

RECLASSIFICATION OF LANDRACE POPULATIONS OF CULTIVATED POTATOES (*SOLANUM* SECT. *PETOTA*)¹

ZÓSIMO HUAMÁN^{2,4} AND DAVID M. SPOONER^{3,5}

²International Potato Center (CIP), Apartado 1558, Lima 12, Peru; and

³United States Department of Agriculture, Agricultural Research Service, Department of Horticulture, University of Wisconsin, 1575 Linden Drive, Madison, Wisconsin 53706-1590 USA

Cultivated potatoes have been classified as species under the International Code of Botanical Nomenclature (ICBN) and as cultivar-groups under the International Code of Nomenclature of Cultivated Plants (ICNCP); both classifications are still widely used. This study examines morphological support for the classification of landrace populations of cultivated potatoes, using representatives of all seven species and most subspecies as outlined in the latest taxonomic treatment. These taxa are *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, *S. phureja* subsp. *phureja*, *S. stenotomum* subsp. *stenotomum*, *S. stenotomum* subsp. *goniocalyx*, *S. tuberosum* subsp. *andigenum*, and *S. tuberosum* subsp. *tuberosum*. The results show some phenetic support for *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, and *S. tuberosum* subsp. *tuberosum*, but little support for the other taxa. Most morphological support is by using a suite of characters, all of which are shared with other taxa (polythetic support). These results, combined with their likely hybrid origins, multiple origins, evolutionary dynamics of continuing hybridization, and our classification philosophy, leads us to recognize all landrace populations of cultivated potatoes as a single species, *S. tuberosum*, with the eight cultivar-groups: Ajanhuiri Group, Andigenum Group, Chaucha Group, Chilotanum Group, Curtilobum Group, Juzepczukii Group, Phureja Group, and Stenotomum Group. We defer classification of modern cultivars, traditionally classified in Tuberosum Group, to a later study.

Key words: cultivated; nomenclature; phenetic; potato; sect. *Petota*; Solanaceae; *Solanum tuberosum*; taxonomy.

The cultivated potatoes of world commerce are collectively designated under the name *Solanum tuberosum*. In total, there are seven cultivated species (including *Solanum tuberosum*), including seven subspecies, according to the latest comprehensive taxonomic treatment of Hawkes (1990; Table 1). The cultivated potato taxonomy of the International Potato Center (CIP) and the United States potato genebank (NRSP-6) follows Hawkes (1990) because it is the latest comprehensive treatment and because he identified many of the cultivated species at CIP and NRSP-6. In addition to the cultivated species there are 199 tuber-bearing wild species relatives, distributed from the southwestern United States to south-central Chile (Spooner and Hijmans, 2001).

Hawkes' (1990) treatment of the seven cultivated species is not universally accepted and is part of a long history of disagreement among potato taxonomists of the treatment of both cultivated and wild species (Spooner and van den Berg, 1992). For example, the Russian potato taxonomists Bukasov (1971) and Lechnovich (1971) recognized 21 species, including separate species status for *S. tuberosum* subsp. *andigenum* (as *S. andigenum*) and subsp. *tuberosum* (as *S. tuberosum*). Ochoa (1990, 1999) recognized nine species (Table 2) and 141 infra-

specific taxa (subspecies, varieties, and forms; including his unlisted autonyms) for the Bolivian cultivated species alone.

There has been much controversy over the distinct species status of *S. andigenum* and *S. tuberosum* and which one gave rise to modern cultivars. Juzepczuk and Bukasov (1929) proposed that modern cultivars of *Solanum tuberosum* subsp. *tuberosum* originated from landraces from Chile. Hawkes (1990) and Hawkes and Francisco-Ortega (1993) suggested an origin of modern cultivars from Andean landraces of *S. tuberosum* subsp. *andigenum*, with later breeding with Andean landraces, Chilean landraces, and wild species. Hawkes (1990) classified Chilean landraces and modern potato cultivars under *Solanum tuberosum* subsp. *tuberosum*, as they have attained a similar morphology of wide leaflets and adaptation to flowering and tuberizing under long-day conditions.

Bukasov (1971), Lechnovich (1971), Hawkes (1990), and Ochoa (1990) classified potatoes as distinct species under the International Code of Botanical Nomenclature (ICBN; Greuter et al., 1999). Dodds (1962), in contrast, treated the cultivated species under the International Code of Nomenclature of Cultivated Plants (ICNCP; the latest version is Trehane et al., 1995). He suggested that there was poor morphological support for most cultivated species, and recognized only *S. ×curtilobum*, *S. ×juzepczukii*, and *S. tuberosum*, with five "groups" recognized in the latter (Table 2). "Cultivar-groups" (the current terminology) are taxonomic categories used by the ICNCP to associate cultivated plants with traits that are of use to agriculturists. The cultivar-group classification of Dodds (1962) was based on comparative morphology, reproductive biology, cytological and genetic data, and cultural practices. He contended that the morphological characters used by Hawkes (1956a, b) to separate species exaggerated the consistency of qualitative and quantitative characters. He showed that Andean farmers grow landraces of all ploidy levels together in the same field and that these can all potentially hybridize. He showed no genetic differentiation of the cultivated

¹ Manuscript received 26 July 2001; revision accepted 3 January 2002.

The authors thank Rene Gomez, Miguel Javier, and Omar Becerra for field assistance; Robert Hijmans for artwork and review; Thomas Lammers and John Wiersema for nomenclatural advice; and Wilbert Hettterscheid, John McNeill, and Ronald van den Berg for review. This work was funded by a grant from the United States Department of Agriculture, Foreign Agricultural Service, Scientific Cooperation Program, and the International Potato Center. Names are necessary to report data. However, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

⁴ Current address: Pro Biodiversity of the Andes (ProBioAndes), Av. R. Ferrero No. 1354, La Molina, Lima 12, Peru.

⁵ Author for reprint requests (e-mail: dspooner@facstaff.wisc.edu).

TABLE 1. Taxonomy and hypotheses of origins of the cultivated potato species (*Solanum* sect. *Petota*) recognized by Hawkes (1990).

Cultivated species	Putative origins (Hawkes, 1990)	Ploidy ($2n = 2x = 24$)	Distribution ^a
<i>Solanum ajanhuiri</i> Juz. and Bukasov, 'Yari' cultigens	<i>S. stenotomum</i> × <i>S. megistacrolobum</i> Bitter	2x	Central Bolivia
<i>Solanum ajanhuiri</i> Juz. and Bukasov, 'Ajawiri' cultigens	<i>Solanum ajanhuiri</i> ('Yari' clones) × <i>S. stenotomum</i>	2x	Southern Peru to central Bolivia
<i>S. chaucha</i> Juz. and Bukasov	<i>S. tuberosum</i> subsp. <i>andigenum</i> × <i>S. stenotomum</i> or <i>S. phureja</i>	3x	Ecuador to northern Peru
<i>S. curtilobum</i> Juz. and Bukasov	<i>S. juzepczukii</i> × <i>S. tuberosum</i> subsp. <i>andigena</i>	5x	Eastern Venezuela; central Peru to northern Argentina
<i>S. juzepczukii</i> Buk.	<i>S. stenotomum</i> × <i>S. acaule</i> Bitter	3x	Central Peru to northern Argentina
<i>S. phureja</i> Juz. and Bukasov subsp. <i>phureja</i>	Divergence from <i>S. stenotomum</i> by selection for rapid maturity and lack of tuber dormancy	2x	Venezuela to central Bolivia
<i>S. phureja</i> subsp. <i>estradae</i> (López) Hawkes	Autotetraploid of <i>S. phureja</i> subsp. <i>phureja</i> ; or <i>S. phureja</i> subsp. <i>phureja</i> × <i>S. tuberosum</i> subsp. <i>tuberosum</i>	4x	Central Colombia (Quindío Department)
<i>S. phureja</i> subsp. <i>hygrothermicum</i> (Ochoa) Hawkes	None stated	4x	Peru (eastern lowlands) ^b
<i>S. stenotomum</i> Juz. and Bukasov subsp. <i>stenotomum</i>	Selection from <i>S. leptophyes</i> Bitter (indigenous to Bolivia and Peru at Lake Titicaca region)	2x	Colombia to northern Argentina
<i>S. stenotomum</i> Juz. and Bukasov subsp. <i>goniocalyx</i>	Divergence from <i>S. stenotomum</i>	2x	Northern Peru to central Bolivia
<i>S. tuberosum</i> L. subsp. <i>andigenum</i> (Juz. and Bukasov) Hawkes ^c	<i>S. stenotomum</i> × <i>S. sparsipilum</i> (Bitter) Juz. and Bukasov	4x	Eastern Venezuela to northern Argentina
<i>S. tuberosum</i> subsp. <i>tuberosum</i>	Two origins, both from selection for long-day length adaptation from <i>S. tuberosum</i> subsp. <i>andigenum</i> ; once in Europe, and once in southern Chile.	4x	Landrace populations in southern Chile (Chiloé Island, Chonos Archipelago, and adjacent areas), modern cultivars grown worldwide.

^a Distributions from Hawkes and Hjerting (1989) and Hawkes (1990); updated by Huamán, Golmirzaie, and Amoros (1997).

^b See Ochoa and Ugent (2000) for recent distributional data.

^c The common tetraploid Andean potato has been widely cited incorrectly as *Solanum tuberosum* subsp. *andigena* Hawkes, but *Solanum tuberosum* subsp. *andigenum* (Juz. and Bukasov) Hawkes is the correct form, which we use throughout this paper.

diploids (Dodds and Paxman, 1962). He contended that his classification was conservative in that it "provides a genetically reasonable classification that disturbs the established usage of words [taxonomic names] as little as possible" (Dodds, 1962, p. 530).

Later data supported Dodds' (1962) hypothesis of poor morphological separation of the cultivated species and suggested that they formed a genetically diverse assemblage of genotypes of multiple and complex hybrid origins. Despite the contention of Jackson, Hawkes, and Rowe (1977) that there was

TABLE 2. Synopsis of taxonomic treatments of cultivated potatoes to the species level, except for *S. tuberosum*, with subspecies listed.

Ploidy	Bukasov (1971), Lechnovich (1971)	Dodds (1962)	Hawkes (1990) ^a	Ochoa (1990, 1999)
2x	<i>S. ajanhuiri</i> Juz. and Bukasov <i>S. canarense</i> Juz. and Bukasov <i>S. erlansonii</i> Bukasov <i>S. goniocalyx</i> Juz. and Bukasov <i>S. macmillanii</i> Bukasov <i>S. phureja</i> Juz. and Bukasov <i>S. rybinii</i> Juz. and Bukasov <i>S. stenotomum</i> Juz. and Bukasov	<i>S. tuberosum</i> Group Stenotomum Subgroup Goniocalyx Subgroup Stenotomum Group Phureja Subgroup Amarilla Subgroup Phureja	<i>S. ajanhuiri</i> <i>S. stenotomum</i> <i>S. phureja</i>	<i>S. ×ajanhuiri</i> <i>S. goniocalyx</i> <i>S. stenotomum</i> <i>S. phureja</i>
3x	<i>S. boyacense</i> Juz. and Bukasov <i>S. chaucha</i> Juz. and Bukasov <i>S. chocclo</i> Bukasov <i>S. ciezae</i> Bukasov and Lechn. <i>S. cuencanum</i> Juz. and Bukasov <i>S. juzepczukii</i> Bukasov <i>S. mamilliferum</i> Juz. and Bukasov <i>S. tenuifilamentum</i> Juz. and Bukasov	<i>S. tuberosum</i> Group Chaucha <i>S. ×juzepczukii</i>	<i>S. chaucha</i> <i>S. juzepczukii</i>	<i>S. ×chaucha</i> <i>S. ×juzepczukii</i>
4x	<i>S. andigenum</i> Juz. and Bukasov <i>S. molinae</i> Juz. <i>S. leptostigma</i> Juz. <i>S. tuberosum</i> L.	<i>S. tuberosum</i> Group Andigena Group Tuberosum	<i>S. tuberosum</i> subsp. <i>andigenum</i> Hawks subsp. <i>tuberosum</i>	<i>S. tuberosum</i> subsp. <i>andigenum</i> subsp. <i>tuberosum</i> <i>S. hygrothermicum</i>
5x	<i>S. curtilobum</i> Juz. and Bukasov	<i>S. ×curtilobum</i>	<i>S. curtilobum</i>	<i>S. ×curtilobum</i>

^a See Table 1 for an expansion of Hawkes' treatment.

limited gene flow between diploid and tetraploid cultivated species, Hawkes (1990) proposed that the triploid *S. chaucha* was of hybrid origin between the diploid species *S. phureja* subsp. *phureja* or *S. stenotomum* and the tetraploid species *S. tuberosum* subsp. *andigenum*. Many studies have shown that potato fields in the Andes contain mixtures of cultivated species at different ploidy levels (Ochoa, 1958; Huamán, 1975; Jackson, Hawkes, and Rowe, 1980; Brush, Carney, and Huamán, 1981; Johns and Keen, 1986; Johns et al., 1987; Quiros et al., 1990, 1992; Zimmerer, 1991). Cultivated species frequently co-occur with different wild potato species (Ugent, 1970; Huamán, 1975; Grun, 1990). The boundary between “cultivated” and “wild” is often vague, and some putative “wild” species may be revertants from cultivation (Spooner et al., 1999). Watanabe and Peloquin (1989, 1991) showed both diploid and unreduced gametes to be common in the South American wild and cultivated species, potentially allowing gene transfer among different ploidy levels. Huamán (1975) showed evidence of natural crosses between the diploid wild species *S. megistacrolobum* and the diploid cultivated species *S. stenotomum*. Open pollinated hybrid fruits were found in all experimental plots containing 10, 25, 50, and 90% of *S. megistacrolobum* plants within isolated plots of *S. stenotomum* grown in Huancayo, Peru. Rabinowitz et al. (1990) tested hypotheses of gene flow between the diploid wild taxon *S. sparsipilum* subsp. *sparsipilum* and the diploid cultivated species *S. stenotomum*. By use of isozyme markers specific to these populations, they were able to document high levels of natural gene flow in experimental field plots in the Andes. Tay (1979) showed extensive overlap of ranges of character states between *S. stenotomum* subsp. *stenotomum* and subsp. *goniocalyx* and questioned their treatment as distinct taxa. Hawkes and Hjerting (1989, p. 376) questioned the distinctness of all three diploid taxa (*S. phureja*, *S. stenotomum* subsp. *stenotomum*, *S. stenotomum* subsp. *goniocalyx*), except *S. ajanhuiri*. They suggested that “in the future they well may need to be classified entirely under *S. stenotomum*, with a subspecies distinction for *S. goniocalyx*, and perhaps also for *S. phureja*” (Hawkes and Hjerting, 1989, p. 376). Hawkes and Hjerting (1989, p. 388) recognized *S. chaucha* (triploid) despite their statement that “it is merely a convenient label for a series of nothomorphic forms resulting from many crosses between various clones of its parental species.”

The ICNCP groups cultivated plant names under denomination classes. A denomination class is a nomenclatural device found in the ICNCP, not the ICBN. It is defined (ICNCP Arts. 6.1, 17.2) as a taxon, or a designated subdivision of a taxon, or a particular cultivar-group, within which cultivated plant epithets must be unique. The botanical genus is the denomination class by default, but *Solanum tuberosum* is the accepted denomination class for cultivated potatoes (Trehane et al., 1995, p. 68). A cultivar epithet must only exist once in every denomination class (Spooner et al., 2002).

Classification and nomenclature of cultivated plants can follow rules of the ICNCP or the ICBN, and classifications of cultivated potatoes in one or the other may reflect differing hypotheses about their evolutionary dynamics. One hypothesis, presented by Ugent (1970; Fig. 1a) postulated extensive gene flow within and among ploidy levels of cultivated and wild species (the crop weed concept; e.g., Harlan, 1992), precluding maintenance of species. Conversely, Hawkes (1962, 1990; Fig. 1b) postulated gene flow to lead to stabilized hy-

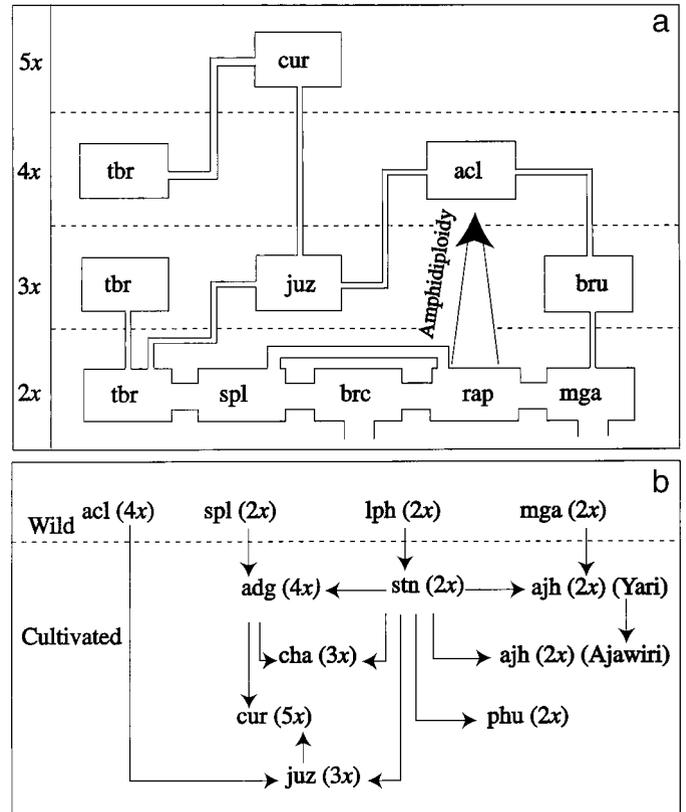


Fig. 1. A comparison of hypotheses of gene flow and hybrid speciation as redrawn from Ugent (1970; Fig. 1a) and Hawkes (1990; Fig. 1b). Ugent (Fig. 1a) postulated extensive gene flow among wild and cultivated species at all ploidy levels and interpreted this as disruptive of maintenance of good species. Hawkes (1990) postulated gene flow to lead to stabilized hybrids (Fig. 1b) and for further hybrids to be eliminated by reduction in their fertility (F_2 breakdown). The three-letter codes follow Spooner and Hijmans (2001). The wild taxa are: acl, *Solanum acaule* Bitter; brc, *S. brevicaulis* Bitter; bru, *S. ×bruecheri* Correll; cur, *S. curtisii* Juz. and Bukasov; lph, *S. leptophyes* Bitter; mga, *S. megistacrolobum* Bitter; rap, *S. raphanifolium* Cárdenas and Hawkes; spl, *S. sparsipilum* (Bitter) Juz. and Bukasov. The cultivated taxa are: adg, *S. tuberosum* subsp. *andigenum*; ajh, *S. ajanhuiri*; cha, *S. chaucha*; juz, *S. juzepczukii*; phu, *S. phureja* subsp. *phureja*; stn, *S. stenotomum* subsp. *stenotomum*; tbr, *S. tuberosum* (for Ugent, 1970), *S. tuberosum* subsp. *tuberosum* (for Hawkes, 1990).

brids and for further hybrids to be eliminated by reduction in fertility in advanced hybrid generations.

Ploidy level has been of great importance in the classification and identification of cultivated potatoes. Bukasov (1939) was the first to count chromosomes of the cultivated potatoes and discovered diploids, triploids, tetraploids, and pentaploids and used these data to speculate on their hybrid origins. In historical and current practice, identifications are frequently made only after chromosome counts are determined, and re-identifications made after chromosome counts do not match that expected for the species. The strong reliance on ploidy levels was clearly stated by Hawkes and Hjerting (1989, p. 389): “The chromosome number of $2n = 36$ largely helps to identify *S. chaucha*, but morphological characters can also be used.”

As taxonomists responsible for the identification and nomenclature of major germplasm holdings of cultivated and wild potatoes, we need to resolve these disagreements in tax-

TABLE 3. Characters used in the phenetic analysis of the cultivated potato species. All measurements for the quantitative characters are in millimeters, except as noted below. The 26 characters followed by an asterisk assess traits used in past treatments of the cultivated potatoes (Tables 1 and 2). The 38 characters followed by a separate number in parentheses were determined by a stepwise discriminant analysis (numbers 1–38 ordered by decreasing order of discriminant utility) to best discriminate the species. The statistical distributions of characters followed by an asterisk or number in parentheses are illustrated in Fig. 3.

Stem and habit characters

1. Stem color: (1) entirely green, (2) mostly green, (3) evenly green and purple, (4) mostly purple, (5) entirely purple.
2. Stem diameter at base.
- 3* (9). Plant height (cm).
- 4*. Plant habit: (1) slightly rosette, (2) semi-erect, (3) erect, (4) decumbent, (5) prostrate.
- 5*. (18). Number of primary stems per plant from base to 30 cm.

Leaf characters

- 6* (21). Length of average adaxial leaf pubescence (μm).
- 7*. Density of adaxial leaf pubescence (number of hairs/cm²).
- 8* (23). Length of average abaxial leaf pubescence (μm).
- 9*. Density of abaxial leaf pubescence (number of hairs/cm²).
- 10* (25). Leaf surface: (0) dull, (1) shiny, (2) very shiny.
11. Length of leaf (cm).
- 12* (20). Ratio: length of leaf/width of leaf.
- 13*. Ratio: length of the most distal lateral leaflet/distance on leaf rachis between the junction of the petiolules of the most distal lateral leaflet and the fourth-most distal lateral leaflet (Salaman leaf index; see text).
14. Ratio: length from widest part of leaf to apex/length of leaf.
- 15 (12). Length of petiolule (cm).
16. Number of lateral leaflet pairs.
17. Number of interjected leaflets.
18. Number of secondary lateral leaflets (= leaflets positioned on the secondary lateral leaflet petiolules).
- 19 (17). Leaflet margin: (0) undulate, (1) straight.
20. Length of terminal leaflet (cm).
- 21* (8). Ratio: length of terminal leaflet/width of terminal leaflet.
- 22 (36). Ratio: length from widest point of terminal leaflet to apex/length of terminal leaflet.
- 23 (7). Width of terminal leaflet from a point 5 mm below apex.
24. Terminal leaflet base: (1) evidently cuneate, (2) truncate to slightly cuneate, (3) truncate to slightly cordate, (4) evidently cordate.
- 25 (34). Length of terminal leaflet petiolule.
- 26 (32). Length of most distal lateral leaflet petiolule.
27. Angle of most distal lateral leaflet from leaf rachis as measured by the ratio: one half of width between apices of most distal lateral leaflet pair/length of most distal lateral leaflet.
28. Ratio: terminal leaflet length/length of most distal lateral leaflet.
29. Width of most distal lateral leaflet.
30. Ratio: length from widest part of most distal lateral leaflet to apex/length of most distal lateral leaflet.
31. Width of most distal lateral leaflet from a point 5 mm below apex.
- 32*. Ratio: length of most distal lateral leaflet/width of most distal lateral leaflet.
- 33* (4). Length of decurrency of first lateral leaflet on basicopic side as measured from leaflet petiolule to end of decurrency (measured from fifth leaf down from apex of plant).
34. Length from widest part of most distal lateral leaflet to apex.
- 35* (28). Ratio: length of third most distal lateral leaflet/length of second most distal lateral leaflet.
- 36* (30). Angle of base of leaf rachis to stem of fifth leaf down from apex of plant, 1 (= 10 degrees diverged from stem) to 9 (= leaf at right angle to stem).
- 37*. Angle of base of leaf rachis to stem on center leaf of plant, 1 (= 10 degrees diverged from stem) to 9 (= leaf at right angle to stem).
- 38* (38). Distal leaf (leaf tip) arching: (1) slightly arched up, (2) straight, (3) slightly arched down, (4) highly arched down.

Floral and fruit characters

39. Length of peduncle (cm).
 40. Number of flowers per inflorescence.
 41. Ratio: Number of flowers per inflorescence/number of peduncle forks per inflorescence.
 - 42 (11). Length of pedicel (cm).
 - 43* (19). Ratio: length of pedicel from base to articulation/length of pedicel.
 - 44* (33). Ratio: width of pedicel 2 mm below the base of the calyx/width of pedicel 2 mm below the articulation.
 - 45* (2). Pedicel articulation: (0) distinct, (1) indistinct.
 - 46* (15). Calyx symmetry: (0) symmetric, (1) asymmetric of 2 + 2 + 1 calyx lobe groupings, (2) asymmetric of 2 + 3 groupings.
 - 47* (3). Calyx base: (0) smoothly arched, (1) slightly angled without ribs, (2) greatly angled and ribbed.
 - 48 (35). Length of calyx acumen.
 49. Length of calyx lobe.
 - 50 (27). Ratio: length of calyx lobe/width of calyx lobe.
 - 51* (31). Radius of corolla (cm).
 - 52* (26). Ratio: length of center to base of corolla lobe/radius of corolla.
 - 53* (5). Ratio: width of corolla lobe at base of junction of corolla lobes/lobe length from base to tip of corolla lobe.
 - 54 (10). Length of anther.
 55. Length of style exertion from apex of anthers to apex of stigma.
 - 56 (13). Color of adaxial interpetolar tissue (see MATERIALS AND METHODS).
 57. Color of abaxial interpetolar tissue.
 - 58 (38). Color of adaxial corolla ray.
-

TABLE 3. Continued.

59.	Color of abaxial corolla ray.
60.	Color of adaxial corolla acumen.
61.	(24). Color of abaxial corolla acumen.
62.	Fruit length (cm).
63.	Ratio: Fruit length/fruit diameter at widest point.
Tuber characters	
64.	Predominant tuber skin color: (1) white-cream, (2) yellow, (3) orange, (4) brownish, (5) pink, (6) red, (7) purplish-red, (8) purple, (9) intensely dark purple.
65.	(29). Secondary tuber skin color: (0) uniform color throughout, (1) white-cream, (2) yellow, (3) orange, (4) brownish, (5) pink, (6) red, (7) purplish-red, (8) purple, (9) intensely dark purple.
66.	(16). Secondary tuber skin color distribution (see Ortiz and Huamán, 1994): (0) uniform throughout, (1) in the eyes, (2) in the eyebrows = the curved depression adjacent to the eye, (3) splashed, when the pigmented areas are around the eyes, (4) spectacled, when the non-pigmented areas are around the eyes, (5) scattered pigmented areas, (6) spots few and scattered, (7) stippled (spots small and uniformly distributed).
67.	(22). Predominant tuber flesh color: (1) white, (2) cream, (3) pale yellow, (4) yellow, (5) intense yellow, (6) red, (7) purple, (8) violet.
68.	Secondary tuber flesh color: (0) uniform color throughout, (1) white, (2) cream, (3) pale yellow, (4) yellow, (5) intense yellow, (6) red, (7) purple, (8) violet.
69.	Distribution of secondary flesh color: (0) uniform color throughout, (1) scattered spots, (2) stippled small spots, (3) scattered areas, (4) in a narrow vascular ring, (5) in a broad vascular ring, (6) in the vascular ring and medulla (pith), (7) in all flesh except medulla.
70.	Tuber shape (for illustrations see Huamán et al., 1977): (1) globose, (2) ovate, (3) obovate, (4) elliptic, (5) oblong, (6) long-oblong, (7) elongate.
71.	(14). Tuber eye position: (1) protruding, (2) shallow, (3) medium deep, (4) deep, (5) very deep.
72.	Tuber knobs: (1) relatively smooth, (2) slightly knobby, (3) strongly knobby, (4) digitate.
73.	Tuber curvature: (1) no curvature, as globose, to elongate, (2) reniform, (3) falcate, (4) spiral.
74.	(6). Tuber compression: (1) symmetrical in cross section, (2) flattened.
75*	(1). Tuber dormancy: (1) tubers with sprouts at harvest, (2) tubers without sprouts at harvest.

onomy. For the wild potato species, our goal is to produce a more stable and natural classification and to pursue monophyletic taxa (e.g., Baum and Donoghue, 1995). Our impression of extensive morphological intergradation among the cultivated species and knowledge of literature (above) led us to suspect, however, that the cultivated species were not monophyletic. The ICNCP recognizes the complex hybrid origins of most crops and focuses on a classification of convenience to users and nomenclatural stability needed for trade (Hatterscheid and Brandenburg, 1995). These are important practical goals. Potato genetic resources provide resistances, sometimes of an extreme type, to the pests and diseases affecting cultivated potato and are sources of improved agronomic traits (Ross, 1986; Hawkes, 1990; Spooner and Bamberg, 1994; Huamán, Golmirzaie, and Amoros, 1997). Publications reporting use of potato genetic resources appear monthly in the scientific literature. The treatments of Dodds (1962) and Hawkes (1990) continue to be widely used as parallel but competing taxonomic systems and maintain confusion among users and instability in taxonomy.

MATERIALS AND METHODS

Species—We planted 267 clonal accessions of landrace populations of cultivated potatoes (listed at <http://ajbsupp.botany.org/v89/>) obtained from CIP (Huamán, Golmirzaie, and Amoros, 1997). We chose up to 48 morphologically most distinct collections from each taxon as recognized by Hawkes (1990) (Tables 1 and 3), if this number was available from the collection (*S. ajanhuiri* had 7 accessions, *S. chaucha* had 37, *S. curtilobum* had 4, *S. juzepczukii* had 14, *S. phureja* subsp. *phureja* had 43, *S. stenotomum* subsp. *goniocalyx* had 32, *S. stenotomum* subsp. *stenotomum* had 42, *S. tuberosum* subsp. *andigenum* had 48, *S. tuberosum* subsp. *tuberosum* had 30, and putative hybrids between *S. stenotomum* subsp. *S. goniocalyx* and *S. stenotomum* subsp. *stenotomum* had 10). These include all species and subspecies of Hawkes (1990), except the rare and localized taxa *S. phureja* subsp. *estradae* and subsp. *hygrothermicum* (Table 1) that were not available for analysis. All

accessions of *S. tuberosum* subsp. *tuberosum* are landrace populations from Chile, not modern commercial cultivars.

We attempted to maximize morphological and geographical coverage of the collection and used putatively indigenous cultivated potatoes from Mexico to southern Chile (Fig. 2), and in the case of *S. tuberosum* subsp. *andigenum*, we used insights from work on establishing a core collection (Huamán and Stegemann, 1989; Huamán, Ortiz, and Gomez, 2000; Huamán et al., 2000). As outlined in Huamán, Golmirzaie, and Amoros (1997), CIP had only 10 accessions for *S. ajanhuiri*, 31 for *S. juzepczukii*, and 11 for *S. curtilobum*. However, the number of distinct genotypes of *S. ajanhuiri* in this collection was thought to be only seven (Huamán, Hawkes, and Rowe, 1980), for *S. juzepczukii* 21 (Schmiediche, Hawkes, and Ochoa, 1980), and for *S. curtilobum* 2 (Schmiediche, Hawkes, and Ochoa, 1980). Huamán (unpublished data) has observed five morphologically distinct types of the latter based on tuber skin color and sprout color, and we include four here. Five tubers of each accession were planted directly in a field plot in Huancayo, Peru (elevation 3200 m above sea level [a.s.l.], 12° S, 75° W). Vouchers were deposited at the herbarium of the International Potato Center in Lima, Peru (herbarium code CIP).

Data measurement—We measured only one plant per accession, as these are clonally maintained and represent one genotype. This differed from a similar study of the putative progenitors of cultivated potatoes, the *S. brevicaulis* complex, that measured six plants per accession, each grown from separate seeds of the accession (van den Berg et al., 1998). The middle of the five plants per row was measured per accession. We assessed 74 morphological characters; 54 were quantitative and 20 were qualitative (Table 3). We also assessed one developmental character used to define *S. phureja* (tuber dormancy at harvest, character 75, Table 3). Of the 54 quantitative characters, 17 were ratios to assess shapes, and none of these ratios weighted characters by using a character more than once. The 74 morphological characters assessed all 13 morphological characters mentioned in keys of Hawkes and Hjerting (1989), Hawkes (1990), and Ochoa (1990) to distinguish the species (Table 4). The raw data file is deposited at <http://ajbsupp.botany.org/v89/>.

Trichomes (characters 6–9) were measured with the aid of a binocular microscope and an ocular micrometer, from fully expanded leaves in the interveinal areas, not from the main vein, where trichomes were typically longer.

TABLE 4. Cultivated potato species as recognized by Hawkes (1990) and taxonomic characters used by Hawkes and Hjerting (1989), Hawkes (1990), and Ochoa (1990).^a Dashes indicate that characters were not mentioned by authors.

Taxon	Habit	Leaflet shape	Leaf arching	Leaf divergence from stem	Leaf pubescence	First lateral leaflet decurrency	Pedicle articulation position	Pedicle articulation presence	Upper pedicel diameter	Calyx symmetry	Calyx base	Corolla shape	Corolla diameter (mm)
<i>Solanum ajanhuiri</i>	semirosette	—	straight	—	soft hairy	broadly decurrent	very high, within 3–4 mm of calyx	indistinct	—	symmetrical	smoothly arched throughout	subrotate to pentagonal, lobes 4–5 mm long, w/o ^b acumens	—
<i>S. juzepczukii</i>	semirosette	—	straight	—	not soft hairy	not or barely decurrent	very high, within 3–4 mm of calyx	indistinct	—	—	smoothly arched throughout	rotate, short lobes (≤1–2 mm long) w/o acumens	small (15–25)
<i>S. curtilobum</i>	semirosette	—	straight	—	not soft hairy	not or barely decurrent	very high, within 3–4 mm of calyx	distinct	—	—	smoothly arched throughout	rotate, short lobes (≤1–2 mm long) w/o acumens	30–35
<i>S. chaucha</i>	branched and ascending	narrow	arched	—	—	not decurrent	lower	distinct	—	usually asymmetrical	smoothly arched throughout	lobes 2–3 × long as broad, broader than corolla radius	—
<i>S. phureja</i> subsp. <i>phureja</i>	branched and ascending	narrow	arched	—	sparsely pubescent	not decurrent	lower	distinct	—	symmetrical or asymmetrical	smoothly arched throughout	corolla lobes broader than length of petals	30–40
<i>S. stenotomum</i> subsp. <i>goniocalyx</i>	branched and ascending	—	arched	—	densely pubescent	not decurrent	lower	distinct	—	—	angled and ribbed	—	—
<i>S. stenotomum</i> subsp. <i>stenotomum</i>	branched and ascending	narrow	arched	—	densely pubescent	not decurrent	lower	distinct	—	variable	smoothly arched throughout	corolla lobes approximately 1/2 as long as length of petals	—
<i>S. tuberosum</i> subsp. <i>andigenum</i>	branched and ascending	narrow	arched	narrow	—	not decurrent	lower	distinct	same above and below	usually symmetrical	smoothly arched throughout	corolla lobes 1/2 long as broad	30–40
<i>S. tuberosum</i> subsp. <i>tuberosum</i>	branched and ascending	wide	arched	broad	—	not decurrent	lower	distinct	pedicels thickened above articulation	usually symmetrical	smoothly arched throughout	corolla lobes 1/2 long as broad	—

^a In addition, *S. chaucha* is mentioned with low seed production, and *S. phureja* subsp. *phureja* with no tuber dormancy.^b w/o = without.

When lengths varied, a mean length was scored. All other characters were measured with digital calipers or for plant height, a ruler. Leaf measurements were made from leaves in the center of the plant unless stated otherwise. Hawkes (1990) used the angle of divergence of the leaf from the stem to distinguish *S. tuberosum* subsp. *andigenum* from *S. tuberosum* subsp. *tuberosum*. To thoroughly assess this trait we measured this character on two different portions of the stem (characters 36 and 37). Floral characters were measured on the uppermost inflorescence. Corolla and tuber colors were measured using color charts that were designed at CIP (Huamán and Gómez, in press) and are available from the authors. Corolla colors are arranged from white to pink, to blue to lilac to violet, and intensities of these colors. The CIP color codes (in parentheses) and equivalent color codes from the Royal Horticultural Society (1986) [in brackets], are: white [155D], cream [10C], light yellow [5A] (1.1, 1.2, 1.3); light pink [65D], medium pink [68D], dark pink [57C] (2.1, 2.2, 2.3); light red [61C], medium red [67A], red-purple [71B] (3.1, 3.2, 3.3); light blue [108A], medium mauve [100D], dark mauve [102D] (4.1, 4.2, 4.3); medium blue [105B], dark blue [105A], blue-purple [94A] (5.1, 5.2, 5.3); light lilac [76C], medium lilac [84B], dark lilac [86D] (6.1, 6.2, 6.3); medium red purple [72A], darker red-purple [77A], dark red-purple [81A] (7.1, 7.2, 7.3); medium-purple [83B], dark purple [86A], dark violet [89A] (8.1, 8.2, 8.3). Tuber colors are explained in Table 3. Ratio characters 12 and 13 are different measures of leaf shape, and we used character 13 to test ideas of Salaman (1949) regarding morphological differences of the subspecies of *S. tuberosum* (long narrow leaves characteristic of subsp. *andigenum*, broad condensed leaves characteristic of subsp. *tuberosum*).

Data analysis—Quantitative characters were analyzed for their means, ranges, and standard deviations. Character distributions among taxa were determined in JMP statistical software (SAS, 1995) by the Tukey-Kramer honestly significant difference (HSD) test. Dendrograms including all accessions were produced by NTSYS-pc version 1.70 (Rohlf, 1992). Means for each character were standardized (STAND) and similarity matrices (in SIMINT) were generated using product-moment correlation (CORR), average taxonomic distance (DIST), Euclidean distance (EUCLID), and Manhattan distance (MANHAT). Clustering was performed using the unweighted pair-group method (UPGMA). Cophenetic correlation coefficients (COPH and MXCOMP) were used to measure distortion between the similarity matrices and the resultant three phenograms (Rohlf and Sokal, 1981; Sokal, 1986). Principal components analysis (PCA) was run with NTSYS-pc, and SAS, version 7 (1998). The PCA with NTSYS-pc used STAND, CORR, and EIGEN. Stepwise discriminant analysis (SDA) was performed with SAS using STEPDISC. Canonical discriminant analysis (CDA) was performed with SAS using CANDISC.

The PCA was performed three times, once with all 267 taxa and 75 characters, with NTSYS-pc that handles missing data. Because of the potential effect of missing data on phenetic results, we ran two additional analyses with no missing data cells, each constructed by elimination of characters or taxa. None of the accessions of *S. tuberosum* subsp. *tuberosum* produced flowers or fruits in Huancayo, Peru, so one analysis was run with all accessions but with the 25 floral characters and two fruit characters (Table 3) deleted for all taxa. Another analysis was made with 201 accessions that excluded the two fruit characters that were the most common missing data across all accessions and eliminated all 30 accessions of *S. tuberosum* subsp. *tuberosum* and 36 accessions of other taxa (also lacking flowers and fruits). Stepwise discriminant analysis was run with SAS on this 201 accession data set.

The SAS does not analyze any accessions with any missing data, and the CDA also was performed twice, using the same reduced data sets as above focused on the elimination characters or taxa. In addition, both these reduced dataset CDA analyses needed to be conducted with the elimination of two characters with only two character states that were invariant within taxa (pedicel articulation, character 45; tuber dormancy at harvest, character 75).

The PCA and CDA are both ordination techniques, but PCA makes no assumptions about group membership of OTUs. It attempts to portray multidimensional variation in the data set in the fewest possible dimensions, while maximizing the variation. The CDA uses assigned groups to derive a linear combination of the variables (morphological characters) that produces

the greatest separation of the groups (SAS, 1998) and is a much more powerful technique than PCA to separate groups. Cluster analysis, like PCA, makes no assumptions about group membership; it produces trees based on average similarity of all data. The PCA and dendrograms, therefore, are more appropriate to explore phenetic structure without any assumptions of species boundaries, while CDA is an appropriate technique to test pre-existing classifications.

RESULTS

Character state variation—Native *S. tuberosum* subsp. *tuberosum* from Chile flowers under the long-day conditions where it naturally grows. Under the short days of Peru, flowers (and fruits) are not produced, making flower and fruit data unavailable for the 30 accessions of *S. tuberosum* subsp. *tuberosum*. In total, data were missing for 5.8% of the 20025 possible data points, but 3.8% of these occurred in the floral and fruit measurements of *S. tuberosum* subsp. *tuberosum*. The SDA of the data set of 201 accessions determined 38 characters to best distinguish species. All 38 of these characters are listed in decreasing order of utility as discriminating factors in Table 3.

The Tukey-Kramer HSD test determined that all the characters were significantly different ($P = 0.05$) between at least two taxa. We show the means, ranges, and standard deviations of 42 of these 75 characters in Fig. 3. We chose them based on using 26 characters we consider to best assess components of characters used in past treatments (listed with an asterisk on Table 3), and all 38 characters of the SDA supported as distinguishing taxa (providing 16 additional characters considering duplicates of these two classes of characters). All characters are highly polymorphic, and the only absolute species-specific character state is for *S. phureja* subsp. *phureja*, distinguished by the one physiological character used in this study (tubers sprouted at harvest).

Phenetic results—A PCA of the entire data set (with NTSYS-pc) using all accessions and characters (5.8% missing data cells) is presented in Fig. 4. Principal components 1, 2, and 3 account for 10.0, 7.9, and 6.9% of the variation, respectively, for a total of 24.8%. This PCA most clearly delineates most accessions of *S. tuberosum* subsp. *tuberosum*, fewer accessions of *S. chaucha*, and yet fewer accessions of *S. phureja* subsp. *phureja*.

The dendrogram of the entire data set produced by DIST (not shown) had the highest cophenetic correlation coefficient (0.65), which is higher than those produced by MANHAT 0.60, CORR 0.55, and EUCLID 0.52. Rohlf (1992) stated that cophenetic correlations below 0.7 were a poor fit of the similarity matrix to the dendrogram. This dendrogram intermixes accessions of many species, including those of *S. tuberosum* subsp. *tuberosum* separated by PCA (above).

A PCA of one of the two reduced data sets (all accessions, only 51 of the 75 characters, no floral or fruit characters, no missing data cells) is presented in Fig. 5. This PCA most clearly separates *S. tuberosum* subsp. *tuberosum*, as in Fig. 4, showing that its morphological distinction is not an artifact of missing floral and fruit characters and that it is supported by vegetative characters. This PCA also provides some morphological support for most accessions of *S. juzepczukii*, but *S. chaucha* and *S. phureja* subsp. *phureja* are less well supported than in Fig. 4.

A PCA (from SAS) of the second of the two reduced data

sets (only 201 accessions, no *S. tuberosum* subsp. *tuberosum*, deleting the two fruit characters) is presented in Fig. 6. The first two factors best separate the taxa, and the third axis is not presented. This PCA shows much better morphological support for *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii*. All other taxa cluster together, but with a tendency for *S. phureja* subsp. *phureja* and *S. stenotomum* subsp. *goniocalyx* in one part of this cluster and *S. chaucha*, *S. stenotomum* subsp. *stenotomum*, and *S. tuberosum* subsp. *andigenum* in another part. The most significant difference between *S. stenotomum* subsp. *goniocalyx* and *S. phureja* subsp. *phureja* is that the former taxa produced dormant tubers, whereas in the latter taxa, the tubers where already sprouting at harvest time.

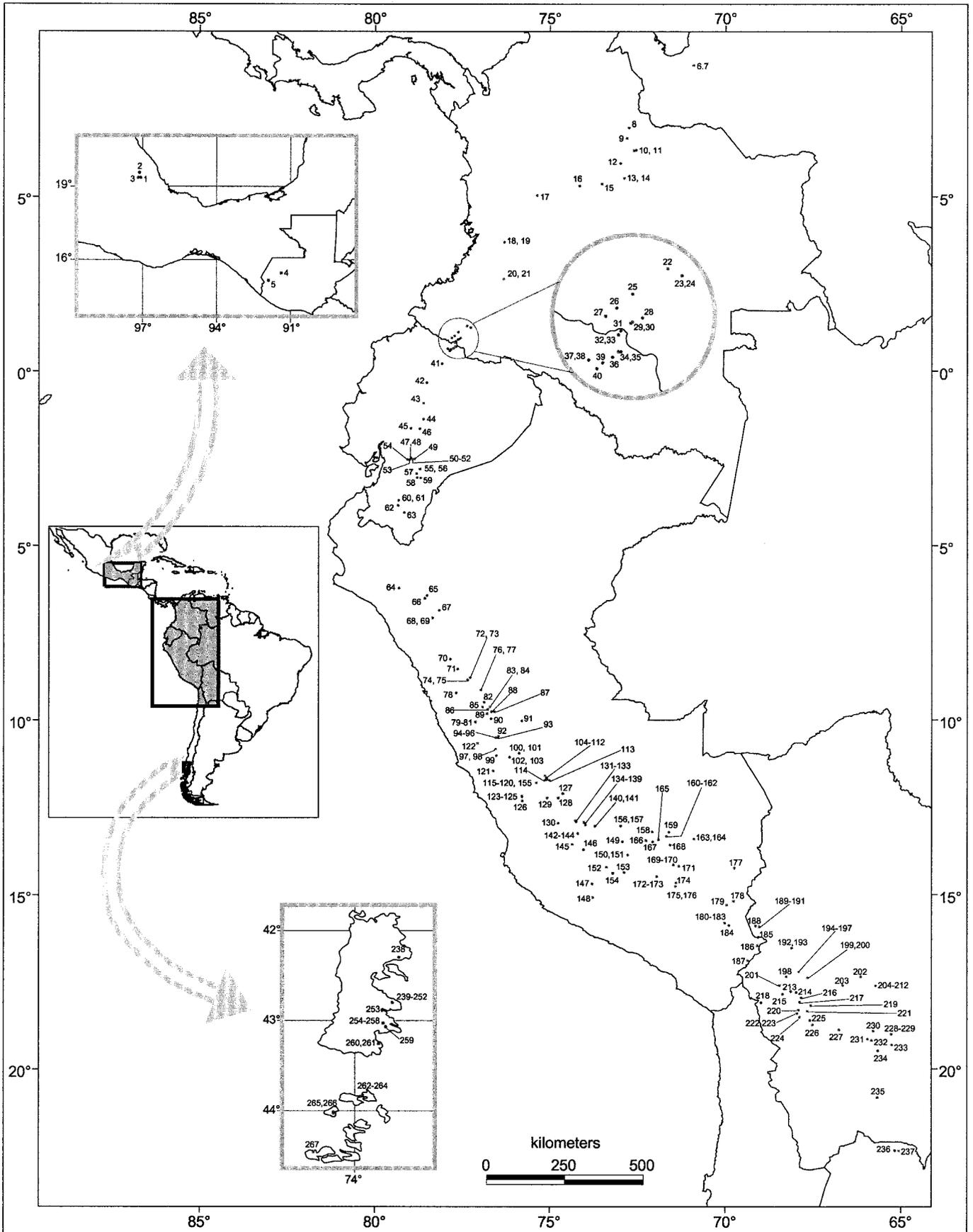
Because of the long controversy about the origin of the early European potato, with competing hypotheses about its origin in Chile (from *S. tuberosum* subsp. *tuberosum*) and the Andes (*S. tuberosum* subsp. *andigenum*) and because of the importance of these accessions for breeding, we investigated the morphological differences of Chilean landraces of subsp. *tuberosum* in detail. We used the Tukey-Kramer HSD test ($P = 0.05$) to find the characters separating *S. tuberosum* subsp. *tuberosum* from its phenetically most similar species *S. chaucha*, *S. stenotomum* subsp. *goniocalyx*, *S. phureja* subsp. *phureja*, *S. stenotomum* subsp. *stenotomum*, and *S. tuberosum* subsp. *andigenum* (excluding *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii*). These are (character numbers follow Table 3) stem color (1), plant height (3), density of adaxial leaf pubescence (7), length of leaf (11), ratio of the length of leaf to the width of leaf (12), ratio of the length of the most distal lateral leaflet to the distance on leaf rachis between the junction of the petiolules of the most distal lateral leaflet and the forthmost distal lateral leaflet (13), length of terminal leaflet (20), ratio of the length of terminal leaflet to the width of terminal leaflet (21), ratio of the length from widest point of terminal leaflet to apex to the length of terminal leaflet (22), width of terminal leaflet from a point 5 mm below apex (23), ratio of the length of most distal lateral leaflet to the width of most distal lateral leaflet (32), length from widest part of most distal lateral leaflet to apex (34), angle of base of leaf rachis to stem on fifth leaf down from apex of plant (36), and angle of base of leaf rachis to stem on center leaf of plant (37). Ten of these characters relate to those used previously to distinguish *S. tuberosum* subsp. *tuberosum* (Table 4) and show it to be distinguished by relatively shorter condensed leaves (the Salaman leaf index, above), wider leaflets, and leaves held more outward from the stem (not pointing upward). All of these characters overlap considerably with other species (Fig. 3).

A CDA of one of the two reduced data sets (all accessions, only 49 of the 75 characters) is presented in Fig. 7. This CDA continues to separate *S. tuberosum* subsp. *tuberosum* and this time not intermixed with a couple of accessions of *S. stenotomum* subsp. *stenotomum*, as in Figs. 4 and 5. It provides better morphological support for *S. ajanhuiri* and *S. juzepczukii* than in Fig. 4.

A CDA of the second of the two reduced data sets (201 accessions, 73 characters) is presented in Fig. 8. This CDA shows total morphological support for *S. ajanhuiri* and *S. juzepczukii* and that *S. curtilobum* is somewhat separated from

the other species. All other taxa form a single cluster, but with much better separation than the PCA in Fig. 6 for *S. phureja* subsp. *phureja* and *S. stenotomum* subsp. *goniocalyx* on one end, and *S. chaucha*, *S. stenotomum* subsp. *stenotomum*, and *S. tuberosum* subsp. *andigenum* on another end.

Our study showed that some key characters used by Hawkes (1990) and Ochoa (1990) overlap in range so much with those of other taxa that they have no or greatly reduced use in key construction. For example, both authors distinguished *S. phureja* subsp. *phureja* from *S. stenotomum* (both subspecies) by the fact that subsp. *phureja* has shiny leaves and *S. stenotomum* has dull leaves. Our results show *S. phureja* subsp. *phureja* to be shiny only 65% of the time and *S. stenotomum* subsp. *stenotomum* to be shiny 40% of the time. Hawkes (1990) distinguished *S. stenotomum* subsp. *goniocalyx* by tubers with bright yellow flesh, and we found only 16% with bright yellow flesh, 34% with yellow flesh, and 19% with pale yellow flesh. However, *S. phureja* subsp. *phureja* showed similar frequencies of yellow flesh to those of *S. stenotomum* subsp. *goniocalyx*. Hawkes (1990) also distinguished *S. stenotomum* subsp. *goniocalyx* from *S. stenotomum* subsp. *stenotomum* by the fact that subsp. *goniocalyx* has a ribbed calyx base and subsp. *stenotomum* has an unribbed base. We found *S. stenotomum* subsp. *goniocalyx* with ribbed bases 88% of the time, while *S. stenotomum* subsp. *stenotomum* had them 10% of the time. A ribbed calyx is also present in *S. phureja* subsp. *phureja* 79% of the time. Hawkes (1990) distinguished *S. tuberosum* subsp. *tuberosum* from *S. chaucha*, *S. phureja* subsp. *phureja*, and *S. stenotomum* by suggesting that *S. tuberosum* subsp. *tuberosum* has an unribbed calyx and *S. chaucha*, *S. phureja* subsp. *phureja*, and *S. stenotomum* had irregular calyx arrangements arranged as 2 + 2 + 1 or 2 + 3 groups. Although *S. tuberosum* subsp. *tuberosum* did not flower in our study, *S. chaucha* was regular 87% of the time; *S. phureja* subsp. *phureja* was 37%, *S. stenotomum* subsp. *stenotomum* was 29%, and *S. stenotomum* subsp. *goniocalyx* was regular 41% of the time. Hawkes (1990) recognized *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* as having the terminal leaflet not arched at the tip and all other taxa as having the terminal leaflet arched. Our data showed *S. ajanhuiri* and *S. curtilobum* to have the terminal leaflet to be slightly arched downward 100% of the time. *Solanum juzepczukii* showed 77% of leaflets slightly arched downward and 23% straight tips. All other species had from 66 to 89% arched downward and 11–34% straight leaf tips. Similarly, Hawkes (1990) considered *S. ajanhuiri* to be distinguished by its pentagonal corollas. Our measure of corolla dissection (ratio of corolla lobe width to lobe length; character 53 in Table 3) ranged from 1.5 to 2.0 in *S. ajanhuiri*, and similar ratios were found in both subspecies of *S. stenotomum* (60%) and in *S. tuberosum* subsp. *andigenum* (55%). The same ratio for other species range between 2.25 and 3.25 that include rotate and very rotate corollas. Hawkes (1990) distinguished *S. juzepczukii* by its smaller flowers. However, the corolla diameter of *S. juzepczukii* ranged from 3.0 to 4.0 cm, and we found similar sizes in *S. tuberosum* subsp. *andigenum* 21% of the time, *S. phureja* subsp. *phureja* 56%, *S. stenotomum* subsp. *stenotomum* 53%, and *S. stenotomum* subsp. *goniocalyx* 75% of the time.



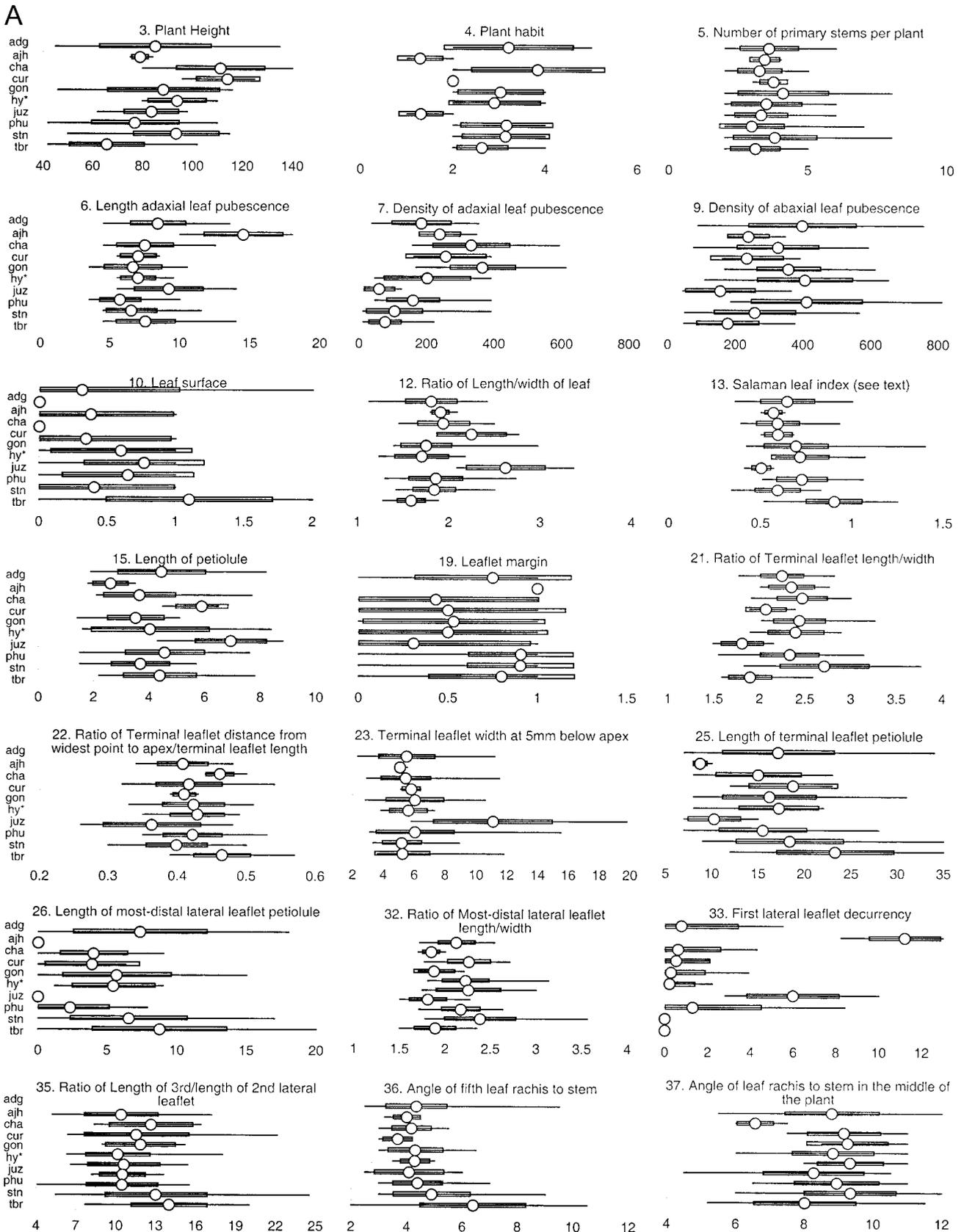


Fig. 3. Means, ranges, and one standard deviation of the mean of 44 of the 75 characters showing greatest separation of the cultivated species. Most characters are highly polymorphic, except pedicel articulation distinctness (character 45, Fig. 3B) and tubers sprouted at harvest (character 75, Fig. 3B). Species codes follow Fig. 1 with the addition of hy*, putative hybrids between *S. stenotomum* subsp. *S. goniocalyx* and *S. stenotomum* subsp. *stenotomum*; and character labels follow Table 3.

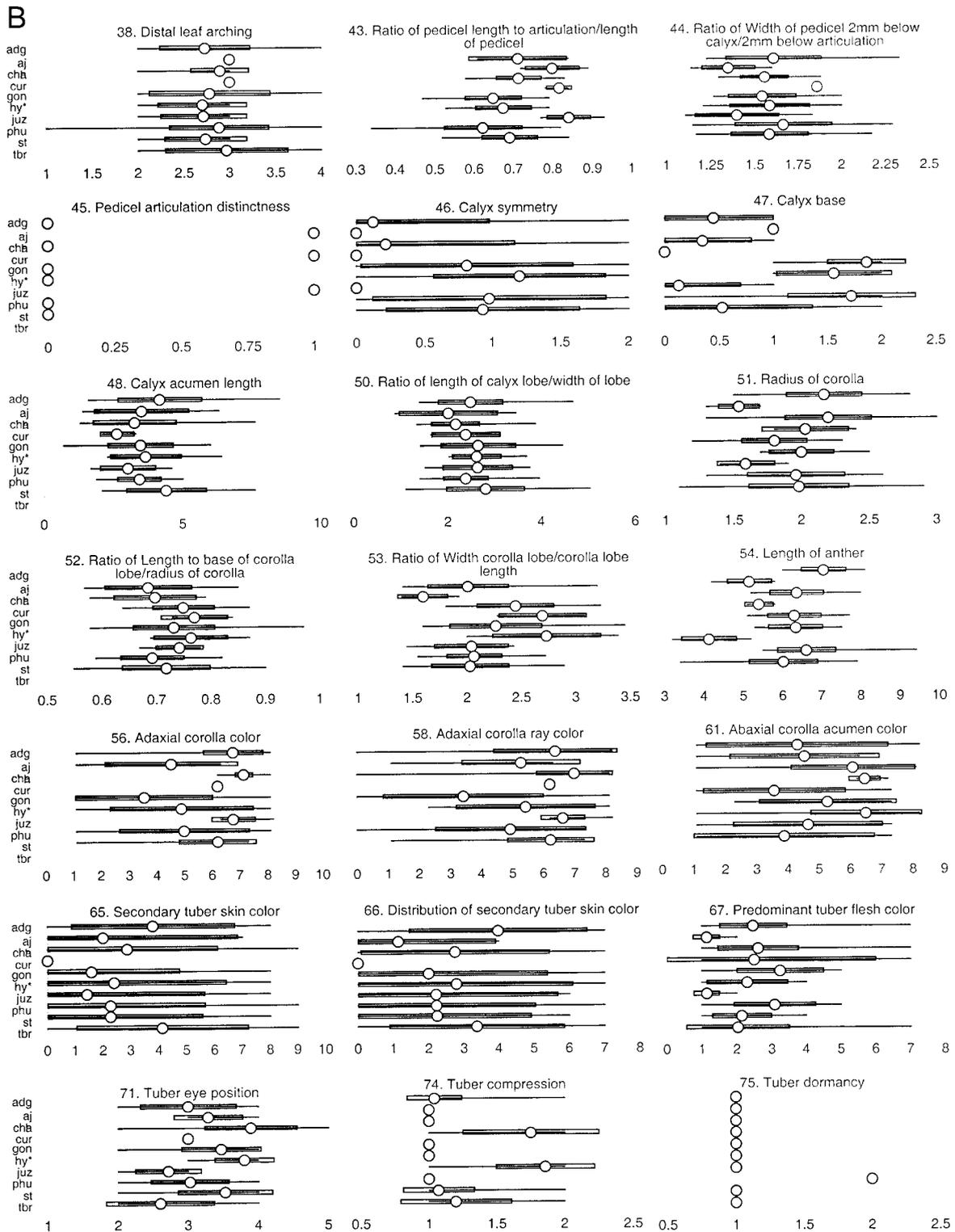


Fig. 3. Continued.

DISCUSSION

Species boundaries—At least some of the results show some degree of morphological support for *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, and *S. tuberosum*

subsp. *tuberosum* as separate taxa, but little to none for *S. phureja* subsp. *phureja*, *S. stenotomum* subsp. *goniocalyx*, *S. stenotomum* subsp. *stenotomum*, and *S. tuberosum* subsp. *andigenum*. Most characters, except tuber dormancy for *S. phureja* subsp. *phureja* and distinctness of pedicel articulation for

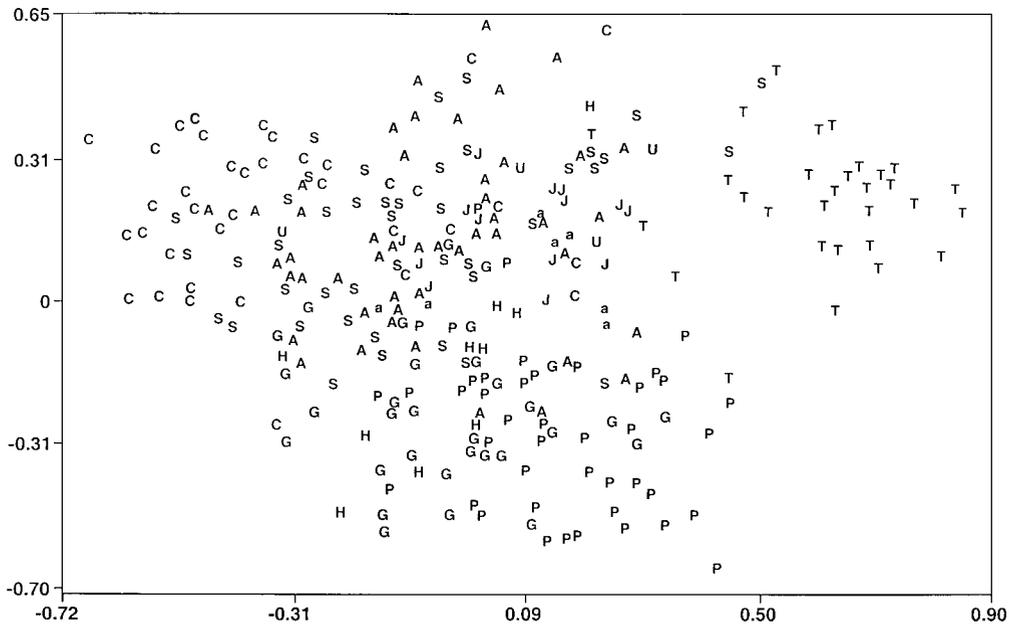


Fig. 4. Principal components analysis of the entire data set of 267 accessions and all characters (5.8% missing data cells, 3.8% of this in missing flower and fruit characters of *S. tuberosum* subsp. *tuberosum*). A, *S. tuberosum* subsp. *andigena*; C, *S. chaucha*; G, *S. stenotomum* subsp. *goniocalyx*; H, putative hybrids between *S. stenotomum* subsp. *goniocalyx* and *S. stenotomum* subsp. *stenotomum*; J, *S. juzepczukii*; P, *S. phureja* subsp. *phureja*; S, *S. stenotomum* subsp. *stenotomum*; T, *S. tuberosum* subsp. *tuberosum*; U, *S. curtilobum*.

S. ajanhuiri, *S. curtilobum*, and *S. juzepczukii*, overlap extensively with those of other species (Fig. 3b). In other words, most morphological support is by provided by a complex of characters that are shared with other taxa (polythetic support). The near sole reliance on polythetic support for taxa is typical

in the wild potato species, e.g., *Solanum* ser. *Demissa* (Spooner, van den Berg, and Bamberg, 1995) and ser. *Longipedicellata* (Spooner, van den Berg, and Miller, 2001).

For the wild species, our goal is to recognize monophyletic taxa (e.g., Baum and Donoghue, 1995), with a realization of

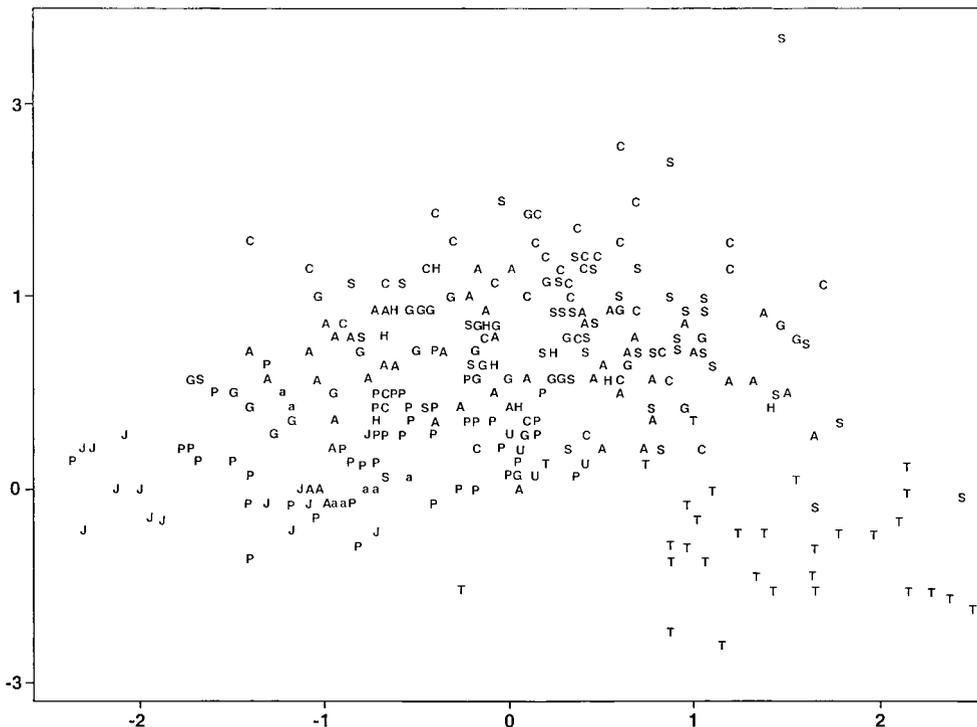


Fig. 5. Principal components analysis of a reduced data set of all accessions, only 51 of the 75 characters (no floral or fruit characters), no missing data cells; species codes as in Fig. 4.

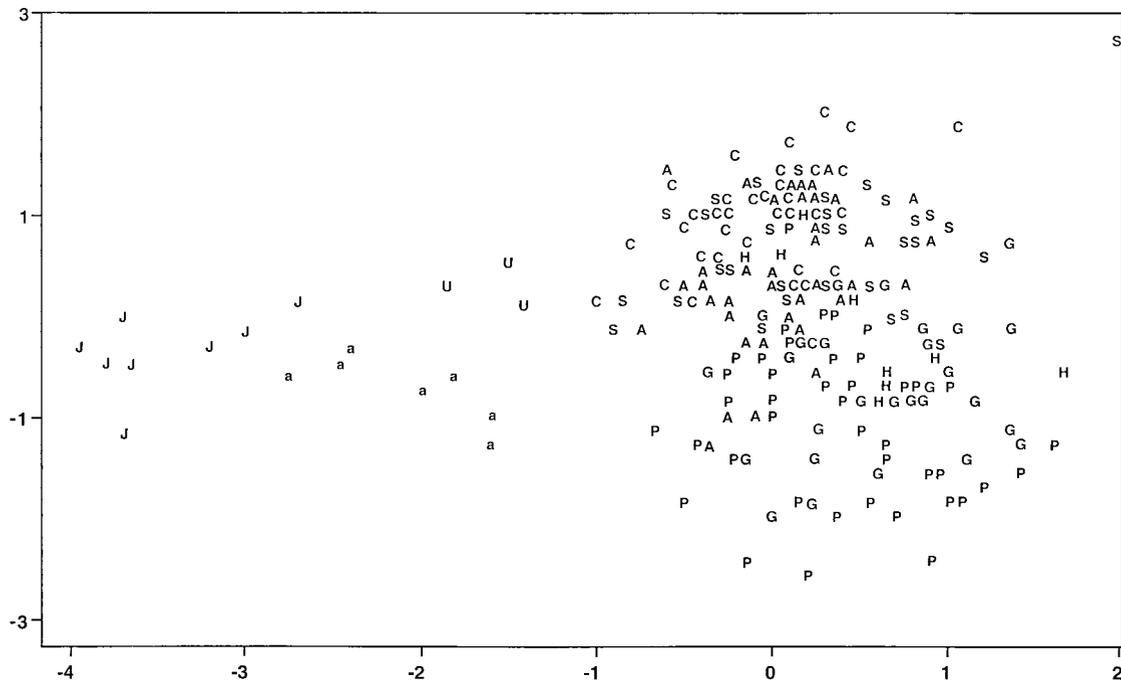


Fig. 6. Principal components analysis of a reduced data set of 201 accessions with complete data, eliminating all 30 accessions of *S. tuberosum* subsp. *tuberosum* and 36 accessions of other species and deletion of the two fruit characters 62, 63 as listed in Table 4; species codes as in Fig. 4.

the likely need to recognize some plesiospecies (e.g., Rieseberg and Brouillet, 1994; Olmstead, 1995). Our data and other data presented above, however, suggest that the cultivated species are of complex hybrid origins, often intergrade morphologically, and are better classified under the rules of the ICNCP that recognizes these phenomena as typical of crops and focuses on a classification of stability and convenience to users (Hetterscheid and Brandenburg, 1995; Spooner et al., 2002). While *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, and *S. tuberosum* subsp. *tuberosum* show some degree of morphological support, we consider treatment as cultivar-groups by the ICNCP to be a more appropriate classification. These "taxa" have common progenitors and/or common hybrid origins (Fig. 1) and undergo hybridization with wild and weedy taxa (except landrace populations of *S. tuberosum* subsp. *tuberosum*, which are geographically isolated from other wild potatoes). Many of the cultivated species likely were selected many times from members of the wild species in the *S. brevicaulle* complex (Ugent, 1970; Grun, 1990; Hosaka, 1995; van den Berg et al., 1998; Miller and Spooner, 1999). The distinction between wild and cultivated species is often vague, and some putative wild species could equally be progenitors or escaped cultivated species. Indeed, some accessions of both groups are so similar that classification as cultivated or wild often rests on whether they are collected in the wild or in a cultivated field (Spooner et al., 1999).

We agree with Hetterscheid and Brandenburg (1995), who argue that the ICBN should be reserved exclusively to name wild species, for which there is a better chance of discerning evolutionary relationships. This is more problematical for cultivated species because of more natural and artificial hybridization, movement of germplasm away from its natural geographic ranges and habitats, and rapid morphological change through artificial selection. Nomenclature in the ICBN is portrayed as a series of nested classification ranks. Each higher

rank (form, variety, subspecies, species, genus, etc.) contains the members of lower ranks, and membership in these ranks implies phylogenetic relationships. These authors advocate classification of cultivated plants as "cultura," not taxa, where no attempt is made to group cultivated plants in classifications implying phylogenetic relationships, except within larger taxa that are part of the denomination class (here *Solanum*, as *Solanum tuberosum* is the denomination class). Our proposed classification places all cultivated populations as cultivar-groups of the single denomination class *S. tuberosum*.

Because of some phenetic support (Figs. 4–8), a reasonable argument can be made to recognize *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, and *S. tuberosum* subsp. *tuberosum* as separate species or subspecies, and all the other taxa as cultivar-groups under a separate cultivated species *Solanum andigenum*. Support for a separate taxon treatment is provided by Raker and Spooner (2002) who demonstrate that most of the landrace populations of *S. tuberosum* subsp. *tuberosum* can be distinguished with microsatellite data from most populations of *S. tuberosum* subsp. *andigenum*, and we expect that molecular support will be provided for *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii*. Distinct species status also could be argued for *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* by their separate hybrid origins involving the phenetically distinct wild species *S. acaule* Bitter or *S. megistacrolobum* Bitter (Fig. 1b). *Solanum phureja*, *S. stenotomum* (both subspecies), and *S. tuberosum* subsp. *andigenum*, on the other hand, possibly evolved from members of the *S. brevicaulle* complex (*S. leptophyes*, *S. sparsipilum*) and the distinction between these wild and cultivated species is often vague (van den Berg et al., 1998; Miller and Spooner, 1999; Spooner et al., 1999). Separate species status also could be reasonably argued by a classification philosophy that focuses on a phenetic rather than a cladistic criteria to define taxa, as argued by McNeill (1998) and in review of our paper.

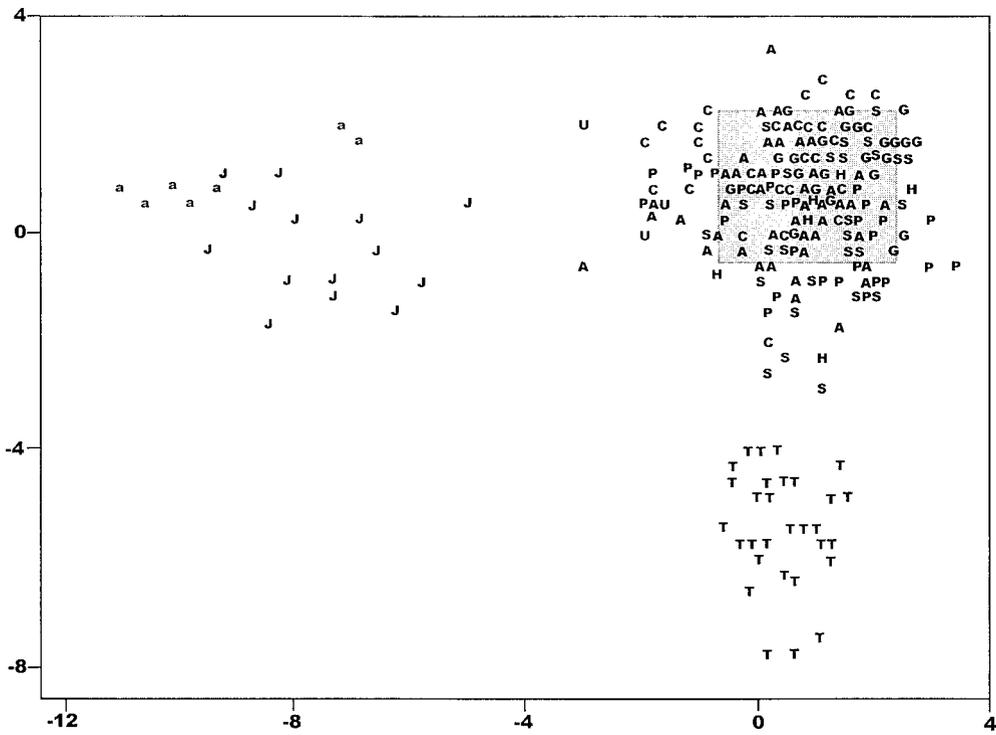


Fig. 7. Canonical discriminant analysis of the reduced data as in Fig. 5 but with tuber dormancy at harvest, character 75, also deleted; species codes as in Fig. 4. The area within the shaded square has 53 points (3As, 8Cs, 9Gs, 4Hs, 15Ps, 14Ss) not drawn because of insufficient space; all of these points fall under other points in this box.

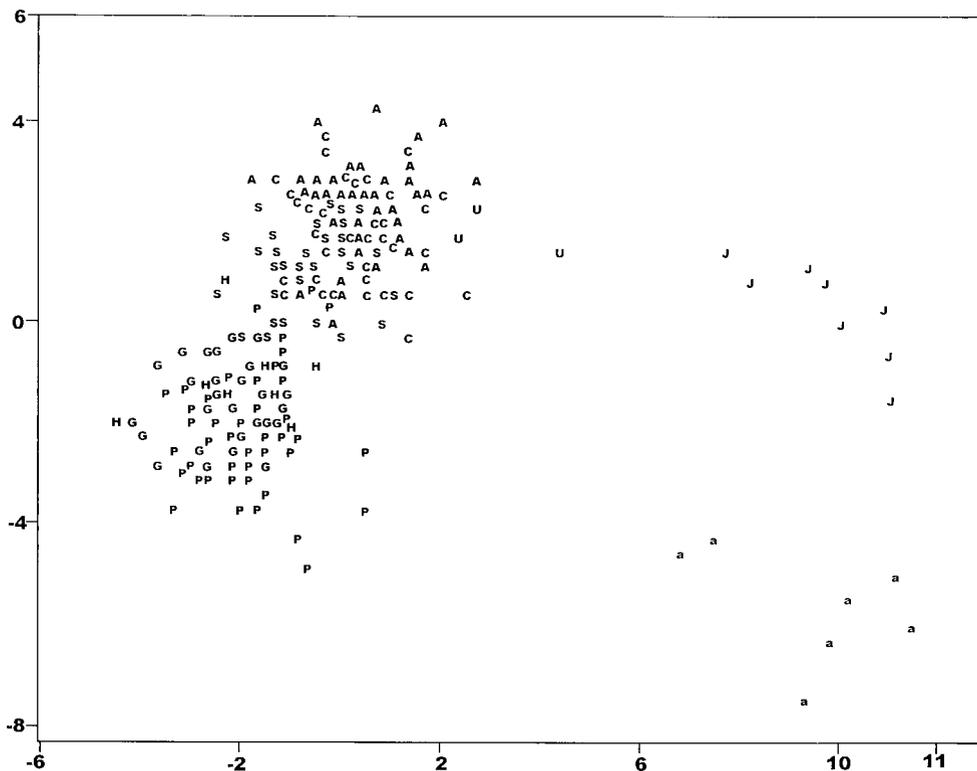


Fig. 8. Canonical discriminant analysis of the reduced data set of Fig. 6 but with pedicel articulation, character 45, and tuber dormancy at harvest, character 75, also deleted; species codes as in Fig. 4.

We classify cultivated species under the single denomination class *S. tuberosum* because of their predominant polythetic morphological support, reticulate origins (Hawkes, 1990; Huamán, Hawkes, and Rowe, 1980, 1982, 1983; Schmiediche, Hawkes, and Ochoa, 1982; Cribb and Hawkes, 1986), possible multiple origins involving common species (Hosaka, 1995), evolutionary dynamics of continuing hybridization, and our classification philosophy of the appropriateness of the ICNCP for cultivated species.

Our proposed classification does not provide synonymy of the many species names to these cultivar-groups. This is an unfinished nomenclatural task because many names published in the Russian literature are of dubious nomenclatural standing and have yet to be typified. However, Hawkes (1990) and Ochoa (1990) list many cultivated species synonyms. The association of species epithets to our cultivar-group names is clear by their similarity of names. We consider most accessions of *S. stenotomum* subsp. *goniocalyx* to be best classified in Stenotomum Group. Groups Andigenum, Chaucha, Phureja, and Stenotomum are clearly the most unnatural by any phylogenetic criterion. We maintain them as cultivar-groups only because they contain useful characters of ploidy or tuber dormancy mentioned in our keys that provide useful traits for breeders. If different classification needs become useful (such as tuber colors or disease resistances), additional and coexisting cultivar-group classifications can be made, as is allowed by the ICNCP.

We key out but do not provide cultivar-group name(s) for the modern advanced tetraploid varieties of potato (classified previously as *S. tuberosum* subsp. *tuberosum* or Group Tuberosum). These modern varieties have resulted from many separate crosses between Andigenum Group, Chilotanum Group, other cultivar-groups, and up to 16 wild species (Ross, 1986; Plaisted and Hoopes, 1989; Grun, 1990). The Chilean landraces and modern varieties differ as a group by isozymes (Ortiz and Huamán, 2001). These complex hybrid origins provide perhaps one of the strongest arguments for the necessity of the treatment of cultivated potatoes as cultivar-groups, rather than as species. We avoid their simple and traditional classification as Tuberosum Group at this time because they are not the subject of study here, and we think that breeders may benefit from cultivar-groups reflecting their actual use in breeding. For example, breeders typically group potatoes by tuber color and shape reflecting market classes such as long reds, round reds, long whites, round whites, yellows, or russets vs. smooth skins, forming potential cultivar-groups. We would make this classification only after consultation and consensus with user groups.

The ICNCP encourages (but does not require) nomenclatural standards (analogous to types) for cultivars, but no system of typification or use of standards is needed for the cultivar-group names. Cultivar-groups are intended to be solely classifications of convenience based on user-defined needs with no implication of relationships. To our knowledge, standards have never been designated for the cultivars. Many names have been published, however, for the Chilean landraces of “subsp. *tuberosum*” (Castronovo, 1949; Kostina, 1978), modern clones of subsp. *tuberosum* (Hamester and Hils, 1998), and landraces in Mexico (Ugent, 1968), South America (Hawkes, 1944, 1947), Peru (Soukup, 1939; Vargas, 1949, 1956; Ochoa, 1958), and Bolivia (Ballivan and Cevallos Tovar, 1914; La Barre, 1947; Ochoa, 1990).

Key to the landrace cultivar-groups of *Solanum tuberosum*—Our study documents that some cultivated species have some morphological support, but that these characters represent only typical traits and are not absolutely cultivar-group specific (Fig. 3). Consequently, our key (below) will not consistently separate these cultivar-groups. We include non-morphological characters of reaction to frost, tuber dormancy, day-length adaptation, and ploidy level that are not appropriate for keys of wild plants but are needed here as they are major traits used in the recognition of these cultivar-groups. The qualifier terms “mostly” or “usually” could be used throughout the key but are not used for simplicity.

1. Plants semi-rossette to semi-erect; articulation indistinct to only slightly distinct, located in the upper 1/5 of the pedicel; frost tolerant (of putative hybrid origin with the frost tolerant species *S. acaule* or *S. megistacrolobum*).
 2. Most distal lateral leaflets broadly decurrent; plants diploid. Ajanhuiri Group.
 2. Most distal lateral leaflets not or only slightly decurrent; plants triploid or pentaploid.
 3. Plants low growing, 62–98 cm tall; triploid. Juzepczukii Group.
 3. Plants of medium height, 96–125 cm tall; pentaploid. Curtilobum Group.
1. Plants ascending to erect; pedicel articulation evident, located below the upper 1/5 of the pedicel; generally not frost tolerant.
4. Plants adapted to long-day flowering and tuberization; upper leaves diverged from stem at angle of 50°–90°; tetraploid.
5. Landrace populations native to south-central Chile. Chilotanum Group.
5. Modern varieties originally derived from breeding populations in the northern hemisphere, now grown worldwide; of many complex hybrid origins from Chilotanum Group, Andigenum Group, other cultivar-groups, and up to 16 wild species. Cultivar-group name(s) yet to be proposed.
4. Plants adapted to short-day flowering and tuberization; upper leaves diverged from stem at 40°–50°; diploid or triploid or tetraploid.
6. Plants tetraploid. Andigenum Group.
6. Plants triploid. Chaucha Group.
6. Plants diploid.
7. Plants with tubers sprouting at harvest. Phureja Group.
7. Plants with tubers not sprouting at harvest. Stenotomum Group.

Descriptions of the landrace cultivar-groups of *Solanum tuberosum*—As documented above, there are different levels of morphological support for the eight cultivar-groups of *S. tuberosum* we recognize here, and many characters providing this support are polythetic in nature. The best morphologically supported cultivar-groups are Ajanhuiri Group, Curtilobum Group, Juzepczukii Group, and Chilotanum Group. The Andigenum Group, Chaucha Group, Phureja Group, and Stenotomum Group are primarily distinguished by tuber dormancy (Phureja Group) and ploidy. Consequently, we provide separate descriptions for Ajanhuiri Group, Curtilobum Group, Juzepczukii Group, and Chilotanum Group. We provide a single description for Andigenum Group, Chaucha Group, Phureja Group, and Stenotomum Group as one morphological unit, and the reader is directed to the key for the useful characters for breeders and other users. The group descriptions are followed with lists of some of the well-known cultivar epithets. Some of these are illegitimate, such as ‘Jancko’ (meaning white) and ‘Azul’ (purple), because colors are not allowed in cultivar names. Some epithets appear under two cultivar-groups (as ‘Azul’ in the Curtilobum Group and Juzepczukii Group) that also are not allowed because a cultivar epithet cannot be re-

peated in a denomination class. These and other errors in nomenclature will have to be corrected in the future.

Solanum tuberosum—*Solanum tuberosum* is here treated as a denomination class for all cultivated potatoes (Trehane et al., 1995, p. 68). Plants semi-rosette to ascending to erect, to 0.4–1.4 m tall; stems 5–19 mm wide at base, green to purple or splotched with green and purple, branched; leaves odd-pinnate, diverging from the main stem at about right angles or upright and at an angle of up to 25° from the main stem, terminal leaf tips straight to arched downwards at tip, with 3–8 pairs of lateral leaflets; interstitial leaflets absent or present, with up to 20 pairs; secondary leaflets on the petiolules absent or present, with up to 40 pairs; leaflets with apex acute to acuminate, base oblique, rounded to cuneate to cordate, leaflets ovate to elliptical, nearly glabrous to densely pubescent, margins straight to undulate, petiolulate to decurrent; pseudostipular leaves auriculate; inflorescence terminal and lateral; peduncles 3–22 cm long; 4–25 flowers per inflorescence; pedicel 10–35 mm long, articulate very near the top to below the middle; calyx smooth at base or with an encircling horizontal rib below the calyx lobes, regular or irregular with lobes in 1 + 2 + 2 or 2 + 3 groups, tube 3–10 mm long, lobes 1–5 mm long, short and acute to long attenuate, acumens 1–8 mm long; corolla 2–6 cm in diameter, rotate to rotate-pentagonal with short acumens, white to blue to purple to pink, lined or mottled; anthers 3–10 mm long, cordate at base; stigma inserted to exerted up to 7 mm from anther tube; fruits globose to long ovoid, medium to deep green, uniform or with white or purple spots or bands, to purple, 1–4 cm long; tubers with skin color white-cream to yellow to pink to red-purple to purple, uniform throughout or with secondary color in the eyes, eyebrows, around the eyes, stippled or scattered, flesh color white to cream to yellow to orange to red to purple to violet, uniform throughout or with secondary color distributed in the vascular ring or medulla, stippled or scattered, tuber shape globose to ovate to obovate to oblong to elliptic to elongated, smooth to knobby to digitate, tuber eyes shallow to deep, sprouting or dormant at harvest, chromosome number $2n = 2x = 24$, $2n = 3x = 36$, $2n = 4x = 48$, or $2n = 5x = 60$.

Landraces distributed throughout the South American Andes to south-central Chile, advanced clones grown worldwide.

Ajanhuiri Group—Plants semi-rosette when young, developing to sub-rosette or to semi-erect, to 0.4–0.7 m tall; stems 8–10 mm wide at base, green to splotched with green and purple, branched; leaves odd pinnate, upright and at an angle of 30–45° from the main stem, terminal leaf tips slightly arched downwards at tip, with 5–6 pairs of lateral leaflets, the uppermost of which are broadly decurrent onto the rachis on the basiscopic side; interstitial leaflets 3–5 pairs, secondary leaflets on the petiolule absent; leaflets with apex distinctly acute, base oblique to rounded, elliptic lanceolate leaflets, densely pubescent on both surfaces, undulate margins; pseudostipular leaves auriculate; peduncle 10–15 cm long; 9–12 flowers per inflorescence; pedicel 21–28 mm long, ratio of length of pedicel from base to articulation/length of pedicel between 0.72 and 0.89; calyx slightly angled, regular, 4–12 mm long, narrowly elliptic lobes shortly acuminate with acumens 1–4 mm long; corolla 2.5–3.5 cm in diameter, rotate-pentagonal, white, white with mauve streaks, blue-mauve, blue-purple; anthers 4–6 mm long; stigma exerted 3–4 mm from anther tube; fruits globose to ovoid, uniformly green or

tinged with purple, 2–3 cm long; tubers with skin color white-cream, white with scattered purplish-red, red-violet, purple, flesh color white to cream, uniform throughout, tuber shape ovate to elongated, smooth to knobby, tuber eyes shallow to deep, dormant at harvest, chromosome number $2n = 2x = 24$.

Landraces originally distributed in the high Andean altiplano between southern Peru and central Bolivia, at elevations between 3700 and 4100 m a.s.l. However, in Peru only the purple skinned 'Ajawiri' is scarcely grown. In the CIP genebank there are 10 cultivars of Ajanhuiri Group. These include 'Jancko Ajawiri', 'Laram Ajawiri', 'Jancko Yari', 'Wila Yari', 'Chañu Yari', 'Alka Yari', and 'Jancko Sisu Yari' reported in Huamán, Hawkes and Rowe (1980). Others from Bolivia are 'Chañu Ajawiri', 'Wila Palta Yari', and 'Wila Anckanche'.

Curtilobum Group—Plants forming a semi-rosette when young, developing to semi-erect and vigorous, to 0.5–0.9 m tall; stems 10–16 mm wide at base, green splotched with purple, branched; leaves odd pinnate, upright and at an angle of 30–40° from the main stem, terminal leaf tips slightly arched downwards at tip, with 5–6 pairs of lateral leaflets; interstitial leaflets 4–6 pairs, secondary leaflets on the petiolule absent; leaflets with apex shortly acuminate, base truncate to rounded to cordate, ovate to elliptical leaflets, sparsely pubescent, undulate to slightly straight margins; pseudostipular leaves auriculate; peduncle 7–8 cm long; 8–14 flowers per inflorescence; pedicel 16–22 mm long, ratio of length of pedicel from base to articulation/length of pedicel between 0.78 and 0.84; calyx smoothly arched, regular, 6–8.5 mm long, elliptic-lanceolate lobes abruptly narrowed at apex to very short pointed acumens 2–3.5 mm long; corolla 3.5–5 cm in diameter, rotate, lilac-purple; anthers 5–6 mm long; stigma exerted 3–4 mm from anther tube; fruits globose to ovoid, green uniform or tinged with purple, 2–3 cm long; tubers with skin color white-cream, white with scattered purple, purple with scattered white, purple, flesh color white, white with scattered purple or purple with scattered white, tuber shape oval-compressed, smooth, tuber eyes shallow to slightly deep, dormant at harvest; chromosome number $2n = 5x = 60$.

Landraces originally distributed throughout the highlands above 3800 m a.s.l. from northern Peru to central Bolivia and very rarely in northern Argentina. In the CIP genebank are cultivars mainly differentiated by the tuber skin color and sprout color. These have many different names including 'Shiri', 'Luki', 'Waña', 'Choquepito', 'Mallku', or 'Ococuri', alone or in combination with names describing the tuber skin color like 'Yuracc' or 'Jancko' (white), 'Yana', 'Laram', or 'Azul' (purple), or 'Pinta' (two colored).

Juzepczukii Group—Plants forming a semi-rosette when young, developing to semi-erect, to 0.4–0.8 m tall; stems 10–15 mm wide at base, green to green splotched with purple, branched; leaves odd pinnate, upright and at an angle of 25–60° from the main stem, terminal leaf tips slightly arched downwards at tip to straight, with 5–7 pairs of lateral leaflets, the uppermost of which are slightly decurrent onto the rachis on the basiscopic side; interstitial leaflets 1–4 pairs, secondary leaflets on the petiolule absent; leaflets with apex obtuse to acute, base cuneate or rounded, broadly ovate to broadly elliptical leaflets, rugose, sparsely pubescent; undulate to slightly straight margins; pseudostipular leaves auriculate; peduncle 7–16 cm long; 10–15 flowers per inflorescence; pedicel 22–35 mm long, ratio of length of pedicel from base to articulation/

length of pedicel between 0.77 and 0.93; calyx smoothly arched, regular, 4–10 mm long, triangular-lanceolate or elliptic-lanceolate lobes terminated in pointed acumens 2–4.5 mm long; corolla 3–4 cm in diameter, rotate, lilac-purple, dark red-purple, medium to dark purple; anthers 3–5 mm long; stigma exerted 1–2 mm from anther tube; fruits globose to ovoid, green to green tinged with purple, 0.5–1 cm long; tubers with skin color white-cream, white with scattered purple, red with scattered white, purple with scattered white, purple, flesh color white to cream, tuber shape ovoid, oblong or elliptical, tuber eyes shallow to medium deep, dormant at harvest; chromosome number $2n = 3x = 36$.

Cultivars originally distributed throughout the highlands above 3800 m from northern Peru to central Bolivia and very scarcely grown in northern Argentina. In the CIP genebank there are 34 different cultivars of Juzepczukii Group including those 21 reported by Schmiediche, Hawkes, and Ochoa (1980). These include 'Jancko Sisu', 'Laram Sisu', and 'Parco Sisu' that are putative natural hybrids between Ajanhuiri Group and *S. acaule* (Johns et al., 1987) and were described by Ochoa (1990). The most common cultivars are 'Kaisalla', 'Kanchillo', 'Pariña', 'Pechuma', 'Pinku', 'Piñaza', 'Mallku', 'Luki', 'Shiri', alone or in combination with the tuber skin color like 'Yuracc' or 'Jancko' (white); 'Yana', 'Chiar', 'Laram', or 'Azul' (Purple), 'Wila' (red-purple); 'Morocc' (two colored).

Chilotanum Group—Plants ascending to erect, to 0.4–1.0 m tall; stems 6–16 mm wide at base, green or spotted with purple, rarely purple spotted with green, branched; leaves odd pinnate, diverging from the main stem at about right angles or upright and at an angle of up to 50° from the main stem, terminal leaf tips slightly to highly arched downwards at tip, with 3–6 pairs of lateral leaflets; interstitial leaflets absent or present, with up to ten pairs, secondary leaflets on the petiolule generally absent, when present with up to five pairs; leaflets with apex acute to shortly acuminate, base generally cordate, sometimes rounded, rarely truncate or cuneate, ovate to ovate-elliptic to broadly elliptic-lanceolate, nearly glabrous to densely pubescent; generally shiny leaf surface, leaflet margins straight, rarely undulate; pseudostipular leaves auriculate to semielliptic, falcate; flowering absent or scarce under short days, peduncle up to 10 cm long; pedicel 10–20 mm long, ratio of length of pedicel from base to articulation/length of pedicel about 0.50; calyx regular, up to 8 mm long; corolla 2–4 cm in diameter, generally rotate with prominent acumens, white to pale pink, pale blue, or blue-purple to red-purple, uniform or with white acumens; anthers 5–7 mm long, cordate at base; stigma inserted to exerted from anther tube; fruits globose, about 2 cm long; tubers with skin color white-cream to light yellow to pink to red-purple to purple, uniform throughout or with secondary color in the eyes, eyebrows, around the eyes, stippled or scattered, flesh color white, cream, light yellow, rarely red to purple, uniform throughout or with secondary color stippled or scattered, rarely in the vascular ring or medulla, tuber shape globose to ovate to oblong, rarely elongated, generally smooth, tuber eyes generally shallow, rarely deep, dormant at harvest, chromosome number $2n = 4x = 48$.

Cultivars originally distributed in the island of Chiloé and adjacent islands in the Chonos Archipelago in Chile. In the CIP genebank there are 143 different accessions of Chilotanum Group native to Chile. Among the most widely distributed

are 'Chapiquina', 'Corahila', 'Chamizuda', 'Clavela', 'Azul', 'Mantequilla', 'Magelanes', 'Michune', 'Palmeta', 'Pichuna', 'Cielo', 'Chaitenera', and 'Camota'. Castronovo (1949) and Kostina (1978) described many of these cultivars.

Andigenum Group, Chaucha Group, Phureja Group, and Stenotomum Group—Plants semi-erect, erect, decumbent or prostrate, 0.4–1.4 m tall; stems 5–19 mm wide at base, green to purple, uniform or spotted with purple or green, branched; leaves odd pinnate, upright and diverging from the main stem at an angle of up to 25°, rarely at about right angles, terminal leaf tips straight to slightly arched downwards at tip, with 3–8 pairs of lateral leaflets; interstitial leaflets absent or present, with up to 20 pairs, secondary leaflets on the petiolule absent or present, with up to 40 pairs; leaflets with apex acute to acuminate, base oblique, rounded to cuneate to cordate, leaflet shape ovate to elliptical, apex acute to acuminate, base cordate to attenuate, leaf surface dull to shiny, nearly glabrous to densely pubescent; leaflet margins straight to undulate, petiolulate; pseudostipular leaves auriculate; peduncle 3–22 cm long; 4–25 flowers per inflorescence; pedicel 10–35 mm long, ratio of length of pedicel from base to articulation/length of pedicel between 0.34 and 0.84; calyx smoothly arched at base to greatly angled and ribbed, regular or irregular with lobes in 1 + 2 + 2 or 2 + 3 groups, 3–10 mm long, short and acute to long attenuate, acumens 1–8 mm long; corolla 2–6 cm in diameter, very rotate to rotate-pentagonal, white to lilac to pink to blue to purple, uniform or with a secondary color stippled, in bands, in the star, or white acumens in the adaxial, abaxial, or both sides; anthers 3–8 mm long, cordate at base; stigma inserted to exerted 7 mm from anther tube; fruits globose to ovoid, green, uniform, or tinged with white or purple spots or bands, 1–4 cm long; tubers with skin color white-cream to yellow to pink to red-purple to purple, uniform throughout or with secondary color in the eyes, eyebrows, around the eyes, stippled or scattered, flesh color white to cream to yellow to orange to red to purple to violet, uniform throughout or with secondary color distributed in the vascular ring or medulla, stippled or scattered, tuber shape globose to ovate to obovate to oblong to elliptic to elongated, smooth to knobby to digitate, tuber eyes shallow to very deep, sprouting or dormant at harvest, chromosome number $2n = 2x = 24$, $2n = 3x = 36$, $2n = 4x = 48$.

Cultivars originally distributed in the highlands of Mexico, Guatemala, Venezuela, Colombia, Ecuador, Peru, Bolivia, and northern Argentina. The characters distinguishing Andigenum Group, Chaucha Group, Phureja Group, and Stenotomum Group are shown in the key above.

In the CIP genebank, out of the 3227 accessions classified in Andigenum Group, 2379 have been found to be morphologically different and/or have different isozyme patterns (Huamán, Ortiz, and Gomez, 2000; Huamán et al., 2000). About half of the remaining 848 accessions could be different. The geographical distribution includes the highlands of Mexico, Guatemala, Venezuela, Colombia, Ecuador, Peru, Bolivia, and northern Argentina, at elevations between 1000 and 4300 m a.s.l. Widely known cultivars in Peru are 'Compis', 'Yana Imilla', 'Yuracc Imilla', 'Huagalina', 'Alka Tarma', 'Hualash', 'Cusi', 'Bole', 'Olones', 'Macctillo', 'Trombus', 'Huaccoto', 'Canteña'; in Bolivia 'Chiar Imilla', 'Sani Imilla', 'Sakampaya', 'Waycha', 'Waca Lajra', 'Pala', 'Koyllu', 'Koyu', 'Runa', 'Sipanacachi'; in Argentina 'Collareja', in Ecuador

'Leona'; in Colombia 'Arbolona'; in Venezuela, 'Criolla'; in Guatemala 'Colima'; and in Mexico 'Yema'.

The CIP genebank holds 167 accessions of Chaucha Group that comprise at least 101 cultivars. These include most cultivars reported by Ochoa (1975) and Jackson, Hawkes, and Rowe (1977). Some cultivars of Chaucha Group are genetically very similar and differ mainly in the tuber skin color. The geographical distribution includes elevations between 2100 and 4100 m a.s.l. throughout Peru, with less frequency in Bolivia, and is scarcely found in Ecuador and Colombia. Widely known cultivars are 'Puca Huayro', 'Muru Warmi', 'Aracc Zapato', 'Coeo Sullu', 'Yana Lenle', 'Puca Muru Rucma', and several colors of 'Suito', 'Chojllu', and 'Piña'.

There are 507 accessions of Stenotomum Group in the CIP genebank. These include 380 different cultivars. The remaining 127 accessions most likely comprise more additional different cultivars. The geographical distribution is throughout the highlands of Peru and Bolivia and is very scarcely found in Argentina, Ecuador, and Colombia, at elevations between 1900 and 4100 m a.s.l. Widely known cultivars are 'Pitiquiña', 'Amarilla', 'Peruanita', 'China Runtush', 'Ishco Puro', 'Huamantanga', 'Puca Fiñu', 'Thuruna', 'Cuchipa Acán', and 'Ichipisa'.

In the genebank at CIP there are 209 accessions of Phureja Group. So far, 131 different cultivars have been identified by morphological and molecular characterization. It is likely that within the remaining 78 accessions there are some additional different cultivars. Their geographical distribution is generally confined to the warmer sites in the Andean valleys between 1700 and 3700 m a.s.l. and very seldom up to 4000 m a.s.l., throughout Bolivia, Peru, Ecuador, and Colombia. Widely known cultivars are 'Yema de Huevo', 'Criolla', 'Phureja', 'Chaucha', 'Mambera', and 'Ratona'.

LITERATURE CITED

- BALLIVAN, M. V., AND W. CEVALLOS TOVAR. 1914. Nota histórica y clasificación de la papa de Bolivia. Ismael Argote, La Paz, Bolivia.
- BAMBERG, J. B., AND D. M. SPOONER. 1994. The United States Potato Introduction Station Herbarium. *Taxon* 43: 489–496.
- BAUM, D. A., AND M. J. DONOGHUE. 1995. Choosing among alternative "phylogenetic" species concepts. *Systematic Botany* 20: 560–573.
- BRUSH, S. B., H. J. CARNEY, AND Z. HUAMÁN. 1981. Dynamics of Andean potato agriculture. *Economic Botany* 35: 70–88.
- BUKASOV, S. M. 1939. The origin of potato species. *Physis (Buenos Aires)* 18: 41–46.
- BUKASOV, S. M. 1971. Cultivated potato species. In S. M. Bukasov [ed.], Flora of cultivated plants, vol. IX, 5–40. Kolos, Leningrad, Russia.
- CASTRONOVO, A. 1949. Papas chilotas, descripciones y clave para el reconocimiento de muestras de papas recogidas en una excursión al sur de Chile. *Revista de Investigaciones Agrícolas* 3: 209–245.
- CRIBB, P. J., AND J. G. HAWKES. 1986. Experimental evidence for the origin of *Solanum tuberosum* subspecies *andigena*. In W. G. D'Arcy [ed.], Solanaceae: biology and systematics, 384–404. Columbia University Press, New York, New York, USA.
- DODDS, K. S. 1962. Classification of cultivated potatoes. In D. S. Correll [ed.], The potato and its wild relatives. *Contributions from Texas Research Foundation, Botanical Studies* 4: 517–539.
- DODDS, K. S., AND G. J. PAXMAN. 1962. The genetic system of cultivated potatoes. *Evolution* 16: 154–167.
- GREUTER, W., J. MCNEILL, F. R. BARRIE, H. M. BURDETT, V. DEMOULIN, T. S. FILGUEIRAS, D. H. NICOLSON, P. C. SILVA, J. E. SKOG, P. TREHANE, N. J. TURLAND, AND D. L. HAWKSWORTH (EDITORS AND COMPILERS). 2000. International Code of Botanical Nomenclature (St. Louis Code). *Regnum Vegetabile* 138: 1–474.
- GRUN, P. 1990. The evolution of cultivated potatoes. In P. K. Bretting [ed.], New perspectives on the origin and evolution of New World domesticated plants. *Economic Botany* (3 Supplement) 44: 39–55.
- HAMESTER, W., AND U. HILS. 1998. World catalogue of potato varieties. Buchedition Agrimedia, Bergen, Germany.
- HARLAN, J. R. 1992. Crops and man, 2nd ed. American Society and Agronomy, and Crop Science Society of America, Madison, Wisconsin, USA.
- HAWKES, J. G. 1944. Potato collecting expeditions in Mexico and South America II: systematic classification of the collections. Imperial Bureau of Plant Breeding and Genetics, Cambridge, UK.
- HAWKES, J. G. 1947. On the origin and meaning of South American Indian potato names. *Journal of the Linnean Society, Botany* 50: 205–250.
- HAWKES, J. G. 1956a. A revision of the tuber-bearing solanums. *Annual Report of the Scottish Plant Breeding Station (1956)*: 37–109.
- HAWKES, J. G. 1956b. Taxonomic studies on the tuber-bearing Solanums. I. *Solanum tuberosum* and the tetraploid species complex. *Proceedings of the Linnean Society of London* 166: 97–144.
- HAWKES, J. G. 1962. The origin of *Solanum juzepczukii* Buk. and *S. curtilobum* Juz. et Buk. *Zeitschrift für Pflanzenzüchtung* 47: 1–14.
- HAWKES, J. G. 1990. The potato: evolution, biodiversity and genetic resources. Belhaven Press, Oxford, UK.
- HAWKES, J. G., AND J. FRANCISCO-ORTEGA. 1993. The early history of the potato in Europe. *Euphytica* 70: 1–7.
- HAWKES, J. G., AND J. P. HUERTING. 1989. The potatoes of Bolivia: their breeding value and evolutionary relationships. Oxford University Press, Oxford, UK.
- HETTERSCHIED, W. L. A., AND W. A. BRANDENBERG. 1995. Culton vs. taxon: conceptual issues in cultivated plant systematics. *Taxon* 44: 161–175.
- HOSAKA, K. 1995. Successive domestication and evolution of the Andean potatoes as revealed by chloroplast DNA restriction endonuclease analysis. *Theoretical and Applied Genetics* 90: 356–363.
- HUAMÁN, Z. 1975. The origin and nature of *Solanum ajanhuiri* Juz. et Buk., a South American cultivated diploid potato. Ph.D. dissertation, University of Birmingham, Birmingham, UK.
- HUAMÁN, Z., A. GOLMIRZAIE, AND W. AMOROS. 1997. The potato. In D. Fuccillo, L. Sears, and P. Stapleton [eds.], Biodiversity in trust: conservation and use of plant genetic resources in CGIAR Centres, 21–28. Cambridge University Press, Cambridge, UK.
- HUAMÁN, Z., AND R. GÓMEZ. In press. Identificación morfológica de duplicados en colecciones de papas cultivadas. Guía de Investigación No. 39. Centro Internacional de la Papa, Lima, Perú.
- HUAMÁN, Z., J. G. HAWKES, AND P. R. ROWE. 1980. *Solanum ajanhuiri*: an important diploid potato cultivated in the Andean altiplano. *Economic Botany* 34: 335–343.
- HUAMÁN, Z., J. G. HAWKES, AND P. R. ROWE. 1982. A biosystematic study of the origin of the diploid potato, *Solanum ajanhuiri*. *Euphytica* 31: 665–675.
- HUAMÁN, Z., J. G. HAWKES, AND P. R. ROWE. 1983. Chromatographic studies on the origin of the cultivated potato *Solanum ajanhuiri*. *American Potato Journal* 60: 361–367.
- HUAMÁN, Z., R. ORTIZ, AND R. GÓMEZ. 2000. Selecting a *Solanum tuberosum* subsp. *andigena* core collection using morphological, geographical, disease and pest descriptors. *American Journal of Potato Research* 77: 183–190.
- HUAMÁN, Z., R. ORTIZ, D. ZHANG, AND F. RODRÍGUEZ. 2000. Isozyme analysis of entire and core collections of *Solanum tuberosum* subsp. *andigena* potato cultivars. *Crop Science* 40: 273–276.
- HUAMÁN, Z., AND H. STEGEMANN. 1989. The use of electrophoretic analyses to verify morphologically identical clones in a potato collection. *Plant Varieties and Seeds* 2: 151–161.
- JACKSON, M. T., J. G. HAWKES, AND P. R. ROWE. 1977. The nature of *Solanum* × *chaucha* Juz. et Buk., a triploid hybrid cultivated potato of the South American Andes. *Euphytica* 26: 775–783.
- JACKSON, M. T., G. J. HAWKES, AND P. R. ROWE. 1980. An ethnobotanical field study of primitive potato varieties in Peru. *Euphytica* 29:107–113.
- JOHNS, T., Z. HUAMÁN, C. M. OCHOA, AND P. E. SCHMIEDICHE. 1987. Relationships among wild, weed, and cultivated potatoes in the *Solanum ajanhuiri* complex. *Systematic Botany* 12: 541–552.
- JOHNS, T., AND S. L. KEEN. 1986. Ongoing evolution of the potato on the altiplano of western Bolivia. *Economic Botany* 40: 409–424.
- JUZEPZUK, S. W., AND S. M. BUKASOV. 1929. A contribution to the question of the origin of the potato. *Trudy Vsesoyuznogo Szeda po Genetike i Seleksii* 3: 593–611. [in Russian, English summary.]
- KOSTINA, L. I. 1978. Native varieties of *Solanum chilotanum* Hawk. *Bulletin of Applied Botany, Genetics and Breeding* 62: 70–101. (Translated from Russian), United States Department of Agriculture, Washington, D.C.

- and National Science Foundation, Washington, D.C., Amerind Publishing Company, New Delhi, India.
- LA BARRE, W. 1947. Potato taxonomy among the Aymara Indians of Bolivia. *Acta Americana* 5: 83–103.
- LECHNOVICH, V. S. 1971. Cultivated potato species. In S. M. Bukasov [ed.], *Flora of cultivated plants*, chapter 2, 41–304. Vol. IX. Kolos, Leningrad, Russia.
- MCNEILL, J. 1998. Culton: a useful term, questionably argued. *Hortax News* 1: 15–22.
- MILLER, J. T., AND D. M. SPOONER. 1999. Collapse of species boundaries in the wild potato *Solanum brevicaulis* complex (Solanaceae, *S.* sect. *Petota*): molecular data. *Plant Systematics and Evolution* 214: 103–130.
- OCHOA, C. M. 1958. Expedición colectora de papas cultivadas a la cuenca del Lago Titicaca. I. Determinación sistemática y número cromosómico del material colectado. Programa Cooperativo de Experimentación Agropecuaria (PCEA), Ministerio de Agricultura, Lima, Perú.
- OCHOA, C. M. 1975. Las papas cultivadas triploides de *Solanum chaucha* y su distribución geográfica en el Perú. *Anales Científicos de la Universidad Agraria, Lima* 13: 31–44.
- OCHOA, C. M. 1990. The potatoes of South America: Bolivia. Cambridge University Press, Cambridge, UK.
- OCHOA, C. M. 1999. Las papas de Sudamérica: Perú. Centro Internacional de La Papa (CIP), Lima, Perú.
- OCHOA, C. M., AND D. UGENT. 2000. *Solanum hygrothermicum*, an endangered cultivated potato species. *Economic Botany* 4: 228.
- OLMSTEAD, R. G. 1995. Species concepts and plesiomorphic species. *Systematic Botany* 20: 623–630.
- ORTIZ, R., AND Z. HUAMÁN. 2001. Allozyme polymorphism in tetraploid potato gene pools and changes due to human selection. *Theoretical and Applied Genetics* 103: 792–796.
- PLAISTED, R. L., AND R. W. HOOPES. 1989. The past record and future prospects for the use of exotic germplasm. *American Potato Journal* 66: 603–627.
- QUIROS, C. F., S. B. BRUSH, D. S. DOUCHES, K. S. ZIMMERER, AND G. HUESTIS. 1990. Biochemical and folk assessment of variability of Andean cultivated potatoes. *Economic Botany* 44: 254–266.
- QUIROS, C. F., R. ORTEGA, L. VAN RAAMSDONK, M. E. HERRERA, P. CISNEROS, E. SCHMIDT, AND S. B. BRUSH. 1992. Increase of potato genetic resources in their center of diversity: the role of natural outcrossing and selection by the Andean farmer. *Genetic Resources and Crop Evolution* 39: 107–113.
- RAKER, C., AND D. M. SPOONER. 2002. Chilean tetraploid cultivated potato, *Solanum tuberosum*, is distinct from the Andean populations; microsatellite data. *Crop Science* 42, in press.
- RABINOWITZ, D., C. R. LINDER, R. ORTEGA, D. BEGAZO, H. MURGUIA, D. S. DOUCHES, AND C. F. QUIROS. 1990. High levels of interspecific hybridization between *Solanum sparsipilum* and *S. stenotomum* in experimental plots in the Andes. *American Potato Journal* 67: 73–81.
- RIESEBERG, L. H., AND L. BROUILLET. 1994. Are many plant species paraphyletic? *Taxon* 43: 21–32.
- ROHLF, F. J. 1992. NTSYS-pc, numerical taxonomy and multivariate system. Exeter Publishing, Ltd., New York, New York, USA.
- ROHLF, F. J., AND R. R. SOKAL. 1981. Comparing numerical taxonomic studies. *Systematic Zoology* 30: 459–490.
- ROSS, H. 1986. Potato breeding: problems and perspectives. *Advances in Plant Breeding Supplement* 13.
- ROYAL HORTICULTURAL SOCIETY. 1986. RHS colour chart. Royal Horticultural Society, London, UK.
- SALAMAN, R. 1949. The character of the early European potato. *Proceedings of the Linnean Society, London* 161: 71–84.
- SAS. 1995. JMP software, version 3.1. SAS Institute, Cary, North Carolina, USA.
- SAS. 1998. SAS proprietary software, version 7. SAS Institute, Cary, North Carolina, USA.
- SCHMIEDICHE, P. E., J. G. HAWKES, AND C. M. OCHOA. 1980. Breeding of the cultivated potato species *Solanum* × *juzepeczukii* Buk. and *S.* × *curtilobum* Juz. et Buk. I. A study of the natural variation of *S.* × *juzepeczukii*, *S.* × *curtilobum* and their wild progenitor, *S. acaule*. *Bitt. Euphytica* 29: 685–704.
- SCHMIEDICHE, P. E., J. G. HAWKES, AND C. M. OCHOA. 1982. The breeding of the cultivated potato species *Solanum* × *juzepeczukii* and *S.* × *curtilobum*. II. The resynthesis of *S.* × *juzepeczukii* and *S.* × *curtilobum*. *Euphytica* 31: 395–707.
- SOKAL, R. R. 1986. Phenetic taxonomy: theory and methods. *Annual Review of Ecology and Systematics* 17: 423–442.
- SOUKUP, V. 1939. La clasificación de las papas del Depto. De Puno. Ministerio de Agricultura y Ganadería, Lima, Perú.
- SPOONER, D. M., AND J. B. BAMBERG. 1994. Potato genetic resources: sources of resistance and systematics. *American Potato Journal* 71: 325–337.
- SPOONER, D. M., W. L. A. HETTERSCHIED, R. G. VAN DEN BERG, AND W. BRANDENBURG. 2002. Plant nomenclature and taxonomy: an horticultural and agronomic perspective. *Horticultural Reviews* 26, in press.
- SPOONER, D. M., AND R. J. HIJMANS. 2001. Potato systematics and germplasm collecting, 1989–2000. *American Journal of Potato Research* 78: 237–268; 395.
- SPOONER, D. M., A. SALAS-L., Z. HUAMÁN, AND R. J. HIJMANS. 1999. Wild potato collecting expedition to southern Peru (Departments of Apurímac, Arequipa, Cusco, Moquegua, Puno, Tacna) in 1998: taxonomy and genetic resources. *American Journal of Potato Research* 76: 103–119.
- SPOONER, D. M., AND R. G. VAN DEN BERG. 1992. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Genetic Resources and Crop Evolution* 39: 23–37.
- SPOONER, D. M., R. G. VAN DEN BERG, AND J. B. BAMBERG. 1995. Examination of species boundaries of *Solanum* series *Demissa* and potentially related species in series *Acaulia* and series *Tuberosa* (sect. *Petota*). *Systematic Botany* 20: 295–314.
- SPOONER, D. M., R. G. VAN DEN BERG, AND J. T. MILLER. 2001. Species and series boundaries of *Solanum* series *Longipedicellata* (Solanaceae) and phenetically similar species in ser. *Demissa* and ser. *Tuberosa*: implications for a practical taxonomy of section *Petota*. *American Journal of Botany* 87: 113–130.
- TAY, C. S. 1979. Evolutionary studies on the cultivated diploid potatoes *Solanum stenotomum*, *S. goniocalyx*, and *S. phureja*. Ph.D. dissertation, University of Birmingham, Birmingham, UK.
- TREHANE, P., C. D. BRICKELL, B. R. BAUM, W. L. A. HETTERSCHIED, A. C. LESLIE, J. MCNEILL, S. A. SPONGBERG, AND F. VRUGTMAN. 1995. International code of nomenclature of cultivated plants. *Regnum Vegetabile* 133: 1–175.
- UGENT, D. 1968. The potato in Mexico: geography and primitive culture. *Economic Botany* 22: 108–123.
- UGENT, D. 1970. The potato: what is the origin of this important crop plant, and how did it first become domesticated? *Science* 170: 1161–1166.
- 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 brevicaulis* complex (Solanaceae: sect. *Petota*). *American Journal of Botany* 85: 92–109.
- VARGAS, C. 1949. Las papas sudperuanas, part I. Publicaciones Universidad Nacional del Cuzco, Cuzco, Peru.
- VARGAS, C. 1956. Las papas sudperuanas, part II. Publicaciones Universidad Nacional del Cuzco, Cuzco, Peru.
- WATANABE, K., AND S. J. PELOQUIN. 1989. Occurrence of 2n pollen and ps gene frequencies in cultivated groups and their related wild species in the tuber-bearing Solanums. *Theoretical and Applied Genetics* 78: 329–336.
- WATANABE, K., AND S. J. PELOQUIN. 1991. The occurrence and frequency of 2n pollen in 2×, 4×, and 6× wild, tuber-bearing *Solanum* species from Mexico, and Central and South America. *Theoretical and Applied Genetics* 82: 621–626.
- ZIMMERER, K. 1991. The regional biogeography of native potato cultivars in highland Peru. *Journal of Biogeography* 18: 165–178.