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A Morphometric Study of Species Boundaries of the Wild Potato *Solanum* Series *Conicibaccata*: a Replicated Field Trial in Andean Peru

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Abstract—*Solanum* series *Conicibaccata* contains about 40 wild potato (section *Petota*) species distributed from southern Mexico to central Bolivia. It contains diploids ($2n = 2x = 24$), tetraploids ($2n = 4x = 48$) and hexaploids ($2n = 6x = 72$) and some polyploids are likely allopolyploids. Our morphological phenetic study in an Andean site in central Peru (12°S, 3200 m altitude) is a replicated study from one done in the north central United States (45°N, 180 m elevation) but uses more species (28 vs. 25), accessions (173 vs. 100), and morphological characters (72 vs. 45) and also includes members of related series *Piurana*. Both US and Peruvian studies provide phenetic support with Canonical Discriminant Analyses (but poorly if at all with Principal Components Analyses) to distinguish the following species or species groups in series *Conicibaccata*: 1) *S. agrimonifolium* and *S. oxycarpum* as a possible single species, and 2) *S. longiconicum* (tetraploids from Mexico and Central America), 3) the South American *Conicibaccata* diploids as a possible single species, except for 4) *S. trinitense* that is distinctive, 5) the South American tetraploids as a group except for 6) *S. flahaultii* that is distinctive. However, character states among these species or species groups are often present only by using a range of widely overlapping character states (polythetic support). We suspect that our continuing molecular studies will support the synonymy of many of these species.

Keywords—Wild potatoes, replicated morphological studies, *Solanum* section *Petota*, series *Conicibaccata*, series *Piurana*.

The potatoes and their wild relatives, *Solanum* L. sect. *Petota* Dumort., grow from the southwestern United States to Argentina, Chile, and Uruguay. The latest comprehensive taxonomic treatment by Hawkes (1990) included 232 tuber-bearing and non-tuber-bearing species. Molecular and morphological studies have redefined sect. *Petota* to be composed of about 190 species, exclusively tuber-bearing (Spooner et al. 1993; Spooner and Salas 2006), and we suspect that the number of species will continue to decrease.

Species boundaries and relationships within sect. *Petota* are unresolved. Due to the large size of the section, we are conducting focused systematic studies in putatively related and taxonomically difficult groups. This study examines species in ser. *Conicibaccata* (see Table 1 for authors of series and species names), the second largest series in sect. *Petota*. Hawkes (1990) included 40 species in ser. *Conicibaccata*, distributed from southern Mexico to central Bolivia, and as elsewhere in sect. *Petota*, the limits of the series and its constituent species are unresolved (Spooner and Salas 2006). The most distinctive features of ser. *Conicibaccata* are the conical fruits and imparipinnate leaves with generally parallel sides; the species also have pentagonal to rotate corollas colored white to blue to purple, in contrast to some other members of the section with stellate corollas of various colors (Figs. 1, 2; Castillo and Spooner 1997; Spooner and Salas 2006), but these are inconstant characters. For example, the conical fruits of sect. *Petota* vary from long to short conical (oblong), and the characteristic leaf shapes sometimes intergrade with members of other series. As a result, authors disagree about what constitutes a species and the affiliation of the species into series (summarized in Table 1 of Castillo and Spooner 1997).

Ploidy in sect. *Petota* ranges from diploid ($2n = 2x = 24$), triploid ($2n = 3x = 36$), tetraploid ($2n = 4x = 48$), pentaploid ($2n = 5x = 60$), to hexaploid ($2n = 6x = 72$), with about 70% of the species diploid (Hijmans et al. 2007). Series *Conicibaccata* has a higher proportion of polyploids, with about one-half of the species tetraploid and hexaploid. Part of the taxonomic confusion in sect. *Petota* has been attributed to hybridization and allopolyploidy (Spooner and van den Berg 1992a; Rodríguez and Spooner 2004).

Castillo and Spooner (1997) studied the taxonomy of ser. *Conicibaccata* with morphological and plastid DNA restriction site data. They found: 1) some species assigned to ser. *Conicibaccata* were better classified in ser. *Piurana* (*S. chomatophilum*, *S. contumazaense*, *S. irosinum*, *S. paucijugum*), 2) the diploid and polyploid members of ser. *Conicibaccata* formed two groups, 3) it was difficult to support many of the species in ser. *Conicibaccata*, and some of the species may need to be placed in synonymy.

The morphological study of Castillo and Spooner (1997) was conducted in a greenhouse environment in the northern United States (45°N, 180 m elevation), and restricted to germplasm accessions available from the US Potato Genebank. Our study is a replicated morphological study in an upland Andean habitat in central Peru (12°S, 3200 m altitude) more similar to the natural habitat of the series, and it combined germplasm from the genebanks of the US Germplasm System and the International Potato Center. It provides replicate results with more species (28 vs. 25), accessions (173 vs. 100), and morphological characters (72 vs. 45). Our goal is to better understand morphological support for species and series boundaries, for an eventual monograph of the series that will draw from additional herbarium specimen and molecular data.

Materials and Methods

Plant Material—A total of 173 accessions from 28 different species of ser. *Conicibaccata* and morphologically similar ser. *Piurana* were selected for the morphological analysis (Appendix 1). The accessions came from the US Potato Genebank in Sturgeon Bay, Wisconsin (http://www.ars-grin.gov/nr6/) and from the International Potato Center (http://www.cipotato.org/). Not all the species had the same number of accessions due to their rarity and restricted geographical distribution, and we chose higher numbers of accessions for some species, as *S. chomatophilum* and *S. colombianum*, because they were widespread, morphologically variable, and apparently intergraded with other species. We chose many

TABLE 1. Tuber characters of *Solanum* ser. *Conicibaccata* and members from ser. *Piurana* examined in this study. [1]Cultivated potatoes and their immediate relatives typically have single tubers form at the end of stolons (b). Moniliform tubers (a) have multiple tubers arranged like beads on a string. Character c is for a single tuber per stolon placed along its length, not at the end. *Solanum sucubunense* Ochoa did not produce tubers.

Taxon	Type: a, moniliform; b, end of stolon; c, along the stolon[1]	Skin color	Eye color	Flesh color
Series *Conicibaccata* Bitter				
Solanum agrimonifolium Rydb.	abc	Light grey-yellow or light violet-purple	Light grey-yellow or light violet-purple	Light cream or light yellow
S. buesii Vargas	b	Light grey-yellow	Light grey-yellow or dark violet-purple	Light cream, yellow or light violet
S. colombianum Dun.	abc	Light grey-yellow	Light grey-yellow	Light cream or light yellow
S. flahaultii Bitt.	ab	Light grey-yellow	Light grey-yellow	Light cream or yellow
S. garcia-barrigae Ochoa	bc	Light grey-yellow	Light grey-yellow	Light cream
S. laxissimum Bitt.	b	Dark grey-yellow	Light grey-yellow or dark violet-purple	Light cream
S. limbaniense Ochoa	ab	Light grey-yellow	Light grey-yellow	Light cream or yellow
S. lobbianum Bitt.	a	Light grey-yellow	Light grey-yellow	Light cream
S. longiconicum Bitt.	ab	Light grey-yellow	Light grey-yellow	Light cream or light grey-yellow
S. moscopanum Hawkes	ab	Light grey-yellow	Light grey-yellow or light violet-purple	Light cream or light grey-yellow
S. nubicola Ochoa	a	Light grey-yellow	Light grey-yellow	Light cream
S. orocense Ochoa	a	Light grey-yellow	Light grey-yellow	Light violet-purple
S. otites Dun.	ab	Light grey-yellow	Light grey-yellow	Light cream
S. oxycarpum Schiede	a	Light grey-yellow	Light grey-yellow	Light cream or light yellow
S. pillahuatense Vargas	b	Dark violet-purple	Light green	Light cream
S. santolallae Vargas	b	Dark grey-yellow or dark violet-purple	Light or dark grey-yellow, or light or dark violet-purple	Light cream
S. tundalomense Ochoa	ab	Light grey-yellow	Light grey-yellow	Light cream
S. trinitense Ochoa	b	Light grey-yellow or light violet-purple	Light grey-yellow or light violet-purple	Yellow
S. urubambae Juz.	b	Dark grey-yellow or dark violet-purple	Light grey-yellow or dark violet-purple	Light cream or light yellow
S. violaceimarmoratum Bitt.	ab	Light grey-yellow or dark violet-purple	Light grey-yellow, or light or dark violet-purple	Yellow
Series *Piurana* Hawkes				
S. andreanum Baker	ac	Light grey-yellow	Light grey-yellow, or light violet-purple	Light cream
S. chomatophilum Bitt.	ab	Light grey-yellow or light cream	Light grey-yellow	Light grey-yellow or light cream
S. contumazaense Ochoa	ab	Light grey-yellow	Light grey-yellow	Light cream
S. irosinum Ochoa	ab	Light grey-yellow or light cream	Light grey-yellow	Light cream
S. paucijugum Bitt.	ab	Light grey-yellow	Light grey-yellow	Light cream
S. solisii Hawkes	a	Light grey-yellow	Light grey-yellow	Light cream
S. tuquerrense Hawkes	ab	Light grey-yellow	Light grey-yellow	Light grey-yellow

accessions from the study of Castillo and Spooner (1997) to compare results from replicated trials, but *S. neovalenzuelae* L. López, *S. pamplonense* L. López and *S. subpanduratum* Ochoa from Castillo and Spooner's (1997) study failed to grow for us. We mapped all accessions of ser. *Conicibaccata* with ArcGIS (ESRI Inc. 2005), and slightly modified map positions to group the accessions into generalized geographic areas (Appendix 1; Suppl. Figs. 1–3).

***Morphological Evaluation*—**Members of ser. *Conicibaccata* and ser. *Piurana* typically grow in rich organic soils in semishade in areas of rain forests and frequently die in exposed experimental fields. As a result, we grew the accessions in pots in organic soils, in greenhouses, and the plants were watered daily and treated with insecticides and fertilized as needed, similar to the study of Castillo and Spooner (1997). Seeds were planted in December, seedlings were transplanted into 8 inch pots, and measurements were made in February to March, except for tubers that were measured in May after plant senescence. Plants were grown at the International Potato Center (CIP) Huancayo Research Station in the central Peruvian Andes (3200 m above sea level, 12°8′ S, 75°8′ W). The plants were hand pollinated to stimulate fruit set. Ten plants were grown per accession, divided into five plants per each of two replicates, and planted in separate greenhouses for each replicate. A total of 72 characters (Table 2) were evaluated for three plants per replicate (a total six plants were measured per accession). Leaf measurements were taken from the middle leaf of each plant when the plants were flowering. Fruits were measured when fully mature. Colors were assessed using the RHS Colour Charts (Royal Horticultural Society 2001). A Hunter Lab Color Quest 45/0 colorimeter obtained measurements from these color charts for CIELab values (Wyszecki 1982), which 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 (positive values) and blue (negative values). Ratios were assessed for characters used by authors to distinguish species. For example, the conical fruit shape is one of the most important characters in ser. *Conicibaccata*, and we assessed this by calculating fruit length/width; as we assessed other ratios of putatively diagnostic shapes of flowers and leaves (Table 2). Our data matrix (as a Microsoft Excel file) is deposited on the *Systematic Botany* supplementary data website.

Principal Components Analyses (PCA) and Canonical Discriminant Analyses (CDA) of standardized averages from each measurement from both replicates (six plants in total) were taken as representative of the accession (thus the accession is the operational taxonomic unit, OTU). PCA was calculated from the correlation matrix of the variance-covariance matrix. Stepwise discriminant analyses (SDA) were used to identify and rank the characters most significant to discriminate 1) species, 2) diploid vs. polyploid members of ser. *Conicibaccata*, 3) ser. *Conicibaccata* vs. *Piurana*. All analyses were done in SAS ver. 9.1 (SAS Institute Inc. 2004). Characters were transformed, when possible (using square root, logarithm and the inverse of the character value), to fit them to

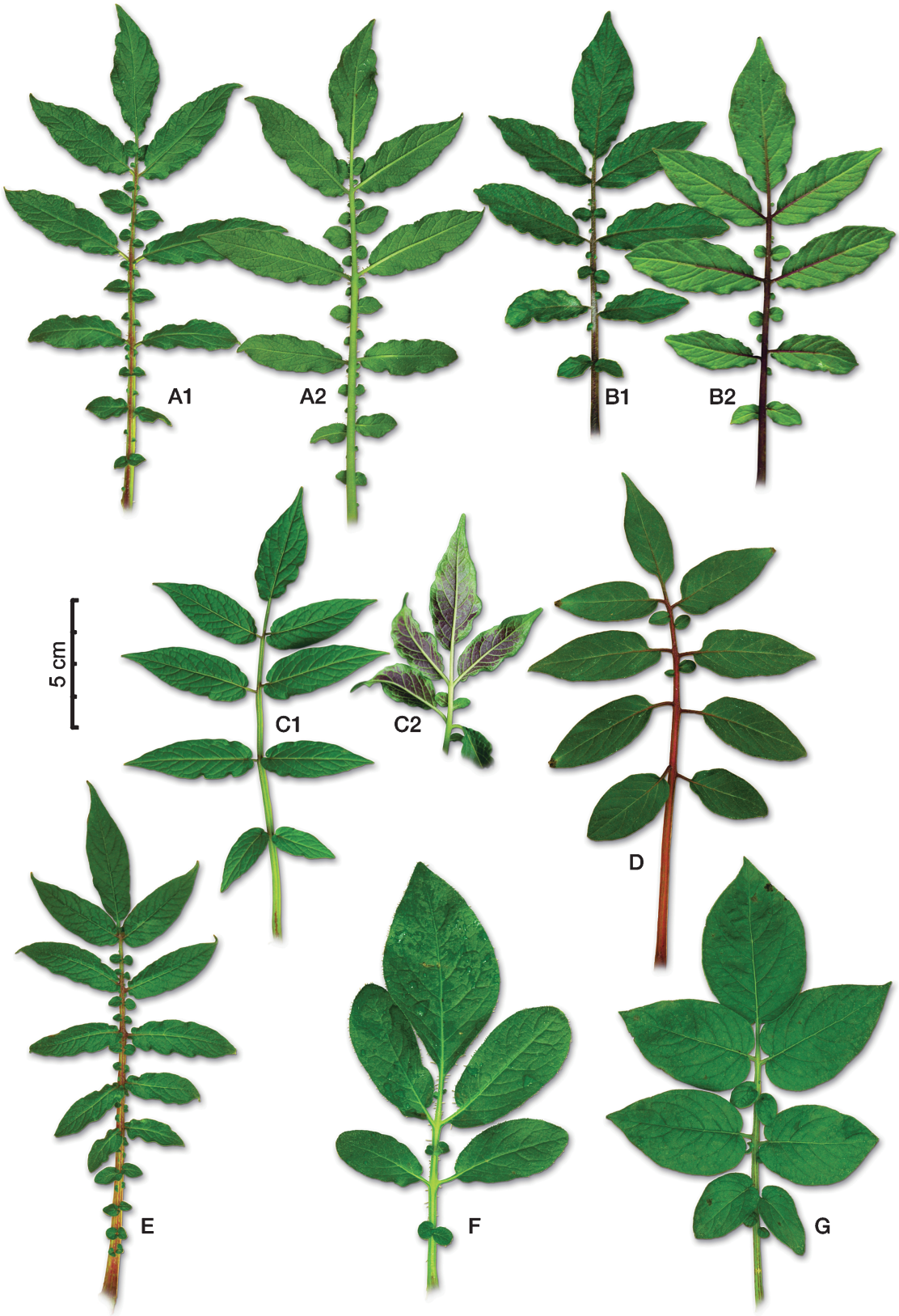

FIG. 1. Leaves of *Solanum* ser. *Conicibaccata* selected to illustrate the range of shapes and colors. A1 and A2. *S. moscopanum* (adaxial and abaxial views respectively). B1 and B2. *S. colombianum* (adaxial and abaxial views). C1 and C2. *S. santolallae* (adaxial and abaxial views). D. *S. longiconicum* (adaxial view). E. *S. agrimonifolium* (adaxial view). F. *S. flahaultii* (abaxial view). G. *S. violaceimarmoratum* (adaxial view).

normality. CDA was performed with all characters and again with the reduced data set of characters that were normally distributed or were able to be normalized.

The data also were analyzed by Gower's similarity coefficient appropriate for mixed data (i.e. qualitative and quantitative data; Podani 1999) by using the *cluster* package (Maechler et al. 2005) in R statistical software version 2.4.1 (R Development Core Team 2006). Principal Coordinates Analyses (PCO) was calculated from the Gower's similarity matrix.

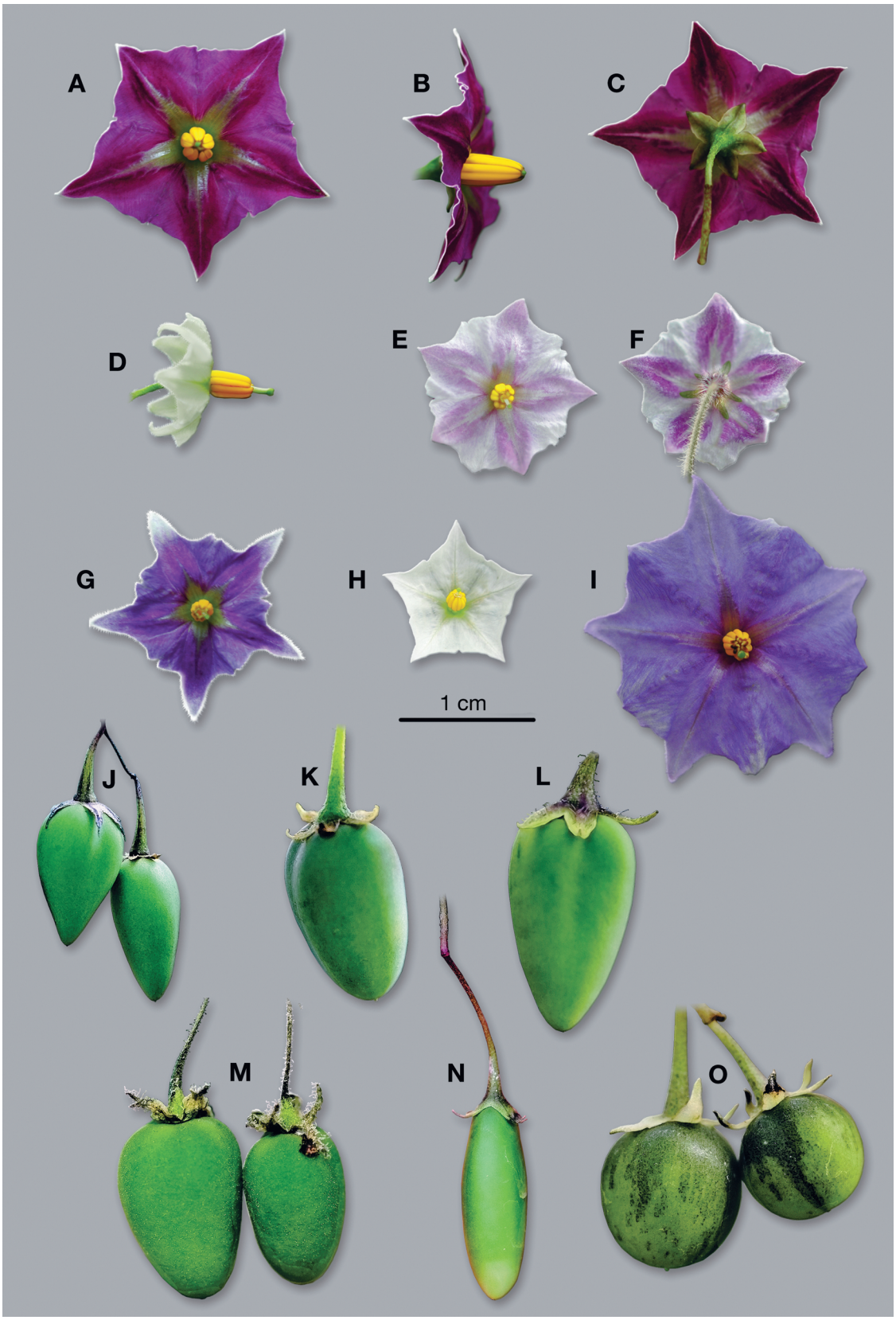

FIG. 2. Corollas (A – I) and fruits (J – O) of *Solanum* ser. *Conicibaccata* selected to illustrate the range of shapes and colors. A, B, C. *S. santolallae* (front, side and back views respectively). D. *S. moscopanum* showing length of exsertion and anther polymorphism present in some species. E, F. *S. garcia-barrigae* (front and back view respectively) G. *S. violaceimarmoratum*. H. *S. longiconicum*. I. *S. tundalomense*. J. *S. agrimonifolium*. K. *S. colombianum*. L. *S. colombianum*. M. *S. lobbianum*. N. *S. longiconicum*. O. *S. urubambae*.

TABLE 2. Characters used in the morphological analysis. *New characters not evaluated by Castillo and Spooner (1997).

Stem characters—**1**. Diameter of stem at the middle part of the plant (cm). **2**. Stem color (1) green, (2) green mottled with purple, (3) purple. **3**. Stem morphology* (1) circular, (2) polygonal, (3) triangular. **4**. Width of stem wings (cm). **5**. Plant height (cm).

Leaf characters (from leaves taken at the middle of flowering plants)—**6**. Length of leaf (cm). **7**. Length of terminal leaflet lamina (cm). **8**. Length of petiolule of terminal leaflet (cm). **9**. Number of pairs of lateral leaflets. **10**. Number of primary interstitial leaflets. **11**. Number of secondary interstitial leaflets. **12**. Margin of leaflets (1) straight, (2) undulate, (3) sinuate. **13**. Width of terminal leaflet 0.5 cm from apex (cm). **14**. Base shape of terminal leaflet*: (1) equilateral, (2) attenuate, (3) auriculate, (4) cordate, (5) cuneate, (6) hastate, (7) oblique, (8) rounded, (9) sagittate, (10) truncate. **15**. Number of interstitial leaflets at base of terminal leaflet. **16**. Length of petiolule of the most distal lateral leaflet (cm). **17**. Length of the largest interstitial leaflet (cm). **18**. Length of widest point of the most distal lateral leaflet (cm). **19**. Length of the most distal lateral leaflet (cm). **20**. Width of most distal lateral leaflet 0.5 cm from apex* (cm). **21**. Width of decurrent tissue under the most distal lateral leaflet as measured 0.5 cm below the insertion point of leaf in the rachis*. **22**. Width of second most distal lateral leaflet between apices* (cm). **23**. Width of third most distal lateral leaflet between apices* (cm). **24**. Color of adaxial surface of leaf* (1) light green, (2) medium green, (3) dark green, (4) purple green. **25**. Color of abaxial surface of leaf* (1) green, (2) green with purple veins, (3) green with purple spots, (4) completely purple. **26**. Density of adaxial pubescence (number of hairs/cm^2). **27**. Length of adaxial pubescence* (cm). **28**. Density of pubescence on abaxial surface of leaf (number of hairs/cm^2). **29**. Length of abaxial pubescence* (cm). **30**. Ratio: leaf length/leaf width. **31**. Ratio: length of axis of widest point of leaf to apex/length of leaf. **32**. Ratio: length of terminal leaflet lamina/width of terminal leaflet. **33**. Ratio: length of axis of widest point of terminal leaflet to apex/length of terminal leaflet lamina. **34**. Ratio: length of most distal lateral leaflet/width of most distal lateral leaflet. **35**. Ratio: length from axis of widest point of most distal lateral leaflet to apex/length of most distal lateral leaflet. **36**. Purple color in rachis at leaflets insertion point* (1) present (2) absent.

Floral characters—**37**. Density of calyx pubescence (hairs/cm^2). **38**. Length of calyx pubescence* (mm). **39**. Length of the peduncle (cm). **40**. Length of pedicel (cm). **41**. Length of pedicel from its base to articulation (cm). **42**. Ratio: length of pedicel articulation/length of pedicel. **43**. Number of peduncle forks*. **44**. Number of flowers per inflorescence. **45**. Length of calyx acumen (cm). **46**. Length of calyx lobe (cm). **47**. Ratio: length of calyx lobe/width of calyx lobe. **48**. Radius of corolla (cm). **49**. Ratio: Length from center of corolla to base of corolla lobes/radius of corolla. **50**. Width of corolla lobe at base of junction of corolla lobes (cm). **51**. Ratio: Width of corolla lobe at base of junction of corolla lobes/length from base to tip of corolla lobe. **52**. Length of anther (cm). **53**. Length of style exertion from apex of anthers to apex of stigma* (cm). **54**. Shape of stigma* (1) capitate, (2) clavate, (3) lobate. **55**. Ratio*: Diameter of style/diameter of stigma. **56**. Diameter of stigma* (mm). **57**. Length of stigma* (mm). **58**. Ratio*: diameter of stigma/length of stigma. **59**. 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. **60**. Color of adaxial corolla interpetolar tissue. **61**. Color of adaxial corolla rays. **62**. Color of abaxial corolla interpetolar tissue. **63**. Color of abaxial surface of corolla rays.

Fruit characters—**64**. Length of fruit (cm). **65**. Width of fruit at 0.5 cm above the fruit apex* (cm). **66**. Ratio: length of fruit/width at widest point of the fruit. **67**. Ratio*: length of fruit/width at its narrowest point. **68**. Ratio*: width of fruit at its widest point/width of fruit at 0.5 cm above the fruit apex. **69**. Ratio*: width of fruit at its widest point/width of fruit at its narrowest point. **70**. Purple dot in the fresh mature seeds* (1) present, (2) absent. **71**. Fruit color distribution* (1) uniform, (2) mottled. **72**. Texture of the external surface of the fruit* (1) rugose, (2) smooth.

Correlation coefficients of similarity matrices were determined using MXCOMP in NTSYS-pc software version 2.02K (Rohlf 1997) of 1) identical accessions and characters from the US vs. Peru, 2) identical US vs. Peru accessions but using all characters measured in Peru, 3) the replicated trials in different greenhouses in Peru.

We used ANOVA to test environment (E) and genotype by environment (G × E) effects for each character in the two locations of the US and Peru, using a randomized complete block (RCBD) with five replications in each location. We analyzed the data with proc GLM (General Linear Model, that is most appropriate for unbalanced data sets) in SAS (SAS Institute Inc. 2004) to determine if environmental factors influenced the replicates in the different locations. The main effects were accession (G) and environment (E), treated as fixed and random effects respectively.

RESULTS

***Tuber Variation*—**Our initial intention was to include four tuber characters in multivariate analyses, but tubers were not formed for 24.8% of the accessions, so we only summarize (Table 1) and comment on tuber variation for future descriptive and comparative studies. Potato tubers are swellings along the stolons (underground stems). Tubers have periderm (skin), indentations in the tuber containing the stem buds (eyes), and internal starch storage tissue (flesh). The typical tuber type for cultivated potatoes and their immediate wild relatives is for a single tuber to be arranged at the end of a stolon. Moniliform tubers are quite different, as they are arranged as serial swellings along a stolon like beads on a string. We also observed single tubers as swellings along the stolon as in the moniliform arrangement but not on the end of the stolon. Tubers in ser. *Conicibaccata* are typically variable within species with the most common arrangements at the end of the stolon or moniliform. Skin colors typically are light grey-yellow and flesh colors whitish to light cream. Rarer types have dark violet-purple skin and flesh (as in four of the diploid species *S. pillahuatense*, *S. santolallae*, *S. urubambae*, and *S. violaceimarmoratum*); rare flesh colors are light violet or light violet-purple in *S. buesii* and *S. orocense*. Tuber eye colors typically are light grey-yellow or violet with a rare light green type in *S. pillahuatense*.

***Multivariate Analyses*—**There were 3.6% missing data averages for the remaining (non-tuber) characters, mostly for fruits that did not develop. Because SAS eliminates entire accessions with any missing data, we estimated these values from averages of other accessions from the same species. The evaluations showed the L*a*b* color values to be highly correlated, and we selected only the parameter a* (colors magenta to green) because it most closely matched the colors of corollas (Fig. 2).

PCA axes 1 and 2 of the entire data set (Fig. 3a) accounted for 13.8% and 10.0% of the total variation for a total of 23.8%; axis 3 accounted for an additional 8.9%, but did not change the overall pattern and is not presented. Axis 1 is most highly influenced (highest positive or negative eigenvector values) by the following characters: width of second most distal lateral leaflet between apices, width of third most distal lateral leaflet between apices, diameter of stem, length of widest point of the most distal lateral leaflet; axis 2 by: length of anther, color of adaxial corolla rays, color of adaxial corolla interpetolar tissue. The PCA (Fig. 3a) only very roughly separated the members of ser. *Conicibaccata* from ser. *Piurana*.

PCA axes 1 and 2 of only members of ser. *Conicibaccata* (Fig. 3b) accounted for 14.6% and 13.2% of the total variation for a total of 27.8%; axis 3 accounted for an additional 7.8%, but did not change the overall pattern and is not presented.

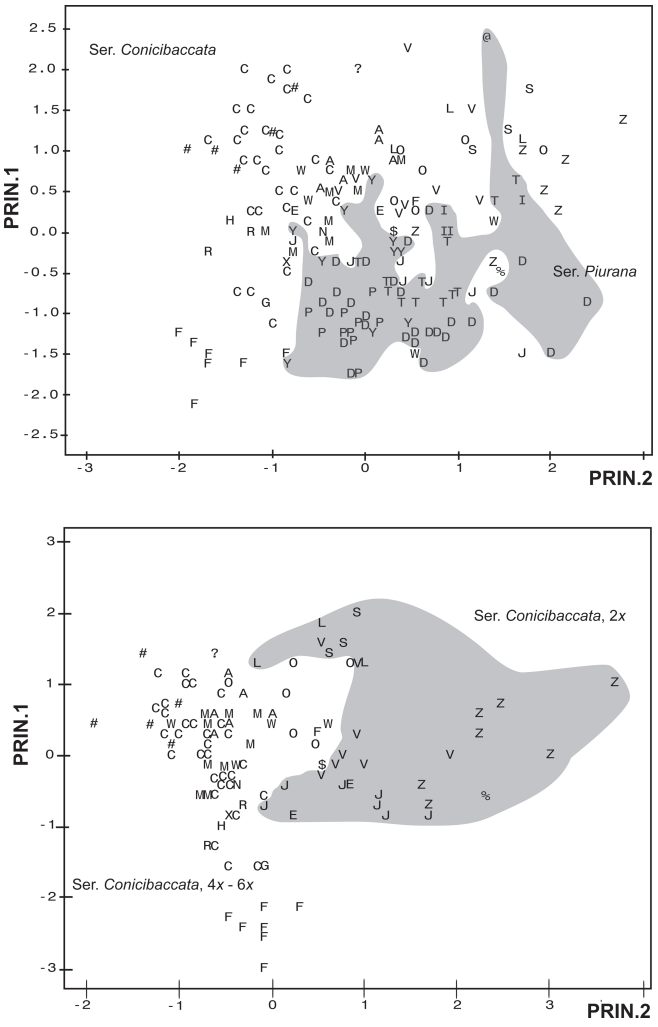

FIG. 3. Principal Components Analyses of members of ser. *Conicibaccata* and *Piurana* based on 72 morphological characters (Table 1). Species codes, following Castillo and Spooner (1997) are: *Solanum andreanum* (Y), *S. agrimonifolium* (A), *S. buesii* (E), *S. chomatophilum* (D), *S. colombianum* (C), *S. contumazaense* (@), *S. flahaultii* (F), *S. garcia-barrigae* (G), *S. irosinum* (I), *S. laxissimum* (L), *S. limbaniense* (J), *S. lobbianum* (H), *S. longiconicum* (#), *S. moscopanum* (M), *S. nubicola* ($), *S. orocense* (N), *S. otites* (R), *S. oxycarpum* (O), *S. paucijugum* (P), *S. pillahuatense* (%), *S. santolallae* (S), *S. solisii* (&), *S. tundalomense* (W), *S. tuquerrense* (T), *S. sucubunense* (X), *S. trinitense* (?), *S. urubambaue* (Z), *S. violaceimarmoratum* (V). Figure 3a is based on all 173 taxa; Fig. 3b is based only on the 108 ser. *Conicibaccata* taxa (see Appendix 1 for localities). Balloons outline ser. *Piurana* from ser. *Conicibaccata* in Fig. 1a, and diploid ser. *Conicibaccata* to the exclusion of polyploid members of ser. *Conicibaccata* in 1b.

Axis 1 is most highly influenced by the following four characters: width of second most distal lateral leaflet between apices, width of third most distal lateral leaflet between apices, width of most distal lateral leaflet 0.5 cm from apex, width of terminal leaflet 0.5 cm from apex; axis 2 by: length of petiolule of terminal leaflet, color of adaxial corolla rays, calyx pubescence, width of fruit at 0.5 cm above the fruit apex. This analysis only roughly separated the South American *Conicibaccata* diploids from polyploids, with seven of the eight accessions of *S. flahaultii* (code F) well differentiated within the South American polyploids.

The SDA identified the following five characters to be the most important in discriminating taxa within the entire data set: ratio - length of fruit/width at widest point of the fruit, length of adaxial pubescence, ratio - length of axis of widest point of terminal leaflet to apex/length of terminal leaflet lamina, presence or absence of a purple dot in the fresh mature seeds, number of interstitial leaflets at base of terminal leaflet; and for the ser. *Conicibaccata* only data set: ratio - length of fruit/width at widest point of the fruit, density of calyx pubescence, ratio - length of axis of widest point of terminal leaflet to apex/length of terminal leaflet lamina, number of pairs of lateral leaflets, color of abaxial corolla interpetolar tissue.

The CDA of the entire data set (Fig. 4a) clearly separated *S. longiconicum* (code #) *S. contumazaense* (@) and *S. trinitense* (?) and did a better job of separating members of ser. *Conicibaccata* from ser. *Piurana* (Fig. 4b). The CDA of the ser. *Conicibaccata* only data set (Fig. 5a, b) well separated *S. longiconicum* and *S. trinitense* (Fig. 5a), *S. agrimonifolium* and *S. oxycarpum* (A, O; tetraploids from Mexico and Central America as a possible single species), the South American *Conicibaccata* diploids, the South American tetraploids, and all eight of the accessions of *S. flahaultii* (F) as a subset of these South American tetraploids. Many of the species of ser. *Conicibaccata* fell into closely adjacent groups, with the exception of *S. lobbianum*, clustering with *S. colombianum*. Despite multivariate

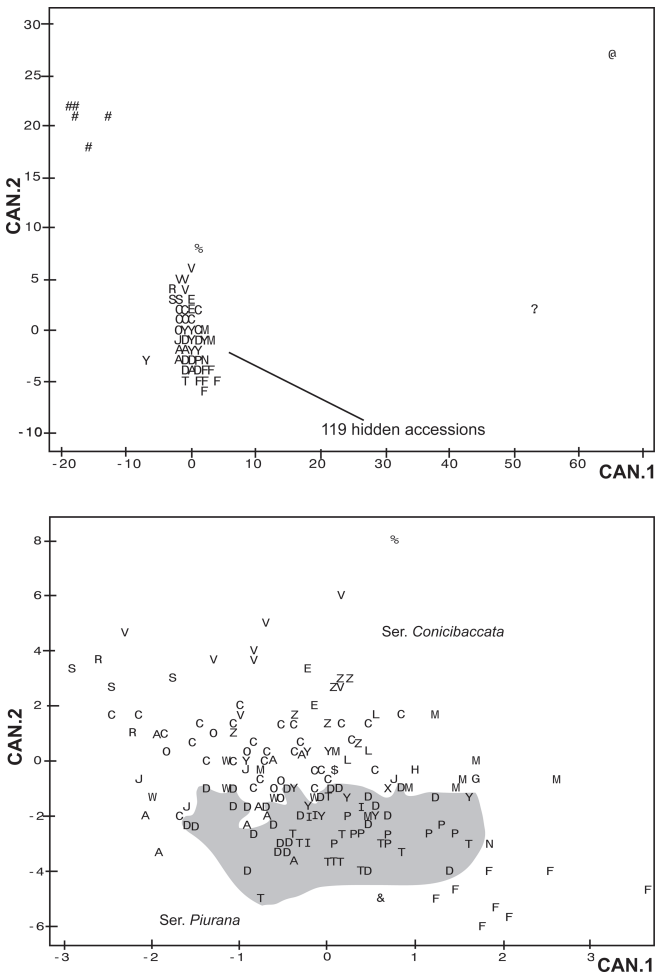

FIG. 4. Canonical Discriminant Analysis based on 72 morphological characters examined in this study. Species codes as in Fig. 3. Figure 4a is based on all taxa; Fig. 4b is redrawn and rescaled showing the window of variation on axis 1 from –3–3.5, and axis 2 from –6–8 showing detail of all species except *S. contumazaense*, *S. longiconicum*, and *S. trinitense* and one accession of *S. andreanum*. The balloon in 4b outlines ser. *Piurana* with the others not so outlined being members of ser. *Conicibaccata*.

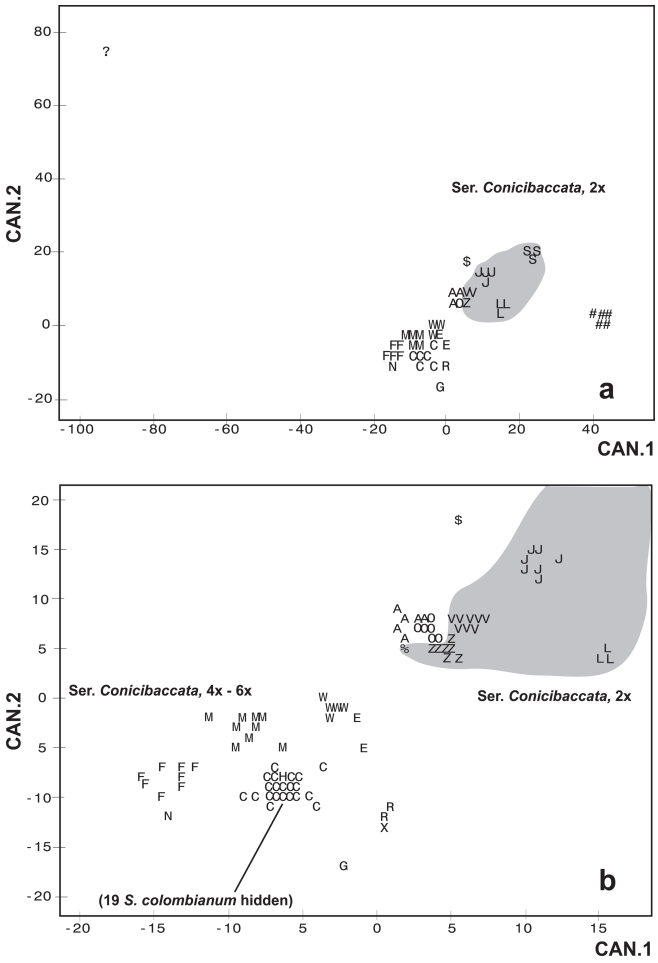

FIG. 5. Canonical Discriminant Analysis based on 72 morphological characters of only members of ser. *Conicibaccata* examined in this study. Species codes as in Fig. 3. Figure 5a is based on all taxa; Fig. 5b is redrawn to scale to show detail of all species except *S. contumazaense*, *S. longiconicum*, and *S. trinitense*. The balloon in 5a and b outlines diploids from polyploid members of ser. *Conicibaccata*.

support of some groups, especially with the CDA, there is much overlap of even the best character states separating the species (Suppl. Fig. 4).

We were able to normalize 28 of the 72 characters for the entire data set and 35 of the 72 characters for the reduced data set of ser. *Conicibaccata*. This reduced number of characters was then used for further CDA analyses for all accessions and for only members of ser. *Conicibaccata*. *Solanum contumazaense*, *S. longiconicum*, and *S. trinitense* were excluded from both of these analyses as they were outliers based on all characters. These new CDA analyses with only the normalized characters showed similar results to those using all characters. That is: 1) there was no good separation of ser. *Piurana* from ser. *Conicibaccata*, 2) *S. agrimonifolium* and *S. oxycarpum* clustered, 3) the South American *Conicibaccata* diploids clustered, 4) the South American tetraploids clustered, 5) *S. flahaultii*, a South American tetraploid clustered (Suppl. Figs. 5a, b).

The plot of the PCO of ser. *Conicibaccata* and *Piurana* (Suppl. Fig. 6a) showed the species from ser. *Piurana* intermixed within ser. *Conicibaccata*. The plot of PCO of the accessions from ser. *Conicibaccata* (Suppl. Fig. 6b), showed a cluster of South American diploids, a cluster of accessions from *S. flahaultii*, and a group of Central and South American polyploids mixed together.

SDA identified the following five characters as the most important to distinguish the diploids from the polyploids: density of calyx pubescence, length of anther, width of corolla lobe at base of junction of corolla lobes/length from base to tip of corolla lobe, width of fruit at 0.5 cm above the fruit apex, number of pairs of lateral leaflets. There was extensive overlap between the individual morphological character states best distinguishing diploid and polyploid *Conicibaccata* (Suppl. Fig. 7), and they were separated only by multivariate techniques.

SDA identified the following five characters as most important to distinguish ser. *Conicibaccata* from ser. *Piurana*: width of decurrent tissue under the most distal lateral leaflet measured 0.5 cm below the insertion point of leaf in the rachis, number of interstitial leaflets at base of terminal leaflet, color of abaxial surface of corolla rays, diameter of stem, number of secondary interstitial leaflets. There was extensive overlap between the characters states best distinguishing ser. *Conicibaccata* and ser. *Piurana* (Suppl. Fig. 8).

Concordance of Data Sets—Correlation coefficients showed: 1) identical accessions and characters from morphological studies in the US and Peru to be correlated at 0.62, 2) identical accessions in US and Peru but to include all 72 characters measured in Peru correlated at 0.58, 3) replicated trials in different greenhouses in Peru correlated at 0.56.

ANOVA analyses were used to determine the environmental effects (E) and genotype by environment effects (G × E) in each character. ANOVA of 100 shared accessions and 45 common characters between US and Peru showed 39 of the 45 shared characters to be significantly different ($P < 0.05$) by environmental factors (E) and all 45 examined characters to be highly significantly different ($P < 0.01$) by genotype by environment factors (G × E). The comparison between the two replicates in Peru showed 47 of the 72 common characters significantly different ($P < 0.05$) between environments, and 53 of the 72 by genotype by environment factors ($P < 0.05$).

DISCUSSION

Tuber Variation—Spooner and Salas (2006) mention moniliform tubers as a character defining ser. *Piurana*. We document moniliform tubers in 13 of the 20 species (Table 1), although many of these species were polymorphic with other tuber types. The use of moniliform tubers to define ser. *Piurana*, therefore, must be reevaluated. The tuber colors we observed are common among many groups of wild potatoes and are not taxonomically useful at the species or series level.

Insights From Replicated Studies—Multivariate studies of germplasm samples of sect. *Petota* in common gardens have tested the morphological support for traditionally recognized species. Some of these (Spooner et al. 1995, 2001b; Lara-Cabrera and Spooner 2005) have provided insights for recent monographic studies in North and Central America (Spooner et al. 2004). This is the first such replicated morphological study in the section that we initiated to provide insights into the stability of morphological characters for monographic studies in South America. The similar correlation between US and Peruvian studies (0.62) and among replicates within Peru (0.56) suggest that the US and Peruvian results are comparable.

The ANOVA analyses showed that there are similar numbers of characters that are significantly different between the US and Peru (45) than are different between the two replications in Peru (47), similar to the results from the correlation coefficients.

Interpretation of Multivariate Analyses—We compared individual characters from the study of Castillo and Spooner (1997) and this study that were determined by the SDA to be most important to distinguish 1) ser. *Piurana* from ser. *Conicibaccata*, 2) species within ser. *Conicibaccata*, and 3) diploids vs. polyploids within ser. *Conicibaccata*. Similar characters were determined to be important in comparisons 1 and 2 although their rankings are different. Different characters are shown to distinguish the ser. *Conicibaccata* ploidy levels. Interestingly, neither study supported fruit shapes to be significant to distinguish ser. *Piurana* from ser. *Conicibaccata*, even though conical fruits have traditionally defined the latter. The results of the CDAs using all characters or only the subset of the characters that were normalized gave similar results to each other. The PCA and PCO provided similar results to each other, and discriminated fewer species than the CDA.

Morphological studies in sect. *Petota*, using PCA, CDA, and ratios to assess taxonomically significant shapes have consistently shown concordance with parallel molecular studies. This suggests that the present morphological results also will correspond to molecular results. For example, van den Berg et al. (1998) showed morphological support for the northern and southern components of the *Solanum brevicaule* complex but poor support for many of the species within the complex, in agreement with low-copy nuclear RFLP and RAPD (Miller and Spooner 1999) and AFLP data (Spooner et al. (2005). Similar concordant results have been shown in *S. berthaultii* Hawkes and *S. tarijense* Hawkes by Spooner and van den Berg (1992b, morphology), Spooner et al. (2007, AFLPs); *S. megistacrolobum* Bitt. and *S. toralapanum* Cárdenas and Hawkes (Giannattasio and Spooner 1994a, morphology), Giannattasio and Spooner (1994b, low-copy nuclear RFLPs); *S. cardiophyllum* Lindl. and *S. bulbocastanum* Dun. (Rodríguez and D.M. Spooner 1997, plastid restriction site data), Rodríguez and Spooner (2002, morphology and low-copy nuclear RFLPs); *S.* ×*rechei* Hawkes and Hjert. (Clausen and Spooner 1998, morphology and low-copy nuclear RFLP data); the species within *Solanum* ser. *Longipedicellata* Bukasov (Spooner et al. 2001a, morphology), van den Berg et al. (2002, AFLPs and RAPDs); the Mexican diploid species (Lara-Cabrera and Spooner (2004, AFLPs), and Lara-Cabrera and Spooner (2005, morphology). In the sister clade to sect. *Petota*, Peralta and Spooner (2001) discovered a "northern" and "southern" group of the wild tomato species *S. peruvianum* L., in agreement with morphological data (Peralta and Spooner 2005).

Our morphological results within ser. *Conicibaccata* support species status in series *Conicibaccata*: 1) *S. agrimonifolium* and *S. oxycarpum* as a possible single species, and 2) *S. longiconicum* (tetraploids from Mexico and Central America), 3) the South American *Conicibaccata* diploids as a possible single species, except for 4) *S. trinitense* that is distinctive, 5) the South American tetraploids as a group except for 6) *S. flahaultii* that is distinctive. The other species are difficult to define with multivariate analyses, matching our observations during our two months of intensive work with these species. Our experience using the keys of Correll (1962), Hawkes (1990), and Ochoa (1999) during this study lead us to conclude that the species within ser. *Conicibaccata* are over-described and that an easy and practical taxonomic treatment of the series will be difficult.

We are continuing to investigate the taxonomy of these species with multiple molecular markers and comprehensive collections of herbarium material worldwide, including types. It is possible that germplasm accessions planted in greenhouses show atypical morphological character expression and that future herbarium and molecular studies will provide better separation than we can support here. However, we suspect that our results highlight taxonomic problems that will require the reduction in the number of species in ser. *Conicibaccata* and a reevaluation of series.

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APPENDIX 1. *Solanum* ser. *Conicibaccata* and ser. *Piurana* used for phenetic analyses. See Hijmans et al. (2007; and accompanying deposited database) for references documenting individual chromosome counts. Full locality data of accessions used in Castillo and Spooner (1997) are published there; accessions new to this study have all locality data here. Vouchers are deposited at PTIS and the herbarium of the International Potato Center (CIP). Accessions with the prefix "CIP" are from the International Potato Center, and those with the prefix "PI" (Plant Introduction) are from the US Potato Genebank in Sturgeon Bay, Wisconsin. See Suppl. Figs. 1-3 for map localities 1-10 in Mexico and Central America, 11 in Venezuela, 12-26 in Colombia, 27-33 in Ecuador, 34-42 in Peru and 43-45 in Bolivia.

***Series Conicibaccata*—**MAP LOCALITY 1: *Solanum oxycarpum* Schiede, PI 607855, 2*n* = 48, *Rivera-Pena et al. 951*, Mexico. Puebla: from Tehuacán to Oaxaca road, turn NE on road to Zoquitlán, 22 km up road, by divergence of road to Coyomeapa, 2640 m, 18.3, -97.07; *S. oxycarpum*, PI 545721, *Tarn et al. 180*, Mexico. Puebla: road from Tehuacán to Oaxaca, turning off at Coxcatlán, 21 km towards Zoquitlán, La Griega, where road divides to Zoquitlán and Coyomeapa, waste place on slope down from the road to cultivated fields and woods, 2660 m, 18.333, -97.067; *S. oxycarpum*, PI 498026, 2*n* = 48, *Tarn et al. 182*, Mexico. Puebla; MAP LOCALITY 2: *S. oxycarpum*, PI 545776, 2*n* = 48, *Tarn et al. 272*, Mexico. Oaxaca; MAP LOCALITY 3: *S. oxycarpum*, PI 607861, 2*n* = 48, *Rivera-Pena et al. 960*, Mexico. Chiapas: 50 m walk down hill from uppermost of antenna cluster on Cerro Zontehuitz, by lower of two shrines, 2950 m, 16.82, -92.58; MAP LOCALITY 4: *S. agrimonifolium* Rydb., PI 558372, 2*n* = 48, *Spooner et al. 4227*, Mexico. Chiapas; MAP LOCALITY 5: *S. oxycarpum*, PI 607862, 2*n* = 48, *Rivera-Pena et al. 961*, Mexico. Chiapas: 17.4 km N of Rt. 190 just S of Motozintla, on road to El Porvenir, ca 50 m W of road, 2410 m, 15.4, -92.18; *S. agrimonifolium*, PI 558370, 2*n* = 48, *Spooner et al. 4208*, Mexico. Chiapas; *S. agrimonifolium*, PI 558371, 2*n* = 48, *Spooner et al. 4211*, Mexico. Chiapas; MAP LOCALITY 6: *S. agrimonifolium*, PI 243350, 2*n* = 48, *Graham 145*, Guatemala. Quezaltenango; *S. agrimonifolium*, PI 243351, 2*n* = 48, *Graham 145A*, Guatemala. Huehuetenango; *S. agrimonifolium*, PI 243352, 2*n* = 48, *Graham 145B*, Guatemala. Huehuetenango; MAP LOCALITY 7: *S. longiconicum* Bitter, PI 208780, 2*n* = 48, *Hope s.n.*, Costa Rica. Alajuela; *S. longiconicum*, PI 604093, 2*n* = 48, *Spooner et al. 7109*, Costa Rica. Alajuela: Monteverde Cloud Forest Preserve, division point of provinces A, P and G, top of Cerro Amigos, around television tower (channel 13), 1830 m, 10.317, -84.795; MAP LOCALITY 8: *S. longiconicum*, PI 604095, 2*n* = 48, *Spooner et al. 7123*, Costa Rica. Heredia: Parque Nacional Braulio Carillo sector Cerro Chompipes, 6.3 km N of San Rafael, along recently cleared path to the top for new road. In wet cloud forest, 2200 m, 10.085, -84.073; MAP LOCALITY 9: *S. longiconicum*, PI 604088, 2*n* = 48, *Spooner et al. 7103*, Costa Rica. Cartago: 13.5 km S of Empalme at the Interamerican Highway. Habitat: Along the road. Common, 9.632, -83.840; MAP LOCALITY 10: *S. longiconicum*, CIP 763031, *Spooner et al. 7411*, Panama. Chiriquí: District and Corregimiento of Boquete, E base of Cerro Pate de Macho, about 100 m S of continental divide at border with Province of Bocas del Toro, 2000 m, 8.82, -82.38; MAP LOCALITY 11: *S. otites* Dunal, CIP 761276, *Ochoa 11779*, Venezuela. Táchira: Mucujabi, 3400 m; *S. otites*, CIP 761277, *Ochoa 11780*, Venezuela. Táchira: Mucujabi, 3400 m; *S. colombianum* Bitter, PI 586950, 2*n* = 48, *Spooner et al. 6314*, Venezuela. Táchira; *S. colombianum*, PI 567826, 2*n* = 48, *Spooner et al. 6315*, Venezuela. Táchira; *S. colombianum*, PI 586951, 2*n* = 48, *Spooner et al. 6316*, Venezuela. Táchira; *S. colombianum*, PI 583325, 2*n* = 48, *Spooner et al. 6319*, Venezuela. Táchira; MAP LOCALITY 12: *S. garcia-barrigae* Ochoa, PI 498158, *Lopez et al. CCC 5170*, Colombia. Norte de Santander: Abreyo, 8.08, -73.22; *S. orocense* Ochoa, PI 583307, 2*n* = 48, *Spooner et al. 1304*, Colombia. Norte de Santander; MAP LOCALITY 13: *S. flahaultii* Bitter, PI 583316, 2*n* = 48, *Lopez et al. CCC 5255*, Colombia. Boyacá: Guicari-La Cueva; MAP LOCALITY 14: *S. flahaultii*, PI 558111, 2*n* = 48, *Lopez et al. CCC 5174*, Colombia. Boyacá; *S. flahaultii*, PI 583317, 2*n* = 48, *Lopez et al. CCC 5259*, Colombia. Boyacá; MAP LOCALITY 15: *S. flahaultii*, PI 597674, 2*n* = 48, *Lopez et al. CCC 5272*, Colombia. Boyacá: Socha-Los Puios; MAP LOCALITY 16: *S. flahaultii*, PI 570620, 2*n* = 48, *Castillo et al. 1272*, Colombia. Cundinamarca: At the farm of San Benito (also called Caldera del Diablo), at a field called Panamá, 12 km from deviation of road to Pacho and San Cayetano from Zipaquirá, 3400 m, 5.1, -74.03; *S. flahaultii*, PI 597672, 2*n* = 24, *Lopez et al. CCC 5233*, Colombia. Cundinamarca: Zipaquirá-Santa Bárbara. Finca de Don Benito; MAP LOCALITY 17: *S. flahaultii*, PI 583313, 2*n* = 48, *Lopez et al. CCC 5232*, Colombia. Cundinamarca; *S. flahaultii*, PI 498167, 2*n* = 48, *Lopez et al. CCC 5168*, Colombia. Cundinamarca; MAP LOCALITY 18: *S. lobbianum* Bitter, PI 567840, 2*n* = 48, *Castillo et al. 1211*, Colombia. Caldas; *S. colombianum*, PI 567831, 2*n* = 48, *Castillo et al. 1212*, Colombia. Caldas; MAP LOCALITY 19: *S. colombianum*, PI 567827, 2*n* = 48, *Castillo et al. 1202*, Colombia. Quindío; *S. colombianum*, PI 567829, 2*n* = 48, *Castillo et al. 1204*, Colombia. Quindío; *S. colombianum*, PI 566750, 2*n* = 48, *Lopez et al. CCC 5157*, Colombia. Quindío; MAP LOCALITY 20: *S. moscopanum* Hawkes, PI 570633, 2*n* = 72, *Castillo et al. 1262*, Colombia. Valle; *S. colombianum*, PI 570616, 2*n* = 48, *Castillo et al. 1264*, Colombia. Valle; *S. moscopanum*, PI 570634, 2*n* = 72, *Castillo et al. 1265*, Colombia. Valle; *S. colombianum*, PI 583312, 2*n* = 48, *Lopez et al. CCC 5218*, Colombia. Valle; MAP LOCALITY 21: *S. colombianum*, PI 583319, *Lopez et al. CCC 5284*, Colombia. Cauca, Silore-Las Cruces, finca Las Locas; MAP LOCALITY 22: *S. colombianum*, PI 584485,

2*n* = 48, *Spooner et al. 1259*, Colombia. Cauca; MAP LOCALITY 23: *S. moscopanum*, PI 567843, 2*n* = 72, *Castillo et al. 1243*, Colombia. Cauca; *S. moscopanum*, PI 570628, 2*n* = 72, *Castillo et al. 1247*, Colombia. Cauca; MAP LOCALITY 24: *S. moscopanum*, PI 570630, 2*n* = 72, *Castillo et al. 1250*, Colombia. Cauca; *S. sucubunense* Ochoa, PI 583320, 2*n* = 72, *Castillo et al. 1255*, Colombia. Cauca; *S. colombianum*, PI 583322, 2*n* = 48, *Lopez 10*, Colombia. Cauca; MAP LOCALITY 25: *S. colombianum*, PI 320346, 2*n* = 48, *Hawkes 2544*, Colombia. Nariño; *S. colombianum*, PI 498150, 2*n* = 48, *Lopez et al. CCC 5141*, Colombia. Putumayo; MAP LOCALITY 26: *S. colombianum*, PI 498151, 2*n* = 48, *Lopez et al. CCC 5143*, Colombia. Nariño; *S. colombianum*, PI 498152, 2*n* = 48, *Lopez et al. CCC 5145*, Colombia. Nariño; MAP LOCALITY 27: *S. colombianum*, PI 561633, 2*n* = 48, *Spooner et al. 5025*, Ecuador. Pichincha; MAP LOCALITY 28: *S. colombianum*, PI 561625, 2*n* = 48, *Spooner et al. 5004*, Ecuador. Pichincha; *S. moscopanum*, PI 561626, 2*n* = 72, *Spooner et al. 5005*, Ecuador. Pichincha; *S. colombianum*, PI 561627, 2*n* = 48, *Spooner et al. 5006*, Ecuador. Pichincha; MAP LOCALITY 29: *S. colombianum*, PI 561647, 2*n* = 48, *Spooner et al. 5119*, Ecuador. Napo; *S. colombianum*, PI 567837, 2*n* = 48, *Spooner et al. 5120*, Ecuador. Napo; MAP LOCALITY 30: *S. colombianum*, PI 561652, 2*n* = 48, *Spooner et al. 5135*, Ecuador. Tungurahua; MAP LOCALITY 31: *S. tundalomense* Ochoa, CIP 761592, 2*n* = 72, *Ochoa 13359*, Ecuador. Azuay: between Cuenca and Quinua, 3200 m; *S. tundalomense*, CIP 761593, 2*n* = 72, *Ochoa 13366*, Ecuador. Azuay: Montes Burgay; *S. tundalomense*, CIP 761594, 2*n* = 72, *Ochoa 13367*, Ecuador. Azuay: between Cuenca and Macas; *S. tundalomense*, PI 473474, 2*n* = 72, *Ochoa et al. 11004*, Ecuador. Azuay; *S. colombianum*, PI 567834, 2*n* = 48, *Spooner et al. 5047*, Ecuador. Azuay; MAP LOCALITY 32: *S. colombianum*, PI 561640, *Spooner et al. 5062*, Ecuador. Cañar; *S. colombianum*, PI 561641, 2*n* = 48, *Spooner et al. 5063*, Ecuador. Cañar; *S. moscopanum*, PI 561659, 2*n* = 72, *Spooner et al. 5139*, Ecuador. Cañar; *S. moscopanum*, PI 561653, 2*n* = 72, *Spooner et al. 5140*, Ecuador. Cañar; MAP LOCALITY 33: *S. moscopanum*, PI 567812, 2*n* = 72, *Spooner et al. 5040*, Ecuador. Loja; MAP LOCALITY 34: *S. trinitense* Ochoa, CIP 763642, 2*n* = 24, *Ochoa et al. 16252*, Peru. Cajamarca: Contumazá, Montaña de Clarín, Totorilla-Cholol, 2700 m; MAP LOCALITY 35: *S. nubicola* Ochoa, CIP 761585, 2*n* = 48, *Ochoa 13335*, Peru. La Libertad: Pataz, Tayabamba, Palo Seco, Tauli to Huarimarca, 3650 m; MAP LOCALITY 36: *S. laxissimum* Bitter, CIP 763644, 2*n* = 24, *Ochoa 16255*, Peru. Pasco: Oxapampa, Chontabamba, Cerro San Crispín, uphill of Oyón, 2500 m; MAP LOCALITY 37: *S. laxissimum*, PI 498252, 2*n* = 24, *Ochoa et al. 11855*, Peru. Junín: Satipo, between Carrizal and Calabaza, 2700 m; MAP LOCALITY 38: *S. urubambae* Juz., CIP 762836, *Spooner et al. 7217*, Peru. Cuzco; *S. santolallae* Vargas, PI 607887, 2*n* = 24, *Spooner et al. 7228*, Peru. Cuzco, 2650 m, -13.18, -72.54; *S. buesii* Vargas, PI 607889, 2*n* = 24, *Spooner et al. 7235*, Peru. Cuzco: Urubamba. Growing about Rio Pacaymayo, at village of Pacaymayo, at crossing of River with Inca Trail N and W of Machu Pichu, 3600 m, -13.23, -72.5; MAP LOCALITY 39: *S. santolallae*, CIP 762857, *Spooner et al. 7237*, Peru. Cuzco: La Convención, 3 km along dirt road E and then S of center of Pistipata (just a few homes), E of Río Chun, 2350 m; MAP LOCALITY 40: *S. pillahuatense* Vargas, CIP 762840, *Spooner et al. 7220*, Peru. Cuzco: Paucartambo, Road Paucartambo-Pillcopata, ca 100 m S of Esperanza (6 km S of Pillahuata), ca 100 m down, 2800 m, -13.3155, -71.5916; *S. santolallae*, PI 473372, 2*n* = 24, *Hawkes et al. 5103*, Peru. Cuzco; *S. urubambae*, CIP 762845, *Spooner et al. 7225*, Peru. Cuzco: Paucartambo, road Amparaez to Pomacocha, footpath ca. 3 km before Hacienda Vilcabamba,300 m after bridge, 2600 m; MAP LOCALITY 41: *S. buesii*, PI 568922, 2*n* = 24, *Ochoa 13637*, Peru. Cuzco; *S. urubambae*, CIP 761795, 2*n* = 24, *Ochoa 13778*, Peru. Cuzco: La Convención, Sta. Teresa, Ccollpapampa y Totora, 2800 m; *S. urubambae*, CIP 761796, 2*n* = 24, *Ochoa 13778A*, Peru. Cuzco: La Convención, Sta. Teresa, Ccollpapampa y Totora, 2800 m; *S. urubambae*, CIP 763314, *Ochoa 13778A1*, Peru. Cuzco; *S. urubambae*, CIP 763315, *Ochoa 13778A2*, Peru. Cuzco; *S. urubambae*, CIP 761797, *Ochoa 13779*, Peru. Cuzco: La Convención, Sta. Teresa, between Pajcha and Wiñay Puquio, 2700 m; MAP LOCALITY 42: *S. limbaniense* Ochoa, CIP 752552, *Ochoa 12594*, Peru. Puno: Sandia, 2.5 km S continuing uphill, in direction away from town of Limbani, of town square of Phara, 3640 m; *S. limbaniense*, CIP 761967, *Ochoa 14288*, Peru. Puno: Sandia, Limbani, Cullucachi, 3500 m; *S. limbaniense*, CIP 761968, 2*n* = 24, *Ochoa 14290*, Peru. Puno: Sandia, Phara, ca. de Palca, 10 km de Phara, 3450 m; *S. limbaniense*, CIP 761970, 2*n* = 24, *Ochoa 14292*, Peru. Puno: Sandia, Phara, ca. de Palca, 10 km de Phara, 3450 m; *S. limbaniense*, CIP 762336, 2*n* = 24, *Ochoa 15601*, Peru. Puno: Sandia, Phara, Cullucachi, de Phara-Patambuco, 3500 m; *S. limbaniense*, CIP 762824, 2*n* = 24, *Salas and Spooner 7205*, Peru. Puno: Sandia; MAP LOCALITY 43: *S. violaceimarmoratum* Bitter, PI 498296, 2*n* = 24, *Ochoa 11901*, Bolivia. La Paz; MAP LOCALITY 44: *S. violaceimarmoratum*, PI 258856, 2*n* = 24, *Gandarillas s.n.*, Bolivia. La Paz; *S. violaceimarmoratum*, PI 473397, 2*n* = 24, *Hawkes et al. 5040*, Bolivia. La Paz; *S. violaceimarmoratum*, PI 473398, 2*n* = 24, *Hawkes et al. 5042*, Bolivia. La Paz; *S. violaceimarmoratum*, PI 631229, 2*n* = 24, *Spooner et al. 6731*, Bolivia. La Paz, Nor Yungas: at Chulumani, starting 15 km from junction of road out of La Paz at road to Caranavi and road to Chuspipata, 2450 m, -16.3, -67.85; *S. violaceimarmoratum*, CIP 760563, *Van Soest et al. 7*, Bolivia. La Paz, 44 km from La Paz tollgate on road to Undavi, near a hut, 3358 m; MAP LOCALITY 45: *S. violaceimarmoratum*, PI 473395, 2*n* = 24, *Hawkes et al. 4436*, Bolivia. Cochabamba; *S. violaceimarmoratum*, PI 473396, 2*n* = 24, *Hawkes et al. 4474*, Bolivia. Cochabamba; Not mapped: *S. colombianum*, PI 266384, 2*n* = 48, *Correll P.749*, Unknown locality; *S. colombianum*, PI 310983, 2*n* = 48, *Erwin Baur Sortiment 2179*, Colombia; *S. colombianum*, PI 566749, 2*n* = 48, *Lopez et al. CCC 5156*, Colombia. Valle; *S. laxissimum*, PI 283088, 2*n* = 24, *Erwin Baur Sortiment 1888*, Peru. Cuzco; *S. limbaniense*, PI 473468, 2*n* = 24, *Ochoa 5123*, Peru; *S. lobbianum*, PI 584488, 2*n* = 48, *Lopez et al. CCC 5166*, Colombia. Cundinamarca; *S. tundalomense*, CIP 761606, *Ochoa 13396*, Ecuador. Bolívar.

Series Piurana*—S. andreanum* Baker, PI 567813, 2*n* = 24, *Castillo et al. 1226*, Colombia. Nariño; *S. andreanum*, PI 247360, 2*n* = 24, *Correll C491*, Colombia. Nariño; *S. andreanum*, PI 320345, 2*n* = 24, *Hawkes 2546*, Colombia. Cauca; *S. andreanum*, PI 498147, 2*n* = 24, *Lopez et al. CCC 5142*, Colombia. Putumayo; *S. andreanum*, PI 597668, 2*n* = 24, *Lopez et al. CCC 5186*, Colombia. Putumayo; *S. andreanum*, PI 567819, 2*n* = 24, *Spooner et al. 5101*, Ecuador. Sucumbios; *S. andreanum*, PI 561658, 2*n* = 24, *Spooner et al. 5133*, Ecuador. Bolívar; *S. andreanum*, CIP 762817, *Spooner et al. 5153*, Ecuador. Morona-Santiago; *S. andreanum*, PI 561661, 2*n* = 24, *Spooner et al. 5155*, Ecuador. Morona-Santiago; *S. chomatophilum* Bitter, PI 266387, 2*n* = 24, *Correll P.862*, Peru. Cajamarca; *S. chomatophilum*, CIP 762649, 2*n* = 24, *Hawkes 2417*, Peru. Ancash; *S. chomatophilum*, PI 310990, 2*n* = 24, *Hawkes 2433*, Peru. Cajamarca; *S. chomatophilum*, PI 243340, 2*n* = 24, *Ochoa 1512a*, Peru. Cajamarca; *S. chomatophilum*, PI 243341, 2*n* = 24, *Ochoa 1664*, Peru. Amazonas; *S. chomatophilum*, PI 473460, 2*n* = 24, *Ochoa 11061*, Peru. Amazonas; *S. chomatophilum*, CIP 761271, 2*n* = 24, *Ochoa 11755*, Peru. La Libertad; *S. chomatophilum*, CIP 761541, 2*n* = 24, *Ochoa 13199*, Peru. Cajamarca; *S. chomatophilum*, CIP 761546, 2*n* = 24, *Ochoa 13204*, Peru. Cajamarca; *S. chomatophilum*, CIP 761549, 2*n* = 24, *Ochoa 13208*, Peru. Cajamarca; *S. chomatophilum*, CIP 761577, 2*n* = 24, *Ochoa 13288*, Peru. La Libertad; *S. chomatophilum*, CIP 761582, 2*n* = 24, *Ochoa 13325*, Peru. La Libertad; *S. chomatophilum*, CIP 763277, *Ochoa 13367a*, Peru. Pasco; *S. chomatophilum*, CIP 760913, *Ochoa S71*, Peru. Amazonas; *S. chomatophilum*, PI 365325, 2*n* = 24, *Ochoa S-42*, Peru. Amazonas; *S. chomatophilum*, CIP 762569, *Ochoa et al. 12561*, Peru. Cajamarca; *S. chomatophilum*, CIP 762575, 2*n* = 24, *Ochoa et al. 12570*, Peru. Cajamarca; *S. chomatophilum*, CIP 762055, 2*n* = 24, *Ochoa et al. 14486*, Peru. La Libertad; *S. chomatophilum*, CIP 763609, *Ochoa et al. 16060*, Peru. Cajamarca; *S. chomatophilum*, PI 365327, 2*n* = 24, *Ochoa et al. S-71*, Peru. Amazonas; *S. chomatophilum*, CIP 762941, 2*n* = 24, *Salas et al. 7322*, Peru. La Libertad; *S. chomatophilum*, CIP 762942, 2*n* = 24, *Salas et al. 7323*, Peru. La Libertad; *S. chomatophilum*, CIP 762946, 2*n* = 24, *Salas et al. 7327*, Peru. La Libertad; *S. chomatophilum*, CIP 762960, 2*n* = 24, *Salas et al. 7341*, Peru. La Libertad; *S. chomatophilum*, CIP 762966, 2*n* = 24, *Salas et al. 7347*, Peru. Ancash; *S. chomatophilum*, PI 310943, 2*n* = 24, *Ugent 5416*, Peru. Cajamarca; *S. contumazaense* Ochoa, CIP 762118, 2*n* = 24, *Ochoa 14751*, Peru. Cajamarca; *S. irosinum* Ochoa, CIP 761252, 2*n* = 24, *Ochoa 11640*, Peru. Cajamarca; *S. irosinum*, CIP 761257, 2*n* = 24, *Ochoa 11667*, Peru. Cajamarca; *S. irosinum*, PI 583305, 2*n* = 24, *Ochoa et al. 15210*, Peru. Cajamarca; *S. irosinum*, CIP 762259, 2*n* = 24, *Ochoa et al. 15225*, Peru. Cajamarca; *S. paucijugum* Bitter, CIP 761595, 2*n* = 48, *Ochoa 13371*, Ecuador. Cubillin; *S. paucijugum*, CIP 761597, 2*n* = 48, *Ochoa 13377*, Ecuador. Chimborazo; *S. paucijugum*, PI 567846, 2*n* = 48, *Spooner et al. 5071*, Ecuador. Chimborazo; *S. paucijugum*, PI 561643, 2*n* = 48, *Spooner et al. 5084*, Ecuador. Chimborazo; *S. paucijugum*, PI 561644, 2*n* = 48, *Spooner et al. 5094*, Ecuador. Cotopaxi; *S. paucijugum*, PI 583303, 2*n* = 48, *Spooner et al. 5096a*, Ecuador. Cotopaxi; *S. paucijugum*, PI 583299, 2*n* = 48, *Spooner et al. 5096b*, Ecuador. Cotopaxi; *S. paucijugum*, PI 561650, 2*n* = 48, *Spooner et al. 5129*, Ecuador. Cotopaxi; *S. paucijugum*, PI 561651, 2*n* = 48, *Spooner et al. 5130*, Ecuador. Cotopaxi; *S. paucijugum*, PI 561654, 2*n* = 48, *Spooner et al. 5151*, Ecuador. Chimborazo; *S. solisii* Hawkes, PI 473472, 2*n* = 48, *Ochoa et al. 10990*, Ecuador. Tungurahua; *S. tuquerrense* Hawkes, PI 338614, 2*n* = 48, *Hawkes 2547*, Colombia. Nariño; *S. tuquerrense*, PI 546033, 2*n* = 48, *Hoopes et al. 298*, Bolivia. Chuquisaca; *S. tuquerrense*, PI 498177, 2*n* = 48, *Lopez et al. CCC 5126*, Ecuador. Nariño; *S. tuquerrense*, CIP 761835, 2*n* = 48, *Ochoa 13835*, Ecuador. Pichincha; *S. tuquerrense*, PI 561628, 2*n* = 48, *Spooner et al. 5007*, Ecuador. Cotopaxi; *S. tuquerrense*, PI 561631, 2*n* = 48, *Spooner et al. 5022*, Ecuador. Pichincha; *S. tuquerrense*, PI 561632, 2*n* = 48, *Spooner et al. 5023*, Ecuador. Pichincha; *S. tuquerrense*, PI 561645, 2*n* = 48, *Spooner et al. 5097*, Ecuador. Cotopaxi; *S. tuquerrense*, PI 583300, 2*n* = 48, *Spooner et al. 5098*, Ecuador. Cotopaxi; *S. tuquerrense*, PI 567849, 2*n* = 48, *Spooner et al. 5100*, Ecuador. Carchi; *S. tuquerrense*, PI 561646, 2*n* = 48, *Spooner et al. 5111*, Ecuador. Imbabura; *S. tuquerrense*, PI 561657, 2*n* = 48, *Spooner et al. 5118*, Ecuador. Napo.