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A Morphometric Study of Species Boundaries of the Wild Potato *Solanum* Series *Piurana* (Solanaceae) and Putatively Related Species from Seven Other Series in *Solanum* Sect. *Petota*

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Abstract—There are about 190 wild potato (*Solanum* L. section *Petota* Dumort.) species distributed from the southwestern United States to central Argentina and adjacent Chile and Uruguay. The morphological similarity of many of its constituent species has led to widely conflicting taxonomic treatments. *Solanum* series *Piurana* Hawkes is one of 21 series recognized in section *Petota* in the latest comprehensive taxonomic treatment by Hawkes in 1990. They are distributed from southern Colombia, south through Ecuador to central Peru. The limits of the series and validity of its constituent species are unresolved. We provide the first comprehensive morphological phenetic study of the series, to include putatively related species in ser. *Conicibaccata*, *Cuneoalata, Ingifolia, Megistacroloba, Simplicissima*, *Tuberosa,* and *Yungasensa*, through an examination 188 living germplasm accessions of 33 species, planted in replicated plots in a field station in Andean Peru. Only four morphologically well-defined groups were supported. Continuing work is exploring molecular support for these species in these eight series.

Keywords—morphometrics, Peru, potatoes, Solanaceae, *Solanum* section *Petota*, *Solanum* series *Piurana*.

The genus *Solanum* L. is one of the most important genera of the Solanaceae. There are about 190 wild tuber-bearing species (*Solanum* sect. *Petota* Dumort.), distributed from the southwestern United States to central Argentina and adjacent Chile and Uruguay. The morphological similarity of many species in the section has led to widely conflicting taxonomic treatments (Spooner and Salas 2006).

Solanum series *Piurana* Hawkes is one of 21 series recognized in section *Petota* in the latest comprehensive taxonomic treatment by Hawkes (1990). They are distributed from southern Colombia, south through Ecuador to central Peru. The limits of the series and its constituent species are unresolved and controversial. The most distinctive features of ser. *Piurana*, used by all major taxonomists of section *Petota* (Correll 1962; Hawkes 1990; Ochoa 1999) are the globose to ovoid fruits and the coriaceous glossy leaves. However, these traits vary so much across the different series that it is difficult to decide what to include in ser. *Piurana.* All the above authors have expressed doubts about the limits of ser. *Piurana*; as stated by Correll (1962: pg.139), "*This series, probably more than any others, may be considered a catchall. Paradoxically, its component species are held together not so much by their similarity as by their differences*."

Different taxonomic treatments illustrate the disagreements regarding the limits of the series. Correll (1962) recognized 15 species, Hawkes (1990) 15, and Ochoa (1999) 13; however, they recognize only six species in common: *S. acroglossum* [see Table 1 for authors of species names], *S. cantense*, *S. cyanophyllum* Corr. (= *S. andreanum* Baker [Spooner et al. 1993]), *S. hypacrarthrum*, *S. piurae,* and *S. solisii* (Table 1).

Plastid DNA restriction site and morphological data (Castillo and Spooner 1997; Spooner and Castillo 1997) suggested that *Solanum* ser. *Piurana* as traditionally circumscribed was paraphyletic. Salas et al. (2001) pointed out that all the species placed by Hawkes (1990) and Ochoa (1999) in ser. *Piurana* possess moniliform tubers (like beads along the stolons, unlike the more typical arrangement of single tubers placed at stolon ends). Spooner and Salas (2006) suggested that the only two distinctive features of ser. *Piurana* might be the coriaceous and glossy leaves (Correll 1962; Hawkes 1990; Ochoa 1999), and the moniliform tubers. Based on the plastid DNA restriction site data, survey of leaf and tuber morphology by Ochoa (1999), and knowledge of these traits in the field and greenhouse, Spooner and Salas (2006) provided hypotheses of a redefined and enlarged monophyletic ser. *Piurana* to include all members of series *Piurana* (all 15 species) as recognized by Hawkes (1990) and selected species in ser. *Conicibaccata* Bitter (four of 40), *Cuneoalata* Hawkes (all three), *Ingifolia* Ochoa (two of two), *Megistacroloba* Cárd. and Hawkes (one of 11), *Olmosiana* Ochoa (one of one), *Simplicissima* Ochoa (one of one), *Tuberosa* (Rydb.) Hawkes (15 of 94), and *Yungasensa* Correll (one of nine). In total, these 43 species represent 19% of the total 225 species recognized by Hawkes.

The primary goal of this study is to analyze the morphological support for the validity of species in this expanded concept of a putatively monophyletic ser. *Piurana* as suggested by Spooner and Salas (2006). The data will be useful to redefine the number of species in sect. *Petota*, for comparison to molecular results, and for a taxonomic monograph of these species that is currently in progress.

Materials and Methods

Plant Material—A total of 188 accessions from 33 of the 43 different species of ser. *Piurana* and putatively related wild potato species (see above) from other series were selected for the morphological analysis (Appendix 1). We did not collect data for the 10 remaining species because they were not available as germplasm (four species) or did not grow well in the greenhouse (six species). These accessions include representatives of all of the nine series listed above except for ser. *Olmosiana,* which grew poorly in our study. Figures 1–3 illustrate the range of variation in tubers, leaves, flowers, and fruits within these eight series. Plants were grown from seeds provided by the US Potato Genebank in Sturgeon Bay, Wisconsin (http://www.ars-grin.gov/nr6/) and the International Potato Center (http://www.cipotato.org/). More than one accession per taxon was analyzed (when available); not all species had the same number of accessions due to their rarity and restricted geographical distribution. Higher numbers of accessions were considered for some species, such as *S. andreanum* and *S. chomatophilum* due to their wide geographic distribution and/or great morphological variation. Herbarium vouchers were deposited at the International Potato Center herbarium (CIP) in Lima, Peru. The evaluated accessions were mapped with ArcGIS (ESRI-Inc., 2005), and grouped by generalized geographic areas (Fig. 4; Appendix 1).

Morphological Evaluation—The accessions were grown in green-

TABLE 1. *Solanum* series *Piurana* and putatively related species evaluated in this study. [a]Endosperm Balance Numbers (EBN) are a hypothetical genetic factors independent of ploidy and empirically determined relative to other EBNs. In potato, these are 2*x*(1EBN), 2*x*(2EBN), 4*x*(2EBN), 4*x*(4EBN), and 6*x*(4EBN). Crosses between species with differing EBNs are almost always unsuccessful due to endosperm unbalance, and crosses between species with the same EBN number are frequently successful, even if they differ by ploidy. EBN forms a major biological isolating mechanism in potato (Fritz and Hanneman 1989). "X" is the basic chromosome number for potatoes, equal to 12.

Species	Number of accessions evaluated	Distribution (Map Locality)	Ploidy (EBN)[a]	Affiliation to series (by author)			
				Original description	Correll 1962	Hawkes 1990	Ochoa 1999
S. acroglossum Juz.	1	Peru (30)	2*x*(2EBN)		PIU	PIU	PIU
S. albornozii Correll	4	Ecuador (12)	2*x*(2EBN)	PIU	PIU	PIU	CON
S. andreanum Baker	11	Colombia, Ecuador (1, 2, 4, 5, 7, 9, 10)	2*x*(2EBN)		TRN	TUB	TUB
S. augustii Ochoa	2	Peru (27, 28)	2*x*(1EBN)	TUB		TUB	TUB
S. cajamarquense Ochoa	8	Peru (19)	2*x*(1EBN)	TUB	MIN	TUB	TUB
S. cantense Ochoa	5	Peru (32)	2*x*(2EBN)	TUB	PIU	PIU	PIU
S. chancayense Ochoa	2	Peru (31)	2*x*(1EBN)	TUB	TRN	TUB	TUB
S. chilliasense Ochoa	2	Ecuador (11)	2*x*(2EBN)	PIU		PIU	PIU
S. chiquidenum Ochoa	10	Peru (18, 19, 20, 21)	2*x*(2EBN)	PIU	PIU	TUB	PIU
S. chomatophilum Bitter	27	Ecuador, Peru (16, 17, 18, 19, 20, 21, 24, 25, 26, 30)	2*x*(2EBN)		PIU	CON	CON
S. contumazaense Ochoa	2	Peru (19)	2*x*(2EBN)	TUB		CON	CON
S. dolichocremastrum Bitter	12	Peru (26, 27, 28)	2*x*(1EBN)		MEG	TUB	MEG
S. huancabambense Ochoa	6	Peru (15)	2*x*(2EBN)	TUB	CON	YUN	TUB
S. huarochiriense Ochoa	4	Peru (27, 32, 33)	2*x*(2EBN)	TUB		TUB	TUB
S. humectophilum Ochoa	1	Peru (16)	2*x*(1EBN)	TUB		TUB	PIU
S. hypacrarthrum Bitter	5	Peru (27, 32, 33)	2*x*(1EBN)		PIU	PIU	PIU
S. immite Dunal	3	Peru (21, 27)	2*x*(1EBN)		PIU	TUB	TUB
S. irosinum Ochoa	4	Peru (18)	2*x*(2EBN)	CON		CON/TUB	CON
S. jalcae Ochoa	6	Peru (19, 21)	2*x*(2EBN)	MEG	ING	PIU	ING
S. marinasense Vargas	11	Peru (34, 35, 36, 37)	2*x*(2EBN)	CON	PIU	TUB	TUB
S. mochiquense Ochoa	8	Peru (15, 19, 22, 23, 31)	2*x*(1EBN)	TUB	PIU	TUB	TUB
S. multiinterruptum Bitter	4	Peru (20, 25, 27, 33)	2*x*(2EBN)		TRN	TUB	TUB
S. paucijugum Bitter	10	Ecuador (6, 8, 9, 10)	4*x*(2EBN)		CON	CON	CON
S. paucissectum Ochoa	6	Peru (15)	2*x*(2EBN)	PIU		PIU	PIU
S. peloquinianum Ochoa	3	Peru (25)	2*x*(2EBN)	CUN		CUN	CON
S. piurae Bitter	3	Peru (13, 15)	2*x*(2EBN)		PIU	PIU	PIU
S. raquialatum Ochoa	2	Peru (13, 14)	2*x*(1EBN)	MEG	ING	ING	ING
S. scabrifolium Ochoa	1	Peru (29)	2*x*	TUB		TUB	TUB
S. simplicissimum Ochoa	2	Peru (32)	2*x*(1EBN)	SMP			SMP
S. sogarandinum Ochoa	5	Peru (21, 25, 28)	2*x*(2EBN)	MEG	MEG	MEG	MEG
S. solisii Hawkes	1	Ecuador (9)	2*x*		PIU	PIU	PIU
S. tuquerrense Hawkes	12	Colombia, Ecuador (3, 4, 5, 6, 7, 8)	4*x*(2EBN)	PIU	ING	PIU	PIU
S. ×*blanco-galdosii* Ochoa	4	Peru (19, 24, 25)	2*x*(2EBN)	CON		PIU	CON

houses at the Experimental Station of the International Potato Center in Huancayo, in the central Peruvian Andes (3200 m above sea level, 12°8′S, 75°8′W). Seeds were planted in organic soils in December, seedlings were transplanted into 8 inch pots, and measurements were conducted from February to April when plants were flowering. Tubers were measured in May after plant senescence. Hand pollination was conducted to stimulate fruit set.

The experimental design included two blocks of accessions planted in separate greenhouses; the first block was organized by species and the second block by collector number. Ten plants were grown per accession, divided into five plants in each of the two blocks. Only three out of the five plants were evaluated for each block so a total of six plants were measured for each accession.

Measurements of 82 morphological characters (Appendix 2) were obtained for the 188 accessions of 33 species. We selected these characters based on prior morphological studies in *Solanum* sect. *Petota* (e.g. Spooner and Castillo 1997; who selected them based on characters used in taxonomic treatments), and added more based on our observations of the variation among species. The measurements were conducted at an accuracy of 0.005 mm with an electronic vernier. Leaf measurements were taken from mature leaves from the middle node of the stem of the plant. Fruits were measured when fully mature, as determined by fruits beginning to turn soft and sometimes turning yellowish. Colors were assessed using the RHS Color Charts (Royal Horticultural Society 2001). A Hunter Lab Color Quest 45/0 colorimeter was used to obtain CIELab values (Wyszecki 1982) from these color charts. The CIELab is a color model used to describe all the colors visible to the human eye developed by CIE (Commission Internationale de l'Eclairage). The L* parameter represents the lightness of the color or luminance (L* = 0 [black] and L* = 100 [white]), a* the position between green (when negative) and magenta (when positive), and b* the position between yellow (negative values) and blue (positive values). Ratios were assessed for traits, and we eliminated one of the measurements to not overweigh characters (Appendix 2).

The correlation coefficient of the similarity matrices was calculated for the two blocks after standardization of the data using MXCOMP in NTSYS-pc software version 2.02K (Rohlf 1997). An operational taxonomic unit (OTU) was the average of three individuals per accession for each block. Stepwise discriminate analysis (SDA) was used to identify and rank the most significant characters to discriminate ser. *Piurana* from other series and also to discriminate species in the larger group to include members of other series. Principal Components Analyses (PCA) and Canonical Discriminate Analyses (CDA) were conducted for the standardized averages of each OTU of averages of six plants. PCA does not take into account a priori group assignment and was thus used to examine phenetic variation independent of taxon assignment and it was calculated from the correlation matrix of the variance-covariance matrix. Unlike PCA, CDA uses preselected groups and provides the greatest separation of groups (Sneath and Sokal 1973); for CDA analysis, the original taxon affiliations were kept. All analyses were done in SAS ver. 9.1 (SAS Institute Inc. 2004).

RESULTS

Results of Analysis in the Two Replicated Blocks—Correlation coefficients showed that identical species and acces-

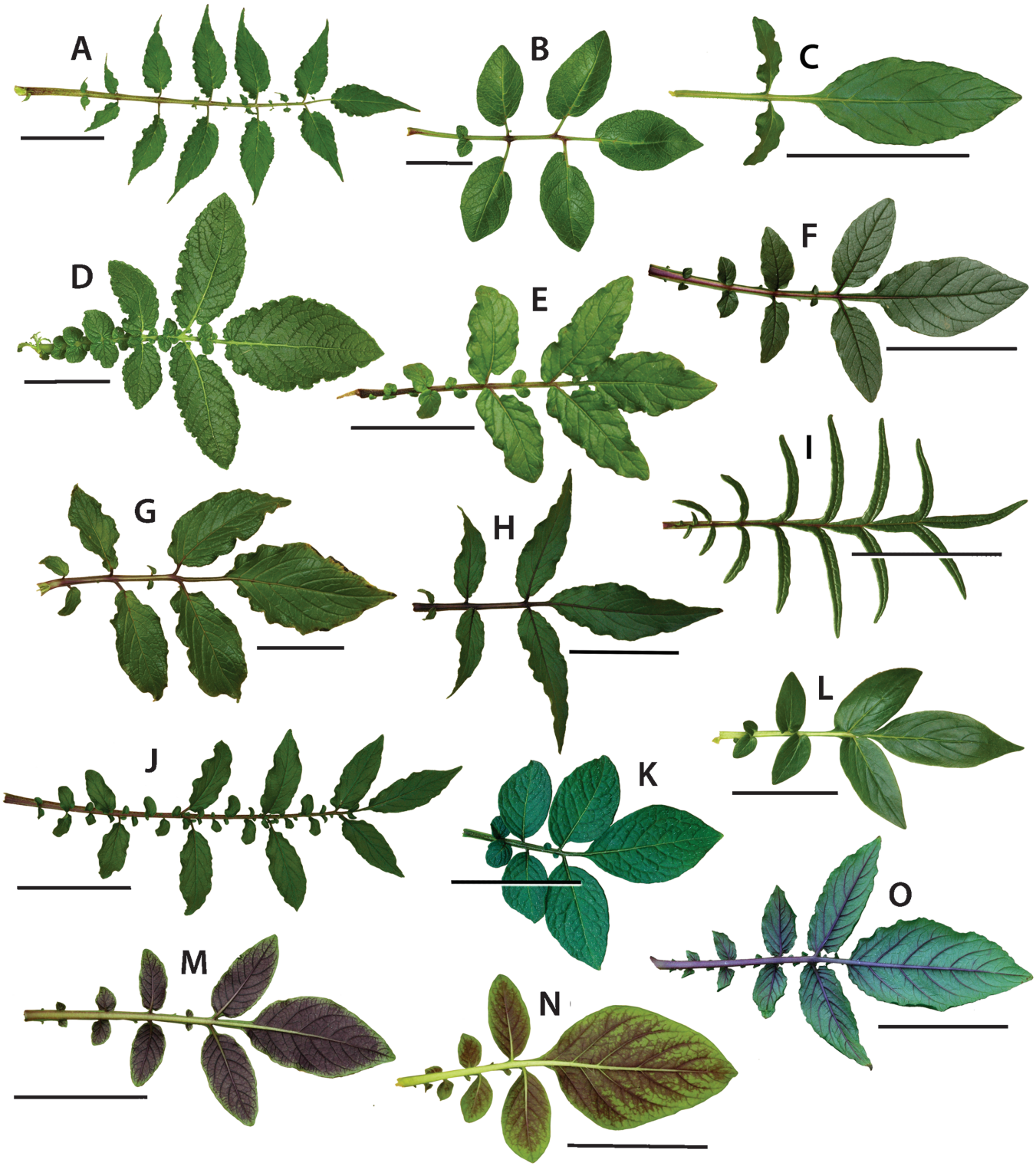

FIG. 1. Morphological variation of leaves among the species included in this study; all figures are from the adaxial surface unless indicated otherwise. (A) *S. immite*, (B) *S. marinasense*, (C) *S. paucissectum*, (D) *S. mochiquense*, (E) *S. scabrifolium*, (F) *S. jalcae*, (G, H) *S. chiquidenum*, (I) *S. peloquinianum*, (J) *S. augustii*, (K) *S. andreanum*, (L) *S. cantense* (M, N) *S. jalcae* (abaxial), (O) *S. piurae* (abaxial). All bars = 5cm.

sions planted in two different greenhouses are correlated at 0.62. ANOVA analysis was used to determine the differences between the two replicated blocks for the evaluated characters. This analysis showed variation between the two environments for 22 out of the 82 characters evaluated ($\alpha = 0.05$). These 22 characters included two out of five characters for stem, three out of 30 characters for leaves, two out of nine fruit characters, eight out of 27 flower characters and seven out of ten tuber characters.

Multivariate Analyses—There were 4.16% missing data averages for the characters. Because SAS eliminates entire accessions with any missing data, we estimated these values

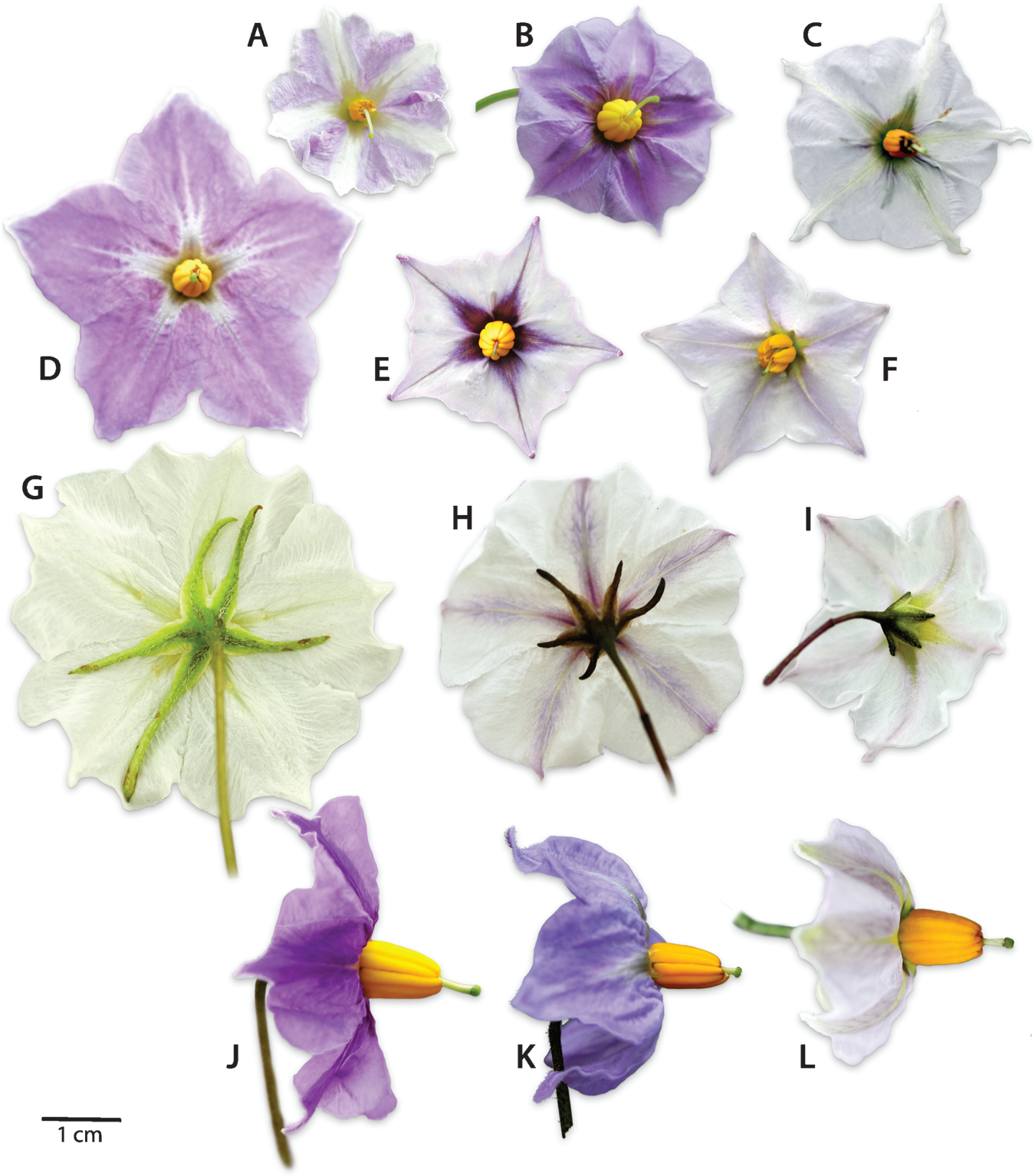

FIG. 2. Morphological variation of corollas among the species included in this study. (A) *S. scabrifolium*, (B) *S. peloquinianum*, (C) *S. chilliasense*, (D) *S. dolichocremastrum*, (E) *S. humectophilum*, (F) *S. albornozii*, (G) *S. hypacrarthrum*, (H) *S. chiquidenum*, (I) *S. albornozii*, (J) *S. chomatophilum*, (K) *S. chomatophilum*, (L) *S. andreanum*.

from averages of other accessions from the same species. Correlation analysis showed the L*a*b* color values to be highly correlated, so we used only the parameter a* (colors magenta to green) because it most closely matched the colors of corollas for the evaluation of flower corollas and only the parameter b* for the assessment of tuber colors (yellow to blue).

PCA analysis was carried out using the complete set of 82 characters. PCA axes 1 and 2 of the entire data set (Fig. 5) accounted for 13.4% and 8.8% of the total variation (for a total

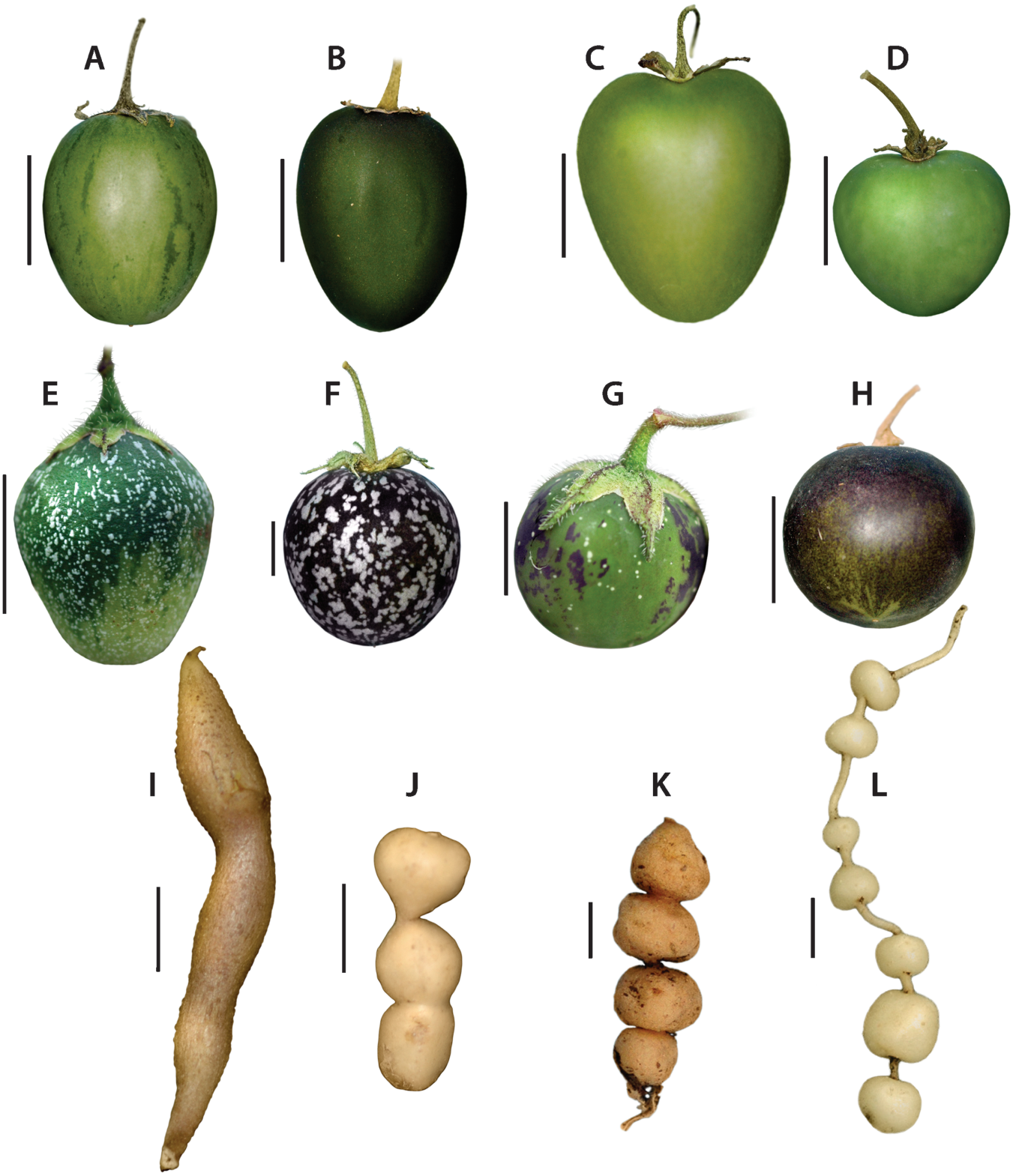

FIG. 3. Morphological variation of fruits (A-H) and tubers (I-L) among the species included in this study. (A) *S. paucijugum*, (B) *S. chomatophilum*, (C) *S. tuquerrense*, (D) *S. mochiquense*, (E) *S. multiinterruptum*, (F) *S. marinasense*, (G) *S. irosinum*, (H) *S. simplicissimum*, (I) *S. andreanum*, (J) *S. sogarandinum*, (K, L) *S. dolichocremastrum*. All bars = 1cm.

of 22.2%); axis 3 accounted for an additional 6.3%, but did not change the overall pattern and is not presented. Axis 1 is highly influenced (highest positive or negative eigenvector values) by the following five characters (Appendix 2): (1) ratio: length of fruit/width at widest point of the fruit, (2) ratio: length of fruit/width at its narrowest point, (3) color of abaxial corolla interpetiolar tissue, (4) color of adaxial corolla rays, and (5) tuber eye color. Axis 2 was mainly influenced by: (1) distance between apices of second most distal lateral leaflets, (2) distance between apices of third most distal lat-

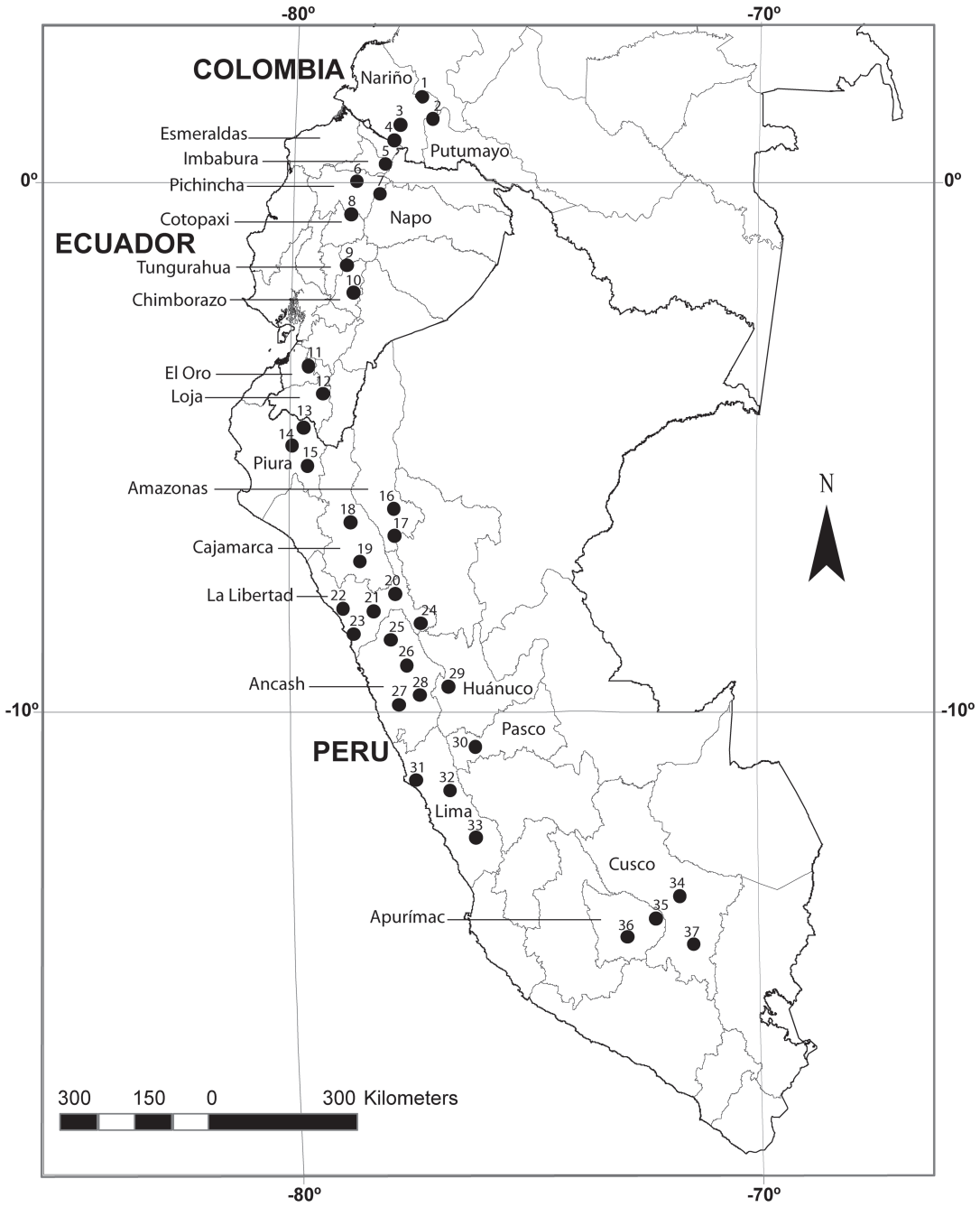

FIG. 4. Map of Colombia, Ecuador, and Peru showing the 37 generalized map localities of the 188 accessions included in this study. Numbers correspond to the generalized map areas in Appendix 1.

eral leaflets, (3) number of primary interstitial leaflets, (4) length of the largest interstitial leaflet, and (5) number of pairs of lateral leaflets. PCA axes 1 and 2 (Fig. 5) distinguished *S. albornozii*, *S. contumazaense*, and *S. hypacrarthrum*.

The SDA analysis identified 56 characters discriminating species. The four most significant characters to distinguish the different species were: (1) length of calyx pubescence (mm), (2) ratio: length of terminal leaflet lamina/width of terminal leaflet lamina, (3) ratio: length from axis of widest point of most distal lateral leaflet to apex/length of most distal lateral leaflet, and (4) density of pubescence on abaxial surface of leaf (number of hairs/cm^2).

The CDA analysis was carried out using only the 56 characters that were selected through the SDA analysis. Four groups were clearly differentiated through CDA analysis: (I) A group constituted by *S. hypacrarthrum* and *S. simplicissimum*, (II) *S. contumazaense*, (III) *S. peloquinianum*, and (IV) an unresolved group of the remaining 29 species (Fig. 6a). A closer look at the phenetic structure of Group IV (Fig. 6b) containing the 29 remaining species provides some morphological support for *S. chancayense*, *S. chilliasense*, *S. acroglosum*, *S. immite*, *S. marinasense*, and *S. cajamarquense*. The means, ranges, and one standard deviation of the mean for the four most important characters identified by SDA to distinguish all taxa is presented in Fig. 7, and for species within Group IV in Fig. 8.

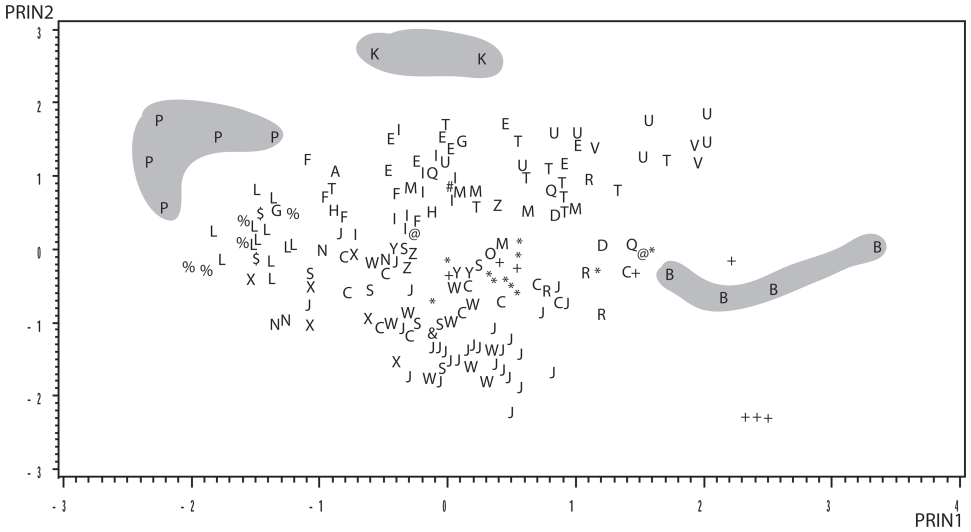

FIG. 5. Principal components analysis based on 82 morphological characters (Appendix 2) examined in this study. Balloons highlight well defined groups. Species codes are: *S. acroglossum* (A), *S. albornozii* (B), *S. andreanum* (C), *S. augustii* (D), *S. cajamarquense* (E), *S. cantense* (F), *S. chancayense* (G), *S. chilliasense* (H), *S. chiquidenum* (I), *S. chomatophilum* (J), *S. contumazaense* (K), *S. dolichocremastrum* (L), *S. huancabambense* (M), *S. huarochiriense* (N), *S. humectophilum* (O), *S. hypacrarthrum* (P), *S. immite* (Q), *S. irosinum* (R), *S. jalcae* (S), *S. marinasense* (T), *S. mochiquense* (U), *S. multiinterruptum* (V), *S. paucijugum* (W), *S. paucissectum* (X), *S. peloquinianum* (Y), *S. piurae* (Z), *S. raquialatum* (@), *S. scabrifolium* (#), *S. simplicissimum* ($), *S. sogarandinum* (%), *S. solisii* (&), *S. tuquerrense* (*), *S. ×blanco-galdosii* (+).

DISCUSSION

Previous taxonomic treatments suggested that ser. *Piurana* contained some of the morphologically most distinctive species in section *Petota* (Correll 1962; Hawkes 1990; Ochoa 1999). While this is certainly true for some of its representatives (e.g. *S. contumazaense*, *S. hypacrarthrum* [to possibly include *S. simplicissimum*]), and *S. peloquinianum*, our results show that many of the species are so similar as to be possibly conspecific. This was shown in a prior morphological and plastid DNA deletion analysis of *S. chomatophilum* and *S. jalcae* by Ames et al. (2007).

Replicated Analysis and Morphological Variation—The correlation value of the similarity matrices of replicates 1 and 2 (0.62) is identical to a study of members of ser. *Conicibaccata* done in the same location and time as our study (Fajardo et al. in press). The ANOVA analyses showed 22 characters to be significantly different between the two replicates, showing the variation of character states. Other taxonomic treatments of ser. *Piurana* (e.g. Correll 1962; Hawkes 1990; Ochoa 1999) relied heavily on the shape of the fruits and the texture of the leaves to define ser. *Piurana*. Most of the characters for fruits and leaves were stable between the two replicates. Spooner and Salas (2006) proposed that moniliform tubers helped to define ser. *Piurana*. While there is a concentration of moniliform tubers in the species we examined relative to the rest of sect. *Petota*, ANOVA analysis documented much variation within accessions for this trait. Multiple alleles have been detected for tuber shape in diploid cultivated potatoes by both qualitative and quantitative genetic analysis, with a major locus explaining 75% of the genetic variation (van Eck et al. 1994). However, there are no similar studies in wild potato species for moniliform tubers.

Interpretation of Multivariate Analysis—Four morphologically distinct groups were revealed by the CDA analysis (Fig. 6a). Group I contained the extremely similar species *S. hypacrarthrum* and *S. simplicissimum*. Ochoa (1999), however, placed these two very similar species in ser. *Piurana* and *Simplicissima* respectively. They are both are 2x(1ENB) species and sympatric, and we suspect that further studies will show them to be conspecific, meaning that we would interpret such minor differences to be part of variation within the species.

Our results also support morphologically coherent species status for *S. contumazaense* (Group II) and *S. peloquinianum* (Group III). *Solanum contumazaense* was originally assigned to ser. *Tuberosa* (Ochoa 1964) and later classified in ser. *Conicibaccata* (Hawkes 1990; Ochoa 1999; Table 1). *Solanum peloquinianum* was originally classified within ser. *Cuneoalata* (Ochoa, 1980) and maintained under that classification by Hawkes (1990) and Ochoa (1999). Under a phenetic morphological species concept (as defined by Sokal and Crovello 1970) where species are "dense regions of hyperdimentional space" (clustering of individuals in ordination analyses), we cannot maintain many of the other species. Regarding the 29 species in Group IV (Fig. 6b), six of them are morphologically distinctive (*S. acroglossum*, *S. cajamarquense*, *S. chancayense*, *S. chilliasense*, *S. immite,* and *S. marinasense*), while the remaining 23 species are difficult to distinguish. These multivariate results concur with our observations in the greenhouse during four months working daily with these species. Based on our observations, we predict that some of these species will be reduced to synonymy, similar to our results with *S. chomatophilum* and *S. jalcae* (above). Similar results showing the need to reduce the number of species have been shown in many groups in sect. *Petota* (Spooner and Salas 2006), such as extensive synonymy sure to occur in the *Solanum brevicaule* complex in the central Andes (van den Berg et al. 1998; Miller and Spooner 1999; Spooner et al. 2005).

Molecular support has been shown to be critical to provide insights into taxonomic patterns and processes elsewhere in sect. *Petota* that affect decisions on recognizing morphologically similar species distinguished only by polythetic support. For example, plastid DNA restriction site data have distinguished the morphologically very similar *S. cardiophyllum* Lindl. and *S. ehrenbergii* (Bitter) Rydb. (Rodríguez and Spooner 1997; Spooner et al. 2004). Nuclear RFLP's have sup-

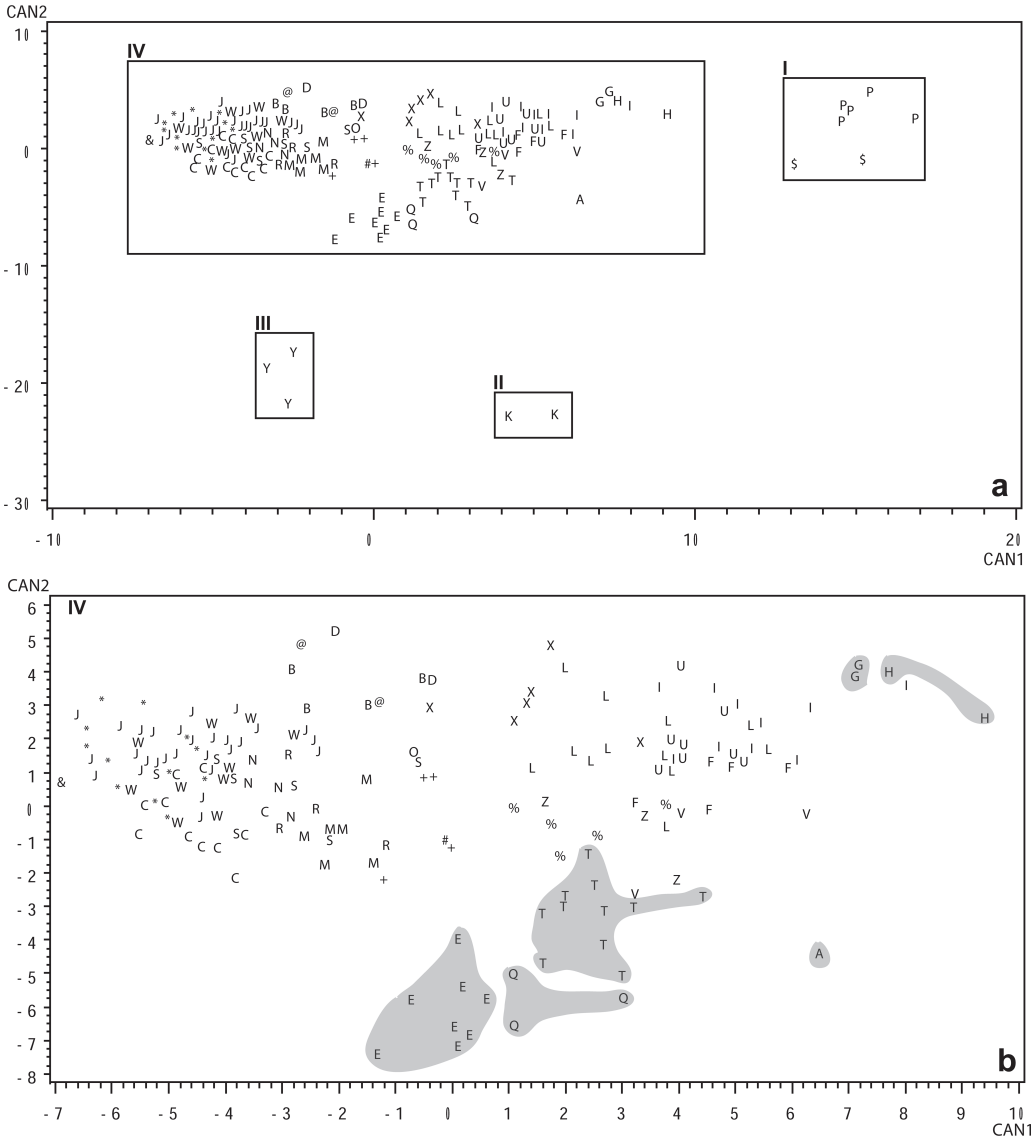

FIG. 6. Canonical discriminant analysis based on 56 morphological characters. Species codes as in Fig. 5. Figure 6a based on all taxa, rectangles highlight morphologically well defined groups I, II, III and IV. Figure 6b is an expansion only the taxa from group IV to highlight detail in the group; balloons highlight some of the better-defined species within group IV.

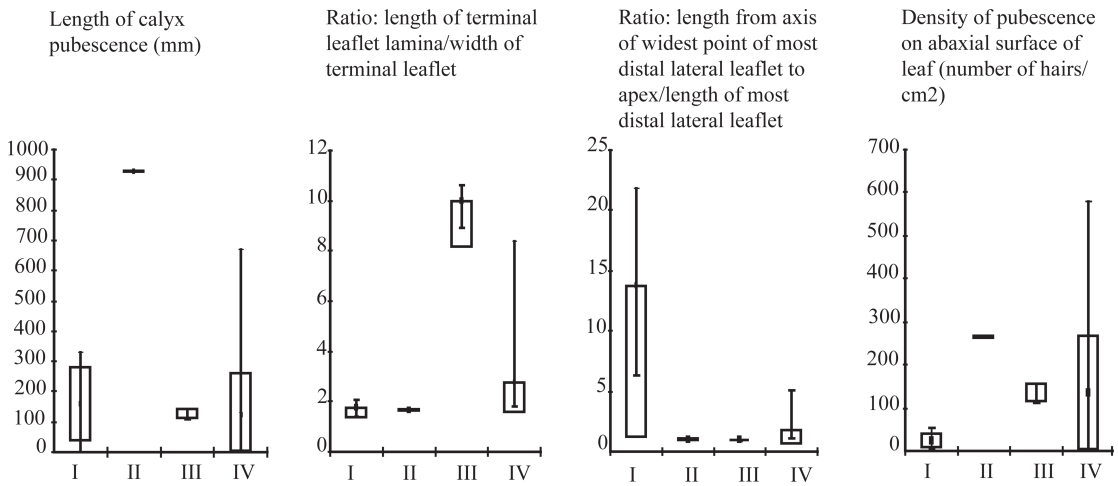

FIG. 7. Means, ranges, and one standard deviation of the mean for four of the most important of the 82 morphological characters (as determined by stepwise discriminant analysis) that distinguish Groups I-IV (Fig. 6a).

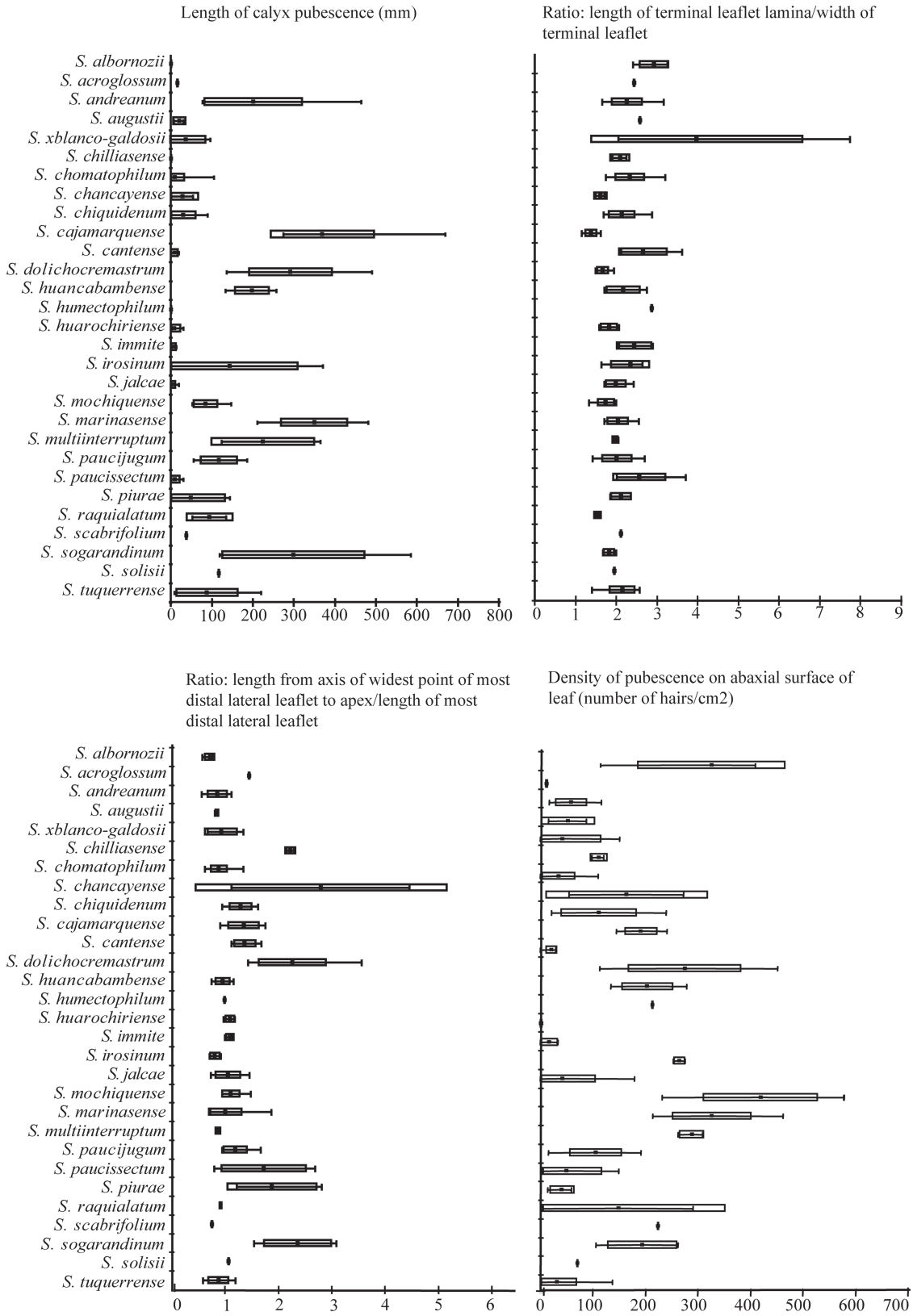

FIG. 8. Means, ranges, and one standard deviation of the mean for four of the most important of the 82 morphological characters (as determined by stepwise discriminant analysis) that distinguish species within group IV (Fig. 6b).

ported the hybrid origin of *S.* ×*rechei* Hawkes and Hjert. (Clausen and Spooner 1998). Microsatellites have helped resolve a long-standing dispute about the species boundaries in the cultivated potatoes (Spooner et al. 2007). Because of the great economic importance of wild potatoes for breeding we seek similar molecular insights and data from examination of herbarium specimens before making final taxonomic decisions on species boundaries and interspecific relationships.

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LITERATURE CITED

Ames, M., A. Salas, and D. M. Spooner. 2007. The discovery and phylogenetic implications of a novel 41 bp plastid DNA deletion in wild potatoes. *Plant Systematics and Evolution* 268: 159–175.

Castillo-T., R. and D. M. Spooner. 1997. Phylogenetic relationships of wild potatoes, *Solanum* series *Conicibaccata* (sect. *Petota*). *Systematic Botany* 22: 45–83.

Clausen, A. M. and D. M. Spooner. 1998. Molecular support for the hybrid origin of the wild potato species *Solanum* × *rechei*. *Crop Science* 38: 858–865.

Correll, D. S. 1962. The potato and its wild relatives. *Texas Research Foundation Botanical Studies* 4: 1–606.

ESRI-Inc. 2005. ArcGIS. Version 9.1. Redlands, California.

Fajardo, D., R. Castillo, A. Salas, and D. M. Spooner. 2008. A morphometric study of species boundaries of the wild potato *Solanum* series *Conicibaccata*: a replicated field trial in Andean Peru. *Systematic Botany* 33: 183–192.

Fritz, N. K. and R. E. Hanneman Jr. 1989. Interspecific incompatibility due to stylar barriers in tuber-bearing and closely related non-tuber-bearing Solanums. *Sexual Plant Reproduction* 2: 184–192.

Hawkes, J. G. 1990. *The potato: evolution, biodiversity and genetic resources*. London: Belhaven Press.

Miller, J. T. and D. M. Spooner. 1999. Collapse of species boundaries in the wild potato *Solanum brevicaule* complex (Solanaceae, *S*. sect. *Petota*): molecular data. *Plant Systematics and Evolution* 214: 103–130.

Ochoa, C. M. 1964. Nuevo *Solanum* tuberifero del Peru. *Anales Científicos Universidad Nacional Agraria Lima* 2: 148–151.

Ochoa, C. M. 1980. *Solanum peloquinianum*: a new wild potato species from the Peruvian Andes. *American Potato Journal* 57: 33–35.

Ochoa, C. M. 1999. *Las papas de Sudamerica: Peru (Parte I)*. Lima: International Potato Center.

Rodríguez-C., A. and D. M. Spooner. 1997. Chloroplast DNA analysis of *Solanum bulbocastanum* and *S. cardiophyllum*, and evidence for the distinctiveness of *S. cardiophyllum* subsp. *ehrenbergii* (sect. *Petota*). *Systematic Botany* 22: 31–43.

Rohlf, F. J. 1997. NTSYS-pc, numerical taxonomy and multivariate system. Version 2.0 New York: Exeter Software.

Royal Horticultural Society. 2001. *RHS colour chart*. London: Royal Horticultural Society.

Salas, A. R., D. M. Spooner, Z. Huamán, R. V. Torres Maita, R. Hoekstra, K. Schüler, and R. J. Hijmans. 2001. Taxonomy and new collections of wild potato species in central and southern Peru in 1999. *American Journal of Potato Research* 78: 197–207.

SAS Institute Inc. 2004. *SAS 9.1.3 Help and Documentation*. Cary, North Carolina: SAS Institute, Inc.

Sneath, P. H. A. and R. R. Sokal. 1973. *Numerical Taxonomy*. San Francisco: Freeman.

Sokal, R. R. and T. J. Crovello. 1970. The biological species concept: a critical evaluation. *American Naturalist* 104: 127–153.

Spooner, D. M. and R. Castillo-T. 1997. Reexamination of series relationships of South American wild potatoes (Solanaceae: *Solanum* sect. *Petota*): evidence from chloroplast DNA restriction site variation. *American Journal of Botany* 84: 671–685.

Spooner, D. M., R. Castillo-T., and L. E. López-J. 1993. Synonymy within wild potatoes (*Solanum* sect. *Petota*: Solanaceae): the case of *Solanum andreanum*. *Systematic Botany* 18: 209–217.

Spooner, D. M., K. McClean, G. Ramsay, R. Waugh, and G. J. Bryan. 2005. A single domestication for potato based on multilocus AFLP genotyping. *Proceedings of the National Academy of Sciences USA* 120: 14694–14699.

Spooner, D. M., J. Núñez, G. Trujillo, M. del Rosario Herrera, F. Guzmán, and M. Ghislain. 2007. Extensive simple sequence repeat genotyping of potato landraces supports a major reevaluation of their gene pool structure and classification. *Proceedings of the National Academy of Sciences USA* 104: 19398–19403.

Spooner, D. M. and A. Salas. 2006. Structure, biosystematics, and genetic resources. Pp. 1–39 in *Handbook of potato production, improvement, and post-harvest management*, eds. J. Gopal and S. M. P. Khurana. Binghampton, New York: Haworth's Press, Inc., pp 1–39.

Spooner, D. M., R. G. van den Berg, A. Rodríguez, J. Bamberg, R. J. Hijmans, and S. I. Lara Cabrera. 2004. Wild potatoes (*Solanum* section *Petota*; Solanaceae) of North and Central America. *Systematic Botany Monographs* 68: 1–209 + 9 plates.

van den Berg, R. G., J. T. Miller, M. L. Ugarte, J. P. Kardolus, J. Villand, J. Nienhuis, and D. M. Spooner. 1998. Collapse of morphological species in the wild potato *Solanum brevicaule* complex (sect. *Petota*). *American Journal of Botany* 85: 92–109.

van Eck, H. J., J. M. E. Jacobs, P. Stam, J. Ton, W. J. Stiekema, and E. Jacobsen. 1994. Multiple alleles for tuber shape in diploid potato detected by qualitative and quantitative genetic analysis using RFLPs. *Genetics* 137: 303–309.

Wyszecki, G. 1982. Color science: concepts and methods, quantitative data and formulae. New York: Wiley.

APPENDIX 1. Accessions of *Solanum* sect. *Petota* examined in this morphological study. Vouchers from greenhouse grown plants are deposited at the herbarium of the International Potato Center (CIP). Accession data are presented in the following order: [generalized map areas from Fig. 4] Species, collector code, Potato Genebank accession number, {locality information}. Final values of locality data represent latitude, longitude, and altitude.

[1] *S. andreanum* Baker, *Correll 491,* 247360, {COLOMBIA. Nariño, La Unión, Pasto, two km E of Santiago on the road to San Francisco. –77.150, 1.600. 1755 m.}. **[2] *S. andreanum,*** *Hawkes 2546,* 320345, {COLOMBIA. Putumayo, San Francisco, valley of Sibundoy, 1.5 km from Santiago on the road to Colón. –76.917, 1.200. 2104 m.}. **[2] *S. andreanum*,** *Colección Central Colombiana 5142,* 762677, {COLOMBIA. Putumayo, Sibundoy. –76.917, 1.200. 2104 m.}. **[2] *S. andreanum*,** *Colección Central Colombiana 5186,* 597668, {COLOMBIA. Putumayo, Sibundoy. –76.917, 1.200. 2104 m.}. **[3] *S. tuquerrense*** Hawkes, *Hawkes 2547,* 762711, {COLOMBIA. Nariño, Ospina, 103 km from Pasto and 30 km from Tuquerres on the road from Pasto to Ipiales, Finca Chautalán. –77.617, 1.083. 3009 m.}. **[4] *S. andreanum,*** *Castillo et al. 1226,* 567813, {COLOMBIA. Nariño, 7.4 km from La Victoria on road to San Jorge. –77.650, 0.700. 3239 m.}. **[4] *S. tuquerrense*,** *Colección Central Colombiana 5126,* 498177, {COLOMBIA. Nariño, Cuaspu de Cumbal. –77.783, 0.900. 3088 m.}. **[4] *S. tuquerrense*,** *Spooner et al. 5100,* 762805, {ECUADOR. Carchi, Tulcán, by houses at Hacienda Troya, 5.8 km E of main road from Tulcán-Quito, less than 1 km S of border with Colombia. –77.680, 0.730. 3230 m.}. **[5] *S. andreanum*,** *Spooner et al. 5101,* 762806, {ECUADOR. Huaca, Sucumbios, 0.5–1.9 km W of Town Square of Santa Bárbara on road to El Carmelo. –77.530, 0.650. 2533 m.}. **[5] *S. tuquerrense,*** *Spooner et al. 5111,* 561646, {ECUADOR. Imbabura, Ibarra, San Pablo del Lago, at Curiquinque, about 6 km E-SE of Ibarra, 17.0 km from main road from Ibarra-Tulcán to El Olivo (on road that passes Yuracruz). –78.067, 0.333. 3284 m.}. **[6] *S. tuquerrense*,** *Ochoa 13835,* 761834, {ECUADOR. Pichincha, Vicinity of Pichincha. 3400 m.}. **[6] *S. paucijugum*** Bitter, *Spooner et al. 5096a,* 583303, {ECUADOR. Pichincha, Mejía, Cotopaxi, in Parque Nacional Cotopaxi, 1.3 km E of center of fenced in deer enclosure at Estación Boliche. –78.633, 0.600. 890 m.}. **[6] *S. tuquerrense,*** *Spooner et al. 5022,* 561631, {ECUADOR. Pichincha, Quito, Nono. Mount Pichincha, on road to antennas, on W side of Quito, about antenna cluster. –78.533, 0.167. 1985 m.}. **[6] *S. tuquerrense*,** *Spooner et al. 5023,* 762788, {ECUADOR. Pichincha, Nono. Mount Pichincha, on road to antennas, on W side of Quito, about antenna cluster. –78.530, –0.170. 3870 m.}. **[7] *S. andreanum*,** *Spooner et al. 5126,* 561648, {ECUADOR. Napo, Quijos, Cosanga, about 2 hr walk W of Baeza-Tena Road, S of Río Bermejo, on farm of José Guaranda Guambi in Nueva Andalucía de Bermejo. –77.917, 0.533. 2761 m.}. **[7] *S. tuquerrense*,** *Spooner et al. 5118,* 763764, {ECUADOR. Napo, Oyacachi. Along Quito-Baeza Road, 7.2 km W of statue of Virgin at crest of sierra. –78.050, –0.220. 3720 m.}. **[8] *S. paucijugum,*** *Sleesman 5129,* 762810, {ECUADOR. Cotopaxi, Macachi, in Parque Nacional Cotopaxi, 10.5 km E of Proyecto Llamas Station 3610m. –78.500, –0.650. 3644 m.}. **[8] *S. paucijugum*,** *Sleesman 5094,* 762802, {ECUADOR. Cotopaxi, Cotopaxi, in Parque Nacional Cotopaxi, on N side of park road. –78.667, –0.600. 3460 m.}. **[8] *S. paucijugum*,** *Sleesman 5096b,* 762803, {ECUADOR. Cotopaxi, Cotopaxi, in Parque Nacional Cotopaxi, 1.3 km E of center of fenced in deer. –78.633, –0.600. 3630 m.}. **[8] *S. tuquerrense*,** *Spooner et al. 5098,* 762804, {ECUADOR. Cotopaxi, Cotopaxi, in Parque Nacional Cotopaxi, at km 6, about 200m N of Río Daule on park road to Mariscal Sucre. –78.650, –0.670. 3567 m.}. **[8] *S. tuquerrense*,** *Spooner et al. 5007,* 561628, {ECUADOR. Cotopaxi, Latacunga, Latacunga, on road from Quito to Latacunga, 8.1 km S of Pichinca-Cotopaxi Provinces; 5.3 km S

from entrance to Cotopaxi National Park, about 60m E of road. −78.667, 0.650. 730 m.}. **[8] *S. tuquerrense***, *Spooner et al. 5097,* 561645, {ECUADOR. Cotopaxi, Latacunga, in Parque Nacional Cotopaxi, at Km 6, about 200m N of Río Daule on park road to Mariscal Sucre. −78.650, 0.667. 605 m.}. **[9] *S. andreanum***, *Spooner et al. 5133,* 561658, {ECUADOR. Bolívar, Chimbo San Miguel de Bolívar, Loma Chuchi, by road to antennas of IETEL station, near El Tambo de Gobierno. −79.011, −1.681. 2466 m.}. **[9] *S. paucijugum,*** *Spooner et al. 5130,* 561651, {ECUADOR. Tungurahua, Ambato Simiatug, 30.5 km SE of Ambato on road to Guaranda, beginning at junction of road in Ambato, at Tamboloma. −78.770, −1.300. 3567 m.}. **[9] *S. solisii*** Hawkes, *Ochoa and Salas 10990,* 761161, {ECUADOR. Tungurahua, Tungurahua, vicinity of Río Yangahua. −78.430, −1.450. 3347 m.}. **[10] *S. paucijugum***, *Ochoa 13377,* 761597, {ECUADOR. Chimborazo, Quishuar. [coordinates unclear] 3200 m.}. **[10] *S. andreanum,*** *Spooner et al. 5153,* 570609, {ECUADOR. Morona Santiago, 13 km NW of San Vicente, on old footpath on S side of Río Upano. −78.420, −2.170. 2.946 m.}. **[10] *S. andreanum,*** *Spooner et al. 5155,* 561661, {ECUADOR. Morona Santiago, about 10 km NW of San Vicente, on old footpath on S side of Río Upano, on the way to San Vicente and Nueve de Octubre. −78.400, −2.167. 2946 m.}. **[10] *S. andreanum***, *Spooner et al. 5155,* 762818, {ECUADOR. Morona Santiago, about 10 km NW of San Vicente, on old footpath on S side of Río Upano. −78.400, −2.170. 2699 m.}. **[10] *S. paucijugum,*** *Ochoa 13371,* 761595, {ECUADOR. Chimborazo, Cubillín. −78.450, −1.830. 3475 m.}. **[10] *S. paucijugum,*** *Spooner et al. 5151,* 762816, {ECUADOR. Chimborazo, Palmira, 36 km from Guamote main N-S road on road to Atillo. −78.617, −2.083. 3600 m.}. **[10] *S. paucijugum***, *Spooner et al. 5071,* 762798, {ECUADOR. Chimborazo, Guaranda, 10.5 km W of San Juan, on road to Guaranda by Loma Tililog, on S side. −78.833, −1.633. 3725 m.}. **[10] *S. paucijugum***, *Spooner et al. 5084,* 762800, {ECUADOR. Chimborazo, Sicalpa, in Quebrada Camal, on N side of road from Sicalpa-Pallatanga. −78.800, −1.733. 3770 m.}. **[11] *S. chilliasense,*** *Spooner et al. 5057,* 567821, {ECUADOR. On Cordillera de Chilla, 1 km S of transmission antenna on top of Cerro Zharayunta, about 4 km SW of Chilla. −79.583, −3.483. 3275 m.}. **[11] *S. chilliasense*** Ochoa, *Ochoa 13350,* 761590, {ECUADOR. El Oro, Cordillera Chillia. −79.583, −3.467. 2699 m.}. **[12] *S. albornozii,*** *Spooner et al. 5030,* 561635, {ECUADOR. Loja, Catamayo, Catamayo, 300–500m S of old road from Loja-Catamayo, about 2 km W of junction with road to Duraznillo. −79.283, −4.000. 2431 m.}. **[12] *S. albornozii,*** *Spooner et al. 5032,* 561636, {ECUADOR. Loja, Catamayo, Catamayo, on old road from Loja to Catamayo, on S slope of Cerro Villonaco, at junction of road to Duraznillo. −79.267, −4.000. 2362 m.}. **[12] *S. albornozii,*** *Spooner et al. 5033,* 561637, {ECUADOR. Loja, Catamayo, 3.6 km SW (on way to Loja), of junction of old Loja-Catamayo road and road to Duraznillo. −79.250, −4.000. 2364 m.}. **[12] *S. albornozii*** **Correll,** *Ochoa and Salas 11007,* 761164, {ECUADOR. Loja, Loja, Km 15 road Loja to Catamayo. −79.220, −4.000. 2165 m.}. **[13] *S. piurae*** **Bitter,** *Ochoa and Salas 11615,* 761072, {PERU. Piura, Ayabaca, Pampa de Lirio. −79.717, −4.633. 2600 m.}. **[13] *S. raquialatum*** **Ochoa,** *Ochoa 13947,* 761863, {PERU. Piura, Ayabaca, Puclus Alto. −79.717, −4.633. 3100 m.}. **[14] *S. raquialatum***, *Ochoa 13950,* 761864, {PERU. Piura, Ayabaca, Maray. −79.950, −4.967. 2600 m.}. **[15] *S. huancabambense*** **Ochoa,** *Huamán 966,* 760955, {PERU. Piura, Huancabamba, Huancabamba Km 22 on road Huancabamba to Canchaque. −79.498, −5.248. 2406 m.}. **[15] *S. huancabambense***, *Ochoa 11619,* 761238, {PERU. Piura, Huancabamba, Huancabamba. −79.458, −5.089. 2908 m.}. **[15] *S. huancabambense,*** *Ochoa 11626,* 761239, {PERU. Piura, Huancabamba, Maraypampa. −79.580, −5.600. 2156 m.}. **[15] *S. huancabambense***, *Ochoa 11627,* 761240, {PERU. Piura, Huancabamba, Huancabamba. −79.458, −5.089. 2909 m.}. **[15] *S. huancabambense***, *Ochoa and Salas 14815,* 762123, {PERU. Piura, Huancabamba, Totoral. −79.630, −5.190. 1275 m.}. **[15] *S. mochiquense*** **Ochoa,** *Ochoa and Salas 20,* 760009, {PERU. Piura, Huancabamba, Huancabamba, Cerro Mishihuaca near Canchaque. −79.584, −5.359. 1767 m.}. **[15] *S. paucissectum*** Ochoa, *Huamán 974,* 760956, {PERU. Piura, Huancabamba, Huancabamba, Sondorillo, Ciénago Largo. −79.475, −5.358. 2809 m.}. **[15] *S. paucissectum***, *Ochoa 11628,* 761241, {PERU. Piura, Huancabamba, Cashcapampa. −79.440, −5.350. 2198 m.}. **[15] *S. paucissectum***, *Ochoa 11633,* 761246, {PERU. Piura, Huancabamba, Cuello del Indio. −79.550, −5.210. 3146 m.}. **[15] *S. paucissectum***, *Ochoa and Salas 14816,* 762124, {PERU. Piura, Huancabamba, Los Canganes. −79.452, −5.244. 3200 m.}. **[15] *S. paucissectum***, *Ochoa and Salas 14817,* 762125, {PERU. Piura, Huancabamba, Los Canganes. −79.452, −5.244. 3200 m.}. **[15] *S. paucissectum***, *Ochoa and Salas 14818,* 762126, {PERU. Piura, Huancabamba, Los Canganes. −79.452, −5.244. 3200 m.}. **[15] *S. piurae***, *Huamán 964,* 760953, {PERU. Piura, Huancabamba, Huancabamba, Culín hill, Hills of Huancabamba. −79.458, −5.089. 2909 m.}. **[15] *S. piurae***, *Ochoa 13959,* 761868, {PERU. Piura, Huancabamba, Cerro Michiwaca. −79.452, −5.244. 2600 m.}. **[16] *S. chomatophilum*** **Bitter,** *Ochoa 11061,* 761173, {PERU. Amazonas, Luya, Cutra Cuello. −77.980, −6.140. 2782 m.}. **[16] *S. chomatophilum***, *Ochoa 1664,* 760057, {PERU. Amazonas, Chachapoyas, Cerro Tinaja, near Chachapoyas. −77.850, −6.217. 2247 m.}. **[16] *S. chomatophilum***, *Ochoa and Salas 42* 760911, {PERU. Amazonas, Cerro Canal, S of Cerro Campanario. −77.400, −6.333. 2864 m.}. **[16] *S. humectophilum*** Ochoa, *Ochoa 11753,* 761052, {PERU. Amazonas, Chachapoyas, Convento. −77.580, −6.230. 2566 m.}. **[17] *S. chomatophilum***, *Ochoa and Salas 71,* 760913, {PERU. Amazonas, Pomacocha, between Leimebamba and Calla-Calla. −77.783, −6.683. 2525 m.}. **[18] *S. chiquidenum,*** *Ochoa and Salas 12568,* 762574, {PERU. Cajamarca, Hualgayoc. −78.630, −6.800. 3885 m.}. **[18] *S. chiquidenum***, *Ochoa and Salas 15240,* 762263, {PERU. Cajamarca, Cutervo, La Ramada. −78.580, −6.260. 2088 m.}. **[18] *S. chiquidenum*** **Ochoa,** *Ochoa and Salas 12566,* 762573, {PERU. Cajamarca, Hualgayoc, Colquerumi. −78.630, −6.800. 3885 m.}. **[18] *S. chomatophilum,*** *Ochoa 13199,* 761541, {PERU. Cajamarca, Hualgayoc, Quinuapampa. −78.630, −6.659. 3553 m.}. **[18] *S. chomatophilum***, *Ochoa 13204,* 761546, {PERU. Cajamarca, Chota, Cerro Calvario. −78.300, −6.480. 1797 m.}. **[18] *S. chomatophilum***, *Ochoa 13212,* 761551, {PERU. Cajamarca, Cajamarca, Silleropata. −78.620, −6.620. 3217 m.}. **[18] *S. chomatophilum***, *Ochoa and Salas 12570,* 762575, {PERU. Cajamarca, Hualgayoc, Mina Carolina. −78.617, −6.767. 3808 m.}. **[18] *S. irosinum*** **Ochoa,** *Ochoa 11640,* 761252, {PERU. Cajamarca, Chota, Cerro Iros. −78.720, −6.420. 2674 m.}. **[18] *S. irosinum***, *Ochoa 11667,* 761254, {PERU. Cajamarca, Cutervo, El Remate. −78.750, −6.270. 2829 m.}. **[18] *S. irosinum***, *Ochoa and Salas 15210,* 762257, {PERU. Cajamarca, Cutervo, Coronilla. −78.750, −6.270. 2829 m.}. **[18] *S. irosinum***, *Ochoa and Salas 15225,* 762259, {PERU. Cajamarca, Cutervo, Laurel. −78.750, −6.270. 2829 m.}. **[19] *S. ×blanco-galdosii*** **Ochoa,** *Ochoa 10673,* 762524, {PERU. Cajamarca, San Marcos, Pencalca, El Mirador. −78.217, −7.183. 3755 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16118,* 762616, {PERU. Cajamarca, Cajamarca, Marcos. −78.580, −6.930. 3819 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16119,* 762617, {PERU. Cajamarca, Cajamarca, Marcos. −78.580, −6.930. 3819 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16121,* 762619, {PERU. Cajamarca, Cajamarca, Chupacatayo. −78.520, −7.250. 2682 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16122,* 762620, {PERU. Cajamarca, Cajamarca, Chupacatayo. −78.520, −7.250. 2682 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16123,* 762621, {PERU. Cajamarca, Cajamarca, Chupacatayo. −78.520, −7.250. 2682 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16124,* 762622, {PERU. Cajamarca, Cajamarca, Chupacatayo. −78.520, −7.250. 2682 m.}. **[19] *S. cajamarquense,*** *Ochoa and Salas 16241,* 763011, {PERU. Cajamarca, Contumazá, Shillar along the route Contumazá - Chilete, on rocky slopes and among large colonies of columnar cactus and Lupinus. −78.817, −7.367. 2578 m.}. **[19] *S. cajamarquense*** **Ochoa,** *Ochoa and Salas 16063,* 762608, {PERU. Cajamarca, Cajamarca, El Potrero. −78.330, −7.120. 2981 m.}. **[19] *S. chiquidenum***, *Ochoa 13963,* 761870, {PERU. Cajamarca, Contumazá, Cajon. −78.765, −6.991. 3033 m.}. **[19] *S. chiquidenum***, *Ochoa and Salas 11059,* 761069, {PERU. Cajamarca, Contumazá, Cerro Chungarrán. −78.900, −7.380. 2544 m.}. **[19] *S. chomatophilum,*** *CORP 862,* 266387, {PERU. Cajamarca, Cajamarca, near the entrance to Hacienda Porcón. −78.583, −7.084. 3204 m.}. **[19] *S. chomatophilum***, *Hawkes 2433,* 310990, {PERU. Cajamarca, Cajamarca, Cajamarca, Hacienda Porcón. −78.583, −7.083. 3240 m.}. **[19] *S. chomatophilum***, *Ochoa 13208,* 761549, {PERU. Cajamarca, Celendín, Tablacucho. −78.230, −6.930. 3014 m.}. **[19] *S. chomatophilum***, *Ochoa and Salas 12561,* 762569, {PERU. Cajamarca, Celendín, Piedra Grande. −78.220, −6.930. 3074 m.}. **[19] *S. chomatophilum***, *Ochoa and Salas 16060,* 763609, {PERU. Cajamarca, Cajamarca, Sinsi. −78.517, −7.167. 2845 m.}. **[19] *S. chomatophilum***, *Ugent 5416,* 310943, {PERU. Cajamarca, Cajamarca, Cajamarca, Hacienda Porcón. −78.583, −7.083. 3240 m.}. **[19] *S. contumazaense*** Ochoa, *Ochoa 14751,* 762118, {PERU. Cajamarca, Contumazá, Guzmango, Cerro Chungarrán. −78.900, −7.380. 2546 m.}. **[19] *S. jalcae*** **Ochoa,** *Ochoa 1512,* 243340, {PERU. Cajamarca, Cajamarca, Cajamarca, Hacienda Porcón. −78.580, −7.080. 3191 m.}. **[19] *S. jalcae***, *Ochoa and Salas 16021,* 763601, {PERU. Cajamarca, Cajamarca, China Linda. −78.517, −7.167. 2844 m.}. **[19] *S. jalcae***, *Ochoa and Salas 16060a,* 763610, {PERU. Cajamarca, Cajamarca, near the entrance to Hacienda Porcón. −78.517, −7.167. 2844 m.}. **[19] *S. mochiquense***, *Ochoa 10728a,* 762989, {PERU. Cajamarca, Cajamarca, Cuesta del Cumbe. −78.550, −7.300. 1761 m.}. **[19] *S. mochiquense***, *Ochoa and Salas 15993,* 762637, {PERU. Cajamarca, Contumazá, Río Andaloy. −78.870, −7.380. 2480 m.}. **[19] *S. mochiquense***, *Ochoa and Salas 16232,* 763002, {PERU. Cajamarca, Contumazá. **[20] *S. chiquidenum***, *Ochoa and Salas 12543,* 762553, {PERU. Cajamarca, Cajabamba, San Nicolás. −78.030, −7.670. 3064 m.}. **[20] *S. chomatophilum***, *Ochoa 11755,* 761271, {PERU. La Libertad, Huamachuco, Pampa de Cóndor. −77.860, −7.790. 3503 m.}. **[20] *S. chomatophilum***, *Ochoa 13288,* 761577, {PERU. La Libertad, Sánchez Carrión, Aricapampa. −77.720, −7.806. 2620 m.}. **[20] *S. chomatophilum***, *Ochoa 13325,* 761582, {PERU. La

Libertad, Pataz, between Gachil and Urpay. –77.590, –7.880. 2214 m.}. **[20] *S. chomatophilum***, *Salas et al. 7327,* 762946, {PERU. La Libertad, Sánchez Carrión, growing at a local place called Macullada, located 14 km S of Molina Viejo, on the road to Huamachuco to Pataz. –77.814, –7.767. 3574 m.}. **[20] *S. multiinterruptum* Bitter,** *Salas et al. 7325,* 762944, {PERU. La Libertad, Sánchez Carrión, growing at a local place called Casasbambul, localed 13 km S of Molino Viejo on the road to Huamachuco to Pataz. –77.783, –7.778. 3924 m.}. **[21] *S. chiquidenum,*** *Ochoa and Salas 14482,* 762052, {PERU. La Libertad, Otuzco, Cerro Songo. –78.64, –7.905. 2630 m.}. **[21] *S. chiquidenum***, *Ochoa and Salas 14487,* 762056, {PERU. La Libertad, Otuzco, Cerro Songo. –78.64, –7.905. 2630 m.}. **[21] *S. chiquidenum***, *Salas et al. 7321,* 762940, {PERU. La Libertad, Santiago de Chuco, on Montana La Botica, ca. 600m uphill walk from the town of Cachiquidán. –78.144, –8.091. 2990 m.}. **[21] *S. chiquidenum***, *Salas et al. 7331,* 762950, {PERU. La Libertad, Julcán, growing at a local place called Chorro Blanco, located 1 km E of community of Victor Julio Roselle, SW of Corrapaldy Chico. –78.436, –8.041. 3599 m.}. **[21] *S. chomatophilum***, *Ochoa and Salas 14485,* 762054, {PERU. La Libertad, Otuzco, Cerro Songo. –78.0, –7.905. 2630 m.}. **[21] *S. chomatophilum***, *Ochoa and Salas 14486,* 762055, {PERU. La Libertad, Otuzco, Cerro Songo. –78.0, –7.905. 2630 m.}. **[21] *S. chomatophilum***, *Salas et al. 7317,* 762936, {PERU. La Libertad, Santiago de Chuco, growing in the "jalcas" (páramo) 9.8 km E of town of Sanro (below Mt. Sanro), in between Motil and Shorey, 200–300 m N of road, among rocks. –78.364, –7.987. 3555 m.}. **[21] *S. chomatophilum***, *Salas et al. 7320,* 762939, {PERU. La Libertad, Santiago de Chuco, 22.5 km from the police station in Shorey on the road to Santiago de Chuco. –78.270, –8.142. 3125 m.}. **[21] *S. chomatophilum***, *Salas et al. 7323,* 762942, {PERU. La Libertad, Santiago de Chuco, growing at Laguna de Torro, under the two overhangin caves on N side of road, 11 km E and N of Quiruvilca on the road to Huamachuco. –78.249, –7.986. 4009 m.}. **[21] *S. immite* Dunal,** *Ochoa and Salas 14491,* 762059, {PERU. La Libertad, Otuzco, Pichullo. –78.64, –7.905. 2630 m.}. **[21] *S. immite***, *Salas et al. 7315,* 762934, {PERU. La Libertad, Otuzco, growing at a local place called La Cascada, located ca 100 m down the road by the big waterfall, 3.1 km S of road from Trujillo to Otuzco and the road to Yamobamba. –78.600, –7.940. 2334 m.}. **[21] *S. jalcae***, *Salas et al. 7316,* 762935, {PERU. La Libertad, Otuzco, growing in the "jalcas" (paramo) 1 km W of town of Sanro (below Mt. Sanro), in between Motil and Shorey, 200–300 m S of road, among rocks. –78.438, –7.996. 3514 m.}. **[21] *S. jalcae***, *Salas et al. 7322,* 762941, {PERU. La Libertad, Santiago de Chuco, growing at Laguna de Torro, by roadside and away fom road, 11 km E and N of Quiruvilca on the road to Huamachuco. –78.249, –7.986. 4009 m.}. **[21] *S. sogarandinum* Ochoa,** *Ochoa 1440,* 762987, {PERU. La Libertad, Santiago de Chuco, Sogarandá, near Santiago de Chuco. –78.183, –8.150. 3550 m.}. **[21] *S. sogarandinum***, *Salas et al. 7332,* 762951, {PERU. La Libertad, Julcán, growing around 1 km NE of Canduall. –78.492, –8.129. 3064 m.}. **[22] *S. mochiquense***, *Ochoa 1822,* 760103, {PERU. La Libertad, Trujillo, Cerro Campana. –79.033, –8.117. 400 m.}. **[22] *S. mochiquense***, *Ochoa and Salas 14870,* 761037, {PERU. La Libertad, Trujillo, Cerro Campana. –79.030, –8.120. 400 m.}. **[23] *S. mochiquense***, *Erwin Baur Sortiment Genebank 2764,* 338616, {PERU. La Libertad, Trujillo, Virú, Cerro La Pileta. –78.750, –8.420. 72 m.}. **[24] *S. ×blanco-galdosii***, *Salas et al. 7339,* 762958, {PERU. La Libertad, Pataz, growing at a local place called Cruz Pata, located 2 km S of Huancaspata. –77.286, –8.470. 3208 m.}. **[24] *S. chomatophilum***, *Salas et al. 7341,* 762960, {PERU. La Libertad, Pataz, growing at a local place called Punya, located ca 30 km N of Huacaspata near the road. –77.306, –8.402. 3989 m.}. **[25] *S. ×blanco-galdosii,*** *Ochoa 13009,* 761466, {PERU. Ancash, Sihuas, Santa Rosa. –77.617, –8.483. 4136 m.}. **[25] *S. chomatophilum***, *Hawkes 2417,* 762649, {PERU. Ancash, Pallasca, Near Consuzo, Cerro Huaura, minas de Huaura, San Luis. –78.017, –8.250. 4000 m.}. **[25] *S. multiinterruptum***, *Ochoa 12066,* 761432, {PERU. Ancash, Sihuas, Recuay, Sicsipampa. –77.600, –8.633. 3172 m.}. **[25] *S. peloquinianum* Ochoa,** *Ochoa 13231,* 761555, {PERU. Ancash, Huaylas, Huaylas. –77.900, –8.870. 2734 m.}. **[25] *S. peloquinianum***, *Salas et al. 7336,* 762955, {PERU. Ancash, Corongo, growing at a local place called Tres Cruces, located 24.9 km N of Yuramarca, 100 m below the road. –77.909, –8.704. 2210 m.}. **[25] *S. peloquinianum***, *Salas et al. 7337,* 762956, {PERU. Ancash, Corongo, growing at a local place called Palillo, located 9.6 km NE of Tres Cruces, 100 m above the road. –77.886, –8.646. 2571 m.}. **[25] *S. sogarandinum***, *Ochoa 13006,* 761465, {PERU. Ancash, Sihuas, Cerro Huinjirca. –77.620, –8.580. 3145 m.}. **[25] *S. sogarandinum***, *Ochoa and Salas-54,* 760018, {PERU. Ancash, Acrana. –77.850, –8.267. 3500 m.}. **[26] *S. chomatophilum***, *Salas et al. 7347,* 762966, {PERU. Ancash, Yungay, at Yurac Corral (Huischa), 18.8 km E of park entrance into Parque Nacional Llanganuco, 11.0 km NE of NE end of the second part of Laguna Llanganuco on the rod to Piscobamba. –77.594, –9.048. 3800 m.}. **[26] *S. dolichocremastrum* Bitter,** *Ochoa 12074,* 761439, {PERU. Ancash, Antonio Raymondi, Chacas, near Llamellín. –77.062, –9.104. 4331 m.}. **[26] *S. dolichocremastrum***, *Ochoa and Salas 16205,* 763621, {PERU. Ancash, Carhuaz, Cuesta de Ulta heading up from Ulta toward Punta Olimpica on the road to Chacas. –77.633, –9.267. 3750 m.}. **[26] *S. dolichocremastrum***, *Ochoa and Salas 16207,* 763623, {PERU. Ancash, Carhuaz, cuesta de Ulta heading up from Ulta toward Punta Olímpica on the road to Chacas. –77.633, –9.267. 3900 m.}. **[26] *S. dolichocremastrum***, *Ochoa and Salas 16208,* 763624, {PERU. Ancash, Carhuaz, cuesta de Ulta heading up from Ulta toward Punta Olímpica on the road to Chacas. –77.633, –9.267. 3900 m.}. **[26] *S. dolichocremastrum***, *Ochoa and Salas 16209,* 762998, {PERU. Ancash, Carhuaz, cuesta de Ulta heading up from Ulta toward Punta Olímpica on the road to Chacas. –77.633, –9.267. 3900 m.}. **[26] *S. dolichocremastrum***, *Salas et al. 7351,* 762970, {PERU. Ancash, Carhuaz, growing at a local place called Ulta, 25.2 km E of Chilla. –77.531, –9.126. 4150 m.}. **[27] *S. augustii* Ochoa,** *Ochoa and Salas 12596,* 762631, {PERU. Ancash, Huaraz, Chamlla. –77.838, –9.680. 3774 m.}. **[27] *S. dolichocremastrum***, *Ochoa and Salas 16218,* 763632, {PERU. Ancash, Recuay, Ayamachay near km 31 on the Cátac-Chavín road, about 5 km before the entrance to the Cawish tunnel toward Chavín. –77.467, –9.717. 4000 m.}. **[27] *S. huarochiriense* Ochoa,** *Ochoa 11699,* 761265, {PERU. Ancash, Aija, Huayán. –77.730, –9.870. 2057 m.}. **[27]** *S. hypacrarthrum* **Bitter,** *Ochoa 11692,* 761259, {PERU. Ancash, Aija, Huayán. –77.730, –9.870. 2056 m.}. **[27] *S. immite***, *Ochoa 11689,* 761040, {PERU. Ancash, Aija, Cotup. –77.720, –9.820. 2898 m.}. **[27] *S. multiinterruptum***, *Ochoa and Salas-27,* 762995, {PERU. Ancash, Aija, Huamanwilca above Huayán. –77.720, –9.817. 2981 m.}. **[28] *S. augustii***, *Ochoa and Salas 12602,* 762633, {PERU. Ancash, Huaraz. –77.533, –9.533. 3045 m.}. **[28] *S. dolichocremastrum***, *Ochoa 12071,* 761043, {PERU. Ancash, Huari, Huari, Tambillo, before the bridge on the Cahuish river. –77.033, –9.400. 3543 m.}. **[28] *S. dolichocremastrum***, *Ochoa 12072,* 761437, {PERU. Ancash, Huari, Huari, Tambillo. –77.033, –9.400. 3542 m.}. **[28] *S. dolichocremastrum***, *Ochoa 13013,* 761470, {PERU. Ancash, Huari, San Marcos, in route from San Luis. –77.233, –9.517. 4000 m.}. **[28] *S. dolichocremastrum***, *Ochoa and Salas 16202,* 763618, {PERU. Ancash, Recuay, Kenuacuto at km 40on the Cátac-Chavín road, past the Cawish tunnel toward Chavín, among large rocks and borders of Polylepis. –77.467, –9.717. 4100 m.}. **[28] *S. dolichocremastrum***, *Salas et al. 7353,* 762972, {PERU. Ancash, Recuay, 31.0 Km from the main Lima-Huaraz road at Cátac, on the road to Chavín de Huántar, along the N side of the road, 6.8 km before reaching Paso Cahuich (at the tunnel through the mountains). –77.276, –9.699. 4200 m.}. **[28] *S. sogarandinum***, *Ochoa 13013a,* 761471, {PERU. Ancash, Huari, San Marcos. –77.230, –9.520. 4200 m.}. **[29] *S. scabrifolium* Ochoa,** *Ochoa and Salas 60,* 760020, {PERU. Huánuco, Huamalíes, Llata. –76.783, –9.417. 2831 m.}. **[30] *S. acroglossum* Juz.,** *Ochoa and Salas 11297,* 761070, {PERU. Pasco, Pasco, Pampania. –76.080, –10.670. 4321 m.}. **[30] *S. chomatophilum***, *Ochoa 13367a,* 763277, {PERU. Pasco [no additional data]. **[31] *S. chancayense***, *Ochoa and Salas 11250,* 761180, {PERU. Lima, Chancay, Lomas de Lachay. –77.380, –11.300. 568 m.}. **[31] *S. chancayense* Ochoa,** *Erwin Baur Sortiment Genebank 2807,* 338615, {PERU. Lima, Huaral, Lachay, Teatinos. –77.383, –11.350. 308 m.}. **[31] *S. mochiquense***, *Gross-Lusewitz Genebank Germany 127/1,* 498411, {PERU. Lima, Chancay, Lomas de Lachay. –77.383, –11.350. 308 m.}. **[32] *S. cantense***, *Salas et al. 7370,* 762888, {PERU. Lima, Canta, Huaytana, 5 km walk NE of Canta on the path to Antura. –76.661, –11.608. 2854 m.}. **[32] *S. cantense***, *Salas et al. 7372,* 762890, {PERU. Lima, Canta, Ugones, 4km NE of square of Canta town on the road to Huaros. –76.622, –11.478. 2975 m.}. **[32] *S. cantense***, *Salas et al. 7382,* 762900, {PERU. Lima, Huarochirí, roadside 30 Km NE of Santa Eulalia on the road to Millo. –76.608, –11.746. 3000 m.}. **[32] *S. cantense* Ochoa,** *Salas et al. 7368,* 762886, {PERU. Lima, Canta, Pallacusco 4 km walk E of Arahuay on a foot path to Cerro Putaca. –76.659, –11.623. 2895 m.}. **[32] *S. huarochiriense***, *Salas et al. 7388,* 762906, {PERU. Lima, Huarochirí, roadside 67.6 Km NE of Santa Eulalia NE of Millo on the road to Huancayo vía Millo. –76.395, –11.605. 3940 m.}. **[32] *S. hypacrarthrum***, *Ochoa 11607,* 473477, {PERU. Lima, Canta, Vicinity of Canta. –76.641, –11.494. 28554 m.}. **[32] *S. hypacrarthrum***, *Ochoa and Salas 11308,* 761204, {PERU. Lima, Canta, Cuesta Huamantanga. –76.750, –11.500. 3377 m.}. **[32] *S. hypacrarthrum***, *Ochoa and Salas 14715,* 762104, {PERU. Lima, Canta, Cuesta Huamantanga. –76.750, –11.500. 3377 m.}. **[32] *S. simplicissimum* Ochoa,** *Ochoa and Salas 15147,* 762233, {PERU. Lima, Canta km. 89 Lima-Canta. –76.624, –11.467. 2600 m.}. **[32] *S. simplicissimum***, *Salas et al. 7378,* 762900, {PERU. Lima, Huaral, NW of the road, 11.4 km NE of Acos, on the road to Pacaraos, about 50 m NE bridge crossing Chancay river. –76.737, –11.260. 2075 m.}. **[33] *S. cantense***, *Ochoa and López Camarena 14828,* 762130, {PERU. Lima, Huarochirí, Collata. –76.233, –12.150. 2974 m.}. **[33] *S. huarochiriense***, *Ochoa 11325,* 761215, {PERU. Lima, Huarochirí, Huarochirí. –76.230, –12.150. 2892 m.}. **[33] *S. huarochiriense***,

Salas et al. 7311, 762930, {PERU. Lima, Huarochirí, growing at a local place called Pacomanta (on the department map but no one living here now), 8 km E of the small village of Izcomarca. –76.300, –12.194. 3875 m.}. **[33]** ***S. hypacrarthrum***, *Ochoa and Salas 14731,* 762111, {PERU. Lima, Huarochirí, Río Huaricanchi. –76.233, –12.150. 2300 m.}. **[33]** ***S. multiinterruptum***, *Ochoa and Salas-36,* 760859, {PERU. Lima, Yauyos, Yauyos, Calchín-Anayán. –75.894, –12.443. 3451 m.}. **[34]** ***S. marinasense*** **Vargas,** *Ochoa and Ortega 14417,* 762051, {PERU. Cusco, Calca, Ruinas de Pisac . –71.850, –13.430. 3350 m.}. **[34]** ***S. marinasense***, *Ochoa 13620,* 761678, {PERU. Cusco, Paucartambo, Paucarpata. –71.500, –13.433. 3639 m.}. **[34]** ***S. marinasense***, *Spooner and Salas 7209,* 762828, {PERU. Cusco, from the Universidad Nacional San Antonio de Cusco on the S side of the town of Cusco, E of main road through town, drive up road going toward Hacienda Kaira San Gerónimo to km 7.5. –71.876, –13.592. 3533 m.}. **[35]** ***S. marinasense***, *Ochoa 13673,* 761714, {PERU. Apurímac, Cotabambas, between Cole and Colesniyoc. –72.220, –13.800. 4289 m.}. **[35]** ***S. marinasense***, *Ochoa 13689,* 761731, {PERU. Apurimac, Cotabambas, Durasnuchayoc. –72.180, –13.850. 4343 m.}. **[36]** ***S. marinasense,*** *Ochoa 14384,* 762024, {PERU. Apurímac, Abancay, Casinchihua. –73.030, –13.880. 2115 m.}. **[36]** ***S. marinasense***, *Ochoa 13608,* 761669, {PERU. Apurímac, Abancay, Tinyayopacta. –73.080, –13.800. 3900 m.}. **[36]** ***S. marinasense***, *Ochoa 13738,* 761775, {PERU. Apurímac, Grau, Maltapay . –72.707, –14.102. 3400 m.}. **[36]** ***S. marinasense***, *Ochoa 13748,* 761783, {PERU. Apurímac, Grau, Puysho. –72.583, –14.083. 3320 m.}. **[36]** ***S. marinasense***, *Ochoa 14386,* 762026, {PERU. Apurímac, Aymaraes, Río Pachaconas. –73.130, –14.200. 2638 m.}. **[37]** ***S. marinasense***, *OCHB 15687,* 762390, {PERU. Cusco, Acomayo, Luruchayocc. –71.436, –14.393. 3400 m.}. **[–]** ***S. ×blanco-galdosii***, *Ochoa 5169,* 442702, {PERU}. **[–]** ***S. contumazaense***, *Salas 089B,* —, {PERU}. ***S. huancabambense***, *Gross-Lusewitz Genebank Germany 155/1,* 498413, {PERU}. **[–]** ***S. jalcae***, *Ochoa and Salas 16036a,* 763602, {PERU}. **[–]** ***S. tuquerrense***, —, 546033, {—}.

APPENDIX 2. Morphological characters and character states used in the phenetic studies. All measurements are in cm unless otherwise stated.

Tuber Characters—1. Tuber type (1) moniliform [Fig. 3J-L], (2) at the end of the stolon, (3) elongated swellings along the stolon [Fig. 3I] 2. Tuber length × width. 3. Tuber length. 4. Number of eyes on tuber. 5. Ratio: tuber weight per plant (gr)/number of tubers. 6. Number of tubers. 7. Tuber primary skin color [see Materials and Methods for color codes here and below] 8. Tuber flesh color. 9. Tuber eye color. 10. Tuber secondary skin color [minor color when there are 2 colors].

Stem Characters—11. Diameter of stem at the middle part of the plant. 12. Stem color (1) green, (2) green mottled with purple, (3) purple. 13. Stem morphology (1) circular, (2) polygonal, (3) triangular. 14. Width of stem wings. 15. Plant height.

Leaf Characters (from leaves taken at the middle of flowering plants)—16. Length of leaf. 17. Length of terminal leaflet lamina. 18. Length of petiolule of terminal leaflet lamina. 19. Number of pairs of lateral leaflets. 20. Number of primary interstitial leaflets. 21. Number of secondary interstitial leaflets. 22. Margin of leaflets (1) straight, (2) undulate, (3) sinuate. 23. Width of terminal leaflet 5 mm from apex. 24. Shape of terminal leaflet base: (1) equilateral, (2) attenuate, (3) auriculate, (4) cordate, (5) cuneate, (6) hastate, (7) oblique, (8) rounded, (9) sagittate, (10) truncate. 25. Number of interstitial leaflets at base of terminal leaflet. 26. Length of petiolule of the most distal lateral leaflet. 27. Length of the largest interstitial leaflet. 28. Length of widest point of the most distal lateral leaflet. 29. Length of the most distal lateral leaflet. 30. Width of most distal lateral leaflet 5 mm from apex. 31. Width of decurrent tissue on the basiscopic side the most distal lateral leaflet measured 5 mm below the insertion point of leaflet lamina on the petiolule. 32. Distance between apices of second most distal lateral leaflets. 33. Distance between apices of third most distal lateral leaflets. 34. Color of abaxial surface of leaf (1) light green, (2) medium green, (3) dark green, (4) purple green. 35. Color of abaxial surface of leaf (1) green, (2) green with purple veins, (3) green with purple spots, (4) completely purple. 36. Density of adaxial pubescence (number of hairs/cm^2). 37. Length of adaxial pubescence (mm). 38. Density of pubescence on abaxial surface of leaf (number of hairs/cm^2). 39. Length of abaxial pubescence (mm). 40. Ratio: leaf length/leaf width. 41. Ratio: length of axis of widest point of leaf to apex/length of leaf. 42. Ratio: length of terminal leaflet lamina/width of terminal leaflet lamina. 43. Ratio: length of axis of widest point of terminal leaflet to apex/length of terminal leaflet lamina. 44. Ratio: length of most distal lateral leaflet/width of most distal lateral leaflet. 45. Ratio: length from axis of widest point of most distal lateral leaflet to apex/length of most distal lateral leaflet. 46. Purple color in rachis at leaflets insertion point (1) present (2) absent.

Floral Characters—47. Density of calyx pubescence (hairs cm^2). 48. Length of calyx pubescence (mm). 49. Length of peduncle. 50. Length of pedicel. 51. Length of pedicel from its base to articulation. 52. Ratio: length of pedicel articulation/length of pedicel. 53. Number of inflorescences axis. 54. Number of flowers per inflorescence. 55. Length of calyx acumen. 56. Length of calyx lobe. 57. Ratio: length of calyx lobe/width of calyx lobe. 58. Radius of corolla. 59. Ratio: Length from center of corolla to base of corolla lobes/radius of corolla. 60. Width of corolla lobe at base of junction of corolla lobes. 61. Ratio: Width of corolla lobe at base of junction of corolla lobes/length from base to tip of corolla lobe. 62. Length of anther. 63. Length of style exertion from apex of anthers to apex of stigma. 64. Shape of stigma (1) capitate, (2) clavate and (3) lobate. 65. Ratio: diameter of style/diameter of stigma. 66. Diameter of stigma (mm). 67. Length of stigma (mm). 68. Ratio: diameter of stigma/length of stigma. 69. Polymorphism in the size of the anthers, (1) no polymorphism, (2) two different sizes, (3) three different sizes, (4) four different sizes, (5) all different 70. Color of adaxial corolla interpetiolar tissue. 71. Color of adaxial corolla rays. 72. Color of abaxial corolla interpetiolar tissue. 73. Color of abaxial corolla rays.

Fruit Characters—74. Length of fruit. 75. Width of fruit 5 mm above the fruit apex. 76. Ratio: length of fruit/width at widest point of the fruit. 77. Ratio: length of fruit/width at its narrowest point. 78. Ratio: width of fruit at its widest point/width of fruit at 5 mm above the fruit apex. 79. Ratio: width of fruit at its widest point/width of fruit at its narrowest point. 80. Purple dot in the fresh mature seeds (1) present, (2) absent. 81. Fruit color distribution (1) uniform (2) mottled. 82. Texture of the external surface of the fruit (1) rugose, (2) smooth.