ163679
<i>S. magnifolium</i> F. Muell.	McDonald 954			
<i>S. melongena</i> L.	Olmstead S-91	AF244726	AY562959	AY998440
<i>S. mitchellianum</i> Domin	Bohs 3583	GQ163607	GQ163539	GQ163680
<i>S. nelsonii</i> Dunal	McClelland 455			
<i>S. nienkui</i> Merr. & Chun	Chow 78313			
<i>S. pancheri</i> Guillaumin	McClelland 557			
<i>S. papuanum</i> Symon	Brass 31172			
<i>S. petrophilum</i> F. Muell.	Bohs 3255	AY998455	GQ163550	AY996454
<i>S. prinophyllum</i> Dunal	Bohs 2725	DQ180407	AY996544	AY996456
<i>S. sandwicense</i> Hook & Arn.	McClelland 450			

Appendix II. Continued.

Taxon	Voucher	GenBank Accession ITS	GenBank Accession <i>trnT-trnL</i>	GenBank Accession <i>waxy</i>
<i>S. schimperianum</i> Hochst.	<i>Olmstead S-97</i>	AY996552	DQ180410	AY996465
<i>S. semiaromaticum</i> F. Muell.	<i>Bohs 3560</i>	GQ163559	GQ163622	GQ163696
<i>S. semisucculentum</i> sp. nov.	<i>McClelland 554</i>			
<i>S. stelligerum</i> Sm.	<i>Bohs 3523</i>	GQ163625	DQ855018 (partial)	ay996469
<i>S. tetrandrum</i> R. Br.	<i>Cowie 14617</i>			
<i>S. torricellense</i> Bitter	<i>Symon ex 13857</i>			
<i>S. torvum</i> Sw.	<i>Olmstead S-101</i>	AF244729	AY266246	AY562972
<i>S. trichostylum</i> Symon	<i>Brass 30725</i>			
<i>S. vaccinioides</i> Schltr.	<i>McClelland 553</i>			
<i>S. viride</i> Sprengel	<i>McClelland 453</i>			
<i>S. viridifolium</i> Dunal	<i>Symon s.n. from Webb & Tracey 8351</i>			

Appendix III. Morphological dataset for the cladistic analysis of the *Solanum dunalianum* group. Polymorphism are within brackets. Dashes indicate inapplicable data. Question marks indicated unknown characters. Bolded taxa belong to the *S. dunalianum* group.

Taxa	Characters					
	1	11	21	31	41	51
1. <i>Solanum abollatum</i>	00-100000-	1001112100	111111200?	??0??01?	??00??010	??????-
2. <i>S. actephilum</i>	0110100101	1000011000	00123101010001	1000111010	1000000000	1210-100
3. <i>S. albertii</i>	00-0000110	1100000000	0012112111	0001111010	0000100011	0000-??0
4. <i>S. amicolorum</i>	10-00000--	1100000000	1102112011	0000111010	1000100011	0101002?00
5. <i>S. artense</i>	00-00000--	1000000000	1002112001	0001111000	1000100000	10002?00
6. <i>S. austro-caledonicum</i>	10-00000??	1001000000	11021120101012]	0001111010	1000100000	1000?120
7. <i>S. bauerianum</i>	00-00000--	1001000000	--02112011	0001111010	1001100010	00002?00
8. <i>S. campanulatum</i>	00-0000110	1101133000	1110112101	01000-0111	1011110000	1100-??1
9. <i>S. camptostylum</i>	0110100101	1000010000	000201012011	00011011010	1000100000	12102?00
10. <i>S. caunii</i>	01000000--	10101000000	11012112011	0011111010	0100101100	00??201010
11. <i>S. chenopodium</i>	00-1000111	100111?000	11012110001	0000101010	1000110000	00002?00
12. <i>S. cinereum</i>	00-1000110	1101122000	10101010101	01000-0111	101110010	1210-131
13. <i>S. denseaculeatum</i>	10-0000100	1111011000	1112112101	0000111010	10000--0001	0002??-
14. <i>S. dunalianum</i>	10-0000100	1110000000	0012112010	0000101000	1000010000	10002?00
15. <i>S. ferocissimum</i>	00-1010110	0101111000	11102101010001	0000110010	1000010000	0000-?00
16. <i>S. furfuraceum</i>	00-1000110	1101122000	111121112001	000?0-0011	1000110000	10002?40
17. <i>S. guamense</i>	00-00000--	1101000000	110102112010	0000101010	1000000010	01002?00
18. <i>S. hillebrandii</i>	00-0000100	1101122000	10101121111111	00?1111000	0?001??011	?0-1-?00
19. <i>S. hugonis</i>	0110111101	0000000000	1112012001	1000111010	1000000000	1210?00
20. <i>S. inamoenum</i>	00-00000--	1001000000	10010211201?	00?1111010	00001??010	0001??0
21. <i>S. incanoalabastrum</i>	10-0000100	11101000000	--02111010101]	00001010?0	1000010000	1000-?00
22. <i>S. incompletum</i>	00-0000100	1101122000	1010112111	0111111110	0100100010	00010000
23. <i>S. insulae-pinorum</i>	00-0111100	0010000000	--0200---1	0000111010	1000000000	1000?020
24. <i>S. labyrinthinum</i>	10-00001--	1100000000	0002111010	000?1010?0	1000010000	1000?00
25. <i>S. leratii</i>	00-00000--	1020000000	1102112000	0001111010	1000100000	10012?00
26. <i>S. magnifolium</i>	00-1000110	1101122000	110121112001	00001-0011	1000110000	1000??124]0
27. <i>S. menaoyanum</i>	00-00000--	1020000000	1102112001	0001111000	1000100000	1000-?00
28. <i>S. milnei</i>	00-00000--	1001000000	1102112011	0001111010	1000100000	10002?00
29. <i>S. missimense</i>	0111000100	1111011001	1112111001	1000111010	1000100000	10002??-

Appendix III. Continued.

Taxa	Characters									
	1	11	21	31	41	51				
30. <i>S. mitchellianum</i>	00-1000110	1101133000	1110112111	0100[01]?101	0100011000	01000??10				
31. <i>S. nelsonii</i>	0120000--	1010000000	110211200100	1111101001	0011110000	010010				
32. <i>S. nudatum</i>	00-0001110	0000010000	--02112001	0000111010	00000-0010	1000-?00				
33. <i>S. pancheri</i>	00-0111100	0000000000	001200---1	1000111010	1000000000	1000?100				
34. <i>S. papuanum</i>	10-0000100	111?022011	111211[02]01?	0000101010	1000110000	?0002?0				
35. <i>S. pekelii</i>	10-0000100	1100000000	0002112010	0000101000	10000??000	10002?00				
36. <i>S. petrophilum</i>	00-1000110	1101122000	1110112101	01000-1111	1011110010	121021?1				
37. <i>S. prinophyllum</i>	00-0000110	1101133000	1110102101	1001011111	0111100001	00021[45]0				
38. <i>S. pseudoranthemoides</i>	00-01100--	0000000000	110200---1	1000111010	1000100000	1000-?10				
39. <i>S. pseudopedunculatum</i>	10-00000--	1000000000	1002111000	0001111010	0000100010	00002?10				
40. <i>S. ratale</i>	10-00000--	1000000000	1002112011	0001111010	0000100010	00002?10				
41. <i>S. sandwicense</i>	10-00000??	1101000000	110[02]11201100	1111101001	0010110000	010010				
42. <i>S. semiarmatum</i>	00-1000111	1101133001	1110112111	01000-1110	1000110000	10002?10				
43. <i>S. semisucculentum</i>	00-00000--	1020000000	--02112001	0001111000	1000100000	1000-?00				
44. <i>S. stelligerum</i>	00-1000110	1100011000	110211[02]001	0000[01]1001	0100011000	01000-?00				
45. <i>S. tetrandrum</i>	00-00000--	1100000000	1102112000	0000111010	1000010000	1[01]00-?00				
46. <i>S. torricellense</i>	10-0000100	1110000100	1012112010	0000101000	1000010000	1000-?00				
47. <i>S. trichosylum</i>	10-0000100	1111022011	111211200?	0000101010	1000110000	10002??0				
48. <i>S. vaccinioides</i>	011011110[01]	0011111000	11131[01][01]001	00001110?0	1000000000	12102120				
49. <i>S. vanuatuense</i>	00-00000--	1001000000	110[012]112011	0001111010	1000100000	11102?00				
50. <i>S. viride</i>	00-00000??	1[01]01000000	?102112011	0011111000	0100100010	0001?000				
51. <i>S. viridifolium</i>	10-00001??	1100000000	0002112010	000[01]111000	1000010000	1000-?00				

Chapter 2

A monograph of *Solanum* section *Dunaliana* (Solanaceae)

Abstract

A treatment for *Solanum* section *Dunaliana* (Bitter) Symon (Solanaceae) is presented. The circumscription of *Solanum* section *Dunaliana* herein is based on the results of a morphological and molecular phylogenetic analysis of the section. *Solanum* section *Dunaliana* is reduced to six species, *S. dunalianum*, *S. incanoalabastrum*, *S. peekelii*, *S. torricellense*, *S. viridifolium*, and *S. labyrinthinum* named herein. The current *Solanum* section *Dunaliana* is morphologically coherent and monophyletic unlike earlier concepts. It is characterized by a large shrub or small tree habit, generally sparse, broad-based prickles, difoliate sympodia, entire leaves with the blade unarmed, many-flowered inflorescence with all flowers bisexual and fertile, corollas with poorly developed interpetalar tissue, and juicy, red fruit. The section is centered on the island of New Guinea extending to Sulawesi, the Solomon Islands, and Queensland, Australia. A key for identifying the species of *Solanum* section *Dunaliana* is provided along with descriptions, distribution maps, and images of type specimens. *Solanum peekelii* is neotypified, and *S. dunalianum* var. *inermis* is lectotypified.

Introduction

Solanum L. (Solanaceae) is a large, cosmopolitan, economically important genus. One of the ten largest genera of angiosperms, *Solanum* is one of only nineteen with more than 1000 species (Frodin, 2004). The genus includes several well known crops including the tomato (*S.*

lycopersicum L.), potato (*S. tuberosum* L.), and eggplant (*S. melongena* L.) as well as many lesser known domesticated species including the scarlet eggplant (*S. aethiopicum* L.), naranjilla or lulo (*S. quitoense* Lam.), and pepino (*S. muricatum* Ait.). Species of *Solanum* can be found on every continent except Antarctica; South America is the most species rich (D'Arcy, 1991) and is likely the geographic origin of the genus. *Solanum* has considerable infrageneric structure, as would be expected for a large genus, and is divided into three subgenera, subgenus *Solanum* L, subgenus *Bassovia* (Aubl.) Bitter, and subgenus *Leptostemonum* (Dunal) Bitter (Nee, 1999).

Solanum subgenus *Leptostemonum* consists of somewhere between 350 and 450 species, almost a third of the genus (Levin *et al.*, 2006). Like the genus as a whole, *Solanum* subgenus *Leptostemonum* has a worldwide distribution with Latin America, Africa, and Australia being the most species rich areas (Levin, *et al.*, 2006). The subgenus is characterized by a suite of three characters: presence of prickles on the stems, leaves, inflorescences, and/or calyces; stellate hairs on any or all above ground organs; and attenuate anthers. However, a few species of *Solanum* subgenus *Leptostemonum* may be missing one or more of these characters, and several of the characters can be found in species outside the subgenus such as the stellate hairs of *S. rugosum* Dunal in *Solanum* subgenus *Solanum* section *Brevantherum* Seithe (Roe, 1967).

The sheer number of species in *Solanum* makes the genus intractable for timely taxonomic study by one worker, and even *Solanum* subgenus *Leptostemonum* is too large. Therefore, most monographic studies since Dunal (1852) have focused on smaller taxa, in particular sections (Bennett, 2008). The major exception is The National Science Foundation funded Planetary Biodiversity Inventory: *Solanum* grant (PBI: *Solanum*) which aimed to produce a genus-wide treatment for *Solanum* by bridging the gaps between individual workers (<http://www.nhm.ac.uk/research-curation/research/projects/solanaceaesource/>); the effort is

ongoing. The study presented here examines one section of *Solanum* subgenus *Leptostemonum*, section *Dunaliana* (Bitter) Symon, and is a contribution to the PBI: *Solanum* project.

Solanum section *Dunaliana* as circumscribed here differs from many of the concepts of previous workers. The history of the group is not simple, and much confusion has been introduced into the literature by various workers (D'Arcy, 1971; Symon, 1981, 1985; Whalen, 1984) through the association of *Solanum* section *Dunaliana* with several other sections particularly *Solanum* section *Irenosolanum* (Bitter) Bitter. In order to prevent future confusion regarding *Solanum* section *Dunaliana*, it is necessary to expound the full history of *Solanum* section *Dunaliana* chronologically. The taxon was not elevated to the rank of section until 1985 (Symon, 1985; however, for simplicity's sake it is consistently referred to here as a section.

The first species of *Solanum* section *Dunaliana* to be described was *Solanum viridifolium*, native to the northeastern coast of Queensland, Australia. This species was originally published by Robert Brown in 1810 (Brown, 1810) under the name *S. viride*, a later homonym of *S. viride* Sprengel from 1807 (Sprengel, 1807). Though *S. viride* R. Br. must be rejected in favor of *S. viridifolium*, as was pointed out by Garnock-Jones (1986), it was nonetheless the first species in *Solanum* section *Dunaliana* to be recognized. Even though *S. viridifolium* and *S. viride* Sprengel differ morphologically and originate from different geographical areas, *S. viride* Sprengel being from the islands of the eastern Pacific, the homonymy of Brown's (1810) and Sprengel's (1807) names led to confusion regarding the identity and distinctiveness of these species.

The second species in *Solanum* section *Dunaliana* to be described and later to become the namesake and type of the section was *S. dunalianum*; published in 1829 by Gaudichaud, *S. dunalianum* is the oldest name in *Solanum* section *Dunalianna*. In his publication, Gaudichaud

(1829) made no hypotheses as to the relationships of his new species other than assigning the genus. It was not until Dunal's (1852) monumental contribution to De Candolle's *Prodromus* that the any relationships of the species of *Solanum* section *Dunaliana* were hypothesized. However, Dunal (1852) did not recognize a group consistent with *Solanum* section *Dunaliana* nor strong affinities among the three names (two species) of the section known to him. In fact, Dunal (1852) separated the two species between his two sections, section *Pachystemonum* Dunal and section *Leptostemonum* Dunal roughly equivalent to the current subgenera *Solanum* and *Leptostemonum* respectively.

The three species recognized by Dunal (1852) were *S. viride* R.Br. (= *S. viridifolium*), *S. viridifolium*, and *S. dunalianum*. Though it is now clear that Dunal's (1852) name *S. viridifolium* applies to the species illegitimately named *S. viride* by Brown, Dunal (1852) considered these two species distinct and not closely related. He placed *S. viridifolium* in section *Pachystemonum* subsection *Dulcamara*. He considered *S. viride* R. Br. to include *S. viride* Sprengel; though he never used Sprengel's (1807) name, Dunal (1852) cited specimens of *S. viride* Sprengel from the Pacific islands. Dunal (1852) placed this conglomeration of two species, in *Solanum* section *Leptostemonum* Dunal under series *Graciliflora* Dunal. Though he also placed *S. dunalianum* in series *Graciliflora*, *S. viride* R. Br. and *S. dunalianum* were separated into the groups *Persicaefolia* and *Aquartia* respectively (Dunal, 1852). Clearly Dunal (1852) did not consider them very closely related.

One additional species in Dunal's (1852) work, *S. tetrandrum* R. Br., must be mentioned as Dunal's treatment of it influenced later workers. Dunal (1852) included *S. tetrandrum* in the group *Aquartia*, along with *S. dunalianum*. Likely, Dunal inferred this relationships as both species have a generally glabrous appearance, paucity of prickles, and red fruits. The *Aquartia*

group consisted of seven species; clearly, Dunal (1852) viewed *S. tetrandrum* and *S. dunalianum* as closely related, and several later workers (Bean, 2004; D’Arcy, 1991; Symon, 1985, 1986a, 1986b; Whalen, 1984) have as well. No one since Dunal (1852) has postulated a relation of either *S. dunalianum* or *S. tetrandrum* with any of the other five species of the group *Aquartia*, however.

In 1919, the first explicit grouping of the species of *Solanum* section *Dunaliana* was made by Bitter (1919). In this publication, Bitter (1919) named Großart *Solanum dunalianum* (literally “big species” *Solanum dunalianum*) consisting of three species, *S. dunalianum*, *S. peekelii*, and *S. torricellense*; latter two species were novel. By providing it a name, Bitter (1919) formally established the taxon. However, since the name is a binary combination rather than a subdivisional epithet, it is automatically altered to *Solanum* [unranked] *Dunaliana* in accordance with McNeill *et al.* (2006) Article 21.4. Additionally, since Bitter (1919) did not designate a type for his taxon, *S. dunalianum* is automatically assigned in accordance with McNeill *et al.* (2006) Article 22.6 as its name is identical to the original taxon name.

After the establishment of *Solanum* section *Dunaliana* as a taxonomic unit, the next major treatment of the genus *Solanum* as a whole was provided by Seithe (1962). However, Seithe (1962) largely neglected the section treating only *S. dunalianum*, which she placed merely to the Subgeneric level. She did not *S. torricellense*, *S. peekelii*, or *S. viridifolium*. Unlike Dunal (1852), Seithe (1962) did not recognize a relationship between *S. tetrandrum* and *S. dunalianum* placing the former in *Solanum* section *Graciliflora*.

Ten years after Seithe (1962), D’Arcy (1972) placed *Solanum* section *Dunaliana* under *Solanum* series *Giganteiformia* Bitter, a series made up of five exclusively African species. In this publication, D’Arcy (1972) did not include a list of species or characters supporting the

grouping. Therefore, it can only be assumed that D'Arcy (1972) strictly adhered to Bitter's (1919) three species concept of *Solanum* section *Dunaliana*. The placement of *Solanum* section *Dunaliana* by D'Arcy (1972) contrasts with the implied concepts of Bitter (1919, 1922), who did not indicate a relationship between *Solanum* section *Dunaliana* and *Solanum* series *Gigantiformia* when he published these taxa. Although, D'Arcy (1972) did not provide justification for his treatment of *Solanum* section *Dunaliana*, it clearly influenced opinions about the relationships of *Solanum* section *Dunaliana* over the next several decades (Whalen, 1984).

The next worker to address *Solanum* section *Dunaliana* was Symon (1981) who over the following few years investigated it more than anyone since Bitter or until the present. In contrast to his later concept, in 1981 Symon placed *Solanum* section *Dunaliana* in the illegitimate *Solanum* section *Irenosolanum* Seithe (a later homonym of *Solanum* section *Irenosolanum* Bitter). This grouping, with *S. sandwicense* (Hawaii) and *S. amicorum* (Tonga), had not been hypothesized before and was in striking contrast with D'Arcy's (1972) placement of *Solanum* section *Dunaliana* within *Solanum* series *Giganteiformia* as it indicated affinities to the east in Oceania rather than to the west in Africa. The other important proposal in this publication was the inclusion *S. tetrandrum* in *Solanum* section *Dunaliana*, the first association of *S. tetrandrum* and *S. dunalianum* since Dunal's (1852) over a hundred years earlier.

The most extensive and influential incarnation of *Solanum* section *Dunaliana* was the "*Solanum dunalianum* group" of Whalen (1984). In all, Whalen (1984) tentatively listed twenty species in the section. Besides size, Whalen's (1984) concept differed from previous concepts in a number of other ways. For example, except for Symon (1981), no previous worker had proposed a relationship between *Solanum* section *Dunaliana* and species from the Pacific Islands; however, unlike Symon (1981), Whalen (1984) separated *Solanum sandwicense* and

most of the other native Hawaiian species of *Solanum*, placing them instead in his *S. sandwicense* group. Also, Whalen (1984) was the first to place the native species of *Solanum* from New Caledonia in *Solanum* section *Dunaliana*. And, like Symon (1981), he included *S. tetrandrum* in the section considering several species from New Caledonia and one from Fiji as conspecific with it.

Whalen (1984) also went the furthest in speculating relationships between *Solanum* section *Dunaliana* and other taxa in *Solanum* subgenus *Leptostemonum*. Of the thirty-three species groups Whalen (1984) recognized within *Solanum* subgenus *Leptostemonum*, he proposed relationships between *Solanum* section *Dunaliana* and three of them. Two of the groups, the *S. sandwicense* group and the *S. macoorai* group, he viewed as more distantly related. In contrast, Whalen (1984) viewed *Solanum* section *Dunaliana* and his *S. giganteum* group, composed of series *Giganteiformia* and *Anomalum* of Bitter, as closely related and perhaps “not meaningfully separable” (p. 216). This is a view Whalen (1984) shared with D'Arcy (1972), though unlike D'Arcy, Whalen provided characters to support this statement: “paucity of prickles on mature growth (these usually small and broad-based when present); entire leaves, often glabrate above and often with closely spaced, upwardly arching lateral veins; inflorescence axes with closely spaced flowers and pedicel scars; all flowers hermaphroditic, often tending to be tetramerous; and juicy, red berries” (p. 216).

Though it would be unreasonable to expect Whalen's (1984) tentative list to be completely accurate and exhaustive, in order to accommodate his concept of *Solanum* section *Dunaliana*, several species not treated by him, including *S. peekelii* from New Guinea and *S. bauerianum* from Lord Howe and Norfolk Islands, would need to be added. Also, given the evidence available even during his time, his *Solanum sandwicense* group would need to be

subsumed within *Solanum* section *Dunaliana*. Also, it is unclear why Whalen (1984) included *Solanum athroanthum* Dunal as it differs from the other species of *Solanum* section *Dunaliana* in a number of ways: deeply lobed juvenile leaves, prickles on the primary and secondary veins of the leaves, and anisandry having three long anthers and two short ones per flower. Perhaps Whalen (1984) knew this species only through the original description, which does not mention anisandry (Dunal, 1852), and never saw herbarium material; it is known from only four collections. Nevertheless, Whalen's (1984) concept strongly influenced all the workers following him. Though some workers contested the inclusion of the New Caledonia species allied with *S. vaccinioides* Schlechter, all were willing to accept the inclusion of the other Pacific species in *Solanum* section *Dunaliana* (Symon 1985, 1986a, 1986b; D'Arcy, 1991; Bean, 2004).

In 1985, Symon assigned *Dunaliana* Bitter [unranked] to the rank of section and the following year published two additional papers including the *Solanum* section *Dunaliana* (Symon, 1986a & 1986b). Though the concepts presented in each of these three papers differed somewhat, when evaluated together, Symon's (1985, 1986a & 1986b) second concept of *Solanum* section *Dunaliana* can be understood. Symon (1985, 1986a & 1986b) had a more restricted concept than did Whalen (1984). He did not accept the inclusion of several New Caledonian species, *S. pseuderanthemoides*, *S. hugonis*, *S. pancheri*, and *S. vaccinioides*, and was unsure about the inclusion of *S. viride* Sprengel and some other species from New Caledonia, *S. camptostylum*, *S. insulae-pinorum*, and *S. styraciflorum*, though he allowed for the possibility. Like Whalen (1984), however, he apparently considered the Hawaiian species of *Solanum* to fall outside of *Solanum* section *Dunaliana*. Symon (1986a) did consider what he termed “the *S. tetrandrum* complex” to belong to the section but had not evaluated species delimitation within the complex and did not detail what entities he included in the complex. It is

likely that Symon(1986a) was referring to the species placed in synonymy under *S. tetrandrum* by Whalen (1984). Pertaining to the relationship of *Solanum* section *Dunaliana* to other taxa of *Solanum* subgenus *Leptostemonum*, Symon (1985, 1986b) agreed with D'Arcy (1972) and Whalen (1984) stating that there was some evidence of an affinity with *Solanum* series *Giganteiformia*; most likely he was referring to the list of shared characteristics proposed by Whalen (1984).

In the nearly twenty years since he last dealt with *Solanum* section *Dunaliana*, D'Arcy's concept of the section had changed (D'Arcy, 1991). He recognized the group at the sectional level in keeping with Symon (1985) and included twenty species. Though he did not provide a list of species, given the number he included, it is likely he employed Whalen's (1984) concept and included the New Caledonian species. In contrast, Bean (2004) mirrored Symon's (1985, 1986a, 1986b) skepticism of the inclusion of some of the diminutive species of *Solanum* native New Caledonian. Bean (2004) maintained a concept similar to Symon (1985, 1986a, 1986b) including about fifteen species but did not provide a list of names.

Until the present, no workers have used phylogenetic methods to assess the circumscription of *Solanum* section *Dunaliana* or its sectional affiliations. The relationships they proposed were morphologically based intuitions. One phylogenetic investigation (Levin *et al.*, 2006) purportedly placed *Solanum* section *Dunaliana* in a clade with *Solanum* section *Irenosolanum*; however, *S. pancheri*, the single representative of *Solanum* section *Dunaliana* sampled by Levin *et al.* (2006), is currently is placed in section *Irenosolanum* (chapter 1). The phylogenetic analysis presented in chapter 1, resolved *Solanum* section *Dunaliana* *s.l.* as polyphyletic contrary to earlier hypotheses. The species native to New Guinea, including *Solanum dunalianum*, fell into a clade with species of *Solanum* section *Graciliflora* (Dunal)

Seithe, also from to New Guinea, and were separate from a clade consisting of *Solanum* section *Irenosolanum*. *Solanum tetrandrum* was not resolved with either *Solanum* section *Dunaliana* s.s. or *Solanum* section *Irenosolanum* falling instead with *S. melongena* from Asia. Therefore, *Solanum* section *Dunaliana* s.s. is restricted to the monophyletic group composed of the following six species: *S. dunalianum*, *S. incanoalabastrum*, *S. labyrinthinum*, *S. peekelii*, *S. torricellense*, and *S. viridifolium*. As it is currently recognized, *Solanum* section *Dunaliana* is consistent with the concept of Bitter (1919) to which three species named after his time are added.

Materials and Methods

During the completion of this monograph 181 collections including types constituting 420 herbarium sheets of the study group were examined. Eleven herbaria with specimens of the study group, BISH, BM, CAS, F, GH (including A), K, L, MO, P, UC, US, were visited. Loans of specimens were received from the following 31 herbaria: A, AD, B, BH, BISH, BM, BRI, C, CANB, CAS, CBG, DS, E, ECON, F, G, GH, GOET, HAM, K, L, M, MEL, MO, MU, NSW, NY, P, S, SING, UC, and US (Theirs [continuously updated]). Additionally, digital images of herbarium specimens from WU were viewed. Of the collections examined in the study, 158 were of species currently included in *Solanum* section *Dunaliana*. Of these specimens about 75% were from just two species, *S. dunalianum* (ca. 27%) and *S. viridifolium* (ca. 48%). The other four species of *Solanum* section *Dunaliana* are known from fourteen or fewer specimens each.

An exhaustive literature review was conducted for all names relevant to *Solanum* section *Dunaliana*. In all, twelve names were applicable to the five previously named species of the

section. Several additional names by Bitter appeared on herbarium specimens; however, these names were never published (they are listed with the appropriate species below). The protologue of every name was consulted and compared with type material where available. Consultation of the protologue was especially important for *Solanum peekelii* the type material of which was destroyed at the Berlin herbarium during World War II. Species were delimited morphologically based on the protologues, type material, and additional herbarium specimens following the phylogenetic species concept of Nixon and Wheeler (1990) and recognizing the least diagnosable unit. Species descriptions were compiled by measuring herbarium specimens and from label data. Habitat descriptions were based on label data and the literature. Species distribution maps were generated from latitude and longitude coordinates recorded on specimen labels or by manually georeferencing specimens.

Morphology

Solanum section *Dunliana* is a morphologically coherent section. The species vary in leaf length to width ratio, pubescence, inflorescence structure, and a few other characters. The section does not have a single synapomorphy uniting the group; nonetheless, based on a suite of characters, its species form a recognizable unit.

Habit

The species of *Solanum* section *Dunliana*, like most species of *Solanum* subgenus *Leptostemonum* are woody perennials. The members of the section are fairly uniform in habit; all are erect, large shrubs or small trees 2–5(–9) m tall. Bean (2004) characterized the section as

rhizomatous; however, Lepshi & Symon (1999) contradicted this, and no herbarium material is available to support a rhizomatous habit in these species. Therefore, they are considered non-rhizomatous here.

Leaves

The leaves of *Solanum* section *Dunaliana* are fairly uniform. All are simple and entire or slightly wavy with weakly brochidromous venation. In *Solanum* subgenus *Leptostemonum*, it is common for juvenile and adult leaves to differ. Typically, the juvenile leaves are lobed, sometimes deeply so, while the adult leaves are entire to shallowly lobed. In *Solanum* section *Dunaliana* however, the leaves are never lobed. The leaves of all species are geminate; in *S. viride* the leaves can be borne individually but this only occurs in fast growing material. The leaves of this section mainly vary in the ratio of length to width, though some variation occurs in pubescence (i.e. *S. torricellense*) and the longitudinal position of the widest part of the leaf.

Armature and indumentum

Most species in *Solanum* section *Dunaliana* have prickles on the stem. These prickles when present are always broad-based. Some species occasionally have prickles on the petioles; however, the laminae of the leaves, the axes of the inflorescences, and the calyces are never armed. Prickles are often lacking on herbarium material of this group especially on mature growth. When prickles are present, they are always sparse.

The species of *Solanum* section *Dunaliana* are typically glabrous at maturity. The exception is *Solanum torricellense* which has tardily deciduous pubescence on the stems and persistent pubescence on the abaxial surfaces of the leaves. Though glabrous at maturity, the

leaves, stems, and inflorescences of many of the species are pubescent when young. All species produce minute glandular hairs and sessile or short stipitate porrect stellae on the leaves; several produce simple glandular hairs on the gynecium as well. Only *S. torricellense* produces multangulate hairs in addition to porrect stellae and glandular hairs.

Sympodial structure

Like all species of *Solanum*, the inflorescences of *Solanum* section *Dunaliana* are developmentally terminal. The sympodial units of *Solanum* section *Dunaliana* are difoliate. Following Child (1979), the specific anthocladial pattern exhibited in *Solanum* section *Dunaliana* can be characterized as monochasial branching, with reduced hypopodia and elongated epipodia concaulescent with the mesopodia of the sympodial unit above. This has the effect of making the inflorescences look lateral in origin and be remote from the geminate clusters of leaves (See Figure 1 redrawn from Danert, 1967).

Inflorescences

The inflorescences of *Solanum* section *Dunaliana* are many-flowered, simple or branching, scorpioid cymes. The inflorescences of *Solanum incanoalabastrum* and *S. viridifolium* represent the extremes of inflorescence structure within the section with those of *S. incanoalabastrum* being tightly congested and those of *S. viridifolium* being lax and branching up to seven times. In all species of *Solanum* section *Dunaliana* except *S. torricellense* and *S. labyrinthinum*, the epipodium is concaulescent with the mesopodium of the sympodial unit above for more than 2/3 the length of the mesopodium. In *S. torricellense* and *S. labyrinthinum* the epipodium is concaulescent with the mesopodium of the sympodial unit above for between

1/3 and 2/3 of the length of the mesopodium. The inflorescences of all species except *S. incanoalabastrum* are pedunculate. *Solanum incanoalabastrum* and *S. labyrinthinum* have pseudo-peduncles with a solitary flower at the base of the inflorescence stalk.

Flowers

The flowers of *Solanum* section *Dunaliana* are typical of *Solanum* subgenus *Leptostemonum*. All species of *Solanum* section *Dunaliana* are basically 5-merous, however, 4- or 6-merous flowers are also present in some species. The calyx of *Solanum* section *Dunaliana* is never armed. The tips of the calyx lobes are typically small and apiculate sometimes even difficult to distinguish. Only in *S. incanoalabastrum* do the lobe tips exceed ca. 2 mm long. The fruiting calyx is not much enlarged and is never accrescent. The corollas of *Solanum* section *Dunaliana* range from white to violet and are deeply stellate with poorly developed interpetalar tissue. All flowers are bisexual with yellow, attenuate poricidally dehiscent anthers.

Fruits

The species of *Solanum* section *Dunaliana* like many other species of *Solanum* produce glabrous, juicy, red berries. According to Symon (1979) *Solanum dunalianum* and *S. viridifolium* are likely bird dispersed. Seeds of *Solanum* have been found in Cassowary dung in the rainforests of North Queensland (Stocker and Irvine, 1983) though none were identified as *S. dunalianum* or *S. viridifolium*. Presumably, the berries of all species of *Solanum* section *Dunaliana* are bird dispersed.

Distribution and ecology

The center of diversity of *Solanum* section *Dunaliana* is the island of New Guinea. All species in the section except *Solanum peekelii* can be found on at least some part New Guinea although *S. viridifolium* is more common in Australia. *Solanum peekelii* is found in the nearby Bismarck Archipelago and the Solomon Islands. The entire section is restricted to the southern tropics from about the equator south in Australia to the Tropic of Capricorn. However, most of the species are much more restricted; only *S. viridifolium* can be found below ca. 11° S. The most widespread species of the section is *S. dunalianum* extending from New Britain in the east onto Sulawesi in the west and the Cape York Peninsula in the south, while the most narrowly distributed species is *S. labyrinthinum* known only from Normanby Island and the adjacent East Cape of New Guinea. The ranges of two species *S. viridifolium* and *S. peekelii* are essentially allopatric to the rest of the section abutting the distributions of the other species, while the remaining four species are sympatric.

Like most species in the genus *Solanum*, the species of *Solanum* section *Dunaliana* are found in disturbed habitat. *Solanum* section *Dunaliana* has been collected in various habitats including roadsides, riverbanks, and old gardens and from sea level to 2400 m elevation.

Phenology

Flowers and fruits have been observed on specimens from all months of the year for the well collected species *S. dunalianum* Gaudich. and nearly all months for *S. viridifolium*. Though there are scant collections of some species, there is no indication that flowering and fruiting is restricted to a specific season for any of them.

Conservation concerns

Several species of *Solanum* section *Dunaliana* are known from only a handful of specimens. Whether these species are rare or are simply under collected, ~~however~~, is impossible to say. *Solanum labyrinthinum* is probably uncommon since it has been collected only a few times from a narrow geographic region. Certainly, more investigation is needed. One species, *Solanum dunalianum*, does seem to be fairly common in New Guinea judging by the number and geographic distribution of specimens. It is, however, rare in Queensland Australia, the southern limit of the species. This has led the Australian government to list it as vulnerable and create a plan for its conservation

(<http://www.environment.gov.au/biodiversity/threatened/species/pubs/13819-conservation-advice.pdf>). This designation however must be seen as somewhat arbitrary, as prior to New Guinea gaining its independence from Australia in 1975, *Solanum dunalianum* would have been fairly common in Australian territory.

Taxonomy

Solanum section *Dunaliana* (Bitter) Symon, J. Adel. Bot. Gard. 8: 129. 1985. *Solanum*

[unranked] *Dunalianum* Bitter, Bot. Jahrb. Syst. 55: 70. 1919 Type species: *Solanum dunalianum* Gaudich., designated by Symon, 1985.

Shrub or small to 2–5(–9), the internodes to 15.0 long. Stems glabrous to densely pubescent with off white or yellow, sessile occasionally stipitate porrect stellae (also with multangulate hairs in

S. torricellense), the stellae typically soon deciduous (or tardily glabrescent in *S. torricellense*), 0.2–0.5 broad, with 6–10 rays, the midpoint erect, ciliate less than 90°, flexed to ±90°, or curved, shorter than to ±equal to the rays; stems unarmed or with scattered prickles, the prickles to 3.2 × 3.6 mm, broad-based, straight, yellow-brown or yellow-ferruginous. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves 8.0–30.0 × 1.4–16.0 cm, ca. 1.7–6.0 times as long as wide, ovate, elliptic, obovate, oval, or lanceolate, chartaceous to subcoriaceous, the minor leaves 1/2 as large to ±equal to the major leaves, both major and minor leaves evenly moderately pubescent or densely pubescent on the proximal portion above with sessile and sometimes stipitate porrect stellae and minute glandular hairs when young, the stellae sometimes lacking (*S. incanoalabastrum*), ±glabrous or sometimes moderately pubescent along the midvein when mature, the stellae 0.2–0.7 mm in diameter, with 5–8(12) rays, the midpoint of the stellae erect, curved, or flexed at the base to ±90°, much shorter than to ±equal to the rays, the glandular hairs 0.04–0.1 mm long, ±glabrous or sparsely to densely pubescent below with sessile and sometimes stipitate porrect stellae (also with multangulate hairs in *S. torricellense*) and typically with minute glandular hairs when young, ±glabrous (or densely pubescent in *S. torricellense*) when mature, the stellae 0.2–0.6 mm in diameter, with 6–10 rays, the midpoint of the stellae erect, curved, ciliate less than 90°, or flexed at the base to ca. 90°, much shorter than to ±equal to the rays, the glandular hairs 0.04–0.08 mm long; blade unarmed, with 5–16 veins on either side of the midvein, the midvein raised abaxially, raised or merely distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially and adaxially; base truncate, rounded, cuneate, short to very long attenuate, or sometimes cordate on one side and truncate on the other, aequilateral or oblique; margin entire or slightly wavy; apex subacute to acuminate; petiole 0.7–9.0 cm long, 0.7–3.0 mm in diameter, terete or channeled above, glabrous, with a few stellae in the channel, or

moderately pubescent all over when young, becoming restricted to the channel or glabrous with age, unarmed or occasionally armed with broad-based, straight, yellow-ferruginous prickles to 6.0×2.5 mm. Inflorescence to 3.3(8.2) cm in flower, 1.5–9.3 cm in fruit, appearing lateral, extra-axillary, in the upper or middle 1/3 of the internode, once to thrice-branched occasionally branching seven times or unbranched, with (20–)30–50(–90) flowers, all apparently fertile or potentially so, the axes glabrous to densely pubescent with stellate hairs, unarmed; true peduncle or pseudo peduncle in flower 4.0–12.6(–21.0) mm long, 0.7–1.9 mm in diameter, the branches to 2.2 cm long, to 0.9 mm in diameter, in fruit 4.0–24.0 mm long, 0.8–2.3 mm in diameter, the branches to 13.0–47.0 mm long, 0.7–1.5 mm in diameter; pedicels 4.3–18.6 mm long, 0.2–0.6 mm width in diameter at the base, 0.5–1.9 mm in diameter below the calyx, straight (sometimes bent to as much as 90° below the calyx *S. viridifolium*), scarcely increasing or gradually increasing in diameter from the base distally in flower, 9.0–2.2(–3.7) cm long, 0.3–1.0 mm in diameter at the base, 0.7–2.2 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally in fruit, rigid, in two rows, articulated at the base. Flowers homostylous, 4–5(–6)-merous. Buds ovoid or conical, the calyx glabrous to densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.4–2.5(–7.0) mm long, unarmed, appearing nearly truncate with apiculate (occasionally caudate in *S. incanoalabastrum*) lobe tips, the tube 1.3–2.0 mm long, the lobe tips 0.1–1.8(–4.8) mm long, the intersepal tissue opaque or translucent when dry; splitting in the sinuses either at anthesis or during fruit development and then the lobes dentate or truncate, glabrous to densely stellate pubescent abaxially, glabrous adaxially, the calyx lobes in fruit $1.2\text{--}3.2(–5.2) \times 1.4\text{--}2.3$ cm, glabrous to densely pubescent, appressed or reflexed in ripe fruit. Corolla 1.0–2.0(–3.5) cm in diameter, stellate with poorly-developed, glabrous interpetalar

tissue, white or lavender to violet, the lobes $3.7\text{--}10.5 \times 1.6\text{--}3.4$ mm, oblong or narrowly triangular to triangular, the midrib $4.6\text{--}11.4 \times 0.8\text{--}2.6$ mm, oblong or lanceolate, densely pubescent with sessile porrect stellae (occasionally \pm glabrous in *S. viridifolium*) abaxially, \pm glabrous or glabrous at the base becoming moderately pubescent $1/3\text{--}1/2$ way towards the apex adaxially. Stamens equal, adnate to the corolla, the free portion of the filament $0.6\text{--}1.9$ mm long; anthers $2.2\text{--}5.9 \times 0.6\text{--}1.4$ mm, straight, attenuate, yellow, connivent, with minute apical pores, the line of dehiscence just below the apex, the pores dorsally inclined, the lateral sutures entire or perforated. Ovary $0.4\text{--}1.3$ mm in diameter, ovoid, globose, or conical, glabrous or with a few sessile porrect stellae or simple glandular hairs at the apex; style $3.7\text{--}9.5$ mm long, $0.2\text{--}0.5$ mm in diameter, typically longer than the stamens, emerging between the anther apices, filiform, straight or curved or hooked at the tip when dry, glabrous or sparsely to moderately stellate pubescent at the base or on the lower $1/3$; stigma $0.3\text{--}0.6$ mm in diameter, capitate or slightly bilobed. Fruit a berry, $4.0\text{--}11.9$ mm in diameter, globose, the immature fruits green or green and white mottled, orange to red when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds $1.5\text{--}2.7 \times 1.4\text{--}2.8$ mm, flattened-orbicular to flattened-reniform or flattened-irregular and notched at the point of attachment, dark tan, yellow-tan, yellow-ferruginous, or light yellow when dry, the surface cancellate or alveolate all over or the central area nearly smooth and the margin alveolate, many per fruit, ca. 23–45. Chromosome number reported as 12 for all species sampled.

Key to species of *Solanum* section *Dunaliana*

1. Mature leaves pubescent below, with multangulate hairs; stems densely pubescent when young the surface fully obscured by the hairs; inflorescence in a mid-internodal position. (New Guinea)

S. torricellense

1. Mature leaves glabrous below, never with multangulate hairs; stems glabrous or nearly so, the surface never obscured; inflorescence in an upper-internodal position (except *S. labyrinthinum*).

2. Leaves narrowly elliptic to slightly lanceolate, 4.5–6 times as long as wide; inflorescence in a mid-internodal position. (New Guinea)

S. labyrinthinum

2. Leaves obovate, ovate, or elliptic, 2–4 times as long as wide; inflorescence emerging from the upper 1/3 of the internode.

3. Inflorescence lax, the pedicels 2.0–7.4 mm apart in fruit, with up to ca. 90 flowers. (Queensland Australia, New Guinea)

S. viridifolium

3. Inflorescence congested, the pedicels to ca. 0.6 mm apart in fruit, with ca. 45 or fewer flowers.

4. Stellate hairs lacking except on the corolla; leaves with 5–11 veins on either side of the midvein; inflorescence with pseudo-peduncle with congested branches of the inflorescence, with ca. 20 flowers. (New Guinea)

S. incanoalabastrum

4. Stellate hairs present on stems and leaves at least when young; leaves with 10–16 veins on either side of the midvein; inflorescence with a true peduncle, with ca. 40–45 flowers.

5. Plants unarmed; leaves widest at or above the middle, 2.4–3.2 times as long as wide, the base attenuate, the apex subacute to acute or short acuminate; axes of the inflorescence densely stellate pubescent in flower; corolla 0.9–1.5 cm in diameter, ±glabrous adaxially; fruit 4.0–7.0 mm in diameter. (New Guinea, Solomon Islands)

S. peekelii

5. Plants sometimes armed with prickles on stems and petioles; leaves widest at or below the middle, ca. 2 times as long as wide, the base rounded to cuneate in non vigorous growth, the apex acuminate; axes of the inflorescence glabrous or with a few stellate hairs on the youngest parts in flower; corolla 1.8–2.2 cm in diameter, stellate

pubescent adaxially; fruit 8.0–11.9 mm in diameter. (Queensland
Australia, New Guinea)

S. dunalianum

***Solanum dunalianum* Gaudich.**, in Freyc., Voy. Uranie 448. 1829. Tab. 58. 1828. Type:

Indonesia. Moluccas Islands, Pisang Island, Dec 1818, *C. Gaudichaud* (Lectotype,
designated by Bean, 2004: P 00369093!; Isolectotype: P 00369092!)

Solanum dunalianum Gaudich. var. *lanceolatum* Witasek Repert. Spec. Nov. Regni Veg. 5:

166. 1908. Type: Papua New Guinea, Island of New Britain. [“Insula “Neupommern”], in
monte ignivomo “Kaia” prope “Matupi” Sept 1905 *Rechinger 4821* (Holotype: WU!)

Solanum dunalianum Gaudich. var. *puberius* Bitter, Bot. Jahrb. Syst. 55: 73. 1919. Syntypes:

New Guinea [“Neu-Guinea, Kaizer-Wilhelmsland”], Hauptlager Malu, *Ledermann 12250*
(B†, no isotypes found), *Ledermann 10718* (B†, no isotypes found)

Solanum pulvinare Scheff., Ann. Jard. Buitenz. 1: 39. 1876. As “*pulvinaris*.” Type: Indonesia.

Irian Jaya [Netherlands New Guinea], Ajambori, near Doré [Dorei?], [1870?], *M. Teysmann*
s.n. (Holotype BO; Isotype MEL!).

Figure 2.

Shrub or small tree 2–3(–4) m tall, the internodes to 10.0 cm long. Stems glabrous or with a few
off white to yellow, sessile porrect stellae and minute glandular hairs when young, the stellae

soon deciduous, ca. 0.2 mm broad, with 6–8 rays, the midpoint erect or curved, shorter than to \pm equal to the rays; stems unarmed or with scattered prickles, the prickles to 3.2×3.6 mm, broad-based, narrowly triangular with the sides concave from a wide base, straight, yellow-ferruginous. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves $19.7\text{--}30.0 \times 9.5\text{--}16.0$ cm, ca. 2.0 times as long as wide, ovate to elliptic, subcoriaceous, the minor leaves $1/2$ as large to \pm equal to the major leaves, both major and minor leaves densely pubescent on the proximal portion above with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae ca. 0.2 mm in diameter, with 6–8 rays, the midpoint of the stellae erect or curved, shorter than to \pm equal to the rays, the glandular hairs to ca. 0.04 mm long, moderately pubescent below with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae ca. 0.2 mm in diameter, with 6–8 rays, the midpoint of the stellae erect or curved, shorter than to \pm equal to the rays, the glandular hairs to ca. 0.04 mm long; blade unarmed, with 12–16 veins on either side of the midvein, the midvein raised abaxially and adaxially, the lateral veins weakly brochidodromous, raised abaxially and adaxially; base short to very long attenuate especially in juvenile growth, aequilateral or oblique, in juvenile growth the attenuate portion often very heavily crisped; margin entire or slightly wavy; apex subacute to acute, or short acuminate; petiole 1.5–9.0 cm long, 1.5–2.5 mm in diameter, channeled above, glabrous or with a few stellae in the channel, the stellae like those of the lamina, unarmed or occasionally armed with broad-based, straight, yellow-ferruginous prickles to 3.9×2.5 mm. Inflorescence to 2.0 cm in flower, 1.5–3.3 cm in fruit, appearing lateral, extra-axillary, in the upper $1/3$ of the internode, once or twice-branched, with ca. 50 flowers, all apparently fertile or potentially so, the axes glabrous or with a few scattered stellate hairs on the youngest parts, the hairs sessile porrect-stellate, unarmed; peduncle in flower 4.0–12.6 mm long, ca. 0.9 mm in

diameter, the branches to 8.0 mm long, to 0.9 mm in diameter, in fruit 4.0–18.0 mm long, 0.8–2.0 mm in diameter, the branches to 13.0 mm long, 0.7–1.2 mm in diameter; pedicels 5.1–18.6 mm long, 0.3–0.4 mm in diameter at the base, 0.7–1.1 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally, glabrous to moderately pubescent, the bases congested in flower, 10.8–18.2 mm long (presumably at least as long as in flower), 0.7–0.9 mm in diameter at the base, 1.5–2.0 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally, the bases congested in fruit, rigid, in two rows, articulated at the base. Flowers homostylous, 4–5-merous. Buds conical, the corolla densely stellate-pubescent, the calyx glabrous or sparsely stellate-pubescent. Calyx 1.5–2.5 mm long, unarmed, the tube 1.4–1.9 mm long, in bud appearing nearly truncate with apiculate lobe tips, 0.1–0.6 mm long, the intersepalar tissue translucent; splitting in the sinuses at anthesis and then the lobes dentate or truncate, 0.7–0.9 × 1.7–1.8 mm at anthesis, glabrous or with a few stellae abaxially, glabrous adaxially, the calyx lobes in fruit 1.5–1.7 × 1.9–2.2 mm, glabrous, reflexed when fruit is ripe. Corolla 1.8–2.0 cm wide in diameter, stellate with poorly developed, glabrous interpetalar tissue, lavender to violet, the lobes 8.2–10.5 × 2.5–2.9 mm, oblong, the midrib 8.5–9.4 × 1.7–2.0 mm, oblong, densely pubescent with sessile porrect stellae abaxially, glabrous at the base becoming moderately pubescent 1/3–1/2 way towards the apex adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.8–1.9 mm long; anthers 3.7–5.7 × 0.8–1.3 mm, straight, attenuate, yellow, connivent, with minute apical pores, the line of dehiscence just below the apex, the pores dorsally inclined, the lateral sutures entire or perforated. Ovary ca. 1.5 mm long, ca. 1.3 mm in diameter at the base, conical, glabrous; style 6.5–9.5 mm long, 0.2–0.4 mm in diameter, longer than the stamens, emerging from between the anther apices, filiform, occasionally straight but more often curved or hooked

towards the tip when dry, glabrous; stigma ca. 0.3 mm in diameter, capitate or slightly bilobed, cream colored. Fruit a berry, 8.0–11.9 mm in diameter, globose, orange to red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds 1.7–2.5 × 2.5–2.8 mm, flattened-orbicular to flattened-reniform or flattened-irregular and notched at the point of attachment, yellow-tan to yellow-ferruginous when dry, the surface cancellate, ca. 40 per fruit.

Distribution and ecology.— *Solanum dunalianum* is the most widespread member of section *Irenosolanum* and one of the most often collected. It is found from Sulawesi east through New Guinea and south to the Cape York Peninsula in Queensland, Australia. It typically occurs in disturbed habitats and has been found in secondary rainforest, along roads, in clearings, along streams, and gardens from sea level to 1200 m elevation. Figure 8.

Phenology.— Flowering and fruiting year round.

Etymology.— *Solanum dunalianum* was named by the French naturalist Charles Gaudichaud-Beaupré (1789-1854) for Michel Félix Dunal (1789-1856) a French Solanologist at Montpellier. Among Dunal's major accomplishments, he contributed the treatment of Solanaceae to De Candolle's *Prodromus*.

Additional specimens examined.

New Guinea, *s.c.*, *s.n.* (L); Mialeo, 21 Jul 1881 (fl, fr), *Betche s.n.* (NSW)

INDONESIA. **Aru:** Elat, W. Bosch. 8 May 1922 (fr, fr), *Jenson 332* (C, L) **Obira:** Laiwoei, Kp. Boeton., 300 m, 30 Oct 1937 (fl, fr), *Nedi 494* (A, B, L×2) **Sulawesi:** Goeroepahii, 600 m, 10 Apr 1917 (fl, fr), *Kaudern 57* (L×2, NY); Mt. Makaleo, around Opa Swamp, 4°05'S, 122°E, 20–150 m, 13 Nov 1978 (fl, fr), *Prawiroatmodjo & Soewoko 1699* (L) **Papua:** Jappen-Biak. G. Wawah. ca. 200 m, 22 Jul 1939 (fl, fr), *Aet & Idjan 39* (L); Baik Island 5 miles SW of Soredo, 1 mile from the coast, ca. 60 m, 28 Apr 1945 (fl, fr), *Britton & Winder 62* (A, F×3, L); Humboldt Bay, ca. 20 m, 15 Jan 1911 (fl), *Gjellerup 423* (L); ca. 10 m, 20 Sep 1911 (fl), *Gjellerup 696* (L×2); near Manokwari Sep 1913 (fl), *Janowski 541* (L); Cycloop-gebergte, by Polymac road, Hollandia, 120 m, 14 May 1956 (fl, fr), *Kalkman 3492* (CANB, L); along river Maro, between Merauke and Tajam, 1 m, 11 Jul 1957 (fr), *Kalkman 3720* (P, L); Merauke, Jul 1904 (fl, fr), *Koch s.n.* (L×3); between Merauke and Wassur, 26 Apr 1967 (fr), *Reksodihardjo 196a* (K, L); Merauke District, Maro River, Tambat [village], 29 Apr 1962 (fr), *Reksodihardjo 199* (G, L); Merauke District, road from Mopa airstrip to Manggatrikke, 8°30'S, 140°22'E [penciled in], ca. 10 m, 3 Aug 1954 (fl, fr), *van Royen 4553* (A, CANB, L)

PAPUA NEW GUINEA. Sepik River, 26 May 1929 (fl), *Herre 333* (DS, F); New Britain, 1901 (fl, fr), *Parkinson 10* (NSW); New Britain slopes of the volcano Kaia, Sep 1905 (fl, fr), *Rechinger 4821* (WU); 1901-1908 (fl, fr), *Schlechter s.n.* (K); New Britain, at Massawa, Nov 1901 (fl, fr), *Schlechter 13749* (BM) **Central:** Sub-district Abau, ca. 15 km along Port Moresby road, 10°05'S, 148°10'E, 25m, 1 Jun 1977 (fl, fr), *Wiakabu & Rauveve 70450* (A, CANB, K, L, M, NSW, US) **East New Britain:** Duke of York Islands, (fl, fr), *Bradtke 62* (NSW) Duke of York Islands, 31 May 1917 (fl, fr), *Bradtke 184* (NSW); Kerawara, 1889 (fl), *Warburg 21251* (BM) **Gulf District:** Summit of Ihu Hill, ca. 1 mile NW of Ihu, Vailala River, 300 ft, 16 Jan

1966 (fl, fr), *Schodde & Craven 4244* (CANB, L) **Madang:** Kalibobo, [in Symon 5°13'S, 145°48'E, [iii.1890 in Symon] 1889–91 (fl), *Weinland 133* (L, M, US) **Milne Bay:** Misima Island Mt. Sisa, northern slopes, 300 m, 22 Jul 1956 (fl, fr), *Brass 27452* (A, L); Esa'ala Sub-district, Normanby Island, Miadeba, 9°50'S, 150°50'E, 0 m, 23 Oct 1971 (fr), *Streimann & Lelean 52624* (A, CANB, K, L) **Morobe District:** Lae Sub-district, Oomsis, ca. 200 ft, 2 Nov 1967 (fr), *Coode, Gillison & Ridsdale 32569* (K, L); Lae Sub-district, Oomsis, 6°45'S, 146°40'E, 600 ft, 27 Feb 1968 (fl, fr), *Coode & Katik 32719* (L); Bewapi Creek, ca. 4 miles W of Lae, 06°40'S, 146°55'E, ca. 200 ft, 27 Mar 1962 (fl, fr), *Hartley 10078* (A, ECON, K, L); Korepa, 7.55°S 147.05°E, 1200 m, 7 Jan 1978 (fr), *Kairo 43* (A, K); vic. of Bulolo, 29 May 1977, *Kairo s.n.* (F); Sub-province Morobe, near Mor River, 7°45'S, 147°25'E, 30 m, 20 Oct 1977 (fr), *Katik 70809* (A, K, L×2, NSW, US); Bulolo, crooked L.A., 1°10'S, 146°40'E, 2400 ft, 8 Mar 1966 (fl, fr), *Streimann & Kairo NGF27523* (A, CANB, K, L); Atzera Range, ridge adjacent to 9-11 mile settlement, 6°37'S, 146°55'E, above 300 m, Jan 1993 (fl, fr), *Takeuchi 9323* (L); Lae Sub-district, Oomsis, 500 ft, 29 Nov 1967 (fl, fr), *Womersley 37098* (L) **Western Province:** Tarara, Wassi Kussa, [8°50'S, 141°52'E in Symon, 1985], Dec 1936 (fl, fr), *Brass 8514* (A, BM, L); Balamuck, 8°52'S, 141°15'E, 10 m, 19 Sep 1979 (fl, fr), *Antiko 57* (M); Balamuk, 8°52'S, 141°15'E, 10 m, 18 Sep 1979 (fl, fr), *Geno 77* (A); Balamuk, 8°52'S, 141°15'E, 10 m, 19 Sep 1979 (fl, fr), *Painap s.n.* (L); Balamuk, 8°52'S, 141°15'E, 10 m, 19 Sep 1979 (fl), *Timothy 37* (MO)

Solanum dunalianum is the type of *Solanum* section *Dunaliana*. It occurs on the island of New Guinea where it is apparently common, as well as Sulawesi and several other Indonesian Islands. The species is also known from northern Queensland, Australia (Symon, 1981; Purdie *et*

al., 1982) though no specimens from there were seen during the completion of this monograph. In Queensland, *S. dunalianum* is not common. The Australian government currently classifies it as vulnerable. In Australia, threats include habitat destruction, herbivory (feral pigs), competition with introduced weeds, and altered fire conditions (s266B of the Environment Protection and Biodiversity Conservation Act 1999).

S. morindaefolium Zipp. herbarium name; (L 202560 L0651807 908246-173)

Solanum gjellerupii Bitter, herbarium name, Hollandia N. N. Guinea, ca. 10 m, 20 Sep 1911 (fl), *Gjellerup 696* [det. Bitter] (L 0651869, L 0651868)

***Solanum incanoalabastrum* Symon**, J. Adelaide Bot. Gard. 8: 132, fig. 66. 1985. Type: Papua New Guinea, on the Wahgi-Sepik divide between Banz and Tabibuga, 15 km from Banz and 45 km from Tabibuga, ca. 2000 m, 27 Jun 1977, *D. Symon 10703* (Holotype: AD 98581507 ex ADW; Isotypes: AD 98581508, BH, CANB, K!, L0003636!, LAE, MO 3318270!, US 3083624!).

Figure 3.

Shrub or slender tree to 2 m, the internodes to 9.0 cm long. Stems glabrous; armed with scattered prickles, the prickles to 2.5×2.5 mm, broad-based, deltate or narrowly triangular, straight, yellow-ferruginous. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves $8.5\text{--}20.5 \times 2.2\text{--}7.5$ cm, 2.75–4.0 times as long as wide, elliptic to lanceolate, chartaceous to subcoriaceous, the minor leaves $3/4$ as large to equal to the major leaves, both major and minor

leaves nearly glabrous above with minute glandular hairs, lacking porrect stellae when young, glabrous when mature, nearly glabrous below with minute glandular hairs, lacking porrect stellae when young, glabrous when mature, the glandular hairs to ca. 0.06 mm long; blade unarmed, with 5–11 veins on either side of the midvein, the midvein prominent adaxially and abaxially, the lateral veins weakly brochidodromous, prominent both adaxially and abaxially; base cuneate to attenuate, aequilateral or oblique; margin entire or somewhat wavy; apex acuminate; petiole 0.7–2.3 cm long, 1.0–1.6 mm in diameter, glabrous, channeled above, unarmed. Inflorescence ca. 1.5 cm long in flower, 1.4–2.0 cm long in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode, forking once or unbranched, with ca. 20 flowers, all apparently fertile or potentially so, the axes glabrous, unarmed; pseudo-peduncle in flower ca. 1.0 cm long, ca. 1.1 mm in diameter, the branches to ca. 9.8 mm long, to ca. 0.6 mm in diameter, in fruit 1.0 cm long, 1.3 mm in diameter, the branches to 1.7 cm long, to 1.1 in diameter; pedicels 1.6–1.7 cm long, 0.4–0.5 mm in diameter at the base, 1.5–1.9 mm in diameter below the calyx, straight gradually increasing in diameter from the base distally in flower, 2.0–3.7 cm long, 0.7–1.0 mm in diameter at the base, 1.1–2.2 mm in diameter below the calyx, and typically straight, gradually increasing in diameter from the base distally in fruit, in two rows, very closely spaced to ca. 0.6 mm apart, articulated at the base. Flowers homostylous, 4–6-merous. Floral buds conical in outline, the corolla densely stellate-pubescent, the calyx glabrous. Calyx 4.5–7.0 mm long, unarmed, the tube 1.5–1.8 mm long, in bud distinctly lobed with apiculate or occasionally caudate lobe tips, 1.5–1.8 (–4.8) mm long, splitting in the sinuses during bud enlargement and continuing to split at anthesis and during fruit development and then the lobes dentate, $2.2\text{--}3.4 \times 1.0\text{--}1.5$ mm at anthesis, glabrous adaxially and abaxially, the calyx lobes in fruit $2.2\text{--}5.2 \times 1.4\text{--}2.0$ mm, glabrous, the lobes \pm appressed in ripe fruit. Corolla 2.0–3.5 cm in diameter, stellate with poorly-

developed, glabrous interpetalar tissue, white or lilac to violet, the tube ca. 2.0 mm long, the lobes 7.5–10.5 × 2.3–3.4 mm, oblong, the midrib 8.0–11.4 × 1.7–2.6 mm, oblong, densely pubescent abaxially, glabrous at the base becoming densely pubescent towards the apex adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 1.1–1.4 mm long; anthers 4.2–5.9 × 0.8–1.4 mm, markedly attenuate, yellow, connivent, with minute apical pores, the line of dehiscence just below the apex, the pores dorsally inclined, the lateral sutures entire. Ovary ca. 1.5 mm in diameter, ±globose, white, glabrous; style ca. 6.8 mm long, ca. 0.3–0.5 mm in diameter, longer than or almost equal to the stamens, filiform, straight, glabrous; stigma 0.5–0.6 mm in diameter, capitate. Fruit a berry, 8.0–12.0 mm in diameter, globose, the immature fruits shiny dark green, maturing red, glabrous; exocarp thin, shiny; endocarp apparently juicy. Seeds 1.8–2.5 × 2.0–2.6 mm, flattened-suborbicular and notched at the point of attachment, dark tan when dry, the central area nearly smooth, the margin alveolate many per fruit. Chromosome number reported as 12 (Symon, 1985).

Distribution and ecology.— *Solanum incanoalabastrum* is distributed across New Guinea in the mountains from 1000 m to 2440 m elevation. It has been collected in Papua New Guinea but not Papua, Indonesia where it most likely also occurs. It is found in rainforest in disturbed areas including roadsides, along river, forest edges, clearings, and old gardens. Figure 9.

Phenology.— Known to flower Mar, May, Jul, Aug–Dec and fruit Mar, May, Aug–Dec. Likely fertile year round.

Etymology.— Symon (1985) in the original protologue stated that the name referred to the hoary pubescence of the buds.

Additional specimens examined.

PAPUA NEW GUINEA. Central: Boridi, ca. 4700ft, 26 Oct 1935 (fr), *Carr 14752* (BM, K, L, NY, SING×3); Port Moresby Subdivision, E of Efogi village in gully, 9°10'S, 147°40'E, 1000–1200 m, 15 Sep 1970 (fl), *Kanis, 1433* (L); **Eastern Highlands:** Purosa, Okapa area, 1950 m, 21 Sep 1959 (fl, fr), *Brass 31613* (A, CANB, K, L, NY 00828107, US); Megabo, 1700 m, 8 Mar 1984 (fl, fr), *Cruttwell 2597* (L); Goroka subdivision, Mountian NE of Kamus village, 05°90'0"S, 144°5'0"E 2200 m, 30 Nov 1984 (fl, fr), *Kerenga & Baker 56923* (CANB, K, L); Goroka subdistrict, below Daulo, 6°05'S, 145°25'E, 8000 ft, 30 Aug 1963 (fl, fr), *Millar & van Royen 15997* (A, CANB, K×2, L) **Milne Bay:** Goodenough Island, east slopes, 1500-1600 m, 11 Oct 1953 (fl, fr), *Brass 24599* (CANB, K, L); **Northern:** Yodda River, ca 4500 ft, 23 Dec 1935 (fl, fr), *Carr 13967* (BM, K, L, NY, SING×3); Isuarava [Isurava], 4500 ft, 5 Mar 1936 (fl, fr), *Carr 15955* (BM, CANB, L, NY, SING×2); Goroup Mountains, Mt. Suckling, Tapan Mayu Riverflats, 9°34'S, 148°56'E, 1400 m, 18 Jul 1972 (fl), *Veldkamp & Stevens 5950* (CANB, L, US); Goropu Mountains, Mt. Suckling, Tapan Mayu Riverflats, 9°34'S, 148°56'E, 1400 m, 18 Jul 1972 (fl), *Veldkamp & Stevens 5957* (CANB, L, US) **Southern Highlands:** Anga Valley near Ebenda, ca. 6300 ft, 25 Jul 1961 (fr), *Schodde 1599* (A, CANB, L) **West Sepik:** Telefomin Subdistrict, Bielga River, below junction with Mongofogola River on Busilmin-Folongonom track, 5°00'S, 141°05'E, 2000 m, 21 May 1975 (fl, fr), *Vinas & Wiakabu LAE-59560* (A, CANB, E, K, L, M, MO, NSW, US).

***Solanum labyrinthinum* D. McClelland sp. nov.**

Type: New Guinea, Normanby Island Sewa Bay, 600 ft, 10° 00' S, 150° 55' E, 20 Apr 1956 (fl),

Womersley & Brass N.G.F.8678 (Holotype: BM 000886237; Isotypes: A!, A!, BO, BRI, CANB, K!, L!, LAE, NSW 594219!, SING 0090088!)

Figure 4.

Apparently unarmed, erect shrub to ca. 2.5 m, the internodes to 6.5 cm long. Stems \pm glabrous, with scattered soon deciduous, sessile porrect stellae when young, the stellae ca. 0.3 mm broad, ferruginous, with 6–7 rays, the midpoint flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, \pm equal the rays, soon glabrescent. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves 8.0–16.0 \times 1.4–3.7 cm, ca. 4.5–6.0 times as long as wide, elliptic to slightly lanceolate, subcoriaceous, the minor leaves \pm equal to the majors, both major and minor leaves above with a few sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.3–0.4 mm in diameter, with 5–8 rays, the midpoint of the stellae clinate less than 90° to flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, much shorter than to about 1/2 as long as the rays, the glandular hairs to 0.04 mm long, glabrous below with a few sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.3–0.4 mm in diameter, with 6–8 rays, the midpoint of the stellae clinate less than 90° , much shorter than to ca. 1/2 as long as the rays, the glandular hairs 0.04 mm long; blade unarmed, with 7–10 veins on either side of the midvein, the midvein raised both abaxially and adaxially, the lateral veins weakly brochidodromous, raised both abaxially and adaxially; base cuneate; margin entire or slightly wavy; apex acute to slightly acuminate; petiole 0.9–1.8 cm

long, 0.8–1.3 mm in diameter, channeled above, glabrous when mature, unarmed. Inflorescence to 2.6 cm long in flower, in fruit the longest observed 2.0 cm but presumably at least equal to the longest inflorescence, appearing lateral, extra-axillary, in the middle 1/3 of the internode, once(thrice)-branched, with ca. 50 flowers, all apparently fertile or potentially so, the axes moderately pubescent when young, soon glabrous, the hairs sessile porrect-stellate, unarmed; pseudo-peduncle in flower 2.0–6.0 mm long, 0.8–0.9 mm in diameter, the branches to 2.0 cm long, to 0.6 mm in diameter, in fruit 2.5–7.5 mm long, 0.8–1.2 mm in diameter, the branches presumably to at least as long as is flower longest observed 0.8 cm long, to ca. 0.9 mm in diameter; pedicels 0.6–1.0 cm long, ca. 0.3 mm in diameter at the base, ca. 0.5 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally, bases congested in flower, 1.2–1.6 cm long, ca. 0.4 mm in diameter at the base, 0.8–0.9 mm in diameter below the calyx, ±straight, gradually increasing from the base distally, the bases congested to 0.9 mm apart in fruit, rigid, in two rows, articulated at the base. Flowers homostylous, 5-merous. Buds conical, the corolla densely stellate-pubescent, the calyx nearly glabrous with few scattered stellate hairs, occasionally with minute glandular hairs, stellate-pubescent, enclosing the corolla when young. Calyx 1.4–1.7 mm long, unarmed, the tube to 0.8–1.2 mm long, in bud appearing nearly truncate with apiculate lobe tips, 0.2–0.5 mm long, splitting in the sinuses at anthesis and then the lobes dentate, 1.1–1.7 × 1–1.4 mm at anthesis, sparsely pubescent with scattered porrect stellae, minute glandular hairs sometimes present on young buds abaxially, glabrous adaxially, the calyx lobes in fruit 1.4–2.2 × 1.0–1.5 mm, glabrous, appressed in ripe fruit. Corolla ca. 1.2 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, purple or deep violet, the lobes 3.7–5.4 × 1.6–2 mm, oblong, the midrib 5.1–5.8 × 0.8–1.1 mm, oblong, densely stellate pubescent abaxially, glabrous with a few

stellae towards the apex adaxially. Stamens adnate to the corolla, the filament not seen; anthers ca. 3.5×0.6 mm, attenuate, connivent, with minute apical pores, the line of dehiscence just below the apex, the pores dorsally inclined, the lateral suture entire or splitting with age. Ovary 1.5 mm long (not seen, Symon, 1985); style ca. 3.0–4.0 mm long, ca. 0.2 mm in diameter, shorter than to \pm equal to the stamens, filiform, straight, glabrous; stigma ca. 0.4 mm in diameter, bilobed. Fruit a berry, 4.0–6.0 mm in diameter, globose, red when mature, glabrous; exocarp thin, shiny; endocarp probably juicy. Seeds $1.8\text{--}2.5 \times 1.5\text{--}1.8$ mm, flattened-suborbicular to flattened-reniform or flattened-irregular and notched at the point of attachment, yellow-ferruginous when dry, the surface alveolate, many per fruit.

Distribution and ecology.— *Solanum labyrinthinum* has been collected along roads in rainforest from 5–185 m elevation. It is the most geographically restricted species of *Solanum* section *Dunaliana*. *Solanum labyrinthinum* is known from Normanby Island and East Cape adjacent on New Guinea. Figure 9.

Phenology.—Known to flower and fruit in Apr. Perhaps fertile year round like the other members of the *Solanum* section *Dunaliana*.

Etymology.— The specific epithet was chosen to reflect the taxonomic labyrinth involving two other species of *Solanum* section *Dunaliana* that was unintentionally created by Symon (1985). Symon (1985) applied the name *S. peekelii* to the unnamed *S. labyrinthinum*. He then applied the name *S. torricellense* to the true *S. peekelii* and provided a new name, *S. mankiense*, for the true *S. torricellense*. As the type of *S. peekelii* was destroyed at B, Symon (1985) also

designated a specimen of *S. labyrinthinum* (Womersley & Brass N.G.F.8678) as the neotype of *S. peekelii*, adding a final twist to the labyrinth. However, the protologue of *S. peekelii* and the neotype designated by Symon (1985) conflict, and this proved key.

Additional specimens examined.

PAPUA NEW GUINEA. Milne Bay: Awaiaama, [in Symon (1985) 10° 14'S, 150° 31'E], Sep 1895 (fr), *Fitzgerald 16* (MEL 625545); Normanby Island, Waikaiuna Bay, inland about ½ mile from coast, 5 m, 17 Apr 1956 (fl, fr), *Brass 25460* (K, L, S);

Solanum labyrinthinum is a typical member of *Solanum* section *Dunaliana*. It is distinguished by its narrow elliptic or somewhat lanceolate leaves. Like *Solanum torricellense*, but unlike the other members of this section, the inflorescence of this species emerges from the middle of the internode. Apparently, this species is not common as only three collections have been seen.

***Solanum peekelii* Bitter**, Bot. Jahrb. Syst. 55: 73. 1917. Type: Bismark Archipelago, New Ireland ["Neu-Mecklenburg"], Buragamata near Namatanai, 12 m, Jul, *G. Peekel 523* (B†).

Neotype, *hic designatus*: New Guinea, West New Britain, West Nakanai, Malalia near Cape Hoskins, 16 Aug 1954 (fl, fr), *Floyd 6549* (Neotype *hic designatus*: K!; Isonotypes: A!, BM 000886258!, CANB, L, NSW 594233!, US 2211029!)

Solanum dunalianum var. *inerme* Witasek ex Rechinger Denkschr. Akad. Wiss. Wien, 89: 601. 1914. Type: Salomonsinseln, Insel Bougainville, Am Strande bei dem

Eingebornendorfe Numa-Numa. *Rechinger 3607* (Lectotype, *hic designatus*: WU 10316!;
Isolectotype: WU 10317!)

Figure 5.

Erect shrub or small tree to 4(5) m tall, the internodes to 13.5 long. Stems pubescent with yellow, sessile porrect stellae, the stellae 0.3–0.4 mm in diameter, with 6–10 rays, the midpoint clinate less than 90° to flexed at the base to $\pm 90^\circ$ and laying flat on the surface of the stem, shorter than to \pm equal to the rays, soon deciduous, reported as armed with prickles (Peekel, 1984) on lower stems. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves 15.0–25.5 \times 6.0–9.0 cm, 2.4–3.2 times as long as wide, obovate to elliptic, chartaceous, the minor leaves 3/4 as large to \pm equal to the majors, both major and minor leaves densely pubescent at the base becoming sparse towards the apex above with sessile porrect stellae and minute glandular hairs when young, \pm glabrous when mature, the stellae 0.3–0.6 mm in diameter, with (5) 6–8-rays, the midpoint of the stellae erect or flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs ca. 0.04 mm long, sparsely pubescent below with sessile porrect stellae and minute glandular hairs when young, \pm glabrous when mature, the stellae 0.4–0.5 mm in diameter, with 6–8-rays, the midpoint of the stellae erect, shorter than to \pm equal to the rays, the glandular hairs ca. 0.04 mm long; blade unarmed, with 10–14 veins on either side of the midvein, the midvein raised abaxially and adaxially, the lateral veins weakly brochidodromous, raised abaxially and adaxially; base rounded to cuneate, occasionally long attenuate in vigorous growth, aequilateral or oblique; margin entire or slightly wavy; apex acuminate; petiole 1.6–5.0 cm long, 1.0–2.2 mm in diameter, channeled above, moderately pubescent all over when young, the

pubescence becoming restricted to the adaxial channel with age and them sparse to moderate, unarmed. Inflorescence to ca. 1.1 cm in flower, 3.5–6.0 cm in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode often just below the leaf, once forking and often with a single pedicel attached below the fork or unbranched, many-flowered with flowers to 45, all apparently fertile or potentially so, the axes densely pubescent with sessile porrect-stellate hairs; peduncle in flower to ca. 7 mm long, 0.7–1.5 mm in diameter, the branches to ca. 5.8 mm long, 0.6–0.9 mm in diameter, in fruit 10.8–12.3 mm long, 1.2–2.1 mm in diameter, the branches to 1.9–4.0 cm long, 0.7–1.1 mm in diameter; pedicels 4.3–11.8 mm long, 0.3–0.4 mm in diameter at the base, 0.5–0.7 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally, the bases congested \pm overlapping in flower, 9.2–15.2 mm long, 0.3–0.7 mm in diameter at the base, 0.7–1.3 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally, the bases congested to ca. 0.6 mm apart in fruit, rigid, in two rows, articulated at the base. Flowers homostylous, 4–5-merous. Buds conical, the corolla densely stellate-pubescent, the calyx moderately to densely stellate-pubescent, fully enclosing the corolla in young bud. Calyx 1.6–2.3 mm long, unarmed, the tube 1.3–1.8 mm long, in bud appearing nearly truncate with lobe tips apiculate or reduced to minute protuberances, 0.1–1.1 mm long, the intersepal tissue transparent when dry, splitting in the sinuses at anthesis and then the lobes dentate, $0.7\text{--}1.7 \times 0.9\text{--}1.5$ mm at anthesis, moderately to densely pubescent abaxially, the hairs sessile porrect-stellate, glabrous adaxially, the calyx lobes in fruit $1.2\text{--}2.3 \times 1.4\text{--}2.0$ mm, sparsely to moderately pubescent, appressed in ripe fruit. Corolla 9.9–14.9 mm in diameter, stellate with poorly-developed, glabrous interpetalar tissue, white or lavender to purple, the lobes $5.7\text{--}6.5 \times 2.8\text{--}3.1$ mm, triangular, the midrib $4.6\text{--}8.8 \times 1.0\text{--}1.3$ mm, lanceolate, densely pubescent abaxially, \pm glabrous adaxially, apparently spread wide at anthesis. Stamens

adnate to the corolla, the free portion of the filament ca. 0.6 mm long; anthers 2.2–4.8 × 0.6–0.9 mm, attenuate, yellow, connivent, with minute apical pores, the line of dehiscence just below the apex, the pores dorsally inclined, the lateral sutures entire or perforated. Ovary 0.4–0.6 mm in diameter, ovoid, glabrous or with a few sessile porrect-stellate hairs at the very apex; style 3.7–5.4 mm long, 0.2–0.3 mm in diameter, emerging from between the anther apices, filiform, straight, sparsely to moderately stellate pubescent at the very base to basal 1/3; stigma ca. 0.4 mm in diameter, capitate or slightly bilobed. Fruit a berry, 4.0–7.0 mm in diameter, globose, the immature fruits green, maturing red, glabrous; exocarp thin, shiny; endocarp apparently juicy. Seeds 1.6–2.3 × 1.4–1.9 mm, flattened-orbicular to flattened-reniform or flattened-irregular, notched at the point of attachment, yellow-ferruginous when dry, the surface the central area nearly smooth, the margin alveolate, ca. 45 per fruit.

Distribution and ecology.—*Solanum peekelii* is spread across the Bismarck Archipelago and Solomon Islands. It is the only species of *Solanum* section *Dunaliana* to be found in the Solomon Islands. It has been collected in disturbed places such as old village gardens, forest edges, and secondary forest. Rechinger (1912) listed it as occurring in strand forest and rainforest on Bougainville Island; sea level–170(–1070) m elevation. Figure 8.

Phenology.— Known to flower and fruit Mar, Aug, Oct–Jan. Likely flowering and fruiting year round.

Etymology.— *Solanum peekelii* was named for P. Gerhard Peekel (1876-1949), a missionary in New Guinea who spent forty-three years collecting plants in the Bismark

Archipelago, primarily on New Ireland, and who prepared a flora of the area. Though Peekel did not consider himself a botanist, he was clearly dedicated to botany. At the outbreak of the Second World War he took measures to preserve his manuscript. Notwithstanding, it suffered from the unfavorable conditions in dugouts and concentration camps; one volume was even pierced by a bullet from an airplane. During the Japanese occupation of New Ireland, Peekel's botanical knowledge saved his life. All whites were brought to a concentration camp where Peekel was the only male not to be killed because the Japanese wanted to take advantage of his botanical knowledge (Peekel, 1984). Peekel's Flora of the Bismarck Archipelago was translated from German into English by Hentley and published in 1984 by the Office of Forests, Division of Botany, Lae, Papua New Guinea.

Additional specimens examined.

PAPUA NEW GUINEA. Bougainville: Kugu-maru, Buin, 150 m, 1 Jun 1930 (fl, fr), *Kajewski 1790* (A, BM, G, P); forest edge at the village Numa-Numa, Sep 1905 (fl, fr), *Rechinger 5365* (WU); on the beach at the village of Numa-Numa, ca. sea level, Sep 1905 (fl, fr), *Rechinger 3607* (WU×2); vic. of Barilo village, ca. 6 miles N of Buin Station, ca. 500 ft, 28 Aug 1964 (fl, fr), *Schodde & Craven 3938* (A, CANB, K, L); Namatoa, ca. 1500 ft, 7 Mar 1932 (fl) *Waterhouse 691* (K) **East New Britain:** Sub-district Gasmata, Torlu River, 5°45'S, 151°10'E, ca. 3500 ft, 27 Mar 1965 (fl, fr), *Sayers NGF24265* (A, K, L) **Madang:** Sub-district Saidor, Long Island, beach of Lake Wisdom, 400 m, 4 Oct 1971 (fl, fr), *Essig & Lelean 55039* (A, BH, CANB, K, L, NY); Sub-district Saidor, Long Island, 5 miles N of Matafuma Village, 5°20'S, 147°05'E, 50 ft, 15 Nov 1969 (fr), *Vandenberg & Katik NGF42331* (A, CANB, K, L) **New Ireland:** St. Matthias Group, Eloaua, 30 m, 16 Nov 1968 (fr) *Lepofsky 466* (BISH).

SOLOMON ISLANDS. Makira. Maru Bay, 550 ft, 28 Nov, 1968 (fr), *Gafui 12869* (K, L)
Malaita: NE Malaita, 450 ft, 21 Nov 1968 (fl, fr), *Mauriasi 13463* (K, L); Su'u area, SE Malaita,
500 ft, 2 Dec 1968 (fl, fr), *Mauriasi 13601* (A, K, L) **Santa Isabel:** Suwa, Toabul, 26 Nov 1932 (fl,
fr), *Brass 3231* (A, L); head of Tatamba Bay, sea level, 1 Jan 1965 (fl, fr), *Hunt 2835* (A, K, P, L).

Morphologically, *Solanum peekelii* is quite similar to *S. dunalianum* from which it differs in robustness, armament, leaf shape, pubescence, flower size, and fruit size. The unity of this species was recognized either at the species or varietal level by a number of workers. Symon (1985) mistakenly treated this species under the name *S. torricellense*, a species from which *S. peekelii* differs markedly (See discussion under *S. torricellense*).

According to Peekel (1984), *Solanum peekelii* is one of the first plants to appear in abandoned gardens. It is or at least was common, and Peekel reported the Pala people used stems from the species to construct graters for taro and yams by binding them crosswise to a grid.

The type of *Solanum peekelii* was destroyed at the Berlin herbarium during the Second World War. As no duplicates seem to exist, Symon (1985) neotypified *S. peekelii* with *Womersley NGF 8678*. However, *Womersley NGF 8678* does not agree with the detailed protologue of *S. peekelii* in the pubescence of the leaves and stem, leaf size or length to width ratio, number of lateral veins per side of the midvein, corolla size, and several other characters. Additionally, the travels and collecting habits of P. G. Peekel are known (Peekel, 1984). Peekel never journeyed to the area where the species represented by *Womersley NGF8678* (*S. labyrinthinum*) is found, and a common species from New Ireland, where Peekel collected, matches the protologue of *S. peekelii*. Therefore under article 10.5 of McNeill *et al.* (2006), the neotypification of *S. peekelii* by Symon (1985) is superseded by the neotype designated here.

Solanum torricellense Bitter, Bot. Jahrb. Syst. 55: 75. 1919. Type: Papua New Guinea, Kaiser

Wilhelmsland, Torricelli Mts., 900 m, Sep, *R. Schlechter 20268* (Holotype B†; Isotypes P!, UC!).

Solanum mankiense Symon, J. Adelaide Bot. Gard. 8: 135, figs. 68, 69. 1985. Type: Papua New

Guinea, Manki area, 7°11'S, 146°33'W, 1350–1400 m, 3 Jun 1984, *D. Symon 13857*

(Holotype AD 98619096 ex ADW; Isotypes AD 98619097, BH, BRI, CANB, K!, L, LAE, MO 3318272!).

Figure 6.

Erect shrub or small tree to 3 m, the internodes to 15.0 cm long. Young stems densely pubescent, with sessile or stipitate porrect stellae, and minute glandular hairs, the surface of the stem totally obscured, the stellae 0.3–0.5 mm broad, light yellow, with 7–8 rays, the stipes of various lengths to 0.2 mm long, the midpoint curved to project ±laterally, slightly shorter than to ±equal to the rays, tardily glabrescent, the minute glandular hairs to 0.04 mm long; stems unarmed or with a few, broad-based prickles, the prickles straight, sometimes very slightly inclined backward, to 3.0 × 1.6 mm, drying yellow-brown, sometimes with a few stellate hairs and scattered glandular hairs. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves 13.0–30.0 × 6.0–14.0 cm, 2.0–2.5 times as long as wide, oval to lanceolate, chartaceous to subcoriaceous, the largest leaves often undulate, the surface rugose particularly around the smaller veins, the minor leaves 2/3 to nearly as large as the majors, both major and minor leaves moderately pubescent above with sessile and a few short stipitate porrect stellae, and minute glandular hairs when young, nearly glabrous with scattered hairs across the lamina, on the midvein sparsely to

moderately pubescent above when mature, the stellae 0.3–0.7 mm in diameter, with 8–12 rays, the midpoint of the stellae erect or flexed to $\pm 90^\circ$ at the base, slightly shorter than the rays, the glandular hairs to ca. 0.08 long, densely pubescent below with sessile porrect stellae, stipitate porrect stellae, and multangulate hairs when young and persisting when mature, the stellae 0.5–0.6 mm in diameter, with 7–10 rays, the midpoint of the stellae erect, \pm equal to the rays, the multangulate hairs with 11–15 rays; blade unarmed, with 11–14 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially and adaxially; base acute to rounded, truncate, or cordate on one side and truncate on the other, oblique; margin entire or somewhat wavy; apex acute; petiole 2.0–11.0 cm long, 1.5–3.0 mm in diameter, channeled above, stellate pubescent all over, unarmed or especially on juvenile leaves with straight, broad-based prickles, to $6.0 \times$ ca. 2.2 mm. Inflorescence 2.8–3.3 cm long in flower, 3.0–3.5 mm long in fruit, appearing lateral, extra-axillary, in the middle 1/3 of the internode, twice or thrice-branched, with 33–54 flowers, with a single flower below the first fork of the inflorescence, all apparently fertile or potentially so, the axes densely, stellate pubescent, the hairs like those of the stem; peduncle in flower 6.2–8.5 mm long, 1.5–1.9 mm in diameter, the branches to 4.9 mm long, to 0.5 mm in diameter, in fruit 0.5–1.0 cm long, 1.5–2.3 mm in diameter, the branches to 1.8 cm long, to 1.5 mm in diameter; pedicels 8.0–11.0 mm long, 0.4–0.6 mm in diameter at the base, 0.7–1.0 mm in diameter below the calyx, straight, scarcely increasing in diameter, the bases congested in flower, 9.0–16.0 mm long, 0.7–0.8 mm in diameter at the base, 1.3–1.8 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally in fruit, in two rows, the bases congested, rigid, in two rows, articulated at the base. Flowers homostylous, 5-merous. Buds ovoid, the calyx and the corolla densely stellate-pubescent. Calyx 2.0–2.5 mm long, unarmed, the tube 1.5–1.9

mm long at anthesis, in bud appearing nearly truncate with apiculate lobe tips, 0.3–0.6 mm long, densely pubescent abaxially with sessile porrect-stellate, glabrous adaxially, the intersepal tissue glabrous, membranaceous, translucent when dry, splitting in the sinuses during fruit development and then the lobes dentate, the calyx lobes in fruit 1.6–2.2 × 1.7–2.3 mm, densely pubescent, appressed in ripe fruit. Corolla ca. 1.3 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white or lavender, the lobes 4.6–5.4 × 2.6–3.4 mm, triangular, the midrib 4.9–7.4 × 1.1–1.4 mm, lanceolate, densely pubescent abaxially with sessile porrect stellae, ±glabrous adaxially. Stamens adnate to the corolla, the free portion of the filament ca. 0.9 mm long; anthers ca. 2.9 × 0.7 mm, slender, attenuate, yellow when dry in well preserved material, connivent, with minute apical pores, the line of dehiscence just below the apex, the pores dorsally inclined, the lateral sutures entire. Ovary ca. 0.9 mm in diameter, globose, nearly glabrous with very few simple glandular hairs at the apex; style ca. 5.5 mm long, ca. 0.3 mm in diameter, longer than the stamens, emerging from between the anther apices, filiform, straight, glabrous with very few simple glandular hairs at the base; stigma ca. 0.4 mm in diameter, capitate. Fruit a berry, 7.0–9.0 mm in diameter, globose, immature fruits green, maturing orange-red, glabrous, shiny; endocarp apparently juicy. Seeds 1.5–1.9 × 1.9–2.2 mm, flattened-suborbicular to flattened-reniform; notched at the point of attachment, yellow-tan when dry, the surface the central area nearly smooth, the margin alveolate, many per fruit. Chromosome number reported as n=12 (Symon, 1985).

Distribution and ecology.— *Solanum torricellense* has been collected along roads in lower and mid-montane forests. It appears to occupy disturbed places like most species of *Solanum*; however, it might be more habitat specific as it is under represented in collections. The two areas

where it has been collected are about 650 km apart, and *Solanums* have been collected from the area in between. Elevation 600–1400 m. Figure 9.

Phenology.—Known to flower and fruit Jan, Jun, and Aug. Likely flowering and fruiting year round.

Etymology.— This species was named for the Torricelli Mountains where it was first collected.

Additional specimens examined.

PAPUA NEW GUINEA. Morobe District: Mauki Bulolo, 600 m, 17 Jan 1979 (fl, fr), *Kairo 67* (A, CANB×2, CBG, K), Upper Watut River, near Nauti Village, 7°19'S, 146°35'E, 1300 m, 13 Aug 1982 (fl, fr), *Kairo 540* (A, BISH, E, K, L, NSW); Manki area, 7°11'S, 146°33'W, 1350–1400 m, 3 Jun 1984, *D. Symon 13857* (AD×2, BH, BRI, CANB, K, L, LAE, MO)

CULTIVATED. Pot grown from seed of *Symon 13857* originally collected Morobe District: Manki, 1300-1400 m, 20 Oct 1985 (fl), *Symon ex 13857* (MO, NY); pot grown from seed of *Symon 13857* originally collected Morobe District: Manki, 1350 m, 26 Apr 1985, *Symon ex 13857* (MO, NY)

The most distinguishing character of this species is its pubescence. While the rest of the members of *Solanum* section *Dunaliana* have glabrous stems and leaves at maturity, the abaxial surface of the leaves are densely and persistently pubescent in *Solanum torricellense*, and the stems

are densely pubescent with tardily deciduous stellate hairs. *Solanum torricellense* also has multangulate stellate hairs on the abaxial surface of the leaves, a hair type present in no other species of *Solanum* section *Dunaliana*.

Save for the pubescence *Solanum torricellense* is a typical member of *Solanum* section *Dunaliana*. Symon (1985) misapplied the name *S. torricellense* to *S. peekelii* and then coined the name *S. mankiense* to use for the true *S. torricellense*.

Solanum viridifolium Dunal, in DC., Prodr. 13(1): 73. 1852. Type: Australia. Queensland [“New South Wales”], Cook District, near Cape Grafton, *J. Banks s.n.* (Holotype BM-Banks; Isotype NY!, P!), pro syn. *Solanum cymosum* Banks ex Dunal, in DC., Prodr. 13(1): 73. 1852. Nom. nud. in syn. *S. viridifolium* Dunal. Cited: New Holland, New South Wales, Grafton promontory, *J. Banks s.n.* (BM-Banks).

Solanum viride R. Br., Prodr. 445. 1810. Lectotype designated by Symon, 1981: Australia, Queensland, coast, Port I, between Curtis Island and Facing Island, *R. Brown s.n.* [Bennett 2664] (Holotype BM!; Isotype K!; possible Isotype NSW!).

Figure 7.

Shrub or small tree to 5 (9) m tall, the internodes to 10.0 cm long. Stems glabrous, reported as armed with simple prickles on seedlings, the mature growth unarmed. Sympodia difoliate. Leaves simple, geminate (occasionally borne individually on fast growth), the blades of major leaves 8.6–18.5 × 2.7–8.8 cm, 1.7–3.4 times as long as wide, elliptic to ovate, chartaceous, the

minor leaves 1/2 as large as to \pm equal to the major leaves, both major and minor leaves sparsely pubescent above with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.2–0.4 mm in diameter, light yellow to ferruginous-yellow, with 6–8 rays, the midpoint of the stellae erect or bent to ca. 90° , \pm equal to the rays, the glandular hairs to 0.1 mm long, sparsely pubescent below with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.2–0.4 mm in diameter, with 6–8 rays, the midpoint of the stellae erect or flexed at the base to ca. 90° , \pm equal to the rays, the glandular hairs to 0.08 mm long; blade unarmed, with 6–10 veins on either side of the midvein, the midvein raised abaxially, slightly recessed in the basal portion adaxially, the lateral veins weakly brochidodromous, raised abaxially and adaxially, the major veins drying straw yellow in well preserved material; base acute to rounded, aequilateral or oblique; margin entire or slightly wavy; apex acute to acuminate; petiole 1.5–4.3 mm long, 0.7–1.6 mm in diameter, channeled above, glabrous or with a few scattered stellate hairs like those of the young leaves.

Inflorescence 2.4–8.2 cm long in flower, to 3.1–9.3 cm in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode, as much as 7-branched, with many flowers to ca. 90, all apparently fertile or potentially so, the axes glabrous; peduncle in flower 1.0–2.1 cm long, 0.7–1.1 mm in diameter, the branches to 2.2 cm long, to 0.7 mm in diameter, in fruit 1.2–2.4 cm long, 0.6–1.4 mm in diameter, the branches to 4.7 cm long, to 0.9 mm in diameter; pedicles 0.8–1.6 cm long, 0.2–0.4 mm in diameter at the base, 0.6–0.8 mm in diameter below the calyx, straight or bent to as much as 90° below the calyx, gradually increasing in diameter from the base distally, the bases congested in flower, 1.2–2.2 cm long, 0.6–0.8 mm in diameter at the base, 1.1–1.5 mm in diameter below the calyx, straight, gradually increasing in diameter from the base distally, the bases well spaced, 2.0–7.4 mm apart in fruit, in two rows, articulated at the base.

Flowers homostylous, 4–5-merous. Buds ovoid to conical, the calyx glabrous or with a few stellate hairs, fully enclosing the corolla when young, the corolla densely stellate-pubescent, the hairs sparser along the center of each petal, occasionally this area nearly glabrous and the hairs restricted to the margins of the petal. Calyx 1.6–2.2 mm long, unarmed, the tube 1.3–2.0 mm long, in bud appearing nearly truncate with apiculate lobe tips, 0.2–0.8 mm long, the intersepal tissue opaque when dry, splitting in the sinuses at anthesis and then the lobes dentate, 1.0–1.8 × 1.1–1.5 mm at anthesis, glabrous abaxially and adaxially, the calyx lobes in fruit 2.3–3.2 × 1.4–1.5 mm, glabrous, appressed in ripe fruit. Corolla 1.4–1.7 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, pale lilac to purple, the lobes 6.3–8.8 × 2.0–2.6 mm, narrowly triangular, the midrib 7.1–9.1 × 1.5–1.9 mm, lanceolate, ±glabrous to moderately pubescent abaxially, glabrous at the base scattered pubescent towards the apex adaxially. Stamens adnate to the corolla, the free portion of the filaments 0.5–0.9 mm long; anthers 3.7–4.7 × 0.8–1.1 mm, yellow, connivent, with minute apical pore, the pore directed distally, the lateral suture perforated. Ovary ca. 1 mm in diameter, globose, mostly glabrous with scattered minute and simple glandular hairs towards the apex; style 5.2–6.0 mm long, 0.2–0.4 mm in diameter, longer than the stamens, emerging from between the anther apices, filiform, straight, glabrous; stigma 0.4–0.6 × 0.3–0.4, entire or slightly bilobed. Fruit a berry, 6.0–9.0 mm in diameter, globose, immature fruits green and white mottled, maturing red, glabrous; exocarp shiny; endocarp soft, juicy. Seeds 2.4–2.7 × 1.8–2.3 mm, flattened-suborbicular to flattened-reniform, notched at the point of attachment, light yellow when dry, the surface cancellate, many ca. 23 per fruit. Chromosome reported as reported as 12 (Randell and Symon, 1976).

Distribution and ecology.— *Solanum viridifolium* primarily occurs on the Cape York Peninsula in Queensland, Australia; however, it can also be found in the southernmost part of New Guinea. It is the only abundant species in *Solanum* section *Dunaliana* in Australia. *Solanum viridifolium* is adapted for disturbed sites. It is found in rainforest especially in rainforest regrowth and margins, in open areas, along roads, along streams, in old garden sites, in old village sites, along the inner edge of mangroves, and in lowland grasslands near old gardens from sea level to 1220 m elevation. Figure 8.

Phenology.— Flowering and fruiting year round.

Etymology.— The specific epithet for this species refers to green leaves, a condition not unusual in *Solanum* or the kingdom Plantae.

Additional specimens examined.

AUSTRALIA. 1802–1805 (fl), *Brown s.n.* (F) **Queensland:** Tinaroo Range, Emerald logging area, 1200 m, 9 Aug 1971 (fl), *Balgooy 1574* (K, L, MO, UC); Atherton, Aug 1901 (fl, fr), *Betche s.n.* (CAS, NSW); E of Ravenshoe, 990 m, 14 Oct 1935 (fl, fr), *Blake 9896* (K, L); Near Clump Point, 12 Nov 1954 (fl, fr), *Blake 19718* (MO); Cape York Peninsula, Iron Range, 20 m, 10 Jun 1948 (fl), *Brass 19120* (A, K, L); Brown's Creek, Pascoe River, 60 m, 15 Jul 1948 (fl, fr), *Brass 19589* (K, L×2); Keppel Bay, (fl, fr), *Brown s.n.* (P); Keppel Bay, 1802–1805 (fl), *Brown s.n.* (NY); Dalrymple Heights, and vic., Jul-Sep 1947 (fl), *Clemens s.n.* (MICH); Mount Fox, Sep-Dec 1949 (fl), *Clemens s.n.* (GH); Fenby Estate, Tully and vicinity, Jan 1950 (fl, fr), *Clemens s.n.* (K); Mission Beach, S of Clump Point, 17°52'S, 146°06'E, 6 Mar 1971 (fl), *Crome 79* (MU); Percy

Islands, Jun 1819 (fl), *Cunningham* 27 (K); Percy Isles, 1819 (fl, fr), *Cunningham* 97 (BM); Cape Grafton, 27 Jun 1821 (fr), *Cunningham* 463 (K); Cape Grafton, 1822 (fl, fr), *Cunningham* s.n. (BM); Cape York, (fl, fr), *Daemel* s.n. (BM) [on sheet with *Cunningham* 222]; Rockingham Bay, (fl, fr), *Dallachy* s.n. (GH, K, P); Port Mackay, (fr), *Dietrich* s.n. (P); Port Makay, 16 May 1864 (fl, fr), *Dietrich* s.n. (HAM); Port Mackay, (fr), *Dietrich* 2489 (BM, HAM ×2, P); Port Macky, (fl, fr), *Dietrich* 2635 (HAM ×2); Wongabel State Forest 191, 17°19'56"S, 145°17'17"E, 760 m, 17 Jan 2002 (fl, fr), *Forster, Booth, & Jensen* 28153 (A); Wongabel State Forest 191, 17°19'46"S, 145°30'39"E, 760 m, 17 Jan 2002 (fr), *Forester, Booth & Jensen* 28156 (K); State Forest 310 Gadgarra, 17°18'13"S, 145°43'26"E, 22 Jan 2002 (fl, fr), *Forster, Booth & Jensen* 28230 (A); State Forest Reserve 194, Western, 17°25'S, 145°25'E, 1200 m, 21 Sep 1981 (fl), *Gray* 2156 (CANB); Cape York, SFR 194, Barron, Plath Road, 17°22'S, 145°27'E, 1000 m, 10 Jan 1983 (fr), *Gray* 02910 (A, K); Cook district, Between Tozer's Gap and Iron Range airport, on road to Coen, just E of the gap, 12°45'S, 143°12'E, 22 Sep 1976 (fl, fr), *Henderson* 2416 (K); near Henrietta Creek [tributary of Johnsonstone River], Palmerston Highway, 21 Sep 1974 (fl), *Hind* 681 (NSW); Cook, Mt. Windsor Tableland, Barcoo Creek, 16°12'S, 145°05'E, 10 Sep 1980 (fl), *Hind* 2737 (NSW); Atherton Tableland S of Atherton, ca. 11 km W of Atherton-Herberton Way, "Eflenwald.", State Forest Reserve 194, 1000 m, 20 Sep 1986 (fl), *Hofmann & Specht* 1803 (GOET); Cook District, Tinaroo Range, Noel Logging area N of Tinaroo Falls Dam, 17°07'S, 145°33'E, 800 m, 18 Nov 1981 (fl), *Hyland* 2150 (MO); State Forest Reserve 652, Cauley, 20°50'S, 148°30'E, 800 m, 31 Jul 1974 (fl), *Hyland* 7382 (L); Clive River, 12°10'S, 143°05'E, 2 m, 14 Sep 1974 (fl), *Hyland* 7518 (L); Mt. Carter, 13°00'S, 143°15'E, 400 m, 15 Sep 1974 (fl), *Hyland* 7545 (L); State Forest Reserve 194, 17°15'S, 145°25'E, 1220 m, 22 Nov 1974 (fr), *Hyland* 7871 (K, L); McIlwraith Range, Leo Creek, Road, T.R. 14 SFR 756, 13°45'S, 143°20'E, 450 m, 22 Sep 1975 (fl), *Hyland* 8431 (CANB, K, L);

Claudie River, 12°45'S, 143°15'E, 60 m, 22 Sep 1976 (fl), *Hyland 9032* (CANB, L); Parish of Jordan, Lower Downey LA, 17°40' 00"S, 145°47' 00"E, 440 m, 30 Jan 1992 (fr), *Hyland 14432* (MO); State Forest Reserve 191, Barron, 17°20'S, 145°30'E, 762 m, 8 Dec 1971 (fl), *Irvine 102* (L); State Forest Reserve 194, 17°17' S, 145°25'E, 1165 m, 15 Dec 1971 (fl), *Irvine 116* (K, L); Gadgarrah, Lake Eacham, Atherton Tableland, 800 m, 4 Jul 1929 (fl, fr), *Kajewski 1171* (A, C, K, NY, P, S×2, UC); Gadgarrah, Heberton Range, 700 m, 18 Nov 1929 (fl, fr), *Kajewski 1373* (A, C, CAS, DS, K, S×2, NY, P, UC); Cook District, Tinaroo Range, Noel Logging area N of Tinaroo Falls Dam, 17°07'S, 145°33'E, 800 m, 18 Nov 1981 (fl), *Kanis 2150* (L); Cook, Ravenshoe, 1921? (fl), *Manuell 2* (NSW); 1886 (fl), *Lea s.n.* (BM); Barnard Isles 10 Jun 1848 (fl, fr), *McGillivray 203* (K); Barnard Isles, 10 Jun 1848 (fl, fr), *Macgillivray 294* (K); Innisfail, (fl), *Michael 360* (GH); Tinaroo Range, Sep 1971 (fl), *Moriarty 823* (L); Bramston Road, 17°18'S, 146°00'E, 5 m, 22 Jan 1976 (fl), *Moriarty 1929* (K, L); Rockingham Bay, 1863 (fl, fr), *Mueller s.n.* (P×2); Rockingham Bay, (fl, fr), *Mueller s.n.* (L); Isles between Cape Flattery and Cape Bedford, Aug 1855 (fl), *Mueller s.n.* (K); Atherton Tablelands, Lake Barrine, Oct 1953 (fl, fr), *O'Grady s.n.* (NSW); Mt. Bellendenker, 1200 ft, 1891-1893 (fr), *Podenzana s.n.* (BM) [on sheet with Cunningham 222]; Halloran's Hill, Atherton, 17°16'S, 145°29'E, 875 m, 21 Aug 1975 (fl), *Stocker 1420* (L); 1936 (fl), *Steers s.n.* (BM); State Forest Reserve 185, Emerald L. A. 17°09'S, 145°39'E, 1000 m, 5 Oct 1971 (fl, fr), *Risley 19* (K, L); Tinaroo Creek Road, ca. 2 miles SW of Mt. Haig, ca. 1150 m, 7 Jan 1966 (fl, fr), *Rodd 273* (NSW); Forestry reserve W of Acherton, 17 May 1967 (fr), *Symon 4753* (B, K); Palmerston Highway, 17°35'S, 145°45'E [penciled in], 29 Sep 1945 (fl), *Webb 1024* (CANB); Whitfield Range W of Cairns 17°0'S, 145°38'E, 600 m, 7 Sep 1972 (fl, fr), *Webb & Tracey 10751* (B, L, MO); MacDowall Range between Daintree River and China Camp, 22 Aug 1972 (fl), *Webb & Tracey 10754* (K); Track near the crest of McDowall Range, 16°06'S, 145°20'E, 480 m, 13 Aug

1986 (fl), *Weston et al.* 530 (NSW); Mt. Spurgeon, Sep 1936 (fl), *White* 10719 (A); Cook District, ETTY Bay, 7 Dec 1941 (fl, fr), *White* 11734 (A, K); South Kennedy District, Nungella Range, 2 Sep 1938 (fl, fr), *White* 12971 (A).

PAPUA NEW GUINEA. Western Province: Mabaduan, Apr 1936 (fl), *Brass* 6498 (A, L); Morehead subdivision, Bula Plains, 9°00'S, 141°15'E, 30 ft, 11 Nov 1972 (fl, fr), *Henty & Foreman* 49372 (CANB, L, NSW); Subdistrict Daru, Sabi, lower Wassi Kussa, 9°05'S, 142°00'E, 0 m, 11 Jun 1973 (fr), *Henty* 49646 (CANB, L); Daru, near Kunini Village, 12 May 1986 (fl, fr), *Simaga* 768 (A, CBG, L).

Cultivated: AUSTRALIA. South Australia. Waite Agricultural Research Institute, from seeds from Bingil Bay Queensland, 20 Mar 1974 (fl), *Symon s.n.* (MO); Waite Research Institute, from seeds from S-660 ex Webb & Tracey 8351, Bingil Bay, Queensland, collected 16 Nov 1969, 19 Jan 1981 (fl), *Symon s.n.* (L)

Solanum viridifolium is the only member of *Solanum* section *Dunaliana* which predominantly occurs in Queensland, Australia and is uncommon on the Island of New Guinea. It also has a lax sometimes highly branched inflorescence instead of the typical condensed few branching inflorescence of *Solanum* section *Dunaliana*. Like all members of *Solanum* section *Dunaliana*, *S. viridifolium* has red fruits. Symon (1979) stated that the seeds of *S. viridifolium* are likely dispersed by birds. Some confusion might occur considering the type locality. The protologue for this species cites the type as from New South Wales. However the type locality is

in present day Queensland. Queensland was separated from New South Wales in 1859. When Dunal named *S. viridifolium* in 1852, Cape Grafton was then in New South Wales.

Excluded species

Solanum section *Dunaliaia* as it is recognized here is much smaller than Whalen's (1984) *Solanum dunalianum* group. Many of the species of Whalen's group belong to section *Irenosolanum* rather than *Solanum* section *Dunaliana* and are treated elsewhere within that section. Below, special mention is made of two species excluded from *Solanum* section *Dunaliana* which also do not belong to section *Irenosolanum*.

***Solanum tetrandrum* R. Br.**, Prodr. 445. 1810. Lectotype [Symon, 1981]: Australia, Northern Territory, Arnheim North Bay, Cotton Island and Pobassoo Island, 14 Feb, 15 Dec, *R. Brown s.n.* [Bennett 2662] (Holotype BM!; Isotypes BM×2!, E, E, K×3!, MEL, P!)

Much confusion has surrounded the circumscription and infrageneric relationships of *S. tetrandrum*. The species was first grouped with *Solanum dunalianum* by Dunal. Later workers, notably Whalen (1984) and Symon (1981), echoed this grouping and expanded the circumscription of *S. tetrandrum* to include species from the islands of the western Pacific. Whalen included *S. artense* Montrouier (New Caledonia), *S. austrocaledonicum* Seem. (New Caledonia), *S. inamoenum* Benth. (Fiji), *S. le-ratii* Schlechter (New Caledonia), *S. neocaledonicum* Bitter & Schlechter (New Caledonia), *S. noumeanum* Bitter (New Caledonia),

and *S. vieillardii* Bitter (New Caledonia) under *S. tetrandrum*. Likewise, Symon extended the range of the species at least as far as New Caledonia. Symon supported his concept with a discussion of morphology. He stated that *S. tetrandrum s.s.*, narrowly distributed along the northeastern coast and offshore islands of Australia, was morphologically very uniform. While he pointed out that *S. tetrandrum s.s.* differed in several ways from the material illustrated by Heine (1976) under that name, he considered the isolated populations of the western Pacific to represent subspecies rather than distinct species. From his discussion of *S. tetrandrum*, it is clear that Symon was comparing the Australian material to the description and illustration of New Caledonian material in Heine (1976) rather than to actual specimens. Close examination of the material from Australia and New Caledonia reveals that they are quite distinct and not simply subspecies. Therefore, the name *S. tetrandrum* must be restricted to the Australian material. Whalen indicated his thoughts on the affinities of *S. tetrandrum* simply by placing it within his *Solanum dunalianum* group. Symon, by contrast, clearly stated that *S. tetrandrum* was most closely related to *S. dunalianum*. However, both molecular and morphological evidence exclude *S. tetrandrum* from *Solanum* section *Dunaliana*. Molecular data places *S. tetrandrum* well outside the clade containing *Solanum* section *Dunaliana* and indicate an affinity with species related to *S. melongena*; several morphological characters exclude *S. tetrandrum* from the section: margins of juvenile leaves repand, leaves almost completely deciduous during the dry season, short, relatively few flowered inflorescences, habit sometimes a liana. No species of *Solanum* section *Dunaliana* exhibit any of these characters.

Solanum athroanthum Dunal, in DC., Prodr. 13(1): 208. 1852. Type: Indonesia, Java, 1846, *H. Zollinger 2907* (Holotype G-DC, =IDC microfiche 800-61.2078:II.8; Isotype BM, P ×3!).

Solanum densiflorum Dunal, in DC., Prodr. 13(1): 208. 1852. Nom. nud. in syn. *S. athroanthum* Dunal. Type: Indonesia, Java, *H. Zollinger 2907* (G-DC).

Whalen (1984) included this species in his large and morphologically heterogeneous “*Solanum dunalianum* group”. While including it in this group based on Dunal’s (1852) description may not have been unreasonable, inspection of the scant herbarium material makes *S. athroanthum* an unlikely candidate for the group and obviously eliminates it from *Solanum* section *Dunaliana*. Whalen (1984) indicated that his list of species in his *Dunalianum* Group was tentative. No evidence has been found that Whalen saw any material of *S. athroanthum*. If he had, it is unlikely he would have included it in his *Dunalianum* Group. *Solanum athroanthum* was excluded here based on the following morphological characters of the species: deeply lobed juvenile leaves, prickles on the primary and secondary veins of the leaves, and anisandry having three long anthers and two short ones per flower. These three conditions are not found in any members of *Solanum* section *Dunaliana*.

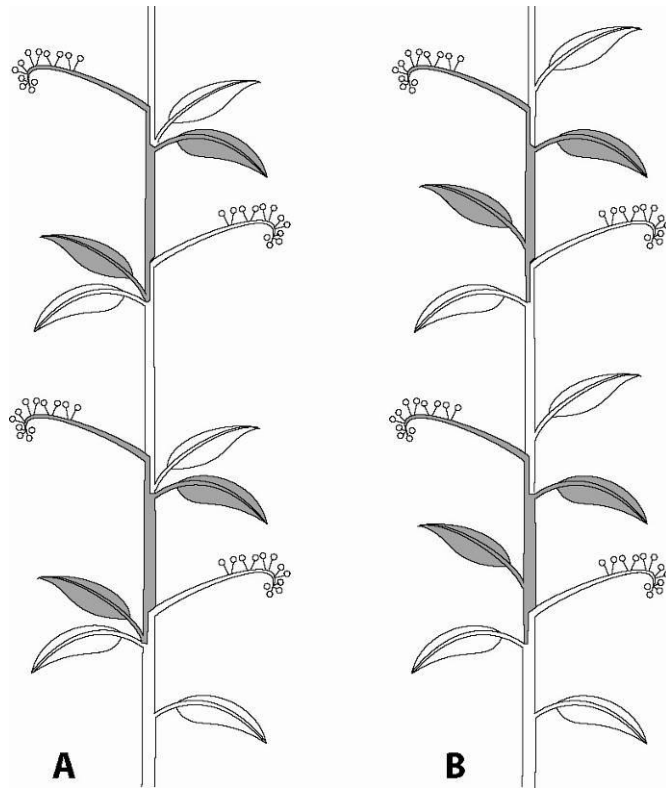


Figure 1. Sympodial growth of *Solanum* section *Irenosolanum* showing successive sympodia (Redrawn from Danert, 1967). A. Geminate leaf arrangement. B. Leaves borne individually.



Figure 2. Holotype of *Solanum dunalianum* (Gaudichaud s.n., P).

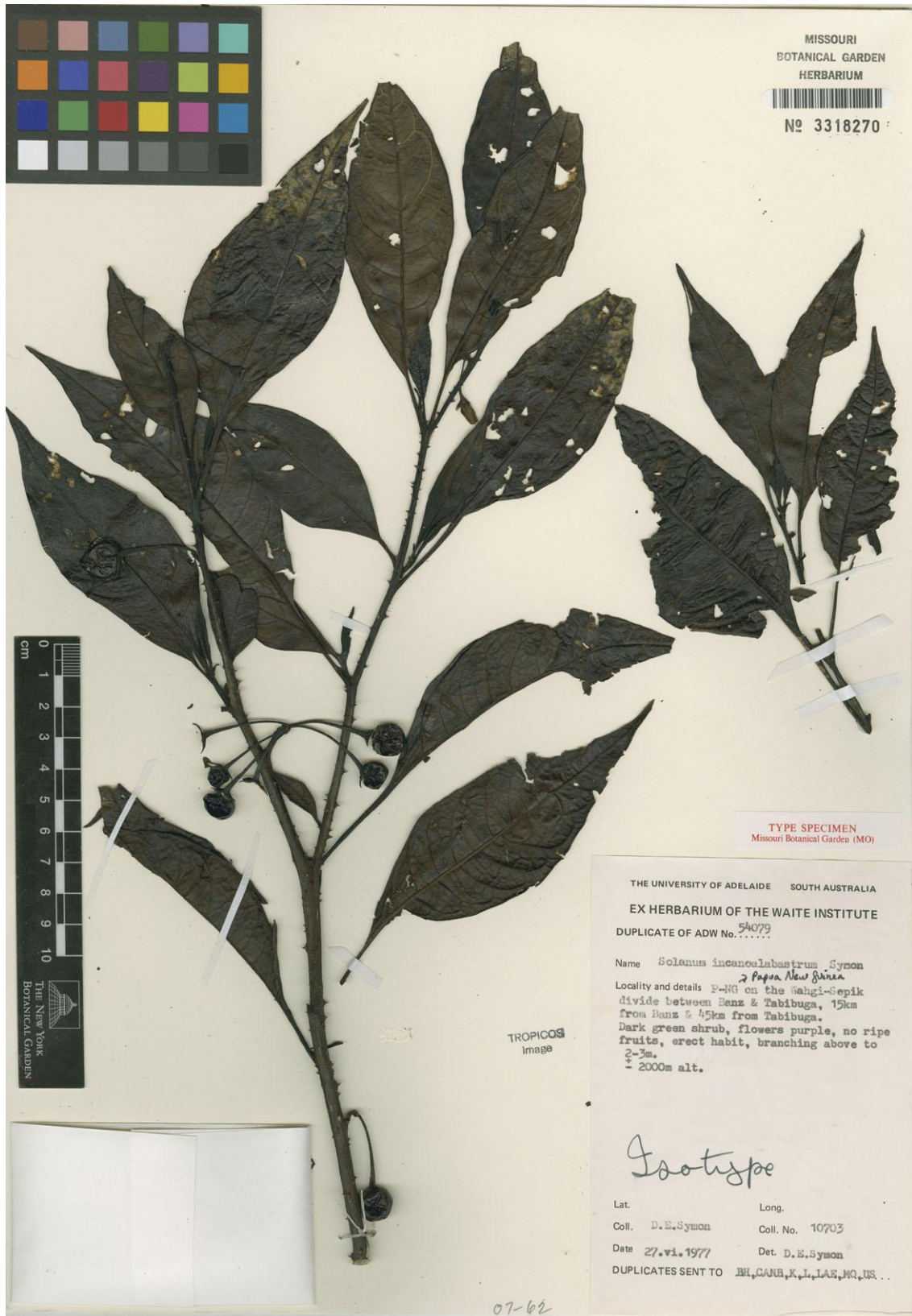


Figure 3. Isotype of *Solanum incanoalabastrum* (Symon 10703, MO).



Figure 4. Holotype of *Solanum labyrinthinum* (Womersley & Brass N.G.F.8678, BM).

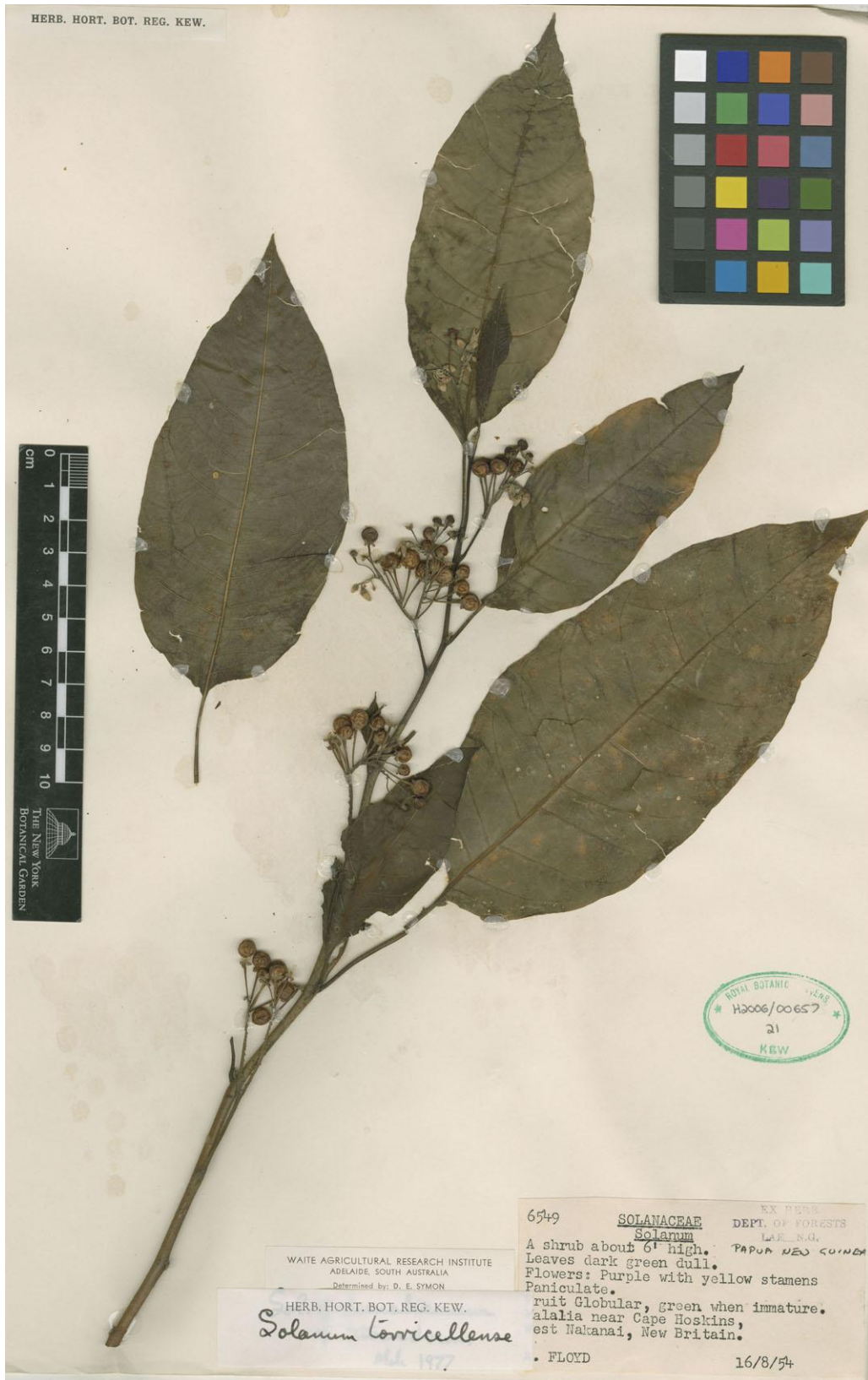


Figure 5. Neotype of *S. peekelii* (Floyd 6549, K).

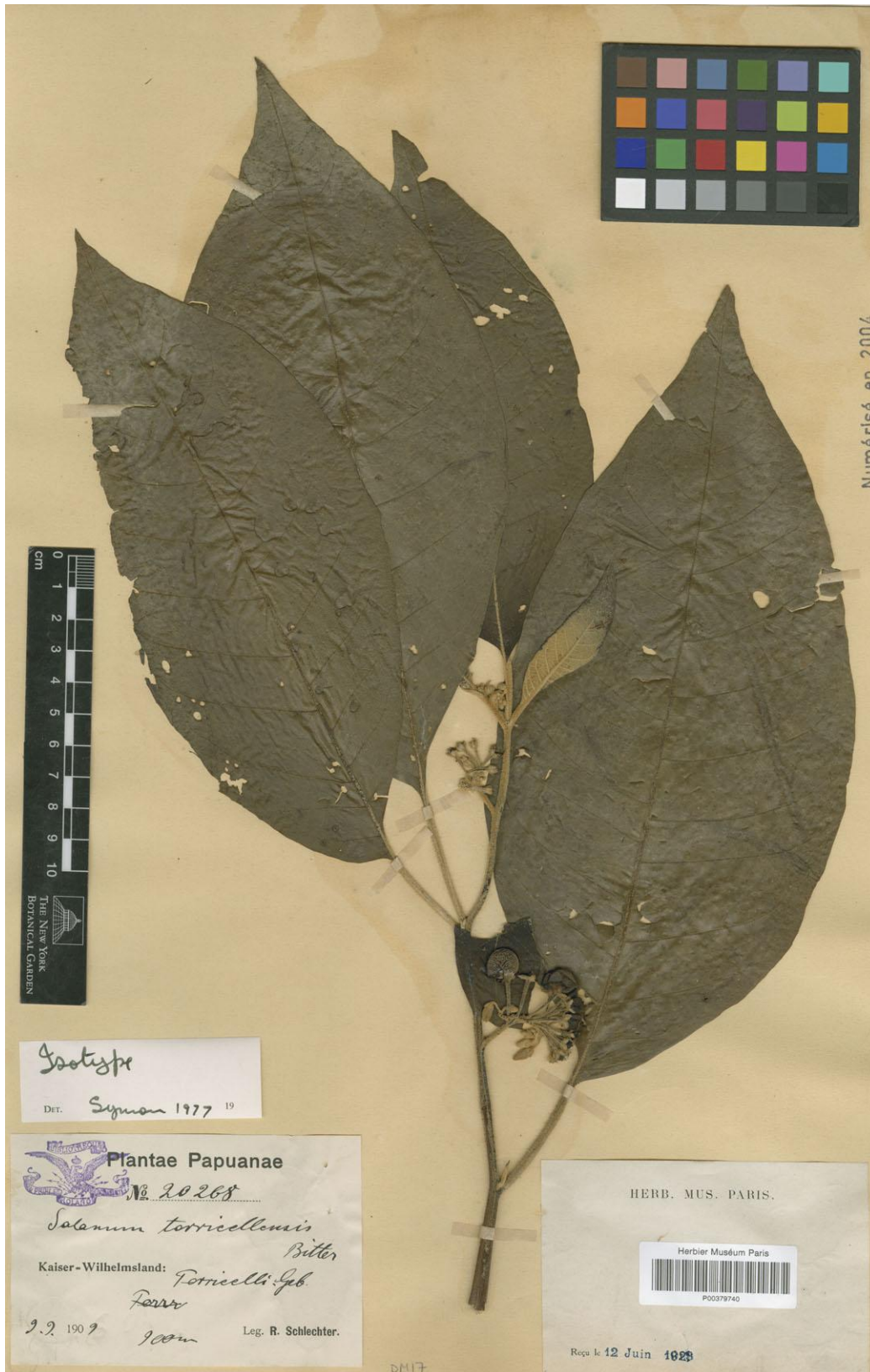


Figure 6. Lectotype of *S. torricellense* (Schlechter 20268, P 00379740).



Figure 7. Isotype of *Solanum viridifolium* (Banks s.n., P).

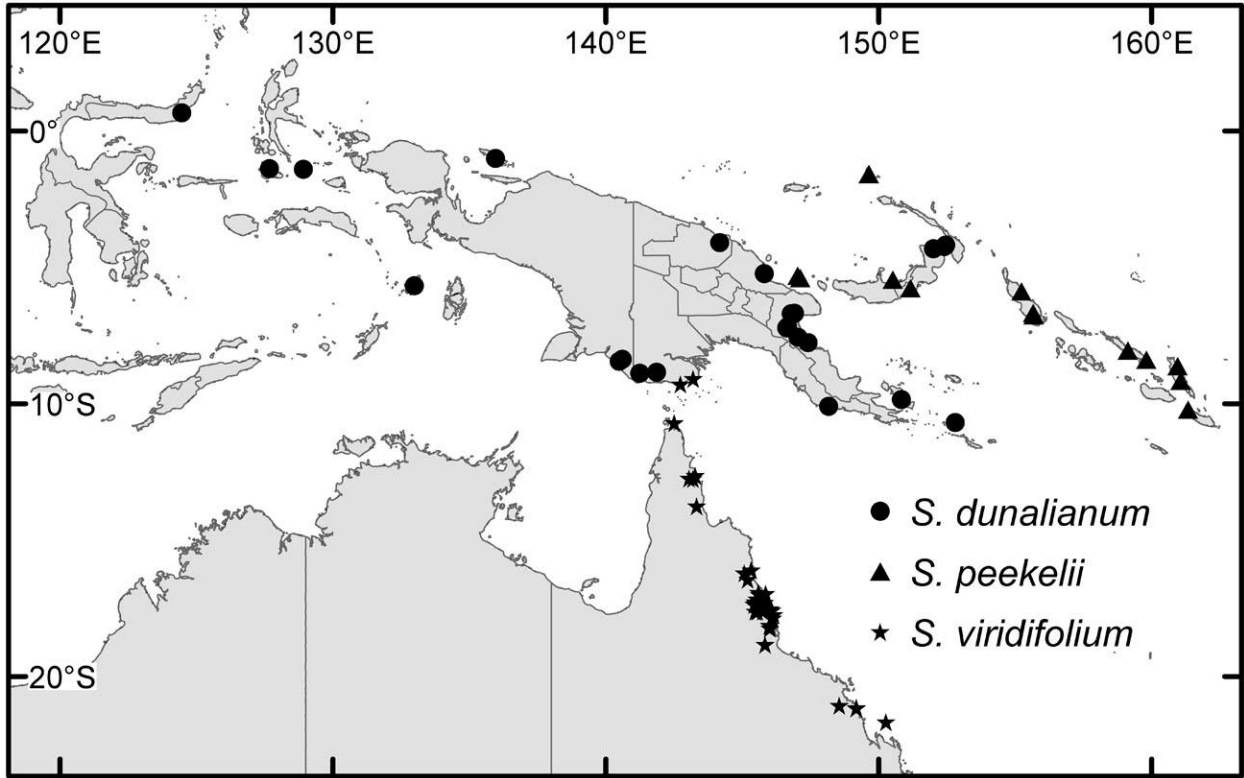


Figure 8. Distributions of *S. dunalianum*, *S. peekelii*, and *S. viridifolium*.

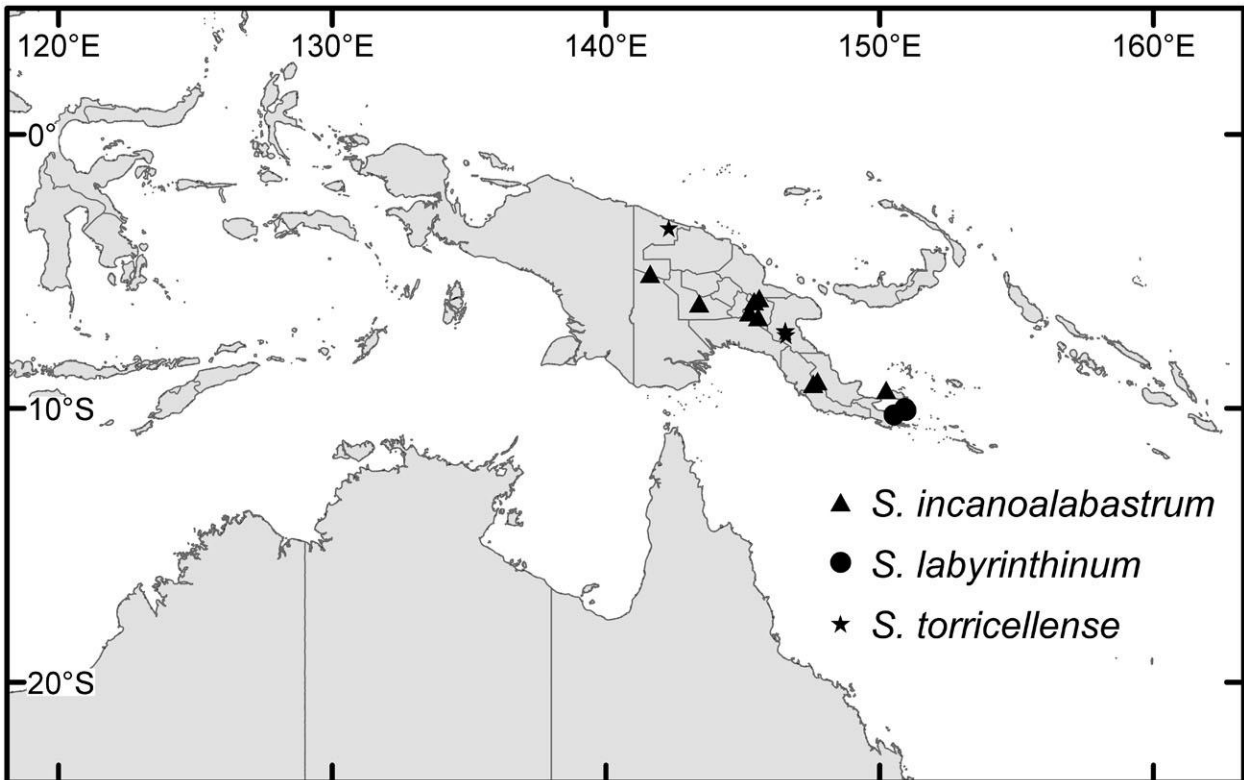


Figure 9. Distributions of *S. incanoalabastrum*, *S. labyrinthinum*, and *S. torricellense*.

Literature Cited

- Bean, A.R.** 2004. The taxonomy and ecology of *Solanum* subg. *Leptostemonum* (Dunal) Bitter (Solanaceae) in Queensland and far north-eastern New South Wales, Australia. *Austrobaileya* 6: 639–816.
- Bennett, J. R.** 2008. Revision of *Solanum* section *Regmandra* (Solanaceae). *Edinburgh Journal of Botany* 65: 69–112.
- Bitter, G.** 1919. Dei papuasischen arten von *Solanum*. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 55: 59–113.
- Bitter, G.** 1921. *Solanum*. In: F. Sarasin and J. Roux (eds.), *Nova Caledonia B. Botanik von Hans Schinz & A. Guillaumin Vol I Livr. III*, Berlin und Wiesbaden, C. W. Kreidels Verlag. 221–228
- Bitter, G.** 1922. *Solana africana*. III. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*. Leipzig. 57: 248–286.
- Brown, R.** 1810. Solanaceae Pp 443–449. In: *Prodromus florae Novae Hollandiae et Insulae Van-Diemen :exhibens characteres plantarum /quas annis 1802–1805 per oras utriusque insulae collegit et descripsit Robertus Brown; insertis passim aliis speciebus, auctori hucusque cognitis, seu evulgatis, seu ineditis, praesertim Banksianis, in primo itinere navarchi Cook detectis*. Volume 1. London.
- Child, A.** 1979. A review of branching patterns in the Solanaceae. Pp.345–356. In: J. G. Hawkes, R. N. Lester and A. D. Skelding, (eds.), *The Biology and Taxonomy of the Solanaceae*. Academic Press Inc. London.
- Danert, S.** 1967. Die Verzweigung als infragenerisches Gruppenmerkmal in der Gattung *Solanum* L. *Die Kulturpflanze*, 15: 275–292.
- D’Arcy, W. G.** 1972. Solanaceae studies II: typification of subdivisions of *Solanum*. *Annals of the Missouri Botanical Garden* 59: 262–278
- D’Arcy, W. G.** 1991. The Solanaceae since 1976, with a review of its biogeography. Pp 75–137. In: J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada-R. Richmond, (eds.), *Solanaceae III: taxonomy, chemistry, evolution*. Royal Botanic Gardens, Kew.
- Dunal, F. M.** 1852. Solanaceae. In: A. De Candolle (ed.), *Prodromus Systematics Naturalis Regni Vegetabilis* 13: 1–690.
- Frodin, D. G.** 2004. History and concepts of big plant genera. *Taxon* 53: 753–776
- Garnock-Jones, P. J.** 1986. South Pacific plants named by K. P. J. Sprengel in 1807. *Taxon* 33: 123–171.
- Gaudichaud-Beaupré, C.** 1829. *Botanique* In: L. C. D. de Freycinet (ed.) *Voy. Uranie*.
- Heine, H.** 1976. Solanaceae. In: A. Aubréville & J. Leroy (eds.), *Flore de La Nouvelle Calédonie et Dépendances* 7: 119–205.
- Levin, R., N. Myers, & L. Bohs.** 2006. Phylogenetic Relationships among the “Spiny Solanums” (*Solanum* subgenus *Leptostemonum*, Solanaceae). *American Journal of Botany* 93: 157–169.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, & N. J. Turland.** 2006. *International Code of Botanical Nomenclature (Vienna Code)*. *Regnum Vegetabile* 146, A.R.G. Gantner Verlag KG, Ruggell, Liechtenstein.

- Nee, M.** 1999. Synopsis of *Solanum* in the New World. Pp. 285–333. *In* M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop (eds.) *Solanaceae IV: advances in biology and utilization*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.
- Nixon, K. C. & Q. D. Wheeler.** 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.
- Peekel, P. G.** 1984. Flora of the Bismarck Archipelago for Naturalists. Office of Forests, Division of Botany, Lae, Papua New Guinea.
- Purdie, R. W., D. E. Symon, & L. Haegi.** 1982. Solanaceae. *In*: A. S. George, R. Robertson, B. Briggs, H. Eichler, L. Pedley, J. Ross, D. Symon, P. Wilson, & A. McCusker (eds.) *Flora of Australia* 29: 1–208
- Randell, B. R. & D. E. Symon.** 1976. Chromosome numbers in Australian *Solanum* species. *Australian Journal of Botany* 24: 369–379.
- Rechinger, K.** 1912. Botanische und zoologische Ergebnisse einer wissenschaftlichen Forschungsreise nach den Samoainseln, dem Neuguinea-Archipel und den Salomonsinseln von März bis Dezember 1905 Part 5.
- Roe, K.** 1967. A revision of *Solanum* sect. *Brevantherum* (Solanaceae) in North and Central America. *Brittonia* 19: 353–373.
- Seithe, A.** 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 81: 3, 261–336.
- Sprengel, K. P. J.** 1807. *In*: J. F. T. Biehler (ed.), *Plantarum novarum ex herbario sprengelii centuriam*. Halle.
- Stocker G. C. & Irvine A. K.** 1983. Seed dispersal by Cassowaries (*Casuaris casuaris*) in North Queensland's Rainforests. *Biotropica*. 15: 170–176.
- Symon, D. E.** 1979. Fruit diversity and dispersal in *Solanum* in Australia. *Journal of the Adelaide Botanic Garden*. 1: 321–331.
- Symon, D. E.** 1981. A Revision of the genus *Solanum* in Australia. *Journal of the Adelaide Botanic Garden*. 4: 1–367.
- Symon, D. E.** 1985. The Solanaceae of New Guinea. *Journal of the Adelaide Botanic Garden*. 8: 1–171.
- Symon, D. E.** 1986a. Solanaceae in New Guinea. Pp. 91–96. *In*: W. G. D'Arcy *Solanaceae Biology and Systematics*. Columbia University Press. New York.
- Symon, D. E.** 1986b. The phylogeography of New Guinea *Solanum* (Solanaceae). *Blumea* 31: 319–328.
- Thiers, B. [continuously updated].** Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>
- Lepschi, B. J. & D. E. Symon.** 1999. A preliminary cladistic analysis of Australasian *Solanum* and *Lycianthes*. Pp. 161–170. *In*: M. Nee, D. E. Symon, R. N. Lester and J. P. Jessop (eds.), *Solanaceae IV: Advances in Biology and Utilization*. Royal Botanic Gardens, Kew.
- Whalen, M.** 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herbarum* 12: 179–282.

Chapter 3

A monograph of *Solanum* section *Irenosolanum* (Solanaceae)

Abstract

A treatment for *Solanum* section *Irenosolanum* (Solanaceae) is presented. The section is comprised of twenty-nine species, the following eight of which are named as new herein: *Solanum albertii*, *S. caumii*, *S. memaoyanum*, *S. nudatum*, *S. pseudopedunculatum*, *S. ratale*, *S. semisucculentum*, and *S. vanuatuense*. The circumscription of the section is based on a morphological and molecular phylogenetic analysis which resolved the section as monophyletic and distinct from *Solanum* section *Dunaliana*. Due to adaptive radiations during the colonization of island groups in the Pacific, section *Irenosolanum* is morphologically diverse and no single morphological character or suite of characters serves to define the section. Morphological tendencies in the section include: general paucity of prickles, some species never having prickles; spreading (non-connivent) anthers; white corollas; and horizontal presentation of flowers at anthesis. The section is geographically unified being restricted to the islands of the Pacific including those of Hawaii, Fiji, French Polynesia, the Marianas Islands, New Caledonia, Samoa, and Tonga. With the exceptions of *S. lasiocarpum* and *S. repandum* of section *Lasiocarpa*, all native species of *Solanum* subgenus *Leptostemonum* from the Pacific belong to section *Irenosolanum*. A key for identifying the species of section *Irenosolanum*, species descriptions, distribution maps, and images of type specimens are provided. *Solanum* section *Irenosolanum* is lectotypified on *S. camptostylum*. Lectotypes are designated for twenty-six species and one variety; neotypes are designated for two species.

Introduction

Solanum L. (Solanaceae) is a species rich, economically important genus with a worldwide distribution. Frodin (2004) listed only nineteen genera of plants with more than 1000 species and included *Solanum* in the top ten largest. Several well known crop plants belong to the genus including the tomato (*S. lycopersicum* L.), potato (*S. tuberosum* L.), and eggplant (*S. melongena* L.), and there are many lesser known domesticated species including the scarlet eggplant (*S. aethiopicum* L.), naranjilla or lulo (*S. quitoense* Lam.), and pepino (*S. muricatum* Ait.). South America, the likely center of origin of *Solanum*, is the most species rich continent (D'Arcy 1991); however, the genus is cosmopolitan, found on every continent except Antarctica. As would be expected for such a large genus, *Solanum* has considerable infrageneric structure. Several major groups are commonly recognized. Nee (1999) recognized these groups as subgenera, subgenus *Solanum* L., subgenus *Bassovia* (Aubl.) Bitter, and subgenus *Leptostemonum* (Dunal) Bitter.

Solanum subgenus *Leptostemonum* constitutes almost a third of *Solanum*, with 350 to 450 species (Levin *et al.*, 2006). It has a cosmopolitan distribution, like *Solanum* as a whole, and is most species rich in Latin America, Africa, and Australia (Levin, *et al.*, 2006). A three character suite defines *Solanum* subgenus *Leptostemonum*: attenuate anthers, stellate hairs on any or all above ground organs, and prickles on the stems, leaves, inflorescences, and/or calyces. However, one or more of these characters can be missing in a few species of the subgenus, and some of the characters can be found in other taxa of *Solanum* such as the stellate hairs of *S. rugosum* Dunal in *Solanum* subgenus *Solanum* section *Brevantherum* Seithe (Roe, 1967).

No one since Dunal (1852) has provided an exhaustive treatment of *Solanum*. The sheer number of species in *Solanum* including those named since Dunal (1852) makes the genus

intractable for a lone worker. Even subgenus *Leptostemonum* is too large; therefore, most monographic studies have focused on smaller taxa, especially sections (Bennett, 2008). The National Science Foundation funded Planetary Biodiversity Inventory: *Solanum* project aimed to bridge the gaps between individual workers to produce a genus-wide treatment for *Solanum* (<http://www.nhm.ac.uk/research-curation/research/projects/solanaceaesource/>); the effort is ongoing. The study presented examines one section of *Solanum* subgenus *Leptostemonum*, section *Irenosolanum* (Bitter) Bitter, and is a contribution to that effort.

Solanum section *Irenosolanum*, composed of twenty-nine species, is found exclusively in the islands of the Pacific. It is morphologically diverse and occupies a wide range of habitats. Unfortunately, several species from the sections are extinct or apparently so, and many others are endangered or threatened.

Taxonomic History

For the sake of simplicity in this discussion, *Solanum* section *Irenosolanum* (Bitter) Bitter is consistently referred to at the section level. While at times anachronistic, this approach is taken to preserve clarity when discussing the taxonomic concepts of the workers involved in the historical recognition of the section.

The first recognition of relationships among the species of *Solanum* section *Irenosolanum* was made by Bentham (1843). Bentham (1843) recognized affinities among *Solanum amicorum*, *S. sandwicense*, *S. inamoenum*, and *S. tetrandrum*. These species are similar in their general appearance, especially *S. amicorum*, *S. sandwicense*, and *S. inamoenum*, and form an obvious group. They have similar leaf sizes and shapes, abundant stellate pubescence, and lack prickles.

Nine years later, Dunal (1852) implied affinities between *S. sandwicense*, *S. amicorum*, and *S. inamoenum* by listing them consecutively within his *Solanum* section *Leptostemonum* (roughly equivalent to the current subgenus *Leptostemonum*) subsection *Torvaria* Dunal. Like Bentham's (1843), Dunal's (1852) ideas were probably spawned by the overall similarity of these species. However, unlike Bentham (1843) and for uncertain reasons, Dunal (1852) did not consider *S. tetrandrum* to be closely related to *Solanum* section *Irenosolanum* placing it instead in *Solanum* section *Leptostemonum* Dunal series *Graciliflora* Dunal group *Aquartia* Dunal. Dunal (1852) also treated several other members of *Solanum* section *Irenosolanum*, *S. viride* Sprengel (as *S. uporo* and *S. viride* R. Br.), *S. incompletum*, and *S. nelsonii*, but he did not consider them to be allied with the other species of section *Irenosolanum*. Probably, his conclusions were reached due to the glabrousness of *S. viride*, presence of prickles in *S. incompletum*, and prostrate habit of *S. nelsonii* which differ striking from *S. sandwicense*, *S. amicorum*, and *S. inamoenum*. Dunal (1852) split *S. viride* Sprengel between two species in his two sections. He recognized it as *S. uporo* in *Solanum* section *Pachystemonum* Dunal (roughly equivalent to the current subgenus *Solanum*) series *Oppositifolia* Dunal group *Leiodendra* Dunal and as *S. viride* R. Br. in *Solanum* section *Leptostemonum* series *Graciliflora*. Dunal (1852) placed *S. incompletum* in section *Leptostemonum* series *Oliganthes* Dunal and *S. nelsonii* in section *Pachystemonum* series *Oppositifolia* Dunal group *Indubitaria* Dunal.

Seemann (1863) provided the earliest comprehensive floristic treatment of *Solanum* from the Pacific. His treatment included nine species (ten names) from *Solanum* section *Irenosolanum*, and for just over half of these, he proposed relationships with other species. Seemann (1863) considered *Solanum bauerianum* and *S. viride* Sprengel (as *S. uporo*) to be very closely related probably due to their shrubby habit, glabrous stems and leaves, lack of prickles, and similarly

sized and shaped leaves. Likewise he considered the morphologically similar species *S. puberulum* (= *S. viride*), *S. sandwicense*, *S. tetrandrum* (including *S. inamoenum*), and *S. austro-caledonicum* to be close. However for four species, *S. amicorum*, *S. incompletum*, *S. milnei*, and *S. nelsonii*, Seemann (1863) did not suggest relationships. While this is understandable for the morphologically dissimilar *S. incompletum* and *S. nelsonii*, it is puzzling for *S. amicorum* and *S. milnei*, which closely resemble *S. sandwicense* and *S. austro-caledonicum* respectively.

Nearly sixty years later in a flora of New Caledonia, Bitter (1921) erected two series for the classification of the native New Caledonian species of *Solanum*. These were: 1. *Solanum* series *Vaccinioides* Bitter made up of two species *S. vaccinioides* and *S. pseuderanthemoides* with small leaves and reduced inflorescences. 2. *Solanum* series *Irenosolanum* Bitter with large leaves and many-flowered inflorescences consisting of six New Caledonian species, *S. camptostylum*, *S. leratii*, *S. neo-caledonicum* (= *S. austro-caledonicum*), *S. styraciflorum* (= *S. artense*), *S. noumeanum* (= *S. austro-caledonicum*) and other “prickleless” species spread across the Pacific as far as the Hawaiian Islands. Though Bitter (1921) did not refer to the non-New Caledonian species by name, he did indicate their subgeneric placement by Dunal (1852). As a result, the non-New Caledonian species included in series *Irenosolanum* by Bitter (1921) can be definitively identified as *S. amicorum*, *S. inamoenum*, *S. incompletum*, *S. nelsonii*, *S. sandwicense*, and *S. woahense* (= *S. sandwicense*). Like the workers before him, Bitter (1921) probably relied on the general morphological similarity of most of these species to form his ideas, but he only indicated the paucity of prickles in these species as a unifying character.

The following year Bitter (1922a) elevated *Solanum* series *Irenosolanum* to the rank of section. In this publication, Bitter (1922a) explicitly identified, by name and number, three species treated by Dunal (1852): *S. woahense* (= *S. sandwicense*), *S. sandwicense*, and *S.*

amicorum. Though he did not list by name any other species from *Solanum* section *Irenosolanum*, Bitter (1922a) stated that he was elevating *Solanum* series *Irenosolanum* to the sectional level. Therefore, it is clear that he was referring to the same taxon. Regardless, some later workers (Symon 1985; Whalen 1984) were confused about Bitter's (1921, 1922a) circumscription of *Solanum* section *Irenosolanum*. They did not consider *Solanum* series *Irenosolanum* and *Solanum* section *Irenosolanum* to include the same species and thus rejected *Solanum* section *Irenosolanum* as invalid. It should also be pointed out that Bitter (1922a) elevated *Solanum* series *Irenosolanum* to the rank of section in a footnote in a publication on *Solanum* series *Giganteiformia* Bitter and series *Anomalum* Bitter from Africa. This may have erroneously influenced later workers (D'Arcy, 1991; Symon, 1985, 1986; Whalen, 1984) who postulated a close relationship between *Solanum* section *Irenosolanum* (within *Solanum* section *Dunaliana* Symon) and series *Giganteiformia* and series *Anomalum*. However, Bitter (1922a) was not suggesting such a relationship as he explicitly called attention to the morphological distinctness of the (supposedly) unarmed *Solanum* section *Irenosolanum* from all other groups of *Solanum* section *Leptostemonum sensu* Dunal (1852).

After Bitter (1921, 1922a), the next worker to address the taxonomy of *Solanum* section *Irenosolanum* was Seithe (1962). In her genus-wide classification of *Solanum*, she named section *Irenosolanum* Bitter ex. Seithe (non (Bitter) Bitter). Seithe (1962) did not cite Bitter (1921) and must have been unaware of the valid establishment of *Solanum* series *Irenosolanum*. Therefore, she logically considered *Solanum* section *Irenosolanum* (Bitter) Bitter to be invalid as Bitter (1922a) did not include a description or diagnosis. Within *Solanum* section *Irenosolanum* Bitter ex Seithe (non (Bitter) Bitter), Seithe (1962) included the three species listed by Bitter (1922a), *S. woahense*, *S. sandwicense*, and *S. amicum*, and designated *S. woahense* the type of the

section. Seithe (1962), like many other workers, treated the morphologically dissimilar species *S. incompletum* and *S. nelsonii* as not related to *Solanum* section *Irenosolanum*. Tentatively, Seithe (1962) included *S. incompletum* in *Solanum* section *Oliganthes* (Dunal) Bitter, like Dunal (1952), and *S. nelsonii* in *Solanum* section *Brevantherum* Seithe.

Solanum section *Irenosolanum* Bitter ex Seithe (non (Bitter) Bitter) became firmly established in the literature (D'Arcy, 1972, 1991; Symon, 1981, 1985; Whalen, 1984; St. John, 1988; Levin *et al.*, 2006, Weese & Bohs, 2007). Whalen (1984), whose argument was repeated by Symon (1985), did address the typification of *Solanum* section *Irenosolanum* Bitter ex Seithe in light of Bitter (1921). However, a combination of errors caused Whalen (1984) to incorrectly reject *Solanum* section *Irenosolanum* (Bitter) Bitter in favor of *Solanum* section *Irenosolanum* Bitter ex Seithe. One of the errors was an inversion of the order in which Bitter (1921, 1922a) published *Solanum* series *Irenosolanum* and *Solanum* section *Irenosolanum* (Bitter) Bitter. The confusion is evident in Whalen's (1984) inconsistent citation of the dates of Bitter's (1921, 1922a) publications. The dates of Whalen's (1984) textual citations are not internally consistent and do not agree with the dates provided in his literature cited. The issue was further confounded in Whalen's (1984) discussion of his *Solanum dunalianum* group by the misattribution of the sectional ranking of *Solanum* section *Irenosolanum* (Bitter) Bitter to Bitter (1921), the publication containing the series ranking. Most likely, this instance was a typographical error in the citation rather than confusion about the content of the publications.

Whalen's (1984) second error was the conclusion that *Solanum* series *Irenosolanum* and *Solanum* section *Irenosolanum* (Bitter) Bitter had no species in common. If this were true, it would invalidate the second name to be published. And, it did lead Whalen (1984) to reject the

series name. However as discussed above, Bitter (1921, 1922a) clearly referred to the same group of “prickleless” species in both publications.

These two errors in combination logically led Whalen (1984) to reject *Solanum* series *Irenosolanum* as a later homonym of *Solanum* section *Irenosolanum* (Bitter) Bitter. However, it is not clear why Whalen (1984) considered *Solanum* section *Irenosolanum* to be validly published without the publication containing *Solanum* series *Irenosolanum*. Bitter (1922a) did not include a diagnosis or description when he elevated *Solanum* section *Irenosolanum* (Bitter) Bitter from series to section. Therefore, had *Solanum* section *Irenosolanum* (Bitter) Bitter been published before *Solanum* series *Irenosolanum* as Whalen (1984) thought, it would have been a *nomen nudum* lacking priority. In that situation, Whalen (1984) could not have rejected *Solanum* series *Irenosolanum* on the grounds that it was a later homonym even if he had been correct about the order of publication and/or the species included by Bitter (1921, 1922a) at the different ranks.

While Seithe (1962) did not treat any of the species of *Solanum* from New Caledonia, Whalen (1984) further disagreed with Bitter (1919, 1921, 1922a) by placing the New Caledonian species and several other prickleless species of *Solanum* from the Pacific in his *Solanum dunalianum* group along with *Solanum* section *Dunaliana* (Bitter) Symon. Symon (1985) doubted Whalen’s (1984) placement of some of the New Caledonian species, believing they were more closely related to *S. ferocissimum*. Presumably, Symon (1985) based this opinion on the small leaves and reduced inflorescence of these New Caledonian species which are similar to *S. ferocissimum*. Symon (1985) did, however, accept Whalen’s (1984) treatment of the rest of *Solanum* section *Irenosolanum*.

In his discussion of *Solanum* section *Dunaliana*, Symon (1985) restated Whalen’s (1984) argument about the taxonomy of *Solanum* section *Irenosolanum* Bitter ex Seithe (non Bitter)

Bitter). However, in the following discussion of *Solanum dunalianum*, he indicated that another earlier publication of *Solanum* section *Irenosolanum* had been overlooked. Symon (1985) stated that this discovery would lead to a different typification of the section, but he did not cite the publication. He also did not cite it in any subsequent publications, and I have been unable to locate any publications of the name “*Irenosolanum*” other than Bitter (1922a) and Seithe (1962). In light of this, it is impossible to recover Symon's (1985) reported discovery. It might be thought that he was referring to Bitter's (1921) publication of *Solanum* series *Irenosolanum*, a publication neglected by Seithe (1962). But, this would contradict the taxonomic evaluation of *Solanum* section *Irenosolanum* he presented.

The next major taxonomic work pertinent to *Solanum* section *Irenosolanum* was that of St. John (1988a, 1988b). St. John, at about 96 years of age, published two works in rapid succession, St. John (1988a, 1988b). The first (St. John, 1988a) was a set of new species of *Solanum* from the Hawaiian Islands with minimal Latin descriptions. The second (St. John, 1988b) was a much more detailed treatment of all the native Hawaiian solanums which included Latin and English descriptions, a key to species, illustrations, and a distribution map. In all, St. John (1988a, 1988b) recognized twenty native Hawaiian species of *Solanum*, thirteen of which were new. He did not consider them to form a coherent group as he distributed them among four sections in two subgenera, *Solanum* section *Irenosolanum* Bitter ex. Seithe (non (Bitter) Bitter), *Solanum* section *Torvaria* (Dunal) Biter, and *Solanum* section *Oliganthes* of subgenus *Leptostemonum*, and *Solanum* section *Brevantherum* of *Solanum* subgenus *Solanum*. Symon (1993) critically reviewed St. John (1988a, 1988b). While acknowledging his remarkable and long botanical career, Symon (1993) noted that in his later years St. John had become a splitter recognizing seemingly every collection as a new species. Though surely St. John (1988a, 1988b)

can be excused given his great age, an honest evaluation of the literature and herbarium material supports Symon's (1993) statement. For example, it is quite likely that several of the specimens lacking collector numbers and cited by St. John (1988a, 1988b) as different species are in fact duplicates of the same collection; St. John (1988b) designated *Forbes 12.L* the holotype of *S. pubinervosum* while citing it in the specimens examined for *S. globosum*, and he muddled the typifications of *S. lanaiense* and *S. popolo* (see explanation under *S. hillebrandii*). Symon (1993) placed a number of St. John's names under synonymy but was unable to resolve others. As was pointed out by Symon (1993), most of St. John's (1988a, 1988b) subgeneric placements are patently wrong; all native Hawaiian species of *Solanum* belong to section *Irenosolanum* (see chapter 1). Before his 1988 works, St. John (1959, 1969) published new names for other species in section *Irenosolanum* from Hawaii and elsewhere in the Pacific. During his career, St. John named eighteen species and one variety in *Solanum* section *Irenosolanum*; only two of these are recognized here as good species.

Until the present, species from *Solanum* section *Irenosolanum* have appeared in two phylogenetic analyses (Levin *et al.*, 2006; Weese & Bohs, 2007). Weese & Bohs (2007) included a single member of the section, *S. sandwicense*, in their analysis; no new conclusions were formed about the phylogenetic relationships of *Solanum* section *Irenosolanum* from their results. Levin *et al.* (2006) included three species from *Solanum* section *Irenosolanum*, *S. sandwicense*, *S. incompletum*, and *S. pancheri*. These three species formed a clade suggesting potential monophyly of the section. Levin *et al.* (2006) also indicated that section *Irenosolanum* is derived from a clade of Australian species. It should be noted that Levin *et al.* (2006) used the taxonomic concepts of Whalen (1984); this led them to conclude that *Solanum* section *Irenosolanum* and *Solanum* section *Dunaliana* form a clade. However the result of a focused analysis of *Solanum*

section *Irenosolanum* and *Solanum* section *Dunaliana* show that this is not the case (see chapter 1).

The current circumscription of *Solanum* section *Irenosolanum* is based on the total evidence phylogenetic analysis presented in chapter 1. In that analysis *Solanum* section *Irenosolanum* was resolved as monophyletic and separate from *Solanum* section *Dunaliana*. *Solanum* section *Irenosolanum* was sister to a clade of Australian and New Guinean species of various sections including *Solanum* section *Dunaliana*. Accounting for new species, *Solanum* section *Irenosolanum* is in line with the concept of Bitter (1922a). Section *Irenosolanum* consists of twenty-nine species and includes all the native species of *Solanum* subgenus *Leptostemonum* from Oceania except *Solanum lasiocarpum* Dunal and *S. repandum* G. Forst. of *Solanum* section *Lasiocarpa* (Dunal) D'Arcy. As concluded in chapter 1, *Solanum* section *Irenosolanum* colonized the islands of the Pacific from west to east. *Solanum* section *Irenosolanum* forms a coherent biogeographic unit, but a morphological synapomorphy or suite of characters for circumscribing the section remains elusive. Several synapomorphies support subclades of *Solanum* section *Irenosolanum* including dimorphic branches, reduced leaves, reduced inflorescences, terminal flexing of the pedicel at anthesis, globose corollas in bud, bicolorous corollas, heterostyly, and sigmoid styles (see chapter 1).

Materials and Methods

During the completion of this monograph about 775 collections, including types, constituting about 1800 herbarium sheets of *Solanum* section *Irenosolanum* were examined. Sixteen herbaria with specimens of the study group, BISH, BM, CAHUP, CAS, F, GH

(including A), K, L, MO, NLUH, NOU, P, PNH, PTBG, UC, and US, were visited. Loans were received from most of the world's relevant herbaria; specimens from the following thirty-one herbaria were examined: A, B, BH, BISH, BM, BRI, C, CANB, CAS, DS, E, F, G, GH, GOET, K, L, M, MICH, MO, NOU, NSW, NY, P, PTBG, RSA, S, U, UC, US, W (Theirs [continuously updated]). Digital images of herbarium specimens from UZH, VT, and WU were also viewed. All specimens listed herein were seen by me unless otherwise noted. To supplement the information available from herbarium specimens, three field trips were taken. In 2008, the Hawaiian islands of Kauai, Hawaii, Lanai, Maui, Oahu, and Molokai were visited. *In situ* individuals of *S. incompletum*, *S. nelsonii*, and *S. sandwicense* were observed. Herbarium specimens and DNA were collected from *ex situ* individuals of *S. caumii*, *S. incompletum*, *S. nelsonii*, *S. sandwicense*, and *S. viride* at The National Tropical Botanical Garden. In 2009, the island of Luzon in the Philippines was visited. Though other endemic solanums were collected, several weeks spent trying to recover *S. retrorsum* (as *S. luzoniense* in Whalen, (1984)) were to no avail. Also in 2009, the Grande Terre and Île des Pins of New Caledonia were visited. Herbarium specimens, DNA collections, and field observations of *S. austro-caledonicum*, *S. insulae-pinorum*, *S. pancheri*, *S. semisucculentum*, and *S. vaccinioides* were made. A set of all collections was deposited at NY; for each trip a complete set of duplicate collections were deposited in "in-country" herbaria: BISH and PTBG in Hawaii; PNH in the Philippines; NOU in New Caledonia.

The literature was exhaustively searched for names applying to *Solanum* section *Irenosolanum*. In all, sixty species names and thirteen varietal names (not including *pro syn.*, *nom. nud.*, and unpublished herbarium names) were applicable to the twenty-one previously named species. The protologues of all pertinent names were consulted and compared with type

material where available. Some type material was destroyed at the Berlin herbarium during World War II. Surviving isotypes were selected as lectotypes, or if none existed, neotypes were designated. Species were delimited following the phylogenetic species concept of Nixon and Wheeler (1990). Herbarium specimens and label data were the primary sources for compiling species descriptions. The literature was used in some instances for missing characters. Label data and the literature were used to compile habitat descriptions. Distribution maps for each species were generated from label information; specimens without latitude and longitude were manually georeferenced.

Morphology

Solanum section *Irenosolanum* is remarkably morphologically diverse. There are general morphological tendencies, such as general paucity of prickles, spreading (non-connivent) anthers, white corollas, and horizontal presentation of flowers at anthesis, but no single character or suite of characters serves to define the section. This is certainly a result of the pattern of diversification of the section *Irenosolanum*. The genus *Solanum* is well known for its morphological plasticity (Anderson *et al.*, 2006), and as *Solanum* section *Irenosolanum* colonized the islands of the Pacific, it encountered and occupied a variety of niches allowing for an adaptive radiation. This compounded with the phenomenon that isolation of organisms on islands often results in the establishment of unusual characters (Carlquist, 1974) likely resulted in the highly varied morphology of the section.

This variability provides the opportunity to study a variety of morphological and anatomical phenomena. For example, though an anatomical investigation of the wood of

Solanum section *Irenosolanum* was not within the scope of this study, such an investigation might provide interesting insights into character evolution of wood in *Solanum*. Variation in the wood features of Solanaceae typically represent ecological patterning rather than taxonomically distributed patterns (Carlquist, 1992). *Solanum* section *Irenosolanum* provides a unique opportunity to study wood anatomy in a single group of closely related species with incredibly diverse habits and habitat preferences.

Habit

All species of *Solanum* section *Irenosolanum*, like most of the species of *Solanum* subgenus *Leptostemonum*, are woody perennials. However, they vary greatly in habit. Many are upright shrubs, but prostrate shrubs, scandent shrubs, and small trees are also found in the section. Most of the species have robust branches, but some species from New Caledonia have gracile branches. Most of the species are not rhizomatous, but one species, *Solanum abollatum* H. St. John, is. Even the texture of the wood itself varies in the section with some species having quite hard wood while the wood of others is soft and light.

Leaves

The leaves of section *Irenosolanum* vary greatly. All are simple, but there is a wide range in size, outline, texture, and pubescence among the species. Most commonly the leaves are pubescent either abaxially or abaxially and adaxially. The hairs are sessile or short-stipitate porrect stellae and minute glandular hairs. The margins range from lobed to entire. As with many species of *Solanum* the margins often vary between juvenile and adult leaves within a species, the juvenile leaves being more lobed while the adult leaves are entire. However, the margins also

may not differ between mature and juvenile growth in which case the margins are typically entire. The leaves of most of the species of the *Solanum* section *Irenosolanum* are chartaceous; however, several species have thicker, tougher leaves. *Solanum semisucculentum*, *S. leratii*, and *S. memaoyanum* have semisucculent leaves, an unusual texture for *Solanum*. This character is most pronounced in *S. semisucculentum*. Leaf size ranges greatly among the species of the section, and the size disparity between the smallest leaved species and the largest is quite striking. The size of the leaves of most species is not remarkable, however several species from New Caledonia have reduced leaves, the smallest of which can be just 0.3×0.3 cm. Another striking difference among the species is leaf outline. The most common outline in *Solanum* section *Irenosolanum* is \pm ovate, however orbicular, lyrate, pandurate, spatulate, cordate, and deltoid leaves are also present. The widest range of shape within a single species is present in *S. vaccinioides*. The leaves of that species can range from spatulate with two deeply dissected basal lobes all the way to orbicular (see discussion of *S. vaccinioides*).

Sympodial structure

The inflorescences of *Solanum* section *Irenosolanum* are developmentally terminal like those of all species of *Solanum*. The sympodial units of the section are difoliate with the exception of *S. nelsonii*. Following Chile's (1979) discussion of the anthocladial pattern in Solanaceae, *Solanum* section *Irenosolanum* typically exhibits monochasial branching which gives the false appearance that the inflorescences are lateral. The epipodia are elongated and often concaulescent with the hypopodium or mesopodium of the sympodial unit above making the inflorescence remote from the leaves. The hypopodia can be reduced or not. When reduced, the leaves are borne in geminate clusters; when not, the leaves are borne individually. (See

Figure 1 redrawn from Danert, 1967). However, several species from New Caledonia bear inflorescences on short shoots. In this case the inflorescences are terminal on these shoots.

Armature and indumentum

Presence of prickles is a synapomorphy for *Solanum* subgenus *Leptostemonum*. Because of the alliteration, the subgenus is commonly, though erroneously, referred to as the “spiny solanums;” however, the armature of the subgenus is clearly epidermal in origin and can appear on many of the above ground structures. The density of prickles in *Solanum* subgenus *Leptostemonum* varies by section and species. Some species have many closely spaced prickles while others have few scattered prickles. Even on less well armed species, prickles are typically present during some growth phase or under certain environmental conditions. In section *Irenosolanum*, however, about 60% of the species never have prickles regardless of growth rate or environmental conditions. For those species in the section that do have prickles, some regularly produce them while others produce them only occasionally. The prickles of *Solanum* section *Irenosolanum* are typically broad based and yellowish to orange. Though the prickles can be abundant they are never dense. For nearly every species of *Solanum* section *Irenosolanum*, unarmed herbarium specimens can be found. Several species native to New Caledonia have retrorse prickles adapted for hooking onto surrounding vegetation allowing these species to scramble up nearby plants.

Stellate hairs are another synapomorphy for *Solanum* subgenus *Leptostemonum*. Nearly all species of *Solanum* section *Irenosolanum* have sessile or short-stipitate stellae. The exceptions are *Solanum nudatum* which is totally glabrous and *S. bauerianum*; while several other species in the section are nearly glabrous, these two species lack stellate hairs all together.

Most of the species of *Solanum* section *Irenosolanum* also have minute glandular hairs on the leaves and sometimes the stems. Minute glandular hairs or simple glandular hairs are also common on the gynoecium.

Inflorescences

Inflorescence structure varies within *Solanum* section *Irenosolanum*. Inflorescences range from many flowered (over 100) with a long axis to few flowered or solitary with a highly reduced or absent axis. A peduncle can be present or lacking. Sometimes a pseudopeduncle is present where one flower is present at the base of the inflorescence above which is a section of the inflorescence axis free of flowers. Often the bases of the pedicels are tightly spaced on the axis of the inflorescence; but, sometimes the pedicels are well spaced, a character which Whalen (1984) used to segregate the native Hawaiian species of *Solanum* section *Irenosolanum*. Most species have rigid pedicels, but some species have limp pedicels that allow flowers and fruit to dangle from the inflorescence. The flowers of many species are positioned \pm parallel to the ground at anthesis, opening towards the ground (See Figure 2). This positioning is typically the result of the pedicel being flexed to $\pm 90^\circ$ just below the calyx (See Figure 2). This flexing of the pedicel is often lost during maturation of the fruit although it is sometimes maintained. At maturity the fruits of some species are held erect while those of other species are inverted.

Flowers

Merousity is relaxed in *Solanum* section *Irenosolanum* with 4- or 6-merous flowers present in addition to the typical 5-merous flowers of Solanaceae. However, no species are

restricted to a merosity other than five with the exception of *S. pancheri*, which is consistently 4-merous.

The calices of *Solanum* section *Irenosolanum* are unarmed with the exception of *Solanum incompletum* which very occasionally has a few prickles on the calyx. The tips of the calyx lobes are typically apiculate or caudate, however *Solanum hugonis* has spatulate lobes. The corolla tissue of section *Irenosolanum* is white with the exception of some of the Hawaiian species, where the entire corolla or just the veins of the corolla can be purple. The outline of the corolla is typically stellate with well developed inter-petalar tissue, however *S. bauerianum* has stellate-rotate corollas and several other species have poorly developed inter-petalar tissue. The abaxial surface of the midribs of the corolla is often moderately to densely stellate-pubescent. The adaxial surface can be glabrous or sparsely stellate pubescent distally.

While most species in *Solanum* section *Irenosolanum* have poricidally dehiscent anthers, typical of *Solanum*, several species have longitudinally dehiscent anthers. Longitudinal dehiscence is sometimes seen in species of other sections of *Solanum* particularly in *Solanum* subgenus *Solanum*, where the anthers initially dehisce from apical pores and then the sutures along the sides of the anthers split as the anthers age. In several species of *Solanum* section *Irenosolanum*, however, the anthers split along the lateral sutures when the anthers are mature rather than dehiscing from apical pores initially. This adaptation is likely a response to available local pollinators though their identities are unknown.

A couple of unusual gynoecial phenomena occur in *Solanum* section *Irenosolanum*. In several species of the eastern Pacific, heterostyly is present. In these species, distinct long and short styled flowers are present both of which are fertile. In New Caledonia and Vanuatu the styles of several species are sigmoid; all styles are apparently deflexed along the vertical axis the

flowers and are not enantiomeric. The deflexion of the styles changes the position and orientation of the stigma, lowering it and directing it upward or back towards the anthers.

Fruits

The fruits of *Solanum* section *Irenosolanum* are fleshy berries, typical of *Solanum*. All are glabrous at maturity. They can be yellow, orange, red, or black and nearly all are globose. The fruits vary in size from 0.3–2.7 cm in diameter with no wild species being larger than 1.9 cm in diameter. One species *S. viride* was domesticated in part for the fruits. In this species some cultivars have fruits as large as 2.7 cm in diameter.

Distribution and ecology

With the exception of *S. milnei*, *S. austro-caledonicum*, and *S. viride*, the species of *Solanum* section *Irenosolanum* are restricted to individual island groups or signal islands. Some island groups have considerably more species while others have fewer. New Caledonia has the most with thirteen species, eleven of which are endemic. Hawaii has the second greatest number of species with seven, six endemics, followed closely by Fiji with six species, five endemics. The Marianas Islands, Tonga, Lord Howe and Norfolk Islands together, and Vanuatu each have a single endemic species. *Solanum milnei* and *S. austro-caledonicum* straddle New Caledonia and Vanuatu, and *S. viride*, the most widely dispersed species, can be found in the Cook Islands, Fiji, French Polynesia, Niue, the Pitcairn Islands, Tonga, Samoa, and Hawaii. *Solanum* section *Irenosolanum* is found from sea level to 2000 m elevation. Its species grow in many habitats including rainforest, dry forest, shrubland, and sand dunes and on various substrates. Several species from

New Caledonia are serpentine endemics while others grow on calcareous soil. One species, *S. nelsonii*, grows on shifting seaside sand dunes, which is unique in *Solanum*.

Solanum, with its poricidally dehiscent anthers, is a classic example of the buzz pollination syndrome. Most of the species in *Solanum* section *Irenosolanum* have poricidally dehiscent anthers, and though no specific pollinators are known, these species are probably pollinated by bees or syrphid flies. *Solanum albertii*, *S. amicorum*, and *S. hillebrandii*, however, have evolved longitudinally dehiscent anthers. The anthers of these species dehisce along the lateral sutures of the pollen sacs exposing the pollen. By allowing for more generalized pollination, this adaptation could be a response to a lack of suitable buzz pollinators such as might be found on isolated, taxonomically depauperate islands.

Etymology of section *Irenosolanum*

Bitter (1921) did not discuss the etymology of *Solanum* section *Irenosolanum* when he originally published it. However, it is easily understood. *Iren* is Greek for peace. In his discussions of the group (Bitter 1921, 1922a), he called attention to the “absence” of prickles in the group and used this characteristic to segregate these species from section *Leptostemonum sensu* Dunal (1852). Clearly, he selected the name *Irenosolanum* to draw attention to the “peacefulness,” i.e. general lack of armature, of the group.

Conservation concerns

The genus *Solanum* is often referred to with the pejorative “weed.” True, the genus typically exploits disturbed areas, and given the right conditions many species of *Solanum* could justifiably be called weeds. However, “weed” cannot be applied to the species of *Solanum*

section *Irenosolanum*. While a few species were once abundant, none are exceedingly common now. Several species are extinct or apparently so, and many others are threatened or endangered (See Table 1 for conservation status of individual species). Wagner *et al.* (1999) reviewed the status of the Hawaiian species of *Solanum*, and Jaffré *et al.* (1998) reviewed the status of New Caledonia species. However, due to the taxonomic realignments presented here, the statuses of these species should be reevaluated. The major threats to the species of *Solanum* section *Irenosolanum* are habitat destruction, seed predation by introduced rodents, and competition with introduced plants (Auld & Hutton, 2004; Keitt, 2008). The one species known to be extinct, *Solanum bauerianum*, was apparently a casualty of seed predation by introduced rats on Lord Howe Island (Auld & Hutton, 2004; Hutton *et al.*, 2007). Seed predation by rats is also a threat to *S. incompletum* (Keitt, 2008) and *S. sandwicense* on Oahu (pers. comm. Stefanie Loo Jefts, The Nature Conservancy). Conservation efforts for the native Hawaiian species of *Solanum* are ongoing at the National Tropical Botanical Garden in HI and for *S. sandwicense* on Oahu and *S. nelsonii* on Molokai by The Nature Conservancy.

Ethnobotany

Two species, *S. bauerianum* and *S. viride*, were used extensively by people in the Pacific. *Solanum bauerianum*, now extinct, was used for bridal bouquets on Lord Howe Island, earning it the common name “bridal flower” (Green, 1994) or “wedding flower” (Rodd & Pickard, 1893). *Solanum viride* was domesticated in the Pacific and dispersed across the Pacific by the Polynesians (Whistler, 1991). This species was used for food, medicine, and decoration (Brewster, 1922; Papy, 1955; Seemann, 1862a, 1862b, 1865–73; Whistler, 1991). The use of *S. viride* in cannibal feasts earned it the English common name “cannibals' tomato” (see discussion

of that species). The Polynesians recognized the affinities of the genus *Solanum* in the Pacific and consistently referred to them as *polo*, *poro*, *boro*, or some derivative thereof (Seemann, 1865–73).

<i>S. abollatum</i>	extinct			endemic in Hawaii (Lanai)	included under <i>S. incompletum</i> by Wagner <i>et al.</i> , 1999
<i>S. actephilum</i>				endemic in New Caledonia	
<i>S. albertii</i>	known only from the type			endemic in Fiji	
<i>S. amicolorum</i>				endemic in Tonga	
<i>S. artense</i>				endemic in New Caledonia	status not evaluated
<i>S. austro-caledonicum</i>				endemic in New Caledonia	
<i>S. banerianum</i>	extinct		Auld & Hutton, 2004; Hutton <i>et al.</i> , 2007; Rodd & Pickard, 1983	Lord Howe Island and Norfolk Island	
<i>S. camplostylum</i>				endemic in New Caledonia	
<i>S. caunii</i>	threatened			endemic in Hawaii (Nihoa)	included under <i>S. nelsonii</i> by Wagner <i>et al.</i> , 1999
<i>S. guamense</i>				endemic in Guam	
<i>S. hillebrandii</i>	extinct			endemic to Hawaii (Lanai and Maui)	included under <i>S. incompletum</i> by Wagner <i>et al.</i> , 1999
<i>S. hugonis</i>	endangered		Jaffré <i>et al.</i> , 1998	endemic in New Caledonia	
<i>S. inamoenum</i>	last collected in 1880			endemic in Fiji	
<i>S. incompletum</i>	endangered		Wagner <i>et al.</i> , 1999	endemic in Hawaii (island of Hawaii)	
<i>S. insulae-pinorum</i>	endangered		Jaffré <i>et al.</i> , 1998	endemic in New Caledonia	

Table 1 continued.

<i>S. leratii</i>			endemic in New Caledonia	included under <i>S. styraciflorum</i> by Jaffré <i>et al.</i> , 1998
<i>S. memaoyanum</i>	known from 3 collections		endemic in New Caledonia	included under <i>S. styraciflorum</i> by Jaffré <i>et al.</i> , 1998
<i>S. milnei</i>			New Caledonia and Vanuatu	status not evaluated
<i>S. nelsonii</i>	threatened	Wagner <i>et al.</i> , 1999	endemic in Hawaii (extant on Molokai and the leeward islands)	
<i>S. nudatum</i>	known only from the type		endemic in Fiji	
<i>S. pancheri</i>	near threatened	Jaffré <i>et al.</i> , 1998	endemic in New Caledonia	
<i>S. pseuderanthemoides</i>	critically endangered	Jaffré <i>et al.</i> , 1998	endemic in New Caledonia	
<i>S. pseudopedunculatum</i>			endemic in Fiji	status not evaluated
<i>S. ratale</i>	known from 3 collections		endemic in Fiji	
<i>S. sandwichense</i>	endangered	Wagner <i>et al.</i> , 1999	endemic to Hawaii (Oahu and Kauai)	
<i>S. semisucculentum</i>	vulnerable	Jaffré <i>et al.</i> , 1998	endemic in New Caledonia	called <i>S. styraciflorum</i> by Jaffré <i>et al.</i> , 1998
<i>S. vaccinioides</i>	endangered	Jaffré <i>et al.</i> , 1998	endemic in New Caledonia	
<i>S. vanuatuense</i>			endemic in Vanuatu	status not evaluated
<i>S. viride</i>			widespread across the Pacific	cultivated and feral on many islands; less commonly cultivated now

Taxonomy

Solanum section *Irenosolanum* (Bitter) Bitter, Bot. Jahrb. Syst. 81: 301. 1922. – *Solanum* series *Irenosolanum* Bitter in Sarasin & Roux, Nova Caled. 1: 221. 1921. – Type species: *Solanum camptostylum* Bitter (*hic designatus*).

Erect, prostrate, lax, or scandent shrub or small tree to 4(–6) m, the internodes to 12.5 cm long. Stems glabrous to densely pubescent with sessile porrect stellae, the stipes to 0.2 mm long, the stellae deciduous or persistent, 0.2–0.9 mm in diameter, with 4–12 rays, the midpoint erect, clinate, or flexed at the base $\pm 90^\circ$, shorter than, \pm equal to, or longer than the rays; bark reddish brown, a transparent layer sloughing off young stems sometimes present; stems unarmed or with scattered prickles, the prickles to 6.0×5.4 mm, typically broad based, straight or retrorse, yellow-ferruginous or orange. Sympodia difoliolate (except *S. nelsonii*). Short shoots absent or present. Leaves simple, borne individually or geminate, $2.3\text{--}21.9 \times 0.4\text{--}12.1$ cm, 1.0–7.3 times as long as wide, orbicular, ovate, obovate, oval, lanceolate to oblong, elliptic, narrowly elliptic, deltate, pandurate, lyrate, spatulate, or spatulate with the distal portion expanded laterally with or without basal lobes, chartaceous, sub-coriaceous, or semisucculent, glabrous to densely pubescent above with deciduous or persistent, sessile or stipitate, porrect stellae and sometimes with minute glandular hairs when young, glabrous to densely pubescent when mature, the stellae 0.1–0.9 mm in diameter, with 4–13 rays, the stipes to 1.2 mm long, the midpoint of the stellae erect, clinate, or flexed at the base $\pm 90^\circ$, shorter than, \pm equal to, or longer than the rays, the glandular hairs 0.03–0.06 mm long, glabrous to densely pubescent below with sessile or stipitate porrect stellae and sometimes minute glandular hairs when young, glabrous to densely pubescent when mature, the stellae 0.2–1.2 mm in diameter,

with 4–11 rays, the stipes to 0.8 mm long, the midpoint of the stellae erect, curved, ciliate, or flexed at the base $\pm 90^\circ$, shorter than, \pm equal to, or longer than the rays, the glandular hairs 0.03–0.07 mm long; blade unarmed or with scattered, straight prickles on the primary vein, primary and secondary veins, or primary, secondary, and tertiary veins adaxially and on the primary vein, primary and secondary veins, or primary, secondary, and tertiary veins abaxially, with 2–16 veins on either side of the midvein, the midvein raised abaxially, distinct or raised adaxially, the lateral veins, craspedodromous, semictaspedodromous, weakly to strongly brochidodromous, or joining a pseudo-intermarginal vein, distinct or raised abaxially, indistinct, distinct or raised adaxially; blade base cordate, subcordate, truncate, rounded, cuneate, shortly attenuate, or attenuate, aequilateral or oblique; margin entire; apex obtuse, acute, short acuminate, or acuminate; petiole 0.3–16.8 cm long, ca. 0.4–2.4 mm in diameter, channeled above, glabrous or densely pubescent all over or on the adaxial surface only when young, unarmed or with scattered broad-based, straight or retrorse prickles. Inflorescence sessile to 12.9 cm in flower, to 14.9 cm in fruit, terminal on short shoots or appearing lateral, extra-axillary, emerging from the middle or upper 1/3 of the internode, occasionally leaf opposed, unbranched or branching to 6(–22) times, with 1–145 flowers, all apparently fertile or potentially so, the axes glabrous to densely pubescent, with sessile or stipitate porrect stellae and sometimes minute glandular hairs, unarmed or occasionally with a few prickles; peduncle lacking or with a true or pseudo-peduncle in, the branches to 8.2 cm in flower, to 8.9 cm long in fruit; pedicels 0.5–2.8 cm long, 0.1–1.3 mm in diameter at the base, 0.4–2.0 mm in diameter below the calyx, not noticeably increasing in diameter or gradually increasing in diameter in the distal 1/4–2/3, glabrous to densely pubescent, the bases congested or well spaced in flower, 1.0–3.2 cm long, 0.3–1.3 mm in diameter at the base, 0.4–4.8 mm in diameter below the calyx, gradually increasing in diameter in the distal ca. 1/3–2/3, glabrous to densely pubescent, the bases congested

or lax in fruit, rigid or limp, in two rows, articulate at the base. Flowers heterostylous or homostylous, (4–)5(–6)-merous. Buds ovate or globose, the calyx glabrous to densely stellate-pubescent, the corolla typically densely stellate-pubescent, the surface of the corolla of the mature bud smooth or ridged. Calyx 0.6–5.5 mm long, unarmed (except *S. incompletum* occasionally), appearing nearly truncate with apiculate to caudate or minute deltate lobe tips, the tube 0.4–3.2 mm long, the tips 0.2–4.2 mm long, the intersepal tissue opaque or translucent when dry; sometimes splitting in the sinuses at anthesis and then the lobes dentate, $0.3\text{--}1.8 \times 0.4\text{--}2.3$ mm at anthesis, glabrous to densely pubescent abaxially, typically glabrous adaxially, the calyx lobes in fruit $0.7\text{--}6.3 \times 0.9\text{--}6.6$ mm, glabrous to densely pubescent, appressed or reflexed. Corolla 0.5–2.3 cm in diameter, stellate with poorly or well developed, glabrous interpetalar tissue, white occasionally purple or the interpetalar and petalar tissue white with purple veins, the lobes $0.8\text{--}7.5 \times 1.6\text{--}8.9$ mm, triangular to deltate, the midrib $4.2\text{--}11.8 \times 1.3\text{--}6.3$ mm, oval, oblong, lanceolate, or elliptic, occasionally glabrous, typically moderately to densely pubescent abaxially, glabrous or glabrous at the base becoming moderately stellate pubescent towards the apex adaxially, spread wide or reflexed at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.4–2.3 mm long; anthers $1.6\text{--}6.2 \times 0.2\text{--}1.7$ mm, acuminate, straight to arcuate, attenuate or oblong, yellow (except sometimes in *S. nelsonii*), typically spreading, occasionally \pm connivent, sometimes longitudinally dehiscent, typically with minute apical pores, the pores directed distally, typically extending around the edge of the apex, the lateral sutures entire or perforated, remaining intact or splitting with age. Ovary 0.5–1.4 mm, globose or ovate, glabrous or with sparsely to densely pubescent with sessile or stipitate porrect-stellate and minute glandular or simple glandular hairs restricted to the apex; styles when homostylous 2.0–11.0 mm long, when heterostylous the short styles 0.7–2.8 mm long, long styles ca. 2.3–8.3 mm long, ca. 0.1–0.3 mm in diameter, shorter than the stamens and not

emerging, \pm equal to the stamens, or longer than the stamens, straight or deflexed and emerging between the sides of two adjacent stamens, filiform, curved or hooked towards the tip, glabrous, white or cream; stigma ca. 0.1–0.7 mm in diameter, capitate, white or green. Fruit a berry, 0.3–2.7 cm in diameter, globose or ovate, yellow, orange, red-orange, red, or black when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds few or many per fruit, 1.3–4.9 \times 1.5–6.5 mm, flattened-reniform, flattened-irregular, or flattened-orbicular and notched at the point of attachment, light brown to brown, red-brown, or yellow-tan when dry, the surface reticulate or completely smooth or with the central area nearly \pm smooth, the margin alveolate or scrobiculate.

Bitter (1921, 1922a) did not designate a type for his taxon. *Solanum camptostylum* was selected as the lectotype for *Solanum* section *Irenosolanum* due to the following: the species was included as *S. camptostylum*, not under a different name, by Bitter (1921); *S. camptostylum* is morphologically uniform, and its circumscription is not likely to change; and Bitter (1921) first mentioned series *Irenosolanum* in his discussion of *S. camptostylum*.

Key to the species of Section *Irenosolanum*

1. Erect or prostrate shrub less than 20 cm tall, the stems persistently pubescent. Leaves densely pubescent across the lamina both abaxially and adaxially when mature.

2. Prostrate shrub. Prickles absent. Lateral veins of the leaves weakly brochidodromous, the margin almost always entire. Corolla 1.3–1.7 cm in diameter. (Hawaiian Islands: various islands)

S. nelsonii

2. Erect shrub. Prickles present or potentially so. Lateral veins of the leaves craspedodromous, the margin sinuate or lobed. Corolla ca. 0.9 cm in diameter. (Hawaiian Islands: Lanai and Hawaii)

S. abollatum

1. Shrub or small trees of various habits taller than 20 cm, the stems glabrous or glabrescent. Leaves glabrous to densely pubescent abaxially, glabrous to sparsely pubescence adaxially when mature.

3. Prickles present on stems, leaves, inflorescences and/or calyces.

4. Plants robust; short lateral shoots absent. Leaves typically large, 5.1–18.8 × 2.3–11.2 cm, 1.5–2.4 times as long as wide. Inflorescences with many flowers, (8–)18–120, the floral buds globose, the styles straight.

5. Stems and pedicles densely armed with yellow prickles. Leaves glabrous, not lobed. Flowers homostylous. Fruit ca. 7.0 cm in diameter. (Fiji)

S. albertii

5. Stems, pedicles, blades of the leaves sparsely armed with red-orange prickles. Leaves densely pubescent abaxially, often lobed or the margin sinuate, sometime entire. Flowers homostylous. Fruits 0.8–1.9 cm in diameter.

6. Leaves with 7–11 lateral veins per side of the midrib, the apices of the lobes acute. Calyx with the intersepalar tissue translucent when dry, the lobes glabrous in fruit; anthers longitudinally dehiscent. (Hawaiian Islands: Lanai and Maui)

S. hillebrandii

6. Leaves with 5–9 lateral veins per side of the midrib, the apices of the lobes rounded. Calyx with the intersepalar tissue opaque when dry, the lobes moderately to densely pubescent in fruit; anthers poricidally dehiscent. (Hawaiian Islands: Hawaii)

S. incompletum

4. Plants gracile, short shoots present (except *S. nudatum*). Leaves typically small, 0.3–6.5(–7.8) × 0.3–2.3 cm, (1–)2–7.3 time as long as wide. Inflorescence with flowers solitary, paired or many, not more than 14 (except *S. camptostylum* with up to 35), the flower buds ovate, the styles sigmoid (or straight in *S. pancheri* and *S. nudatum*).

7. Erect shrub, totally glabrous; short shoots absent. Corollas ca. 0.6 cm in diameter. Styles straight. (Fiji)

S. nudatum

7. Erect or scandent shrub, pubescent; lateral short shoots present. Corollas 0.9–2.5 cm in diameter (except *S. ratale*, ca. 0.5 cm). Styles sigmoid. (except *S. pancheri* and *S. insulae-pinorum*)

8. Leaves typically more than 3 times as long as wide.

9. Erect shrub, the stems glabrous, prickles infrequent and often lacking on herbarium specimens. Leaves spatulate, never lobed, glabrous. Inflorescences with flowers solitary or occasionally paired. Flowers 4-merous, the style straight. (New Caledonia)

S. pancheri

9. Scandent shrub, the stems glabrous to moderately pubescent, prickles frequent. Leaves variously shaped, sometimes lobed, glabrous to moderately pubescent. Inflorescences with 1–14 flowers. Flowers 5-merous, the styles sigmoid.

10. Stems with a transparent sloughing layer. Leaves 0.3–6.5 × 0.3–1.2 cm, typically moderately pubescent, variously shaped, ovate, obovate, orbicular, pandurate, lyrate, oval, elliptic, spatulate, spatulate with the distal portion expanded laterally with or without basal lobes, the widest portion typically above the midpoint of the leaf, the apices rounded, marginal prickles never present. Fruit 0.4–0.7 cm in diameter, yellow when mature. Seeds alveolate. (New Caledonia)

S. vaccinioides

10. Stems lacking a transparent sloughing layer. Leaves $2.3\text{--}7.8 \times 0.4\text{--}2.3$ cm, glabrous, typically elliptic to narrowly elliptic, occasionally lanceolate to oblong, never spatulate, never with basal lobes, the widest portion typically at or below the midpoint of the leaf, the apices acute, marginal prickles sometimes present. Fruit 0.5–1.3 cm in diameter, red when mature. Seeds smooth. (New Caledonia)

S. actephilum

8. Leaves less than 3 times as long as wide.

11. Young stems lacking a transparent sloughing layer. Inflorescences with up to 35 flowers in the inflorescence. Fruit 0.6–1.3 cm in diameter, orange when mature. (New Caledonia)

S. camptostylum

11. Young stems with a transparent layer sloughing off. Inflorescence with 1–6 flowers. Fruit 0.5–0.8 cm in diameter, orange-red or yellow when mature.

12. Prickles infrequently present. Stems glabrous. Leaves glabrous when mature. Inflorescence lacking a rachis, with 1–2(–3) flowers. Calyx lobes ca. 0.3 mm long, apiculate. Style straight. Fruit orange-red when mature. (New Caledonia)

S. insulae-pinorum

12. Prickles frequently present. Stems sparsely to moderately pubescent.

Leaves sparsely pubescent when mature. Inflorescence with the rachis 1.1–1.6 cm long in flower, with 3–6 flowers. Calyx lobes 2.2–4.0 mm long, spatulate. Style sigmoid. Fruit yellow when mature. (New Caledonia)

S. hugonis

3. Prickles never present on any organ.

13. Leaves semisucculent.

14. Leaves and stems glabrous. Calyx lobes 0.7–4.2 mm long. (New Caledonia)

S. semisucculentum

14. Leaves and stems densely pubescent. Calyx lobes 0.9–1.6 mm long.

15. Shrub to 3 m tall. Leaves pubescent across the blades. Midpoints of the stellae on the stems and leaves shorter than to \pm equal to the rays. Inflorescences with 2–7 flowers. Corolla glabrous at the base becoming pubescent towards the apex adaxially. Found in rainforest 1300–1500 m elevation. (New Caledonia)

S. memaoyanum

15. Shrub to 1 m tall, Leaves pubescent along the mainvein, glabrous across the blade. Midpoints of the stellae on the stems and leaves much longer than the rays. Inflorescences with up to 21 flowers. Corolla glabrous adaxially. Found in maquis, 100–250 m elevation. (New Caledonia)

S. leratii

13. Leaves chartaceous.

16. Stems and leaves glabrous; or an occasional hair may be present.

17. Inflorescences branching up to 22 times. Flower buds ovoid. Flowers homostylous, the corolla outline stellate-rotate, the abaxial surface sparsely pubescent with simple hairs flexed at the base; filaments 1.4–2.3 mm long. Fruits 0.6–1.0 cm in diameter, the mesocarp never fleshy. (Lord Howe Island and Norfolk Island)

S. bauerianum

17. Inflorescence forked once or unbranched. Flower buds globose. Flowers heterostylous, the corolla outline stellate, the abaxial surface moderately to densely pubescent with stellate hairs; filaments 0.7–1.0 mm long. Fruits 0.9–2.7 cm in diameter, the mesocarp sometimes fleshy. (widespread across the Pacific)

S. viride

16. Stems and leaves pubescent

18. Flower buds globose. Flowers heterostylous.

19. Semi-erect shrub to 1.5 m tall. Leaves deltoid to ovate, 3.5–8.0 × 2.2–6.4 cm, 1.3–1.6 times as long as wide. Inflorescence typically unbranched occasionally forked, with 10–16 flowers. (Hawaiian Islands: Nihoa)

S. caumii

19. Erect shrub or small tree over 1.5 m tall. Leaves lanceolate to ovate, 4.5–21.9 × 1.8–12.1 cm, 1.5–2.6 times as long as wide. Inflorescence unbranched or branching up to 10 times, with 17–145 flowers.

20. Stems and leaves glabrescent or sparsely pubescent. Inflorescence typically unbranched, sometimes forking, occasionally branching 3 times. Fruit 0.8–1.1 cm in diameter. (widespread across the Pacific)

S. viride

20. Stems and leaves densely pubescent. Inflorescence unbranched or branching up to 10 times. Fruit 0.7–1.7 cm in diameter.

21. Leaves with sessile and stipitate stellae, the stipes to 0.7 mm long, the lateral veins weakly brochidodromous or semicraspedodromous.

Pedicels to 10.5 mm apart in fruit. Mature flower buds ridged. Corolla 1.2–2.3 cm in diameter. Anthers arcuate. Seeds 3.2–4.9 × 3.9–6.5 mm. (Hawaiian Islands: Oahu and Kauai)

S. sandwicense

21. Leaves with sessile stellae, the lateral veins weakly brochidodromous. Pedicels to 2.0 mm apart in fruit. Mature flower buds smooth. Corolla 1.1–1.5 cm in diameter. Anthers slightly incurved. Seeds ca. 2.8 × 2.8 mm. (Fiji)

S. inamoenum

18. Flower buds ovate or globose in *S. pseudopedunculatum* and *S. ratale*. Flowers homostylous.

22. Mature leaves densely pubescent across the surface of the lamina abaxially

23. Leaves deltate to ovate, geminate, typically less than 2 times as long as wide.

24. Pubescence on the abaxial surface of the blades distinctly different between the veins and across the lamina. Inflorescence with up to 35 flowers. Corolla 1.5–2.0 cm in diameter. Anthers longitudinally dehiscent. Fruit 0.7–1.5 cm in diameter, red when mature. (Tonga)

S. amicorum

24. Pubescence uniform across the adaxial surface. Inflorescence with up to 95 flowers. Corolla 1.1–1.6 cm in diameter. Anthers poricidally dehiscent. Fruit 0.3–0.6 cm in diameter, black when mature. (Guam)

S. guamense

23. Leaves lanceolate to elliptic, borne individually (sometimes geminate in *S. vanuatuense*), typically more than 2 times as long as wide.

25. Pubescence of the stems and leaves bicolorous, ferruginous and yellow respectively. Leaves 1.5–4.0 × 0.6–2.1 cm. Inflorescence with 1–2 flowers. Fruit black when mature. (New Caledonia)

S. pseuderanthemoides

25. Pubescence of the stems and leaves concolorous. Leaves (2.2–)5.3–16.6 × (0.9–)1.6–7.5 cm. Inflorescence with many flowers up to 130. Fruit yellow, orange or red when mature.

26. Leaves sometimes geminate, and often lobed. Corolla 1.1–1.3 cm in diameter. Anthers 2.5–2.9 × 0.9–1.1 mm. Style sigmoid. (Vanuatu)

S. vanuatuense

26. Leaves borne individually, seldom or never lobed. Corolla 1.3–2.2 cm in diameter. Anthers 3.2–4.5 × 0.8–1.4 mm. Style straight.

27. Leaves lanceolate to ovate, 2.6–3 times as long as wide, sparsely pubescent across the blade, the margin typically minutely undulate-crenate, the apex typically long acuminate, with 7–10 veins per side of the midvein. Inflorescence branching 4–6 times. Calyx lobes reflexed in fruit. Fruit 0.5–0.8 cm in diameter. (Vanuatu and New Caledonia (Loyalty Islands))

S. milnei

27. Leaves lanceolate to elliptic, 1.7–2.4 times as long as wide, moderately to densely pubescent across the blade, the margin entire, the apex acute to acuminate, with 5–7 veins per side of the midvein, Inflorescence unbranched or branching to 3(–5) times. Calyx lobes appressed in fruit. Fruit 0.6–1.1 cm in diameter. (New Caledonia)

S. austro-caledonicum

22. Mature leaves sparsely to moderate pubescent but never densely pubescent across the surface of the lamina abaxially.

28. Shrub to 1 m tall. Leaves pubescent only on the petiole or main veins.
Fruit 1.1–1.5 cm in diameter, red when mature. (New Caledonia)

S. artense

28. Shrub or small tree over 1.5 m tall. Leaves pubescent across the blade but not dense at maturity. Fruits 0.5–1.0 cm in diameter, black when mature.

29. Shrub or small tree to 4 m tall. Inflorescence with a pseudopeduncle. Pedicels 0.8–1.4 cm long in flower, 1.7–2.3 cm long in fruit. Corolla ca. 1.5 cm in diameter. Anthers 1.5–2.1 × 1.0–1.2 mm. Fruit 0.7–1.0 cm in diameter. (Fiji)

S. pseudopedunculatum

29. Shrub or small tree to 1.5 m tall. Inflorescence with a true peduncle. Pedicels 0.6–0.8 cm long in flower, 0.8–1.4 cm long in fruit. Corolla ca. 0.5 cm in diameter. Anthers ca. 1.3 × 0.6 mm. Fruit 0.5–0.7 cm in diameter. (Fiji)

S. ratalae

***Solanum abollatum* H. St. John**, *Phytologia* 64: 169. 1988. Type: U.S.A., Hawaiian Islands, Lanai Island, 1 Aug 1922 (fl), *G. C. Munro s.n.* (Holotype: BISH 70009!; Isotype: NY 00759141!).

Solanum nelsonii Dunal var. *vadosum* H. St. John, *Phytologia* 64: 170. Jan. 1988. Type: U.S.A., Hawaiian Islands, Hawaii, Kaulananauna, *L. W. Croft 110* (Holotype: BISH 523451!; Isotypes: BISH 523452!, K!).

Figure 3.

Low shrub to at least 20 cm, rhizomatous, the internodes to 1.3 cm long. Stems densely pubescent with yellow-ferruginous to ferruginous, sessile and short-stipitate porrect stellae, the stipes to 0.13 mm long, the stellae persistent, 0.2–0.4 broad, with 7–12 rays, the midpoint erect, shorter than to longer than the rays; bark reddish brown, a transparent sloughing layer absent on young stems; stems unarmed. Sympodial structure unknown. Short shoots absent. Leaves simple, borne individually, 2.5–4.0 × 1.9–3.3 cm, 1–1.5 times as long as wide, ovate, chartaceous, densely pubescent above with sessile and short-stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.3–0.5 mm in diameter, with 6–9 rays, the stipes to 0.1 mm long, the midpoint of the stellae erect or clinate less than 90°, shorter than to ±equal to the rays, very densely pubescent below with sessile and short-stipitate porrect stellae when young, very densely pubescent when mature, the stellae 0.3–0.8 mm in diameter, with 8–11 rays, the stipes to 0.15 mm long, the midpoint of the stellae ±erect, shorter than the rays; blade unarmed or with a few straight prickles on the primary vein abaxially and the primary vein or the primary and secondary veins adaxially, with 4–6 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins craspedodromous, raised abaxially, distinct adaxially; blade base subcordate, truncate, or rounded, aequilateral or occasionally oblique; margin sinuate or lobed, the apices of the lobes obtuse; apex obtuse; petiole 0.6–1.6 cm long, 0.7–1.1 mm in diameter, channeled above, densely

pubescent, unarmed or occasionally with a prickle. Inflorescence to 1.3 cm in flower, not seen in fruit, appearing lateral, extra-axillary, just below the leaf or leaf opposed, unbranched, with 6–8 flowers, all apparently fertile or potentially so, the axes densely pubescent, with sessile and stipitate porrect stellae, unarmed; peduncle in flower ca. 6.3 mm long, ca. 0.9 mm in diameter; pedicels ca. 4.5 mm long, ca. 0.5 mm in diameter at the base, ca. 0.6 mm in diameter below the calyx, straight, not noticeably increasing in diameter, densely pubescent, the bases congested to ca. 0.9 mm apart in flower, rigid, in two rows, articulate at the base. Flowers heterostylous, 5-merous. Buds globose, the calyx very densely stellate-pubescent, the corolla very densely stellate-pubescent, the surface of the corolla of the mature bud not seen. Calyx 2.3–3.2 mm long, with deltoid lobe tips, the tube 1.3–1.8 mm long, the lobe tips $1.0\text{--}1.6 \times 1.1\text{--}1.3$ mm long, the intersepal tissue opaque when dry; not splitting at anthesis, densely pubescent abaxially, glabrous adaxially. Corolla ca. 0.9 cm in diameter, stellate with well developed, glabrous interpetalar tissue, the lobes ca. 3.1×1.6 mm, deltoid, the midrib ca. 4.2×2.6 mm, lanceolate, densely pubescent abaxially, glabrous adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 0.8 mm long; anthers ca. 1.6×0.8 mm, acuminate, globolunate, scarcely attenuate, with minute apical pores, the pores directed adaxially, extending around the edge of the apex, the lateral sutures entire remaining intact with age. Ovary ca. 0.5 mm, globose, glabrous or with a few minute glandular hairs restricted to the apex; short styles ca. 0.7 mm long, ca. 0.1 mm in diameter, shorter than the stamens, not emerging from among the stamens, long styles ca. 3.0 mm long, ca. 0.2 mm in diameter, longer than the stamens, emerging between the anther apices, cylindrical or filiform, straight, sparsely pubescent with sessile porrect-stellate the rays much reduced, minute glandular; stigma ca. 0.1 mm in diameter, truncate. Fruit not seen. Seeds not seen.

Distribution and ecology.— Found from sea level to ca. 300 m elevation in dry habitats. The species is primarily known from the island of Lanai. However, there is one specimen from the island of Hawaii, *Croft 110*, creating an unusual disjunct distribution, but see discussion below. Figure 35.

Phenology.— Flowering January, May, August, and November; fruiting period unknown.

Etymology.— St. John (1988) named this species after what he characterized as the lanate coating of the leaves. Though the leaves are densely pubescent, it should be noted that the indumentum does not fit the typical definition of lanate.

Additional specimens examined. **USA. Hawaiian Islands. Hawaii:** South Kona District, Ahupua'a of Kaulananauna, immediately before Ahuloa Pt., 35 feet from jeep road, 75–50 feet from shore, 25 Nov 1977 (fl), *L. W. Croft 110* (BISH×2, K). **Lanai:** Kalulu, May 1921 (fl), *Munro s.n.* (BISH); Maunalei, 23 May 1921 (fl), *Munro s.n.* (BISH); Kahoolani, Maunalei, 1 May 1922 (fl), *Munro 495* (BISH 70011); Kahoolani, Maunalei, ca. 1000 ft, 5 Jan 1922 (fl), *Munro 693* (BISH).

Solanum abollatum is unusual within section *Irenosolanum* due to its rhizomatous habit. This condition is not known from any other species of the section.

With reservation, I include *Croft 110* in *S. abollatum*. St. John (1988a; 1988b) placed *Croft 110* into *S. nelsonii* and erected a new variety, var. *vadosum*, for it. However, *Croft 110* differs from *S. nelsonii* in a number of ways, including habit, corolla size, anther size and shape, and leaf armament. A few prickles are present on *Croft 110*, and unlike *S. abollatum*, *Solanum*

nelsonii never has prickles. *Croft 110* most closely resembles *S. abollatum*, however it does differ slightly in the lobing of the leaves. Inclusion of *Croft 110* within *S. abollatum* also creates an unusual, and somewhat suspicious, disjunct distribution for the species, but from the herbarium material available, I do not feel at this time that *Croft 110* warrants taxonomic recognition.

Unfortunately, *Solanum abollatum* could well be extinct. It was last collected in 1977. In 2008, I made a special search for this species. I visited both the collection locality of *Croft 110* and the island of Lanai but was unable to locate living material in either place. The locality of Croft's collection was heavily disturbed by people with trash strewn about and a fire pit; a search of the surrounding area yielded nothing. The collection localities on Lanai are vague at best; however, several days of fruitless searching indicate that the *S. abollatum*, if it is still extant on Lanai, is very uncommon.

***Solanum actephilum* Guillaumin** Bull. Soc. Bot. France 88: 465. 1941. Type: France. New

Caledonia. Ouroue, at the mouth of the Dothio, s.d. (fl, fr) *B. Balansa 3527* (Lectotype, first stage, designated by Heini, 1976: P×3; Lectotype, second stage, *hic designatus*: P 00298907!; Isolectotypes: A!, K!, L 0531771!, L 0531770!, NY00172270!, P 00298908!, P 00298909!, UC103825!, Z).

Solanum deplanchei Guillaumin, Bull. Mus. Hist. Nat., 16: 84. 1944. Type: France. New

Caledonia, Uarai *Pancher s.n.* in *Vieillard 1032* (Lectotype, *hic designatus*: P 00298941!)

Other syntypes: *s. loc.*, 1861, *Deplanche s.n.* (P 298923!); *s. loc.*, 1861, *Deplanche s.n.* (P

298924!); *s. loc. Deplanch 142* (P 298942!); Nené, *Deplanche 484, 3040, 142* (P 521098!);
Nené, 1861, *Deplanche 484* (P 298922!)

Figure 4.

Scandent shrub to 2(–6) m, the internodes to 6.6 cm long. Stems glabrous or sparsely pubescent with yellow-ferruginous to ferruginous, sessile porrect stellae, the stellae soon deciduous, 0.3–0.4 mm in diameter, with 6–8 rays, the midpoint flexed at the base $\pm 90^\circ$, \pm equal to or longer than the rays; bark reddish brown, a transparent layer sloughing off young stems; stems with scattered prickles, the prickles to 2.2×5.4 mm, broad based, broadly triangular, retrorse, yellow-ferruginous. Sympodia difoliate. Short shoots present. Leaves simple, borne individually, $2.3\text{--}7.8 \times 0.4\text{--}2.3$ cm, 2.6–7 times as long as wide, lanceolate to oblong or elliptic, chartaceous to sub-coriaceous, glabrous to moderately pubescent above with soon deciduous, sessile, porrect stellae and minute glandular hairs when young, \pm glabrous when mature, the stellae 0.3–0.4 mm in diameter, with 6–10 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$, \pm equal to or longer than the rays, the glandular hairs 0.04 mm long, glabrous to moderately pubescent below with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.3–0.4 mm in diameter, with 6–8 rays, the midpoint of the stellae curved or flexed at the base $\pm 90^\circ$, longer than the rays, the glandular hairs 0.04 mm long; blade unarmed or with scattered, straight prickles on the primary vein adaxially and on the primary vein or primary and secondary veins abaxially, with 4–16 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins strongly brochidodromous or joining a pseudo-intermarginal vein, distinct or occasionally raised abaxially, indistinct or distinct adaxially; blade base rounded to cuneate, aequilateral or oblique; margin entire,

sometimes with prickles extending laterally; apex obtuse to acute; petiole 0.3–2.2 cm long, ca. 0.5 mm in diameter, channeled above, glabrous or densely pubescent all over when young, unarmed or with scattered broad-based, retrorse, yellow-ferruginous prickles to 1.9×1.7 mm. Inflorescence to 2.3 cm in flower, to 3.2 cm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, once forked or unbranched, with 2–14 flowers, all apparently fertile or potentially so, the axes glabrous or sparsely pubescent, with sessile porrect stellae, unarmed; pseudo-peduncle in flower 1.7–9.2 mm long, 0.6–0.9 mm in diameter, the branches not seen in flower, in fruit 2.3–6.6 mm long, 0.7–1.4 mm in diameter, the branches to 2.5 mm long, ca. 1.1 mm in diameter; pedicels 1.4–2.8 cm long, ca. 0.3 mm in diameter at the base, ca. 0.7 mm in diameter below the calyx, gradually increasing in diameter in the distal 1/4–1/3, glabrous, the bases congested or lax to 4 mm apart in flower, 1.3–2.8 cm long, 0.5–0.6 mm in diameter at the base, 1.4–1.6 mm in diameter below the calyx, gradually increasing in diameter in the distal ca. 1/2, glabrous, the bases congested or lax to 4.3 mm apart, in fruit, apparently limp, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx \pm glabrous, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.0–3.2 mm long, unarmed, appearing nearly truncate with apiculate or minute deltate lobe tips, the tube 1.6–2.3 mm long, the tips 0.6–1.0 mm long, the intersepalar tissue opaque when dry; splitting in the sinuses at anthesis and then the lobes dentate, $1.3\text{--}1.8 \times 1.6\text{--}1.8$ mm at anthesis, \pm glabrous abaxially, sparsely pubescent adaxially with minute glandular hairs, the calyx lobes in fruit $1.6\text{--}2.1 \times 1.4\text{--}2.2$ mm, glabrous, appressed. Corolla 1.6–2.0 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white, the lobes $5.2\text{--}7.5 \times 3.6\text{--}3.9$ mm, deltoid, the midrib $6.9\text{--}10.3 \times 2.2\text{--}2.9$ mm, lanceolate, moderately pubescent abaxially, glabrous at the base becoming moderately stellate pubescent towards the apex adaxially, spread wide or somewhat reflexed at anthesis. Stamens adnate to the corolla, the free portion of the

filament 0.5–0.8 mm long; anthers 4.5–5.2 × 1.2–1.6 mm, acuminate, somewhat incurved, attenuate, yellow, ±connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact or splitting with age. Ovary ca. 1.0 mm, ovate, glabrous; style ca. 8.0 mm long, ca. 0.3 mm in diameter, longer than the stamens, deflexed and emerging between the sides of two adjacent stamens, filiform, curved or hooked towards the tip, glabrous, white or cream; stigma ca. 0.7 mm in diameter, capitate, green. Fruit a berry, 0.5–1.3 cm in diameter, globose, red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds few per fruit, 1.6–1.7 × 1.7–2.3 mm, flattened-orbicular and notched at the point of attachment, yellow-tan when dry, the surface completely smooth.

Distribution and ecology.— Restricted to the Grande Terre of New Caledonia, this species is found across a wide elevation range from ca. sea level to 1000 m elevation in humid forest. Whalen (1985) reported this species as a serpentine endemic. It is a scandent shrub adapted to scramble up surrounding vegetation with its prickles. *McKee 34476* reported it as scrambling to 6 m up neighboring vegetation. Figure 38.

Phenology.— Flowering April and December and fruiting April, March, and December.

Etymology.— The specific epithet is Greek for beach-loving. This must be somewhat humorous for anyone who collects the species in the mountains at 500 or 1000 m elevation.

Additional specimens examined. **FRANCE. New Caledonia.** Mt. Kujua [Mt. Koujoua], ca. 600 m, 27 Mar 1980, *s.c. s.n.* (P×2); (fl) *Hennecart s.n.* (A, P); Mar 1870 (fl), *Pancher s.n.* (K, L); Chez M.

Nagles, 5 Dec 2007 (fl, fr), *Hequet & Butin 3781* (NOU). **North Province:** entrée de Népoui, 21° 18' 6" S, 165° 25" E, ca. 1500 ft, 20 Nov 2007 (fr), *Hequet & Butin 3794* (NOU); Vallée du Ouen Koura, Haute Dothio, 300–400 m, 26 May 1970, *MacKee 21989* (NOU 016987, P×2); Poya, Népou, 5 m, 31 Dec 1973 (fr), *McKee 27719* (K, L, NOU, P); Poya, Népou, 5 m, 25 Apr 1974 (fl, fr), *McKee 28565* (K, L, P); Pouembout, Embouchure de la Tiaoué, 30 Dec 1977 (fr), *McKee 34476* (L, NOU, P); Hienghene, Crete Tindo-Coulna, 500 m, 16 Jun 1979, *McKee 35176* (P); Poya, Moindah, station de Beaupre, 29 Jun 1987 (fl), *Veillon 6379* (NOU, NSW, P). **South Province:** Mt. Ninga, 1000 m, 2 Mar 1976 (fr), *Jaffre 1731* (NOU); Col d'Amieu, Toili, 500 m, 14 Nov 1970, *McKee 22928* (NOU, NSW, P×2); Mt. Nakada, south slope, 600 m, 4 Dec 1980 (fl), *McKee 38393* (P).

There is considerable morphological variability in the leaves of *S. actephilum* especially between specimens from lower and higher elevations. However, from the material available, no taxa can be segregated. I include *S. deplanchei* Guillaumin here, but if *S. actephilum* were to be split it would likely result in the resurrection of *S. deplanchei* for at least some of the low altitude material. *Solanum actephilum* is most similar to *S. camptostylum*; however, *S. actephilum* can be easily distinguished by its longer leaf length to width ratio, poorly developed interpetalar tissue, and red fruit. One remarkable feature of *S. actephilum* is the occasional presence of prickles that project out horizontally from the margin of the blade in the same plane as the blade.

Solanum actephilum is part of a group of native New Caledonian *Solanums* with relatively small leaves and short shoots which typically bear the inflorescences. Though not common this species is one of the few New Caledonian *Solanums* not currently threatened (Jaffré *et al.*, 1998)

The syntypes are variously and confusingly cross numbered, but all were annotated by Guillaumin. The Deplanch collections may well form a single gathering from Nené under *Deplanche 484* and later 142 which is a Mus. Neocal. number and 3040 which is a Viellard herbarium number. Two sheets of Deplanche bear no numbers or locality but undoubtedly belong with the collection.

The lectotype was chosen as it was the most complete of the three specimens designated by Heine.

***Solanum albertii* D. McClell. sp. nov.**

Type: Fiji. Fulanga Island. 24 Feb 1934 (fl, fr), *Smith 1180* (Holotype: NY 00828297!;

Isotypes: GH!, K!, P 00315309!, UC 601472!, US 1674821!).

Figure 5.

Shrubs 1–2 m tall, the internodes to 9.0 cm long. Stems with a few scattered, yellow, sessile porrect stellae, the stellae soon deciduous, 0.3–0.5 mm broad, with 4–8 rays, the midpoint ciliate less than 90° to flexed at the base $\pm 90^\circ$, shorter than the rays; a transparent sloughing layer absent on young stems; stems armed, the prickles to 6.0×2.0 mm, aciculate, constricted just above the base the sides concave from a wider base, to 0.8 mm in diameter just above the base, straight, sometimes inclined backward, yellow. Sympodia difoliolate. Short shoots absent. Leaves simple, geminate, the blades of major leaves $12.5\text{--}18.8 \times 6.6\text{--}9.7$ cm, ca. 1.5–2 times as long as wide, ovate, chartaceous, the minor leaves $2/3\text{--}3/4$ times as large as the majors, both major and minor leaves sparsely pubescent above

with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.4–0.6 mm in diameter, with 6–8 rays, the midpoint of the stellae ciliate less than 90° to flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, shorter than to \pm equal to the rays, the glandular hairs to ca. 0.08 mm long, sparsely pubescent below with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.4–0.6 mm in diameter, with 5–10 rays, the midpoint of the stellae ciliate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs to 0.06 mm long; blade unarmed, with 6–9 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base truncate to rounded, occasionally subcordate, aequilateral or oblique; margin entire or sinuate; apex acute to short acuminate; petiole 2.6–6.1 cm long, 1.2–1.6 mm in diameter, channeled above, with scattered hairs when young, glabrous when mature, unarmed or with a few straight, aciculate, light yellow prickles to 4.0×0.8 mm. Inflorescence to 3.8 cm in flower, to 4.0 cm in fruit, appearing lateral, extra-axillary, in the middle or upper 1/3 of the internode, branching 1–2 times, with 18–25 flowers, all apparently fertile or potentially so, the axes with a few scattered sessile porrect stellae and minute glandular hairs when young, glabrous when mature, unarmed or sometimes with a few straight, light yellow aciculate prickles to 4.6×0.6 mm; peduncle 1.2–2.5 mm long in flower and fruit, ca. 0.9 mm in diameter in flower, ca. 1.1 mm in diameter in fruit, in flower the branches to 9.2 mm long, to 0.7 mm in diameter, in fruit to 11.7 mm long, to 1.1 mm in diameter; pedicles 1.1–1.2 cm long, ca. 0.7 mm in diameter at the base, ca. 1.1 mm in diameter below the calyx, arching, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal 1/2–2/3, bases congested to 0.7 mm apart, in flower, 1.1–1.7 cm long, 0.5–0.7 mm in diameter at the base, 1.4–2.0 mm in diameter below the calyx, gradually increasing in diameter in the distal ca. 1/2, straight, bases well spaced to 2.5 mm

apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous on the type, 5-merous. Buds globose, the calyx glabrous or with a few hairs sessile porrect stellae, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.2–3.1 mm long, unarmed, appearing nearly truncate with caudate lobe tips, the tube 1.1–1.2 mm long, the lobe tips 1.1–1.7 mm long, the intersepal tissue opaque when dry, splitting during fruit development and then the lobes dentate, glabrous abaxially, glabrous adaxially, the calyx lobes in fruit 1.4–2.1 × 1.3–1.8 mm, glabrous, appressed. Corolla ca. 1.5 cm in diameter, stellate with well developed, glabrous interpetalar tissue, white, the lobes ca. 6.5 × 4.9 mm, deltoid, the midrib ca. 8.0 × 3.1 mm, oblong, sparsely pubescent abaxially, with sessile porrect stellae, glabrous adaxially, spreading at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 1.2 mm long; anthers 2.0 × 1.0 mm, oblong, straight, not attenuate, yellow, spreading, longitudinally dehiscent. Ovary ca. 0.8 mm in diameter, ovate, glabrous; style ca. 5.5 mm long, 0.2–0.3 mm in diameter, longer than the stamens, emerging between the anthers apices, filiform, straight, glabrous; stigma 0.3–0.4 mm in diameter, capitate. Fruit a berry, ca. 0.7 cm in diameter, globose, glabrous; exocarp thin, glossy; endocarp juicy. Seeds few per fruit, 2.0–2.4 × 2.6–2.7 mm, flattened-reniform to sub-orbicular and notched at the point of attachment, light brown when dry, the surface reticulate.

Distribution and ecology – Known only from the type locality: Fiji, Fulanga Island, southwestern part of the island. In thickets on limestone from sea level to 80 m. Figure 41.

Phenology – Flowers and young fruits are present in February, their presence at other times of year is unknown.

Etymology – The name is given to honor the preeminent botanist Albert C. Smith (1906–1999) who collected the type and only specimen of the species.

Albert Smith collected this species in 1934. Fifty-seven years later, Smith (1991) described the specimen as a *species novum* but declined to provide a name. He was unsure whether it was distinct from *Solanum viride* since the most obvious difference was the abundant prickles on *S. albertii* and presence of prickles is notoriously variable in *Solanum*. Some species of the section including *S. viride*, a well collected species, never have prickles. And, a close examination of material of both *S. viride* and *S. albertii* reveals several other differences. *Solanum albertii* differs from *S. viride* by having smooth corollas in mature flower buds, stamens with the filaments ca. 1.2 mm long, and longitudinally dehiscent anthers, ca. 2.0×1.0 mm vs. having ridged corollas in mature flower buds, stamens with filaments 0.7–1.0 mm long, and poricidally dehiscent anthers, $2.2\text{--}3.1 \times 0.9\text{--}1.2$ mm.

***Solanum amicorum* Benth.**, London J. Bot. 2: 227. 1843. Type: Friendly Islands [Tonga], s.d. (fl) *Barclay s.n.* (Holotype: BM 000846954!; Isotype: K 000195708!).

Figure 6.

Unarmed shrub or small tree to 1.5 m, the internodes to 9.5 cm long. Stems densely pubescent with yellow to yellow-ferruginous, sessile or short-stipitate porrect stellae, the stipes to 0.2 mm long, the stellae tardily glabrescent, 0.3–0.5 mm broad, with 4–9 rays, the midpoint \pm erect to flexed at the

base $\pm 90^\circ$, shorter than than the rays. Sympodia difoliate. Leaves simple, geminate, the blades of major leaves $8.1\text{--}17.1 \times 5.5\text{--}11.1$ cm, 1.5–1.9 times as long as wide, deltoid to ovate, chartaceous, the minor leaves $3/4$ to \pm equal as the major leaves, both major and minor leaves densely pubescent along the veins and scattered across the lamina above with sessile or short-stipitate porrect stellae and minute glandular hairs when young, moderately to densely pubescent along the veins only when mature, the stellae 0.4–0.6 mm in diameter, with 6–10 rays, the stipes to 0.04 mm long, the midpoint of the stellae cliniate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs ca. 0.05 mm long, densely pubescent below with sessile and short-stipitate porrect stellae when young, densely pubescent when mature, denser along the veins than across the lamina, the stellae 0.5–0.7 mm in diameter, with 4–8 rays, the stipes to 0.1 mm long, the midpoint of the stellae \pm erect to flexed at the base $\pm 90^\circ$, shorter than the rays; blade with 5–7 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded to cuneate, \pm aequilateral or oblique; margin entire to sinuate; apex acute; petiole 1.5–4.0 cm long, 1.0–1.8 mm in diameter, channeled above, densely pubescent. Inflorescence to 3.8 cm in flower, to 3.2 cm in fruit, appearing lateral, extra-axillary, in a the middle $1/3$ of the internode, branching up to 3 times or unbranched, with to ca. 35 flowers, all apparently fertile or potentially so, the axes densely pubescent; peduncle in flower to 2.1 cm long, 0.9–1.2 mm in diameter, the branches to 2.1 cm long, to 0.8 mm in diameter, in fruit 3.0–11.1 mm long, 1.2–2.3 mm in diameter, the branches to 2.2 cm long, 0.9–1.3 mm in diameter; pedicels 0.9–1.2 cm long, ca. 0.3 mm in diameter at the base, 0.6–1.2 mm in diameter below the calyx, straight, swelling very little or gradually increasing in diameter in the distal $1/3$, pubescence, the bases congested, \pm overlapping in flower, 1.5–2.1 cm long, 0.9–1.1 mm in diameter at the base, 1.9–3.4 mm in diameter below the calyx, arching, gradually increasing in

diameter in the distal 1/2–2/3, moderately pubescent, the bases well spaced, to 2.6 mm apart, in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.4–1.8 mm long, the tube 0.8–1.0 mm long, appearing nearly truncate with apiculate lobe tips, 0.4–0.7 mm long, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, at anthesis densely pubescent abaxially, with sessile porrect stellae, glabrous adaxially, the calyx lobes in fruit 1.8–3.5 × 2.7–3.0 mm, ±glabrous to sparsely pubescent, typically reflexed though sometimes appressed. Corolla 1.5–2.0 cm in diameter, stellate with poorly-developed, glabrous interpetalar tissue, white, the lobes 4.2–5.5 × 3.1–4.2 mm, deltoid, the midrib 7.1–9.1 × 1.7–2.1 mm, oblong, moderately pubescent abaxially, ±glabrous adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 0.6 mm long; anthers 2.5–2.6 × 0.7–0.8 mm, oblong, straight, yellow, spreading, longitudinally dehiscent. Ovary ca. 1.4 mm in diameter, globose, glabrous or with sessile porrect stellae and simple glandular hairs restricted to the apex; style ca. 7.5 mm long, ca. 0.3 mm in diameter, longer than the anthers, emerging between the anther apices, filiform, ±straight or hooked, glabrous; stigma 0.4 mm in diameter, capitate. Fruit a berry, 0.7–1.5 cm in diameter, globose, orange-red to red when mature, glabrous; exocarp thin, shiny; endocarp juicy. Seeds many per fruit, 1.9–2.2 × 1.8–2.3 mm, flattened-orbicular and notched at the point of attachment, yellow-tan when dry, the surface with the central area nearly ±smooth, the margin alveolate.

Distribution and ecology.— Restricted to the island nation of Tonga in coastal thickets, edges of littoral forest, and disturbed areas from sea level to 7 m elevation. Figure 33.

Phenology.— Known to flower and fruit in January, February, October, and November.

Etymology.— The name of this species is literally the *Solanum* of friends. Presumably the epithet refers to the origin of the species in Tonga, the Friendly Islands.

Additional specimens examined. (fl, fr) *Foster s.n.* (BM). **TONGA**. cultur in hortis (fl), *Nelson s.n.* (BM); (fl, fr) *Vieillard 1855* (P); 1838–1842 *Wilkes* (GH). **Eua**: on the coast at Matalanga a Maui on the south end of the island, 5 Feb 1987 (fl, fr), *Whistler 5991* (K, US). **Niuatoputapu**: Funga'ana, 5 m, 14 Oct 1976 (fl, fr), *Kirch 302* (BISH). **Tafahi**: south end of the island, 18 Nov 1987 (fl), *Whistler 6217* (BM, US). **Tofua**: Hota'ane, at boulder beach, 24 Jun 1982 (fl, fr), *Buelow 2677* (US); Jan 1967 (fl, fr), *Scarth-Johnson 96* (K). **Tongatapu**: Liku, Tokomololo, 5–7 m, 31 Jan 1979 (fl, fr), *Buelow 1784* (BISH); Ha'atafu, sea level, 5 Nov 1958 (fl, fr), *Soakai 220* (A, K). **Vavau**: *s.c. s.n.* (P); Oct 1892 (fl, fr), *Crosby s.n.* (K); Vavau and Lifuka, Aug Oct 1855 (fl, fr), *Harvey s.n.* (GH, K, NY); (fl, fr), *Hombroon s.n.* (P, US).

Cultivated. USA. Hawaii: National Tropical Botanical Garden, 21 Apr 1989 (fl, fr), Accession No. 870074001-003 (From Tonga: Tongatapu, cliff top at Keleti Beach Resort, *Hume 388 Sd*) *Flynn 3340* (PTBG); National Tropical Botanical Garden, 16 May 1990 (fl, fr), Accession No. 870074001 (from Tonga: Tongatapu, Keleti, Feb 1987, *Hume s.n.*) *Hume 505* (PTBG).

Solanum amicorum is easily recognized by its large, deltate to ovate leaves with the pubescence of the veins on the abaxial leaf surface distinct from the pubescence of the rest of the

blade. It is most similar *S. sandwicense* but differs by its more compact inflorescence, longitudinally dehiscent anthers, and orange-red to red fruits.

Solanum artense Montr., Mem. Acad. Lyon 10: 245. 1860. France. New Caledonia. Île Art. No type designated. Type: France. New Caledonia, Île Art, bordure de piste en forêt, 150 m, 28 Feb 1978 (fl, fr), *McKee 34860* (Neotype, *hic designatus*: P 00299986!; Isoneotype: NOU 017064!)

Solanum styraciflorum Schlechter, Bot. Jahrb. Syst. 40 Beibl. 92: 34. 1908. Type: France. New Caledonia, Süd-Bezirk, Tchambonon unweit Voh, 50 m, Nov 1902, *Cribs 1244* (Holotype: B† “Herb. Noumeens”). No isotypes found. Neotype: Koumac, crête calcaire rocheuse au nord du ruisseau Grande Forêt, 250 m, 1 Jul 1972 (fl), *McKee 26004* (Neotype, *hic designatus*: P 00288473!; Isotypes: A!, L 0651813!, NOU 017105!).

Solanum linearisepalum Guillaumin, Bull. Mus. Hist. Nat. Paris, ser. 2, 16: 84. 1944. Type: France. New Caledonia Tanlé, 1867 (fl, fr) *Deplanche 77* [“Dupl. 483”] (Lectotype, *hic designatus*: P 00299989!)

Other syntypes: France. New Caledonia, Balade [specimen does not say Balade], Apr–May 1792 (fl), *Lahaie 1355* (P 00299959!); Tanlé, *Deplanche 483* [“423”] (P 00299984!, P 00299985!; L 3667!); Tanlé, *Vieillard 3038* (P!, L!); Tanlé, *Pancher 141* [also “V. no 3038”] (P 00299990!, P 00299991!); Tanlé, *s.c. s.n.* (K!).

Figure 7.

Unarmed erect shrub to ca. 1 m, the internodes to 4.7 cm long. Stems typically sparsely to densely pubescent with yellow-ferruginous, sessile or short-stipitate porrect stellae, occasionally nearly glabrous, the stipes of various lengths length to 0.08 mm long, the stellae soon or tardily deciduous, 0.3–0.9 mm broad, with 6–12 rays, the midpoint ciliate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays; bark reddish brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, the blades 3.1–13.7 \times 2.0–7.6 cm, ca. 1.4–3.0 times as long as wide, borne individually, ovate to oval, chartaceous, sparsely to densely pubescent along the midvein above with sessile and short-stipitate porrect stellae and minute glandular hairs when young, glabrous to densely pubescent along the midvein when mature, the stellae 0.3–0.6 mm in diameter, with 8–13 rays, the stipes to 1.2 mm long, the midpoint of the stellae erect, ciliate less than 90°, or flexed at the base $\pm 90^\circ$, shorter than, \pm equal to, or longer than the rays, the glandular hairs to 0.06 mm long, \pm glabrous to moderate pubescent below with sessile and short-stipitate porrect stellae and minute glandular hairs when young, \pm glabrous to sparsely pubescent when mature, the stellae 0.3–0.5 mm in diameter, with 7–8 rays, the stipes to 0.8 mm long, the midpoint of the stellae ciliate less than 90°, or flexed at the base $\pm 90^\circ$, shorter than, \pm equal to, or longer than the rays, the glandular hairs to 0.07 mm long; blade with 5–8 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly brochidodromous, raised abaxially, raised adaxially; blade base rounded, aequilateral or occasionally slightly oblique; margin entire; apex acute; petiole 0.6–2.8 cm long, 0.7–1.6 mm in diameter, channeled above, pubescence on the adaxial surface or all over. Inflorescence to 2.0 cm in flower, 1.9–2.9 cm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, unbranched (one specimen *McKee 4602* observed with a trifurcating inflorescence), with ca. 18 flowers, all apparently fertile or potentially so, the axes \pm glabrous to densely pubescent,

sessile and short-stipitate porrect-stellate; peduncle in flower 7.7–11.2(–19.0) mm long, 0.4–0.6(–0.9) mm in diameter, the branches not seen in flower, in fruit 9.5–14.2(–31.0) mm long, 0.7–1.8 mm in diameter, the branches to 2.9 cm long, ca. 0.9 mm in diameter; pedicels 0.8–1.5 cm long, 0.3–0.5 mm in diameter at the base, 0.7–1.4 mm in diameter below the calyx, straight, bent $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal $1/2$ – $2/3$, \pm glabrous to moderately pubescent, the bases congested, to 2.1 mm apart in flower, 1.3–1.8 cm long, 0.6–1.3 mm in diameter at the base, 2.1–3.7 mm in diameter below the calyx, straight or arching not bent below the calyx, gradually increasing in diameter in the distal $1/2$ – $2/3$, glabrous to moderately pubescent, the bases laxly spaced, to 2.5 apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx \pm glabrous to moderately stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.8–4.9 mm long, appearing nearly truncate with caudate lobe tips, the tube 0.8–1.2 mm long, the tips 1.1–3.7 mm long, the intersepal tissue translucent when dry; splitting in the sinuses during fruit development and then the lobes dentate, at anthesis \pm glabrous to moderately pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 2.5 – 3.8×2.1 – 3.3 mm, glabrous or sparsely pubescent, reflexed. Corolla 1.5–2.1 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes 5.1 – 6.6×3.6 – 4.6 mm, deltoid, the midrib 8.5 – 9.5×1.5 – 2.3 mm, oblong, densely pubescent abaxially, glabrous at the base becoming \pm densely stellate pubescent towards the apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.8–1.1 mm long; anthers 3.2 – 3.7×0.9 – 1.3 mm, acuminate, straight, markedly attenuate, yellow, connivent, with minute apical pores, the pores directed dorsally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 1.3 mm in diameter, ovate, densely pubescent with sessile porrect stellae; style 5.2–7.7 mm long, 0.3–0.5 mm in diameter, longer than

the stamens, emerging between the anther apices, filiform, straight, sparsely to moderately pubescent with sessile porrect stellae; stigma ca. 0.6 mm in diameter, capitate. Fruit a berry, 1.1–1.5 cm in diameter, globose, the immature fruits not seen, red when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 1.8–2.2 × 1.7–2.6 mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, yellow-tan when dry, the surface ±evenly cancellate over the entire surface.

Distribution and ecology.— Found from 10–250 m elevation on the Île of Art and the northern tip of the Grande Terre, New Caledonia, on calcareous substrates. Figure 37.

Phenology.— Known to flower January–April, July–December and fruit January–May, September, November–December.

Etymology.— This species was name for the Île of Art.

Additional specimens examined. **FRANCE. New Caledonia.** 1861–1867 (fl), *Vieillard s.n.* (G); 1868 (fl), *Vieillard s.n.* (G); 1861–1867 (fl, fr), *Vieillard 3036* (P). **North Province:** Île Art, 7 Apr 1874 (fr), *Balansa 3178* (P); Île Art, Dec 1978 (fl, fr), *Bourret 1870* (NOU); auf den Glügeln in Küstennähe, Paagoumene, 22 Mar 1925 (fl, fr), *Däniker 1485* (L, P); bei Friedhof von Paagoumene, 22 Mar 1925 (fl), *Däniker 1485a* (P); Tanlé, (fl, fr), *Deplanche 141* (P×2); Île Art, plateau Nord, bord de chemin, 10 Dec 1975 (fr), *Jaffre 1671* (NOU); Poum, 10 m, 20 May 1956 (fr), *McKee 4602* (K, P); Vallee de Koumac, 200 m, 2 Oct 1968 (fl), *McKee 19685* (K, L, NOU, P); Poum, Anse de Pouani, [ca. sea level], 5 Jan 1971 (fl, fr), *McKee 23149* (A, K, L, NOU, NSW, P); sud-est de la

Corne de Koumac, ca. 250 m, 10 Jul 1972 (fl), *McKee 25672* (A, K, L, NOU, P); Nord du Ruisseau Grand Forêt, 250 m, 1 Dec 1972 (fl), *McKee 26004* (A, K, NOU 017105, P); Île Mouac, 40 m, 15 [16 in NOU spec.] Feb 1977 (fl, fr), *McKee 32807* (L, MO, NOU, P); Gomen, Toela 400 m, 16 Jun 1979 (fr), *McKee 34993* (L); Île Art, 24 Aug 1978 (fl), *Morat 6153* (NOU, P); Poum, 13 Apr 2006 (fl, fr), *Munzinger & Rigault 3394* (NOU); Ouaieme, Nov 1973 (fl, fr), *Schmid 4879* (NOU, P); en haut des grotte de Koumac, 26 Sep 1978 (fl, fr), *Suprin 455* (NOU).

Solanum artense is most similar to *Solanum semisucculentum*, however the species differ in a number of ways. *Solanum artense* is sparsely to densely pubescent on the stems, along the midvein of the leaves adaxially, and sometimes the inflorescence; its leaves are chartaceous and typically have a greater leaf length to width ratio than *S. semisucculentum*. Also, *S. artense* is found below 250 m on calcareous soils while *S. semisucculentum* is typically found at high elevation on lateritic soils.

The syntypes of *S. linearisepalum* are variously and confusingly numbered with *Deplanche 77* apparently a duplicate of *Deplanche 483*. None of the Deplanche collections are numbered “423” as reported in the protologue. The lectotype was chosen as it a good quality specimen and had the clearest notation of collection and herbarium numbers.

***Solanum austro-caledonicum* Seem.**, J. Bot. 1: 209. 1863. Type: France. New Caledonia. Isle of Pines, Observatory [illegible] & main lanes, Oct. 1853 (fl, fr), [“*Milne s.n*”] *Milne 137* (Lectotype, *hic designatus*: K 000195698!; Isolectotypes: K 000195697!, K 000195696!)

Other syntypes: France. New Caledonia. Loyalty Islands, *G. Grey s.n.* (K-Hook.); France. New Caledonia, *E. Home s.n.* (BM 000846935!).

Solanum neocaledonicum Bitter & Schlechter, in Sarasin & Roux, Nova Caled. 1: 223. 1921.

Type: France. New Caledonia, Îlot Amédée, Jan 1903 (fl), *Le Rat 291* (Lectotype, *hic designatus*: P 00299967!; Isolectotypes: B†, P 00299968!).

Other syntypes: New Caledonia. *Le Rat 376A* (B†).

Solanum noumeanum Bitter, in Sarasin & Roux, Nova Caled. 1: 224. 1921. Type: France. New

Caledonia. Nouméa, bords de la mer, Jan 1905 (fl, fr), *Franc 682* (Holotype: B†; Lectotype, *hic designatus*: G 00035441!; Isotypes: A!, BM 000846932!, CAS!, K×2!, NY 00828278!, P 00288351!, P 00288352!, UC 390803!, US 1527491!).

Figure 8.

Unarmed shrub to 3.5 m, the internodes to 7.6 cm long. Stems densely pubescent with yellow-ferruginous, sessile or occasionally short-stipitate porrect stellae, stipes of various lengths to 0.2 mm long, the stellae soon or tardily deciduous, 0.3–0.5 mm broad, with 6–8 rays, the midpoint erect, much longer than the rays; bark gray-brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, 2.2–14.0 × 0.9–7.5 cm, 1.7–2.4 times as long as wide, borne individually, lanceolate to elliptic, chartaceous, occasionally sparsely pubescent, typically moderately to densely pubescent above with sessile or occasionally very short-stipitate porrect stellae and minute glandular hairs when young, sparsely to moderately pubescent when mature, the stellae 0.1–0.5 mm in diameter, with 4–8 (10) rays, the stipes to 0.06 mm long, the midpoint of the stellae erect, much longer than the rays, the glandular hairs ca. 0.04 mm long,

densely pubescent below with sessile and occasionally short-stipitate porrect stellae and minute glandular hairs when young, moderately to densely pubescent when mature, the stellae 0.2–0.4 mm in diameter, with 4–8 rays, the stipes to 0.08 mm long, the midpoint of the stellae \pm erect, much longer than the rays, the glandular hairs 0.04 mm long; blade with 5–7 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded to cuneate, aequilateral or oblique; margin entire or sinuate; apex acute to acuminate; petiole 0.4–2.4 cm long, 0.4–1.3 mm in diameter, channeled above, densely pubescent all over. Inflorescence to 8.4 cm in flower, to 6.8 cm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, unbranched or branching 1–3(–5) times, many-flowered with up to 56 flowers, all apparently fertile or potentially so, the axes densely pubescent, with sessile or occasionally short-stipitate porrect-stellae; peduncle in flower 7.8–26.9 mm long, 0.7–0.8 mm in diameter, the branches to 4.7 cm long, to 0.8 mm in diameter, in fruit 13.2–27.8 mm long, 0.9–1.5 mm in diameter, the branches to 5.0 cm long, to 1.0 mm in diameter; pedicels 0.6–2.0 cm long, 0.3–0.7 mm in diameter at the base, 0.7–1.6 mm in diameter below the calyx, straight, not bent below the calyx, gradually increasing in diameter in the distal ca. 1/3, densely pubescent, the bases \pm congested to ca. 4.0 mm apart in flower, observed as 1.0–1.9 cm (presumably as long as in flower) long, 0.6–0.9 mm in diameter at the base, 1.2–2.8 mm in diameter below the calyx, straight, not bent below the calyx, gradually increasing in diameter in the distal 1/3–2/3, moderately to densely pubescence, the bases \pm congested observed to ca. 2.9 mm apart in fruit (presumably as long as in flower), rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.8–4.2 mm long, appearing nearly truncate with apiculate lobe tips, the tube 1.8–2.3 mm long, the lobe tips 0.9–1.9

mm long, the intersepal tissue translucent when dry; splitting in the sinuses during fruit development and then the lobes dentate, densely pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 1.6–2.2 × 2.0–3.2 mm, moderately to densely pubescent, appressed. Corolla 1.3–2.2 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes 5.8–8.3 × 3.8–4.8 mm, deltoid, the midrib 7.7–9.2 × 1.8–2.2 mm, oblong, moderately to densely pubescent abaxially, glabrous at the base becoming sparsely to moderately pubescent to the apex adaxially, reflexed at anthesis especially the apices of the lobes. Stamens adnate to the corolla, the free portion of the filament ca. 1.0 mm long; anthers 3.5–4.5 × 1.1–1.4 mm, acuminate, straight, scarcely attenuate, yellow, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 0.6 mm, ovate, white or cream, glabrous; style 5.8–7.4 mm long, ca. 0.3 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, moderately to densely pubescent on the basal 1/2–2/3; stigma ca. 0.7 mm in diameter, capitate, green. Fruit a berry, 0.6–1.1 cm in diameter, globose, the immature fruits light green with darker green stripes, yellow or yellowish-green when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 1.6–1.9 × 1.8–2.3 mm, flattened-reniform or flattened-irregular, yellow-tan or red-brown when dry, the surface evenly alveolate all over.

Distribution and ecology.— Widespread particularly on the southern half of the Grande Terre, on small coastal islands, the Loyalty Islands, and Île des Pins, New Caledonia, typically near sea level but occurring up to 600 m elevation on calcareous and serpentine soils. Figure 38.

Phenology.— Flowering and fruiting year round.

Etymology.— The specific epithet refers New Caledonia as the Southern Scotland.

Additional specimens examined. MacGillivray s.n. (P). FRANCE. New Caledonia. 1868, (fl, fr), *Baudouin 260 (P×3); Blanchard s.n. (P);* 20 Oct 1950 (fl, fr), *Catala 7286 (P);* s.d. (fl, fr) *Caldwell (K); (fl, fr) Deplanche s.n. (W);* 1861 (fl, fr), *Deplanche 320 (P);* 1862 (fl, fr), *Deplanche 321 (K, P×3);* 1861 (fl, fr), *Deplanche 322 (P);* 1874–1876 (fl, fr), *Germain s.n. (A, K, L, P×2);* 1860 (fl), *Gillivray & Cuming s.n. (G); Pancher s.n. (A); Pancher s.n. (BM); (fl, fr) Pancher s.n. (K); Pancher s.n. (NY);* 1847 (fl, fr), *Védel s.n. (P×2). North Province: Koe,* 22 Feb 1881 (fl, fr), *Broucmiche 120 (P);* Canala, Dec 1808 (fl, fr), *Delacour 49 (K, L, P);* Mt. Koniambo, 21 Dec 1950 (fl), *Guillaumin & Baumann-Bodenheim 9454 (A, NY, US);* Mt. Koniambo, 400 m, 21 Dec 1950 (fr), *Guillaumin & Baumann-Bodenheim 9502 (A, G, MO, US);* Mt. Koniambo, 21 Dec 1950 (fr), *Guillaumin & Baumann-Bodenheim 9516 (A, NY);* Mt. Kaféaté, 22 Dec 1950 (fl), *Guillaumin & Baumann-Bodenheim 9699 (A, NY, P, RSA, US);* Mt. Kaféaté, 30 m, 22 Dec 1950 (fl, fr), *Guillaumin & Baumann-Bodenheim 9720 (G, K, MO, P, US);* Baie Naya, 24 Mar 1951 (fr), *Guillaumin & Baumann-Bodenheim 11497 (P, RSA);* Mt. Kaféaté, 10 Apr 1951 (fr), *Guillaumin & Baumann-Bodenheim 12052 (P, S, US);* Nékoru, 13 Mar 2007 (fl), *Hequet et al. 3619 (NOU);* Mgne. de Poum, 100–200 m, 20 May 1956 (fl), *McKee 4603 (K, L);* Mueo, 19 Jun 1968 (fl), *McKee 19024 (K, L, NOU, P);* Mt. Tiaoue, 200–400 m, 17 Sep 1968 (fl, fr), *MacKee 19551 (L×2);* Monéo, 5 m, 20 Jan 1970 (fl, fr), *McKee 21180 (K, P);* Oundjo, 26 Jan 1970 (fl, fr), *McKee 21477 (L, MO×2, NOU, P×2, US);* Tindo, 11 Oct 1966 (fl), *Nothis 293 (NOU, P);* Poya, Presqu'île de Pindai, 17 Jun 1997 (fl, fr), *Veillon 7976 (NOU);* Balade 1855–1860, (fl, fr) *Vieillard 1025 (P×5, G×2);* Gatope, 1861–67 (fl, fr), *Vieillard 3037 (GH, P×3). South Province: Île Nou,* Jan 1868 (fl,

fr), *s.c. 18* (K); Vallée du Dothio, Dec 1971 (fl), *Balansa 3528* (MO, P×2); Île Ndié, 24 Sep 1950 (fl), *Bass.-B. 6186* (G); Île Moro, 24 Sept 1950 (fr), *Baas.-B. 11147* (G, P); Île Moro, 24 Sep 1950 (fr), *Baas.-B. 11151* (G); Nouméa, Sep 1968, (fl, fr), *Balansa 488* (GH, P×3, W); Bourail, 7 Apr 1869 (fr), *Balansa 1345* (P×3); Vallée de Tontouta, rte le long de la rivière du Humboldt (près côte 20), *Blanchon 507* (P); la région de Nouméa, 11 Jun 1948 (fl, fr), *Barrau 14* (P); Île des Pins, Île Kouibandian, 25 May 1951, *Baumann-Bodenheim 13449* (P); Île des Pins, Anse Kaminéra, 27 May 1951 (fr), *Baumann-Bodenheim 13603* (NY, P); ÎlotSignal, Apr 1948 (fl), *Catala 1* (P); Nouméa, Port Despointes, 31 Jan 1914 (fl), *Compton 226* (BM); Mont Dore, 1 May 1914 (fr), *Compton 843* (BM); Goro, 150 m, Oct 1903, *Cribs 1714* (P); bei der Tontautafähre, 1 Nov 1924 (fl), *Däniker 420* (P); Île Nou, Jan 1868 (fl, fr), *Delacour 18* (P); Île Hugon, 19 May 1961 (fl, fr), *Denizot s.n.* (P); Île Hugon, 26 May 1961 (fl), *Denizot s.n.* (P); ÎlotSignal, 13 Aug 1961 (fl), *Denizot s.n.* (P); near the Kalouéhola River, about 15 km east of Tontouta, ca. 80 m, 15 Dec 1963 (fl, fr), *Green 1832* (A, K, NOU); Îlotde Freycinet, Aug 1884 (fl, fr), *Grunou s.n.* (W); Nouméa, ÎlotMaître, 23 Jan 1951 (fl), *Guillaumin & Hürlimann 695* (A, NY, P, RSA, US); Nouméa Ouen-Toro, 5–20 m, 14 Oct 1950 (fl), *Guillaumin & Baumann-Bodenheim 6834* (A, G, US); Prèsqu'île Ducos, 28 Feb 1951 (fl, fr), *Guillaumin 11049* (A, G, MO, NY); Île Page, 5 Mar 1951 (fl, fr), *Guillaumin & Baumann-Bodenheim 11073* (NY, P); Île Hugon, 5 Mar 1951 (fl, fr), *Guillaumin & Baumann-Bodenheim 11081* (A, P); Île Moro, 6 Mar 1951 (fr), *Guillaumin & Baumann-Bodenheim 11131* (P); Île Moro, 6 Mar 1951 (fl, fr), *Guillaumin & Baumann-Bodenheim 11147* (P); Île Moro, 6 Mar 1951 (fr), *Guillaumin & Baumann-Bodenheim 11152* (P); Île N'Ducé, 6 Mar 1951, *Guillaumin & Baumann-Bodenheim 11165* (P, US); ÎlotAmédée, Aug 1909 (fl, fr), *Le Rat 143* (P×3); Bourail [“Ourail”], Sep 1876 (fl, fr), *Lécard s.n.* (K); Prony, zone maritime, (fl, fr), *Le Rat 197* (P); Prony, bord de mer, (fl, fr), *Le Rat 341* (P); Isle of Pines, 1854 (fl), *McGillivray s.n.* (BM); Isle of Pines, Sep 1853 (fl),

MacGillivray 806 (K); Presqu'île de Uitoé, eastern end of the summit of the section hill from the souther tip of the peninsula, 22° 04' 47.5" S, 166° 08' 42.0" E, 75 m, 11 Jul 2009 (fl, fr),

McClelland & Nee 550 (A, BM, MO, NOU, NY, P, US, UT); Presqu'île de Uitoé, summit of the section hill from the souther tip of the peninsula, 22° 04' 46.5" S, 166° 08' 39.1" E, 85 m, 11 Jul 2009 (fl, fr), *McClelland & Nee 551* (BISH, BM, F, L, MO, NOU, NY, P, US); Île des Pins, by visitor parking lot for La Mériden, general area of la piscine naturelle, 22° 34' 52.8" S, 157° 31' 1.9" E, 8 m, 19 Jul 2009 (fl, fr), *McClelland & Nee 559* (BM, F, MPU, MO, NOU, NY, P, US); Île des Pins, along road to Baie d'Oro and la piscine naturelle at intersection of the road to Gîtes d'Oro Régis and La Mériden, 22° 34' 52.8" S, 157° 31' 1.9" E, 8 m, 19 Jul 2009 (fl, fr), *McClelland & Nee 560* (A, BISH, LY, MO, NOU, NY, P, UT) Nouméa, foot of Ouen-Toro, 13 Feb 1955 (fl, fr),

McKee 2112 (A, K, L, P, US); Upper Tontouta Valley, 500–600 m, 20 Nov 1955 (fl, fr), *McKee 3481* (A, L, P, UC, US); Dumbea, 17 Mar 1956 (fl), *McKee 4072* (P); Nouméa, Ouen-Toro, 10 m, 28 Apr 1956 (fl), *McKee 4470* (A, K, L, P); Thio, Bota Méré, ca. 60 m, 7 Dec 1965 (fl, fr), *McKee 14021* (K, L, NOU, P×2); Thio, Bota Méré, 60 m, 8 Aug 1966 (fl), *McKee 15473* (K, P); Vallée de Mamie, 0–20 m, 7 Oct 1966 (fl, fr), *McKee 15759* (A, K, L, NOU, P); Tontouta, 20–100m, 30 Jan 1967 (fl, fr), *McKee 16356* (K, L, NOU, P); Vallée de la Kalouehola, 60 m, 28 Oct 1967 (fl, fr),

McKee 17795 (K, L, NOU, NY, P); Île des Pins, plateau central, 100 m, 1 Apr 1971 (fl, fr), *McKee 23495* (NOU, P); Île des Pines plateau central, 100 m, 1 Apr 1971 (fl), *McKee 23498* (P); Bourail, Basse Barendeu, 100m, 23 Sep 1976 (fl, fr), *McKee 31994* (L, MO, NOU, P×2); ÎlotUa, 15 Oct 1979 (fr), *McKee 37465* (P); Nouméa, ÎlotMaître, 9 Aug 1982 (fl), *McKee 40672* (P); Tontouta, Uitoé, 60 m, 23 Apr 1986 (fl, fr), *McKee 43082* (L, NOU, P); Tontouta, Uitoé, 60 m, 23 Apr 1986 (fr), *McKee 43085* (NOU, P); Valley of the Tontouta, along riverside road, ca. 100 m, 3 Nov 1981 (fl, fr), *McPherson 4302* (MO, NOU, PTBG); Île Nou, Jan 1898 (fl, fr), *de Pompéry s.n.* (P);

ÎlotN'Da, 6 Jun 1974 (fl, fr), *Schmid 5054* (NOU); Îlot Améré, réserve intégrale, 20 Apr 1982 (fl, fr), *Suprin 1805* (NOU); Bourail, Le Cap, 12 Oct 1982 (fl, fr), *Suprin 2079* (NOU); Îlot Léprédour, 7 Feb 1886 (fl, fr), *Toutain s.n.* (NOU); Nouméa, ÎlotCanard, zone littorale, 25 May 1964 (fl), *Uhe 1098* (NOU); Nouméa, Ouen-Toro, vallée du Sud Ouest, ca. 100 m, 24 Mar 1967 (fr), *Veillon 1118* (NOU); Thio, Bota Méré, 12 Oct 1967 (fl), *Veillon 1415* (NOU, P); ÎlotKoutomo, 20 Jan 1971 (fl, fr), *Veillon 2247* (NOU, P); Îlot Améré, 10 Dec 1981 (fl, fr), *Veillon 4709* (NOU); Nouméa, ÎlotMaître, 16 Sep 1982 (fl, fr), *Veillon 5253* (NOU); Port de France [Nouméa], 1856 (fl, fr), *Vieillard 25* (P×6); Île Ngéa, partie sud-orientale, ca 20 m, 26 Dec 1941 (fl, fr), *Virots 568* (A, NOU, P); Nouméa, base du Ouen-Toro, ca. 15 m, 26 Nov 1942 (fl), *Virots 869* (A×2, MO); Île des Pins, Presqu'île de Kuto, ca. 5 m, 2 Mar 1943 (fl, fr), *Virots 1049* (NOU, P); Sentier du Dzumac, ca. 200 m, 8 Aug 1943 (fl, fr), *Virots 1215* (A, NOU); Île Ngéa, partie centrale, 31 Jan 1945 (fl), *Virots 1488* (A, K, L, MO×2, P); Nouméa, versants sud du Ouen-Toro [South slopes of Ouen-Toro], ca. 40 m, 4 Feb 1945 (fl), *Virots 1493* (P); Vallée de la Noubée, Route de Yaté, 25 Dec 1945 (fl, fr), *Virots 1549* (A, MO, P). **Loyalty Islands Province:** (fl), *Franc 1022* (UC) Lifou: Mou, 60 m, 21 Feb 1974 (fl, fr), *McKee 28261* (A, K, L, P 00288474, US 2996776); Maré, 1938–1939 (fl), *Leenhardt 476* (P); Île Maré, 1911–1912 (fl), *Sarasin 473* (P).

VANUATU. [“New Hebrides”], *s.c. s.n.* (W). **Anatom:** secteur de UMEC, Nov 1974 (fl), *Schmid 5149b* (P). **Erromango:** south Erromango, 22 Jun 1982 (fl, fr) *Cabalion 1744* (P).

Solanum austro-caledonicum is the most widespread and common species of section *Irenosolanum* in New Caledonia. Heine (1976) placed this species under synonymy with *S. tetrandrum* from Northern Australia. Symon (1985) agreed with Heine's (1976) treatment though he believed some subspeciation had likely occurred as some characters illustrated by Heine disagreed

with the Australian *S. tetrandrum* s.s. Symon (1985) dubbed what he believed to be a species complex involving *S. tetrandrum* s.s., *S. austro-caledonicum* as a few other species the “*S. tetrandrum* complex.” While there is a complex of similar species in the western Pacific corresponding to Symon's (1985) none are closely related to *S. tetrandrum* (see chapter 1). The complex is composed of *S. austro-caledonicum*, *S. inamoenum*, *S. vanuatuense*, and *S. milnei*. The morphological similarity of these species has confounded many workers. Careful, synchronous examination of a large quantity of herbarium specimens revealed the different taxa.

Like most Solanums, *Solanum austro-caledonicum* is morphologically plastic. It can be a short shrub or small tree depending on the local environment. The leaf size can vary greatly, and the inflorescence can be unbranched or branched several times. Before, the species was so well represented in the herbarium, some of these forms were named. Field observations were especially useful for understanding the morphological variation of herbarium specimens. Still, there are several unusual specimens which I place under *S. austro-caledonicum* with some hesitation. Some of these may represent distinct taxa, but more and higher quality collections are needed.

Unpublished name: Bitter annotated *Vieillard* s.n. (G 00035452) with an unpublished epithet “*stero-trichandrum*” under the species *S. neocaledonicum*.

***Solanum bauerianum* Endl.**, Prodr. Fl. Norf. 54. 1833. Type: Norfolk Island, Oct. (fl), *F. Bauer* s.n. (Holotype: W 0015500!; possible Isotype: K 000449108!)

Figure 9.

Unarmed shrub or small tree to 3 m, the internodes to ca. 4 cm long. Stems lacking stellate hairs, with yellow or yellow-ferruginous, minute, glandular hairs when young; bark reddish brown on mature stems, transparent sloughing layer lacking. Sympodia difoliate. Short shoots absent. Leaves simple, typically borne individually, occasionally geminate, 4.0–12.0 × 1.9–5.5 cm, 2–3 times as long as wide, lanceolate to oblong, chartaceous, the minor leaves when present \pm equal to major leaves, both major and minor leaves without stellate hairs, with minute glandular hairs above when young, glabrous when mature, the glandular hairs 0.03 mm long, with minute glandular hairs below when young, glabrous when mature, the glandular hairs 0.03 mm long; blade with 7–10 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly brochidodromous, raised abaxially, raised adaxially; blade base subacute to rounded, or shortly attenuate, aequilateral or oblique; margin entire, sinuate or with short lobes to 0.7 cm long, the apices of the lobes acute; apex subacute to acute; petiole 1.0–3.5 cm long, 1.0–1.6 mm in diameter, channeled above, glabrous. Inflorescence to 8.2 cm in flower, 2.2–6.3 cm in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode, branching up to 22 times, with many to ca. 55 flowers, all apparently fertile or potentially so, the axes glabrous when mature, when young with simple glandular hairs and minute; peduncle in flower 0.7–3.7 cm long, 0.8–1.7 mm in diameter, the branches to 4.8 cm long, to 1.3 mm in diameter, in fruit (0.3–)0.8–3.5 cm long, 1.0–1.5 mm in diameter, the branches to 4.7 cm long, to 1.7 mm in diameter; pedicels 1.1–1.4 cm long, ca. 0.3 mm in diameter at the base, 0.6–0.7 mm in diameter below the calyx, arching, gradually increasing in diameter in the distal 1/4–1/3, glabrous or with stellate pubescence, with sparse to moderate glandular pubescence when young, the hairs minute glandular and stipitate glandular hairs, the bases irregularly, and well spaced, to 5.0 mm apart in flower, 1.4–1.7 cm long, ca. 0.6 mm in diameter at

the base, 1.5–2.5 mm in diameter below the calyx, straight or slightly arching, very occasionally bent to 90° below the calyx, gradually increasing in diameter in the distal 1/3–1/2, glabrous, the bases well spaced to 6.0 mm apart, in fruit, rigid, in two rows though not always obviously so, articulate at the base. Flowers homostylous, 5-merous. Buds oval in outline, the apex flattened, the calyx sparsely to moderately glandular pubescent, the glandular hairs minute or stipitate, the corolla sparsely to moderately pubescent, stellate hairs lacking, with minute glandular hairs and simple hairs, the simple hairs flexed at the base and lying against the surface of the corolla, all directed distally, the surface of the corolla of the mature bud smooth. Calyx 1.5–2.0 mm long, appearing nearly truncate with apiculate lobe tips, the tube 0.8–1.1 mm long, the tips ca. 0.5 mm long, the intersepal tissue opaque when dry; splitting in the sinuses either at anthesis or during fruit development and then the lobes dentate, 0.3–0.6 × 0.4–1.2 mm at anthesis, becoming glabrous as the bud matures abaxially, glabrous adaxially, the calyx lobes in fruit 1.0–1.5 × 1.5–1.8 mm, glabrous, reflexed. Corolla 1.3–1.6 cm in diameter, rotate-stellate with well developed, glabrous interpetalar tissue, white, the lobes 1.3–3.7 × 4.9–5.8 mm, deltoid, the midrib 6.9–10.3 × 2.3–2.6 mm, oblong, nearly glabrous to sparsely pubescent abaxially with minute glandular hairs and simple, eglandular hairs, flexed near the base, glabrous adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 1.4–2.3 mm long; anthers 2.2–2.5 × 9.0–1.0 mm, acuminate, straight, scarcely attenuate, yellow, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 0.9 mm, ovate, pale yellowish green, with scattered simple glandular hairs; style 3.0–4.5 mm long, ca. 0.3 mm in diameter, ±equal to the stamens, emerging between the anther apices, filiform, ±straight, glabrous; stigma ca. 0.5 mm in diameter, capitate, green. Fruit a berry, 0.6–1.0 cm in diameter, globose to ovate, red when mature, glabrous; exocarp thin, glossy;

endocarp apparently juicy. Seeds many per fruit, 2.6–2.9 × 2.2–2.8 mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, yellow-tan or red-brown when dry, the surface the central portion ±smooth, the margin scrobiculate.

Distribution and ecology.— Known only from Lord Howe Island and Norfolk Island, this species is now extinct on both islands. Green (1994) cited *Boorman s.n.* (NSW not seen by me) which indicated the species occurred “near Ned's Beach in rocky formation of land overlooking the ocean” at ±sea level. Based on this locality, *S. bauerianum* likely grew on on calcareous substrate. Figure 33.

Phenology.— Known to flower January and November and fruit January, April, and November.

Etymology.— This species was named to honor Ferdinand Bauer (1760–1826), the Austrian botanical illustrator.

Additional specimens examined. **AUSTRALIA. New South Wales:** Lord Howe Island (fl, fr) *s.c.* 58 (MEL), Lord Howe Island, (fl, fr), *Fullagar s.n.* (MEL possible dupl. of *Fullagar & Lind 66*) Lord Howe Island, (fl, fr), *Fullagar & Lind 66* (MEL×4); Lord Howe Island, Apr 1893 (fr), *Maiden s.n.* (NSW); Lord Howe Island, Jan 1937 (fl, fr), *McComish 142* (NSW); Lord Howe Island, Nov 1913 (fl, fr), *Oliver s.n.* (NSW). **Territory of Norfolk Island:** (fl), *s.c. s.n.* (W); (fl), *Caley s.n.* (G, W).

It is rare for a plant species to be known to be extinct. Unfortunately, *S. bauerianum* holds this dubious distinction and is one of only two species of plants from Lord Howe Island to have become extinct (Auld & Hutton, 2004; Hutton *et al.*, 2007). *Solanum bauerianum* was last collected on Lord Howe Island in 1937 and on Norfolk Island in 1830 (Green, 1994). The likely cause of the extinction of *S. bauerianum* on Lord Howe Island was the introduction of rats in 1918 from the vessel “Makambo” (Auld & Hutton, 2004; Paramonov, 1960). Rats are seed predators and have heavily impacted species in *Solanum* section *Irenosolanum* on other islands, most notably the Hawaiian Islands.

A reconstructed painting of *S. bauerianum* was published by Mabblerly *et al.* (2007). By decoding Bauer's color coding scheme, the appropriate colors could be filled into Bauer's unfinished illustration of *S. bauerianum*. For the description presented here, the reconstructed painting was used to determine several color characters not noted on specimen labels, i.e. petal color, stigma color, and fruit color.

Solanum bauerianum is one of only two species in section *Irenosolanum* to have been extensively used by people. On Lord Howe Island, the common name for the species was “bridal flower” (Green, 1994) or “wedding flower” (Rodd & Pickard, 1893); the showy inflorescences were used by the islanders as bridal bouquets. Besides its anthropological interest, *S. bauerianum* is notable because of its lack of stellate hairs. This species is one of two in section *Irenosolanum* that lack stellate hairs the other being *S. nudatum*. While *S. nudatum* bears no hairs, *S. bauerianum* has simple hairs, flexed at the base and directed distally on the corolla abaxially as well as the typical minute glandular hairs of section *Irenosolanum* on the stems, leaves, inflorescence, and flowers. The simple nonglandular hairs are likely reduced stellate hairs and are unique in section *Irenosolanum*.

Solanum bauerianum resembles *S. viride* superficially. However, *S. bauerianum* can be differentiated easily by its showy inflorescences and unusual pubescence on the abaxial surface of the corolla.

***Solanum camptostylum* Bitter**, in Sarasin & Roux, Nova Caled. 1: 221. 1921. Type: France. New Caledonia. Mt. Kanala, ca. 600 m, 11 Jan 1912 (fl), *Sarasin 392* (Lectotype, designated by Heine, 1976: BAS; Isolectotype: P 00298943!).

Figure 10.

Erect or scandent shrub or small tree to 4 m, the internodes to 8.5 cm long. Stems scarcely to moderately pubescent with yellow-ferruginous, sessile porrect stellae, the stellae soon deciduous, 0.3–0.4 mm broad, with 8 rays, the midpoint ciliate less than 90° to flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, \pm equal to the rays; bark reddish brown, a transparent sloughing layer absent on young stems; stems unarmed or with scattered prickles, the prickles to 2.0×4.0 mm, broad based, broadly triangular, retrorse, yellow-ferruginous. Sympodia difoliate. Short shoots present. Leaves simple, borne individually, $2.7\text{--}5.7 \times 1.3\text{--}2.5$ cm, 2–3 times as long as wide, lanceolate to oval, chartaceous to subcoriaceous, moderately to densely pubescent above with sessile porrect stellae and minute glandular hairs when young, \pm glabrous when mature, the stellae 0.2–0.3 mm in diameter, with 4–8 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, longer than the rays, the glandular hairs ca. 0.05 mm long, densely pubescent below with sessile porrect stellae and minute glandular hairs when

young, \pm glabrous when mature, the stellae 0.2–0.3 mm in diameter, with 4–8 rays, the midpoint of the stellae curved to flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, longer than the rays, the glandular hairs ca. 0.04 mm long; blade unarmed or occasionally with 1–3 retrorse prickles on the primary vein abaxially, with 4–7 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded, aequilateral or sometimes oblique; margin entire to slightly sinuate; apex acute; petiole 0.6–1.9 cm long, 0.4–0.6 mm in diameter, channeled above, sparsely to densely pubescent, unarmed or occasionally with broad-based, retrorse prickles. Inflorescence to 3.8 cm in flower, to 6.4 cm in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode, unbranched or branching up to 3 times, with up to ca. 35 flowers, all apparently fertile or potentially so, the axes sparsely to densely pubescent becoming \pm glabrous, the hairs sessile porrect-stellate, unarmed; peduncle in flower (0–)2.5–11.0 mm long, 0.6–1.0 mm in diameter, the branches to 3.0 cm long, 0.4–0.7 mm in diameter, in fruit 0.9–2.0 cm long, 1.0–2.0 mm in diameter, the branches to 3.4 cm long, to 1.7 mm in diameter; pedicels 1.0–1.5 cm long, 0.3–0.5 mm in diameter at the base, 1.1–1.3 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal ca. 1/3, nearly glabrous to \pm dense on the proximal 2/3 and sparsely pubescent on the distal 1/3, the bases well spaced to ca. 5.0 mm apart in flower, 1.3–1.8 cm long, 0.5–0.7 mm in diameter at the base, 0.8–1.8 mm in diameter below the calyx, straight, swelling evenly from the base to the base of the calyx or the distal 1/3 portion gradually swelling to the base of the calyx, nearly glabrous to \pm dense on the proximal 2/3s and sparsely pubescent on the distal 1/3, the bases well spaced to 10.8 mm apart, in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx sparsely stellate-pubescent, the corolla moderately stellate-pubescent, the surface of the corolla

of the mature bud smooth. Calyx 1.5–1.9 mm long, unarmed, distinctly lobed, the tube 0.8–1.1 mm long, the lobes deltoid, 0.9–1.3 × 1.3–1.6 mm long, the intersepal tissue opaque when dry; at anthesis sparsely pubescent abaxially, glabrous adaxially; splitting in the sinuses during fruit development, the calyx lobes in fruit 1.5–2.2 × 1.4–2.2 mm, dentate, ±glabrous, appressed or reflexed. Corolla 1.7–1.9 cm in diameter, stellate with well developed, glabrous interpetalar tissue, white, the lobes 4.6–6.0 × 7.0–8.9 mm, deltoid, the midrib 8.3–10.9 × 2.9–4.0 mm, lanceolate, moderately pubescent abaxially, ±glabrous adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 1.2–1.6 mm long; anthers 3.8–4.9 × 1.2–1.7 mm, acuminate, somewhat incurved, markedly attenuate, yellow, connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary 0.9–1.2 mm, ovate, with ±glabrous to moderately pubescent; style 7.8–11.0 mm long, ca. 0.3 mm in diameter, longer than the stamens, deflexed and emerging between the sides of two adjacent stamens, filiform, sigmoid, sparsely pubescent, the hairs simple glandular, restricted to the basal 1/4–1/3 portion; stigma 0.5–0.8 mm in diameter, capitate. Fruit a berry, 0.6–1.3 cm in diameter, globose, orange when mature, glabrous; exocarp thin, glossy; apparently juicy. Seeds many per fruit, 2.1–2.9 × 2.8–3.1 mm, flattened-reniform to flattened-orbicular and notched at the point of attachment, yellow-tan when dry, the surface alveolate.

Distribution and ecology.— In humid forest from 500–850 m elevation on the Grande Terre of New Caledonia. Figure 36.

Phenology.— Known to flower November–February and fruit February–June and September.

Etymology.— The name of this species refers to bent, i.e. sigmoid, style of this species.

Additional specimens examined. **FRANCE. New Caledonia.** Mt. Rembai, 700 m, 31 May 1990 (fr), *McKee 44914* (NOU); Mt. Rembai region above Col d'Amieu, ca. 650 m, 6 Jun 1983 (fr), *McPherson 5720* (K, NOU, NSW, PTBG); Along road from Cascade de Ciu (south of Canala) toward Koindé and La Foa, ca. 750 m, 9 Dec. 1983 (fl), *McPherson 6108* (MO, NOU, NSW, PTBG). **North Province:** Aoupinié, 165° 17' 12" E, 21° 10' 38" S, 900 m, 18 Feb 2007 (fl, fr), *Fambart-Tinel 122* (NOU); Mt. Koniambo, about 400 m, 5 May 1961 (fl), *McKee 7968* (K, L×2, P×2, US); Haute Neaoua, Ouen Sieu, 500–600 m, 12 Feb 1970 (fr), *McKee 21602* (P×3, NOU); Ponérihouen, Pente est du Mt. Aoupinie, Exploitation forestière Devillers, 500 m, 27 Apr 1972 (fr), *McKee 25398* (A, K×2, L, NOU, NSW, P, US); Ponérihouen, Pente est du Mt. Aoupinie, Exploitation forestière Devillers, 500–700 m, 7 Nov 1972 (fl), *McKee 25796* (A, K, L, NOU, NSW, P); Ouen Sieu, 600 m, 27 Feb 1978 (fl, fr), *McKee 34768* (L, MO, NOU, NSW, P); Aoupinié, 15 Jan 2004 (fl), *Munzinger 1956* (NOU); Mt. Aoupinié above Poya, 700 m, 9 Mar 1984 (fr), *McPherson 6381* (K, MO, NOU, PTBG); Massif de l'Aoupinié, 850 m, 2 Sep 1981 (fr), *Suprin 1343* (NOU, NY); Gatope, Montagne de Temala, 1861–1867 (fl, fr), *Vieillard 3039* (P×3). **South Province:** Route de la Ouenghi, 1000 m, 16 Dec 1970 (fl), *Jaffré 432* (NOU); Ridge north of Upper Poueo Valley, 17 km to the east of Col des Roussettes, 500 m, 27 Dec 1962 (fl), *McKee 9859* (NSW, P).

This species is part of a group of native New Caledonian *Solanums* with relatively small leaves and short shoots which typically bear the inflorescences. *Solanum camptostylum* is most similar to *S. actephilum*, but differs in a number of ways. See the discussion of *S. actephilum*.

***Solanum caumii* (F. B. H. Brown) D. McClell. comb. et stat. nov.**

Basionym: *Solanum nelsonii* Dunal var. *caumii* F. B. H. Brown, in Christophersen & Caum, Bull. Bish. Mus. 81: 36, pl. 15B. 1931. U.S.A., Hawaiian Islands, Leeward Islands, Nihoa, 75 m, 19 Jun 1923 (fl, fr), *E. Caum* 84 (Holotype: BISH 581193!; Isotypes: BISH 581194!, K!, NY 00172288!, UC 505079!).

Solanum nelsonii Dunal var. *acuminatum* F. B. H. Brown, in Christophersen & Caum, Bull. Bish. Mus. 81: 36, pl. 16A. 1931. Type: U.S.A., Hawaiian Islands, Leeward Islands, Nihoa, 75 m, 19 Jun 1923 (fl, fr), *E. Caum* 68 (Holotype: BISH 581186!; Isotypes: BISH 581185!, K!, NY 00172287!).

Figure 11.

Unarmed, sprawling shrub to ca. 1.5 m, the internodes to 6.6 cm long. Stems densely pubescent with yellow-ferruginous, short-stipitate porrect stellae, stipes of various lengths to ca. 0.1 mm, the stellae tardily deciduous, 0.3–0.4 mm broad, with 6–10 rays, the midpoint ±erect, shorter than the rays; bark reddish brown, a transparent sloughing layer absent on young stems.

Sympodia difoliate. Short shoots absent. Leaves simple, geminate or borne individually, the blades of major leaves 3.5–8.0 × 2.2–6.4 cm, 1.3–1.6 times as long as wide, deltoid to ovate,

chartaceous, the minor leaves when present $\frac{2}{3}$ as large to \pm equal to the major leaves, both major and minor leaves densely pubescent above with short-stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.2–0.4 mm in diameter, with 6–9 rays, the stipes to ca. 0.1 mm long, the midpoint of the stellae \pm erect, much shorter than the rays, densely pubescent below with short-stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.4–0.5 mm in diameter, with 7–9 rays, the stipes to ca. 0.1 mm long, the midpoint of the stellae \pm erect, much shorter than the rays; blade with 4–6 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous or semicraspedodromous, raised abaxially, distinct adaxially; blade base cordate, truncate, or rounded, \pm aequilateral; margin entire or with short lobes; apex acute to acuminate; petiole 0.8–3.3 cm long, 1.0–1.4 mm in diameter, channeled above, densely pubescent all over. Inflorescence to 8.1 cm in flower, to 4.2 cm long in fruit, appearing lateral, extra-axillary, emerging from the upper $\frac{1}{3}$ of the internode, typically unbranched occasionally forked, with 10–16 flowers, all apparently fertile or potentially so, the axes densely pubescent, with short-stipitate porrect-stellate; peduncle in flower 5.4–17.7 mm long, 0.9–1.3 mm in diameter, the branches when present to 2.3 cm long, ca. 0.8 mm in diameter, in fruit 11.1–21.2 mm long, 1.1–1.3 mm in diameter, the branches not seen; pedicels 0.9–1.2 cm long, 0.3–0.6 mm in diameter at the base, 0.5–0.9 mm in diameter below the calyx, straight, to $\pm 90^\circ$ below the calyx, not significantly increasing in diameter distally, densely pubescent, the bases well spaced to 8.8 mm apart in flower, 1.1–1.9 cm long, 0.9–1.1 mm in diameter at the base, 2.1–2.3 mm in diameter below the calyx, straight, not bent below the calyx, gradually increasing in diameter in the distal $\frac{1}{3}$ – $\frac{1}{4}$, moderately to densely pubescent, the bases well spaced to 9.2 mm apart in fruit, limp, in two rows, articulate at the base. Flowers heterostylous, 4–5-merous. Buds globose,

the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud ridged. Calyx 3.1–4.9 mm long, appearing nearly truncate with deltoid lobe tips, the tube 1.7–1.8 mm long, the lobe tips $1.1\text{--}3.5 \times 1.2\text{--}2.1$ mm, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, densely pubescent abaxially, densely pubescent adaxially, the calyx lobes in fruit $3.4\text{--}6.3 \times 1.8\text{--}2.5$ mm, moderately to densely pubescent, appressed. Corolla 1.3–2.0 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the veins purple, the lobes $5.1\text{--}5.7 \times 7.2\text{--}7.4$ mm, deltoid, the midrib $8.8\text{--}10.3 \times 3.7\text{--}4.5$ mm, oval, moderately pubescent abaxially, \pm glabrous adaxially, spread at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 1.5 mm long; anthers $2.9\text{--}3.2 \times 0.8\text{--}0.9$ mm, acuminate, arcuate, markedly attenuate, purple sometimes appearing almost black, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 0.8 mm, ovate, white or cream, densely pubescent; short styles 2.1–2.5 mm long, 0.1–0.2 mm in diameter, shorter than the stamens, not emerging from between the anthers, long styles ca. 3.8 mm long, ca. 0.4 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, densely stellate pubescent on the basal 2/3; stigma ca. 0.3 mm in diameter, capitate, white or cream. Fruit a berry, 1.0–1.5 cm in diameter, globose, the immature fruits evenly green, red or black when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, $2.8\text{--}3.5 \times 3.5\text{--}4.1$ mm, flattened-reniform, red-brown when dry, the surface evenly reticulate over the entire surface.

Distribution and ecology.— Restricted to the island of Nihoa in shallow rocky soil from 10–270 m elevation. Figure 34.

Phenology.— Known to flower March–April and June–September and fruit March and June–July.

Etymology.— The varietal name elevated here was given to honor Edward Leonard Caum (1893–1952), an American botanist who collected the type.

Additional specimens examined. **USA. Hawaiian Islands. Nihoa:** 13 Jun 1923 (fl), *Bryan 3* (BISH); 19 Jun 1923 (fl, fr), *Caum 68* (BISH, K, NY); 19 Jun 1923 (fl, fr), *Caum 84* (BISH, K, NY, UC); Miller Valley, 22 Apr 1983 (fl), *Conant 102* (BISH); base of Miller Valley, ca. 30 ft, 26 Aug 1968 (fl), *Herbst 1210* (BISH, US); Middle Valley, ca. 500 ft, 27 Jul 1980 (fl, fr), *Herbst & Takeuchi 6544* (US); East Palm Valley, ca. 300 ft, 27 Jul 1980 (fl, fr), *Herbst & Takeuchi 6555* (BISH; US); (fr), *Judd s.n.* (K); Rocky Gulch, 100 m, 20 Jun 1923 (fr), *Judd 6* (BISH); Rocky Gulch, 100 m, 20 Jun 1923 (fr), *Judd 7* (BISH); Rocky Gulch, 100 m, 20 Jun 1923 (fl), *Judd 8* (BISH); lower slopes above the east cove, 23 Sep 1964 (fl), *Long 2424* (US); top of Millers Peak in crevice at top of “Devil's Slide”, north side of peak, 24 Sep 1964 (fl), *Long 2434* (US); lower slopes west valley near water-course, ca. 350 ft, 24 Sep 1964 (fl), *Long 2439* (US); near helicopter landing, 6 Mar 1964 (fl, fr), *Munro s.n.* (BISH); Kawaewae, 75 ft, 12 Aug 1947 (fl), *St. John 22731* (K, PTBG, RSA, US).

Cultivated. USA. Hawaiian Islands. Kauai: National Tropical Botanical Garden McBryde Garden, plant propagation range, 19 Apr 2008 (fl), *McClelland 452* (BISH, NY, PTBG).

This species had been recognized as a taxonomic entity by previous workers. Brown (1931) recognized it as two varieties of *S. nelsonii*. St. John (1988b) placed *S. nelsonii* var. *acuminatum* under synonymy with *S. nelsonii* var. *caumii*. *Solanum caumii* is most similar to *S. nelsonii*; however it can be distinguished by its semi-erect habit, larger leaf length to width ratio, and sometimes red fruit, and it remains distinct when grown in a common garden alongside *S. nelsonii*. In 2008, pot grown individuals from Molokai were observed next to pot grown individuals from Nihoa. Under identical growing conditions the species maintained their distinct forms. This material was made available through the conservation program at the National Tropical Botanical Garden by Drs. David and Lida Burney and their staff.

Endemism on the small island of Nihoa is not without precedent. There are three other species of endemic plants and the entire island was designated critical habitat for them (Mitchell *et al.*, 2005). The island also hosts two endemic birds, at least seventeen endemic arthropods, and six endemic land snails (Mitchell *et al.*, 2005). Recognition of *S. caumii* at the species level has conservation consequences. Wagner *et al.* (1999) included *S. caumii* within *S. nelsonii*. At that time *S. nelsonii* was listed as vulnerable. Due to the small size of the island of Nihoa, *Solanum caumii* is certainly endangered, and the segregation of the species may change the status of *S. nelsonii*. Threats to *S. caumii* include habitat destruction from natural causes and herbivory by an introduced grasshopper (Mitchell *et al.*, 2005).

***Solanum guamense* Merrill**, Philipp. J. Sci., Bot. 9: 139. 1914. Type: U.S.A., Marianas Islands, Guam, Cabras Island, s.d. (fl) *Guam Experiment Station 446* (Lectotype, *hic designatus*: US 902498!; Isolectotypes: K 000195710!, P 00316599!).

Solanum saipanense Bitter, Bot. Jahrb. Syst. 56: 559. 1921. Type: Marianas Islands, Saipan, Feb, *Hofer 14* (Not traced, likely B†). [Placed under synonymy of *S. guamense* by Bitter (1922b).]

Figure 12.

Unarmed shrub or small tree to 1(–3) m, the internodes to 12.5 cm long. Stems densely pubescent with yellow to yellow-ferruginous, sessile or short-stipitate porrect stellae, the stipes to 0.17 mm long, the stellae tardily glabrescent, 0.3–0.6 mm broad, with 6–10 rays, the midpoint erect to clinate less than 90°, shorter than the rays. Sympodia difoliate. Leaves simple, geminate or borne individually on fast growth, the blades of major leaves 8.3–18.0 × 3.9–12.2 cm, as wide as long to 2.1 times as long as wide, deltate to ovate, chartaceous, the minor leaves 1/4–3/4 as large as the major leaves, both major and minor leaves densely pubescent above with short-stipitate porrect stellae and minute glandular hairs when young, moderately pubescent when mature, the stellae 0.3–0.5 mm in diameter, with 4–11 rays, the stipes to 0.08 mm long, the midpoint of the stellae erect to clinate less than 90°, shorter than to ±equal to the rays, the glandular hairs ca. 0.4 mm long, very densely pubescent below with short-stipitate porrect stellae, densely pubescent when mature, the stellae 0.3–0.6 mm in diameter, with 4–8 rays, the stipes to 0.13 mm long, the midpoint of the stellae erect or curved, ±equal to the rays; blade with 4–6 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded to cuneate, aequilateral or oblique; margin entire to sinuate or lobed; apex acute; petiole 1.2–6.3 cm long, 1.0–2.0 mm in diameter, channeled above, densely pubescent with yellow to yellow-

ferruginous short-stipitate porrect stellae. Inflorescence to 2.7 cm long in flower, to 5.0 cm long in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode, branched 1–3 times, with up to 95 flowers, all apparently fertile or potentially so, the axes densely pubescent, with yellow to yellow-ferruginous, short-stipitate porrect stellae; peduncle in flower 2.3–5.1 cm long, 0.7–0.8 mm in diameter, the branches to 1.5 cm long, ca. 0.7 mm in diameter, in fruit 0.3–3.9 cm long, 0.8–1.3 mm in diameter, the branches to 2.8 cm long, 0.6–0.7 mm in diameter; pedicels 0.5–1.3 cm long, ca. 0.4 mm in diameter at the base, 0.8–1.0 mm in diameter below the calyx, straight, evenly increasing from the base to below the calyx, densely pubescent, the bases congested, overlapping to 1.7 mm apart in flower, 1.0–1.6 cm long, 0.4–0.8 mm in diameter at the base, 1.2–1.7 mm in diameter below the calyx, straight evenly increasing from the base to below the calyx, the bases congested, overlapping to 1.8 mm apart, in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.9–2.2 mm long, the tube 1.2–1.7 mm long, appearing nearly truncate with apiculate or occasionally caudate lobe tips, 0.2–0.6(–1.6) mm long, the intersepal tissue opaque when dry; splitting in the sinuses either at anthesis and continuing to split during fruit development and then the lobes dentate, 0.9–1.3 × 1.3–1.6 mm at anthesis, densely, stellate pubescent abaxially, glabrous or with a few stellae adaxially, the calyx lobes in fruit 1.5–3.4 × 1.3–2.0 mm, densely pubescent abaxially, appressed to the fruit. Corolla 1.1–1.6 cm in diameter, stellate with poorly-developed, glabrous interpetalar tissue, white, the lobes 5.1–6.2 × 2.2–2.9 mm, oblong, the midrib 5.7–7.7 × 1.7–2.5 mm, lanceolate, moderately pubescent abaxially, nearly glabrous with a few stellae towards the apex adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.5–1.0 mm long; anthers 2.3–2.5

× 0.8–1.0 mm, oblong, straight, yellow, spreading, with minute apical pores, the pores directed upright, restricted to the apex, the lateral sutures entire. Ovary ca. 0.8 mm, globose, glabrous or with few simple glandular hairs apically; style 5.8–6.6 mm long, ca. 0.2 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, typically curved or hooked towards the apex, sparsely pubescent with simple glandular and eglandular hairs and sessile, porrect stellae; stigma ca. 0.3 mm in diameter, discoid. Fruit a berry, 0.3–0.6 cm in diameter, globose, red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds few per fruit, 1.6–1.8 × 1.8–2.2 mm, flattened-orbicular and notched at the point of attachment, yellow-tan when dry, the surface ±smooth, the very edge scrobiculate.

Distribution and ecology.— This species is restricted to the Marianas Islands where it can be found between 2–320 m elevation. This species is disjunct from the rest of section *Irenosolanum* the nearest species geographically being in Vanuatu, a distance of about 4000 km. No explanation readily presents itself to explain this phenomenon other than long distance dispersal by some unknown bird. Figure 33.

Phenology.— Known to flower February–March and July–November and fruit March and July–November.

Etymology.— This species is named after the Island of Guam in the Mariana Islands.

Additional specimens examined. *Gaudichud s.n.* (P×2) **USA. Guam:** Ritidian Point Light, 185m, 1 Sep 1949 (fl, fr), *Anderson 102* (UC, US); Tarague Beach, west end, near caves, where cliffs come

close to water's edge, 2–3 m, 14 Oct 1949 (fl, fr), *Anderson 233* (NY, POM, US); 17 Nov 1913 (fr), *Guam Experiment Station 138* (K); Jul 1916 (fl, fr), *Guerrero 739* (BISH, P); Ritidian Pt., 400 ft, 1 Jul 1946 (fl, fr), *Hosaka 3108* (L, NY, US); 1 mile east of Barrigada area, 400–600 ft, 25 Nov 1945 (fl fr), *Moore 51* (MICH, UC, US); Guae, 13°28'N 144°51'E, 14 Aug 1954 (fl, fr), *Moran 4613* (BISH, K, MICH, MO, POM, UC, US); 1919 (fl, fl), *Nelson 385* (BISH, F, GH, NY, US); Andersen Air force Base, Late Point to Pati Point, 420 ft, 5 Jul 1994 (fl, fr), *Perlman & Wood 14284* (BISH, PTBG, US); Road to Piti Point, North of North West Field, 500 ft, 7 Nov 1945 (fl, fr), *Steere 166* (US); Ypan Point, 22 Jul 1962 (fl, fr), *Stone 4299* (L, US); Andersen Air force Base, between Pati and Late Point, 300–550 ft, 5 Jul 1994 (fl), *Wood & Perlman 3329* (MO, PTBG)

COMMONWEALTH OF THE NORTHERN MARIANA ISLANDS. Guguan:

Southwest coast at beginning of southwest ravine, ca. 7 m, 11 Jul 1975 (fl, fr), *Falanruw 3104* (NY, POM, US). **Maug:** mid west island, 100 ft, 24 Nov 1977 (fl, fr), *Moore 799* (US). **Rota:** 320 m, 25–27 Feb 1950 (fl), *Fosberg 31856* (L, NY, POM, US); 1932 (fl, fr), *Kanehira 1832* (NY). **Saipan:** Kagman Point (Puntan Hagman) east coast of island, 150 m, 1 Mar 1950 (fl, fr), *Fosberg 31933* (L, NY, POM, US). **Tinian:** Ponape, 3 Jul 1934 (fl, fr), *Hosokawa 7713* (BISH, MICH, US); Ponape, 1925 (fl), *Kariyone 30* (UC).

Morphologically, *S. guamense* is similar to *S. sandwicense* and *S. amicum*. It can easily be distinguished from *S. sandwicense* by its totally white corollas, straight anthers with restricted pores, and small fruit. From *S. amicum* it can be distinguished by its poricidal dehiscence, small, black fruits and the distinctive pubescence of veins of the abaxial surface of the leaves of *S. amicum*.

Solanum hillebrandii H. St. John, Pacific Sci. 23: 352, fig. 2. 1969. Type: U.S.A. Hawaiian

Islands, Hawaii, Kohala Range and base of Mauna Kea, 5000 ft, s.d. (fl, fr) *W. Hillebrand 116* (Holotype: K!; Isotype: BISH!).

Solanum incompletum Dunal var. *glabratum* Hillebr., Fl. Hawaiian Isl. 306. 1888. *Solanum globosum* H. St. John, Phytologia 64: 169. 1988. Type: U.S.A., Hawaiian Islands, Lanai, *W. Hillebrand & J. M. Lydgate s.n.* (Lectotype, designated by St. John, 1988b: BISH 70006!; Isolectotypes: K [not found], US 809480!).

Other syntype: East Maui, Hamakua, *Lydgate s.n.* was not traced.

Solanum incompletum Dunal var. *mauiense* Hillebr., Fl. Hawaiian Isl. 305. 1888. *Solanum semilobatum* H. St. John, Phytologia 64: 171. 1988. Type: U.S.A., Hawaiian Islands, Maui, Ulupalakua, *W. Hillebrand s.n.* (Lectotype, *hic designatus*: US 809481 [barcode 00027617]!; Isotypes: GH!, K 000449109!, MEL 1520575!).

Solanum haleakalaense H. St. John, Pacific Sci. 23: 350, fig. 1. 1969. Type: U.S.A., Hawaiian Islands, East Maui, S side of Haleakala, *W. Hillebrand 113* (Holotype: K 000449110!; Isotype: BM 000846688!).

Solanum forbesii H. St. John, Phytologia 64: 169. 1988. Type: U.S.A., Hawaiian Islands, Maui Island, Kipahulu, *C. N. Forbes 1647.M* (Lectotype, *hic designatus*: BISH 70000!; Isotypes: BISH 644749!, K!, NY 00759140!).

Solanum lanaiense H. St. John, Phytologia 64: 170. 1988; Native Hawaiian species of *Solanum*, Hawaiian Plant Studies 82. Jun 1988. *Solanum popolo* H. St. John, Phytologia 64: 171. Jan. 1988. Type: U.S.A., Hawaiian Islands, Lanai Island, *W. Hillebrand s.n.* (Holotype: US 809480 [barcode 00288742]!; Isotype: BM 000846690!).

Solanum lydgatei H. St. John, *Phytologia* 64: 170. Jan 1988. Type: U.S.A., Hawaiian Islands
[“Sandwich Islands”], *Menzies s.n.* (Holotype: BM 000846698!). [St. John (1988b)
incorrectly cited the holotype.]

Solanum nesophilum H. St. John, *Phytologia* 64: 170. 1988. Type: U.S.A., Hawaiian Islands,
Maui Island, *H. Mann & W. T. Brigham 458* (Holotype: BH; Isotypes: BISH 614817!, GH!,
L 0651873!, NY 00759138!). [St. John (1988b) incorrectly cited the holotype.]

Solanum pubinervosum H. St. John, *Phytologia* 64: 171. 1988. Type: U.S.A., Hawaiian Islands,
Lanai Island, Kaiholea Valley, *C. N. Forbes 12.L* (Holotype: BISH 70002!; Isotypes: K!,
MO 818975!).

Solanum tonsum H. St. John, *Phytologia* 64: 171. Jan. Type: U.S.A., Hawaiian Islands, west
Maui Island, *H. Mann & W. T. Brigham 457* (Holotype: BISH 70001!; Isotypes: BH!, GH!,
NY 0079139!).

Figure 13.

Shrub, the internodes to 4.3 cm long. Stems densely pubescent with yellow-ferruginous, sessile or stipitate porrect stellae, stipes of various lengths to 0.13 mm, the stellae soon deciduous, 0.4–0.6 mm broad, with 5–8 rays, the midpoint flexed at the base $\pm 90^\circ$, shorter than to \pm equal to than the rays; bark reddish brown, a transparent sloughing layer absent on young stems; stems unarmed or with scattered prickles, the prickles to 5.4×4.2 mm, broad based, narrowly triangular, straight, red-orange. Sympodia difoliate. Short shoots absent. Leaves simple, geminate, the blades of major leaves $5.2\text{--}17.8 \times 2.5\text{--}11.2$ cm, ca. 1.5–2.4 times as long as wide, ovate to elliptic, chartaceous, the minor leaves ca. $2/3$ as large as the major leaves, both major

and minor leaves moderately pubescent above with sessile and short stipitate porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.3–0.6 mm in diameter, with 5–8 rays, the stipes to 0.06 mm long, the midpoint of the stellae flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs ca. 0.5 mm long, densely pubescent below with sessile and short stipitate porrect stellae and minute glandular hairs when young, glabrous to densely pubescent when mature, the stellae 0.3–0.5 mm in diameter, with 5–9 rays, the stipes to 0.04 long, the midpoint of the stellae erect to flexed at the base $\pm 90^\circ$, shorter than the rays, the glandular hairs ca. 0.4 mm long; blade unarmed or with a few scattered, straight prickles on the primary or primary and secondary veins abaxially and adaxially, with 7–11 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded to cunate, aequilateral or oblique; margin entire, sinuate, or lobed, the lobe apices acute; apex acute; petiole 1.0–5.5 cm long, 0.7–2.3 mm in diameter, channeled above, densely pubescent when young, the hairs becoming sparse with age, unarmed or with scattered straight prickles. Inflorescence to 9.8 cm in flower, to 9.1 cm in fruit, appearing lateral, extra-axillary, emerging from an upper internodal position, branching to 5 times, with 8–120 flowers, all apparently fertile or potentially so, the axes densely pubescent becoming glabrous, the hairs sessile and stipitate porrect-stellate and minute glandular, unarmed or with scattered straight, broad-based prickles; peduncle in flower 0.7–2.3 cm long, 0.4–0.9 mm in diameter, the branches to 7.0 cm long, 0.5–1.1 mm in diameter, in fruit 1.5–2.1 cm long, 2.0–3.9 mm in diameter, the branches to 4.4 cm long, 0.8–2.5 mm in diameter; pedicels 1.1–1.4 cm long, 0.4–0.7 mm in diameter at the base, 1.3–2.0 mm in diameter below the calyx, arching, gradually increasing in diameter in the distal 1/4–1/3, glabrous to densely pubescent, the bases well spaced to 5.0 mm apart in flower, 1.6–2.5 cm long, 0.7–1.0

mm in diameter at the base, 2.2–2.8 mm in diameter below the calyx, gradually increasing, gradually increasing in diameter in the distal 1/3–1/2, glabrous, the bases well spaced to 7.0 mm apart, in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 5-merous. Buds globose, the calyx glabrous or densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud ridged. Calyx 1.7–2.7 mm long, unarmed, appearing nearly truncate with apiculate lobe tips, the tube 1.4–2.4 mm long, the lobe tips 0.4–0.5 mm long, the intersepal tissue translucent when dry; splitting in the sinuses at anthesis and then the lobes dentate, 1.1–1.7 × 1.6–2.3 mm at anthesis, glabrous to densely pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 3.4–3.6 × 2.2–2.6 mm, glabrous, appressed or reflexed. Corolla 1.2–2.0 cm in diameter, stellate with well developed, glabrous interpetalar tissue, the lobes 3.1–3.8 × 4.0–5.4 mm, deltoid, the midrib 6.0–6.6 × 2.4–3.2 mm, lanceolate, moderately to densely pubescent abaxially, glabrous at the base scattered pubescent towards the apex adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.5–1.3 mm long; anthers 2.2–2.9 × 1.2–1.5 mm, oblong, somewhat incurved, not attenuate, spreading, longitudinally dehiscent, the slit extending 1/2–2/3 the length of the anther. Ovary ca. 1.3 mm, globose, glabrous; short styles 1.2–1.7 mm, long styles ca. 3.8 mm long, both long and short styles 0.2–0.3 mm in diameter, the short styles shorter than the stamens not emerging, the long styles longer than the stamens emerging between the anther apices, filiform, straight, with a few sessile porrect-stellate hairs restricted to the basal ca. 1/3 portion; stigma 0.3–0.4 mm in diameter, capitate. Fruit a berry, 0.9–1.9 cm in diameter, globose, probably orange to red when mature, glabrous; exocarp thin, glossy; apparently juicy. Seeds many per fruit, 2.8–3.0 × 3.2–3.8 mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, yellow-tan when dry, the surface reticulate.

Distribution and ecology.— *Solanum hillebrandii* likely grew in dry habitats on the islands of Lanai and Maui, but the exact conditions and elevation are unknown due to the minimal label information of the collections. Figure 35.

Phenology.— Known to flower and fruit January, March, June, September, and November. Likely this species flowers and fruits year round.

Etymology.— This species was named to honor William Hillebrand (1821–1886) a German physician who studied the native flora during his twenty year stay in Hawaii.

Additional specimens examined. **USA. Hawaiian Islands.** (fr) *Hillebrand s.n.* (BM); Sandwich Island *Menzies s.n.* (BM), 1851–1855 (fl), *Rémy 448* (P×2). **Lanai:** Kaiholena Valley, Jun 1913 (fl, fr), *Forbes 12.L* (BISH, K, MO); (fl, fr) *Hillebrand s.n.* (BM); (fl, fr), *Hillebrand s.n.* (GH); (fl), *Hillebrand & Lydegate s.n.* (BISH) 22 Sep 1916 (fr), *Hitchcock 14704* (US); Kaiholena 19 Jan 1915 (fl, fr), *Munro s.n.* (BM, BISH); Kaiholena, 30 Mar 1919 (fl, fr), *Munro 322* (BISH). **Maui:** Ridge right side Kipahulu, 20 Nov 1919 (fl, fr), *Forbes 1697.M.* (BISH×2, K, NY); (fl, fr) *ex herb. Hillebrand* (US); Maui (fl), *Hillebrand s.n.* (MEL); east Maui (fl, fr), *Hillebrand s.n.* (GH, K); east Maui, Haleakala South, Sep 1870 (fl, fr), *Hillebrand s.n.* (BM); west Maui (fl, fr), *Mann & Brigham 457* (BH, BISH, NY, GH); 1851–1855 (fl), *Rémy s.n.* (P); 1851–1855 (fl, fr), *Rémy 447* (P); 1851–1855 (fl, fr), *Rémy 449* (P×2).

All eleven of the specific level names for this species were published by Harold St. John. It was recognized as two varieties of *S. incompletum* by Hillebrand (1888). There are differences among the specimens some corresponding with Hillebrand's varieties, but intermediate forms exist. St. John (1969) elevated these two varieties to species, *S. hillebrandii* and *S. haleakalaense*. Since both names were published at the same time, either name could be used for the single taxon. I chose to use *S. hillebrandii* for two reasons: first, to honor William Hillebrand for his major contribution to Hawaiian botany; second, since the species was not restricted to Mount Halaekala. With some reservations, I include *S. nesophilum* within *S. hillebrandii*. St. John (1988) named *S. nesophilum* from a single specimen and although it differs from other specimens of *S. hillebrandii* in a number of ways, most notably the density of its pubescence, the wide range of variation in *S. hillebrandii* makes me inclined to consider it an aberrant individual. Unfortunately, *S. hillebrandii* is likely extinct. It was last collected in 1919, and though not exhaustive, a week of focused searching by me on the islands of Lanai and Maui in 2008 failed to turn up any specimens.

The nomenclature of this species is complex due to the many superfluous names proposed by St. John (1988a). Of special note, St. John (1988a) named both *Solanum lanaiense* and *S. popolo* from the same specimen at US; he listed no isotypes for either name. St. John (1988b) listed an isotype of *S. lanaiense* at BM and his illustration indicated as “from holotype” is unquestionably of the specimen at BM; however, the holotype was designated as the US specimen by St. John (1988a) and therefore must be used.

Solanum hugonis **H. Heine**, Fl. N. Caled. & Depend. 7: 170, pl. 39. 1976. Type: France. New Caledonia, Pouembout, 30 m, 15 Feb 1972 (fl, fr), *MacKee 25016* (Lectotype, *hic designatus*: P 00300157!; Isotypes: A 00077586!, K!, L 0003635!, NOU 006614!, NSW 594207!, P 00300158!, P 00300159!).

Figure 14.

Shrub to 2 m, the internodes to ca. 4 cm long. Stems sparsely to moderately pubescent with yellow, sessile and short stipitate porrect stellae, stipes of various lengths to 0.2 mm long, the stellae soon deciduous, 0.5–0.8 mm broad, with 4–6 rays, the midpoint erect to flexed at the base $\pm 90^\circ$, \pm equal to the rays; bark reddish brown, a transparent layer sloughing off young stems; stems with scattered prickles, the prickles to 2.5×4.6 mm, broad based, deltate to broadly triangular, retrorse, yellow-ferruginous. Sympodia difoliate. Short shoots present. Leaves simple, the blades $1.4\text{--}4.4 \times 0.9\text{--}1.1$ cm, 1.5–4 times as long as wide, borne individually, lanceolate, elliptic, or ovate, sub-coriaceous, leaves moderately pubescent above with short stipitate porrect stellae and minute glandular hairs when young, sparsely pubescent when mature, the stellae 0.5–0.9 mm in diameter, with 4(–10) rays, the stipes to 0.1 mm long, the midpoint of the stellae erect or occasionally clinate to $\pm 45^\circ$, \pm equal to the rays, the glandular hairs ca. 0.04 mm long, moderately pubescent below with short stipitate porrect stellae and minute glandular hairs when young, sparsely pubescent when mature, the stellae 0.5–0.9 mm in diameter, with 4(–10) rays, the stipes to 0.1 mm long, the midpoint of the stellae erect or occasionally clinate to $\pm 45^\circ$, \pm equal to the rays, the glandular hairs ca. 0.04 mm long; blade unarmed, with 4–7 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins strongly brochidodromous, raised abaxially, distinct adaxially; blade base

typically rounded, occasionally sub-cordate or truncate, aequilateral or oblique; margin entire to slightly sinuate; apex obtuse; petiole 2.0–11.0 mm long, 0.3–0.5 mm in diameter, channeled above, sparsely to moderately pubescent, unarmed or with scattered, straight, broad-based prickles. Inflorescence 1.1–1.6 cm in flower, 1.4–2.3 cm in fruit, appearing terminal on short shoots, unbranched, with 3–6 flowers, all apparently fertile or potentially so, the axes sparsely pubescent, the hairs sessile and stipitate porrect-stellate and minute glandular, unarmed; peduncle in flower 4.6–7.0 mm long, ca. 0.3 mm in diameter, in fruit 7.7–9.2 mm long, ca. 0.5 mm in diameter; pedicels 1.0–1.5 cm long, 0.2–0.4 mm in diameter at the base, 0.4–0.5 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal 1/2–1/3, sparsely pubescent, the bases well spaced to 3.4 mm apart in flower, 1.3–1.6 cm long, 0.3–0.4 mm in diameter at the base, 1.0–1.3 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal 1/2–1/3, sparsely pubescent, the bases well spaced to 4.8 mm apart, in fruit, probably rigid, in two rows, articulate at the base. Flowers, 5-merous. Buds ovate, the calyx sparsely to moderately stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 3.3–4.9 mm long, unarmed, distinctly lobed with spatulate lobe tips, the tube ca. 0.9 mm long, the lobe tips $2.2\text{--}4.0 \times 0.6\text{--}1.3$ mm, the intersepal tissue opaque when dry; not splitting or splitting in the sinuses during fruit development, sparsely pubescent abaxially, sparsely pubescent adaxially, the calyx lobes in fruit $1.5\text{--}2.4 \times 5.5\text{--}6.6$ mm, sparsely pubescent, appressed. Corolla ca. 1.8 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white, the lobes ca. 7.2×2.3 mm, oblong, the midrib ca. 9.0×2.3 mm, oblong, densely pubescent abaxially, glabrous at the base scattered pubescent towards the apex adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 1.2 mm long; anthers ca. 3.8×2.5 mm, acuminate, somewhat incurved, markedly attenuate, yellow, apparently connivent, with minute

apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures entire or perforated, not splitting with age. Ovary not seen; style ca. 10.0 mm long, ca. 0.3 mm in diameter, longer than the stamens, deflexed and emerging between the sides of two adjacent stamens, filiform, sigmoid, glabrous; stigma 0.4 mm in diameter, slightly bilobed but nearly capitate. Fruit a berry, 0.5–0.6 cm in diameter, globose, orange-red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds ca. 27 per fruit, 1.8–2.0 × 2.1–2.3 mm, flattened-orbicular to suborbicular and notched at the point of attachment, yellow-tan when dry, the surface alveolate or scrobiculate.

Distribution and ecology.— This species is only known from the type locality in the vicinity of Pouembout at ca. 30 m on the Grande Terre, New Caledonia. It is likely that this species is highly geographically restricted like *S. insulae-pinorum* rather than simply under collected.

Figure 36.

Phenology.— Known to flower February, April, and October and fruit February, but likely fertile year round.

Etymology.— This species was named to honor Hugh S. MacKee (1912–1995), a prolific plant collector in New Caledonia.

Additional specimens examined. **FRANCE. New Caledonia. North Province:** Pouembout, 30 m, 16 Apr 1972 (fl), *MacKee 25305* (K, P 00300160); Pouembout, ca. 30 m, 10 Oct 1995 (fl), *Veillon 7843* (NOU 016998, P 00070161).

Solanum hugonis is most similar to *S. vaccinioides* but is easily distinguished by the leaf shape and texture and by its spatulate calyx lobes which are unique within section *Irenosolanum*. Few collections of this species have been made as it is only known from the type locality. Jaffré *et al.* (1998) listed *S. hugonis* as critically endangered because of its highly restricted distribution. The species is part of a group of native New Caledonian Solanums with relatively small leaves and short shoots which typically bear the inflorescences.

***Solanum inamoenum* Benth.**, in Hook. Lond. J. Bot. 2: 228. 1843. Type: Fiji, 1841 (fl), *R. Hinds s.n.* (Holotype: K 000195699!; Isotype: BM).

Figure 15.

Unarmed shrub, the internodes to 5.6 cm long. Stems densely pubescent with yellow to yellow-ferruginous, sessile or short-stipitate porrect stellae, stipes of various lengths to 0.06 mm long, the stellae soon deciduous, 0.4–0.7 mm broad, with 6–9 rays, the midpoint clinate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to than the rays; bark reddish brown, a transparent sloughing layer absent on the young stems. Sympodia difolate. Short shoots absent. Leaves simple, geminate, the blades of major leaves 6.4–19.8 \times 3.6–8.1 cm, ca. 1.8–2.4 times as long as wide, lanceolate to ovate, chartaceous, the minor leaves ca. 2/3 to as large as the major leaves, both major and minor leaves densely pubescent above with sessile porrect stellae and minute glandular hairs when young, \pm glabrous when mature, the stellae 0.4–0.5 mm in diameter,

with 4–8 rays, the midpoint of the stellae erect to flexed at the base $\pm 90^\circ$, \pm equal to to longer than the rays, the glandular hairs to 0.6 mm long, densely pubescent below with sessile porrect stellae when young, moderately pubescent when mature, the stellae 0.4–0.6 mm in diameter, with 4–8 rays, the midpoint of the stellae erect, \pm equal to the rays; blade with 6–10 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded, cuneate, or shortly attenuate, aequilateral or oblique; margin entire to wave, or occasionally lobed in juvenile growth, the apices of the lobes acute; apex acuminate; petiole 1.0–4.1 cm long, 0.7–1.7 mm in diameter, channeled above, densely pubescence. Inflorescence to 3.1 cm in flower, to 4.9 cm long in fruit, appearing lateral, extra-axillary, in the upper 1/3 of the internode, unbranched or branching to as many as 4 times, with up to ca. 50 flowers, all apparently fertile or potentially so, the axes densely pubescent, the hairs sessile porrect-stellate; peduncle in flower 0.8–1.9 cm long, 1.1–1.2 mm in diameter, the branches to 2.3 cm long, ca. 0.6 mm in diameter, in fruit 0.8–2.9 cm long, ca. 1.2 mm in diameter, the branches not seen in fruit; pedicels 0.7–0.8 cm long, 0.4–0.6 mm in diameter at the base, 0.8–2.0 mm in diameter below the calyx, straight, scarcely swelling or the distal 1/3–1/2 portion gradually swelling to the base of the calyx, densely pubescent, the bases congested to ca. 0.7 mm apart in flower, ca. 1.4 cm long, 0.8–1.2 mm in diameter at the base, 3.1–3.8 mm in diameter below the calyx, arching, gradually increasing in diameter in the distal 1/3–1/2, sparsely pubescent, the bases congested to 2.0 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 5-merous. Buds globose, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.7–2.1 mm long, appearing nearly truncate with apiculate lobe tips, the tube 1.1–1.4 mm long, the lobe tips 0.3–0.8 mm long, the intersepal tissue opaque when dry;

densely pubescent abaxially, glabrous adaxially, splitting in the sinuses during fruit development and then the lobes dentate, the calyx lobes in fruit $1.6\text{--}2.7 \times 1.4\text{--}2.3$ mm, densely pubescent, reflexed. Corolla $1.1\text{--}1.5$ cm in diameter, stellate poorly developed, glabrous interpetalar tissue, probably white, the lobes $3.8\text{--}4.6 \times 3.7\text{--}4.0$ mm, deltoid, the midrib $5.5\text{--}6.6 \times 2.4\text{--}2.7$ mm, elliptic, densely pubescent abaxially, glabrous adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament $1.1\text{--}1.2$ mm long; anthers $2.2\text{--}2.8 \times 0.9\text{--}1.2$ mm, oblong, somewhat incurved, not attenuate, probably yellow, spreading, with minute apical pores, the pores directed adaxially, extending around the edge of the apex, the lateral sutures entire, remaining intact with age. Ovary $0.7\text{--}0.8$ mm, globose, sparsely pubescent with sessile pectinate stellae and minute glandular hairs; short styles ca. 0.9 mm long, long styles ca. 3.8 mm long, both short and long styles ca. 0.2 mm in diameter, short styles shorter than the stamens, long styles longer than the stamens, short styles not emerging from the stamens, long styles emerging between the anther apices, filiform, straight, glabrous; stigma 0.4 mm in diameter, capitate. Fruit a berry, $1.3\text{--}1.6$ cm in diameter, globose, color unknown, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds many per fruit, ca. 2.8×2.8 mm, flattened-orbicular and notched at the point of attachment, brown when dry, the central area nearly smooth, the margin alveolate.

Distribution and ecology.— The habitat in which this species occurs is unknown due to the minimal label information provided on the herbarium specimens. Likely it occurred at low elevations near the coast as it was collected mainly on smaller islands and the interiors of the large islands remained relatively unexplored until the late nineteenth century due to the ferocity of the native Fijians. Figure 41.

Phenology.— Known to flower June and September–November and fruit March and October–November.

Etymology.— Literally, this species is named the unpleasant *Solanum*. But, what Bentham found unpleasant about this species will likely remain unknown as he published no indication.

Additional specimens examined. **FIJI**. 1877–1878 (fl, fr), *Horne s.n.* (K, GH); Nairia, Nov 1855 (fl), *Milne 151* (K); 1860 (fl), *Seemann 343* (BM, G, GH, K, P, W); 1860 (fl), *Seemann 345* (BM, K); 1838–1842 (fl), *Wilkes s.n.* (GH, K, NY, P). **Kanacea**: [“Kanathia”] Mar 1880 (fr), *Graeffe 1481* (K, HAM). **Matuku**: [“Matuaku”] 5 Oct 1855, *Milne 373* (K) **Ngau**: [“Angua”] 5 Sep 1855 (fl), *Milne 161* (K). **Nukuloa**: [“Nukalua”] 30 May – 14 Jun 1840 (fl), *Barclay 3446* (BM, P). **Ovalau**: [“Balaou”] (fl) *Hombron s.n.* (P); Levuka [“Lavouka”] (fl, fr) *Jacquinot s.n.* (P); [“Balaou”] 1838–1840 (fl), *Le Guillou 12* (P); Oct 1854 (fl), *McGillivray s.n.* (BM); 1856 (fl), *Vieillard s.n.* (P); Oct 1855 (fl, fr), *Vieillard 27* (P). **Totoya**: Aug 1855 (fl, fr), *Milne 81* (K). **Viwa**: Nov 1855 (fl, fr), *Harvey 472* (BM, GH, K).

This species has not been collected since 1880. Modern collections often determined as this species are actually *S. pseudopedunculatum*. Smith (1991) misapplied the name *S. inamoenum* to *S. pseudopedunculatum*. However, the two species are not particularly similar, the species differing notably in density of leaf pubescence and inflorescence structure. Considerable confusion has surrounded the distinctiveness of *S. inamoenum* from *S. austro-caledonicum* from New Caledonia and *S. tetrandrum* from Australia. While *S. austro-caledonicum*, *S. inamoenum*,

S. milnei, and *S. vanuatuense* form a species complex, none are closely related to *S. tetrandrum*. See the discussion of *S. austro-caledonicum* for a discussion of this complex.

***Solanum incompletum* Dunal**, in DC., Prodr. 13(1): 311. 1852. *pro syn. Solanum sandwichianum*

Dunal, in DC., Prodr. 13(1): 311. 1852. Type: Hawaiian Islands, s.d., *D. Nelson s.n.*

(Holotype: BM-Banks 000846689!).

Figure 16.

Shrub to ca. 1.5 m, the internodes to ca. 12.0 cm long. Stems densely pubescent with yellow-ferruginous or ferruginous, sessile and short stipitate porrect stellae, the stipes to 0.13 mm, the stellae tardily deciduous, 0.2–0.6 mm broad, with 6–8 rays, the midpoint erect to flexed at the base $\pm 90^\circ$, \pm equal to the rays; bark reddish brown, a transparent sloughing layer absent on young stems; stems unarmed or with scattered prickles, the prickles to 5.7×2.3 mm, broad based, narrowly triangular, straight, red-orange. Sympodia difoliate. Short shoots absent. Leaves simple, geminate or borne individually, the blades of major leaves $5.1\text{--}15.4 \times 2.3\text{--}6.8$ cm, 1.5–2.4 times as long as wide, ovate to oblong, chartaceous to subcoriaceous, the minor leaves 1/2 as large to \pm equal to the major leaves, both major and minor leaves densely pubescent above with sessile and short stipitate porrect stellae and minute glandular hairs when young, glabrous or sparsely pubescent when mature, the stellae 0.3–0.6 mm in diameter, with 4–8 rays, the stipes to 0.01 mm long, the midpoint of the stellae erect, slightly shorter than the rays, the glandular hairs to 0.06 mm long, densely pubescent below with sessile and short stipitate porrect stellae and minute

glandular hairs when young, moderately to densely pubescent when mature, the stellae 0.3–0.6 mm in diameter, with 4–8 rays, the stipes to 0.08 mm long, the midpoint of the stellae \pm erect, slightly shorter than the rays, the glandular hairs to 0.4 mm long; blade unarmed or with few to many straight prickles on the primary vein or on the primary and secondary veins abaxially and adaxially, with 5–9 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins craspedodromous or semicraspedodromous, raised abaxially, distinct adaxially; blade base rounded to cuneate, aequilateral or oblique; margin sinuate or lobed, the apices of the lobes rounded; apex subacute to acute; petiole 1.4–4.7 mm long, 0.9–1.5 mm in diameter, channeled above, densely pubescent, unarmed or with scattered straight prickles. Inflorescence 1.1–7.7 cm in flower and fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, unbranched or branching to 4 times, with up to ca. 90 flowers, all apparently fertile or potentially so, the axes densely pubescent, the hairs sessile porrect-stellate, unarmed or occasionally with scattered prickles; peduncle in flower 6.5–16.0 mm long, 0.6–1.0 mm in diameter, the branches to 4.3 cm long, to 0.6 mm in diameter, in fruit 2.6–3.7 cm long, 0.6–2.2 mm in diameter, the branches with fruits and flowers to 6.3 cm long, to 1.4 mm in diameter; pedicels 7.0–1.4 cm long, 0.4–0.6 mm in diameter at the base, 0.9–1.3 mm in diameter below the calyx, straight, bent to $\pm 90^\circ$ below the calyx, increasing in diameter in the distal immediately below the calyx, densely pubescent, the bases congested to somewhat well spaced to 2.6 mm apart in flower, 1.0–2.1 cm long, 0.6–0.9 mm in diameter at the base, 1.5–3.1 mm in diameter below the calyx, straight, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal 1/3–1/2, moderately to densely pubescent, the bases well spaced to 5.2 mm apart, in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 5-merous. Buds globose, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface

of the corolla of the mature bud ridged. Calyx 2.2–3.1 mm long, unarmed or occasionally with several, straight prickles, appearing nearly truncate with deltoid lobe tips, the tube 1.4–1.5 mm long, the lobe tips 0.8–1.5 × 0.6–1.3 mm, the intersepal tissue opaque when dry; splitting in the sinuses at anthesis and then the lobes dentate, 1.9–2.6 × 1.2–1.9 mm at anthesis, densely pubescent abaxially, glabrous or sparsely pubescent adaxially, the calyx lobes in fruit 2.6–4.8 × 1.9–3.2 mm, moderately to densely pubescent, appressed or reflexed,. Corolla 1.4–1.9 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white or white with purple veins, the lobes 5.2–6.3 × 3.2–6.2 mm, triangular to deltate, the midrib 6.9–9.2 × 3.1–4.0 mm, lanceolate, densely pubescent abaxially, glabrous at the base, scattered pubescence towards the apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.8–1.2 mm long; anthers 1.8–2.3 × 1.0–1.2 mm, oblong, somewhat incurved, not attenuate, yellow, spreading, with minute apical pores, the pores directed slightly adaxially, extending around the edge of the apex, the lateral sutures perforated remaining intact or splitting with age. Ovary ca. 1.0 mm in diameter, globose, green, glabrous or densely pubescent at the apes with sessile porrect stellae and minute glandular hairs; short styles ca. 1.0 mm long, long styles ca. 4.9 mm long, ca. 0.2 mm in diameter, short styles shorter than the stamens, not emerging from the stamens, long styles longer than the stamens, emerging between the anther apices, filiform, straight, glabrous or moderately pubescent with sessile porrect stellae, the hairs when present restricted to the basal 2/3 portion; stigma ca. 0.6 mm in diameter, capitate, green. Fruit a berry, 0.8–1.4 cm in diameter, globose, the immature fruits evenly green, red to orange when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 2.5–2.9 × 3.5–3.8 mm, flattened-reniform, red-brown when dry, the surface the central portion lightly pitted, the margin alveolate.

Distribution and ecology.— On the island of Hawaii, on old lava flows or old cinder cones in dry shrubby or forested habitats from 1000–2000 m elevation. Figure 35.

Phenology.— Known to flower February, March, June, and August and fruit March and August.

Etymology.— Dunal (1952) named this species from the sterile, and thus incomplete, material collected by David Nelson on Captain Cook's third voyage.

Additional specimens examined. **U.S.A. Hawaiian Islands.** (fl, fr) *sin nom* (P); (fl), *Hillebrand 112* (K); (fl, fr), *Hillebrand 114* (GH, K); 1838–1842 (fl, fr) *Wilkes s.n.* (GH, NY). **Hawaii:** Puu Huluhulu, near Saddle Road, 20 Aug 1949 (fl, fr), *Degener & Greenwell 19980* (A, B, BH, BISH, BRI, G, K, MO, NY, NSW, US); Puuwaawaa, 8–14 Jun 1911 (fl), *Forbes 38H* (BH, CAS, P, UC, US); Puuwaawaa, 17 Jun 1911 (fl, fr), *Forbes 189H* (A, BH, CAS, K, UC, M, NY, P, US); Kona, Kanehaha [Kanahaha], 23 Jun 1911 (fl), *Forbes 239H* (K, MO, NY); Omaokaili, 17 Jun 1915 (fl), *Forbes 876H* (BISH, K, UC, NY, P, US); N. Kona, Puuwaawaa, Mar 1912 (fl, fr), *Rock 10047a* (A, BH, BISH, K, UC, GH, M, NY, P, US); edge of the path to Kiholo, Jan 1851–1855 (fl, fr), *Rémy 451* (GH, L, P×3); N. Kona, Puuwaawaa, Mt. Hualalai, Mar 1912 (fl, fr), *Rock 10047* (GH); Mauna Loa, Puuoaikaaka crater, 13 Feb 1912 (fl), *Rock 10047* (GH, NY); 1838–1842 (fr), *Wilkes* (GH).

Cultivated. **U.S.A. Hawaiian Islands. Kauai:** National Tropical Botanical Garden McBryde Garden, plant propagation range, living collection accession no. 070386, 19 Apr 2008, *McClelland 451* (BISH, NY, PTBG).

Once thought to be extinct this species persists on the United States Army Pōhakuloa Training Area. Several conservation measures have been taken since the discovery of living material, including *ex situ* conservation and fencing of *in situ* individuals. Threats to this species include seed predation by rats, herbivory by feral goats, and destruction from military training (VanderWerf & Young, 2008). This is the only species of section *Irenosolanum* with prickles sometimes present on the calyx. Wagner *et al.* (1999) listed *S. incompletum* as endangered. My recognition of *S. hillebrandii* which Wagner *et al.* (1999) included under *S. incompletum* will not alter the conservation status of *S. incompletum* as no living individuals *S. hillebrandii* would be “removed” from the population of *S. incompletum*.

***Solanum insulae-pinorum* H. Heine**, Fl. N. Caled. & Depend. 7: 186, pl. 44. 1976. Type: France.

New Caledonia, Îlot Ouate, ile des Pins, 10 m, 24 Jul 1970 (fl, fr), *MacKee 22370*

(Lectotype, *hic designatus*: P 00300168!; Isotypes: MO 2816537!, NOU 006615!, P

00300169!, P 00300170!).

Figure 17.

Shrub to 1(–1.75) m, the internodes to ca. 4.5 cm long. Stems glabrous; bark reddish brown, a transparent layer sloughing off young stems; stems unarmed or with scattered prickles, the prickles to 0.9×1.2 mm, broad based, deltoid, slightly retrorse, yellow-ferruginous. Sympodial structure unknown. Short shoots present. Leaves simple, $1.1\text{--}6.5 \times 0.5\text{--}2.3$ cm, 2–3 times as long as wide, borne individually, lanceolate, ovate to elliptic, coriaceous, with a few scattered hairs to

sparsely pubescent above with sessile porrect stellae when young, glabrous when mature, the stellae 0.2–0.3 mm in diameter, with 6–8 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$, shorter than the rays, with a few isolated hairs to sparsely pubescent below with sessile porrect stellae when young, glabrous when mature, the stellae 0.2–0.3 mm in diameter, with 6–8 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays; blade unarmed, with 4–5(–6) veins on either side of the midvein, the midvein raised abaxially, slightly but raised adaxially, the lateral veins weakly brochidodromous, distinct abaxially, distinct adaxially; blade base rounded to shortly attenuate, sometimes sub-cordate, aequilateral; margin entire to slightly sinuate, typically revolute; apex obtuse; petiole 0.3–2.1 cm long, ca. 1.5 mm in diameter, channeled above, glabrous to sparsely pubescent, unarmed or occasionally present. Inflorescence with a \pm absent rachis in flower and fruit, typically appearing terminal on short shoots occasionally appearing lateral on fast growth and then extra-axillary, emerging from the middle 1/3 portion of the internode, unbranched, with 1–2(–3) flowers, all apparently fertile or potentially so; pedicels ca. 1.8 cm long, ca. 0.2 mm in diameter at the base, 0.9–1.2 mm in diameter below the calyx, gradually increasing in diameter in the distal 1/4–1/3, glabrous, 2.1–3.0 cm long, ca. 0.3 mm in diameter at the base, 1.7–2.2 mm in diameter below the calyx, gradually increasing in diameter in the distal 1/4–1/3, glabrous in fruit, apparently limp in flower and fruit, articulate at the base. Flowers homostylous, 4–5-merous. Buds not seen. Calyx 1.7–2.1 mm long, unarmed, appearing nearly truncate with apiculate lobe tips, the tube 1.4–1.8 mm long, the lobe tips ca. 0.3 mm long, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, glabrous abaxially, glabrous adaxially, the calyx lobes in fruit 1.2–2.2 \times 1.6–2.5 mm, glabrous, appressed. Corolla ca. 1.5 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white, the lobes 4.3–5.9 \times 3.2–3.5

mm, deltoid, the midrib $5.2\text{--}7.2 \times 2.2\text{--}3.0$ mm, lanceolate, nearly glabrous with a few stellate hairs towards the apex abaxially, glabrous adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 0.8 mm long; anthers $3.8\text{--}4.6 \times 0.9\text{--}1.0$ mm, acuminate, \pm straight, markedly attenuate, yellow, connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 0.8 mm in diameter, ovate, glabrous; style ca. 7.0 mm long, 1.1 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, \pm glabrous with a few simple glandular hairs on the lower 1/2; stigma 0.4 mm in diameter, capitate. Fruit a berry, 0.5–0.8 cm in diameter, globose, yellow when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds many per fruit, $1.9\text{--}2.4 \times 2.2\text{--}2.5$ mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, yellow-tan when dry, the surface alveolate.

Distribution and ecology.— Restricted to the forest understory and forest edge of ocean-side *Pandanus-Arocaria* forest ca. 10 m elevation, *Solanum insulae-pinorum* is a calciferous endemic (Morat *et al.* 2001). It is restricted to a small area on Île des Pins, New Caledonia, in the vicinity of *la piscine naturelle*. Figure 39.

Phenology.— Known to flower May and July and to fruit February.

Etymology.— The species is named for the Île des Pins in New Caledonia where the species is endemic.

Additional specimens examined. **FRANCE. New Caledonia. South Province:** Île des Pins, in forest by la piscine naturelle, 22° 34' 57.0" S, 167° 31' 40.2" E, 10 m, 18 Jul 2009 *McClelland & Nee* 558 (MO, NOU, NY, P); Île des Pins, Ouaté côte Est, bordure d'une laisse sableuse entre 2 ilots, 6 Feb 1967 (fr), *Schmid* 2163 (NOU); Île des Pins, south east, 3 May 1974 (fl), *Schmid* 4973 (NOU).

This species has an extremely localized distribution. By sheer coincidence the locality is also one of the most beautiful in all of New Caledonia. *Solanum insulae-pinorum* is found only on Île des Pins in the vicinity of *la piscine naturelle*, a large tidal pool and popular vacation spot for New Caledonians and visiting tourists. Few species have postcards made of the type locality, but this is one. The proximity of the only known population of this *Solanum insulae-pinorum* to such a tourist attraction naturally puts it at risk from human disturbance. Such disturbance for the time being is limited to foot traffic along the trails in the area, however accidental fire is a real concern. Fortunately, the proximity of the locality to *la piscine naturelle* likely saves it from development. This species is part of a group of native New Caledonian Solanums with relatively small leaves and short shoots which typically bear the inflorescences.

***Solanum leratii* Schlechter**, Bot. Jahrb. Syst. 40, Beibl. 92: 34. 1908. Type: France. New

Caledonia, Sud-Bezirk, Koniambo, Aug 1902 (fl), A. *Le Rat* 249 (Lectotype, *hic designatus*: P 00299966!; Isolectotype: B†). Other syntype: Voh, 50–100 m, Nov 1902, *Cribs* 1249 (B†, P 00300020!, P 00300021!).

Figure 18.

Unarmed shrub to ca. 1 m, the internodes to 2.5 cm long. Stems densely pubescent with yellow to yellow-ferruginous, sessile or short-stipitate porrect stellae, stipes of various lengths to 0.2 mm, the stellae soon deciduous, 0.2–0.6 mm broad, with 6–12 rays, the midpoint erect or clinate less than 90°, much longer than the rays; bark lacking a transparent sloughing layer on young stems. Sympodia difoliolate. Short shoots absent. Leaves simple, borne individually, 1.6–9.2 × 0.7–3.4 cm, 2.1–3.8 times as long as wide, lanceolate, oblong, or ovate, semisucculent, densely stellate-pubescent along the veins only, glandular-pubescent across the blade above with sessile or short-stipitate porrect stellae and minute glandular hairs when young, moderately to densely stellate-pubescent along the main vein becoming glabrous distally when mature, the stellae 0.4–0.8 mm in diameter, with 8(–10) rays, the stipes to 0.1 mm long, the midpoint of the stellae erect or clinate less than 90°, much longer than the rays, the glandular hairs ca. 0.04 mm long; moderately to densely pubescent across the blade or along the main vein only below with sessile or short-stipitate porrect stellae and minute glandular hairs when young, ±glabrous when mature, the stellae 0.3–0.7 mm in diameter, with 7–8 rays, the stipes to 0.1 mm long, the midpoint of the stellae erect or clinate less than 90°, ±equal to to much longer than the rays, the glandular hairs ca. 0.04 mm long; blade with 5–8 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded, aequilateral or slightly oblique; margin entire; apex acute to short acuminate; petiole 6.8–15.2 mm long, 0.6–1.3 mm in diameter, channeled above, pubescence all over. Inflorescence to 3.5 cm in flower, to 4.9 cm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode sometimes subopposite, twice-branched or

unbranched, with up to 21 flowers, all apparently fertile or potentially so, the axes moderately to densely pubescent, sessile and short-stipitate porrect stellae and minute glandular hairs; peduncle in flower 8.0–14.5 mm long, 0.5–0.6 mm in diameter, the branches to 1.5 cm long, ca. 0.7 mm in diameter, in fruit 8.5–15.8 mm long, 0.8–1.2 mm in diameter, the branches not seen; pedicels 0.7–1.2 cm long, 0.3–0.4 mm in diameter at the base, 0.8–1.0 mm in diameter below the calyx, straight, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal 1/2–2/3, moderately to densely pubescent, the bases congested overlapping to 1.5 mm apart in flower, 0.7–1.7 cm long, 1.1–1.3 mm in diameter at the base, 2.0–2.8 mm in diameter below the calyx, straight, not bent below the calyx, gradually increasing in diameter in the distal 1/2–2/3, moderately pubescence, the bases well spaced to 6.6 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 5-merous. Buds ovate, the calyx moderately to densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.5–2.7 mm long, appearing nearly truncate with apiculate to caudate lobe tips, the tube 0.5–1.1 mm long, the lobe tips 1.0–1.6 mm long, the intersepal tissue opaque when dry; splitting in the sinuses either during fruit development and then the lobes dentate, moderately to densely pubescent abaxially, sparsely pubescent at the tip adaxially, the calyx lobes in fruit 1.5–2.5 \times 2.1–2.4 mm, moderately pubescent, appressed and slightly accrescent. Corolla 1.4–2.0 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes 4.5–6.2 \times 3.5–7.2 mm, deltoid, the midrib 7.1–9.7 \times 1.3–2.0 mm, oblong, moderately to densely pubescent abaxially, glabrous adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.7–1.3 mm long; anthers 2.4–5.1 \times 0.7–1.1 mm, acuminate, straight, markedly attenuate, yellow, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining

intact with age. Ovary ca. 0.9 mm, ovate, with a few sessile porrect stellae and simple glandular hairs at the apex; short styles 2.4–2.8 mm long, ca. 0.3 mm in diameter, shorter than the stamens, long styles 5.4–7.1 mm long, ca. 0.3 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, with sessile porrect stellae and simple glandular hairs on the basal 1/3–1/2; stigma ca. 0.3 mm in diameter, capitate. Fruit a berry, 0.7–1.0 cm in diameter, globose, probably orange to red when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 1.7–1.8 × 2.0–2.3 mm, flattened-oval and notched at the point of attachment, yellow-tan when dry, the surface smooth all over, the coat transparent revealing a cancellate pattern beneath.

Distribution and ecology.— In the vicinity of Tsiba on the Grand Terre, New Caledonia, in shrubby vegetation on serpentine substrate (maquis) from 100–250 m elevation. Figure 36.

Phenology.— Known to flower December–January and fruit December–January and April.

Etymology.— Name for Auguste-Joseph Le Rat (1872-1910) a botanist in New Caledonia and collector of the type specimen.

Additional specimens examined. **FRANCE. New Caledonia.** (fl, fr), *Rotton s.n.* (NOU). **North Province:** Voh, Tiéta 20 m, 24 Jun 1971 (fl, fr), *McKee 23625* (L, MO×2, US), Ouaco, Tsiba, 200 m, 31 Dec 1977 (fl, fr), *McKee 34495* (B, L, MO, NOU, NSW, P); Tsiba radio tower near Ouaco, north of Voh, ca. 250 m, 7 Jan 1983 (fl), *McPherson 5341* (MO, P); above Tinip river, near Ouaco, north of Voh, ca. 100 m, 8 Jan 1983 (fl, fr), *McPherson 5353* (MO, NOU, NSW, P).

Solanum leratii is most similar to *S. semisucculentum* but can be distinguished by its pubescent stems, petioles, and midveins of the leaves with the midpoints of the stellae much longer than the rays, persistent pubescence on the inflorescences, robust pedicels, the adaxial surface of the corolla nearly glabrous, and ovate fruits held erect and sometimes a nipple at the apex. *Solanum leratii* was treated as a synonym of *S. tetrandrum* (= *S. austro-caledonicum*) by Heine (1976) therefore it was not treated by Jaffré *et al.* (1998); in light of its resurrection, the conservation status of *S. leratii* needs to be reevaluated.

***Solanum memaoyanum* D. McClell. sp. nov.**

Type: France. New Caledonia. contrefort oest du Mé Maoya audessus de la Mine Emma, 1450 m, 23 Apr 1970 (fr), *McKee 21797* (Holotype: P 00300081!; Isotypes: A!, K×2!, L 0651811!, MO 2816917!, NOU 017079!, NSW 594231!, U 0182899!).

Figure 19.

Unarmed shrub to 3 m, the internodes to 2.8 cm long. Stems densely pubescent with yellow-ferruginous, sessile porrect stellae, the stellae tardily glabrescent, 0.1–0.3 mm broad, with 8 rays, the midpoint ciliate less than 90° to flexed at the base ±90° and laying flat on the surface of the leaf, shorter than to ±equal to the rays; bark brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, borne individually, 3.9–9.9 × 2.0–3.3 cm, ca. 2.0–3.4 times as long as wide, lanceolate to elliptic, semisucculent, densely

pubescent along the veins and sparsely pubescent across the lamina above with sessile porrect stellae and minute glandular hairs when young, glabrous or with moderate to dense pubescence on the midvein towards the base when mature, the stellae 0.2–0.5 mm in diameter, with (4–)8(–12) rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs ca. 0.04 mm long, densely pubescent below with sessile porrect stellae and minute glandular hairs when young, sparsely pubescent when mature, the stellae 0.2–0.4 mm in diameter, with 6–8 rays, the midpoint of the stellae clinate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs ca. 0.04 mm long; blade with 5–8 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded, aequilateral or oblique; margin entire; apex acute to short acuminate; petiole 1.0–2.2 cm long, 0.7–1.2 mm in diameter, channeled above, densely pubescent all over. Inflorescence to 2.0 cm long in flower, 1.0–2.2 cm long in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, unbranched, with 2–7 flowers, all apparently fertile or potentially so, the axes densely pubescent, with sessile porrect stellae; peduncle in flower ca. 0.8 cm long, ca. 0.5 mm in diameter, in fruit 1.0–1.7 cm long, ca. 0.6 mm in diameter; pedicels 0.7–1.3 cm long, 0.3–0.4 mm in diameter at the base, 0.6–0.9 mm in diameter below the calyx, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal 1/4–1/2, sparsely pubescent, the bases congested to 3.5 mm apart in flower, 1.3–2.6 cm long, 0.6–1.0 mm in diameter at the base, 1.7–2.5 mm in diameter below the calyx, arching, gradually increasing in diameter in the distal 1/3–2/3, glabrous to sparsely pubescent, the bases congested to 1.2 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers 5-merous. Buds ovate, the calyx densely stellate-pubescent, the lobe tips glabrous, the corolla densely stellate-pubescent, the surface of the corolla of the

mature bud smooth. Calyx ca. 2.6 mm long, appearing nearly truncate with caudate lobe tips, the tube ca. 0.9 mm long, the lobe tips 1.4–1.7 mm long, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, the calyx lobes in fruit 2.6–4.0 × 1.7–3.8 mm, glabrous, reflexed. Corolla ca. 2.4 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes ca. 0.8 × 0.3 cm, triangular, the midrib ca. 10.0 × 2.6 mm, oblong, moderately pubescent abaxially, glabrous at the base with scattered pubescent towards the apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 1.7 mm long; anthers ca. 5.1 × 1.3 mm, acuminate, straight, attenuate, yellow, connivent, with minute apical pores, the pores directed outward, extending around the edge of the apex, the lateral sutures perforated. Ovary ca. 1.3 mm, globose, glabrous. Fruit a berry, 0.7–1.1 cm in diameter, globose, red when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 1.8–2.3 × 2.2–2.6 mm, flattened-orbicular and notched at the point of attachment, yellow-tan when dry, the surface cancellate all over.

Distribution and ecology.— Restricted to the mountain of Mé Maoya in rainforest from 1300–1500 m elevation on the Grande Terre, New Caledonia. Figure 38.

Phenology.— Known to flower in January and fruit in April and August.

Etymology.— This species is named after Mé Maoya the mountain on which is found.

Additional specimens examined. **FRANCE. New Caledonia.** contrefort oest du Mé Maoya audessus de la Mine Emma, 1350–1500 m, 13 Jan 1970 (fl), *McKee 21422* (NOU, P); Mt. Mé

Maoya, above Mine Emma, ca 27 air-km northwest of Bourail, ca. 1300 m, 8 Aug 1980 (fr),
McPherson 2948 (MO, NOU, NSW, PTBG).

Solanum memaoyanum is most similar to *S. semisucculentum*. From herbarium material it appears to have semisucculent leaves like *S. semisucculentum*, but it differs in having a taller habit, pubescent stems, leaves, and inflorescences, and seeds with a cancellate surface. Also, *Solanum memaoyanum* occupies a much different habitat growing in rainforest from 1300–1500 m as opposed to *S. semisucculentum* which grows in open shrubby habitat (maquis) and is typically not found above 700 m.

***Solanum milnei* Seem.**, J. Bot. 1: 210. 1863. Type: Vanuatu [“New Hebrides”]. Anatom [“Aneiteum”], Nov 1853 (fl), *MacGillivray 926* (Lectotype, *hic designatus*: K 000195704!). Other syntypes: Vanuatu [“New Hebrides”], Futuna Island, “table land”, *Milne s.n.* (K-Hook.!) = *S. vanuatuense*; Anatom [“Aneiteum”], *Milne 269* (K!). Possible syntype: Vanuatu [“New Hebrides”], Anatom [“Aneiteum”], 1858. *MacGillivray 28* (BM 000846950!, G 00025447!, G 00035451!, K 000195695!, P 00315263!, P 00315264!, S!, W 14897!, W14898!).

Solanum vieillardii Bitter, in Sarasin & Roux, Nova Caled. 1: 226. 1921. Type: Ins. Loyauté. Lifou, Vieillard 1026 (Lectotype, *hic designatus*: P 00288324!; Isolectotype: P 00288325!).

Figure 20.

Unarmed shrub to 2 m, the internodes to 4.9 cm long. Stems densely pubescent with light yellow nearly white to light yellow-ferruginous, sessile or short-stipitate porrect stellae, stipes of various lengths to 0.2 mm, the stellae tardily deciduous, 2.0–3.2 mm broad, with 6–8 rays, the midpoint clinate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to than the rays; bark lacking a sloughing, transparent layer on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, borne individually, 5.3–16.6 \times 1.6–4.5 cm, 2.3–4.4 times as long as wide, ovate to elliptic, chartaceous, densely pubescent along the veins, sparsely pubescent across the lamina above with sessile and short-stipitate porrect stellae and minute glandular hairs when young, \pm glabrous when mature, the stellae 0.3–0.5 mm in diameter, with 6–12 rays, the stipes to 0.1 mm long, the midpoint of the stellae clinate less than 90° to flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs 0.05 mm long, densely pubescent below with sessile and short-stipitate porrect stellae and minute glandular hairs when young, sparsely to moderately pubescent when mature, the stellae 0.2–0.5 mm in diameter, with 6–8 rays, the stipes to 0.2 mm, the midpoint of the stellae clinate less than 90° to flexed at the base $\pm 90^\circ$, \pm equal to the rays, the glandular hairs 0.03 mm long; blade with 7–10 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly brochidodromous, raised abaxially, distinct adaxially; blade base rounded to cuneate, aequilateral or oblique; margin entire or sinuate; apex acuminate; petiole 0.9–2.0 long, 0.6–0.9 mm in diameter, terete becoming channeled above towards the base of the petiole, densely pubescent all over. Inflorescence to 3.2 cm long in flower only, to 8.1 cm in fruit and flower, appearing lateral, extra-axillary, emerging from the middle or upper 1/3 of the internode, branching 4–6 times, with many, to 130 flowers, all apparently fertile or potentially so, the axes densely pubescent with sessile and stipitate

porrect-stellate; peduncle in flower 6.3–18.5 mm long, 0.7–0.9 mm in diameter, the branches to 4.0 cm long, to 0.9 mm in diameter, in fruit 14.6–16.5 mm long, 0.9–1.4 mm in diameter, the branches to 5.0 cm long, to ca. 0.9 mm in diameter; pedicels 0.9–1.3 cm long, ca. 0.2 mm in diameter at the base, 0.6–0.8 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal ca. 1/3, densely pubescent, the bases ±well spaced to 5.1 mm apart in flower, 0.9–1.3 cm long, 0.4–0.6 mm in diameter at the base, 0.9–1.4 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal 1/2–2/3, moderately to densely pubescent, the bases well spaced to 4.5 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.3–3.0 mm long, appearing nearly truncate with apiculate lobe tips, the tube 0.9–1.3 mm long, the lobe tips 1.3–1.8 mm long, the intersepal tissue translucent when dry; splitting in the sinuses during fruit development and then the lobes dentate, at anthesis densely pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 1.8–2.5 × 1.4–2.4 mm, sparsely to moderately pubescent, reflexed. Corolla 1.5–1.7 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes 6.8–7.8 × 3.4–3.7 mm, triangular, the midrib 7.4–9.1 × 1.7–2.3 mm, oblong, densely pubescent abaxially with sessile porrect and stipitate porrect-stellate, glabrous at the base, moderately pubescent towards the apex adaxially with sessile, very short, and reduced sessile porrect-stellate, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 1.0–1.3 mm long; anthers 3.2–3.8 × 0.8–1.0 mm, acuminate, straight, scarcely attenuate, yellow, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 1.0 mm, globose, densely pubescent with sessile and stipitate porrect-stellate

restricted to the apex; style 5.7–6.6 mm long, ca. 0.3 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, sparsely to densely pubescent, the sessile and stipitate porrect-stellate restricted to the basal ca. 1/2; stigma ca. 0.4 mm in diameter, capitate. Fruit a berry, 0.5–0.8 cm in diameter, globose, probably orange or red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds few per fruit, ca. 2.2×1.6 mm, flattened-reniform, yellow-tan when dry, the surface evenly reticulate over the entire surface.

Distribution and ecology.— On the island of Anatom, Vanuatu, and the Loyalty islands of New Caledonia. Figure 40.

Phenology.— Known to flower in March and October. Fruiting period unknown.

Etymology.— This species was named to honor William Grant Milne, a botanist on the HMS Herald expedition to the South Pacific (1852–1856) and collector of the type.

Additional specimens examined. **FRANCE. New Caledonia. Loyalty Islands Province:** Lifu, 27 Oct 1925 (fl), *Daniker 2318* (P); Lifu, 1869 (fl,fr), *Deplanche s.n.* (P×2); Lifu, *Whitmee s.n.* (BM×2); Lifou, falaise de Mou et Région de Wé, 16 Mar 1966 (fl), *Schmid 1080* (K, P).

The typification of *S. milnei* is complicated by two factors. First, Seemann did not cite collector numbers in the protologue, and second, two species are amongst the syntypes. Even though Seemann referenced specimens by collector name and location only, the description in the protologue is detailed enough to allow them to be identified. Herein *S. milnei* is lectotypified on the

specimen best fitting the original description, and *S. vanuatuense*, the second species, is separated. *Milne 28* has been indicated as the type by some herbaria, however this material does not fit well with the protologue though it is material of *S. milnei*. I doubt that Seemann used *Milne 28* in the preparation of his description, but I list it as a possible syntype as the possibility can not be totally ruled out. *Milne 269* and *MacGillivray 926* may represent the same collection. For both specimens the 9 in the collector number is larger and somewhat offset from the 26 the only difference being whether the 9 precedes or follows the 26.

Solanum milnei is most similar to *S. austro-caledonicum* and *S. vanuatuense*. It differs from the former by having lanceolate to ovate leaves 2.6–3 times as long as wide with sparse pubescence across the blade, margin of the leaves typically minutely undulate-crenate, leaf apices typically long acuminate, and 7–10 veins on either side of the midvein. The inflorescences are also more branched, the calyx lobes reflexed in fruit, and it has smaller fruits. It differs from *S. vanuatuense* by having unlobed leaves borne individually, larger corollas and anthers, straight styles.

***Solanum nelsonii* Dunal**, in DC., Prodr. 13(1): 123. 1852. Type: U.S.A., Hawaiian Islands, *D.*

Nelson s.n. (Holotype: BM-Banks 000846708!).

Solanum nelsonii Dunal var. *thomasiifolium* Seem., J. Bot. 1: 209. 1863 Type: Pacific Islands,

Atoi, *T. Nuttall s.n.* (Holotype: BM).

Solanum laysanense Bitter, Abh. Naturw. Vereins Bremen 16: 433, tab. 4a–d. 1900. Type:

U.S.A., Hawaiian Islands, Leeward Islands, Laysan Island, 1896–1897, *H. Schauinsland s.n.*

(BREM; Isotypes: BISH No. α 581202! [“14 Jul 1896”], BISH ex BREM, No. β 581201!).

Solanum nelsonii Dunal var. *intermedium* F. B. H. Brown, in Christophersen & Caum, Bull.

Bish. Mus. 81: 35, pl. 15A. 1931. Type: U.S.A., Hawaiian Islands, Leeward Islands,

Midway Island, central plain, 18 Apr 1923 (fl), *E. Caum 12* (Holotype: BISH!).

Solanum nelsonii Dunal var. *typicum* F. B. H. Brown, in Christophersen & Caum, Bull. Bish.

Mus. 81: 35, pl. 14B. 1931. Nom. illegit. for var. *nelsonii*, but “syntypes” cited as: U.S.A.,

Hawaiian Islands, Molokai, Moomomi shore, Mar 1910 (fl, fr), *J. F. Rock A* (BISH);

Moomomi, 24 Mar 1915, *C. N. Forbes 613Mo*.

Figure 21.

Unarmed prostrate shrub, the internodes to 5.8 mm long. Stems densely pubescent with yellow-ferruginous, short-stipitate porrect stellae, stipes of various lengths to ca. 0.2 mm, the stellae persistent, 0.7–0.8 mm broad, with 8–11 rays, the midpoint erect or flexed at the base $\pm 90^\circ$, shorter than the rays; a transparent sloughing layer absent on young stems. Sympodia trifoliate though more often appearing tetrafoliate. Short shoots absent. Leaves simple, the blades of leaves 2.3–6.4 \times 2.1–6.2 cm, \pm as long as wide, borne individually, ovate, orbicular, oval, to deltoid or cordate, chartaceous to sub-coriaceous, densely pubescent above with short-stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.5–0.7 mm in diameter, with 7–9 rays, the stipes to 0.2 mm long, the midpoint of the stellae erect or curved, shorter than the rays, densely pubescent below with short-stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.4–1.2 mm in diameter, with 7–9 rays, the stipes to 0.2 mm long, the midpoint of the stellae erect, shorter than the rays; blade with 4–6 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly

brochidodromous, raised abaxially, distinct adaxially; blade base cordate to rounded, aequilateral; margin entire or very occasionally lobed; apex obtuse; petiole 1.0–3.4 mm long, 1.1–1.8 mm in diameter, channeled above, densely pubescent all over. Inflorescence to 7.6 cm long in flower, observed to 3.6 cm long in fruit but presumably at least equal to length in flower, appearing lateral, extra-axillary, emerging from the 1/3 of the internode, unbranched, with 7–17 flowers, all apparently fertile or potentially so, the axes densely pubescent, stipitate porrect stellae; peduncle in flower observed 10.3–14.5 mm long but presumably as short as in fruit, 0.9–1.0 mm in diameter, in fruit 8.0–33.1 mm long, 1.3–1.7 in diameter; pedicels 1.2–1.9 cm long, 0.6–0.9 mm in diameter at the base, 1.1–1.5 in diameter below the calyx, straight, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal ca. 1/4, densely pubescent, the bases well spaced to 1.8 mm apart in flower, 1.9–2.6 cm long, 0.8–1.1 mm in diameter at the base, 1.9–2.7 mm in diameter below the calyx, straight or arching, not bent below the calyx, gradually increasing in diameter in the distal 1/4–1/3, with a distinct bulge directly below the calyx, densely pubescent, the bases well spaced to 1.8 cm apart in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 5-merous. Buds globose, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud ridged. Calyx 2.8–4.2 mm long, with deltoid lobe tips, the tube 1.7–2.8 mm long, the lobe tips $0.9\text{--}1.5 \times 1.2\text{--}1.4$ mm, the intersepalar tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, at anthesis densely pubescent abaxially, densely pubescent at the apex, glabrous towards the base adaxially, the calyx lobes in fruit $4.3\text{--}6.2 \times 3.2\text{--}3.5$ mm, densely pubescent, appressed. Corolla 1.3–1.7 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, purple or the interpetalar and petalar tissue white with purple veins, the lobes $4.1\text{--}6.3 \times 4.3\text{--}4.8$ mm, deltoid, the midrib $5.7\text{--}7.8 \times 3.1\text{--}3.8$ mm,

lanceolate, densely pubescent abaxially, glabrous adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 1.2 mm long; anthers 2.8–2.9 × 0.9–1.2 mm, acuminate, arcuate, markedly attenuate, yellow to dark purple appearing nearly black, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures entire or perforated, remaining intact with age. Ovary 0.7–1.3 mm, globose, white to cream, densely pubescent at the apex, glabrous towards the base; short styles ca. 1.5 mm long, ca. 0.2 mm in diameter, cylindrical, shorter than the stamens, long styles 3.5–4.8 mm, ca. 0.2 mm in diameter, filiform, longer than the stamens, emerging between the anther apices, straight, the basal ¼ moderately pubescent; stigma ca. 0.3 mm in diameter, capitate, green. Fruit a berry, 0.8–1.3 cm in diameter, globose, the immature fruits evenly green, black when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 2.2–2.9 × 2.3–3.3 mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, red-brown to yellow-brown when dry, the surface evenly reticulate all over.

Distribution and ecology.— *Solanum nelsonii* used to occur on several of the main islands of Hawaii in addition to the leeward islands. Now it is restricted to Moomomi Dunes on Molokai where it grows in shifting and fixed sand dunes and in central areas of some of the leeward islands from 2–10 m elevation. The sea side is not a typical location for Solanums; *S. nelsonii* is the only *Solanum* known to live in shifting dunes. Figure 34.

Phenology.— Known to flower January–June, August–October, and December and fruit January–June and August–September, but likely flowering and fruiting year round.

Etymology.— This species is named in honor of the botanist David Nelson, who in addition to another fateful voyage, participated in Captain Cook's third and final voyage to the Pacific. The type of this species was collected by David Nelson on that voyage.

Additional specimens examined. **USA. Hawaiian Islands. Hawaii:** east of South Point, 16 Sep 1929 (fl, fr), *Degener 7369* (BRI, CAS, F, K, MICH, NY). **Kure Island:** 12 Sep 1961 (fl), *Lamoureux 1878* (NSW, P); 12 Sep 1961 (fl), *Lamourex 1897* (BISH). **Maui:** 1838–1942 (fl), *Wilkes s.n.* (NY, US). **Midway Atoll:** Sand Island, 25 Jun 1944 (fl, fr), *Caura s.n.* (BISH); (fl) *Meagher s.n.* (BISH). **Molokai:** west of Moomomi, 25 Apr 1928 (fl, fr), *Degener 7370* (B, BRI, CAS, F, K, MICH, MO, NY, S, US); between Kaa and Kalani, 19 Apr 1928 (fl, fr), *Degener 7371* (A, BH, DS×2, F, GH, MO, NY×2, US×2); Beaches of western end, Jun 1912 (fl, fr), *Forbes 111MO* (A, BH, K, M, MO, NY, P, UC, US); Moomomi Beach, 23 Feb 1948 (fl, fr), *Fosberg 29609* (BISH, BH, US); Moomomi Beach, 23 Jun 1979 (fl), *Gustafson 1297* (RSA); Kaluakoi district, Moomomi Kaiehu Pint, 30 ft, 11 Mar 1976 (fl), *Herbst 5760* (UC); Moomomi, 30 Oct 1986 (fl), *Imada & Takeuchi 1000* (BISH); between Moomomi Beach and Kawaaloa Beach, 21.2°N, 157.1°W, 10 m, 14 Jun 1962, *Krajina & Lamoureux 620614006* (NY); Moomomi, Mar 1910 (fl, fr), *Rock s.n.* (BH, GH×2, K, NY, UC, US); Moomomi, 20 May 1918 (fl, fr), *Rock 14016* (A, NY, PTBG, US); Moomomi, Kaluakoi, 20 ft, 3 Jan 1939 (fl, fr), *St. John et al. 19962* (K, NY, P, UC, US); Moomomi, Kaluakoi, 30 ft, 24 Dec 1948 (fl), *St. John et al. 23489* (A). **Oahu:** Atoo-ai, 1853 (fl), *Nuttall s.n.* (BM); Atooi, (fl), *Nuttall 78* (K); 1851–1855 (fl, fr), *Rémy 442* (G, GH, K, L×2, P×5). **Pearl and Hermes Reef:** Southeast Island, central portion of both eastern and western halves of islet, 25 Sep 1966 (fl, fr), *Carlquist 2333* (BISH); 2 m, 27 Apr 1923 *Caum 49* (K); North Island,

interior of island, 2 m, 10 Aug 1983 (fl, fr), *Conant 199* (BISH); Feb 1928(fl, fr), *Pietschmann s.n.* (W×2).

Cultivated. USA. Hawaiian Islands. Kauai: Koloa District, Lawai Valley, Cultivated at the National Tropical Botanical Garden, grown from seed collected Moomomi, Molokai, 30 Mar 1995 (fl), *Flynn 5749* (MO, NY, PTBG); National Tropical Botanical Garden, Makauwahi Cave restoration site, source Molokai, 18 Apr 2008 (fl, fr), *McClelland 455* (BISH, NY, PTBG).

The most striking characteristic of *S. nelsonii* besides its unusual habitat preference is its habit—a mat forming prostrate shrub, unique within section *Irenosolanum*. *Solanum nelsonii* is most similar to *S. caumii* but differs in habit, leaf length to width ratio, sometimes in fruit color, and habitat preference. Wagner *et al.* (1999) listed *S. nelsonii* (including *S. caumii*) as vulnerable. Following the segregation of *S. caumii* herein, the conservation status of *S. nelsonii* may need to be reassessed as recognizing *S. caumii* effectively reduces the population size of *S. nelsonii*.

Other names: *S. rotundifolium* Nutt. ex Seem. J. Bot. 1: 209. 1863. *nom. nud.*

***Solanum nudatum* D. McClell. sp. nov.**

Type: Fiji, Oct 1838 (fl, fr), *D. Jacquinet s.c.* (Holotype: P 00315200!)

Figure 22.

Shrub probably erect, the internodes to 1.7 cm long. Stems glabrous; bark reddish brown, a transparent layer sloughing off young stems; stems with scattered prickles, the prickles to 1.6×1.4 mm, broad based, the base circular in outline rather than the typical oval, a hump just above the base, the prickle then narrowing to have straight sides up to the tip, straight, yellow-ferruginous. Sympodia difoliate. Short shoots present though not as distinct as in some other species. Leaves simple, geminate or borne individually, the blades of leaves $2.9\text{--}5.0 \times 0.3\text{--}0.7$ cm, 6–7 times as long as wide, very narrowly elliptic, chartaceous, glabrous when young, glabrous when mature, glabrous below when young, glabrous when mature; blade unarmed or with an occasional prickle on the primary vein adaxially, with 10–15 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly brochidodromous, distinct abaxially, distinct adaxially; blade base long cuneate, aequilateral; margin entire to sinuate, revolute; apex acute; petiole 2.6–6.6 mm long, 0.3–0.4 mm in diameter, channeled above, glabrous, unarmed. Inflorescence 0.3 mm in flower, 0.1–6.2 mm in fruit, lateral though appearing nearly terminal on short shoots, extra-axillary, emerging from the very upper internode, appearing nearly leaf opposed, unbranched, with 2–5 flowers, all apparently fertile or potentially so, the axes glabrous, unarmed; peduncle in flower to 1.8 mm long, ca. 0.3 mm in diameter, in fruit to 3.1 mm long, ca. 0.4 mm in diameter; pedicels ca. 0.9 cm long, ca. 0.3 mm in diameter at the base, ca. 0.9 mm in diameter below the calyx, straight or arching in herbarium material, gradually increasing in diameter in the distal 1/4, glabrous, the bases congested to ca. 0.4 mm apart in flower, 1.3–1.5 cm long, ca. 0.4 mm in diameter at the base, 1.0–1.1 mm in diameter below the calyx, straight or arching in herbarium material, gradually increasing in diameter in the distal 1/3, glabrous, the bases congested to 2.8 mm apart in fruit, probably limp, in two rows, articulate at the base. Flowers homostylous (on a single plant), 5-

merous. Buds globose, the calyx glabrous stellate-pubescent, the corolla glabrous stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx ca. 0.6 mm long, unarmed, appearing nearly truncate with apiculate lobe tips, the tube ca. 0.4 mm long, the lobe tips ca. 0.2 mm long, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, glabrous abaxially, glabrous adaxially, the calyx lobes in fruit ca. 0.7×0.9 mm, glabrous, appressed or reflexed. Corolla ca. 0.6 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, the lobes 2.3×1.5 mm, oval, the midrib 2.7×1.3 mm, lanceolate, glabrous abaxially, glabrous adaxially, probably spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 0.4 mm long; anthers ca. 1.8×0.2 mm, oblong, the inner surface straight, the outer surface curved, not attenuate, connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures entire, remaining intact with age. Ovary ca. 0.4 mm in diameter, globose, glabrous; style 2.0–2.2 mm long, ca. 0.2 mm in diameter, \pm equal to the stamens, filiform, straight, glabrous; stigma 0.3 mm in diameter, capitate to slight bilobed. Fruit a berry, 0.4–0.6 cm in diameter, globose, probably orange or red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds relatively few per fruit, $1.3\text{--}1.5 \times 1.6\text{--}1.8$ mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, yellow-tan when dry, the surface the central portion \pm smooth, the margin scrobiculate.

Distribution and ecology.— Known only from the type on which the locality is given only as Fiji.

Phenology.— Known to flower and fruit in October.

Etymology.— The specific epithet draws attention to the total lack of pubescence in this species.

This species is tantalizing as it is known from the type alone and the locality is given only as “Viti”. The type was collected by Honoré Jacquinot. Mr. Jacquinot was the surgeon and naturalist on board the *Zélée* which accompanied the *Astrolabe* in a voyage of discovery for the French from 1837–1840. During the voyage, the ships were in Fiji throughout most of the month of October, 1838. One other specimen of the genus *Solanum* was collected by Jacquinot, a specimen of *S. inamoenum* collected in Levuka (spelled Lavouka) on the island of Ovalau. Specimens of other taxa collected by Jacquinot at Levuka are also known. These other collections give a possible lead as to the type locality of *S. nudatum*. A close reading of reports of the voyage of the *Astrolabe* and the *Zélée* would also be necessary to identify possible localities for *S. nudatum*, and its rediscovery.

***Solanum pancheri* Guillaumin**, Bull. Soc. Bot. France, 88: 465. 1941. Type: France. New Caledonia. 1862 (fl), *Pancher s.n.* (Lectotype, designated by Heine 1976: P 00300140! [does not have the locality “Uaraï” or no “142” but was determined by Guillaumin and is annotated “type” apparently in his hand]) Other syntypes: New Caledonia, *Vieillard 3040* (P); *Deplanche 323* (P 00300124!); *June J. Pancher s.n.* (P 00300141!); *Pancher s.n. et 142* (P 00300137!); *Lecard s.n.* (A 00139598!, A 0013635!, P 00300129!); Anse Vata, *Brousmitche s.n.* (A 00139636!, P 00300122!, P 00300123!); Poïta, *Vieillard 1032* (G 00035456!, GH 00139605!, P 00300142!, P 00300147!, P 00300148!, P 00300149!, P00300150!. P00578016!, P00578017!, NY 00172290!, W 61472!); between Néoua and

Mt. Mi, *B. Balansa* 1365 (P 00300120!); Toni, *Deplanche s.n.* (P); Uarai, *Pancher s.n.* ["262" written on later] (P 00298940!).

Solanum desmodioides Guillaumin, Mém. Mus. Hist. Nat., 15: 89. 1964. Type: France. New Caledonia, Mt. Koniambo, 21 Dec 1950, A. *Guillaumin & M. Baumann-Bodenheim* 9474 (Holotype: P 00300126!; Isotypes: G!, GH 00077855!, US 2909315!).

Figure 23.

Shrub to 2 m, the internodes to 2.3 cm long. Stems glabrous; bark typically reddish brown, a transparent layer sloughing off young stems; stems unarmed or with scattered prickles, the prickles to ca. 1.7×2.3 , broad based, deltate, straight, yellow-ferruginous. Sympodial structure unknown. Short shoots present. Leaves simple, $0.9\text{--}4.8 \times 0.2\text{--}1.0$ cm, 3–7.3 times as long as wide, borne individually, spatulate, very occasionally narrowly elliptic, chartaceous to subcoriaceous, with isolated, sessile porrect stellae along the midvein above when young, glabrous when mature, the stellae 0.2–0.3 mm in diameter, with 6–8 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, \pm equal to to slightly longer than the rays, yellow to yellow-ferruginous, with isolated, sessile porrect stellae along the midvein below when young, \pm glabrous when mature, the stellae ca. 0.3 mm in diameter, with 6–9 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, \pm equal to to slightly longer than the rays, yellow to yellow-ferruginous; blade unarmed, with 3–6 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous, distinct abaxially, distinct or indistinct adaxially; blade base rounded to cuneate, aequilateral to oblique; margin entire; apex obtuse; petiole 0.5–4.0 mm

long, ca. 0.3 mm in diameter, channeled above, densely pubescent on the adaxial side, unarmed or occasionally with scattered, broad-based prickles to 1.0×0.8 mm. Inflorescence sessile, appearing terminal on short shoots or lateral on long shoots, extra-axillary, in the middle or lower 1/3 of the internode, with 1 or very occasionally 2 flowers, all apparently fertile or potentially so; pedicels 1.3–2.6 cm long, 0.1–0.2 mm in diameter at the base, 0.7–1.0 mm in diameter below the calyx, gradually increasing in diameter in the distal ca. 1/3, glabrous in flower, 1.7–3.2 cm long, 0.3–0.7 mm in diameter at the base, 1.3–1.5 mm in diameter below the calyx, gradually increasing in diameter in the distal ca. 1/3, glabrous, in fruit, limp in flower and fruit, articulate at the base. Flowers homostylous, 4-merous. Buds ovate, the calyx \pm glabrous, the corolla moderately stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.5–1.7 mm long, unarmed, appearing nearly truncate with apiculate lobe tips, the tube 1.0–1.5 mm long, the lobe tips 0.2–0.5 mm long, the intersepal tissue opaque when dry; splitting in the sinuses at anthesis and then the lobes dentate, $0.5\text{--}1.3 \times 1.0\text{--}1.4$ mm at anthesis, glabrous abaxially, glabrous adaxially, the calyx lobes in fruit $1.8\text{--}2.5 \times 1.4\text{--}1.6$ mm, glabrous, appressed. Corolla 1.2–1.6 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white, the lobes $4.9\text{--}7.0 \times 2.2\text{--}2.7$ mm, oblong, the midrib $6.3\text{--}7.7 \times 1.8\text{--}2.0$ mm, oblong, sparsely to moderately stellate pubescent abaxially, glabrous adaxially, reflexed at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 0.5 mm long; anthers $3.8\text{--}4.8 \times 0.8\text{--}0.9$ mm, acuminate, straight, markedly attenuate, yellow, connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 0.6×0.5 mm, ovate, with a few minute glandular hairs restricted to the apex; style 5.5–6.5 mm long, ca. 0.2 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, glabrous; stigma ca. 0.3 mm

in diameter, capitate, green. Fruit a berry, 0.5–0.6 cm in diameter, globose, the immature fruits light and dark green striped and mottled, red when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds many per fruit, 1.5–1.9 × 1.7–2.2 mm, flattened-orbicular and notched at the point of attachment to flattened-irregular, yellow-tan when dry, the surface evenly alveolate over the entire surface.

Distribution and ecology.— Restricted to the Grande Terre of New Caledonia, *S. pancheri* is found in low forest from 5–200 m elevation. This species can be an understory shrub in intact forest which is very unusual for a *Solanum*. *Solanums* in general prefer disturbance such as forest edges or openings. Whalen (1984) listed it as a serpentine endemic, but several specimens indicate it growing on calcareous substrates as well. Figure 39.

Phenology.— Known to flower March, June–July, September, and November–December and fruit March, June–July, and September–December. Likely flowering and fruiting year round.

Etymology.— This species was named to honor Jean Armand Isidore Pancher (1814–1877) a French gardener and botanist who collected in New Caledonia.

Additional specimens examined. **FRANCE. New Caledonia.** *Lécard* (P); (fl, fr) *Pancher s.n.* (A, K, L, UC); (fl) *Pancher 144* (P). **North Province:** Pindai Baie des Sapins, 5 Mar 2007 (fl), *Hequet & Butin 3591* (MO, NOU); Pindai Baie des Sapins 5 Mar 2007 (fl), *Hequet & Butin 3594* (NOU); Presqu'île de Pindai, vicinity of Baie des Sapins, 21° 20' 05.1" S, 164° 58' 13.2" E, 20 m, Jul 16 2009 (fr), *McClelland et al. 556* (MO, NOU, NY, P); Presqu'île de Pindai, vicinity of Baie des

Sapins, 21° 20' 05.1" S, 164° 58' 13.2" E, 20 m, Jul 16 2009 (fr), *McClelland et al. 557* (MO, NOU, NY, P); Bourail, Cap Goulvain, 50 m, 23 Mar 1983 (fl, fr), *McKee 41366* (K, NOU, P×2); Nepoui, Presqu'île de Moueo, 5 m, 12 Jun 1975 (fl, fr), *McKee 30071* (A, K×2, L×2, NSW, NOU, P, US); Bourail, Le Cap, 14 Oct 1982 (fr), *Suprin 2104* (NOU); Presqu'île de Pindai, Plaine des Gaiacs, 1 Jul 1987 (fl), *Veillon 6410* (NOU, NSW, NY, P); Presqu'île de Nepoui, Pindai, 100 m, 18 Nov 1987 (fl, fr), *Veillon 6567* (NOU, P). **South Province:** Poita *s.c. s.n.* (K); Île Moro, 6 Mar 1951 (fr), *Guillaumin & Baumann 11144* (A, GOET, P); 6 Mar 1951 (fr), *Guillaumin & Baumann 11160* (G, P); Tontouta, Untoé [Uitoé], 60 m, 29 Mar 1986 (fl, fr), *MacKee 43061* (L, NOU, P); Mont Maa, au peid du pic Taureau versant sud vers, 150 m, 18 Sep 1989 (fl, fr), *Veillon 7165* (NOU, Y); Bourail, forêt Vallicole, ca. 200 m, 14 Dec 1990 (fl, fr), *Veillon 7302* (NOU).

Cultivated. AUSTRALIA. South Australia: Adelaide Botanical Garden. 34°55'S, 138°37'E, 30 m, 16 Sep 1994 (fr), *Nee 45559* (MO, NY); Adelaide Botanical Garden. 10 Jun 1988 (fr), *Symon s.n.* (MO×2, NY).

Solanum pancheri is part of a group of native New Caledonian Solanums with relatively small leaves and short shoots which typically bear the inflorescences. However, it does not closely resemble any other species of section *Irenosolanum*; its spatulate leaves appearing clustered on the short shoots give it a very unusual aspect. Furthermore, it is the only member of section *Irenosolanum* for which only 4-merous flowers are known. Though prickles are infrequently on specimens of *S. pancheri*, the species can have them. This is an important character since prickles are absent in many species of section *Irenosolanum*. Jaffré *et al.* (1998) listed *S. pancheri* as near threatened.

Unpublished name: The epithet “*longipedunculatum*” appears on *Pancher s.n.* (P 00300141), a syntype.

***Solanum pseuderanthemoides* Schlechter**, Bot. Jahrb. Syst. 40, Beibl. 92: 33. 1908. *pro syn.*

Solanum horizontale Panch. ex Guillaumin, Ann. Mus. Col. Marseille, ser. 2, 9: 202.

1911. Type: France. New Caledonia, (“Sud-Bezirk, Plaine des Lacs”) Yahoué, forêt sentier de la Cascade, 200 m, Jan 1906 (fl, fr), *I. Franc 201a* (Holotype: B†; Lectotype, designated by Heine, 1976: P 00300030!; Isolectotypes: G 0035457!, UC 390808!, VT!; probable Isotypes: A!; BM 000846937!; K 000195703!; L; E “Yahoué”; NY 00172291!).

Figure 24.

Unarmed shrub to 2 m, the internodes to ca. 4.5 cm long. Stems moderately to densely pubescent when young with ferruginous, sessile porrect stellae, the stellae glabrescent, sometimes tardily so, ca. 0.3 mm broad, with 4–6(–8) rays, the midpoint flexed at the base $\pm 90^\circ$ and laying flat on the surface of the stem, typically directed distally, to ca. 4 times longer than than the rays.

Sympodia difoliate. Leaves simple, borne individually, 1.5–4.0 \times 0.6–2.1 cm, ca. 2–2.5 times as long as wide, ovate to elliptic, chartaceous, densely pubescent above with sessile porrect stellae when young, sparsely pubescent when mature, the stellae 0.2–0.3 mm in diameter, with 4–8 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, much longer than the rays, densely pubescent below with sessile porrect stellae when young, sparsely pubescent when mature, the stellae ca. 0.3 mm in diameter, with 6–8 rays, the midpoint of the

stellae nearly erect to strongly curved, longer than the rays; blade with 3–5 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly brochidodromous, distinct abaxially, nearly indistinct adaxially; blade base rounded to acute, \pm aequilateral; margin entire; apex acute to rounded; petiole 1.5–9.0 mm long, 0.3–0.7 mm in diameter, channeled above, densely pubescent in bud becoming sparsely pubescent with age. Inflorescence sessile, appearing lateral, extra-axillary, in the middle 1/3 of the internode, with 1–2 flowers, all apparently fertile or potentially so; pedicels 1.6–1.8 cm long, ca. 0.2 mm in diameter at the base, 0.7–0.8 mm in diameter below the calyx, straight to slightly arching, gradually increasing in diameter in the distal ca. 1/3, with scattered stellate hairs in flower, 1.5–1.9 cm long, 0.2–0.3 mm in diameter at the base, 0.9–1.2 mm in diameter below the calyx, straight to slightly arching, gradually increasing in diameter in the distal ca. 1/2, with scattered stellate hairs in fruit, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx moderately stellate-pubescent along the midrib of the sepals, the inter-sepal tissue of the calyx tube glabrous or nearly so, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.3–5.5 mm long, unarmed, appearing nearly truncate with caudate lobe tips, the tube 1.5–2.0 mm long, the tips to 3 mm long, the intersepal tissue slightly translucent when dry; splitting in the sinuses at anthesis and then the lobes dentate, $1.3\text{--}3.0 \times 1.2\text{--}1.5$ mm at anthesis, moderately stellate pubescent abaxially, glabrous adaxially, the calyx lobes in fruit $2.0\text{--}3.1 \times 1.3\text{--}1.5$ mm, sparsely pubescent with persistent hairs mainly along the midrib, appressed. Corolla ca. 2.0 cm in diameter, stellate with well developed, glabrous interpetalar tissue, white, the lobes ca. $6.0\text{--}6.2 \times 5\text{--}5.4$ mm, deltoid, the midrib $8.3\text{--}10.0 \times 1.6\text{--}2.5$ mm, oblong, moderately pubescent abaxially, glabrous with a few scattered stellae towards the apex adaxially, probably wide spread at anthesis. Stamens adnate to the corolla, the free

portion of the filament ca. 0.7 mm long; anthers 3.7–5.4 × 0.6–1.1 mm, straight, attenuate though not dramatically so, yellow, connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated. Ovary ca. 1.0 mm, globose, glabrous; style ca. 7.0 mm long, 0.3–0.4 mm in diameter, slightly longer than the stamens, emerging between the anther apices, filiform, straight, with a few sessile porrect stellae on the lower 1/3; stigma 0.4–0.5 mm in diameter, capitate. Fruit a berry, 0.4–0.7 cm in diameter, globose, black when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds many per fruit, 2.0–2.2 × 1.7–1.8 mm, flattened-reniform to flattened-orbicular and notched at the point of attachment, brown when dry, the surface the central area nearly smooth, the margin alveolate.

Distribution and ecology.— Along streams in humid forest from 100–200 m elevation in the southwestern part of the Grande Terre of New Caledonia. Figure 37.

Phenology.— Known to flower January–February, June, and November and fruit January, June, September–October. Likely flowering and fruiting year round.

Etymology.— The specific epithet refers to the genus *Pseuderanthemum* Radlk. (Acanthaceae).

Additional specimens examined. **FRANCE. New Caledonia.** *Franc s.n.* (P); (fl), *Franc s.n.* (S); Feb 1906 (fl), *Franc* (K); (fr) *Pancher s.n.* (C); 1861 (fr), *Pancher s.n.* (BM); *Pancher s.n.* (G×2); Jan (fr), *Pancher s.n.* (K); (fr), *Pancher s.n.* (L); (fr), *Pancher s.n.* (P); Jan (fr), *Pancher s.n.* (P); 100m, Jan (fr), *Pancher s.n.* (BM); Jan (fl), *Pancher s.n.* (P); Jan (fl, fr), *Pancher s.n.* (K, P); Jan (fl,

fr), *Pancher* 263 (P); Oct. *Pancher* 602 (P×2); 3 Oct (fr), *Pancher s.n.* (K). **South Province:**
Modile, près de Nouméa, Sep 1868 (fr), *Balansa* 487 (P); Thy Valley, Shangri La Track, 200 m, 12
Nov 1983 (fl), *Brinon* 1572 (NOU); Dumbea near Hermitage Stream, 500 ft, 26 Jan 1914 (fl),
Compton 150 (BM, NSW); Yahoué (fl), *Franc* 287A (A); Yahoié, Feb 1906 (fl), *Franc* 287(P);
Yahoué 20 Feb 1907 (fl), *Franc* 287A (P.); Koghi, 2 Feb 1909 (fl), *Franc* 287 (BM); Yahoui, 2 Feb
1909 (fl), *Franc* 287 (G); Yahoué 2 Feb 1909 (fl), *Franc* 287A (A, UC); Nouméa, Jun 1906 (fl, fr),
Gandoger s.n. (MO); Pont des Français, *Pancher* 438 (P).

Solanum pseuderanthemoides is quite distinctive. Though it has small leaves like several other species of *Solanum* from New Caledonia, it does not have short shoots or prickles. The species has been reported as holding its branches horizontal, giving herbarium specimens a natural two-dimensional look unlike the flattened look of most herbarium specimens. The species also has a pronounced difference between the ferruginous pubescence of the stem and the yellow pubescence of the petioles, which is unique within *Solanum* section *Irenosolanum*. In 2009, the type locality, along Hermitage Stream, was visited but no living material was discovered. Jaffré *et al.* (1998) listed this species as critically endangered; it has been collected once in the last ca. 100 years.

The probable isotypes from A, BM, K, and NY have skeletal labels and the number 201. However, it is very likely that these are duplicates of *Franc* 201a.

***Solanum pseudopedunculatum* D. McClell. sp. nov.**

Type: Fiji. Vanua Levu. Mathuata, Summit ridge of Mt. Numbuiloa, east of Lambasa, 500–590 m, 29 Oct – 6 Nov 1947 (fl, fr), *Smith 6467* (Holotype: US 1966675!; Isotypes: A!, BISH 181936!, K!, L 0531787!, NY 00828289!, P 00315297!, S!)

Figure 25.

Unarmed shrub or small tree to 4 m, the internodes to 6.5 cm long. Stems densely pubescent with yellow, sessile or stipitate porrect stellae, the stipes to ca. 0.2 mm, the stellae rate of tardily deciduous, 0.3–0.4 mm broad, with 4–8 rays, the midpoint erect or clinate less than 90° to flexed at the base $\pm 90^\circ$, shorter than the rays; bark reddish brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, geminate, the blades of major leaves 6.0–15.0 \times 2.0–4.7 cm, ca. 2.5–4.2 times as long as wide, oval to elliptic, chartaceous, the minor leaves \pm equal as the major leaves, both major and minor leaves moderately pubescent above with sessile and stipitate porrect stellae and minute glandular hairs when young, with scattered pubescence when mature, the stellae 0.4–0.7 mm in diameter, with 4–8 rays, the stipes to ca. 0.2 mm long, the midpoint of the stellae erect to flexed at the base $\pm 90^\circ$, \pm equal to to longer than the rays, the glandular hairs 0.05 mm long, densely pubescent below with sessile and stipitate porrect stellae and minute glandular hairs when young, sparsely to moderately pubescent when mature, the stellae 0.5–0.8 mm in diameter, with 4–8 rays, the stipes to ca. 0.2 mm long, the midpoint of the stellae erect, curved, clinate less than 90°, \pm equal to to longer than the rays, the glandular hairs ca. 0.05 mm long; blade with 6–8 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly

brochidodromous, raised abaxially, distinct adaxially; blade base cuneate to attenuate, aequilateral or oblique; margin entire; apex acuminate, occasionally obtuse; petiole 0.8–2.0 cm long, 0.5–1.0 mm in diameter, channeled above, pubescent all over. Inflorescence to ca. 6 mm in flower, 4.0–12.5 mm in fruit, appearing lateral, extra-axillary, in the middle 1/3 of the internode, unbranched, with few to 8 flowers, all apparently fertile or potentially so, the axes densely pubescent in flower, moderately pubescent in fruit, with sessile and stipitate porrect-stellate; pseudopeduncle in flower to 4.3 mm long, ca. 0.5 mm in diameter, in fruit 2.6–6.5 mm long, 0.6–1.0 mm in diameter; pedicels 0.8–1.4 cm long, 0.4–0.5 mm in diameter at the base, 0.8–1.4 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal 1/4–1/3, moderately to densely pubescent, the bases congested, to ca. 1.0 mm apart in flower, 1.7–2.3 cm long, 0.3–0.6 mm in diameter at the base, 1.1–1.6 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal 1/3–1/2, sparsely pubescent, the bases congested to ca. 2.4 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds globose, the calyx moderately stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.0–1.6 mm long, appearing nearly truncate with minute deltate or apiculate lobe tips, the tube 0.4–0.8 mm long, the lobe tips 0.5–0.8 mm long, the intersepal tissue opaque when dry; not splitting or splitting in the sinuses during fruit development and then the lobes dentate; lobes sparsely to moderately pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 0.5–0.9 × 1.5–1.7 mm, sparsely appressed. Corolla ca. 1.5 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white, the lobes 3.1–4.2 × 2.2–2.9 mm, deltoid, the midrib 5.2–6.0 × 2.1–2.7 mm, lanceolate, moderately abaxially, ±glabrous adaxially, apparently spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.6–0.9 mm long; anthers 1.5–2.1

× 1.0–1.2 mm, acuminate, straight, scarcely attenuate, yellow, spreading, with minute apical pores, the pores directed distally, ±restricted to the apex, the lateral sutures entire, remaining intact with age. Ovary ca. 1.2 mm, globose, with a few stellate hairs and a few minute and simple glandular hairs; style 3.1–4.0 mm long, 0.3–0.4 mm in diameter, longer than the stamens, emerging between the anther apices, filiform, straight, sparsely pubescent with minute glandular hairs restricted to the basal ca. 1/3; stigma 0.5–0.6 mm in diameter, capitate. Fruit a berry, 0.7–1.0 cm in diameter, globose, variously reported as orange, red becoming black, and purple when mature, glabrous; exocarp thin, glossy; apparently juicy. Seeds many per fruit, 1.8–2.0 × 2.3–2.8 mm, flattened-orbicular and notched at the point of attachment to flattened-reniform or flattened-irregular, yellow-tan when dry, the surface with the central area nearly smooth, the margin alveolate.

Distribution and ecology.— In forest and secondary thickets on the islands of Kanduvau, Vanua Levu, and Viti Levu, Fiji, from 50–1150 m elevation. Figure 41.

Phenology.— Known to flower and fruit February–March and July–December.

Etymology.— The specific epithet is derived from the pseudo-peduncle of the inflorescence of this species.

Additional specimens examined.

FIJI. Dec 1904 – Mar 1905 (fr), *Goddard s.n.* (NSW). **Kandavu:** Hills above Namalata and Ngaloa Bays, 200–400 m, 13–18 Oct 1933 (fl, fr), *Smith 141* (BISH, GH, K, NY, P, S, UC, US). **Vanua Levu:** Mt. Delaikoro, Macuata, 3050 ft, 21 Aug 1962 (fl, fr), *Parham & Koroi 12792* (BISH); Thakaundrove, Southwestern slope of Mt. Mbatini [Batini], 300–700 m, 28–29 Nov 1933 (fl, fr), *Smith 603* (GH, K, NY, P, S, UC, US). **Viti Levu:** Serua district, 500 ft, 14 Jun 1961 (fl, fr), *Bola 42* (K); Mba [“Tholo North”], Sovutawambu, near Nandrivatu, 750–800 m, 27 Feb – 4 Mar 1941 (fl, fr), *Degener 14594* (A, K, NY, US); Nadarivatu, 2700 ft, 1907 (fl, fr), *Gibbs 615* (BM×2); Mba (formerly Tholo North), Western and southern slopes of Mt. Tomanivi (Mt. Victoria), 850–1150 m, 7 Jul – 18 Sep 1947 (fl, fr), *Smith 5273* (A, K, L, NY, P, S, US); Serua, Hills west of Waivunu Creek, between Ngaloa and Korovou, 50–150 m, 23 Nov – 7 Dec 1953 (fl, fr), *Smith 9223* (BISH, GH, K, L, NY, P, S, UC, US); Nadarivatu, road to Suva, 27 Nov 1906 (fl, fr), *Thurn 294* (K).

Smith (1991) misapplied the name *S. inamoenum* to this species though the two species are not very similar morphologically, with notable differences in leaf and stem pubescence, inflorescence structure, and habitat preference. *Solanum pseudopedunculatum* is much more similar to *S. ratale* but can be distinguished by its taller habit, inflorescence with a pseudo-peduncle, longer pedicels, and much larger corolla, anthers, and fruit.

***Solanum ratale* D. McClell. sp. nov.**

Type: Fiji. Viti Levu: Western division. Tholo North. Village of Nadarivatu, Fish Hatchery 2600 ft, 9 Feb 1941 (fl, fr), *Degener 14324* (Holotype: A!; Isotypes: K!, UC 1016245!, US 1943693!)

Figure 26.

Unarmed shrub or small tree to 1.5 m, the internodes to 3.4 cm long. Stems densely pubescent with yellow-ferruginous, sessile or stipitate porrect stellae, stipes of various lengths to 0.2 mm long, the stellae tardily glabrescent, 0.3–0.5 mm broad, with 6–8 rays, the midpoint \pm erect or clinate less than 90° , \pm equal to to longer than the rays; bark reddish brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, geminate, the blades of major leaves $4.3\text{--}10.4 \times 1.3\text{--}2.6$ cm, 2.8–5.2 times as long as wide, narrowly lanceolate to narrowly elliptic, chartaceous to subcoriaceous, the minor leaves $2/3$ as large to \pm equal to the major leaves, both major and minor leaves densely pubescent at the base becoming sparsely pubescent distally above with sessile and stipitate porrect stellae and minute glandular hairs when young, with isolated, regularly distributed hairs across the lamina and moderate pubescence along the midveins when mature, the stellae 0.4–0.6 mm in diameter, with 4–8 rays, the stipes to 0.6 mm long, the midpoint of the stellae \pm erect, longer than the rays, the glandular hairs ca. 0.04 mm long, very densely pubescent below with sessile and stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.5–0.7 mm in diameter, with 6–8 rays, the stipes to 0.1 mm long, the midpoint of the stellae erect, longer than the rays; blade with 5–7 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the

lateral veins weakly brochidodromous, raised abaxially, raised adaxially; blade base cuneate or rounded, aequilateral or oblique; margin entire; apex acuminate; petiole 0.4–1.3 cm long, 0.6–1.0 mm in diameter, channeled above, moderately to densely pubescent all over. Inflorescence to 1.3 cm long in flower, 1.1–1.8 cm long in fruit, appearing lateral, extra-axillary, emerging from the middle 1/3 of the internode, typically unbranched, occasionally forked, with 4–13 flowers, all apparently fertile or potentially so, the axes moderately to densely pubescent, with sessile and stipitate porrect stellae; peduncle in flower to 4.3 mm long, to 0.6 mm in diameter, the branches to 4.3 mm long, ca. 0.5 mm in diameter, in fruit 2.2–4.6 mm long, to 0.6 mm in diameter, the branches not seen; pedicels 0.6–0.8 cm long, ca. 0.3 mm in diameter at the base, ca. 0.6 mm in diameter below the calyx, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal ca. 1/3, moderately to densely pubescent, the bases congested to 1.4 mm apart in flower, 0.8–1.4 cm long, ca. 0.5 mm in diameter at the base, 1.4–2.0 mm in diameter below the calyx, straight, gradually increasing in diameter in the distal ca. 2/3, sparsely to moderately pubescent, the bases congested to 2.2 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds globose, the calyx moderately stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.5–2.3 mm long, appearing nearly truncate with caudate lobe tips, the tube 0.6–1.1 mm long, the lobe tips 0.9–1.3 mm long, the intersepal tissue opaque when dry; not splitting or splitting in the sinuses during fruit development and then the lobes dentate, moderately pubescent abaxially, glabrous adaxially, the calyx lobes in fruit $0.8\text{--}2.3 \times 1.3\text{--}1.6$ mm, sparsely to moderately pubescent, appressed. Corolla ca. 0.5 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes $3.2\text{--}3.8 \times 1.9\text{--}2.2$ mm, oblong, the midrib $4.5\text{--}4.9 \times 1.3\text{--}2.0$ mm, oblong, moderately pubescent abaxially, glabrous adaxially, spread wide at anthesis.

Stamens adnate to the corolla, the free portion of the filament ca. 0.5 mm long; anthers ca. 1.3 × 0.6 mm, oblong, somewhat incurved, apparently yellow, spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures entire. Ovary ca. 0.8 mm, globose, with a few simple glandular hairs at the apex; style ca. 2.8 mm long, ca. 0.3 mm in diameter, longer than the stamens, emerging between the anther apices, cylindrical, straight, glabrous; stigma ca. 0.5 mm in diameter, capitate. Fruit a berry, 0.5–0.7 cm in diameter, globose, black when mature, glabrous; exocarp thin, glossy; endocarp apparently juicy. Seeds few per fruit, 2.3–2.5 × 1.5–1.9 mm, flattened-reniform, yellow-tan when dry, the surface with the central area nearly smooth, the margin alveolate.

Distribution and ecology.— This species has been collected in several areas on Viti Levu. It is known from elevation of 200–800 m but may grow at lower elevation near Suva. *Degener 14324* was found in logged off forest. Figure 41.

Phenology.— Known to flower and fruit February, May, and June.

Etymology.— The specific epithet which means “pertaining to rafts” references a note on *Horne 679* indicating that the light wood was used for making rafts.

Additional specimens examined. **FIJI. Viti Levu: Central Division.** near Lutu, May 1878 (fl, fr), *Horne 595* (K, GH); near Suva, Jun 1978 (fl, fr) *Horne 679* (K, GH).

Very little is known about *S. ratale* due to the limited herbarium material. It is most similar to *S. pseudopedunculatum* but can be distinguished by its shorter habit, inflorescence with a true peduncle, shorter pedicels, and much smaller corolla, anthers, and fruit.

Solanum sandwicense Hook. & Arn., Bot. Beech. Voy. 92. 1832. Type: U.S.A., Hawaiian Islands.

cf. Oahu, s.d. (fl), *Beechey s.n.* (Lectotype, *hic designatus*: E 00243620!; Isotypes: K×2!, BM 000846694!).

Solanum sandwicense Hook. & Arn. var. *kavaiense* A. Gray, Proc. Amer. Acad. Arts 6: 43.

1866. *Solanum kavaiense* (A. Gray) Hillebr., Fl. Hawaiian Isl. 305. 1888. U.S.A., Hawaiian Islands, Kauai, 1831-1842 (fl), *Wilkes s.n.* (Holotype: US 78691!).

Solanum woahense Dunal, in DC., Prodr. 13(1): 268. 1852. *pro syn.* *Solanum sandwichense*

Dunal, in DC., Prodr. 13(1): 268. 1852. Cited: U.S.A., Hawaiian Islands, Oahu [“Woahoo”], May 1825, *Macrae s.n.* (G-DC (at K)!, E00243617!, possible duplicate W 0015502! though this specimen does not have date). Type: U.S.A., Hawaiian Islands, Oahu [“Woahoo”], *Macrae 239* (Holotype: G-DC, =IDC microfiche 800-61.2082:I.6!).

Solanum woahense Dunal var. *erosocrenulatum* Dunal, in DC., Prodr. 13(1): 269. 1852. Type:

Hawaiian Islands, *C. Gaudichaud 238* (Holotype: G-DC, =IDC microfiche 800-61.2082:I.7!).

Solanum honopuenes H. St. John, Phytologia 64: 170. Jan. 1988. Type: U.S.A., Hawaiian

Islands, Kauai Island, Kalalau Trail, 3 Jul–18 Aug 1917 (fl, fr), *C. Forbes 1081.K* (Holotype: BISH 70019!).

Figure 27.

Unarmed shrub or small tree to ca. 6 m, the internodes to 6.9 cm long. Stems densely pubescent with yellow-ferruginous to ferruginous, sessile or stipitate porrect stellae, stipes of various lengths to 3.8 mm, the stellae tardily deciduous, 0.3–0.8 mm broad, with 6–10 rays, the midpoint erect or clinate less than 90°, shorter than to longer than the rays; bark reddish brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, geminate, the blades of major leaves 4.5–21.9 × 1.8–12.1 cm, 1.5–2.5 times as long as wide, lanceolate to ovate, chartaceous, the minor leaves 2/3 as large as to ±equal to the major leaves, both major and minor leaves densely pubescent above with sessile and stipitate porrect stellae and sometimes minute glandular hairs when young, ±glabrous or very sparsely pubescent when mature, the stellae 0.2–0.9 mm in diameter, with 4–9 rays, the stipes to 0.7 mm long, the midpoint of the stellae erect, shorter than to longer than the rays, the glandular hairs ca. 0.04 mm long, densely pubescent below with stipitate porrect stellae when young, densely pubescent when mature, the stellae 0.4–1.2 mm in diameter, with 5–8 rays, the stipes to 0.1 mm long, the midpoint of the stellae erect, shorter than to ±equal to the rays; blade with 5–7 veins on either side of the midvein, the midvein raised abaxially, distinct adaxially, the lateral veins weakly brochidodromous or semicraspedodromous, raised abaxially, distinct adaxially; blade base truncate, rounded, or cuneate, aequilateral or oblique; margin entire to lobed with several acute lobes on either side of the midrib; apex acute to acuminate; petiole 0.5–5.8 cm long, 0.6–2.4 mm in diameter, terete or channeled above, densely pubescent all over. Inflorescence to 12.9 cm in flower, to 14.9 cm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, sometimes appearing nearly leaf opposed, unbranched or forking up to 10

times, with 17–145 flowers, all apparently fertile or potentially so, the axes densely pubescent, with sessile or stipitate porrect stellae; peduncle in flower 1.1–8.3 cm long, 0.5–1.4 mm in diameter, the branches to 8.2 cm long, 0.4–1.3 mm in diameter, in fruit 0.8–3.4 cm long, 1.0–4.5 mm in diameter, the branches to 8.9 cm long, 0.5–2.2 mm in diameter; pedicels 0.6–1.6 cm long, 0.3–0.6 mm in diameter at the base, 0.6–1.0 mm in diameter below the calyx, straight, bent to $\pm 90^\circ$ below the calyx, increasing in diameter in the distal 1/4 or less, densely pubescent, the bases well spaced to 8.8 mm apart in flower, 1.2–2.6 cm long, 0.6–2.6 mm in diameter at the base, 1.6–4.8 mm in diameter below the calyx, straight or arching, not bent or bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal 1/4–1/3 with a distinct bulge directly below the calyx, \pm glabrous to moderately pubescent, the bases well spaced to 10.5 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 4–6-merous. Buds globose, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud ridged. Calyx 1.4–4.0 mm long, appearing nearly truncate with apiculate to caudate lobe tips, the tube 0.6–1.2 mm long, the lobe tips 0.8–2.9 mm long, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, densely pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 1.1–3.4 \times 1.0–2.6 mm, glabrous to moderately pubescent, appressed or reflexed. Corolla 1.2–2.3 cm in diameter, stellate with poorly or well-developed, glabrous interpetalar tissue, white or white with purple veins, the lobes 5.1–8.7 \times 3.2–7.0 mm, oval, the midrib 5.8–11.4 \times 2.8–6.3 mm, lanceolate to ovate, moderately to densely pubescent abaxially, glabrous at the base becoming sparsely pubescent towards that apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.5–1.5 mm long; anthers 1.9–2.8 \times 0.8–1.3 mm, acuminate, arcuate, markedly attenuate, yellow, spreading, with minute apical pores, the pores

directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact. Ovary 0.8–1.2 mm, globose, white or cream, densely pubescent all over with sessile and stipitate porrect stellae; short styles 0.9–1.9 mm long, shorter than the anthers, long styles 2.3–3.1 mm long, longer than the anthers, emerging between the apices of the anthers, both short and long styles 0.2–0.3 mm in diameter, filiform, straight, moderately to densely stellate pubescent on the basal 2/3, the hairs sessile and stipitate porrect stellae; stigma 0.4–0.5 mm in diameter, capitate, green or white to cream. Fruit a berry, 0.7–1.7 cm in diameter, globose, the immature fruits evenly green, black when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 3.2–4.9 × 3.9–6.5 mm, flattened-reniform, yellow-tan when dry, the surface ±smooth in the central area, reticulate along the margin.

Distribution and ecology.— Rainforest on the islands of Kauai and Oahu, Hawaiian Islands, from 230–1100 m elevation. Figure 35.

Phenology.— Flowering and fruiting February–October.

Etymology.— This species is named for the Sandwich Islands, an early name for the Hawaiian Islands.

Additional specimens examined. **USA. Hawaiian Islands.** (fl, fr), *Andersson s.n.* (S×2); (fl), *Beechey s.n.* (K); (fl, fr), *Gaudichaud s.n.* (L); Sep and Oct 1836 (fl, fr), *Gaudichaud s.n.* (L×2, P×2); (fl, fr) *Hillebrand s.n.* (K); (fr), *Hillebrand s.n.* (B); (fl, fr), *Hillebrand s.n.* (BM); (fr), *Hillebrand s.n.* (S); (fl, fr), *Hillebrand s.n.* (W); (fl, fr), *Hillebrand 115* (GH, K). **Oahu:** Honolulu,

(fl, fr), *Andersson s.n.* (S); Honolulu, 1852 (fl, fr), *Andersson s.n.* (S×3); Nuuanu Pali, Jun 1852 (fl, fr), *Andersson s.n.* (S); Puu Hapapa, 2600 ft, 16 Mar 1930 (fl, fr), *Bean et al. 489* (UC); 1845–47 (fr), *Didrichsen 3475* (W); Between Puu Manawahua and Palikea along ridge, 27 Sep 1931 (fl, fr), *Degener s.n.* (NY); Ekahanui, 19 Apr 1936 (fl, fr), *Degener et al. 10850* (BH, BRI, CAS, F, G, GH, MICH, MO, NY, P, US); Palikea, near von Holt cabin, 27 Sep 1931 (fl, fr), *Degener 18229* (A, MO, NY); Punaluu, May 1910, (fl, fr), *Faurie 867* (A, BM, G, P); Koulanloa Mts. Between Punahu and Kaipapau, 5–13 May 1909 (fl, fr), *Forbes 137.O* (M); Mokaha Valley, Koala Range 12–19 Feb 1909 (fl, fr), *Forbes 1115O* (BH, MO, P, US); Koolauloa Mts. between Punaluu and Kaipapau, 8–13 May 1909 (fl), *Forbes & Thompson 137O* (BISH, K, M, MO, UC); Palehua, Waianae Range, 1–4 Apr 1911 (fl, fr), *Forbes 1687O* (A, F, NY); (fl, fr), *Gaudichaud s.n.* (GH); 1300 ft, 1897 (fl, fr), *Guppy s.n.* (K×2); Puu Hapapa, Waianaueka, 2000 ft, 16 Mar 1930 (fl, fr), *Hosaka 171* (CAS); (fl, fr), *Hillebrand s.n.* (L); 1850 (fl, fr), *Leemann 2273* (K); May 1825 (fl, fr), *Macrae s.n.* (E, K); (fl), *Macrae s.n.* (W); 1867 (fl, fr), *Mann & Brigham 202* (BH, BM, F×2, G, GH×2, MO, NY×2, US); Waianea Mts. Napepeiauolelo Gulch in subgulch east of Pritchardia Gulch, 2400 ft, 21 Apr 1987 (fl, fr), *Perlman & Obata 5677* (BISH, F, MO, PTBG, RSA); Waianae Mts., Honouliuli, North Palawai Gulch, north facing slope, 2400 ft, 12 Jul 1987 (fl, fr), *Perlman & Obata 6160* (PTBG, US); 1851–1855 (fl, fr), *Rémy 443* (P); 1851–1855 (fr), *Rémy 445* (P×2, US); 1851–1855 (fl, fr), *Rémy 446* (P×2); Punaluu, Koolau Mts, Aug 1911 (fl, fr), *Rock 8829* (A×2, BH, BISH, GH, K, L, NY, R, UC, US); Puu Hapapa, Waianea Mts., Honouliuli, 2600 ft, 16 Mar 1930 (fl), *St. John 10421* (CAS, K, NY, P, US); Palikea, Waianae Mts., Honouliuli, 2800 ft, 30 May 1947 (fl, fr), *Sakimura s.n.* (BISH); Puu Hapapa, Waianea Mts., Honouliuli, 2600 ft, 25 Oct 1931 (fl, fr), *Sideris s.n.* (NY); Waianea, near Palehua, 650 m , 25 Aug 1922 (fr), *Skottsberg 323* (S); Mt. Kalena, 14 Sep 1924 (fr), *Topping 2855* (UC); 1868–1871 (fl, fr), *Wawra 1769* (W×2); Waianae

Range, South Palawai Gulch, Honouliuli, 2500 ft, 27 Mar 1948 (fl, fr), *Webster 1437* (NY, US); Ewa District, Waianea Mountains, North Palawai Gulch south fork and south branch, 750–850 ft, 12 Sep 1991 (fl), *Wood et al. 1213* (PTBG). **Kauai:** Kokee, at head of Kumuweia Ridge, 1200 m, 25 Jul 1940 (fl, fr), *Bryan 1441* (BISH, L); Kokee, Puu ka Ohelo trail, 13 Aug 1938 (fl), *Cranwell et al. 2860* (S); Kohua ridge, Kawaia trail, ca. 1200 m, 19 Aug 1938 (fl, fr), *Cranwell et al. 3909* (S); Waimea Drainage Basin, west side, 3 Jul – 18 Aug 1917 (fl, fr), *Forbes 788.K* (BISH); Kokee State Park, Kumuwela Ridge Rd ca 1.5 miles from Mohini Rd, 3700 ft, 1 Jul 1987 (fl), *Flynn et al. 2233* = *Lorence et al. 5277* [a hand written note on *Flynn 309* (PTBG) specimen says “Same plant as *Flynn 2233* and *Lorence 5277* Flynn 14.X.1996”] (BISH); ridge west of the Hanapepe River, 29 Jul 1985 (fl, fr), *Heller 2638* (L×2); Kokee, in a gulch about one mile east of Kalalau Lookout, 26 Aug 1960 (fl, fr), *Lamoureux 1525* (BISH); Halemanu, 17 Feb 1927 (fl, fr), *MacDaniels 763* = *MacDaniels 382* (BISH); Kokee, Nov 1938 (fl, fr), *Meebold 26344* (M×2); Kokee, Kokee-Haena Road, on edge of open woods, 4,000 ft, 9 Jul 1959 (fl), *Pearsall 438* (K, M); Halemanu, 14–26 Feb 1909 (fl), *Rock 1628* (M); Kaholuamano, Oct 1911 (fl), *Rock 9014* (K); Lihue, Oct 1929 (fl, fr), *Russ s.n.* (BISH); Kokee, Waimea, Na Pali-Kona Forest Reserve, 26 Dec 1930 (fr), *St. John et al. 10702* (K); Kilauea Lookout, Kalalau Valley, 4000 ft, 21 Dec 1947 (fr), *St. John et al. 22897* (L), Waimea, forest of Kokee, 27 Oct 1922 (fl, fr), *Skottsberg 973* (BISH, S); near Kokee, along road to Kalalau Lookout, ca. 2500 ft, 19 Jun 1955 (fl), *Stone 854* (BISH); 1868–71 (fl, fr), *Wawra 2081* (W×3); Mokuone Flats, along Mokuone River, 3200 ft, 13 Jun 1985 (fl), *Williams s.n.* (BISH).

Cultivated. U.S.A. Hawaiian Islands. Kauai: National Tropical Botanical Garden, McBryde Garden, plant propagation range, cultivated from *Agurajua s.n.* Kauai, Kokee, 19 Apr 2008 (fl, fr), *McClelland 450* (BISH, NY, PTBG); National Tropical Botanical Garden, McBryde

Garden plant propagation range, source Kauai, 19 Apr 2008 (fl, fr) *McClelland 454* (BISH, NY, PTBG)

Once widespread and frequent (MacCaughey, 1917), on Oahu *S. sandwicense* is restricted to one reintroduced population. On Kauai, about fifteen wild individuals are known. Wagner *et al.* (1999) listed *S. sandwicense* as endangered. Conservation International and the National Tropical Botanical Garden include this species in their conservation efforts on Oahu and Kauai respectively.

The specimens from Oahu and Kauai have at times been recognized as different species. Some specimens from Kauai have large lobes on leaves and ferruginous hairs with much longer stipes on the stems and leaves; however, these simply represent an extreme variant of the species. Still, all surviving forms of the species need to be protected. And, study on the “population” level may reveal genetic differences between the individuals of Oahu and Kauai.

The lectotype was selected from one of the most complete specimens with flowers and fruiting pedicles though the fruits are missing.

Unpublished name: The variatal epithet “*globosifructum*” appears on several specimens, (*Wawra 1769* (W 0015497, W 0015498), *Andersson s.n.* (S)).

***Solanum semisucculentum* D. McClell. sp. nov.**

Type: France. New Caledonia. North Province, Tiébaghi Massif, ca. 12 air-km northwest of Koumac, 8 Nov 1980 (fl, fr), *McPherson 3303* (Holotype: NOU 017344!; Isotypes: MO 2924404!, NSW 594228!, PTBG 032935!).

Figure 28.

Unarmed shrub 1.5 m, the internodes to 4.5 m long. Stems glabrous or with the occasional yellow-ferruginous, sessile porrect stellae, the stellae soon decedious, 0.1–0.3 mm broad, with 7–11 rays, the midpoint flexed at the base $\pm 90^\circ$ or more and laying flat against the other rays of the hair, \pm equal to the rays; bark grey, the young stems bright purple, lacking a sloughing layer. Sympodia difoliate. Short shoots absent. Leaves simple, borne individually, 2.3–11.2 \times 1.0–3.4 cm, 2.3–3.6 times as long as wide, lanceolate to elliptic, semisucculent, \pm glabrous to very sparsely pubescent above with sessile porrect stellae and minute glandular hairs when young, glabrous when mature, the stellae 0.2–0.3 mm in diameter, with 8–10 rays, the midpoint of the stellae flexed at the base $\pm 90^\circ$ or more and laying against the rays, \pm equal to the rays, the glandular hairs 0.7 mm long, glabrous below when young, glabrous when mature; blade with 6–8(–9) veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly or strongly brochidodromous, raised abaxially, distinct adaxially; blade base rounded, cuneate, or shortly attenuate, aequilateral or oblique; margin entire; apex acute to acuminate; petiole 0.6–3.0 cm long, 0.6–0.9 mm in diameter, channeled above, glabrous or sparsely pubescent on the adaxial surface. Inflorescence to 3.8 cm in flower, to 34.8 mm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, unbranched, with

up to 23 flowers, all apparently fertile or potentially so, the axes nearly glabrous, with sessile porrect stellae and minute glandular hairs; peduncle in flower 1.0–1.4 cm long, 0.4–0.6 mm in diameter; pedicels 0.9–1.2 cm long, 0.2–0.4 mm in diameter at the base, 0.6–0.8 mm in diameter below the calyx, straight, bent $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal $1/3$ – $1/2$, glabrous, the bases laxly spaced to 4.9 mm apart in flower, 1.5–2.4 cm long, 0.6–1.1 mm in diameter at the base, 1.6–2.9 mm in diameter below the calyx, straight or arching, gradually increasing in diameter in the distal $1/2$ – $2/3$, glabrous, the bases laxly spaced to 6.9 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5(–6)-merous. Buds ovate, the calyx \pm glabrous to sparsely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 1.3–5.3 mm long, appearing nearly truncate with apiculate to caudate lobe tips, the tube 0.5–1.1 mm long, the lobe tips 0.7–4.2 mm long, the intersepal tissue translucent when dry; splitting in the sinuses during fruit development and then the lobes dentate, sparsely pubescent abaxially, glabrous adaxially, the calyx lobes in fruit 1.8 – 2.8×0.9 – 3.5 mm, glabrous, appressed or reflexed. Corolla 1.2–2.5 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes 5.5 – 8.9×5.4 – 6.8 mm, deltoid, the midrib 5.8 – 11.8×1.7 – 2.6 mm, oblong, moderately to densely pubescent abaxially, glabrous at the base becoming densely stellate pubescent towards the apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.6–1.0 mm long; anthers 4.2 – 6.2×1.3 – 1.7 mm, acuminate, straight, markedly attenuate, yellow, \pm spreading, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact with age. Ovary ca. 1.0 mm, globose, with mostly glabrous, densely pubescent at the apex only; short styles 1.0–1.3 mm long, ca. 0.2 mm in diameter, shorter than the anthers, long styles 7.7–8.3 mm long, ca. 0.3 mm in

diameter, longer than the stamens, emerging between the anther apices, filiform, straight, moderately to densely pubescent on the basal 1/2–2/3 portion; stigma 0.4–0.6 mm in diameter, capitate, green. Fruit a berry, 0.8–1.3 cm in diameter, globose, the immature fruits evenly green, red to orange when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, ca. 2.2×2.3 –2.8 mm, flattened-orbicular and notched at the point of attachment, red-brown or tan when dry, the surface alveolate under a \pm smooth, translucent seed coat.

Distribution and ecology.— *Solanum semisucculentum* is a serpentine endemic and is restricted to the ultramaphic mountains of the western side of the Grande Terre. It is found in the North Province from (50–)100–700(–1200) m elevation. This species grows in an open shrubby habitat (maquis) on lateritic soils which are fast draining; the semisucculent leaves of this species are likely an adaptation for these harsh conditions. Figure 39.

Phenology.— Flowering and fruiting year round.

Etymology.— The specific epithet indicates the texture of the leaves and stems. This texture is best described as semisucculent and is highly unusual in the genus *Solanum*.

Additional specimens examined. **FRANCE. New Caledonia.** Mine Oubliée, 650 m, 7 Jan 1962 (fl, fr), *Catala-Stucki 160* (G); 1861–1867 (fl), *Vieillard s.n.* (G). **North Province:** Dôme de Tiébaghi, 22 Jan 1976 (fl, fr), *Blanchon 1444* (NOU, P); Tiébaghi, 24 Sep 1961 (fl, fr), *Denizot s.n.* (P); Dôme de Tiébaghi, 8 Nov 1980 (fl), *Hoff 2975* (NOU); Massif de Boulinda, 500 m, 9 Nov 1971 (fl, fr), *Jaffré 492* (L, NOU, P); Massif du Boulinda, 100 m, Mar 1974 (fl, fr), *Jaffré 1283* (NOU \times 2, P);

Dôme de Tiébaghi, 350 m, 15 Nov 1975 (fr), *Jaffré 1415* (NOU, P); Plateau de la Tiébaghi, 500 m, 15 Nov 1976 (fl, fr), *Jaffré 1824* (NOU, P); Massif de Boulinda, above river Ouaha, east of Muéo, 100–200 m, 21.20 S, 165.05 E, 12 Dec 1973 (fl), *Jaffré 19234* (NOU, P); Massif Boulinda, secteur Col Nekoro, 27 Jul 1972 (fl), *Jaffré 2183* (NOU); Dôme de Tiébaghi, on the plateau south of the old town, 20° 27' 23.7" S, 164° 12' 48.5" E, 590 m, 15 Jul 2009 (fl, fr), *McClelland & Nee 554* (MO, NOU, NY, P); Dôme de Tiébaghi, Pente Sud-Ouest du Dôme de Tiébaghi, 300–500 m, 9 May 1966 (fl), *McKee 14921* (K, P); pente nord du Mt. Kaala, 400–700 m, 9 Jul 1966 (fl, fr), *MacKee 15272* (L); pente Nord du Mont Kaala, 700 m, 25 Dec 1966 (fl, fr), *MacKee 16152* (K, L, NOU, NY); Haute Népoui, Oué Péoué, contrefort sud du Kopéto, 500 m, 8 Jul 1970 (fl), *McKee 22193* (P); Mt. Boulinda, 1200 m, 1 Jun 1972 (fl, fr), *McKee 25571* (P); Dôme de Tiébaghi, 400 m, 30 Nov 1972 (fl, fr), *McKee 25953* (K, L, P); Nekoro, 200 m, 21 May 1977 (fr), *McKee 33195* (NOU, P); Dôme de Tiébaghi, Plateau central, 550 m, 8 Jul 1978 (fl, fr), *McKee 35432* (L, NOU, P); Koumac, Chagrin, 300 m, 8 Jan 1983 (fr), *McKee 41156* (P); Tiébaghi Massif, north of Koumac, 550 m, 20 Dec 1983 (fl, fr), *McPherson 6169* (MO, NOU, PTBG); Pindai pres de Nekoro, 50 m, 1 Apr 1988 (fl), *Morat 8049* (P); Boulinda, base, 165° 5' 55.6" E, 21° 18' 52.8" S, 23 Jan 2008 (fl, fr), *Munzinger et al. 4959* (NOU); Dôme de la Tiébaghi, 400–600 m, 25 Jul 2007 (fl, fr) *Pillon et al. 775* (NOU); pentes du Dôme de Tiébaghi, 13 Jun 1974 (fl, fr), *Sévenet 685* (NOU); route minière d'accès ou Bulinda [Boulinda], 20 Feb 1978 (fl, fr), *Suprin 254* (NOU); Mt. Boulinda, 550 m, 26 Apr 1965 (fr), *Veillon 129* (NOU); Dôme de Tiébaghi, plateau, ca. 550 m, 17 Aug 1965 (fl), *Veillon 361* (NOU); Mt. Boulinda, ca. 400 m, 26 Jul 1967 (fl), *Veillon 1268* (K, NOU); Dôme de Tiébaghi, ca. 550 m, 25 Nov 1967 (fl, fr), *Veillon 1457* (NOU, P); pentes ouest du Dôme de Tiébaghi, ca. 500 m, 27 Oct 1943 (fl, fr), *Virot 1274* (A, NOU).

Cultivated. AUSTRALIA. South Australia. Waite Agricultural Research Institute, from seeds of *McKee 41156* ex New Caledonia, 30 Aug 1984 (fl), *Symon s.n.* (NY).

Heine (1976) applied the name *S. styraciflorum* to *S. semisucculentum*. The type of *S. styraciflorum* was probably destroyed at B during the Second World War, and no duplicates have been traced. However, the name *S. styraciflorum* clearly does not apply to *S. semisucculentum* because the protologue disagrees with in a number of ways. Also, specimens matching the protologue of *S. styraciflorum* exist. Notable differences between *S. semisucculentum* and the protologue of *S. styraciflorum* include pubescence of the petiole and fruit size. The petioles of *S. styraciflorum* were described as densely stellate-subvillose above whereas those of *S. semisucculentum* are glabrous or very sparsely pubescent and could never be described as subvillose. The fruits of *S. styraciflorum* were reported as ca. 6.0 mm in diameter while those of *S. semisucculentum* are larger at 7.5–12.5 mm in diameter. *Solanum semisucculentum* also differs in elevation from the protologue of *S. styraciflorum* and the specimens matching it. *Solanum styraciflorum* was reported at an elevation of ca. 50 m while *S. semisucculentum* typically occurs at higher elevation, such as the plateau of the Dôme de Tiébaghi, at 300–500 m elevation. I place *S. styraciflorum* in synonymy under *S. artense*.

Perhaps the most remarkable feature of *S. semisucculentum* is its semisucculent leaves. Many species of *Solanum* wilt shortly after collecting; however, *S. semisucculentum* is well adapted for water deprivation. With no difficulty, I was able to keep a specimen alive after collecting it with a few roots but no soil and carrying it for a couple hours on a warm tropical afternoon. After a couple of days this specimen opened a flower which had been in bud when it was collected. For a *Solanum* this was impressive. *Solanum semisucculentum* also has vividly purple stems which are

quite striking in living material. This coloration probably provides a certain amount of protection of the high levels of solar radiation this species receives in its open habitat.

***Solanum vaccinioides* Schlechter**, Bot. Jahrb. Syst. 40, Beibl. 92: 34. 1908. Type: France. New Caledonia, Sud-Bezirk, Kafeate, 500 m, Nov 1902 (fl), *Cribs 1253* (Holotype: B† “Herb. Noumeens”); Lectotype, designated by Heine, 1976: P×2; Lectotype, second stage, *hic designatus*: P 00288416!; Isolectotype: P 00288417!)

Other syntype: Koniambo, Mar 1903, *A. Le Rat 456* (B†, P 00288423!).

Solanum vaccinioides Schltr. var. *muhlenbeckiiifolium* Bitter Repert. Spec. Nov. Regni Veg. 11: 487. 1913. Type: France. New Caledonia: In insulae parte boreali-occidentali, 18[illegible] (fl), *Alf. Krieger* (?illegible), herb. Vindob. (Holotype: W 0015510!)

Solanum lyciifolium Daniker, Vierteljahrsschr. Naturforsch. Ges. Zurich, Beibl. 19: 78 (Mitt. Bot. Mus. Univ. Zurich 142): 420–421. 1933 [1943 distributed]. Type: France. New Caledonia. Kone, Hang des mt. Koniambo bei den Hütten der Mine Boum I., 14 Jan 1925 (fl, fr). *A. U. Daniker 877* (Lectotype, *hic designatus*: Z 000027802!; Isolectotypes: Z 000027803!, Z 000027804!)

Solanum kafeateense Guillaumin, Mém. Mus. Hist. Nat. 8: 168. 1959. Type: France. New Caledonia, lower slopes of Mt. Kafeate (Konoe to Voh), 30–100 m, 30 Mar 1956 (fl), *H. S. McKee 4220* (Lectotype, *hic designatus*: P 00288427!; Isolectotypes: E, K!, P 00288428!).

Solanum koniamboense Guillaumin, J. Agric. Trop. & Bot. Appliq. 11: 192. 1964. Type:
France. New Caledonia, Mt. Koniambo, 400 m, 5 Jan 1961 (fl), *H. S. MacKee* 7966
(Lectotype, *hic designatus*: P 00288433!; Isolectotypes: K!, L 177132!).

Figure 29.

Shrubs to 1.5 m, often sprawling on surrounding vegetation, the internodes to 4.5 cm long. Stems sparsely to densely pubescent with yellow-ferruginous, sessile or occasionally short-stipitate porrect stellae, the stipes to ca. 0.1 mm long, the stellae tardily deciduous, 0.4–0.6 mm broad, with 4–8 rays, the midpoint erect to flexed at the base $\pm 90^\circ$ and \pm laying flat on the surface of the stem, shorter than the rays; stems unarmed or with scatter prickles, the prickles to 1.8×2.3 mm, broad based, deltate, straight, yellow-ferruginous. Sympodia difoliate. Short shoots present. Leaves simple, the blades $0.3\text{--}6.5 \times 0.3\text{--}1.2$ cm, 1–6.5 times as long as wide, borne individually, often appearing clustered on short shoots, of various shapes ovate, obovate, orbicular, pandurate, lyrate, oval, elliptic, spatulate, spatulate with the distal portion expanded laterally with or without basal lobes, the basal lobes to ca. 7.0×3.5 mm, coriaceous, \pm glabrous to moderately pubescent above with sessile porrect-stellate or occasionally along the main vein stipitate porrect-stellate when young, \pm glabrous to moderately pubescent when mature, the stellae 0.3–0.7 mm in diameter, with 4–10(–11) rays, the stipes to ca. 0.2 mm long when present, the midpoint of the stellae erect to flexed at the base $\pm 90^\circ$ and laying flat on the surface of the leaf, much shorter than to $2/3$ as long as the rays, sometimes reduced to a stub, densely pubescent below with sessile or occasionally stipitate porrect stellae when young, \pm glabrous to densely pubescent when mature, the stellae 0.3–0.6 mm in diameter, with 4–10 rays, the stipes when present to ca. 0.1

mm long, the midpoint of the stellae \pm erect to clinate less than 90° , shorter than the rays, sometimes little more than a stub; blade unarmed or with a few scattered prickles on the primary vein adaxially and abaxially, with 2–3(–5) veins on either side of the midvein, the midvein raised abaxially, raised or merely distinct adaxially, the lateral veins strongly brochidodromous, forming a pseudo-marginal vein, indistinct or sometimes distinct abaxially, indistinct or sometimes distinct adaxially; blade base rounded to shortly attenuate or truncate, typically aequilateral or sometimes oblique; margin entire or lobed, the lobes rounded, typically a single basal lobe per side a second lobe per side occasionally present; apex obtuse to occasionally subacute; petiole 0.7–12 mm long, 0.4–0.5 mm in diameter, channeled above, \pm glabrous to densely pubescent, unarmed or with a few broad-based prickles like those of the blade, to 2.6×1.5 mm. Inflorescence sessile to 1.3(–2.6) cm in flower, to 0.8 cm in fruit, appearing lateral, extra-axillary, emerging from the upper 1/3 of the internode, unbranched, with 1–8 flowers, all apparently fertile or potentially so, the axes \pm glabrous to densely pubescent with sessile porrect-stellate, unarmed; pseudo-peduncle in flower to 9.0 mm long, ca. 0.4 mm in diameter, in fruit to 1.2 cm long, ca. 0.7 mm in diameter; pedicels 0.8–1.7 cm long, ca. 0.2 mm in diameter at the base, 0.4–0.8 mm in diameter below the calyx, straight to arching, gradually increasing in diameter in the distal 1/3–1/2, \pm glabrous to densely pubescent, the bases congested, to ca. 1.5 mm apart in flower, 1.0–1.8 cm long, 0.6–0.8 mm in diameter at the base, 0.4–0.8 mm in diameter below the calyx, straight or arching, gradually increasing in diameter in the distal 1/3–1/2, \pm glabrous to moderately pubescent, the bases congested to ca. 1.5 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx \pm glabrous to densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.6–3.5 mm long, unarmed, appearing nearly truncate

or with more well developed lobe tips, the tube 0.8–1.1 mm long, the lobe tips deltoid to caudate lobe tips, 1.3–2.5 mm long, the intersepular tissue glabrous, slightly translucent when dry; typically splitting in the sinuses at anthesis and then the lobes dentate, 1.9–2.9 × 1–1.7 mm, ±glabrous to moderately pubescent abaxially, glabrous adaxially; in fruit the calyx lobes 2.3–3.4 × 1.7–2.6 mm, ±glabrous to moderately pubescent, appressed. Corolla 1.3–1.9 cm in diameter, stellate with poorly developed, glabrous interpetalar tissue, white, the lobes 5.8–8.9 × 2.8–3.4 mm, narrowly lanceolate, the midrib 7.1–9.8 × 2.3–2.8 mm, narrowly lanceolate, densely pubescent abaxially, glabrous with a few stellae towards the apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.5–1.2 mm long; anthers 3.7–4.9 × 1.2–1.5 mm, acuminate, slightly incurved, markedly attenuate, yellow, connivent, with minute apical pores, the pores directed distally, extending around the edge of the apex, the lateral sutures perforated, remaining intact. Ovary ca. 0.5 mm, ±globose, with glabrous with a few stipitate glandular hairs at the apex; style 7.1–10.0 mm long, ca. 0.2 mm in diameter, longer than the stamens, emerging between the sides of the stamens, filiform or swelling below the stigma, sigmoid, ±white, with scattered stalked glandular hairs and/or sessile porrect-stellate hairs on the lower ca. 1/3; stigma 0.4–0.6 mm in diameter, capitate, green. Fruit a berry, 0.4–0.7 cm in diameter, globose, the immature fruits very light green nearly white with some darker green mottling, yellow when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds many per fruit, 2.2–2.6 × 1.7–2.3 mm, flattened-reniform to flattened-orbicular and notched at the point of attachment, yellow-tan or brown when dry, the surface alveolate.

Distribution and ecology.— Restricted to a single ultramafic formation which forms Mt. Koniambo and Mt. Katépahié on the Grande Terre, New Caledonia. It is found in lino-herbaceous scrub on hypermagnesian brown soils (Brooks, 1987) from 10–500 m elevation. Figure 37.

Phenology.— Known to flower and fruit January–August, October, and December. Likely flowering and fruiting year round.

Etymology.— This species is named for its resemblance to some species of the genus *Vaccinium* of the Ericaceae.

Additional specimens examined. **FRANCE. New Caledonia. North Province:** Oundjo, 4 Aug 1977 (fl), *Carlquist 15339* (RSA); Vavouto, site de l'usine Flaconbridge, 30 Jan 2004 (fl, fr), *Dagostini 731* (NOU); Mt. Kaféaté, 300m 22 Dec 1950 (fl), *Guillaumin & Baumann-Bodenheim 9606* (L×2); Mt Kaféaté, 300 m, 22 Dec 1950 (fl), *Guillaumin & Baumann-Bodenheim 9636* (G, MO, P, RSA, US); Mt. Kaféaté, 300 m, 22 Dec 1950 (fl, fr), *Guillaumin & Baumann-Bodenheim 9671* (G, MO, P, US); ca. 6 km north of Koné, lower slopes of east face of Massif de Koniambo, ca. 300 m, 5 Dec 1963 (fl), *Green 1745* (A, K, NOU, P); Base du Koniambo côté Voh, 200 m, 21 Feb 1972 (fr), *Jaffré 672* (NOU, P); Massif du Koniambo, 1 Jun 1972 (fl), *Jaffré 758* (NOU, P×2); (fl), *Le Rat 730* (P); southern slope of Mt. Katépahié, ca. 0.25 km from the main road on side road at base of the slope, ca. 80 m up the slope, 21° 03' 13.8" S, 164° 43' 14.6" E, 33 m, 14 Jul 2009 (fl), *McClelland & Nee 552* (MO, NOU, NY, P); southern slope of Mt. Katépahié, ca. 0.25 km from the main road on side road at base of the slope, ca. 80 m up the slope, 21° 03' 13.8" S, 164° 43' 14.6" E, 33 m, 14 Jul 2009 (fl), *McClelland & Nee 553* (MO, NOU, NY, P); slopes of Mt Koniambo, 400–

800 m, 31 Mar 1956 (fr), *McKee 4255* (P); Oundjo, 0–100 m, 9 Sep 1958 (fr, fl), *McKee 6516* (A, K, P, US); Oundjo, 0–100 m, 9 Sep 1958 (fr), *McKee 6518* (A, K, P); Voh, Mt. Katépahié, ca. 400 m, 20 Jan 1963 (fl, fr), *McKee 10063* (P); Voh, Mt. Katépahié, ca. 400 m, 20 Jan 1963 (fl, fr), *McKee 10064* (K, L, P); Voh, Mt. Katépahié, ca. 400 m, 20 Jan 1963 (fl, fr), *McKee 10065* (L, P); Voh, Mt. Katépahié ca. 400 m, 20 Jan 1963 (fr), *McKee 10066* (K, L, P); Voh, Mt Katépahié, 400 m, 20 Jan 1963 (fl, fr), *McKee 10067* (K, L, NOU, NSW, P); Oundjo, 50 m, 8 May 1966 (fl, fr), *McKee 14903* (A, K, L, P); Oundjo, 50 m, 8 May 1966 (fl), *McKee 14904* (P); Oundjo, 10 m, 5 Jul 1966 (fl), *McKee 15186* (A, K×2, L, MO, NOU, NSW, P); Mt. Koniambo, 400–700 m, 21 May 1967 (fl, fr), *McKee 16777* (K, L, NOU, P); Voh, base sud-ouest du Mt. Katépahié, 50–200 m, 7 Jun 1967 (fl, fr), *McKee 16836* (K, L, NOU, NY, P); Oundjo, 26 Jan 1970 (fl, fr), *McKee 21478* (NOU, P×2); Oundjo, 400 m, 26 Jan 1970 (fl), *McKee 21486* (NOU, P×2); Voh, base sud-est du Tahafé, 50–200 m, 7 Jul 1970 (fl, fr), *McKee 22143* (P); Oundjo, 10 m, 7 Apr 1971 (fl, fr), *McKee 23604* (MO, NOU, P×2); Koné, Kataviti, 20 m, 16 Aug 1970 (fl), *McKee 22435* (A, K×2, L, NOU, NSW, P, U, US); Koné, Kataviti, 20 m, 10 Oct 1970 (fl, fr), *McKee 22756* (P); Mont Koniambo, Base Sud-Ouest, 100 m, 24 Apr 1974 (fl), *McKee 28528* (K, P); Koniambo, base massif côté, 12 Feb 1974 (fr), *Sévenet 592* (NOU); base du Katépahié, 23 Mar 1982 (fl, fr), *Suprin 1719* (NOU); near Oundjo, 18 Oct–8 Nov 1959 (fl, fr), *Thorne 28006* (P, RSA); Massif du Koniambo, 21° 0' 27"S, 164° 45' 52"E, 400 m, 6 Jan 2003 (fl), *Tronchet & Roumagnac 683* (MO); Montagnes de Gomouex, Gatape [Gatope], 1867 (fl, fr), *Vieillard 3041* (BM, K, NSW, P×5); 1861–1867 (fl), *Vieillard 3043* (P); Maquis ca. 16 km north of Koné, 12 Dec 1972 (fl), *Webster & Jaffré 19269* (P, RSA); Oundjo, 21.05S, 164.41E, 20–50 m, 14 Dec 1973 (fl), *Webster & Jaffré 19294* (NOU, P); ca. 8 km north of Koné on hill with relay station, 11 Feb 1982 (fl), *Weston & Carolin 18090* (NSW); northwest slopes of Mt. Kafate, 50 m, 2 Aug 1977 (fl, fr), *Whaite 4604/8* (L, NOU, NSW).

This species is remarkable due to its wide range of variability in leaf shape. This amazing variability in leaf shape lead to the species being given four different specific epithets by various workers. *Solanum vaccinioides* is most similar to *S. hugonis*; see discussion of that species. *Solanum vaccinioides* is part of a group of native New Caledonian Solanums with relatively small leaves and short shoots which typically bear the inflorescences. Jaffré *et al.* (1998) listed this species as endangered in part due to its restricted distribution.

The lectotypes for these names were selected based on completeness of the collections.

***Solanum vanuatuense* D. McClell. sp. nov.**

Type: Vanuatu. Efate. lower slopes of Pic Fatamalapa, 17°33'S, 168°22'E, 200 m, 15 Jul 1971 (fl, fr), *Green 1103* (Holotype: P 00315286!; Isotypes (A!, K!, L 0531790!, NSW 594210!))

Figure 30.

Unarmed shrub to 2 m, the internodes to 5.1 cm long. Stems densely pubescent with yellow to yellow-ferruginous, sessile and stipitate porrect stellae, stipes of various lengths to 0.1 mm long, the stellae soon or tardily deciduous, 0.4–0.6 mm in diameter, with 6–8 rays, the midpoint cliniate less than 90° to flexed at the base $\pm 90^\circ$, \pm equal to the rays; bark reddish brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, geminate or borne individually, the blades of major leaves 4.9–11.2 \times 1.9–3.9 cm, 2.6–3 times as

long as wide, lanceolate to ovate, chartaceous, the minor leaves when present $1/2$ – $2/3$ as large as the major leaves, both major and minor leaves densely pubescent above with sessile or very short-stipitate porrect stellae and minute glandular hairs when young, sparsely to moderately pubescent when mature, the stellae 0.3–0.5 mm in diameter, with 4–8 rays, the stipes to 0.06 mm long, the midpoint of the stellae ciliate less than 90° or flexed at the base $\pm 90^\circ$, \pm equal to or longer than the rays, the glandular hairs to 0.05 mm long, densely pubescent below with sessile and short-stipitate porrect stellae when young, sparsely to moderately pubescent when mature, the stellae 0.4–0.7 mm in diameter, with 4–8 rays, the stipes to 0.3 mm long, the midpoint of the stellae erect or ciliate less than 90° , \pm equal to or longer than the rays; blade with 4–6 veins on either side of the midvein, the midvein raised abaxially and adaxially, the lateral veins weakly brochidodromous or semictaspedodromous, or craspedodromous in lobed leaves, raised abaxially, distinct adaxially; blade base rounded, typically oblique though occasionally aequilateral; margin entire, sinuate, or lobed; apex acute or acuminate; petiole 6.2–16.8 mm long, 0.6–1.3 mm in diameter, channeled above, densely pubescent all over. Inflorescence to 2.0 cm in flower, to 8.9 cm in fruit, appearing lateral, extra-axillary, emerging from the middle or upper $1/3$ of the internode, forking 1–3 times, with many to 61 flowers, all apparently fertile or potentially so, the axes densely pubescent, with sessile porrect stellae; peduncle in flower 3.1–16.0 mm long, ca. 0.6 mm in diameter, the branches to 1.2 cm long, ca. 0.4 mm in diameter, in fruit 4.9–18.5 mm long, 1.3–1.8 mm in diameter, the branches to 7.8 cm long, 0.5–1.4 mm in diameter; pedicels 0.7–1.0 cm long, ca. 0.3 mm in diameter at the base, 0.6–0.9 mm in diameter below the calyx, straight, not bent below the calyx or bent to $\pm 90^\circ$, swelling \pm evenly from the base to the base of the calyx, densely pubescent, the bases congested, overlapping to 0.4 mm apart in flower, 11.1–16.2 mm long, ca. 0.4 mm in diameter at the base, 1.3–1.7 mm in diameter

below the calyx, straight, not bent below the calyx, gradually increasing in diameter in the distal $1/2-2/3$, sparsely to moderately pubescence, the bases well spaced to 5.7 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers homostylous, 5-merous. Buds ovate, the calyx densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud smooth. Calyx 2.2–2.8 mm long, appearing nearly truncate with caudate lobe tips, the tube 0.5–0.9 mm long, the lobe tips 1.2–2.0 mm long, the intersepal tissue opaque when dry; splitting in the sinuses during fruit development and then the lobes dentate, moderately to densely pubescent abaxially, glabrous adaxially, the calyx lobes in fruit $1.7-2.4 \times 1.3-1.5$, sparsely to moderately pubescent, appressed. Corolla 1.1–1.3 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes $3.9-4.5 \times 2.2-3.5$ mm, deltoid, the midrib $4.9-5.5 \times 1.6-2.2$ mm, lanceolate, densely pubescent abaxially, glabrous or with a few scattered sessile porrect stellae adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament ca. 0.8 mm long; anthers $2.5-2.9 \times 0.9-1.1$ mm, acuminate, straight, markedly attenuate, yellow, spreading, with minute apical pores, the pores directed dorsally, extending around the edge of the apex, the lateral sutures perforated, remaining intact. Ovary ca. 0.6 mm, globose, color, moderately pubescent at the apex with simple glandular hairs; style 5.6–6.4 mm long, ca. 0.2 mm in diameter, longer than the stamens, deflexed and emerging between the sides of two adjacent stamens, filiform, curved or hooked towards the tip, glabrous or sparsely pubescent with simple glandular hairs on the basal $1/3$; stigma 0.3–0.6 mm in diameter, capitate. Fruit a berry, 0.6–0.8 cm in diameter, globose, apparently orange or red when mature, glabrous; exocarp thin, glossy; endocarp juicy. Seeds few per fruit, $1.5-1.8 \times 1.5-2.0$ mm, flattened-orbicular and notched at the point of attachment to flattened-reniform, red-brown when dry, the surface evenly reticulate.

Distribution and ecology.— On various islands in Vanuatu. Reported in grass or low herbage, sea side, and on outcroppings of limestone from sea level–200 m elevation. Figure 34.

Phenology.— Known to flower and fruit February, July, and October–November.

Etymology.— This species is named for Vanuatu, the country where it is found.

Additional specimens examined. **VANUATU.** “Nendroz” Oct 1883 (fl, fr), *Levat s.n.* (P).

Anatom: entre Umetch et Aneghowhat, edge of the sea, 12 Feb 1986 (fl, fr), *Bourdy 442* (K, P); (fl) *McGillivray s.n.* (BM); secteur de UMEC, Nov 1974 (fl, fr), *Schmidt 5149* (P). **Erromango:** entre Cook Bay et Ipota, ca. 5 m, 25 Jul 1983 (fl, fr), *Cabalion 2247* (K, P); tableland, 600 ft, 26 Jul 1930 (fl), *Cheeseman 38* (K). **Espiritu Santo:** Hog Harbour, 24 Nov 1933 (fl, fr), *Baker 58* (BM) **Futuna:** tableland, Dec 1858 (fl, fr), *Milne 391* (K). **Pentecost Island:** north end, ca. 1972, *Walsh 208* (NSW).

Specimens of what is here recognized as *Solanum vanuatuense* were included in *S. milnei* by Seemann when he named the latter species; however, it is distinct. *Solanum vanuatuense* is also similar to *S. austro-caledonicum*. It can be distinguished from both species by its leaves being geminate sometimes and often lobed, its smaller corolla and anther, and its sigmoid style.

- Solanum viride* Sprengel, Beihler, Pl Nov. herb. Spreng. no. 28 pp. 14. 1807. Type: Tahiti
 [“Taheetee”], s.d. (fl, fr), *Foster s.n.* (Lectotype, designated by Garnock-Jones, 1986: K
 000195705!).
- Solanum uporo* Dunal, in DC., Prodr. 13(1): 138. 1852. Type: Tahiti, *Morrenhout s.n.*
 (Holotype: G-DC, =IDC microfiche 800-61.2072:III.4!).
- Solanum anthropophagorum* Seem., Bonplandia 10: 274, tab. 14. 1862.; Bonplandia 9: 258.
 1861, *nom. nud.* Type: Fiji, s.d. (fl, fr), *B. Seemann 341* (Lectotype, *hic designatus*: K
 000195707!; Isolectotypes: BM 000846951!, GH!, K 000195706!, P 00315246!).
- Solanum puberulum* Nutt. ex Seem., J. Bot. 1: 207. 1863. *pro syn.* *Solanum pulverulentum* Nutt.
 ex Seem., J. Bot. 1: 208. 1863. Type: U.S.A. Hawaiian Islands, Oahu, s.d. (fl, fr), *T. Nuttall*
s.n. (Lectotype, *hic designatus*: BM 00084669!, photo at NY!). Other Syntype: U.S.A.
 Hawaiian Islands, *S. Menzies s.n.* (BM).
- Solanum ornans* Witasek, Repert. Spec. Nov. Regni Veg. 5: 165. 1908. Type: Samoa, Upolu,
 Moa-Moa, 1905 (fl, fr), *K. Rechinger 1775* (Holotype: W 2134!).
- Solanum patameense* Witasek Repert. Spec. Nov. Regni Veg. 5: 163. 1908. *Solanum*
patameense var. *grandifolium* Witasek Repert. Spec. Nov. Regni Veg. 5: 163. 1908. Type:
 Samoa, Savaii, Patamea, Jul 1905 (fl, fl), *Rechinger 92* (Lectotype, *hic designatus*: W
 2157!)
- Solanum patameense* var. *parvifolium* Witasek, Repert. Spec. Nov. Regni Veg. 5: 164. 1908.
 Type: Samoa, Savaii, Patamea, Jul 1905 (fl), *Rechinger 92* (Holotype: W 2156!).
- Solanum savaiense* Witasek, Repert. Spec. Nov. Regni Veg. 5: 163. 1908. Type: Samoa, Savaii,
 Malo, Jul 1905, *Rechinger 1117* (Lectotype, *hic designatus*: W 2136!)

Other syntypes: Samoa, Lealatele, Jul 1905 (fl, fr), *Rechinger 1183* (W 2137!); Lealatele, Jul 1905, *Rechinger 76* (W 2135!).

Solanum upolense Witasek, Repert. Spec. Nov. Regni Veg. 5: 164. 1908. Type: Samoa, Upolu, Laulii, Jun 1905 (fr), *K. Rechinger 482* (Holotype: W 2160!).

Solanum polynesianum St. John, J. Jap. Bot. 34: 333, fig. 1. 1959. Type: Society Islands, Raiatea Island, 25 Dec 1926 (fl, fr), *J. W. Moore 463* (Lectotype *hic designatus*: BISH 515280!; Isotypes: BISH 581176!, BISH 581179!, L 0651830!).

Solanum tongaense St. John, J. Jap. Bot. 34: 335, fig. 2. 1959. Type: Tonga Island, Eua Island, between Mua and Ha'aluma, SW side of island, 1 Apr 1953 (fr), *T. Yuncker 15584* (Holotype: BISH 586943!; Isotypes: BM 000846712!, CANB 251283!, GH!, NY 00828353!, NY ex DPU 00828352!, U 0182896!, US 2128443!)

Solanum tuamotuense St. John, J. Jap. Bot. 34: 337, fig. 3. 1959. Type: Tuamotu Archipelago, Hiti Atoll, 5 May 1923 (fl, fr), *Whitney Expedition 2059* (Holotype: BISH 581174!).

Solanum angustior H. St. John. Phytologia 64: 169. 1988. Type: U.S.A., Hawaiian Islands, Kauai Island, s.d. (fl, fr) *Lygate s.n.* (Holotype: BISH 523450!)

Solanum macdanielsii H. St. John, Phytologia 64: 170. Jan. 1988. Type: U.S.A., Hawaiian Islands, Kauai Island, Haupu, 16 Feb 1927 (fl, fr), *L. H. MacDaniels 732* (Holotype: BISH 14286!; Isotype: K!).

Figure 31 and 32.

Unarmed shrub to 3 m, the internodes to 5.8 cm long. Stems glabrous to densely pubescent with yellow-ferruginous, sessile or short-stipitate porrect stellae, the stipes of various lengths to 0.1

mm long, the stellae tardily glabrescent, 0.3–0.7 mm broad, with 4–8 rays, the midpoint \pm erect to flexed at the base $\pm 90^\circ$, shorter than the rays; bark reddish brown, a transparent sloughing layer absent on young stems. Sympodia difoliate. Short shoots absent. Leaves simple, geminate or borne individually, the blades of major leaves 4.6–12.9 \times 2.4–5.0 cm, 1.9–2.6 times as long as wide, lanceolate, ovate, or oval, chartaceous, the minor leaves $\frac{2}{3}$ to \pm as large as the major leaves, both major and minor leaves glabrous to moderately pubescent above with sessile porrect stellae and minute glandular hairs when young, glabrous to sparsely pubescent across the lamina and moderately pubescent along the veins when mature, the stellae 0.3–0.6 mm in diameter, with 4–8 rays, the midpoint of the stellae clinate less than 90° or flexed at the base $\pm 90^\circ$, shorter than to \pm equal to the rays, the glandular hairs to 0.08 mm long, nearly glabrous to sparsely pubescent across the lamina and densely pubescent on the veins below with sessile and short-stipitate porrect stellae and minute glandular hairs when young, glabrous to sparsely pubescent across the lamina and moderately to densely pubescent along the veins when mature, the stellae 0.4–0.7 mm in diameter, with 4–8 rays, the stipes to 0.06 mm long, the midpoint of the stellae erect to clinate less than 90° , shorter than to \pm equal to the rays, the glandular hairs to 0.06 mm long; blade with 7–10 veins on either side of the midvein, the midvein raised abaxially, raised adaxially, the lateral veins weakly brochidodromous, raised abaxially, raised or merely distinct adaxially; blade base rounded, cuneate, or shortly attenuate, aequilateral or oblique; margin entire, sinuate, or lobed; apex acute to acuminate; petiole 0.5–2.4 cm long, 0.5–1.1 mm in diameter, channeled above, glabrous to densely pubescent all over. Inflorescence to 11.2 cm in flower, to 5.3 cm in fruit, appearing lateral, extra-axillary, emerging from the upper $\frac{1}{3}$ of the internode, forked or unbranched, sometimes branching 3 times, with 7–67 flowers, all apparently fertile or potentially so, the axes \pm glabrous to densely pubescent, with sessile and short-stipitate

porrect stellae; peduncle in flower to 7.5 mm long, 0.5–1.0 mm in diameter, the branches to 2.2 cm long, ca. 0.5 mm in diameter, in fruit to 9.0 mm long, 0.7–3.0 mm in diameter, the branches to 2.9 cm long, to 1.1 mm in diameter; pedicels 0.8–1.1 cm long, 0.3–0.5 mm in diameter at the base, 0.8–1.5 mm in diameter below the calyx, straight, bent to $\pm 90^\circ$ below the calyx, gradually increasing in diameter in the distal $1/4$ – $1/3$, glabrous to moderately pubescent, the bases congested or well spaced to 4.0 mm apart in flower, 0.8–2.2 cm long, 0.5–2.0 in diameter at the base, 1.5–4.8 mm in diameter below the calyx, straight or arching, bent or not below the calyx, gradually increasing in diameter in the distal $1/3$ – $1/2$, glabrous to sparsely pubescent, the bases well spaced to 8.8 mm apart in fruit, rigid, in two rows, articulate at the base. Flowers heterostylous, 4–5-merous. Buds globose, the calyx glabrous to densely stellate-pubescent, the corolla densely stellate-pubescent, the surface of the corolla of the mature bud ridged. Calyx 1.4–2.9 mm long, appearing nearly truncate with apiculate to caudate lobe tips, the tube 0.9–1.8 mm long, the lobe tips 0.2–1.3 mm long, the intersepal tissue translucent when dry; splitting in the sinuses as the bud develops or at anthesis then the lobes dentate, 0.4 – 2.0×0.9 – 1.5 mm at anthesis, glabrous to moderately pubescent abaxially, glabrous or densely pubescent on the tip adaxially, the calyx lobes in fruit 1.1 – 5.8×1.2 – 4.9 mm, glabrous to sparsely pubescent, appressed or reflexed. Corolla 0.9–1.6 cm in diameter, stellate with well-developed, glabrous interpetalar tissue, white, the lobes 3.2 – 6.4×2.6 – 5.1 mm, deltate to widely deltate, the midrib 4.6 – 8.5×1.5 – 3.5 mm, lanceolate to ovate, moderately to densely pubescent abaxially, glabrous or glabrous at the base scattered pubescent towards the apex adaxially, spread wide at anthesis. Stamens adnate to the corolla, the free portion of the filament 0.7–1.0 mm long; anthers 2.2 – 3.1×0.9 – 1.2 mm, acuminate or oblong, straight or somewhat incurved, not or scarcely attenuate, yellow, spreading, with minute apical pores, the pores directed ventrally or distally, extending

around the edge of the apex, the lateral sutures entire. Ovary 0.5–1.3 mm in diameter, globose to ovate, glabrous or with few minute glandular hairs at the apex; short style 1.0–1.8 mm, shorter than the stamens, not emerging from the stamens, the long styles ca. 3.7–4.1 mm long, longer than the stamens, emerging between the apices of the anthers, both short and long styles 0.2–0.4 mm in diameter, filiform, straight, glabrous or with a few glandular hairs on the basal 1/2; stigma 0.2–0.6 mm in diameter, capitate, green. Fruit a berry, 0.8–2.7 cm in diameter, globose, the immature fruits evenly green, red when mature, glabrous; exocarp thin, mesocarp thin or thick, glossy; endocarp juicy. Seeds many per fruit, 2.2–2.6 × 2.3–2.8 mm, flattened-reniform to flattened-orbicular and notched at the point of attachment, yellow-tan when dry, the surface with the central area nearly smooth, the margin alveolate.

Distribution and ecology.— Distributed across the Pacific from Fiji to the Pitcairn Islands and in Hawaii from sea level–300 m elevation. This species is both cultivated and feral in forests, thickets, and along beaches. Figure 33.

Phenology.— Known to flower and fruit January–November; undoubtedly flowering and fruiting in December as well.

Etymology.— The specific epithet refers to the color green in Latin.

Additional specimens examined. Insulae Oceanae Pacifici, (fl, fr), *Forster & Forster s.n.* (BM, BM); Nova Caledonia aut Friendly Islands, *Forster & Forster s.n.* (BM); Place name illegible, *Wilkes s.n.* (K).

FIJI. 1860 (fl, fr), *Seemann 341* (K×2); 1838–1842 (fl, fr), *Wilkes s.n.* (B, GH, NY).
Fulaga: 0–80 m, 22–26 Feb 1934 (fr), *Smith 1178* (A, GH, NY, P, S, UC, US) **Kabara:** 2–7 Mar 1934 (fl, fr), *Smith 1286* (GH, K, P, NY, S, UC, US). **Marabo:** 26 Aug 1924 (fl), *Bryan 516* (A).
Matuku: Aug 1855 (fl), *Milne 115* (K).

FRANCE. French Polynesia. Austral Islands. Raivavae: Rairua Village, 147° 40' W, 23° 52' S, 2 m, 4 May 1992 (fr), *Florence & Sykes 11192* (BISH, P); Beach south of Pic Rouge, 2 m, 5 Aug 1934 (fl, fr), *St. John & Fosberg* (BISH). **Rimatara:** Anapoto, 3 m, 4 Sep 1934 (fl, fr), *St. John & Fosberg 16811* (BISH). **Rurutu:** Moerai, at beach, 4 ft, 14 Jan 1921 (fl), *Stokes 44* (BISH); Mato Arei, 50 ft, 10 Feb 1921 (fl, fr), *Stokes 50* (BISH, BISH). **Marquesas. Fatu Hiva:** Omoa, 30 m, 20 Jun 1922 (fl, fr), *Brown 941* (BISH); Omoa, along streets of village and in yards, 10 m, 9 Feb 2003 (fr), *Perlman 18412* (BISH, PTBG). **Ua Huka:** Papuaieikaha, at the arboretum on the grounds of the Service Development Ruale, 55m, 14 Dec 2003 (fl, fr), *Dunn 414* (BISH, NY, PTBG). **Society Islands. Tahiti:** Arue, valley bottom of Papaoha. 17° 32' S, 149° 32' W, 50 m, 18 Sep 1987 (fr), *Florence 8557* (P); 1834 (fl, fr), *Morrenhout s.n.* (P×2).
Tuamotu Archipelago. Tenarunga: 3–4 m, 13 Jun 1922 (fl, fr), *Quayle 513* (A, BISH, K, UC). **Ahunui:** 3–6 m, 26 Jun 1922 (fl, fr), *Quayle 558* (BISH). **Apataki:** Jul 1923 (fr), *Quayle 2163* (BISH). **Hiti:** 5 May 1923 (fl, fr), *Quayle 2057* (BISH). **Mataiva:** Jul 1923 (fr), *Quayle 2099* (BISH). **Puka-Puka:** 1838–1842 (fr), *Wilkes s.n.* (GH); 1838–1842 (fl, fr), *Wilkes s.n.* (P).
Raroia: Papakobuha, Opakea, 16° S, 142° 26' W, 15 Aug 1952 (fl, fr), *Doty & Newhouse 11793* (BISH). **Takapoto:** 2–5 m, Aug 29 1922 (fr), *Jones 1004* (BISH); 2–5 m, Mar 1923, *Quayle 1954* (BISH); 2–5 m, Mar 1923 (fl, fr), *Quayle 1967* (BISH). **Tepoto [no North or South indication]:** in interior, 2 m, 16 May 1934 (fl, fr), *St. John 14327* (BISH, K, L). **Wallis and**

Futuna. Wallis Islands: 1847 (fl), *Védel s.n.* (P). ‘**Alofi:** 200–300 m, 26 Oct 1968 (fl, fr), *McKee 19786* (BISH, K, L).

NEW ZEALAND. Cook Islands. Aitutaki: at a house at Vaepae, 11 Mar 1894 (fl, fr), *Whistler 5220* (BM). **Atiu:** Tengtangi District, Vai Momori Swamp, 26 Jul 1991 (fr), *Sykes 3829/CI* (BISH). **Pukapuka:** Apr 1935 (fl, fr), *Beaglehole 44* (BISH); 2–4 m, 3 Mar 1924 (fr), *Bryan 14a* (A, BISH). **Rarotonga:** near Saipara 100 ft, 2 Sep 1969 (fl), *Philipson 10181* (L, US). **Tokelau. Fakaofu:** 4–5 m, 3 Apr 1924 (fl, fr), *Bryan 69* (A, BISH×2); Fenuatapu Motu, 14 Aug 1980 (fl, fr), *Whistler 4650* (B, K).

NIUE. Niue: Nr. Hakupu, 8 Oct 1965 (fl, fr), *Sykes 569* (L); near the sea north of Alofi, 15 m, 5 Feb 1940 (fl, fr), *Yunker 10039* (A, BISH, NY×2); near the village of Makefu; 20 m, 7 Feb 1940, *Yunker 10103* (K).

SAMOA. Aug 1875(fl), *Whitnee 185*(K); (fl) *Gräffe s.n.* (BM); Feb 1880 (fl), *Powell 366* (K); (fl, fr) *Whitnee s.n.* (BM×2, GH×2); (fl, fr) *Whitnee s.n.* (K); Aug, 1875 (fr), *Whitnee 333* (K); 1838–42 (fl, fr), *Wilkes s.n.* (GH, P). **Apolima:** Jun 1905 (fl, fr), *Rechinger 474* (W). **Savai'i:** Gagamalae, ca. 5 m, 4 Nov 1931 (fl), *Christophersen 3053* (BISH); *Gräffe 235* (HBG). ‘**Upolu:** Lefafa, Gagaifoolevao, central village clearing, sea level, 9 Aug 1968 (fl, fr), *Bristol 2240* (BISH, GH, NY, US); Vailele, 100 m, 5 Mar 1921 (fr), *Eames 168* (B, BISH, K, NY); (fl) *Gräffe 22* (HBG); (fr), *Gräffe 86* (HBG); (fl), *Gräffe 1477* (HBG, K); Falefa village au bord de la mer, 30 Mar 1905 (fr), *Hochreutiner 3457* (G); 1846 (fl, fr), *Horne s.n.* (BM); Vailele, Jun 1905 (fr), *Rechinger 518* (W×2).

TONGA. 1889–1890 (fl), *Lister s.n.* (K×2); Sep 1920–Jun 1921 (fr), *McKern 59* (BISH); (fl, fr), *Nelson* (BM, NSW); 1838–42 (fr), *Wilkes s.n.* (GH). ‘**Eua:** east side of Koloaki lupe, 27 Sep 1960 (fl, fr), *Hotta 5570* (BISH); Terrace south of Vaingana, 21° 30’S, 13 Nov 1951 (fl, fr),

Hürlimann 281 (NY); Niua, 320 ft, 8 Aug 1987 (fl, fr), *O'Rourke 254* (GH); 'Ohonua village, 174° 57' 18" W, 21° 20' 43" S, 55 m, 27 Mar 2002 (fl, fr), *Suzuki et al. T00347* (BISH); 'Ohonua, 1 Jul 1977 (fl, fr), *Sykes 443/T* (US); forest just north of Musie a Monomono, 28 Jun 1990 (fl, fr), *Whistler 7435* (BISH, K, US); along road between Maua and Ha'aluma on the southwestern side of the island, 1 Apr 1953 (fl, fr), *Yuncker 15584* (BM, GH, NY). **'Euaiki:** close to the beach, 0–15 ft, 26 Aug 1959 (fl, fr), *Soakai 1048* (K×2). **Tongatapu:** Mar 1880 (fr), *Gräffe & Luerssen s.n.* (K); near Houma, 17 Jan 1972 (fl, fr), *Helu 194* (RSA); Jun–Aug 1926, *Setchell & Parks 15407* (UC); Nuioua, ca. sea level, 19 Nov 1958 (fl, fr), *Soakai 229* (A, BISH, K); near Mu'a, 4 Oct 1969 (fl, fr), *Weiner T1a* (BISH); in a yard in Halaleva in Nuku'alofa, 1 Jun 1989 (fl, fr), *Whistler 6748* (B, K, NTGB); near the sea on the eastern side of the island near the village of Niutoua, 2 Mar 1953 (fr), *Yuncker 15131* (BISH, BM, GH, NY, U, US, W). **Vava'u:** (fl, fr), *Barclay s.n.* (K); 22 May 1840 (fl, fr), *Barclay 3363* (BM); (fl, fr), *Hombron s.n.* (P, US); (fl, fr), *Leguillon s.n.* (P); slopes of Mt. Talau, near Neiafu, 25 Aug 1926 (fl, fr), *Setchell 15660* (UC).

UNITED KINGDOM. Pitcairn Islands. Oeno: Pointe Sud-Est, 130° 45' W, 23° 57' S 2 m, 29 May 1991 (fl, fr), *Florence, Chepstov-Lusty & Waldren 10937* (BISH, BM, K, P×2, PTBG, US); 2 m, 23 Jun 1934 (fl, fr), *St. John & Fosberg 15185* (BISH×2, K, L NSW); 3 m, 23 Jun 1934 (fr), *St. John & Fosberg 15186 a* (P).

USA. American Samoa. Ta'u: slopes of Laufuti Stream, ca. 60 m, 8 Oct 1993 (fl, fr), *Whistler 9304* (PTBG×2). **Nuu Islet:** Ofu, 10 ft, 4 Jul 1925 (fr), *Garber 1107* (BISH). **Nu'utele:** end of the ridge on the north side of the bay, 17 Sep 1991 (fl, fr), *Whistler 8332* (BM, PTBG, US) **Savai'i:** behind Manase, 100 m, 16 Nov 1905 (fl, fr), *Vaiipel 479* (M); Falealupo, 8 Oct 1906 (fl), *Vaiipel 534* (M). **Tutuila:** Pago Pago, 23 May 1904 (fr), *Kuntze 23009* (NY×2); Pago

Pago, Feb 1930 (fr), *Meebold* 8236 (BISH, K); near Nuuli [sic Nuuuli], Jun 15 1920 (fl, fr), *Setchell* 123 (UC); north end of the ridge just to the west of Afono Bay, 11 Apr 1991, *Whistler* 8067 (PTBG); Tafuna, 23 Jan 1959 (fl), *Wisner* 34 (BISH×2). **Hawaiian Islands. Kauai:** Hii Valley, (fl, fr), *Lygate s.n.* (BM); north side of Haupu 300 m, 16 Feb 1927 (fl, fr), *MacDaniels* 732 (BISH, K); 1851–1855 (fl, fr), *Rémy* 444 (P×2); Haupu (Hoary Head Mts.), Kipu, 800 ft, 25 Dec 1933 (fr), *St John Fosberg* 13658 (PTBG).

Cultivated. AUSTRALIA. South Australia: pot grown, Waite Institute, 10 Sep 1984 (fl, fr), *Symon s.n. ex Buelow & Sykes* 172 (L); in glasshouse, Adelaide Botanic Gardens, 15 May 1989 (fr), *Symon s.n.* (NY). **U.S.A. Hawaiian Islands. Kauai:** National Tropical Botanical Garden McBryde Garden, plant propagation range, living collection accession no. 050495, 19 Apr 2008 (fl, fr), *McClelland* 453 (BISH, NY, PTBG).

Within section *Irenosolanum*, *Solanum viride* is of particular interest because it was domesticated. Both the leaves and fruits were eaten and desirable traits were selected for in both. As would be expected, leaves and fruit were selected for increased size, and leaves were also selected for glabrousness. Since two organs were the object of selection, the various domesticates of *S. viride* display a wide range of morphology. Some domesticates have large glabrous leaves but relatively small fruits while others have both glabrous leaves and large fruits. Some large fruited types have a thickened mesocarp which adds fleshiness to the fruits while others do not. Besides uses as food, the leaves of *S. viride* are used medicinally in Tonga (Whistler, 1991), and the decorative fruits are made into crowns in the Society Islands (Papy, 1955) and garlands on Niue (*Yuncher* 10039). The variability of the different domesticates could be recognized at the varietal level, but more investigation, especially in the field, is needed.

The exact area of domestication of *S. viride* remains unknown. The matter is complex because many domesticated forms can become established in the wild as was noted by Whistler (1991) and as can be seen from herbarium material. Though Fiji cannot be ruled out at this time, perhaps the best candidate for the domestication is Samoa (including American Samoa). The widest range of domesticated forms comes from Samoa, and specimens with many small fruits and pubescent leaves are found there. These specimens could represent the wild progenitor because of these undesirable/less palatable traits, but again more investigation is needed.

The existence of many domesticates on many islands has resulted in *S. viride* being the most over-named species in section *Irenosolanum*. The most colorful name given to the species was *S. anthropophagorum*, literally *Solanum* of the man eaters. Sadly, *S. anthropophagorum* is a superfluous name, but this might be just as well since the species was used by non-cannibals, too.

Use of *S. viride* during cannibal feasts in Fiji has led to a general macabre fascination with the species, and provided it with the English common name “Cannibal's Tomato.” Several authors wrote about the use of *S. viride*. The most extensive reports were provided by Seemann (1862a, 1862b, 1865–73) and Brewster (1922). According to Seemann (1862a, 1862b, 1865–73), the Fijians believed human flesh or “boloka” as they called it was difficult to digest and could cause constipation lasting two to three days or result in death. Apparently to aid in digestion, the leaves of three species, *Trophis anthropophagorum* Seem. (Moraceae), *Omаланthus* [sic *Homаланthus*] *pedicellatus* Benth. (Euphorbiaceae), and *S. viride*, were always eaten as a condiment being wrapped around the flesh before cooking (Seemann, 1862a, 1862b, 1865–73). The Fijians name for *S. viride* was *boro dina* (Seemann, 1862a, 1862b, 1865–73), sometimes spelled *mboro ndina* (Brewster, 1922); it is translated as “true spinach” (Brewster, 1922). To insure a regular and fresh supply, *Solanum viride* was grown next to the *Bure-ni-sa* or “stranger's house” where the bodies

were brought prior to consumption (Seemann, 1862a, 1862b, 1865–73). The fruits of *S. viride* are described as having a faint aromatic smell (Brewster, 1922; Seemann, 1862a, 1862b, 1865–73) and were occasionally made into a “tomato sauce.” The last documented act of cannibalism in which *S. viride* was used occurred in July 1867 when the Reverend Thomas Baker, a British missionary, was eaten (Brewster, 1922). However, there is no reason to believe that *S. viride* was not used in subsequent cannibal activities extending through 1874. In Fiji, *Solanum viride* was also utilized by white settlers (Brewster, 1922; Seemann, 1862a, 1862b, 1865–73) presumably with a different main course.

Due to its lurid reputation, there has been some renewed interest in *S. viride* as a novelty in recent years. Several seed supply companies purportedly sell seeds of *Solanum viride* often under the name *S. uporo* Dunal. Unfortunately, many of these are not *S. viride*, but in fact *S. aethiopicum* L. In 2009, The New York Botanical Garden (NYBG) purchased seeds of *S. viride* from the seed company Trade Winds Fruit. These turned out to be *S. aethiopicum* instead (voucher *McClelland 564* (NY)), a disappointment for everyone involved at NYBG. Cultivation of *S. viride* in the Pacific seems to be waning. The people of the Pacific and of the rest of the world stand to lose one of the few crops domesticated in and perfectly adapted to the Pacific.

No autonym variety was published for *Solanum patameense*. Therefore, the species is lectotypified on *Solanum patameense* var. *grandifolium* as the holotype of that variety is more complete than the holotype of *Solanum patameense* var. *parvifolium*. It has two inflorescences with several flower buds and fruiting pedicel though the fruit is missing. The lectotypes for the other names were selected based on completeness of the collections.

The 1861 appearance of the name *S. anthropophagorum* was in a list of species without a description in.

Other names: *Solanum viride* Soland. ex G. Forster, Pl. Esc. 72. 1786. *nom. nud.*; Fl. Ins. Austr. 89. 1786. fide Ind. Kew.

Excluded species

Solanum retrorsum Elmer, Leaflets Philipp. Bot. 1: 342. 1908. *pro syn.* *S. reflexispinosum* Merrill, in Gibbs, Phytogeogr. & Fl. Arfak Mts. 178. 1917. Type: Philippines, Luzon, Prov. Benguet [plus Baguio at K], Mar 1907, A. Elmer 8719. (Lectotype *hic designatus*: K000195910!; Isotypes: A!, E 00243613!, PNH!).

Solanum luzoniense Merrill, Philipp. J. Sci., Bot. 13: 58. 1918. Type: Philippines, Luzon, Prov. Nueva Ecija, Mount Umingan, 3 Aug 1916, M. Ramos & G. Edaña (*Bur. Sci.*) 26487 (Lectotype, *hic designatus*: US 1376054!; Isotype: K).

Solanum luzoniense var. *glabrum* Merrill Philipp. J. Sci., Bot. 13: 59. 1918. Type: Philippines, Luzon, Prov. Pampanga, Calumpit, Sep 1905, Merrill 4237 (Lectotype, *hic designatus*: US 00027663!)

There are no compelling reasons to include *S. retrorsum* in section *Irenosolanum*. It neither resembles any species of the section nor does it occur within the geographic distribution. Whalen (1984) included *S. luzoniense* in his *Solanum dunalianum* group, roughly equivalent to section

Dunaliana and section *Irenosolanum* together. Inspection of the available herbarium material shows that *S. luzoniense* is conspecific *S. retrorsum*, a species not treated by Whalen (1984). As herbarium material of this species is scarce, Whalen (1984) probably was not well acquainted with it. Given that the species lists for his different groups were preliminary, less weight can be attributed to the inclusion of this species with the species of section *Irenosolanum*. Elmer (1908), in the protologue of *S. retrorsum* suggested a distant relationship with *S. ferocissimum* Lindl. from Australia. It is also possible that *S. retrorsum* is related to *S. lianoides* Elmer also from the Philippines. For the time being, the affinities of *S. retrorsum* remain unclear. Certainly, much more investigation of the native species of *Solanum* from the Philippines is necessary to understand their sectional relationships.

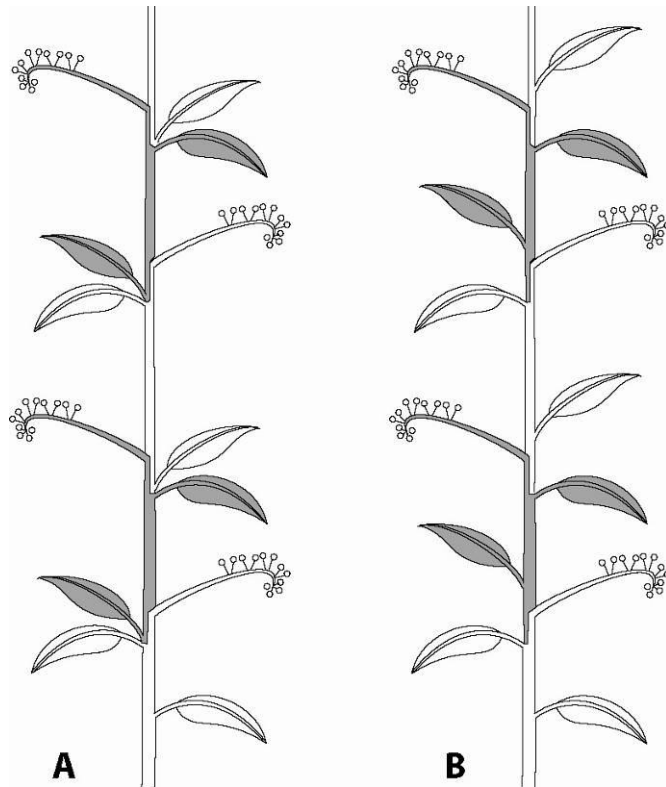


Figure 1. Sympodial growth of *Solanum* section *Irenosolanum* showing successive sympodia (Redrawn from Danert, 1967). A. Geminate leaf arrangement. B. Leaves borne individually.



Figure 2. Inflorescence and anther characteristics of *Solanum* section *Irenosolanum*. A. Inflorescence of *S. viride* showing the characteristic \pm horizontal presentation of open flowers and spreading anthers. B. Flower of *S. sandwicense* showing the characteristic flexing of the pedicel to $\pm 90^\circ$ below the calyx and the unusual arcuate anthers of this species.



Figure 3. Isotype of *Solanum abollatum* (Munro s.n., NY) courtesy of the C. V. Starr Virtual Herbarium NYBG.

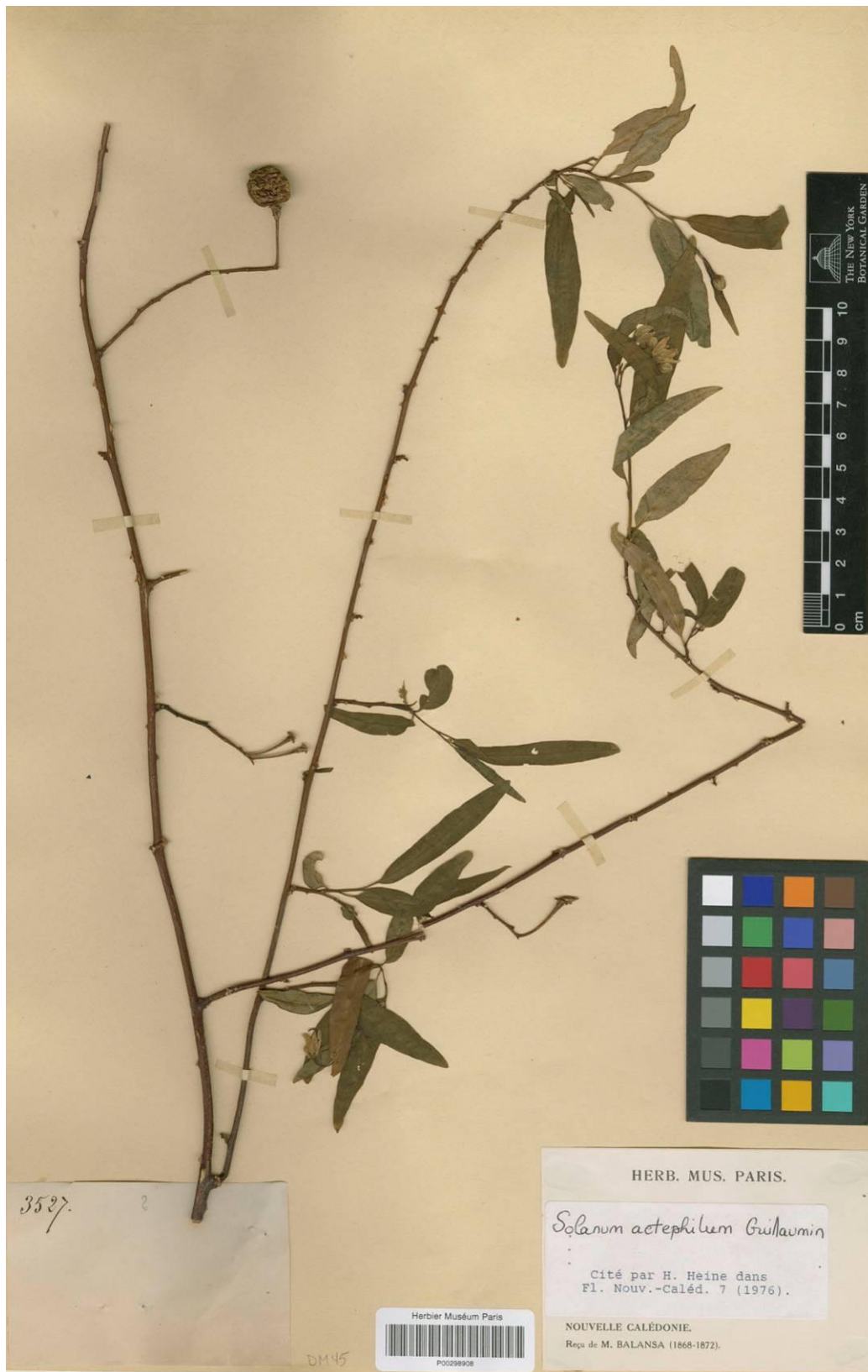


Figure 4. Isotype of *Solanum actephilum* (B. Balansa 3527, P 00296908).



Figure 5. Isotype of *Solanum albertyi* (Smith 1180, P 00315309).

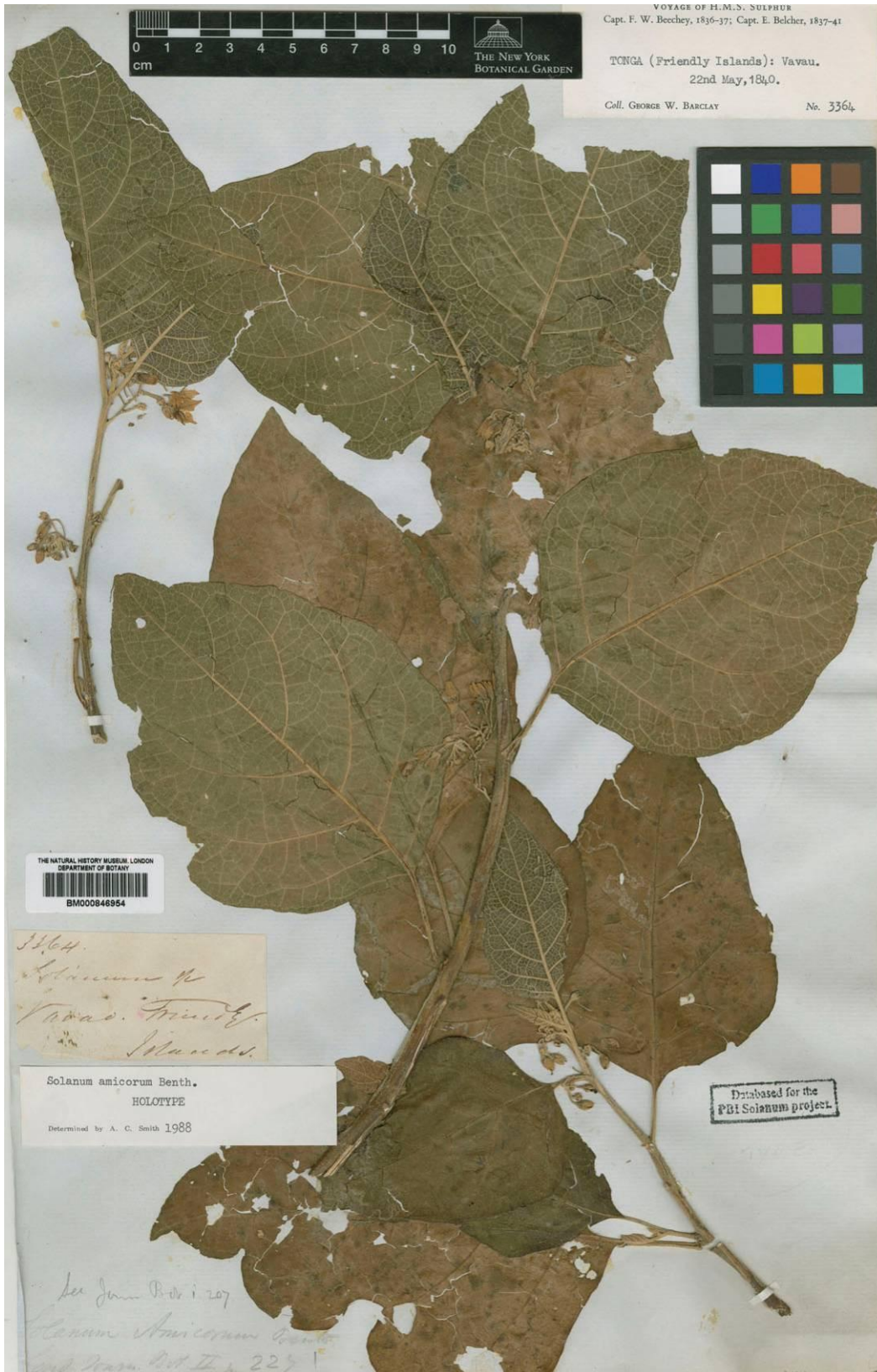


Figure 6. Holotype of *Solanum amicorum* (Barclay s.n., BM 000846954).



Figure 7. Specimen of *Solanum artense* (MacKee 23149, P 0030067).



Figure 8. Lectotype of *Solanum austro-caledonicum* (Milne 137, K 000195698).



Figure 9. Possible isotype of *S. bauerianum* (Bauer s.n., K 000449108).



Figure 10. Isotype of *Solanum camptostylum* (Sarasin 392, P 00298943).



Figure 11. Isotype of *Solanum caumii* (Caum 84, BISH 581194).



Figure 12. Isotype of *Solanum guamense* (Guam Experiment Station 446, P 00316599).



Figure 13. Holotype of *Solanum hillebrandii* (Hillebrand 116, K).



Figure 14. Lectotype of *Solanum hugonis* (McKee 25016, P 00300157).



Figure 15. Holotype of *Solanum inamoenum* (R. Hinds s.n., K 000195699).



Figure 16. Holotype of *Solanum incompletum* (Nelson s.n., BM 000846689).

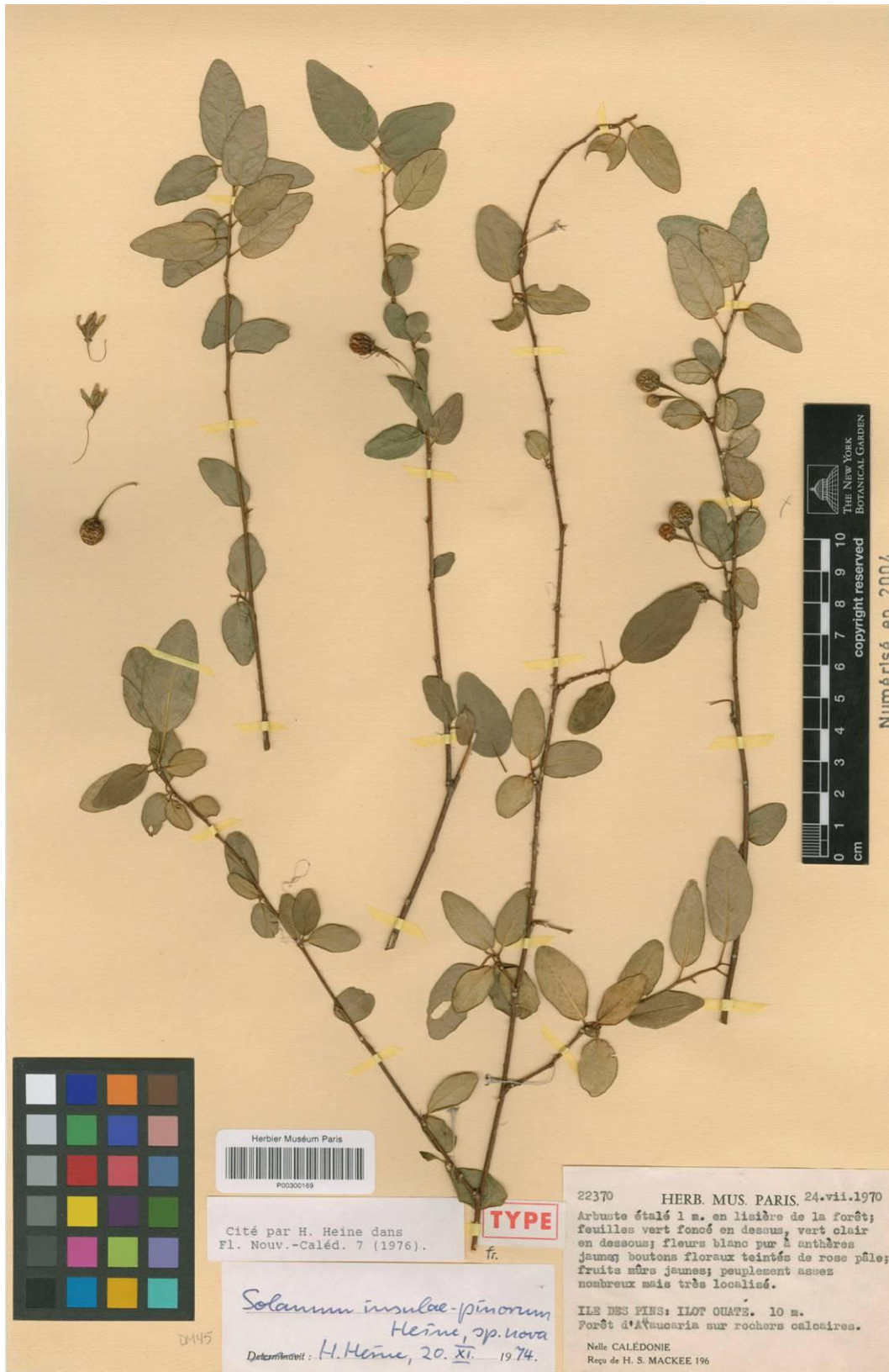


Figure 17. Isotype of *Solanum insulae-pinorum* (MacKee 22370, P 00300169).



Figure 18. Lectotype of *Solanum leratii* (Le Rat 249, P 00299966).

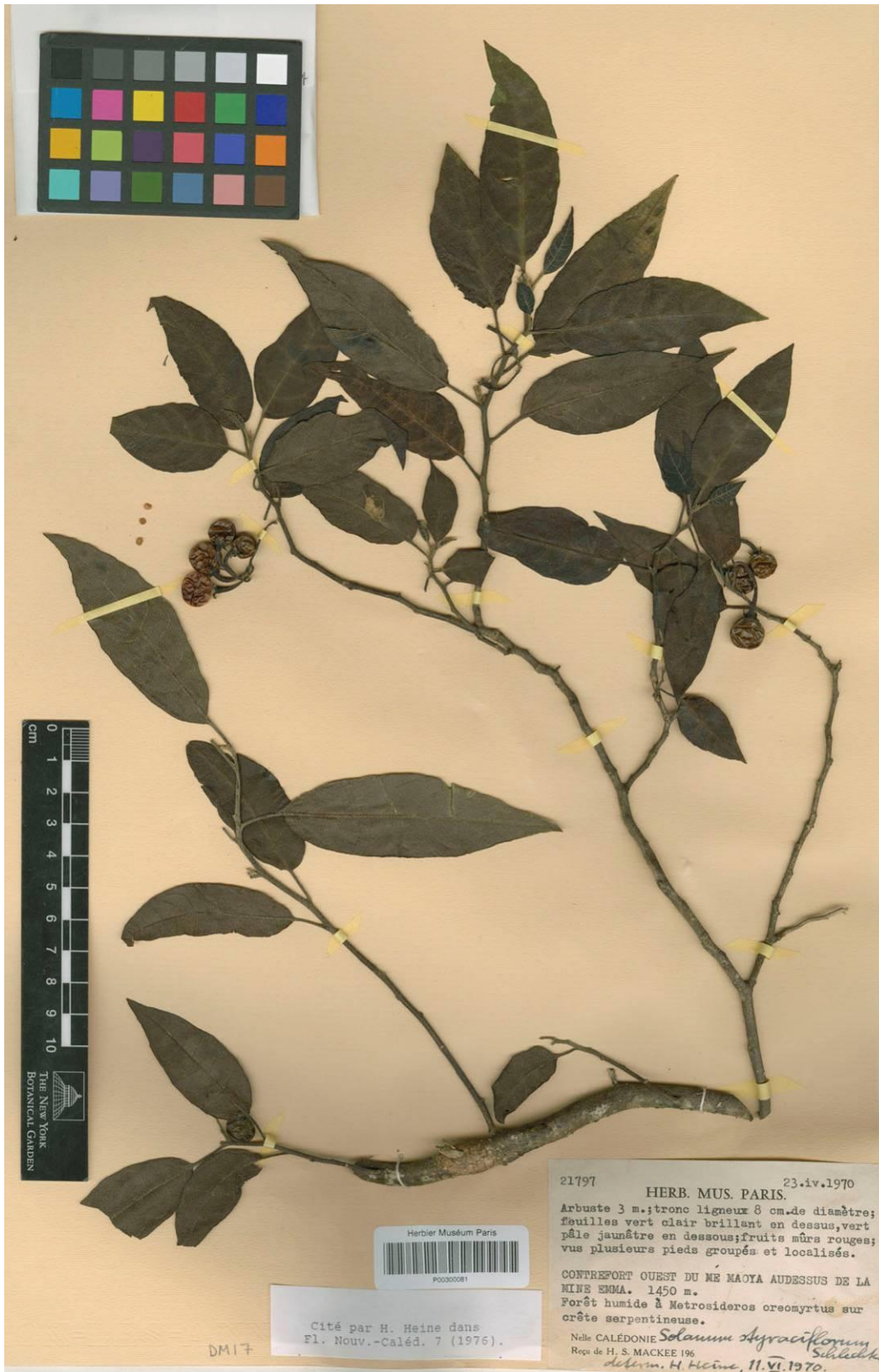


Figure 19. Holotype of *Solanum memaoyanum* (MacKee 21787, P 00300081).



Figure 20. Lectotype of *Solanum milnei* (MacGillivray 926, K 000195704).



Figure 21. Holotype of *Solanum nelsonii* (Nelson s.n., BM-Banks 000846708).



Figure 22. Holotype of *Solanum nudatum* (Jacquinot s.n., P 00315200).



Figure 23. Lectotype of *Solanum pancheri* (Pancher s.n., P 003000140).

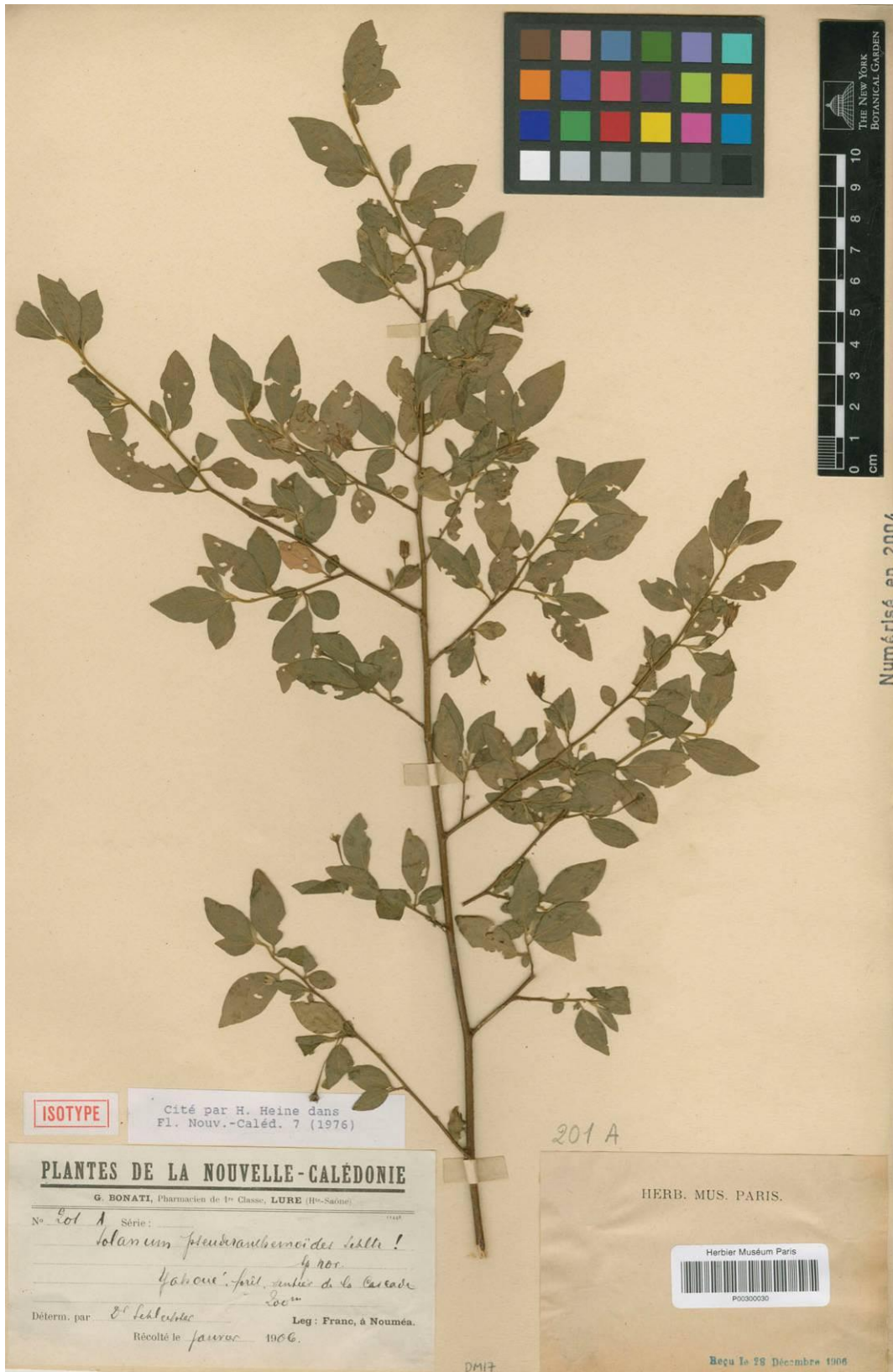


Figure 24. Lectotype of *Solanum pseuderanthemoides* (Franc 201a, P 00300030).



Figure 25. Holotype of *Solanum pseudopedunculatum* (Smith 6467, US 1966675).

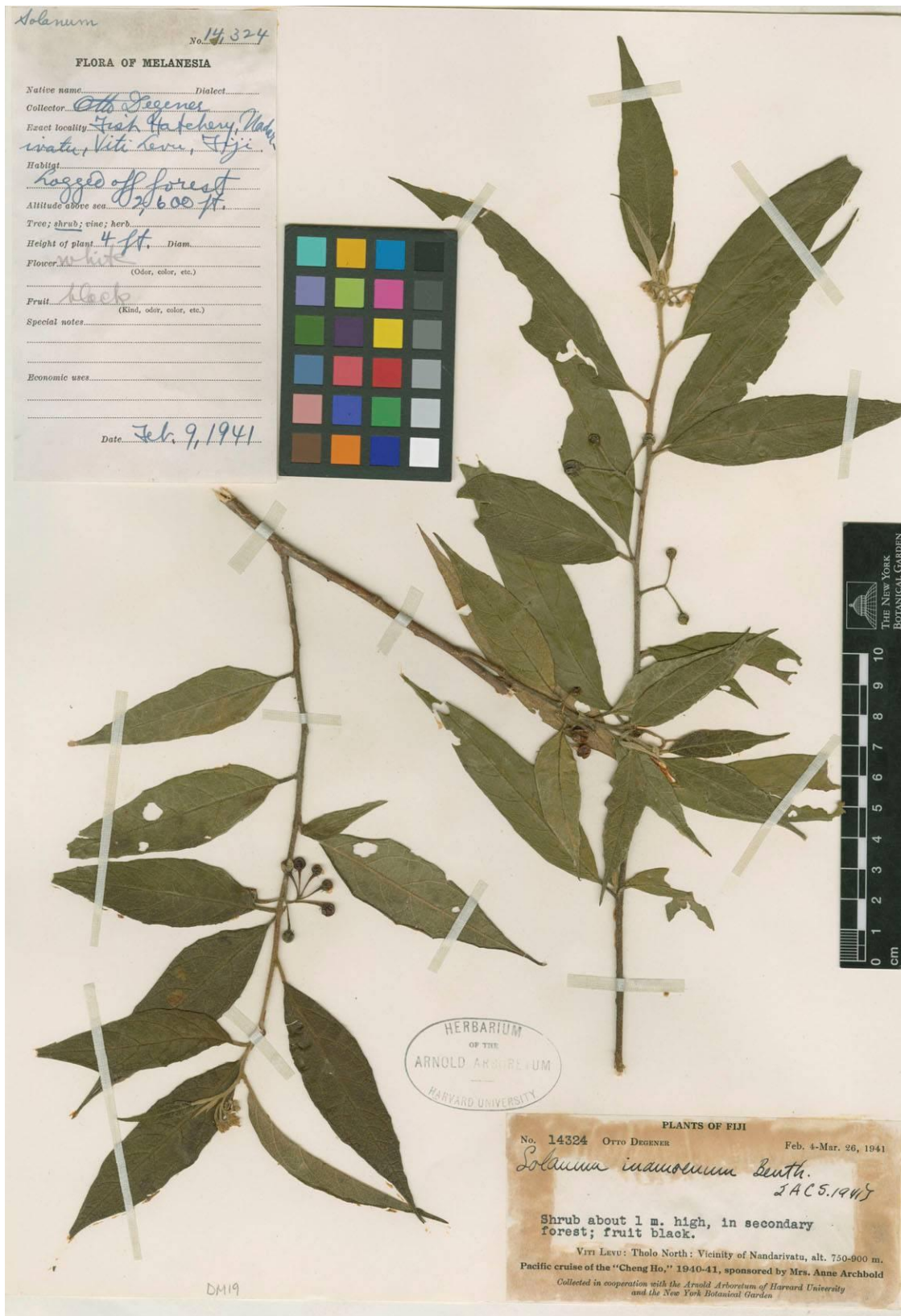


Figure 26. Holotype of *Solanum ratale* (Degener 14324, A).

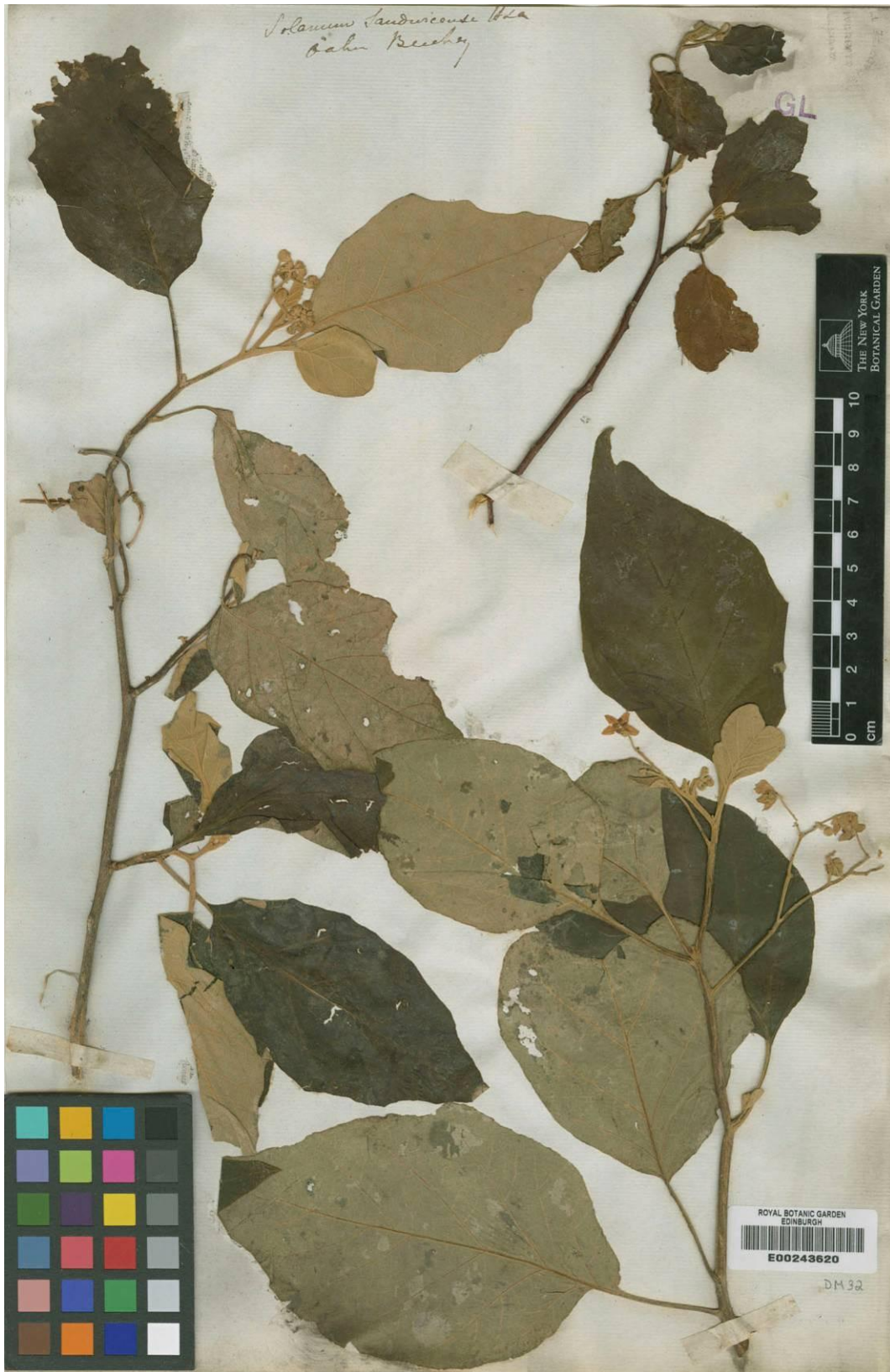


Figure 27. Lectotype of *Solanum sandwicense* (Beechey s.n., E 00243620).



Figure 28. Isotype of *Solanum semisucculentum* (McPherson 3303, MO 2924404).



Figure 29. Isotype of *Solanum vaccinioides* (Cribbs 1253, P 00288416).

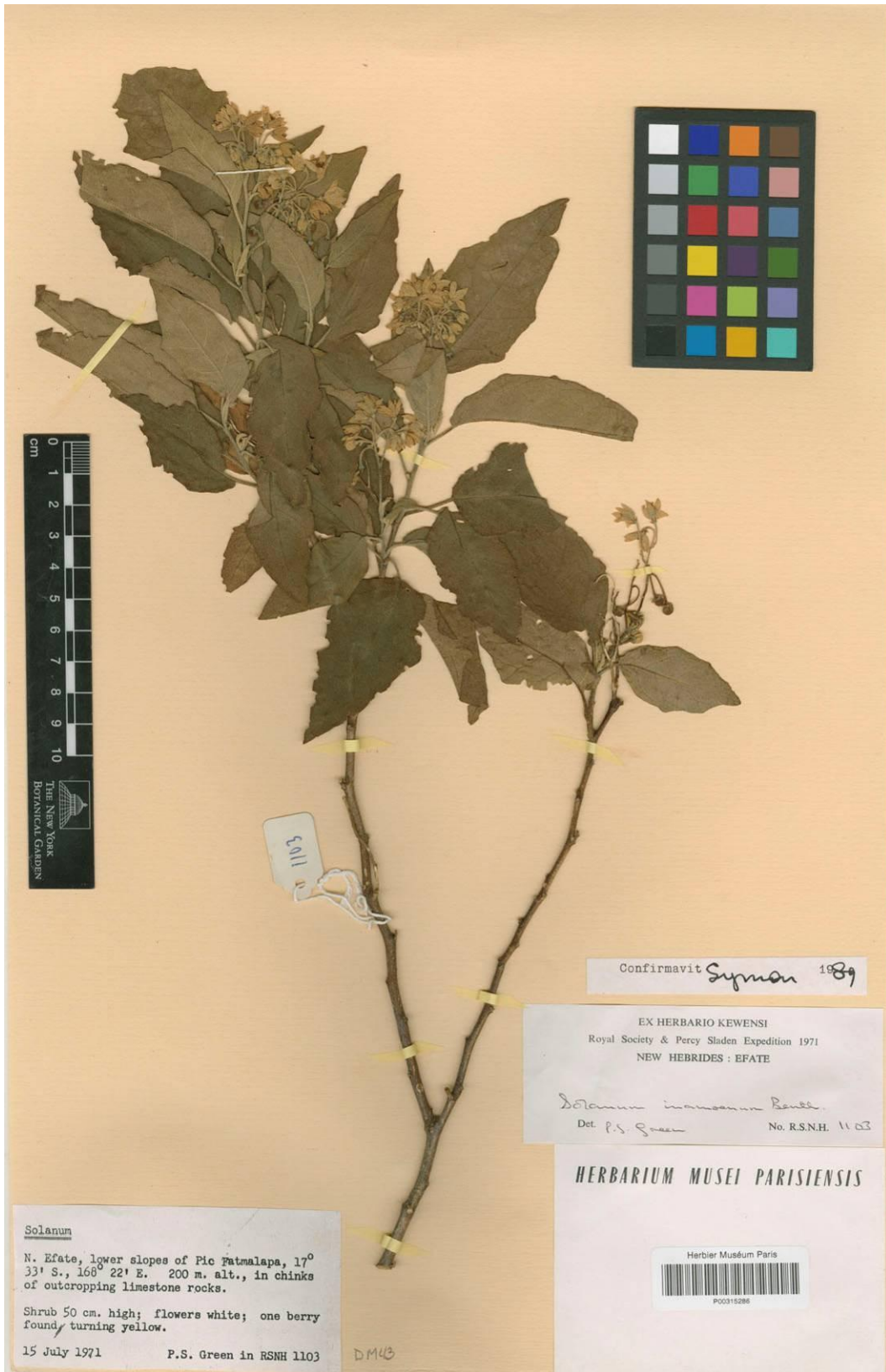


Figure 30. Holotype of *Solanum vanuatuense* (Green 1103, P 00315286).

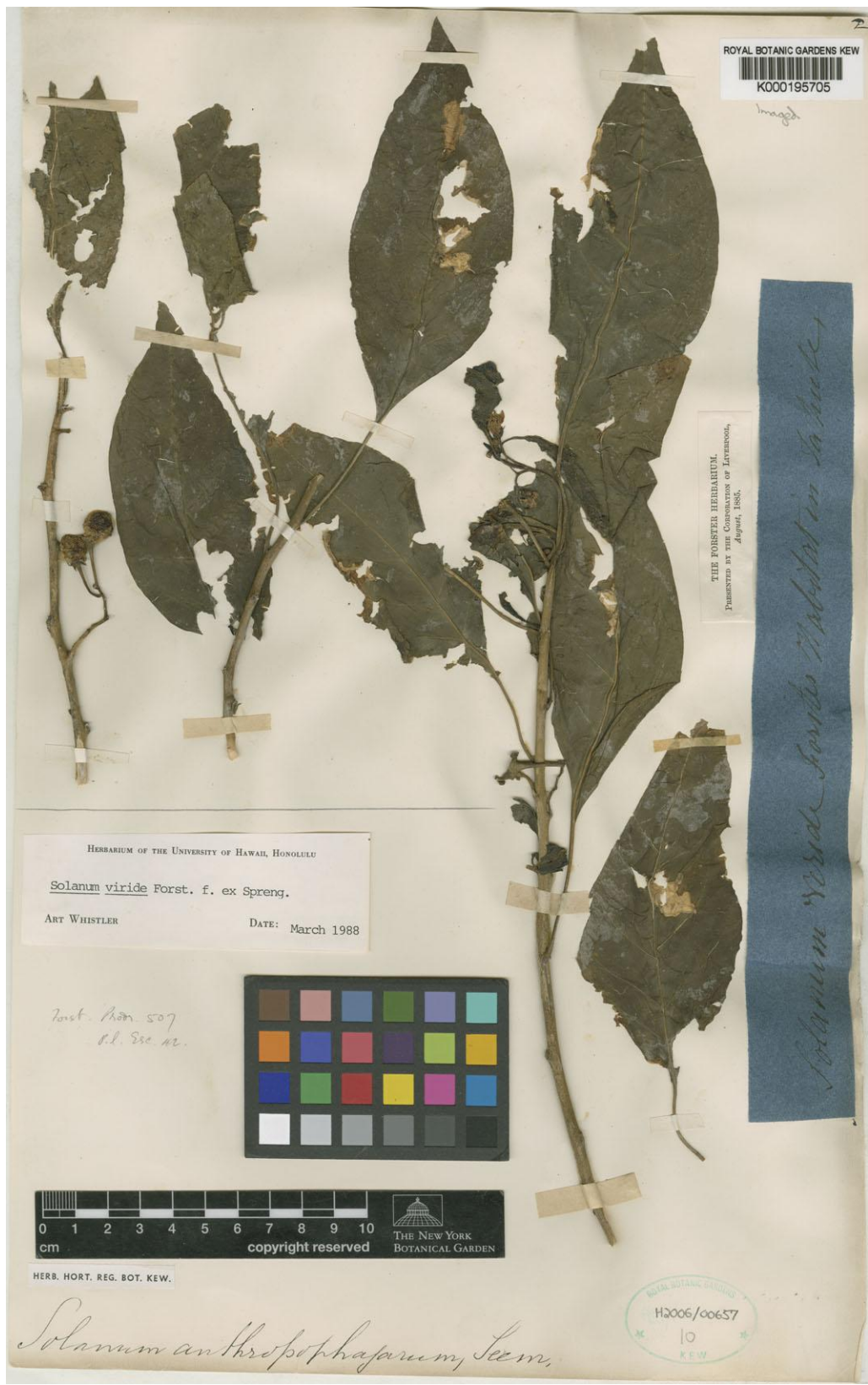


Figure 31. Isotype of *Solanum viride* (Morrenhout s.n., K 000196705).

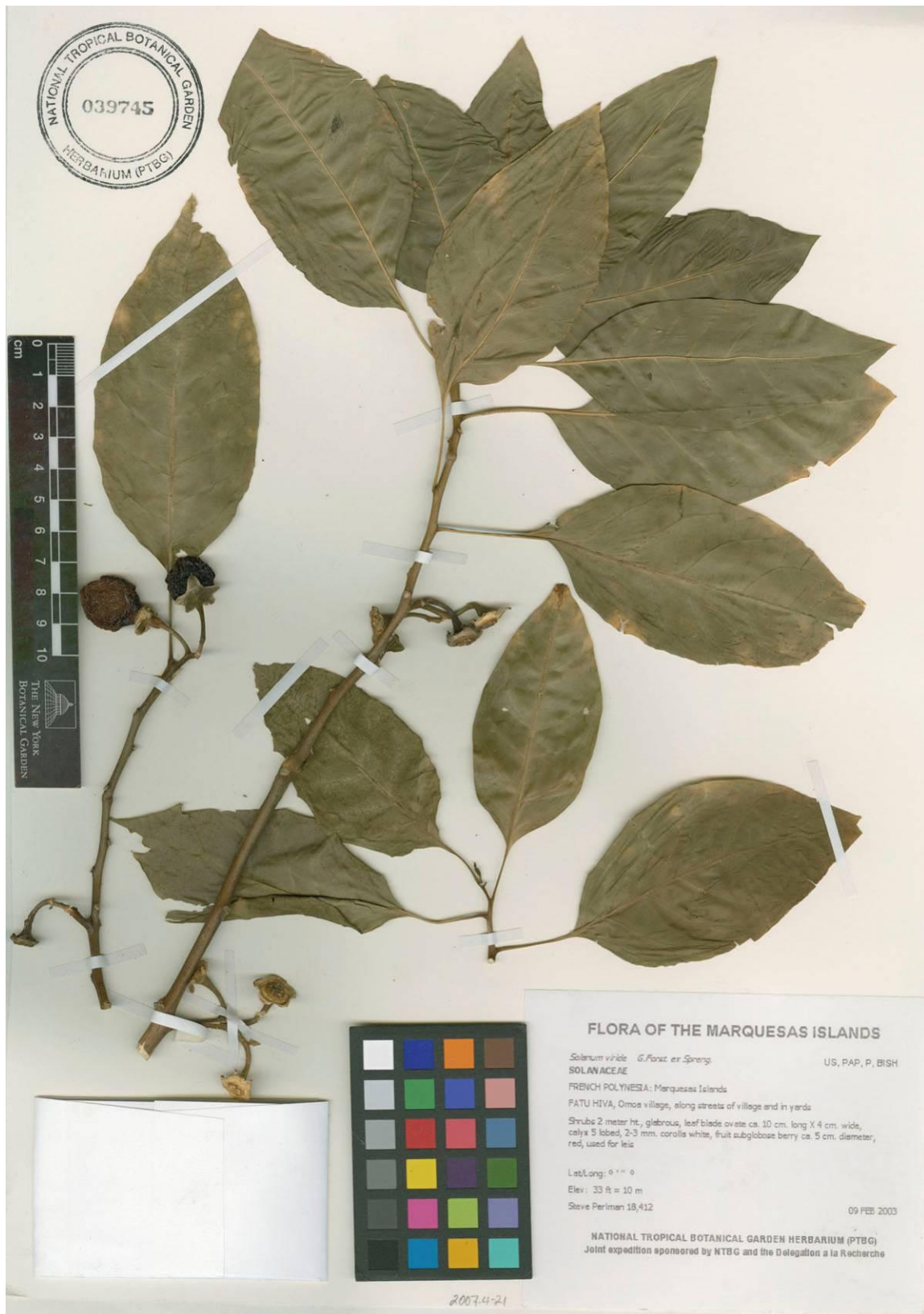


Figure 32. A large fruited domesticated of *Solanum viride* from the Marquesas Islands (Perlman 18412).

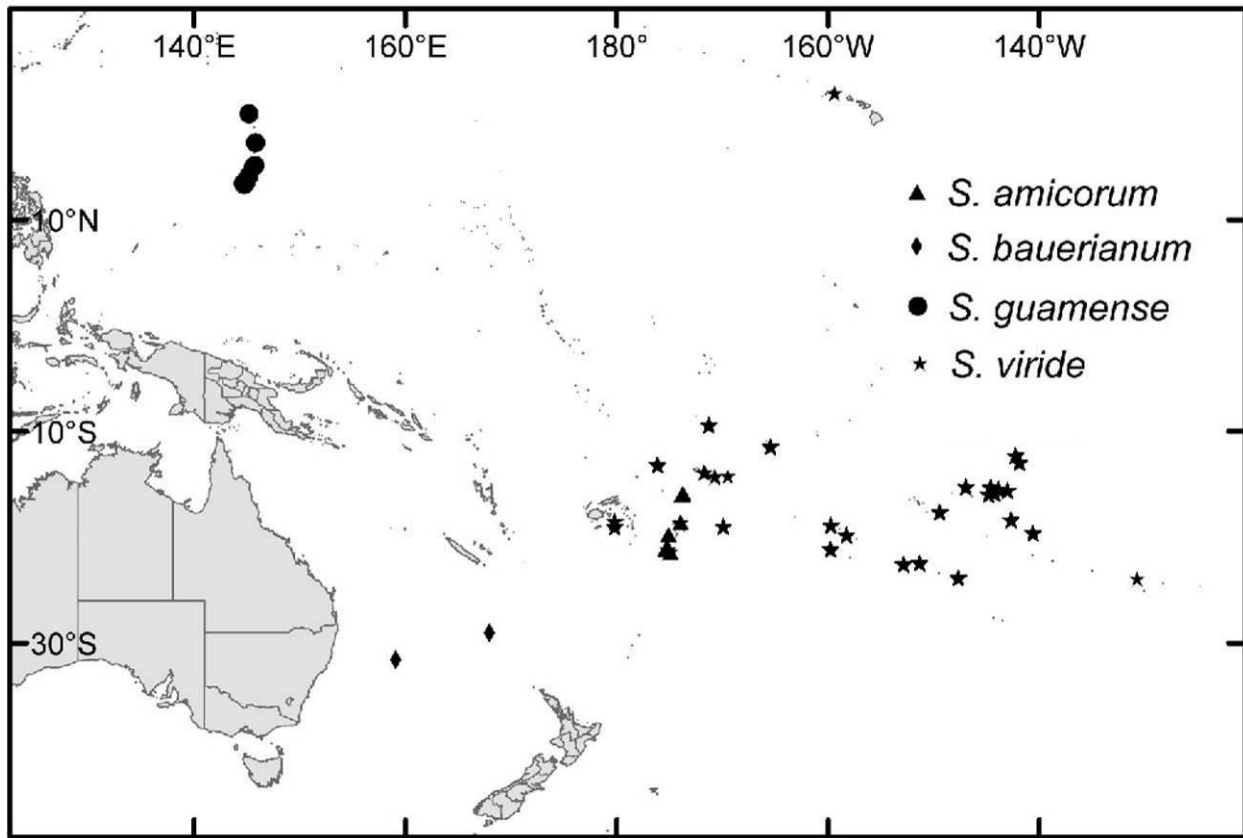


Figure 33. Distributions of *S. amicorum*, *S. bauerianum*, *S. guamense*, and *S. viride*.

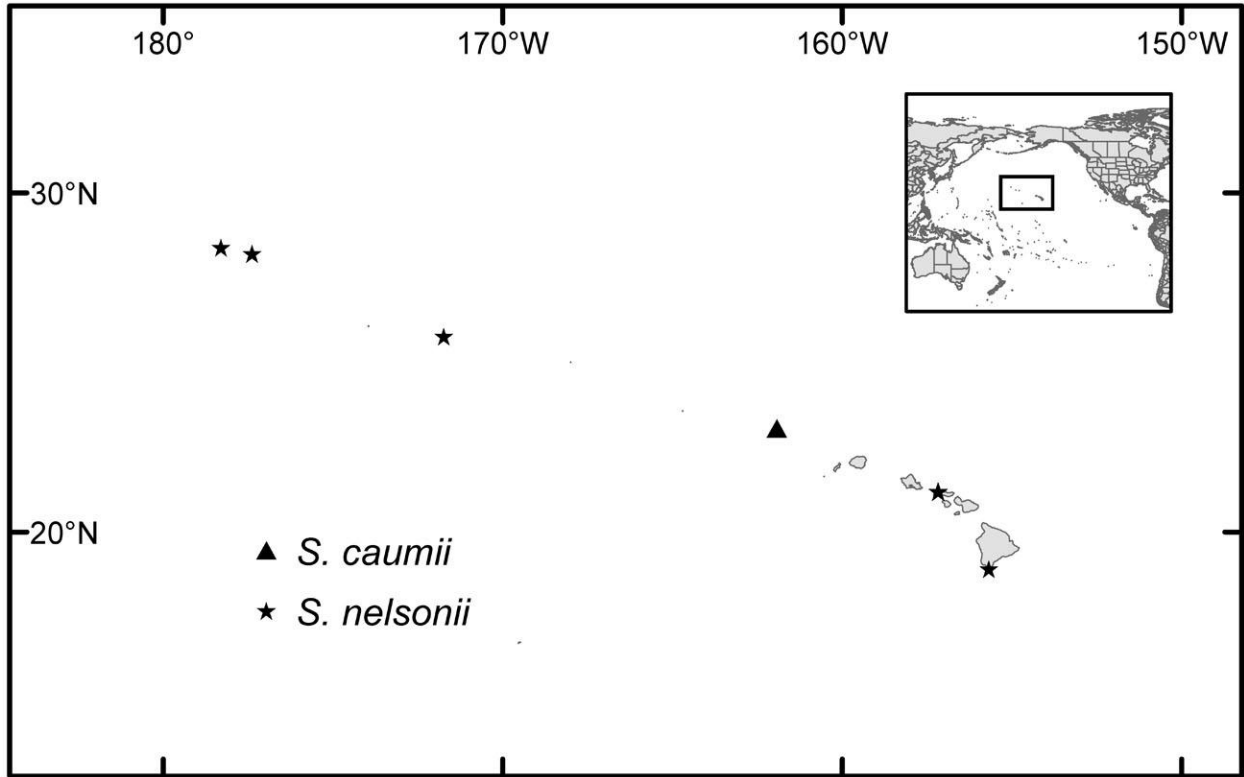


Figure 34. Distributions of *S. caumii* and *S. nelsonii*, in the Hawaiian Islands.

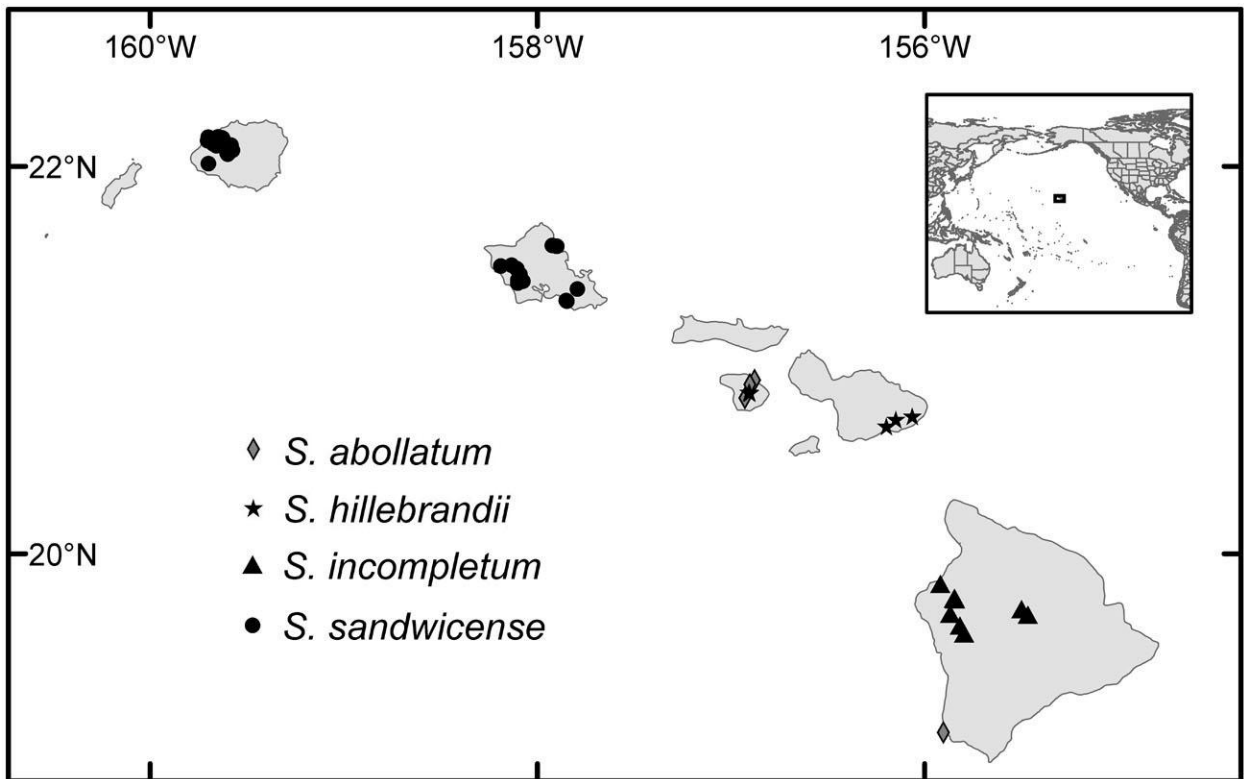


Figure 35. Distributions of *S. abollatum*, *S. hillebrandii*, *S. incompletum*, and *S. sandwicense*, in the Hawaiian Islands.

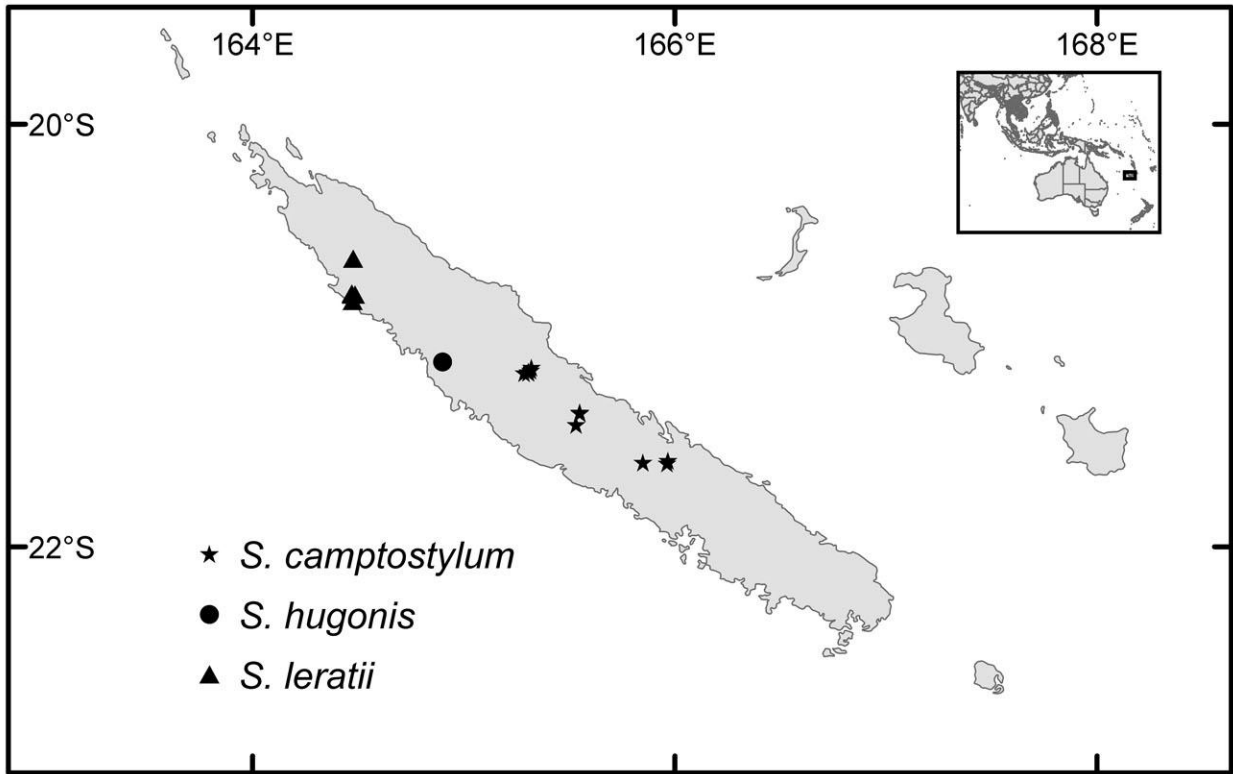


Figure 36. Distributions of *S. camptostylum*, *S. hugonis*, and *S. leratii*, in New Caledonia.

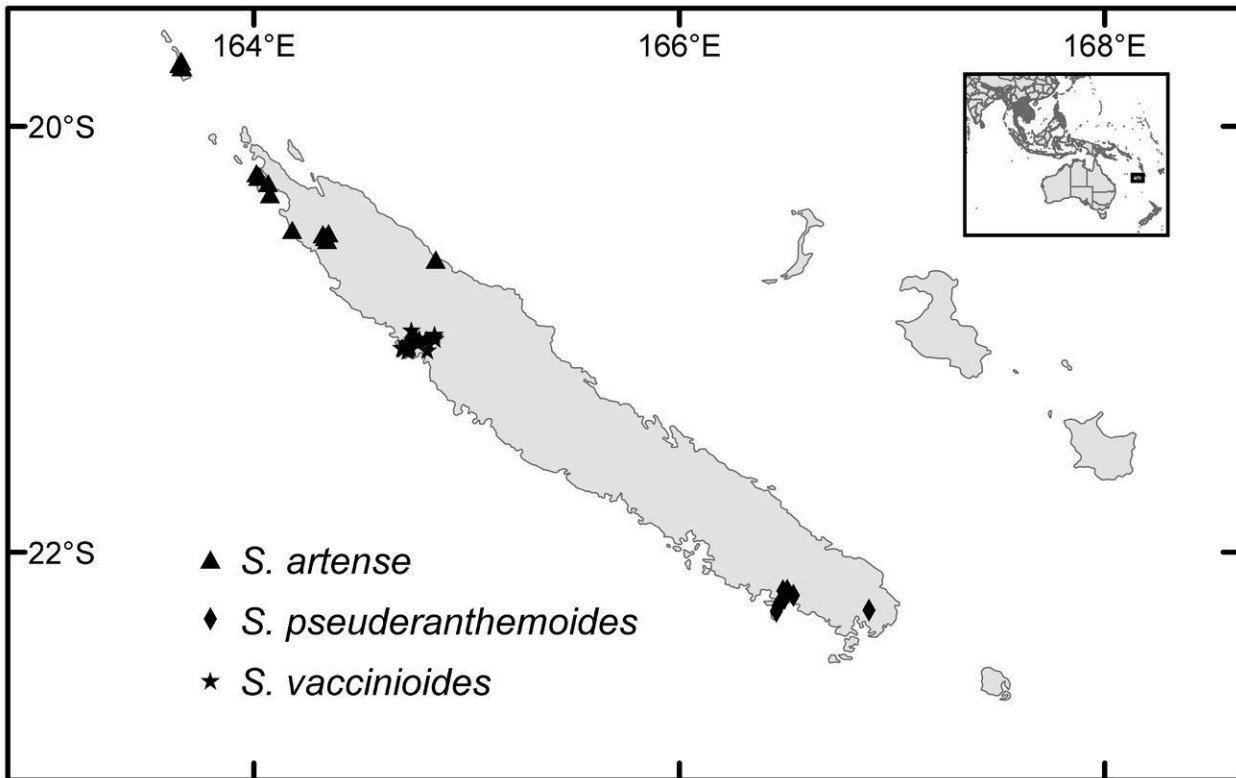


Figure 37. Distributions of *S. artense*, *S. pseuderanthemoides*, in New Caledonia.

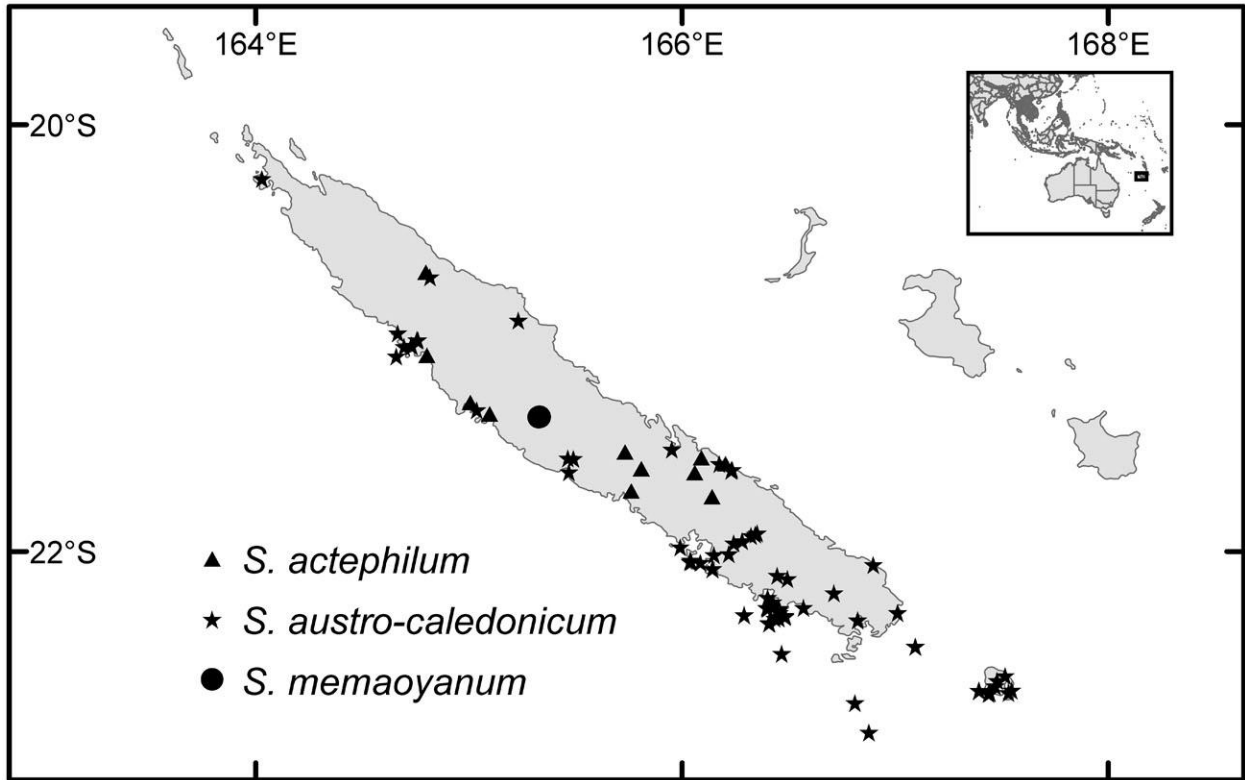


Figure 38. Distributions of *S. actephilum*, *S. austro-caledonicum*, and *S. memaoyanum*, in New Caledonia.

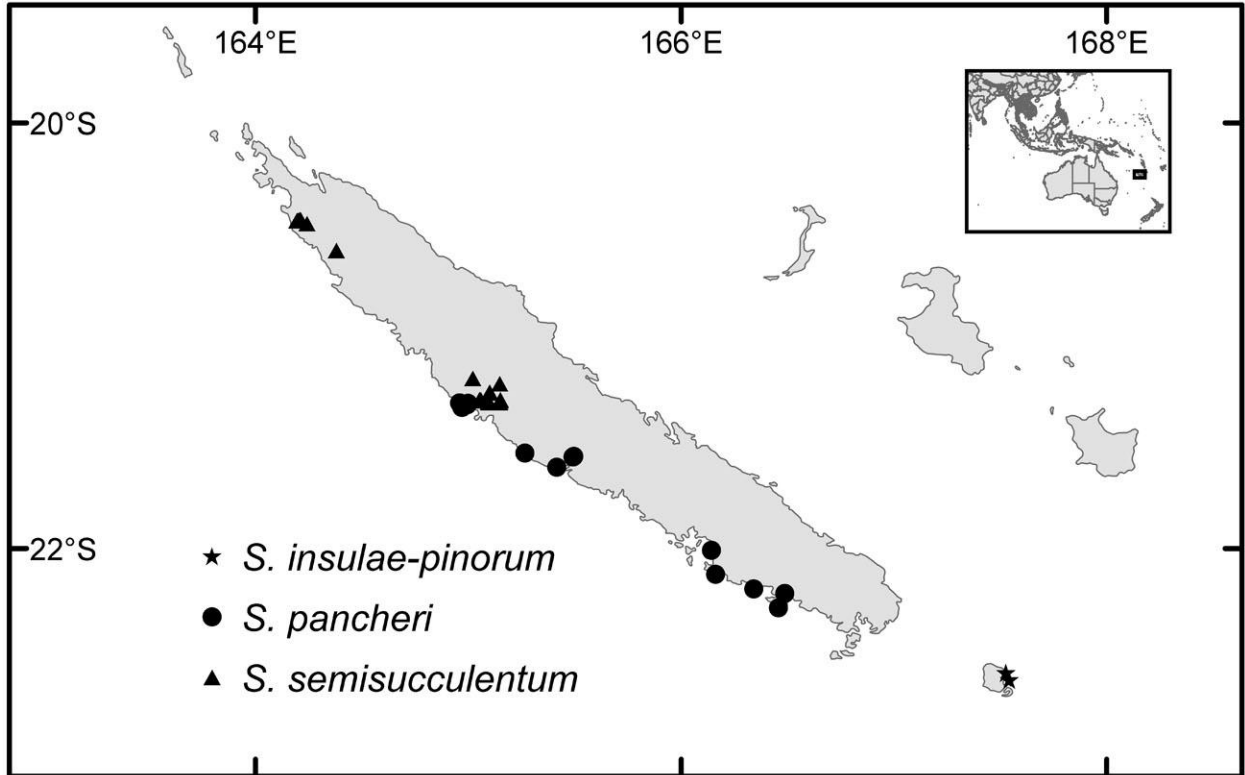


Figure 39. Distributions of *S. insulae-pinorum*, *S. pancheri*, and *S. semisucculentum*, in New Caledonia.

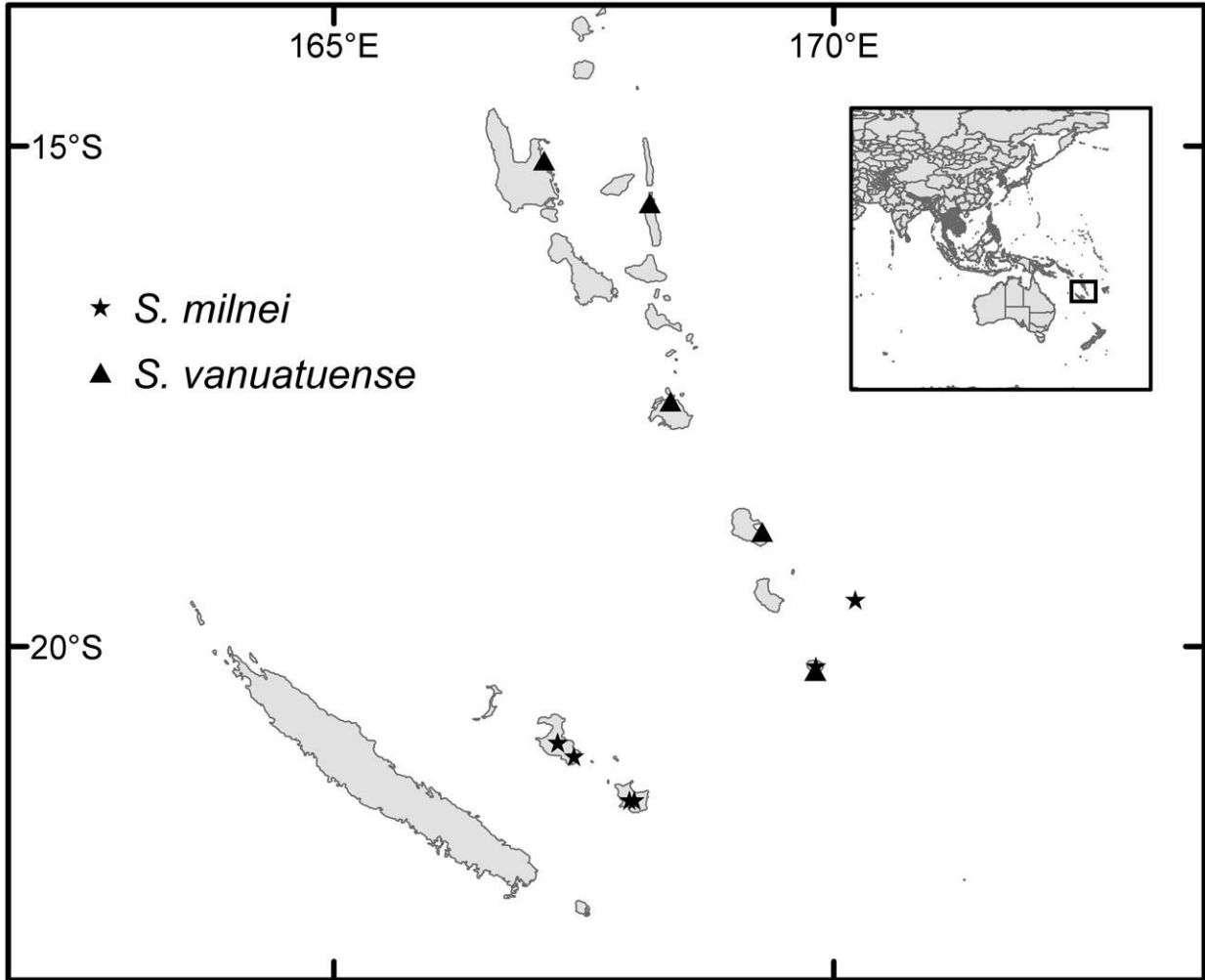


Figure 40. Distributions of *S. milnei* and *S. vanuatuense*, in Vanuatu and the Loyalty Islands of New Caledonia.

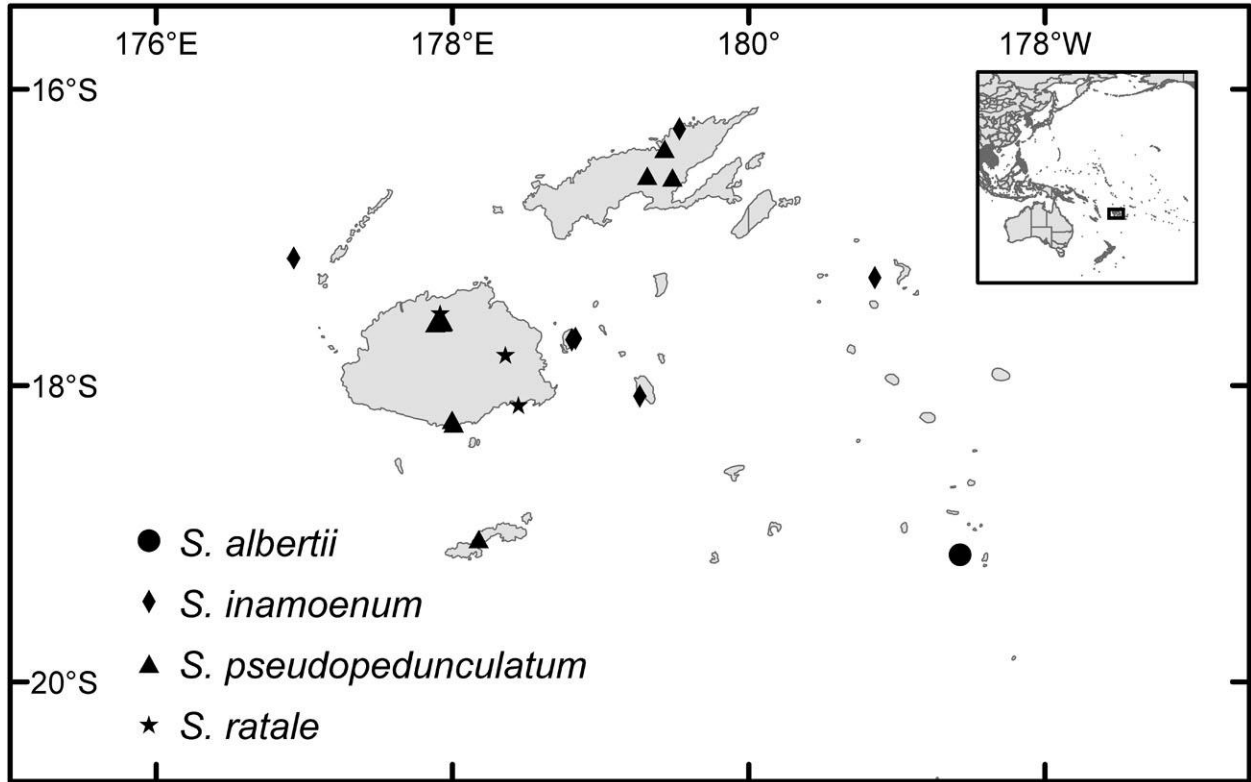


Figure 41. Distributions of *S. albertii*, *S. inamoenum*, *S. pseudopedunculatum*, and *S. ratale*, in Fiji.

Literature Cited

- Anderson, G., G. Bernardello, L. Bohs, T. Weese & A. Santos-Guerra.** 2006. Phylogeny and biogeography of the Canarian *Solanum vespertilio* and *S. lidii* (Solanaceae). *Anales del Jardín Botánico de Madrid*. 63: 159–167.
- Auld, T. & I. Hutton.** 2004. Conservation issues for the vascular flora of Lord Howe Island. *Cunninghamia* 8: 490–500.
- Bennett, J. R.** 2008. Revision of *Solanum* section *Regmandra* (Solanaceae). *Edinburgh Journal of Botany* 65: 69–112.
- Bitter, G.** 1921. *Solanum*. Pp. 221–228. *In*: F. Sarasin and J. Roux (eds.), *Nova Caledonia B. Botanik von Hans Schinz & A. Guillaumin Vol I Livr. III*, Berlin und Wiesbaden, C. W. Kreidels Verlag.
- Bitter, G.** 1922a. *Solana africana*. III. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*. 57: 248–286.
- Bitter, G.** 1922b. *Solana nova vel minus cognita*. XXI. *Repertorium Specierum Novarum regni Vegetabilis*. 18: 301–309.
- Brown, F. B. H.** 1931. Solanaceae. Pp. 35–37. *In*: E. Christophersen and E. L. Caum (eds.), *Vascular Plants of the Leeward Islands, Hawaii*. Bernice P. Bishop Museum Bulletin 81.
- Brewster, A. B.** 1922. The hill tribes of Fiji a record of forty years' intimate connection with the tribes of the mountainous interior of Fiji with a description of their habits in war & peace, methods of living, characteristics mental & physical, from the days of cannibalism to the present time. J. B. Lippincott Company. London.
- Carlquist, S.** 1974. *Island biology*. Columbia University Press, New York, New York. USA.
- Child, A.** 1979. A review of branching patterns in the Solanaceae. Pp. 345–356. *In*: J. G. Hawkes, R. N. Lester and A. D. Skelding, (eds.), *The biology and taxonomy of the Solanaceae*. Academic Press Inc. London.
- Danert, S.** 1967. Die Verzweigung als infragenerisches Gruppenmerkmal in der Gattung *Solanum* L. *Kulturpflanze* 15: 275–292.
- D'Arcy, W. G.** 1972. Solanaceae studies II: typification of subdivisions of *Solanum*. *Annals of the Missouri Botanical Garden* 59: 262–278.
- D'Arcy, W. G.** 1991. The Solanaceae since 1976, with a review of its biogeography. Pp 75–137. *In*: J. G. Hawkes, R. N. Lester, M. Nee, and N. Estrada-R. Richmond, (eds.), *Solanaceae III: taxonomy, chemistry, evolution*. Royal Botanic Gardens, Kew.
- Dunal, F. M.** 1852. Solanaceae. Pp. 1–690. *In*: A. P. DeCandolle (ed.), *Prodromus* 13.
- Elmer, A. D. E.** 1908. A century of new plants. *Leaflets of Philippine Botany* 1: 272–359.
- Garnock-Jones, P. J.** 1986. South Pacific plants named by K. P. J. Sprengel in 1807. *Taxon* 33: 123–171.
- Green, P.** 1994. *Solanaceae*. Pp. 1–208. *In*: Orchard, A. E., A. J. G. Wilson, L. G. Adams, B. Barnsley, K. Mallett, J. C. Mowatt, T. S. Rand, K. Thomas, H. S. Thompson (eds.), *Flora of Australia* Volume 49, Oceanic islands 1, Australian Government Publishing Service, Canberra, Australia.
- Heine, H.** 1976. Solanaceae. Pp. 119–205. *In*: A. Abréville and J. Leroy (eds.), *Flore de la Nouvelle Calédonie et Dépendances*. Muséum National D'Histoire Naturelle. Paris.
- Hillebrand, W.** 1888. *Flora of the Hawaiian Islands a description of their phanerogams and vascular cryptogams*. New York. New York. USA

- Hutton, I., J. P. Parkes & A. R. E. Sinclair.** 2007. Reassembling island ecosystems: the case of Lord Howe Island. *Animal Conservation* 10: 22–29.
- Jaffré, T., P. Bouchet, J. Vellon.** 1998. Threatened plants of New Caledonia: Is the system of protection areas adequate? *Biodiversity and Conservation* 7: 109–135.
- Keitt, B. S.** 2008. Predator-proof Fencing for Invasive Species Control in Hawaii: A Comprehensive Prioritization and Implementation Plan to protect native species. Department of Defense Legacy Resource Management Program Project 07-339 Report.
- Levin, R., N. Myers, & L. Bohs.** 2006. Phylogenetic Relationships among the “Spiny Solanums” (*Solanum* subgenus *Leptostemonum*, Solanaceae). *American Journal of Botany* 93: 157–169.
- Nixon, K. C. & Q. D. Wheeler.** 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–23.
- Mabberely, D., Crika Pignatti-Wikus, and Christa Riedl-Dorn.** 2007. An extinct tree ‘revived’. *Curtis’s Botanical Magazine*, 24: 190–195.
- McCaughey, V.** 1917. The phytogeography of Manoa Valley, Hawaiian Islands. *American Journal of Botany* 4: 561–603.
- McNeill, J., F. R. Barrie, H. M. Burdet, V. Demoulin, D. L. Hawksworth, K. Marhold, D. H. Nicolson, J. Prado, P. C. Silva, J. E. Skog, J. H. Wiersema, & N. J. Turland.** 2006. International Code of Botanical Nomenclature (Vienna Code). *Regnum Vegetabile* 146, A.R.G. Gantner Verlag KG, Ruggell, Liechtenstein.
- Mitchell, C, C. Ogura, D. W. Meadows, A. Kane, L. Strommer, S. Fretz, D. Leonard, & A. McClung.** 2005. Hawaii’s Comprehensive Wildlife Conservation Strategy. Department of Land and Natural Resources. Honolulu, Hawai‘i.
- Morat, P., T. Jaffré, J. Veillon.** 2001. The flora of New Caledonia’s calcareous substrates. *Adansonia*, sér. 3, 23: 109–127.
- Nee, M.** 1999. Synopsis of *Solanum* in the New World. Pp. 285–333. *In* M. Nee, D. E. Symon, R. N. Lester, and J. P. Jessop (eds.) *Solanaceae IV: advances in biology and utilization*. Royal Botanic Gardens, Kew, Richmond, Surrey, UK.
- Nixon, K. C. & Q. D. Wheeler.** 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.
- Papy, H. R.** 1955. La végétation des Îles de la Société et de Makatéa (Océanie française) *Travaux du Laboratoire forestier de Toulouse*. Tome V, Géographie forestière du monde. Deuxième section, L’Océanie. vol. 1, article 3: 1–386.
- Paramonov, S. J.** 1960. Lord Howe Island, a riddle of the Pacific. Part II. *Pacific Science* 14: 75–85.
- Rodd, A. & J. Pickard.** 1983. Census of vascular flora of Lord Howe Island. *Cunninghamia* 1:267–280.
- Roe, K.** 1967. A revision of *Solanum* sect. *Brevantherum* (Solanaceae) in North and Central America. *Brittonia* 19: 353–373.
- Seithe, A. & D. v. Hoff.** 1962. Die Haararten der Gattung *Solanum* L. und ihre taxonomische Verwertung. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie*. 81: 3, 261–336.
- Seemann, B.** 1862a. Viti: an account of the government mission to the Vitian or Fijian Islands in the years 1860–61. MacMillan & Co. London.
- Seemann, B.** 1862b. *Plantae Vitienses*. *Bonplandia* 10: 274–275.
- Seemann, B.** 1863. The Solana of Tropical Polynesia. *Journal of Botany* 1: 206–211.

- Seemann, B.** 1865–73. *Flora Vitiensis: a description of the plants of the Viti or Fiji Islands with an account of their history, uses, and properties.* L. Reeves and Co. London.
- Smith, A. C.** 1991. *Flora vitiensis nova: A new flora of Fiji Part 5.* Pacific Tropical Garden, Lawai, Hawaii.
- St. John, H.** 1969. Hawaiian novelties in the genus *Solanum* (Solanaceae). *Hawaiian Plant Studies* 30. *Pacific Science* 23: 350–352.
- St. John, H.** 1988a. Diagnoses of *Solanum* species (Solanaceae). *Hawaiian Plant Studies* 163. *Phytologia* 64: 169–171.
- St. John, H.** 1988b. Native Hawaiian species of *Solanum* (Solanaceae). *Hawaiian Plant Studies* 82. Privately published. Honolulu.
- Symon, D. E.** 1981. A revision of the genus *Solanum* in Australia. *Journal of the Adelaide Botanic Garden*. 4: 1–367.
- Symon, D. E.** 1985. The Solanaceae of New Guinea. *Journal of the Adelaide Botanic Gardens* 8: 1–171.
- Symon, D. E.** 1986. The phylogeography of New Guinea *Solanum* (Solanaceae). *Blumea* 31: 319–328.
- Symon, D. E.** 1993. Hawaiian species of *Solanum*. *Solanaceae Newsletter* 3: 18–25.
- Thiers, B. [continuously updated].** Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium.
<http://sweetgum.nybg.org/ih/>
- Warren, L. W., M. M. Bruegmann, D. M. Herbst, J. Q. C. Lau.** 1999. Hawaiian vascular plants at risk: 1999. *Bishop Museum Occasional Papers*. 60: 1–58.
- Weese, T. & L. Bohs.** 2007. A three gene phylogeny of the genus *Solanum* (Solanaceae). *Systematic Botany* 32: 445–463.
- Whistler, W. A.** 1991. The ethnobotany of Tonga: The plants, their Tongan names, and their uses. *Bishop Museum Bulletins in Botany* 2.