Relationships among wild relatives of the tomato, potato, and pepino

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Abstract With ca. 200 species, the informally named Potato clade represents one of the larger subgroups of the estimated 1500 species of *Solanum*. Because its members include the potato (*S. tuberosum*), tomato (*S. lycopersicum*), and pepino (*S. muricatum*), it is the most economically important clade in the genus. These crop species and their close relatives have been the focus of intensive research, but relationships among major lineages of the Potato clade remain poorly understood. In this study, we use sequences from the nuclear ITS and *waxy* (GBSSI), and plastid *trnT-trnF* and *trnS-trnG* to estimate a phylogeny and further explore relationships within the Potato clade. With increased sampling over past studies, the Potato clade emerges as a strongly supported clade and comprises 12–13 subclades which, for the most part, correspond to traditionally recognized sections. *Solanum* sect. *Regmandra* is sister to the rest of the lineages of the Potato clade which are, in turn, organized into two major subclades: (1) sections *Anarrhichomenum*, *Articulatum*, *Basarthrum*, *Etuberosum*, *Juglandifolia*, *Lycopersicoides*, *Lycopersicon*, and *Petota*, and (2) sections *Herpystichum* and *Pteroidea*. As in all other studies including these groups, sections *Etuberosum*, *Juglandifolia*, *Lycopersicoides*, *Lycopersicon*, and *Petota* form a strongly supported clade. *Solanum oxycoccoides*, a high-elevation species endemic to north-central Peru, was tentatively assigned to several groups within *Solanum* based on morphological evidence, but instead the species represents an independent lineage within the Potato clade, sister to the first major subclade. A key to the sections of the Potato clade is provided.

Keywords Americas; phylogeny; potato; Solanaceae; *Solanum*; taxonomy

Supplementary Material The Electronic Supplement (Figs. S1–S4) is available in the Supplementary Data section of the online version of this article at http://ingentaconnect.com/content/iapt/tax; DNA sequence alignment is available from TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S19117)

■ INTRODUCTION

Infrageneric classification of *Solanum* L. has undergone dramatic changes during the shift from schemes stemming from morphological data (e.g., Dunal, 1816, 1852; D'Arcy, 1972; Nee, 1999) to those based on molecular data (Bohs, 2005; Weese & Bohs, 2007; Särkinen & al., 2013). Among the biggest surprises to emerge from this revolution was the realization that the tomato (*S. lycopersicum* L.) and its close relatives, long considered as a separate genus by many authors, are instead deeply nested within *Solanum* and, in fact, are closely related to the potato (*S. tuberosum* L.; Spooner & al., 1993). Also, molecular data has allowed for the identification of many monophyletic lineages, some of which are consistent with groups recognized by morphology, while others are wholly unexpected. One of the clades that has been redefined by molecular data is the Potato clade, which includes the potato, tomato, and pepino (*S. muricatum* Aiton), and is one of the world's most economically important clades of plants. Relationships among these crops and their wild relatives have been the focus of many studies and are well established (e.g., Lester, 1991; Spooner & al., 1993, 2005a; Blanca & al., 2007; Peralta & al., 2008). Other lineages within the Potato clade that are less economically important have not received the same attention. Several of these lesser-known groups have been the focus of recent taxonomic or phylogenetic studies, including *Solanum* sect. *Pteroidea* Dunal (Knapp & Helgason, 1997; Tepe & Bohs, 2010), sect. *Regmandra* (Dunal) Ugent (Bennett, 2008), and sect. *Herpystichum* Bitter (Tepe & Bohs, 2011; Tepe & al., 2011), but others such as sect. *Anarrhichomenum* Bitter have not been the focus of such comprehensive studies and remain poorly understood.

Despite strong molecular support for the Potato clade, a clear morphological synapomorphy for the group has not been identified. Nevertheless, once familiar with the group, accurately identifying a plant as a member of the Potato clade is straightforward. There are, however, a number of characters that in combination can be used to characterize members of the clade. These include compound leaves in most species (otherwise rare in *Solanum*; Child, 1990), a largely herbaceous to weakly woody habit, stems that are often lax to weakly

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scandent to truly viny, unbranched multicellular trichomes in most species (but see exceptions below), tubers borne on rhizomes exclusively in all species of section *Petota*, and the presence of well-developed pseudostipules in most lineages (Child & Lester, 1991; Spooner & al., 2004; Peralta & al., 2008).

The concept of the Potato clade, as presented herein, came together slowly over time. Dunal (1816) arranged all *Solanum* species known to him into a series of infrageneric groupings. In the group with *S. tuberosum*, he included other members of *S.* sect. *Petota* Dumort along with members of sect. *Anarrhichomenum*, sect. *Basarthrum* (Bitter) Bitter, sect. *Juglandifolia* (Rydb.) A.Child, sect. *Pteroidea*, and sect. *Regmandra*. This collection of lineages encompasses a wide range of morphological variation (e.g., Fig. 1), but all are included in the Potato clade as circumscribed today (Särkinen & al., 2013). Dunal's (1816) concept of the group, however, was much broader and also included species now recognized as belonging to the Cyphomandra and Dulcamaroid clades (Weese & Bohs, 2007). Furthermore, he excluded the tomatoes and their relatives (*S.* sect. *Lycopersicon* (Mill.) Wettst.) from the group, as they were considered to belong to the segregate genus *Lycopersicon* Mill. Species in the former genus *Lycopersicon* have now been transferred to *Solanum* (Spooner & al., 1993; Peralta & al., 2008). Dunal (1816) also excluded sect. *Herpystichum* and some species of sect. *Pteroidea* from his concept of the potatoes, and placed them together in the genus *Bassovia* Aubl., but both groups have since been recognized as relatives of the potato based on morphological (Child, 1990) and molecular data (Bohs, 2005; Weese & Bohs, 2007). The present study builds on these previous molecular studies and includes the broadest sampling of the Potato clade to date.

Although the potato, tomato and, to a lesser degree, the pepino, are cultivated around the world, all species of the Potato clade are native to the New World. They range from ca. 38° N in western North America to ca. 41° S in central Chile and Argentina, with highest species diversity concentrated in the central Andes (Ecuador, Peru, Bolivia, Argentina) and central Mexico (Hijmans & Spooner, 2001). Habitats vary from sea-level beaches to high-Andean meadows up to 4650 m in elevation (D.M. Spooner, pers. obs.) and include arid deserts and mesic pine forests to wet rainforests, with the greatest diversity of species between 2000 and 4000 m (Correll, 1962; Hijmans & Spooner, 2001). Despite the nearly 200 years of research since Dunal's (1816) treatment, new species continue to be discovered in the Potato clade (Anderson, 1975; Anderson & Bernardello, 1991; Peralta & al., 2005; Nee & al., 2006; Anderson & al., 2006; Bennett, 2008; Tepe & Bohs, 2009; Tepe & al., 2012; Särkinen & al., 2015) and we expect this list to grow as exploration of under-collected areas continues.

The genus-wide phylogenies of Bohs (2005) and Weese & Bohs (2007) that first defined the Potato clade as presented here included relatively few species. Särkinen & al. (2013) also recognized the Potato clade, expanding its circumscription to include sect. *Regmandra*. Spooner, Peralta, and colleagues have extensively studied the relationships among the species of sect. *Etuberosum*, sect. *Petota* and sect. *Lycopersicon*, respectively (Spooner & al., 2004, 2005a, b; Peralta & al., 2008; Rodríguez & Spooner, 2009; Spooner, 2009; Ames & Spooner, 2010; Rodríguez & al., 2010; Fajardo & Spooner, 2011; Ovchinnikova & al., 2011; Spooner & al., in press). Similarly, Anderson and colleagues have studied the biosystematics of species of sect. *Basarthrum*, sect. *Anarrhichomenum*, and sect. *Articulatum* (Correll) A.Child including studies of morphology and interfertility (Anderson, 1975, 1977; Seithe & Anderson, 1982), breeding systems (Anderson 1979; Anderson & Levine, 1982; Mione & Anderson, 1992), pollen (Anderson & Gensel, 1976), karyotypes (Bernardello & Anderson, 1990), and restriction fragment analysis (Anderson & al., 1999). The purpose of our present work is to increase sampling of taxa in smaller, lesser-known groups that have been underrepresented in other studies to give a more complete picture of the composition and relationships among lineages that form the Potato clade. We also provide a key for identification of the major groups and discuss characters of the sections of *Solanum* that comprise the clade.

■ MATERIALS AND METHODS

Taxon sampling. — We sampled 81 accessions representing 77 species of *Solanum*, including representatives of all known subgroups of the Potato clade (Spooner & al., 1993; Weese & Bohs, 2007) and 62 of the 203 species of the Potato clade (Table 1). The sample also includes 15 accessions from most of the other major clades in the genus (Bohs, 2005; Weese & Bohs, 2007) in order to test the monophyly and broader relationships of the clade. *Solanum graveolens* Bunbury from southeastern Brazil was also sampled because various authors have postulated that it is related to taxa of the Potato clade (e.g., Bitter, 1913a, b; Bohs, 1994); others, however, allied it with the Cyphomandra clade (e.g., D'Arcy, 1972; Child, 1984). The trees were rooted using *S. thelopodium* Sendtn., a member of the Thelopodium clade that was sister to the rest of *Solanum* in previous phylogenetic studies (Bohs, 2005; Levin & al., 2006; Weese & Bohs, 2007). All accessions, vouchers, and GenBank accession numbers are listed in Appendix 1.

Molecular methods and phylogenetic analysis. — DNA was extracted from silica gel-dried leaves collected in the field or greenhouse or from herbarium material using the DNeasy plant mini extraction kit (Qiagen, Valencia, California, U.S.A.) following the manufacturer's protocol, or a modified protocol described by Tepe & al. (2011). PCR amplification followed the procedures described in Tepe & al. (2011) for ITS, GBSSI, and *trnT-trnF*, and Levin & al. (2005) for *trnS-trnG*. PCR reactions of 15 µl each contained 1.5 µl 10× Mg-free buffer, 1.5 mmol/l $MgCl_2$, 0.25 mmol/L dNTPs, 0.08 µmol/L of each primer, 0.7 µl DNA, and 1 unit of AmpliTaq Gold *Taq* polymerase (Applied Biosystems, Foster City, California, U.S.A.). For recalcitrant samples, DNA stocks were diluted from ½ to ⅕₀₀ and/or additives were used in various combinations. These additives included 0.75 µl of a 50% glycerin/water solution, 0.75 µl DMSO, or 0.9 µl of a 10× PVP-40 solution. Illustra PuRe Taq Ready-To-Go PCR Beads (GE Healthcare, Buckinghamshire, England) were used to amplify the most difficult samples. PCR products were cleaned with the Promega Wizard SV Gel and PCR

Fig. 1. Diversity in the Potato clade. **A,** *Solanum* sect. *Regmandra* (*S. remyanum* Phil.); note the distinctly enlarged stigma (photo by P. Pelser*); **B,** *S. oxycoccoides* Bitter; **C,** sect. *Basarthrum* (*S. canense* Rydb.); note interjected leaflet (arrowhead); **D,** sect. *Basarthrum* (*S. caripense* Dunal); mature fruits; **E,** sect. *Basarthrum* (*S. basendopogon* Bitter); note mirror image pair of pseudostipules (arrowhead); **F,** sect. *Anarrhichomenum* (*S. baretiae* Tepe); note the single pseudostipule at each node (arrowhead and inset); **G,** sect. *Anarrhichomenum* (*S. brevifolium* Dunal); mature fruit; **H,** sect. *Juglandifolia* (*S. juglandifolium* Dunal); **I,** sect. *Lycopersicon* (*S. pimpinellifolium* L.); **J,** sect. *Petota* (*S. candolleanum* Berthault); note articulation in the upper ¼ of the pedicel; **K,** sect. *Herpystichum* (*S. pentaphyllum* Bitter; photo by J.D. Tovar Durán); **L,** sect. *Pteroidea* (*S. anceps* Ruiz & Pav.). — All photos by E.J. Tepe unless otherwise indicated. [*Nickrent, D.L., Costea, M., Barcelona, J.F., Pelser, P.B. & Nixon, K. (2006–) PhytoImages. Available from: http://www.phytoimages.siu.edu]

Clean-up system (Promega, Madison, Wisconsin, U.S.A.) and sequenced on an ABI automated DNA sequencer at the University of Utah Core Facilities. Overlapping forward and reverse sequences were produced for all samples, and contigs were assembled and proofread with Sequencher v.4.8 (GeneCodes, Ann Arbor, Michigan, U.S.A.). Standard nucleotide ambiguity codes were used to code all instances of polymorphic peaks in the chromatograms. Dubious sequences at the extreme 3′ and 5′ ends of reads were excluded from the analyses. The sequences were manually aligned using Se-Al v.2.0a11 (Rambaut, 1996). Descriptive statistics and substitution models used for each data matrix are listed in Table 2; aligned datasets are available from TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S19117 and the University of Cincinnati (https://drc.libraries.uc.edu/handle/2374.UC/743972).

Phylogenetic relationships were estimated under Bayesian inference (BI) and maximum parsimony (MP) optimality criteria for individual markers and concatenated matrices. MP analyses were performed using a full heuristic analysis in PAUP* v.4.0b10 (Swofford, 2003) with 100 random addition

Table 1. A list of the sections of the Potato clade, including the number of species in each group according to the most recent revision (if available), and the number of species included in this study.

Section of *Solanum* L.	No. of species	No. of species included in this study	Most recent comprehensive revision
Regmandra (Dunal) Ugent	11	4	Bennett, 2008
Clade I			
Anarrhichomenum Bitter	ca. 15	6	Correll, 1962, in part
Articulatum (Correll) A.Child	2	2	–
Basarthrum (Bitter) Bitter	14	5	Correll, 1962
Etuberosum (Bukasov & Kameraz) A.Child	3	2	Spooner & al., in press
Juglandifolia (Rydb.) A.Child	2	2	Peralta & al., 2008
Lycopersicoides (A.Child) Peralta	2	2	Peralta & al., 2008
Lycopersicon (Mill.) Wettst.	13	6	Peralta & al., 2008
Petota Dumort	112	12	Spooner & al., in press
Clade II			
Herpystichum Bitter	10	10	Tepe & Bohs, 2011
Pteroidea Dunal	10	10	Knapp & Helgason, 1997

A dash (–) indicates that a comprehensive revision for the group is not available.

Table 2. Summary of sequence data matrix and analysis parameters.

					MP analyses					BI analyses	
Data partition	*N*	Aligned length	No. variable sites	No. possibly parsimony-informative sites	No. MP trees	L	CI	RI	No. supp. nodes[a]	Substitution model	No. supp. nodes[a]
ITS	76	707	426	264	10,000[c]	1197	0.389	0.700	15	GTR+I+G	28
GBSSI (*waxy*)	79	2275	741	433	10,000[c]	851	0.646	0.882	34	GTR+G	42
trnT-trnF	67	1842	305	122	–	–	–	–	–	GTR+G	–
trnS-trnG	61	736	138	72	–	–	–	–	–	GTR+I+G	–
cp combined[b]	76	2543	447	196	10,000[c]	634	0.795	0.867	15	Partitioned[d]	10
nuc. combined[e]	80	2982	1167	699	1,584	3024	0.556	0767	29	Partitioned[d]	58
all combined	80	5591	1607	851	1,237	2560	0.505	0.735	34	Partitioned[d]	59
all w/o conflict[f]	69	5515	1516	809	96	2415	0.504	0.789	37	Partitioned[d]	52

N, number of accessions; L, length of the most parsimonious tree; CI, consistency index; RI, retention index

[a] The number of nodes supported by ≥90 bootstrap support (for the MP analyses) or ≥0.95 posterior probability (for the BI analyses).

[b] Concatenated matrix of *trnT-trnF* and *trnS-trnG*.

[c] The maximum number of trees was set at 10,000.

[d] Models for each individual marker were maintained in the partitioned analyses.

[e] Concatenated matrix of ITS and GBSSI.

[f] Concatenated matrix with accessions removed which cause conflict among the trees in Fig. 2 and Electr. Suppl.: Figs. S1 & S2.

sequence replicates, TBR swapping, steepest descent, all characters weighted equally, and gaps treated as missing data. All other settings were kept as the defaults. Bootstrap (BS) values for nodes were estimated from full heuristic searches of 5000 replicates with MaxTrees set at 10,000 and TBR branch swapping. Analysis of the concatenated plastid dataset did not run to completion due to limitations of computer memory.

Prior to Bayesian inference analyses, the model of nucleotide evolution was determined using the Akaike information criterion (AIC) as implemented in MrModeltest v.2.2 (Nylander, 2004). Analysis of individual markers and partitioned concatenated datasets was performed using MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). Using random starting trees, MrBayes was run for 10 million generations, with one tree sampled every 1000 generations to estimate phylogenies and to calculate posterior probabilities (PP) on the Oakley cluster at the Ohio Supercomputer Center or on a personal computer. Burn-in, the consensus tree, and posterior probabilities were calculated in MrBayes.

To evaluate the compatibility of the individual markers, we compared the topologies of the nuclear and plastid markers to each other and to the concatenated results to identify the presence of well-supported incongruence (i.e., differences supported by high posterior probabilities and/or bootstrap values; Seelanan & al., 1997; Wiens, 1998). Throughout this study, we conservatively considered nodes to be well-supported if they had both PP ≥ 0.95 and BS ≥ 90; however, when evaluating the congruence of the nuclear and plastid trees, we used PP ≥ 0.95 and BS ≥ 70 as a more conservative approach in this step to minimize false negative results. We considered both measures of support together because PP values are known to frequently be inflated relative to BS (Cummings & al., 2003; Erixon & al., 2003; Simmons & al., 2004). To control for any impact of accessions in conflict among trees on the topology in Fig. 2, and following the guidelines described in Pirie (2015), analyses were re-run with eleven accessions of ten species excluded from the matrix. These include *S. dolichorhachis* Bitter and *S. trifolium* Dunal (sect. *Herpystichum*), *S. anceps* Ruiz & Pav.-1, *S. mite* Ruiz & Pav.-2, and *S. uleanum* Bitter (sect. *Pteroidea*), *S. lycopersicoides* Dunal (sect. *Lycopersicoides* (A.Child) Peralta), *S. bulbocastanum* Dunal and *S. pinnatisectum* Dunal (sect. *Petota*), *S. palustre* Schltdl. (sect. *Etuberosum*), and both accessions of *S. oxycoccoides* Bitter. The concatenated matrix was then reanalyzed under BI and MP criteria.

■ RESULTS

Congruence of datasets. — The BI post burn-in majority-rule tree and the MP strict consensus trees based on the concatenated matrix of all four markers (the 4-gene matrix) differ only in the degree of resolution (Fig. 2). The BI tree has more resolved nodes than the MP tree (Table 2), and most nodes are more highly supported in the BI tree. Analysis of the two nuclear markers together produced an overall topology that is nearly identical to the 4-gene topology, but that differs only in somewhat lower resolution and support (Electr. Suppl.: Fig. S1). Analysis of the concatenated plastid markers resulted in trees with much lower resolution and support than either the 4-gene tree or the nuclear markers analyzed together (Table 2; Electr. Suppl.: Fig. S2).

Twelve nodes in the nuclear tree (Electr. Suppl.: Fig. S1) are incongruent with the plastid tree (Electr. Suppl.: Fig. S2), whereas nine nodes in the plastid tree are in conflict with the nuclear tree. Seventeen of these nodes, including the seven of the eight nodes with support according to the criteria identified above, are within sect. *Herpystichum* and sect. *Pteroidea* and do not impact the conclusions discussed herein. The relationships among these two sections are discussed in more detail below. There are five instances of topological divergence between the plastid tree (Electr. Suppl.: Fig. S2, asterisks) and the 4-gene topology (Fig. 2). Two of these involve the placement of *S. lycopersicoides* (sect. *Lycopersicoides*) which is nested within sect. *Lycopersicon*, and *S. polyadenium* Greenm. (sect. *Petota*) which is in a polytomy with species of sect. *Juglandifolia*, sect. *Lycopersicoides*, and sect. *Lycopersicon*; however, neither of these nodes are well supported and *trnT-trnF* in all of these species is represented by only partial sequences, which may influence their placement in the tree. The only other supported node in conflict outside of sect. *Herpystichum* and sect. *Pteroidea* determines the placement of *S. oxycoccoides*. However, the node in the plastid tree that places *S. oxycoccoides* as sister to Clades I and II is present only in the BI tree and is unsupported (PP < 0.5).

Removal of the eleven accessions responsible for these conflicts did not have an effect on the relationships of the remaining taxa (Electr. Suppl.: Fig. S3). Consequently, the conclusions drawn herein are based on the BI analysis of the concatenated matrix of all markers (Fig. 2) because this analysis provides the most highly resolved and supported topology. This tree is not in conflict with the 4-gene MP analysis or the nuclear or plastid markers analyzed separately based on the criteria outlined above (Electr. Suppl.: Figs. S1–S4), except for the nodes within Clade II and the placement of *S. oxycoccoides*, which are discussed below in more detail.

Phylogenetic relationships. — The Potato clade is supported as monophyletic (PP: 1.0; BS: 84) and contains 12–13 well-supported subclades or monospecific lineages, depending on the uncertain monophyly of sect. *Herpystichum* (Fig. 2). A clade comprising species of the Archaesolanum, Dulcamaroid, and Morelloid clades is sister to the Potato clade (see Weese & Bohs, 2007 for discussion of outgroup lineages). *Solanum graveolens* emerges as a member of the Cyphomandra clade with moderately strong support. Within the Potato clade, sect. *Regmandra* is moderately supported as sister to all other groups. Section *Regmandra* is strongly supported as monophyletic in all analyses. The remaining lineages are distributed between two clades (Clades I and II; Fig. 2).

Clade I, with *S. oxycoccoides* resolved as sister to all other species in the group, is strongly supported in the BI, but only moderately in the MP analyses. *Solanum oxycoccoides* is followed by a clade comprising sect. *Articulatum* and sect. *Basarthrum*; each of these sections is strongly supported as monophyletic. These two groups are followed by sect. *Anarrhichomenum*, which is sister to a large clade that includes sect.

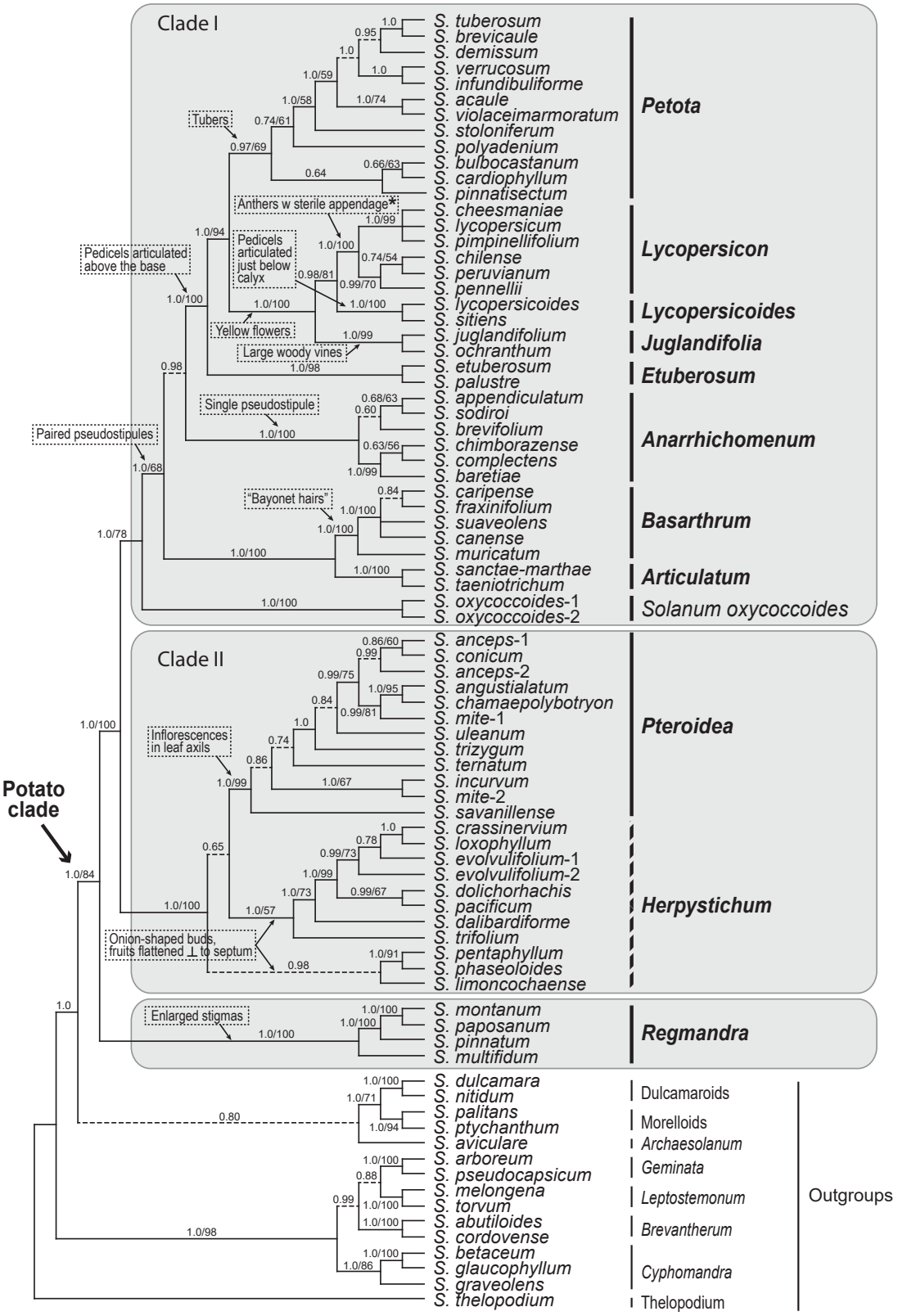

Fig. 2. The 50% majority-rule post-burn-in tree from Bayesian analysis of the combined *trnS-trnG*, *trnT-trnF*, GBSSI (*waxy*), and ITS data. Branches not present in the MP strict consensus tree are indicated by dashed lines. Branch support values are Bayesian posterior probabilities >0.5/maximum parsimony bootstrap >50. The three major lineages of the Potato clade are indicated by the gray boxes. Sections of *Solanum* are in italics; informal clade names are not italicized. The diagonally hatched bar indicates that sect. *Herpystichum* is paraphyletic on this tree. Synapomorphies for clades with clear defining characters are provided in dotted boxes. *All species have anthers with a sterile apical appendage except for *S. pennellii* (see text).

Etuberosum (Bukasov & Kameraz) A.Child, sect. *Juglandifolia*, sect. *Lycopersicoides*, sect. *Lycopersicon*, and sect. *Petota*. This large clade of five sections is well-supported. Section *Juglandifolia*, sect. *Lycopersicoides*, and sect. *Lycopersicon* form a strongly supported clade, and within this clade, we recovered a strongly supported relationship between sect. *Lycopersicon* and sect. *Lycopersicoides*.

The second major lineage within the Potato clade, Clade II (Fig. 2) is strongly supported and contains sect. *Herpystichum* and sect. *Pteroidea*. Support for the monophyly of sect. *Pteroidea* is strong, but it appears to be nested within sect. *Herpystichum* in the BI analysis. However, the early-branching relationships in Clade II are poorly supported and collapse in the MP strict consensus tree. The analysis with the eleven problematic accessions removed (Electr. Suppl.: Fig. S3) was not in conflict with the BI topology in Fig. 2.

■ DISCUSSION

Our results reflect the composition of the Potato clade suggested by Bohs (2005), Weese & Bohs (2007), and Särkinen & al. (2013); however, our increased sampling of lesser-known taxa and use of the more variable ITS and *trnS-trnG* markers have provided a more robust understanding of the composition of the groups within the Potato clade and a well-supported estimation of relationships among the groups. The circumscription of the well-supported lineages within the Potato clade corresponds, for the most part, to traditionally recognized taxonomic sections and/or series of *Solanum*.

We acknowledge that the topology of the concatenated analyses largely reflects the topology of the nuclear markers. The plastid markers that were included provide poor resolution and support and, consequently, had relatively little impact on the topology in Fig. 2. Our decision to concatenate our data follows the guidelines described by Pirie (2015) and our decision to base our conclusions on the concatenated topology comes from our collective experience of working the groups considered here. Nevertheless, an informative next step would be to analyze an expanded dataset with additional plastid and single-copy nuclear markers using coalescent species tree methods. This could shed light on questionable parts of the tree such as the placement of *S. oxycoccoides* and the nature of the relationships among species of sect. *Herpystichum* and sect. Pteroidea.

Key to the sections of the Potato clade

1. Flowers yellow (carotenoid pigments) …… 2
1. Flowers white to cream, pink, violet, or blue (anthocyanin pigments) …… 5
2. Anthers strongly connivent, elongate, and evenly narrowed toward the slender, sterile tip; anther dehiscence not visible unless anther column opened (e.g., Fig. 1I) … …… ***Solanum*** sect. ***Lycopersicon*** (p.p.)
2. Anthers free to weakly connivent, lacking long sterile tip; anthers dehiscing initially by apical pores that elongate into introrse, longitudinal slits with age (e.g., Fig. 1H) …… 3
3 Anthers distinctly unequal in length and curved apically to form a beak-like structure; corollas asymmetrical, stellate …… ***Solanum*** sect. ***Lycopersicon*** (p.p., *S. pennellii*)
3. Anthers more or less equal in length and straight; corollas symmetrical, rotate to pentagonal …… 4
4. Leaflets with deeply divided margins; plants herbs to subshrubs 0.5–2.5 m tall; inflorescences bracteate; pedicels articulated just below the calyx; fruits 1–1.3 cm diam., with a thin, leathery pericarp …… …… ***Solanum*** sect. ***Lycopersicoides***
4. Leaflets with entire margins; plants woody vines to 5 m or more long; inflorescences ebracteate; pedicels articulated near the middle; fruits 1.5–5+ cm diam., with a thick, hard pericarp …… ***Solanum*** sect. ***Juglandifolia***
5. Stigma usually markedly enlarged apically (e.g., Fig. 1A); plants low-growing herbs; leaves simple to deeply pinnatifid to tri-pinnatifid, the margins often crenate to coarsely dentate; sympodial units typically unifoliate (i.e., inflorescence(s) associated with each node) …… ……***Solanum*** sect. ***Regmandra***
5. Stigmas not markedly enlarged apically (e.g., Fig. 1L); plants vines to herbs and weakly woody shrubs; leaves simple to compound, the margins entire to somewhat wavy; sympodial units typically plurifoliate (one or more sterile nodes between inflorescences) …… 6
6. Pseudostipules present on at least some nodes (e.g., Fig. 1E & F) …… 7
6. Pseudostipules absent at all nodes (a prominent axillary bud may be present, but this plainly not leaf-like) …. 11
7. Pseudostipules one per node or, if two, then strongly anisomorphic; plants slender woody vines, rooting at most nodes; inflorescences usually terminal on short, axillary spur shoots bearing reduced leaves (occasionally terminal on main shoot); pedicels articulated at base …. …… ***Solanum*** sect. ***Anarrhichomenum***
7. Pseudostipules two per node (a mirror-image pair); plants herbs to shrubs, sometimes scandent or viny, but very rarely rooting at the nodes; inflorescences terminal, axillary, or extra-axillary, but not terminal on axillary spur shoots with reduced leaves; pedicels articulated at or above base …… 8
8. Pedicels articulated distinctly above the base (e.g., Fig. 1J); plants with rhizomes bearing tubers …… …… ***Solanum*** sect. ***Petota***
8. Pedicels articulated at or near the base (e.g., Fig. 1D); plants without tubers …… 9
9. Pubescence of 2-celled "bayonet hairs" (trichomes with a long, cylindrical basal cell and a much shorter, sharply pointed apical cell) …… ***Solanum*** sect. ***Basarthrum***
9. Pubescence, if present, of single- to multi-celled "finger hairs" (uniseriate trichomes with >2 cells of similar length), or if 2-celled, then cells ± equal in length or basal cell much shorter than apical cell …… 10
10. Plants upright to spreading (but not vines), herbaceous; distribution limited to southern South America (Chile, Argentina, Juan Fernández Islands) …… …… ***Solanum*** sect. ***Etuberosum***

10. Plants viny, herbaceous to woody; distribution limited to Central and northern South America (Costa Rica, Panama, Colombia) …… ***Solanum*** sect. ***Articulatum***
11. Inflorescences in leaf axils, often paired (rarely 1 or 3); sympodial units unifoliate …. ***Solanum*** sect. ***Pteroidea***
11. Inflorescences terminal on leafy shoots, extra-axillary (but occasionally close enough to the node to appear leaf-opposed or axillary), solitary; sympodial units usually plurifoliate (occasionally unifoliate in *S. crassinervium* of sect. *Herpystichum*) …… 12
12. Petioles >3 cm long; leaves simple to 3- or 5-foliate; decumbent, weak-stemmed, ground-trailing or low-climbing vines (Fig. 1K) …… ***Solanum*** sect. ***Herpystichum*** (p.p.)
12. Petioles <2 cm long; leaves simple; climbing vines to slender lianas …… 13
13. Flowers with rotate-stellate corollas with clearly visible interpetalar tissue; occurring at 3000–4300 m elevation or higher …… ***Solanum oxycoccoides***
13. Flowers with deeply stellate corollas with sparse to no interpetalar tissue; occurring from sea level to 3400 m …… ***Solanum*** sect. ***Herpystichum*** (p.p.)

Solanum sect. ***Regmandra*** (Dunal) Ugent in Ann. Missouri Bot. Gard. 59: 273. 1973 ("1972")[1] ≡ *Solanum* [unranked] *Regmandra* Dunal in Candolle, Prodr. 13(2): 28, 60. 1852 – Lectotype (designated by Ugent in Ann. Missouri Bot. Gard. 59: 273. 1973 ("1972")): *S. montanum* L. — Fig. 1A.

Solanum sect. *Regmandra* has been included in the Potato clade in one study (Särkinen & al., 2013), but not in others (Bohs, 2005; Weese & Bohs, 2007) due to lack of resolution. Based on both molecular data and morphological similarity to other lineages, we include sect. *Regmandra* under our definition of the Potato clade.

Solanum sect. *Regmandra* was the focus of a revision by Bennett (2008) and the 11 species of this section can be recognized by their herbaceous habit, enlarged stigmas, and usually somewhat fleshy leaves with margins that range from slightly lobed to deeply pinnatifid or tripinnatifid. Some individuals of *S. montanum* develop a swollen caudex that has been used locally as a food source (Bennett, 2008). This swollen, underground stem, however, is not homologous to the tubers found in *S.* sect. *Petota*. Species of sect. *Regmandra* occur in Chile and Peru and, with the exception of the more widespread *S. paposanum* Phil., are restricted to lomas habitats. Lomas form in western Peru and northwestern Chile on near-coastal hills and low mountains where moisture comes almost exclusively from ocean fog, resulting in a series of "islands" of vegetation surrounded by the extremely dry deserts (Dillon, 2005). *Solanum paposanum* has been collected as high as 3500 m, but the rest of the species of this group occur between sea level and 2300 m (Bennett, 2008).

Clade I. — This lineage contains the potato and the taxa long considered to be its close relatives (e.g., Correll, 1962; Fig. 1A–J). The large clade that includes sect. *Etuberosum*, sect. *Juglandifolia*, sect. *Lycopersicoides*, sect. *Lycopersicon*, and sect. *Petota* has been the focus of much research and, although the relationships among these taxa are generally well-supported in our trees, they are quite variable among studies using different types of data and different numbers of markers (e.g., Spooner & al., 1993, 2005a; Peralta & Spooner, 2005; Peralta & al., 2008; Rodríguez & al., 2009). There is considerable discordance among these studies with respect to the relationships of sect. *Juglandifolia*, sect. *Lycopersicoides*, and sect. *Lycopersicon*, and most studies did not report the strongly supported sect. *Lycopersicon*–sect. *Lycopersicoides* relationship found in our analyses. The relationships among these three sections, however, collapse into a polytomy when *S. lycopersicoides* is excluded from the analysis. The relationships recovered here are likely due to missing data since most of the accessions of these three lineages are missing *trnS-trnG* and have only partial *trnT-trnF* sequences (Appendix 1).

With the exception of *S. oxycoccoides*, all lineages in Clade I are characterized by pseudostipules, interpreted as the first, reduced leaf or pair of leaves of an axillary shoot (Fig. 1E, F; see Peralta & al., 2008 for further discussion). Many lineages have small interjected leaflets interspersed among the larger leaflets (Fig. 1C), and have at least some species with glandular pubescence. Clade I is also distinguished by its peculiar seed morphology. The anticlinal walls of the seed coat cells possess characteristic outgrowths forming a marginal wing in mature seeds (Anderson, 1979), giving them a densely pubescent appearance when subjected to partial enzyme etching. Within the Potato clade, these "hairy" seeds are not found in sect. *Regmandra*, nor in the sections that comprise Clade II (Lester, 1991). This character has not been examined in *S. oxycoccoides*.

Solanum oxycoccoides Bitter in Repert. Spec. Nov. Regni Veg. 16: 14. 1919. — Fig. 1B and http://sweetgum.nybg.org/vh/specimen.php?irn=860341

The affinities of *S. oxycoccoides* have been ambiguous, with very different relationships proposed by different authors. Bitter (1919) included *S. oxycoccoides* in sect. *Anarrhichomenum* when he originally described the species, whereas Nee (1999) placed it in sect. *Dulcamara* (Moench) Dumort. Its position here, not associated with either group, is something of a surprise. Nevertheless, the inclusion of *S. oxycoccoides* in the Potato clade was consistent across all analyses. The specific placement of the species, however, was not consistent. It was sister to all other species of Clade I in analyses of the nuclear data and all data combined, whereas it was in a large polytomy or sister to the species of Clades I and II in analyses of the plastid data. *Solanum oxycoccoides* is a slender-stemmed, herbaceous to woody vine with simple, deltoid to ovate, coriaceous to somewhat fleshy leaves, pubescence of unbranched "finger hairs" (Seithe & Anderson, 1982), pedicels articulated at the base, corollas with considerable interpetalar tissue, and small fruits with apparently only 3 or 4 seeds. Based on examination of living material and herbarium specimens, it appears that this species lacks the pseudostipules characteristic of all other lineages in Clade I. *Solanum oxycoccoides* is endemic to

1 Ann. Missouri Bot. Gard. 59(2): 105–322 was published on 28 March 1973; see note on p. 478 of the same volume.

Peru and occurs on steep, rocky slopes, mossy cliff ledges, and among grasses and shrubs in northern Peru (Depts. Ancash, Cajamarca, and Huánuco) at 3000–4280 m in elevation.

Three other sections in Clade I have simple-leaved species, some of which are sympatric with *S. oxycoccoides*. The entirely simple-leaved species of sect. *Anarrhichomenum* can be distinguished by their deeply stellate corollas (vs. rotate-stellate corollas in *S. oxycoccoides*). Simple-leaved species of sect. *Petota* can be identified by pedicels articulated above the base (vs. at the base), and sect. *Basarthrum* is easily identified by its unique "bayonet hairs" (see below).

Solanum sect. ***Anarrhichomenum*** Bitter in Repert. Spec. Nov. Regni Veg. 11: 247. 1912 – Lectotype (designated by Seithe in Bot. Jahrb. Syst. 81: 294. 1962): *S. sodiroi* Bitter. — Fig. 1F, G.

The ca. 15 species of sect. *Anarrhichomenum* form a strongly supported clade in all analyses. Morphologically, species of the section can be separated from all other groups in Clade I by their habit as herbaceous to woody vines rooting readily at the nodes and by the presence of a single pseudostipule per node (Fig. 1F) or, more rarely, highly anisophyllous pseudostipules where one of the pair is many times larger than the other. The leaves are simple to pinnately compound and lack interjected leaflets. The pedicels are articulated at the base, the fruits are orange to red at maturity, and the seeds have a conspicuous marginal wing (Anderson, 1979). Trichomes are primarily uniseriate, multicellular, unbranched "finger hairs"; however, branched (dendritic) trichomes are found in several species (Seithe & Anderson, 1982). These are the only known examples of branched pubescence in the Potato clade (Seithe & Anderson, 1982). This section includes *S. appendiculatum* Dunal, the first described cryptically/functionally dioecious species in the genus (Anderson, 1979). Like *S.* sect. *Basarthrum*, most of these species occupy mid-elevation habitats in the mountains of Central and South America, growing in moist sunny or shady habitats.

Most species of sect. *Anarrhichomenum* fall into two geographic groups, each with a characteristic inflorescence structure. The inflorescences of the Central American species are produced terminally on the primary axis and are usually branched one or more times. The inflorescences are pushed laterally by the continuation shoot to become leaf-opposed to extra-axillary (Child & Lester, 1991). Inflorescences of the South American species are either highly condensed, branched inflorescences borne terminally on the primary axis as above, or produced as distinctive axillary spur shoots. These axillary spur shoots are unlike any other inflorescences in the Potato clade and, when present, make this section easy to recognize at a glance.

Solanum sect. ***Articulatum*** (Correll) A.Child in Feddes Repert. 101: 221. 1990 ≡ *Solanum* ser. *Articulata* Correll in Contr. Texas Res. Found., Bot. Stud. 4: 62. 1962 – Type: *S. sanctae-marthae* Bitter.

The two species comprising sect. *Articulatum*, *S. sanctae-marthae* and *S. taeniotrichum* Correll, have long been isolated and problematic elements in Potato clade taxonomy (Correll, 1962; Anderson, 1977, 1979; Child, 1990). Correll (1962) included both species under his concept of sect. *Basarthrum*. Anderson (1977, 1979) followed Correll's lead, but expressed doubts about their relationships and informally proposed sectional status for *S. taeniotrichum* (Anderson & Jansen, 1998). Child (1990) elevated *S. sanctae-marthae* to sectional status (sect. *Articulatum*), leaving *S. taeniotrichum* in sect. *Basarthrum.* He later reconsidered and created the monotypic sect. *Taeniotrichum* A.Child (Child, 1998) to accommodate this species that differs from sect. *Basarthrum* in several important characters. None of these authors, however, placed these two species together or even suggested a close relationship. Nevertheless, the section is strongly supported as monophyletic and sister to sect. *Basarthrum*. The two species share a general morphological similarity, with pubescence of multicellular trichomes, winged seeds, and large, often branched inflorescences (Correll, 1962; Anderson, 1977, 1979; Seithe & Anderson, 1982; Child, 1990). The overall morphology of these plants resembles sect. *Basarthrum* (Anderson, 1977), but they lack the unique "bayonet hairs" that characterize that section (Seithe & Anderson, 1982; see below). Further differences between the sections are mature fruits that are red to purple (Anderson, 1977; Child, 1998) vs. green and striped in sect. *Basarthrum*, and seeds that possess a distinct marginal wing vs. inconspicuously winged in sect. *Basarthrum* (e.g., Anderson, 1979). The sectional name is derived from the observation that the petiolules of the leaflets of *S. sanctae-marthae* are articulated, resulting in deciduous leaflets in some specimens (Correll, 1962; Child, 1990); however, this character is often difficult to detect and, since it is apparently absent from *S. taeniotrichum*, is not a diagnostic character for the section (Anderson, 1977). Both species are rare or uncommon. *Solanum sanctae-marthae* is endemic to the Santa Marta mountains in northern Colombia, whereas *S. taeniotrichum* is found in Costa Rica and Panama. Both species grow in rich soils as scrambling vines covering other vegetation and occur in moist montane to cloud forest habitats at elevations of 2500–3400 m.

Solanum sect. ***Basarthrum*** (Bitter) Bitter in Repert. Spec. Nov. Regni Veg. 13: 101. 1914 ≡ *Solanum* subsect. *Basarthrum* Bitter in Repert. Spec. Nov. Regni Veg. 11: 350. 1912 – Lectotype (designated by Seithe in Bot. Jahrb. Syst. 81: 293. 1962): *S. suaveolens* Kunth & C.D.Bouché. — Fig. 1C–E.

This clade of 14 highly variable species is defined by the presence of "bayonet hairs", which are 2-celled trichomes consisting of a large, cylindrical basal cell and a much smaller, sharply pointed apical cell (Seithe & Anderson, 1982; Anderson & Jansen, 1998). Species of the section are upright to scrambling, herbaceous to shrubby vines, rarely rooting at the nodes. Fruits are typically green and striped at maturity (Fig. 1D), although they can sometimes be tinged with purple where exposed to sun. Fruits in morphologically similar groups (i.e., sect. *Anarrhichomenum* and sect. *Articulatum*) are orange to red to purple at maturity. Similarly, the conspicuous marginal

seed wing found in most species of sect. *Anarrhichomenum* and sect. *Articulatum* is reduced and inconspicuous in sect. *Basarthrum* (Anderson, 1979). The leaves range from simple to pinnately compound with frequent interjected leaflets (Fig. 1C) and pseudostipules at most nodes in mirror image pairs (Fig. 1E). The pedicels are articulated at the base (Fig. 1D), and the sectional name is derived from this character. With the exception of *S. trachycarpum* Bitter & Sodiro, the species all grow in moist to cloud forest habitats in Central and South American mountains. *Solanum trachycarpum* is an exception in several respects and grows in somewhat drier habitats at mid elevations in the Andes, and it is an upright plant, lacking the trailing viny habit of most of the other species in the section. Two species, *S. canense* Rydb. and *S. suaveolens*, grow in moist habitats, but are more herbaceous than the other species in the section. These latter three species are, along with the domesticated *S. muricatum*, the only three self-compatible autogamous species in the section (Anderson & Jansen 1998). The range of sect. *Basarthrum* is from Guatemala to Peru, from sea level to nearly 4000 m.

Correll (1962) provided the most recent full taxonomic treatment of the section, but Anderson and colleagues have studied the group extensively, along with members of sect. *Anarrhichomenum* and sect. *Articulatum*, using multiple lines of evidence including morphology, crossing studies, cytology, chemosystematics, and molecular data (Anderson, 1975, 1977, 1979; Anderson & Gensel, 1976; Anderson & Levine, 1982; Seithe & Anderson, 1982; Anderson & al., 1987, 1996, 1999, 2006; Bernardello & Anderson, 1990; Anderson & Bernardello, 1991; Mione & Anderson, 1992; Spooner & al., 1993; Anderson & Jansen, 1998; Stiefkens & al., 1999; Prohens & al., 2006; Blanca & al., 2007). The section includes the cultivated *S. muricatum*, known as the pepino, pepino dulce, and pear melon; the fruit is grown in local gardens and commercially in tropical America, and occasionally exported worldwide. Pepino fields are often in areas adjacent to where some of the wild species still grow. Thus, there are abundant opportunities for introgressive gene flow from the wild species to the domesticate (Anderson & Jansen 1998; Anderson & al., 1996; Blanca & al., 2007).

Solanum sect. ***Etuberosum*** (Bukasov & Kameraz) A.Child in Feddes Repert. 101: 218. 1990 ≡ *Solanum* ser. *Etuberosum* Bukasov & Kameraz, Osnovy Selektsii Kartofelia [= Bases of Potato Breeding]: 18. 1959 – Lectotype (designated by D'Arcy in Ann. Missouri Bot. Gard. 59: 268. 1973 ("1972")): *S. etuberosum* Lindl.

Spooner & al. (in press) provided a revision of the three species that make up sect. *Etuberosum* (*S. etuberosum*, *S. fernandezianum* Phil., *S. palustre* Schltdl.). This group is a strongly supported clade in this study and others that is distinct from the tuber-bearing potatoes in sect. *Petota* (Spooner & al., 1993, 2005a). Morphologically, they are upright herbs that are similar to species in sect. *Petota*, but they lack tubers and possess pedicels that are articulated at or near the base. The pinnately compound leaves have 4–7 pairs of lateral leaflets with frequent interjected leaflets, and pseudostipules are present in mirror image pairs. Section *Etuberosum* occurs in Argentina and Chile, including one species, *S. fernandezianum*, on the remote Juan Fernández Islands. The three species of this group are somewhat divergent ecologically. *Solanum etuberosum* can be found in dry scrub, typically along streams or in the mist of waterfalls, in full sun, and in rocky soils from 430–2500 m. *Solanum palustre* occurs in mesic habitats, often following fires, in fertile soils, and can tolerate partial shade from 40 to 1170 m. *Solanum fernandezianum* grows in diverse mesic habitats including the edges of woods, shady rock walls, and valley floors from 100 to 610 m (Spooner & al., in press).

The flowers of all species in the clade formed by sect. *Juglandifolia*, sect. *Lycopersicoides*, and sect. *Lycopersicon* are pigmented with carotenoids and range from pale to golden yellow. The yellow flower color in these three groups is in marked contrast with all other lineages of the potato clade whose flowers have anthocyanin pigments and range from white or creamy white to violet to deep purple. These three sections were the subject of a revision by Peralta & al. (2008).

Solanum sect. ***Juglandifolia*** (Rydb.) A.Child in Feddes Repert. 101: 220. 1990 ≡ *Solanum* ser. *Juglandifolium* Rydb. in Bull. Torrey Bot. Club 51: 146. 1924 – Lectotype (designated by D'Arcy in Ann. Missouri Bot. Gard. 59: 269. 1973 ("1972")): *S. juglandifolium* Dunal. — Fig. 1H.

The two species in this section, *S. juglandifolium* and *S. ochranthum* Dunal, are large, woody vines with stems reaching 5 m in length or more, pinnately compound leaves with interjected leaflets, leaflets with entire margins, pseudostipules that are either very small and deciduous (*S. juglandifolium*) or large (up to 1.5 × 1.5 cm) and persistent (*S. ochranthum*), bright yellow corollas, and typically highly branched inflorescences (4–5 times branched; Peralta & al., 2008). The pedicels are articulated near the middle. Both species are typically found in tree fall gaps, road cuts and other sunny, disturbed areas in cloud forests. *Solanum juglandifolium* occurs in Colombia and Ecuador from 1200 to 3100 m, whereas *S. ochranthum* is found between 1900 and 4100 m from Colombia to Peru.

Solanum sect. ***Lycopersicoides*** (A.Child) Peralta in Syst. Bot. Monogr. 84: 57. 2008 ≡ *Solanum* subsect. *Lycopersicoides* A.Child in Feddes Repert. 101: 224. 1990 – Type: *S. lycopersicoides* Dunal.

Solanum sect. *Lycopersicoides* includes two species, *S. lycopersicoides* and *S. sitiens* I.M.Johnst. They are both upright shrubs to subshrubs with pinnatifid to pinnately compound leaves with deeply and irregularly lobed margins and frequent interjected leaflets (Peralta & al., 2008). The well-developed pseudostipules are in mirror image pairs and are lobed like the leaflets. The inflorescences are relatively large and branched (2–3 times or more), and the pedicels are articulated just below the calyx. The anthers of the yellow flowers are straight, equal in length, and pale yellow to nearly white. Species of this section are adapted to very dry habitats and are found on the dry, rocky, western slopes of the Andes in southern Peru and northern Chile between 1500 and 3700 m.

Solanum sect. ***Lycopersicon*** (Mill.) Wettst. in Engler & Prantl, Nat. Pflanzenfam. IV(3b): 24. 1891 ≡ *Lycopersicon* Mill., Gard. Dict. Abr., ed. 4. 1754 – Lectotype (designated by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 3: 168. 1913): *Lycopersicon lycopersicum* (L.) H.Karsten (= *S. lycopersicum* L.). — Fig. 1I.

We sampled 6 of the 13 species of this section, including the cultivated tomato, *S. lycopersicum*. Species of sect. *Lycopersicon* are upright herbs to herbaceous vines with complex leaves ranging from pinnately to bipinnately compound with frequent interjected leaflets. Pseudostipules, where present, are in mirror image pairs, but are absent in the four species of the "*Lycopersicon* Group" (Peralta & al., 2008). The flowers are yellow and, in most species, radially symmetrical and borne on pedicels articulated above the middle. The most distinctive character of this section are the anthers, which are usually straight (curved only in *S. corneliomulleri* J.F.Macbride, *S. pennellii* Correll, and *S. peruvianum* L.), coalesced into a tube, and with distinct, sterile apical appendages (Fig. 1I). *Solanum pennellii* is exceptional among the species of sect. *Lycopersicon* in that it has pedicels articulated at the base, somewhat zygomorphic corollas, and strongly curved anthers lacking the sterile apical appendages. In the combined tree, *S. pennellii* is sister to *S. chilense* Dunal+*S. peruvianum*, but this relationship is supported only in the BI analysis. Native species of sect. *Lycopersicon* occur in Ecuador (including the Galapagos Archipelago), Peru, Bolivia, and Chile in a variety of habitats ranging from premontane humid forests to hyperarid deserts from sea level to 3600 m. Most species, however, occur on dry rocky western slopes of the Andes in Peru and Chile.

Solanum sect. ***Petota*** Dumort., Fl. Belg.: 39. 1827 – Lectotype (designated by D'Arcy in Ann. Missouri Bot. Gard. 59: 272. 1973 ("1972")): *S. tuberosum* L. — Fig. 1J.

This lineage of 112 species (Spooner & al., 2014) is the largest in the Potato clade and, because it contains the cultivated potato, *S. tuberosum*, has been the focus of intensive and multifaceted research (see Spooner & al., 2004, 2014, in press, and references therein). Section *Petota* is strongly supported in the BI, but unsupported in the MP analyses. Nevertheless, the section has been strongly supported as monophyletic in numerous studies with much greater species sampling (e.g., Spooner & al., 1993, 2005a; Rodríguez & al., 2010) and is a morphologically coherent group. All species of sect. *Petota* have tubers borne along the length or at the ends of stolons. The pedicels are articulated ¼ of the way above the base or higher (Fig. 1J). The leaves in this group range from simple to twice pinnate, with the leaves of most species once pinnate with 1–13 pairs of lateral leaflets and frequent interjected leaflets (these lacking on simple-leaved species). Pseudostipules are present in mirror image pairs. Species of this section range from the SW U.S.A. to Argentina and Chile from sea level to 4650 m. Species abundance is highest in the Andes and in the highlands of central Mexico. The high species diversity among tuberous potatoes is accompanied by a high degree of habitat diversity, but most species can be found between 1500 and 4000 m elevation in moist to wet montane habitats (Hijmans & Spooner, 2001; Spooner & al., 2014). The ecological tolerances of species of sect. *Petota* are further expanded by the frequent polyploidy among species in the group (Hijmans & al., 2007).

Clade II. — Despite strong molecular support for Clade II, a reliable morphological synapomorphy of the group remains elusive. Child (1990), using morphological data, considered sect. *Herpystichum* and sect. *Pteroidea* to be part of the potato lineage and closely related to each other (a relationship supported by our results). Species in this clade range from upright herbs to node-rooting herbaceous or woody vines. With the exceptions of *S. dalibardiforme* Bitter and *S. trifolium* (both sect. *Herpystichum*), which have rotate-stellate to rotate corollas, the corollas of all species are stellate and range from white or cream-colored to violet. All species in Clade II have stout, elliptical, and blunt-tipped anthers, but this anther morphology is not unique to the group. In contrast to the majority of species in Clade I, members of Clade II lack pseudostipules and interjected leaflets.

Solanum sect. ***Herpystichum*** Bitter in Repert. Spec. Nov. Regni Veg. 17: 331. 1921 – Lectotype (designated by Seithe in Bot. Jahrb. Syst. 81: 292. 1962): *S. trifolium* Dunal. — Fig. 1K.

The ten species of sect. *Herpystichum* were the focus of a revision by Tepe & Bohs (2011). They do not form a clade in the present analyses, and instead sect. *Pteroidea* is either nested within sect. *Herpystichum* (Fig. 2), or forms a polytomy with two clades of sect. *Herpystichum*. In contrast, Tepe & al. (2011) found support for a monophyletic sect. *Herpystichum* (PP: 1.0, BS: 98) based on sequences of seven nuclear and three plastid markers, but the analysis included only one species of sect. *Pteroidea*. Despite not recovering a monophyletic sect. *Herpystichum* in the analyses reported here, we feel that it is conservatively appropriate to continue to recognize the morphologically cohesive section as described by Tepe & Bohs (2011). Furthermore, the molecular evidence is currently inconclusive due to the weak support for the branching order at the base of Clade II and the limited sampling of sect. *Pteroidea* in Tepe & al. (2011). Additional data is clearly needed to resolve the uncertain relationships among the species of these two groups.

Species of *Solanum* sect. *Herpystichum* are ground-trailing or climbing vines that root at the nodes and have simple or three- to five-foliate pinnately compound leaves. The section is distinguished by characters unique within *Solanum*, including onion-shaped flower buds at certain stages of development and fruits that are flattened perpendicular to the septum in most species (Tepe & Bohs, 2011). Species of the section occur in wet forests from southern Mexico to northern Peru and range from near sea level to 3500 m.

Solanum sect. ***Pteroidea*** Dunal, Hist. Nat. Solanum: 43. 1813 – Lectotype (designated by D'Arcy in Ann. Missouri Bot. Gard. 59: 272. 1973 ("1972")): *S. mite* Ruiz & Pav. — Fig. 1L.

Knapp & Helgason (1997) revised sect. *Pteroidea* and the ten species of the section form a clade in this study and in Tepe & Bohs (2010). Species of sect. *Pteroidea* are herbs or vines with simple or pinnately compound leaves. The most useful diagnostic characters are unifoliate sympodial units and inflorescences that emerge from the leaf axils (although not truly axillary; see Knapp & Helgason, 1997). Also, many species of sect. *Pteroidea* have unusual, sharply pointed, and sometimes coarsely rugose fruits (Fig. 1L). The group occurs from southern Mexico to Bolivia, Brazil, and the Guianas at elevations from sea level to 3200 m. One species, *S. trizygum*, is found in Central America, with the remaining nine restricted to South America. Species of sect. *Pteroidea* can be found in a wide range of wet lowland forests to premontane and montane cloud forests, and from deep shade to forest edges and clearings.

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Appendix 1. Accessions used in this study.

Taxon (clade), voucher (herbarium code), source, and GenBank numbers for ITS, GBSSI (*waxy*), *trnT-trnF*, *trnS-trnG*. Missing data are indicated by a dash (–). Material collected from seed-grown plants are identified by the BIRM (Solanaceae Collection at the University of Birmingham, U.K.) and NIJ (Botanic Garden of Radboud University, Nijmegen, The Netherlands) accession numbers. The BIRM collection is now held at NIJ (http://www.bgard.science.ru.nl/solanaceae/). LA numbers are accession numbers of the C.M. Rick Tomato Genetics Resource Center (http://tgrc.ucdavis.edu/), PI numbers are USDA Plant Introduction Number (http://www.ars-grin.gov/nr6/), and CPC are Commonwealth Potato Collection numbers (http://germinate.scri.ac.uk/germinate_cpc/app/cpc/species_list.pl). # Sequences from different accessions combined for species. * Sequences newly generated for this study.

Solanum abutiloides (Griseb.) Bitter & Lillo (Brevantherum), *Olmstead S-73* (WTU), Seed: BIRM S.0655, AF244716, AY562948, AY266236, AY555453. ***S. acaule*** Bitter# (Petota), PI-472735, Argentina, –, AY875420, –, –. ***S. acaule*** Bitter# (Petota), PI-310923, Bolivia, AY875782, –, –, –. ***S. acaule*** Bitter# (Petota), PI-472659, Argentina, –, –, –, GU143630. ***S. anceps*** Ruiz & Pav.-1 (Pteroidea), *Tepe 2600* (MU), Ecuador, GQ221544, GQ221596, GQ221571, KR919660*. ***S. anceps*** Ruiz & Pav.-2 (Pteroidea), *Bohs 2790* (UT), Bolivia, GQ221541, GQ221593, GQ221568, HQ856087. ***S. angustialatum*** Bitter (Pteroidea), *Tepe 2368* (UT), Peru, GQ221547, GQ221599, GQ221574, KR919659*. ***S. appendiculatum*** Dunal (Anarrhichomenum), *Anderson 1401* (CONN), Mexico, KR872954*, DQ169018, DQ180461, KR919658*. ***S. arboreum*** Dunal (Geminata), *Bohs 2521* (UT), Costa Rica, AF244719, AY996381, DQ180424, AY998380. ***S. aviculare*** G.Forst. (Archaesolanum), Seed: BIRM S.0809, AF244743, AY562952, AY562952, AY555458. ***S. baretiae*** Tepe (Anarrhichomenum), *Tepe 2882* (UT), Peru, KR872955*, KT424063*, KT001410*, KR919657*. ***S. betaceum*** Cav. (Cyphomandra), *Bohs 2468* (UT), Bolivia, AF244713, AY996387, DQ180426, AY998386. ***S. brevicaule*** Bitter# (Petota), PI-234009, Bolivia, AY875826, –, –, –. ***S. brevicaule*** Bitter# (Petota), *Hawke 6701* (PTIS), Bolivia, –, DQ169019, DQ180443, –. ***S. brevifolium*** Dunal (Anarrhichomenum), *Bohs 3112* (UT), Ecuador, GQ221562, GQ221614, GQ221589, HQ856089. ***S. bulbocastanum*** Dunal (Petota), *Tarn 153* (PTIS), Mexico, GQ221564, DQ169020, DQ180444, HQ856091. ***S. canense*** Rydb.# (Basarthrum), *Anderson 46* (CONN), Panama, –, KR820002*, –, –. ***S. canense*** Rydb.# (Basarthrum), *Tepe 2717* (UT), Ecuador, KR872953*, –, KT001409*, KR919656*. ***S. cardiophyllum*** Lindl.# (Petota), PI-595465, Mexico, AY875759, HM561739, –, –. ***S. cardiophyllum*** Lindl.# (Petota), PI-283062, Mexico, –, –, –, GU143634. ***S. caripense*** Dunal (Basarthrum), *Bohs 3149* (UT), Ecuador, GQ221563, GQ221615, GQ221590, HQ856090. ***S. chamaepolybotryon*** Bitter (Pteroidea), *Tepe 2371* (NY), Peru, GQ221548, GQ221600, GQ221575, KT447210*. ***S. cheesmaniae*** (L.Riley) Fosberg# (Lycopersicon). LA0437, Peru, –, AB515419, AB515399, –. ***S. cheesmaniae*** (L.Riley) Fosberg# (Lycopersicon), LA0137, Ecuador, AJ300202, –, –. ***S. chilense*** Dunal# (Lycopersicon), LA2884, Chile, –, AY875629, –, –. ***S. chilense*** Dunal# (Lycopersicon), LA2930, Chile, AJ300203, –, –, –. ***S. chilense*** Dunal# (Lycopersicon), Unknown, Chile, –, –, AB515412, –. ***S. chimborazense*** Bitter & Sodiro (Anarrhichomenum), *Anderson 858* (CONN), Ecuador, KR872952*, KT424071*, KT001411*, KR919655*. ***S. complectens*** M.Nee & G.J.Anderson (Anarrhichomenum), *Bohs 2452* (UT), Bolivia, KR872951*, KT424062*, KT001412*, KR919654*. ***S. conicum*** Ruiz & Pav. (Pteroidea), *Tepe 2270* (UT), Peru, GQ221549, GQ221601, GQ221576, KR919653*. ***S. cordovense*** Sessé & Moc. (Brevantherum), *Bohs 2693* (UT), Costa Rica, AF244717, AY996401, DQ180480, AY998400. ***S. crassinervium*** Tepe (Herpystichum), *Tepe 2729* (NY), Ecuador, HQ856119, HQ856216, HQ856062, HQ856080. ***S. dalibardiforme*** Bitter (Herpystichum), *Mora 924* (COL), Colombia, HQ856123, HQ856220, HQ856066, HQ856084. ***S. demissum*** Lindl.# (Petota), PI-558482, Mexico, AY875794, –, –, –. ***S. demissum*** Lindl.# (Petota), PI-545757, Mexico, –, AY875451, –, –. ***S. demissum*** Lindl.# (Petota), CPC 8, Mexico, –, –, –, GU143637. ***S. dolichorhachis*** Bitter (Herpystichum), *Mexia 6617* (US), Ecuador, –, HQ856212, HQ856057, HQ856074. ***S. dulcamara*** L. (Dulcamaroid), No voucher, U.S.A., cultivated, AF244742, AY996410, AY266231, AY998409. ***S. etuberosum*** Lindl. (Etuberosum), *Contreras 1322* (UAC), Chile, KR872950*, DQ169027, DQ180463, KR919652*. ***S. evolvulifolium*** Greenm.-1 (Herpystichum), *Knapp 7198* (BM), Panama, HQ856113, DQ169028, DQ180464, HQ856070. ***S. evolvulifolium*** Greenm.-2 (Herpystichum), *Tepe 2585* (NY), Ecuador, HQ856116, HQ856211, HQ856056, HQ856073. ***S. fraxinifolium*** Dunal (Basarthrum), *Bohs 2558* (UT), Costa Rica, AY996511, AY996416, DQ180465, AY998415. ***S. graveolens*** Bunbury (Cyphomandra), *Agra 7261* (JPB), Brazil, KR872949*, KT424064*, KT001413*, –. ***S. incurvum*** Ruiz & Pav. (Pteroidea), *Tepe 2294* (UT), Peru, GQ221550, GQ221602, GQ221577, KR919650*. ***S. infundibuliforme*** Phil. (Petota), PI-472857, Argentina, AY875818, HM561753, –, GU143638. ***S. juglandifolium*** Dunal (Juglandifolia), *Rick 7546* (PTIS), Colombia, KR872948*, DQ169034, DQ180449, KR919651*. ***S. limoncochaense*** Tepe (Herpystichum), *Tepe 2627* (NY), Ecuador, HQ856120, HQ856217, HQ856063, HQ856081. ***S. loxophyllum*** Bitter (Herpystichum), *Tepe 2726* (QCNE), Ecuador, HQ856117, HQ856213, HQ856058, HQ856075. ***S. lycopersicoides*** Dunal# (Lycopersicoides), *Marshall s.n.* (K; LA2407), Chile, AJ300212, –, –, –. ***S. lycopersicoides*** Dunal# (Lycopersicoides), unknown (LA1990), Peru, –, AY875569, –, –. ***S. lycopersicoides*** Dunal# (Lycopersicoides), "*ASP* 029" , Unknown, –, –, DQ855063, –. ***S. lycopersicum*** L. (Lycopersicon), No voucher, U.S.A., cultivated, GQ221566, DQ169036, DQ180450, HQ856092. ***S. melongena*** L. (Leptostemonum), *Olmstead S-91* (WTU), Seeds: NIJ 954750114, GU591078, AY562959, DQ180406, AY998440. ***S. mite*** Ruiz & Pav.-1 (Pteroidea), *Bohs 3627* (UT), Ecuador, GQ221554, GQ221606, GQ221581, KR919648*. ***S. mite*** Ruiz & Pav.-2 (Pteroidea), *Bohs 2750* (UT), Bolivia, GQ221552, GQ221604, GQ221579, KR919649*. ***S. montanum*** L. (Regmandra), *Bohs 2870* (UT), Seeds: NIJ 904750205, AY996531, AY996443, DQ180468, AY998443. ***S. multifidum*** Lam. (Regmandra), *Stern 85* (UT), Peru, KR872947*, KT424065*, KT001414*, KR919647*. ***S. muricatum*** Aiton (Basarthrum), *Olmstead s-93* (WTU), Colombia, KT921783*, DQ169038, DQ180469, –. ***S. nitidum*** Ruiz & Pav. (Dulcamaroid), *Nee 31944* (NY), Bolivia, AF244740, DQ169039, DQ180451, KR919646*. ***S. ochranthum*** Dunal (Juglandifolium), *Rick 7710* (WIS), Peru, –, AY875567, –, –. ***S. oxycoccoides*** Bitter-1 (Potato Clade I), *Tepe 2881* (UT), Peru, KR872946*, KT424066*, KT001415*, KR919645*. ***S. oxycoccoides*** Bitter-2 (Potato Clade I), *Henning 160* (B), Peru, KR872945*, –, –, KR919644*. ***S. pacificum*** Tepe (Herpystichum), *Tepe 2696* (NY), Ecuador, HQ856122, HQ856219, HQ856065, HQ856083. ***S. palitans*** C.V.Morton (Morelloid), *Bohs 2449* (UT), Seeds: BIRM 50837170, AF244739, AY996449, DQ180452, AY998450. ***S. palustre*** Schltdl.# (Etuberosum), *Spooner 4329* (PTIS), Chile, PI 558233, –, –, –. ***S. palustre*** Schltdl.# (Etuberosum), *Sortiment 388* (PTIS), Chile or Argentina, –, AY875561, –, –. ***S. paposanum*** Phil. (Regmandra), *Aedo 10976* (MA), Peru, KF720746,

Appendix 1. Continued.

KF720781, KF720769, KR919643*. ***S. pennellii*** Correll# (Lycopersicon), LA1376 , Peru, –, AY875635, –, –. ***S. pennellii*** Correll# (Lycopersicon), *Marshall 105* (BM), Unknown, AJ300205, –, –, –. ***S. pentaphyllum*** Bitter (Herpystichum), *Grant 99-03335* (US), Venezuela, –, HQ856215, HQ856061, HQ856079. ***S. peruvianum*** L. (Lycopersicon), LA2744, Chile, AJ300210, AY875627, AB515411, –. ***S. phaseoloides*** Pol. (Herpystichum), *Bohs 2485* (UT), Costa Rica, GQ221567, GQ221617, GQ221592, HQ856077. ***S. pimpinellifolium*** L.# (Lycopersicon), LA2184, Peru, –, AY875579, –, –. ***S. pimpinellifolium*** L.# (Lycopersicon), LA3910, Ecuador, –, –, AB515402, –. ***S. pimpinellifolium*** L.# (Lycopersicon), *Marshall 103* (BM), Unknown, AJ300196, –, –, –. ***S. pinnatisectum*** Dunal (Petota), *Tarn 205A* (PYIS), Mexico, KR872944*, DQ169042, DQ180453, KR919642*. ***S. pinnatum*** Cav. (Regmandra), *Bohs 2994* (UT), Cultivated, KR872943*, KT424067*, KT001416*, KR919641*. ***S. polyadenium*** Greenm.# (Petota), PI-161728, Mexico, AY875766, HM561784, –, –. ***S. polyadenium*** Greenm.# (Petota), CPC 3501, Unknown, –, –, –, GU143641. ***S. pseudocapsicum*** L. (Geminata), no voucher, Seeds: BIRM S-0870, AF244720, AY562963, DQ180436, AY555469. ***S. ptycanthum*** Dunal (Morelloid), *Olmstead S-94* (WTU), U.S.A., AF244735, AY996457, DQ180454, AY998458. ***S. sanctae-marthae*** Bitter (Articulatum), *Anderson 84-6* (CONN), Colombia, KR872942*, KT424068*, KT001417*, KR919640*. ***S. savanillense*** Bitter (Pteroidea), *Bohs 3444* (UT), Ecuador, GQ221556, GQ221608, GQ221583, KR919639*. ***S. sitiens*** I.M.Johnst.# (Lycopersicoides), LA1974 (PTIS), Chile, DQ118129, –, –, –. ***S. sitiens*** I.M.Johnst.# (Lycopersicoides), *Rick 7603* (PTIS), Chile, –, AY875571, –, –. ***S. sodiroi*** Bitter (Anarrhichomenum), *Bohs 3118* (UT), Ecuador, KR872941*, KT424069*, KT001418*, KR919638*. ***S. stoloniferum*** Schltdl.# (Petota), PI-251740, Mexico, AY875809, AY875516, –, –. ***S. stoloniferum*** Schltdl.# (Petota), CPC 4018, Unknown, –, –, –, GU143642. ***S. suaveolens*** Kunth & C.D.Bouché (Basarthrum), *Anderson 40-9* (CONN), cultivated (Peru), KR872940*, KT424070*, KT001419*, KR919637*. ***S. taeniotrichum*** Correll (Articulatum), *Anderson 1423* (CONN), cultivated (Costa Rica), KR872939*, AY875407, KT001420*, KR919636*. ***S. ternatum*** Ruiz & Pav.# (Pteroidea), *Bohs 3395* (UT), Ecuador, GQ221557, GQ221609, GQ221584, –. ***S. ternatum*** Ruiz & Pav.# (Pteroidea), *Tepe 2320* (NY), Peru, –, –, –, KR919635*. ***S. thelopodium*** Sendtn. (Thelopodium), *Nee 50858* (NY), Bolivia, AY996556, AY996471, DQ180470, AY998472. ***S. torvum*** Sw. (Leptostemonum), *Olmstead S-101* (WTU), Seeds: BIRM S.0839, AF244729, AY562972, AY266246, AY555478. ***S. trifolium*** Dunal (Herpystichum), *Tepe 2682* (MU), Ecuador, HQ856125, HQ856221, HQ856068, HQ856086. ***S. trizygum*** Bitter (Pteroidea), *Moran 7678* (UT), Costa Rica, GQ221559, GQ221612, GQ221587, KR919634*. ***S. tuberosum*** L.# (Petota), PI-195188, Peru, AY875827, –, –, –. ***S. tuberosum*** L.# (Petota), PI-234011, Bolivia, –, AY875555, –, –. ***S. tuberosum*** L.# (Petota), UPG 0078, Hungary, –, –, HM006842, –. ***S. tuberosum*** L.# (Petota), CPC 843, Unknown, –, –, –, GU143643. ***S. uleanum*** Bitter (Pteroidea), *Bohs 3628* (UT), Ecuador, GQ221561, GQ221613, GQ221588, KR919633*. ***S. verrucosum*** Schltdl.# (Petota), PI-558488, Mexico, AY875796, –, –, –. ***S. verrucosum*** Schltdl.# (Petota), PI-545745, Mexico, –, HM561829, –, –. ***S. verrucosum*** Schltdl.# (Petota), CPC 7127, Mexico, –, –, –, GU143644. ***S. violaceimarmoratum*** Bitter# (Petota), PI-473396, Bolivia, AY875788, AY875557, –, –. ***S. violaceimarmoratum*** Bitter# (Petota), CPC 7128, Bolivia, –, –, –, GU143645.