

What Is the Origin of the European Potato? Evidence from Canary Island Landraces

Domingo Ríos, Marc Ghislain, Flor Rodríguez, and David M. Spooner*

ABSTRACT

The modern cultivated potato (*Solanum tuberosum* L.) was first recorded in Europe in the Canary Islands in 1567, but its origin has long been in dispute. Two competing hypotheses have proposed an “Andean” area (somewhere from the Andean uplands from Venezuela to northern Argentina) or a lowland south-central “Chilean” area, but the Andean origin hypothesis is today generally accepted. The identity of extant Canary Island potato landraces as exclusively of upland Andean origin is one part of a multicomponent argument that the European potato originated from there, rather than from Chile. We reassess these two competing hypotheses with nuclear microsatellite and chloroplast DNA analyses of 19 Canary Island landraces, 14 Andean landraces, 11 Chilean landraces, and two wild potato species as outgroups, and with chloroplast DNA data of 150 landraces from South America. Our molecular results document a wide variation of Andean- and Chilean-type cultivars on the Canary Islands and possible hybrids of the two. Our new data, integrated with historical, molecular, agronomic, and crossing data, support a hypothesis that there were multiple introductions of Andean and Chilean germplasm to the Canary Islands and that the early European potato was selected from Chilean introductions long before the late blight epiphytotics of the 1840s.

D. Ríos, Centro de Conservación de la Biodiversidad Agrícola de Tenerife, Carretera Tacoronte-Tejina, 20 A. Tacoronte, 38.350, Tenerife, and Univ. of La Laguna, ETSIA, Carretera de Geneto 2, Campus de Anchieta, 38206, La Laguna, Tenerife; M. Ghislain, International Potato Center, P.O. Box 1558, La Molina, Lima 12, Peru; F. Rodríguez and D.M. Spooner, USDA-ARS, Dep. of Horticulture, Univ. of Wisconsin, 1575 Linden Dr., Madison, WI 53706-1590. Received 22 May 2006. *Corresponding author (dsponer@wisc.edu).

Abbreviations: CIP, International Potato Center; NJ, neighbor-joining; PCR, polymerase chain reaction; PIC, polymorphic information content; SSR, simple sequence repeat or microsatellite.

THE CANARY ISLAND Archipelago (Spain) contains seven islands in the Atlantic Ocean about 100 km west of Morocco, 1200 km southwest of Spain, and 5000 km northeast of northern South America. At about 28° N lat near the Tropic of Cancer, they are similar to the southern latitude at the Tropic of Capricorn in northern Argentina at the southern limit of Andean landraces. About 1000 ha are today devoted to the growth of potato (*Solanum tuberosum* L.) landraces in the Canary Islands (Ríos et al., 1999), with about 90% of these in Tenerife Island and much smaller amounts in La Palma and Lanzarote Islands. They are grown at 600 to 1200 m, in areas of dense cloud cover. Most landraces are for the fresh market and consumed locally, but there is a small export market as specialty potatoes. In addition, about 4600 ha on Tenerife Island are devoted to the growth of advanced commercial varieties for the local fresh market (Servicio de Estadística, 2004).

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Classification of Cultivated Potato

Cultivated potatoes have been classified as species under the International Code of Botanical Nomenclature (ICBN; Greuter et al., 2000) and as cultivar groups under the International Code of Nomenclature of Cultivated Plants (ICNCP; Brickell et al., 2004). Huamán and Spooner (2002) examined morphological support for the classification of potato landraces, and on the basis of poor morphological support and an ongoing dynamic of hybridization (Ugent, 1970; Grun, 1990), they recognized a single species, *Solanum tuberosum* L., with eight cultivar groups: Ajanhuiri Group (diploid, $2n = 2x = 24$), Andigenum Group (tetraploid, $2n = 4x = 48$), Chaucha Group (triploid, $2n = 3x = 36$), Chilotanum Group (tetraploid, $2n = 4x = 48$), Curtilobum Group (pentaploid, $2n = 5x = 60$), Juzepczukii Group (triploid, $2n = 3x = 36$), Phureja Group (diploid, $2n = 2x = 24$), and Stenotomum Group (diploid, $2n = 2x = 24$). All occur in the Andes from western Venezuela to northern Argentina, except the Chilotanum Group (= *S. tuberosum* subsp. *tuberosum*), which occurs in lowland south-central Chile of Chiloé Island, the Chonos Archipelago immediately to the south (where they occur as ruderal plants growing on beaches), and the adjacent low elevation mainland. Remnant landrace populations outside of South America were all introduced in post-Columbian times.

History of the Potato in the Canary Islands

The potato was first seen by European explorers in lowland Chile in 1551 (Salaman, 1949) and in the Andes in 1552 (López de Gómara, 1552) (Table 1). The first known written record of potatoes in Europe was on 28 Nov. 1567 in the Canary Islands. Lorenzo Palenzuela, a notary public, recorded that potatoes were sent from Grand Canary Island to Antwerp, Belgium (Lobo-Cabrera, 1988; Hawkes and Francisco-Ortega, 1993): “y asi mismo recibo tres barriles medianos que decis lleven patata y naranjas e lemons berdes” (and in the same way I received three medium-size barrels that you said carried potatoes, oranges, and green lemons) [orange, *Citrus sinensis* (L.) Osbeck; lemon, *Citrus limon* (L.) Burm. F.]. Hawkes and Francisco-Ortega (1993) speculated that potatoes were introduced into the Canary Islands at least 5 yr earlier (1562) to develop an export crop. A second record from the Canary Islands on 24 Apr. 1574 from the notary public Luis de Balboa noted a shipment of potatoes from Tenerife to Rouen France (Hawkes and Francisco-Ortega, 1993). Potatoes were reported in continental Europe in 27 Dec. 1573 in the records of the Hospital de la Sangre y de las Cinco Llagas in Spain. These records are deposited in the Archivo Hispalense (Spanish Archives) in Seville (Hamilton, 1934; Salaman, 1937; Hawkes and Francisco-Ortega, 1992).

The first date of introduction of potatoes into the Canary Islands from a known place was in 1622, nearly

100 yr after their documented introduction, when D. Juan Bautista de Castro sowed potatoes that he brought from Peru to his land Icod El Alto (Bandini, 1816; Viera y Clavijo, 1866). Icod El Alto is probably the area in Tenerife Island where the cultivation of potato landraces is now common. At that time, some farmers were growing these potatoes from botanical seed (in contrast to tubers, which are referred to in the trade as “seed” potatoes; Viera y Clavijo, 1866). By 1681 potatoes had reached such value in Tenerife that they fulfilled tithing requirements to the Catholic Church. By 1776 the potato was only surpassed

Table 1. Key dates bearing on the history of potato (*Solanum tuberosum* L.) in the Canary Islands.

Date	Event
1532	Pizarro discovered Peru.
1551	Valdivia mentioned the growth of potatoes in Valdivia (160 km north of Chiloé Island, Chile) by Araucarian Indians (Salaman, 1949).
1552	First mention of potato from Peru (López de Gómara, 1552).
1559	Discovery of Chiloé Island, Chile (160 km south of Valdivia Chile).
1567	Potato was first documented from the Canary Islands (Grand Canary Island) for consumption (Lobo-Cabrera, 1988; Hawkes and Francisco-Ortega, 1993). Hawkes and Francisco-Ortega (1993) speculated that potato was brought to the Canary Islands as early as 1562.
1573	First mention of potato consumption in continental Spain (Hamilton, 1934, as quoted by Salaman, 1937; Hawkes and Francisco-Ortega, 1992). Hawkes and Francisco-Ortega (1992) speculated that these potatoes were cultivated in continental Spain.
1574	Second record of potato from the Canary Islands (Tenerife Island) as shipments to Rouen France (Hawkes and Francisco-Ortega, 1993).
1587	Potatoes were recorded as crated for shipment from Chile to Europe.
1622	First record of potato arriving to the Canary Islands (Tenerife) from a known place (Peru) [Viera y Clavijo, 1866 (but written in 1799 from historical archives from the Catholic Church; Bandini, 1816)]. Both references report that the Canary Island growers used true seed.
1681	First record of potatoes from the Canary Islands used as payment of tithe to the Catholic Church (Macías, 1986).
1776	Potatoes were documented as the second most important crop for the Canary Islands (after wine grapes (<i>Vitis vinifera</i> L.); Macías, 1986). Today, potato is the third most important crop after grapes and bananas (<i>Musa acuminata</i> Colla) (Servicio de Estadística, 2004).
1797	Doyle (1797) described three different potato groups from the Canary Islands that were distinguished by harvest dates (July, December, May).
1800	Jose de Bethencourt and Castro reported that the poor people of Tenerife preferred to eat potatoes more than grains (Rodríguez, 1992).
approx. 1800	First record of seed potato (tuber-stock for planting) imported from Europe (Holland) to the Canary Islands (Sánchez-Manzano, 1984; Régulo, 1973).
1868	Alvarez-Rixo (1868) described 20 cultivars of Canary Island potatoes; most of his names are still in use there.
1955	Zubeldia et al. (1955) identified, based on morphological and ploidy data, Canary Island potatoes as landraces of <i>S. tuberosum</i> ssp. <i>andigenum</i> (tetraploid), ssp. <i>tuberosum</i> (tetraploid), and <i>S. mamilliferum</i> (triploid). Hawkes and Francisco-Ortega (1993) later identified <i>S. mamilliferum</i> as <i>S. chaucha</i> .

by the wine grape (*Vitis vinifera* L.) as an agricultural commodity (Macías, 1986).

By 1797 a large diversity of potato landraces was present in the Canary Islands, as Doyle (1797) recognized three groups based on harvest dates of July (Veraneras), December (Tempranas), and May (de Mayo). Potatoes were a preferred food on the islands by 1800 (Rodríguez, 1992). At that time, additional varieties were imported into the islands from continental Europe (Sánchez-Manzano, 1984; Régulo, 1973). The variation of potatoes on the islands was maintained, as Alvarez-Rixo (1868) described 20 Canary Island landraces; most of Alvarez-Rixo's names are still in use.

Why Is the Study of Canary Islands Landraces Significant to Address the Origin of European Potato?

Remnant populations of early potato introductions in India (Swaminathan, 1958) and in the Canary Islands (Hawkes and Francisco-Ortega, 1992) have been thought to have undergone little to no morphological change since their export from South America. These populations, like those in South America, also are referred to as landraces. The identity of these populations as Andean or Chilean form one component of a multifaceted and long-standing argument (described below) about the origin of "European" potato, here defined as the first group of cultivars imported and further developed in Europe that then spread worldwide. The European potato has been widely referred to as *Solanum tuberosum* L. subsp. *tuberosum*, although modern cultivars contain mixtures through breeding efforts of different cultivar groups and up to 16 wild potato species (Plaisted and Hoopes, 1989; Grun, 1990). The present study is parallel to a similar study of the Indian landraces first recorded in that country in 1615 (Spooner et al., 2005b), which unexpectedly showed Indian landraces to be of Chilean, rather than of Andean origin. For comparative purposes, we use the same Andigenum Group and Chilotanum Group accessions from South America as comparator accessions, but generate new data from these here. This study of the Canary Island landraces is even more significant than the Indian landrace study for the European introduction question as they represent the first putative introduction of potato outside of South America (Hawkes and Francisco-Ortega, 1993) and were believed to form the initial breeding stock for the European potato.

More recent studies suggested that the Canary Island potatoes was mixtures of Andean and Chilean landraces (Zubeldia et al., 1955; Chico, 1986; Marrero, unpublished data, 1992; Alvarez and Gil, 1996; Gil, 1997; Cédres, 1998; Ríos et al., 1999; Gil et al., 2000; Rodríguez, 2000; López, 2001; Casañas et al., 2002; Ríos, 2002), but these were ignored in the argument of the origin of the European potato. Most recently, Barandalla et al. (2006) used

19 nuclear microsatellite (simple sequence repeat, SSR) primers on 41 Canary Island accessions, representing all of the diversity on Tenerife Island, and classified their wide diversity into 10 phenetic groups. They did not classify them into taxonomic species or cultivar groups, but in concert with morphological data of landraces of Tenerife Island from Ríos (2002), they inferred the presence of landraces from the Andigenum Group (4x), Chaucha Group (3x), and Chilotanum Group (4x).

The purpose of the present study is to identify representative Canary Island landrace potatoes as Andean or Chilean in order to address the long-standing controversy of the origin of the first European potato. Our study differs from other studies in the use of comparative data from Andean and Chilean landraces and outgroups, and in the broader extrapolation of our results to the question of the origin of the European potato through integration with other historical, molecular, agronomic, and crossing data. We use microsatellite primers developed for optimal utility in *S. tuberosum* regarding polymorphism, quality scores, and genomic coverage (Ghislain et al., 2004) and the 241-bp chloroplast assay deletion distinguishing most populations of Chilean from Andean potato landraces (Kawagoe and Kikuta, 1991; Hosaka, 2002, 2003).

MATERIALS AND METHODS

Plant Material

We examined 44 landraces and three outgroup accessions (initially, but reduced to two accessions as discussed below) of wild potato [two of *S. bukasovii* (potato landrace sister group), one of *S. chillasense* (more distant outgroup)] based on phylogenetic studies of Spooner et al. (2005a). Nineteen of the forty-four cultivated accessions were chosen to represent the diversity of triploid and tetraploid genotypes of Canary Island landraces as determined by prior microsatellite and morphological studies of Ríos (2002) and Barandalla et al. (2006) (Table 2). The remaining 25 South American landraces are from the Andigenum Group (4x), Chilotanum Group (4x), Chaucha Group (3x), Phureja Group (2x), and Stenotomum Group (2x). On the basis of the unexpected results of the chloroplast DNA deletion marker (below), we further analyzed all 150 CIP (International Potato Center) accessions of the Chaucha Group (3x) from South America (increased from the 97 accessions listed in Huamán et al. [1997], as a result of re-identifications) with this chloroplast DNA deletion marker.

DNA Extraction, Microsatellite and Chloroplast Primers, and PCR Conditions

Genomic DNA was purified using the DNAeasy Plant Mini Kit from Qiagen (Valencia, CA). DNA concentration was estimated by visually comparing with the staining intensity of 1 µg of λDNA (Gibco-BRL, Gaithersburg, MD) digested with 1.6×10^{-8} katal of *Pst*I and subjected to electrophoresis on a 1% agarose gel.

We chose 23 SSR primers (24 loci as STM0019 amplifies two loci) based on quality of amplification and polymorphic information content (PIC) observed in a large sample of cultivated potato

Table 2. Cultivar groups of *Solanum tuberosum*, and three outgroup wild species (*S. bukasovii* and *S. chilliasense*) used in this microsatellite and chloroplast DNA deletion study. Members of the Andigenum and Chilotanum Groups are tetraploid ($2n = 4x = 48$), Chaucha Group triploid ($2n = 3x = 36$), and all other accessions diploid ($2n = 2x = 24$). In addition, all 150 accessions of the Chaucha Group from the International Potato Center (CIP) collection (all Andean) were examined for the chloroplast DNA deletion.

Cultivar groups or wild species	Accession [†]	Cultivar	Location
Cultivar group accessions			
Andigenum Group	CV1	Bonita Blanca	Tenerife Island, La Orotava
Andigenum Group	CV15	Azucena Negra	Tenerife Island, Buenavista
Andigenum Group	CV21	Bonita Negra	Tenerife Island, Los Realejos
Andigenum Group	CV30	Bonita Llagada	Tenerife Island, La Guancha
Andigenum Group	CV44	Bonita Colorada	Tenerife Island, Los Realejos
Andigenum Group	CV50	De Baga	Tenerife Island, Los Realejos
Andigenum Group	CV51	Azucena Negra	Tenerife Island, La Guancha
Andigenum Group	CV52	Azucena Blanca	Tenerife Island, La Guancha
Andigenum Group	CV53	Colorada de Baga	Tenerife Island, La Guancha
Andigenum Group	CV61	Terrenta	Tenerife Island, Tacoronte
Andigenum Group	CV8	Azucena Blanca	Tenerife Island, Tacoronte
Andigenum Group	700031	Hualash	Peru, Carrion Palca
Andigenum Group	700223	Yana or Chiar Imilla	Peru, Puno
Andigenum Group	700921	Ccompis	Peru, Cuzco
Andigenum Group	702477	Yana Puma Maqui	Peru, Tambillo
Andigenum Group	703240	Sani Imilla	Bolivia, Cochabamba
Andigenum Group	703243	Imilla Blanca	Bolivia, Cochabamba
Andigenum Group	703284	Puca Ticka	Bolivia, Cochabamba
Andigenum Group	703346	Huaycha Pacena	Bolivia, Cochabamba
Andigenum Group	703748	Huagalina	Peru, La Libertad
Andigenum Group	704353	Puna	Ecuador, Chimborazo
Andigenum Group	704429	Guincho Negra	Peru, Chachapoyas
Andigenum Group	705665	Pellejo de Cuy	Peru, Santa Cruz de Miopapa
Chaucha Group	CV63	Negra Yema de Huevo	Tenerife Island, Tacoronte
Chaucha Group	CV9	Blanca Negra	Tenerife Island, Tacoronte
Chaucha Group	702230	Huayro	Peru, Ayacucho
Chaucha Group	704710	Unknown	Peru, Huanuco
Chilotanum Group	CV18	Melonera	Tenerife Island, Buenavista
Chilotanum Group	CV20	Peluca Negra	Tenerife Island, Buenavista
Chilotanum Group	CV25	Peluca Rosada	Tenerife Island, La Matanza
Chilotanum Group	CV36	Palmera Lagarteadada	Tenerife Island, Anaga
Chilotanum Group	CV37	Brasileña or Grasiñeña	Tenerife Island, Anaga
Chilotanum Group	CV58	Peluca Colorada	Tenerife Island, Fasnía
Chilotanum Group	703606	Papa Chonca	Chile, Chiloé, Chonos Archipelago
Chilotanum Group	703610	Papa Cacho	Chile, Chiloé, Chonos Archipelago
Chilotanum Group	703611	Papa Colorada	Chile, Chiloé, Chonos Archipelago
Chilotanum Group	705040	Unknown	Chile, Chiloé, Chonos Archipelago
Chilotanum Group	705045	Estrella	Chile, Chiloé, Chonos Archipelago
Phureja Group	705154	Unknown	Colombia, Dep. Nariño
Phureja Group	705825	Unknown	Colombia, Mercaderes
Stenotomum Group	703783	Unknown	Peru, Puno
Stenotomum Group	705987	Perla Limeña	Peru, Cajamarca
Stenotomum Group	706025	Puca Runtush or Cibra	Peru, Carrion, Chinchí
Stenotomum Group	706668	Yana Huayro	Peru, Canchaplaca
Wild potato species accessions used as outgroups			
<i>S. bukasovii</i>	761220		Peru, Huarochiri
<i>S. bukasovii</i>	761223		Peru, Huarochiri
<i>S. chilliasense</i>	761590		Ecuador, Cordillera Chillia

[†]The accessions preceded by "CV" are from the genebank of the Centro de Conservación de la Biodiversidad Agrícola de Tenerife, and the six-digit accessions from the CIP Genebank.

Table 3. Simple sequence repeat primers used in this study, and their characteristics.

Name	Repeat	Primer sequences (5'–3')	Linkage group	Annealing temperature °C	Allele range bp	No of alleles detected	PIC [†]
STG006	(AC) ₉	TGAAAACCTGGTTCCGCATT TAAGCAAGCTCTCTCCAGGG	II	55	127–171	7	0.7624
STG016	(AGA) ₈	AGCTGCTCAGCATCAAGAGA ACCACCTCAGGCACCTTCATC	I	55	119–154	9	0.7663
STG021	(AAGA) ₇	TGCCTACTGCCAAAACATT ACTGGCTGGGAAGCATACAC	n.d. [‡]	58	114–142	8	0.7578
STGBSS	(TCT) ₉	AATCGGTGATAAATGTGAATGC ATGCTTGCCATGTGATGTGT	VIII	53	125–144	7	0.7680
STI003	(ACC) _n	ACCATCCACCATGTCAATGC CTCATGGATGGTGTCAATGG	VIII	61	136–187	9	0.7993
STI004	(AAG) _n	GCTGCTAAACACTCAAGCAGAA CAACTACAAGATTCATCCACAG	VI	61	75–104	8	0.7460
STI012	(ATT) _n	GAAGCGACTTCCAAAATCAGA AAAGGGAGGAATAGAAACCAAAA	IV	55	167–197	8	0.8132
STI014	(TGG) _n (AGG) _n	AGAAACTGAGTTGTGTTGGGA TCAACAGTCTCAGAAAACCCCTCT	IX	55	122–131	4	0.6699
STI022	(ACCCG) _n	TCTCCAATTACTTGATGGACCC CAATGCCATACACGTGGCTA	VIII	61	113–133	5	0.7178
STI023	(CAG) _n	GCGAATGACAGGACAAGAGG TGCCACTGCTACCATAACCA	X	61	151–236	14	0.7252
STI030	(ATT) _n	TTGACCCTCCAACATATAGATTCTTC TGACAACCTTAAAGCATATGTCAGC	XII	58	87–107	8	0.7969
STI032	(GGA) _n	TGGGAAGAATCCTGAAATGG TGCTCTACCAATTAACGGCA	V	61	110–135	8	0.7680
STI036	(AC) _n (TC) _n	GGAATGCTGACCATGAACT TTACAGGAAATGCAAACCTCG	n.d. [‡]	53	117–165	10	0.8308
STM0019-a	(AT) ₇ (GT) ₁₀ (AT) ₄ (GT) ₅ (GC) ₄ (GT) ₄	AATAGGTGACTGACTCTCAATG TTGAAGTAAAAGTCCTAGTATGTG	VI	48	79–124	10	0.7243
STM0019-b	(AT) ₇ (GT) ₁₀ (AT) ₄ (GT) ₅ (GC) ₄ (GT) ₄	AATAGGTGACTGACTCTCAATG TTGAAGTAAAAGTCCTAGTATGTG	n.d. [‡]	48	157–235	13	0.6894
STM0030	compound (GT/ GC) (GT) ₈	AGAGATCGATGTAACACCGT GTGGCATTGATGGATT	XII	53	121–165	14	0.8540
STM0031	(AC) ₂ (GCAC) ₂	CATACGCACGCACGTACAC TTCAACCTATCATTGTTGTGAGTCG	VII	55	154–196	9	0.8088
STM0037	(TC) ₅ (AC) ₆ AA (AC) ₇ (AT) ₄	AATTTAACTTAGAAGATTAGTCTC ATTTGGTTGGGTATGATA	XI	53	71–103	11	0.8187
STM1016	(TCT) ₉	TTCTGATTCATGCATGTTTCC ATGCTTGCCATGTGATGTGT	VIII	53	243–270	8	0.7857
STM1052	(AT) ₁₄ GT(AT) ₄ (GT) ₆	CAATTTTCGTTTTTTCATGTGACAC ATGGCGTAATTTGATTTAATACGTAA	IX	50	199–259	12	0.8036
STM1104	(TCT) ₅	TGATTCTCTTGCCTACTGTAATCG CAAAGTGGTGTGAAGCTGTGA	VIII	53	164–184	7	0.7603
STM1106	(ATT) ₁₃	TCCAGCTGATTGGTTAGGTTG ATGCGAATCTACTCGTCATGG	X	55	128–195	12	0.7564
STM5127	(TCT) ₅	TTCAAGAATAGGCAAAACCA CTTTTTCTGACTGAGTTGCCCTC	I	55	240–277	9	0.8101
STWAX-2	(ACTC) ₅	CCCATAACTGTGCGATGAGCA GAATGTAGGGAACATGCATGA	VIII	53	220–252	12	0.7949

[†]Polymorphic information content = $1 - \sum(p_i^2)$, where p_i is the frequency of the i^{th} allele detected in all accessions.

[‡]n.d. = not determined.

(manuscript in preparation) using published microsatellite markers (Ghislain et al., 2004; Feingold et al., 2005; NSF Potato Functional Genomics, 2004). Primers were synthesized by Prologo (Boulder, CO) by license by Beckman Coulter, Inc. (Fullerton, CA), to supply WellRED oligos designed for use with the CEQ Genetic Analysis Systems. Only the forward primer was labeled with D4-PA at the 5' end. PCRs were performed in a 10- μ L volume of: 1X buffer, 2.5 mM MgCl₂, 0.2 mM of each dNTP, 5 pM of each primer pair (forward and reverse), 0.5 units Taq polymerase (SIGMA JumpStart

Taq polymerase, Saint Louis, MO) and 5 ng of genomic DNA. All reactions were amplified in a DNA Engine DYAD Peltier thermal cycler (MJ Research, Inc., Watertown, MA) at the following times and temperatures: 3 min at 94°C, 2 min at annealing temperature (Table 3), 1 min 30 s at 72°C, 30 cycles of 1 min at 94°C, 2 min at annealing temperature, and 1 min 30 s at 72°C, with a final extension step of 5 min at 72°C.

By a polymerase chain reaction (PCR)-marker assay, we determined the presence or absence of a 241-bp chloroplast

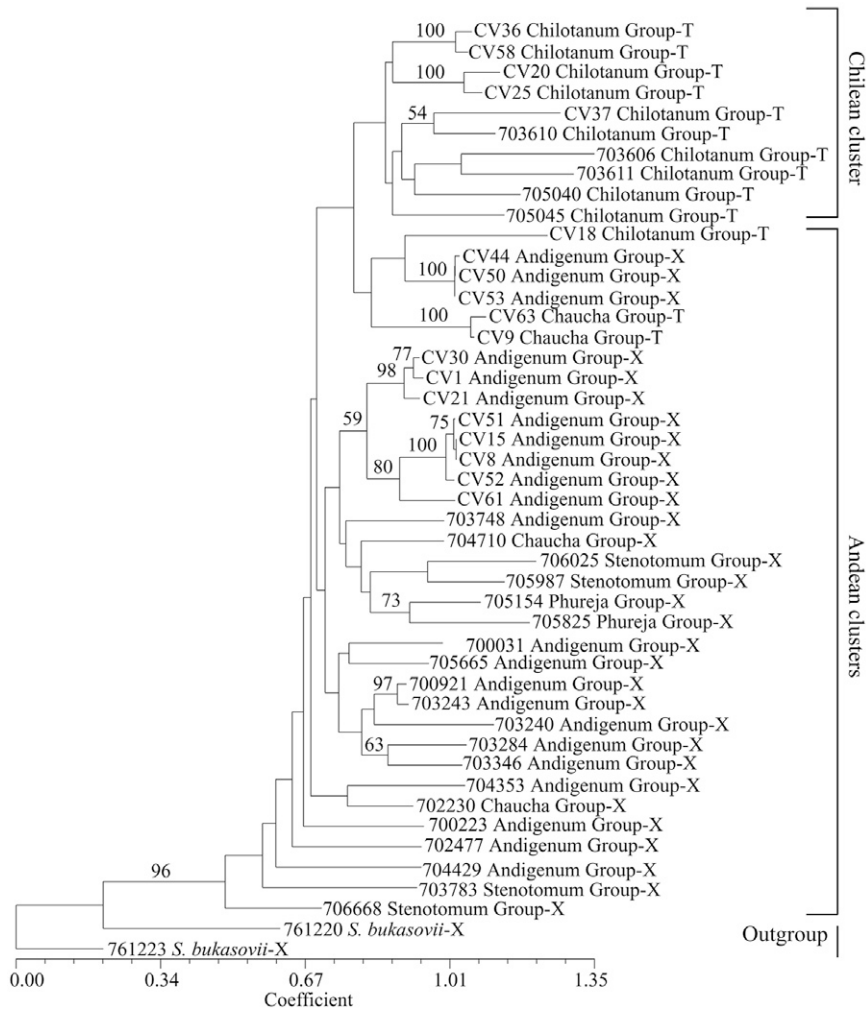


Figure 1. Neighbor-joining tree of potato (*Solanum tuberosum* L.) landrace cultivar groups from the Canary Islands (CV accessions) and from South America (seven-digit accessions) corresponding to Table 1, with bootstrap values (1000 replicates) in bold italic. The letters T and X after the accessions refer to the presence or absence, respectively, or to a 241-bp chloroplast DNA deletion generally characteristic of germplasm from lowland south-central Chile (Kawagoe and Kikuta, 1991; Hosaka, 2002, 2003), in contrast to germplasm from higher elevations in the Andes from western Venezuela to northern Argentina.

DNA deletion in an intergenic region flanking the 3' end of the *trnV-UAC* gene that characterizes most populations of the Chilotanum Group landraces from all other potato landraces from the Andes (Hosaka and Hanneman, 1988; Kawagoe and Kikuta, 1991; Hosaka, 2002).

Data Analyses

Microsatellite amplicons were separated and sized on a CEQ 8000 Genetic Analysis System (capillary electrophoresis; Beckman Coulter, Inc. (Fullerton, CA) under the manufacturer's "frag-3" method: capillary temperature, 50°C; denaturing temperature, 90°C; and time, 120 s; injection voltage, 2.0 kV for 30 s; and separation voltage 6.0 kV for 35 min. One microliter of dilution of PCR product (diluted in 10 or 20 µL of water, depending on height of the peak from the CEQ machine), was added to the sample plate containing 40 µL of sample loading solution (Beckman Coulter, Inc.) and 0.25 µL of DNA size standard-400 (Beckman Coulter, Inc.) in each well. The

fragments were analyzed by Genetic Analysis System Program-Version 5.0. These data were converted to presence (1) and absence (0) data for phylogenetic analysis.

We used a combination of an infinite allele similarity model (Nei72) with the neighbor-joining (NJ) tree-building procedure, based on results of Raker and Spooner (2002). They showed that these combinations of similarity and tree-building algorithms grouped germplasm in *S. tuberosum* much better than stepwise mutation similarity algorithms and unweighted pair group tree-building methods, based on the ability to group replicate germplasm samples together and based on expectations of results from prior taxonomic data. The NJ method developed by Saitou and Nei (1987) estimates phylogenetic trees. While the method is based on the idea of parsimony (it does yield relatively short estimated evolutionary trees), the NJ method does not attempt to obtain the shortest possible tree for a set of data. Rather, it attempts to find a tree that is usually close to the true phylogenetic tree (Rohlf, 1992). This method allows the rooting of trees on outgroups (in this case the two accessions of *S. bukasovii*). All of the analyses used programs in NTSYS-pc Ver. 2.02 K (Applied Biosystematics, Setauket, NY), except bootstrap analyses (1000 replicates) run on PAUP (Swofford, 2001). We calculated the PIC as follows: $PIC = 1 - \sum(p_i^2)$, where p_i is the frequency of the i^{th} allele detected in all accessions (Smith et al., 1997).

The cophenetic correlation coefficient was calculated comparing the Nei72 similarity matrix and NJ tree using the procedures COPH and MXCOMP in NTSYS-pc. This coefficient indicates the correlation between a similarity matrix and the phenetic tree resulting from it after a cluster analysis, indicating goodness-of-fit of the cluster analysis to the similarity matrix. Clustering methods and similarity coefficients are described in Rohlf (1992).

RESULTS

The number of alleles per microsatellite primer ranged from 4 to 14 (average = 9.375). In total, the 24 microsatellite loci produced 222 alleles (Table 3) with relatively high PIC (as expected based on the criteria to select the primers) ranging from 0.6699 to 0.8540. The cophenetic correlation coefficient of Nei72/NJ was 0.70. The Nei72/NJ tree (Fig. 1) clustered 10 of the 11 accessions of the Chilotanum Group from both Chile and the Canary Islands together (we label this the Chilean cluster). All the remaining 34 landraces (1 accession of the Chilotanum Group from the Canary Islands, 4 Chaucha Group, 4 Stenotomum Group, 2 Phureja Group, and 23 Andigenum Group) clustered separately in "Andean clusters" but did not form a cultivar group-specific cluster as in the Chilean cluster; 6 accessions, including 1 Chilean

accession (CV18), form a separate branch to the 10 Chilean accessions. This clustering was only effective, however, after the removal of the distant outgroup *S. chillasense* from the analysis. As pointed out by Raker and Spooner (2002) and Lara-Cabrera and Spooner (2005), microsatellite primers developed from cultivated potato have lesser utility outside of cultivated potato and immediately related germplasm. The microsatellite primers used here similarly were developed from a cultivated potato database (Ghislain et al., 2004; Feingold et al., 2005; NSF Potato Functional Genomics, 2004). The wild species *S. bukasovii* (sister group to the cultivars) are well supported as distinct from the cultivars (96% bootstrap value) as expected based on prior phylogenetic results (Spooner et al., 2005a). All other bootstrap values above 50% are in more internal nodes, not in the branch separating the Andean or Chilean clusters. All of the Chilotanum Group accessions from the Canary Islands group in one of two clusters, separate from the remaining Andean accessions.

One “misplaced” accession of the Chilotanum Group (CV18 from the Canary Islands) was in the Andean cluster but it possessed the 241-bp chloroplast deletion characteristic of this cultivar group. The only other accessions known to possess this deletion were the two accessions of the Chaucha Group from the Canary Islands, but not the two accessions of the Chaucha Group from the Andes. On the basis of this unexpected result we then screened all 150 accessions of the Chaucha Group in the CIP collection (accession numbers available on request), all from South America. None of these 150 accessions possess this deletion.

DISCUSSION

Our data provide the first unambiguous documentation of the occurrence of Chilean as well as Andean landrace potatoes in the Canary Islands, using comparative molecular data from accessions from these islands, the Andes, Chile, and outgroups. All Chilean and Canary Island Chilotanum Group landraces possess the 241-bp chloroplast DNA deletion, including the one accession clustering with the Andean accessions.

Our chloroplast results provide the first discovery of triploid landraces possessing the 241-bp chloroplast DNA deletion. No triploid landraces examined from the Andes possess this deletion (Sukhotu et al., 2004; and our new data of 150 Chaucha Group accessions from the CIP). It is possible that these two Canary Island triploid landraces are recent hybrids on the Canary Islands with Chilean landraces that possess this deletion, but it is unclear what the other parents of this hybrid would be, as both Canary Island triploids have six alleles found in no other accessions examined. As pointed out by Viera y Clavijo (1866), farmers from the Canary Islands sometimes grew potatoes from true seed, and Sánchez-Manzano (1984) and Régulo (1973) documented the import of advanced cultivars to the Canary Islands from Europe. In addition, the historical records of

early introductions of potatoes are at best sparse and indefinite (Salaman, 1949; Glendinning, 1983). These data, and our present molecular results, document a wide variation in germplasm of potatoes, including Andean, Chilean, and possibly, advanced varieties of potatoes developed in Europe, some of which may be of hybrid origin after introductions from South America. The clustering of all Andean Canary Islands accessions together may be a result of such inbreeding, or it may be a result of few related introductions from South America. Our results document that the Canary Islands are a repository of diverse germplasm from unknown sources worldwide, and it is impossible, therefore, to use germplasm from these islands to support an exclusive Andean origin of the first European potato.

A logical extension of this study is to discover the clone-specific sources of the landraces of Canary Island potatoes. This would be greatly facilitated by a combined morphological and microsatellite database of the landraces from the Andes and from Chile, and CIP is in the process of constructing such a database. However, discovery of the sources of Canary Islands landraces may forever be frustrated by genetic erosion of possible imports from the Andes and from Chile up to 450 yr ago, and by hybridization of germplasm from Canary Island landraces among each other and from possible advanced varieties later brought in from Europe as early as 1800 (Sánchez-Manzano, 1984; Régulo, 1973).

What Is the Source of the Early European Potato?

Juzepczuk and Bukasov (1929) proposed Chile (Chilotanum Group) as the source of the first European potato because of shared morphology and long daylength adaptation of Chilean landraces and modern cultivars. Alternatively, Salaman (1937), Salaman and Hawkes (1949), Hosaka and Hanneman (1988), Grun (1990), and Hawkes (1990) proposed the Andes (Andigenum Group). The Andean introduction hypothesis invokes: (i) a convergent rapid selection of European potato to the morphology and daylength adaptation shown by members of the Chilotanum Group, and (ii) that the late blight epidemics beginning in 1845 in the UK and later spreading worldwide displaced most existing European cultivars by Chilean germplasm or hybrids with this germplasm. These researchers collectively suggested the following:

1. *Solanum tuberosum* in Chile arose from Andean landraces, either directly, or through a cross with an unidentified wild species. Grun (1979, 1990) found that the cytoplasmic types of Chilean landraces and modern potatoes were identical and that both differed from Andean landraces by a unilateral incompatibility when Chilean germplasm is used as a female (but not as a male).
2. Hosaka (2002, 2003) identified, through a chloroplast DNA deletion, a likely wild species contributor to

- Chilean tuberosum as the Bolivian and Argentinean species progenitor *S. tarijense* Hawkes.
- The first European potatoes were introduced from the Andes, with the first record in the Canary Islands in 1567 (Hawkes and Francisco-Ortega, 1993). Putative late harvest dates (“putative” because the data are for late purchases, not late harvests) of early potatoes in Spain implied Andean introductions, as would be expected from short-day adapted Andigenum Group. (The Chilotanum Group is long-day adapted.)
 - Early herbarium specimens of potato in Europe had the narrow-leaved phenotype thought to distinguish the Andigenum Group from the Chilotanum Group (Salaman and Hawkes, 1949).
 - The trip from Chile to Europe took longer than from Peru (or Colombia) to Europe, and tubers from Chile would have less chance to survive.
 - Artificial selection of Andigenum Group produced some Chilotanum Group-like clones (“neo-tuberosum”) having greater flowering, shorter stolons, greater yield, earlier tuberization, reduction of cytotesterility, and greater late blight resistance (Simmonds, 1966; Glendinning, 1975; Huarte and Plaisted, 1984; Vilaro et al., 1989), suggesting the possibility for rapid selection of Andean to Chilean types. Putative early Andean introductions in Europe rapidly evolved into a wider leaf morphology with long-day adaptation, a parallel event to long-day selection in Chile.
 - The fungal disease late blight [*Phytophthora infestans* (Mont.) de Bary] in Europe killed most of these evolved Andean types in the 1840s, but the modern potato was rapidly mass selected and bred for blight resistance with subsp. *tuberosum*, purchased in Panama (as cultivar Rough Purple Chile) but believed to have come from Chile (Plaisted and Hoopes, 1989; Grun, 1990).

Spooner and Hettterscheid (2005) questioned this hypothesis and suggested that early introductions of potato came from both the Andes and from Chile, with the Chilean introductions rapidly being selected as the European potato, long before the late blight epiphytotics of the 1840s. Their proposition was later supported by new molecular evidence derived from microsatellites and the 241-plastid deletion marker, like this study, but of potato landraces of India that also were thought to be solely of Andean origin (Spooner et al., 2005b). They argued the following:

- The leaf-shape data of Salaman and Hawkes (1949) was insufficient to identify early herbarium specimens as Andean rather than Chilean because Huamán and Spooner (2002, Fig. 3, Char. 13) quantified considerable overlap of leaf shapes between landraces from both areas that would make such conclusions highly problematic.

- The argument that Chilean tubers would not have survived the long trip from the Andes to Europe (Hawkes, 1967) ignored the simple possibility of transport of true seeds, of potted plants, or even well-preserved tubers. Potatoes were documented as an item of ship’s stores from Chile, and there are records as early as 1587 of potatoes crated for shipment in storehouses (Glendinning, 1983).
- The vast majority (>99%) of extant advanced potatoes have T-type DNA typical of most Chilean germplasm (Hosaka, 1993, 1995; Powell et al., 1993; Provan et al., 1999). This includes a clone released before the 1840s (cultivar Yam, released in 1836; Powell et al., 1993). The proponents of Andean introduction explain these facts by an elimination of Andigenum Group clones after the late blight epidemics and breeding with Chilotanum Group clones, but only a cross with Chilotanum Group as female would confer the T-type cpDNA, as plastids are not transferred in pollen in the Solanaceae (Corriveau and Coleman, 1988).
- Chilotanum Group clones are not known for late blight resistance and would have been poor breeding stock to combat this disease.
- A similar argument that putative remnant populations of Andean potatoes from India supported Andean introductions was discounted by Spooner et al. (2005b), who showed, with microsatellite and cpDNA evidence, that these potatoes were Chilean, not Andean.
- Juzepczuk and Bukasov’s (1929) argument that Chilean landraces were preadapted to the long days of Europe are compelling, and early introductions from Chile would rapidly be selected over Andean clones. Although neo-tuberosum clones show the possibility to select for long-day adaptation from Andigenum clones (Simmonds, 1966; Glendinning, 1975; Huarte and Plaisted, 1984; Vilaro et al., 1989), Chilean introductions would not require such intentional selection.

CONCLUSIONS

Our data, and prior studies of Zubeldia et al. (1955), Chico (1986), Marrero (unpublished data, 1992), Alvarez and Gil (1996), Gil (1997), Ríos et al. (1999), Gil et al. (2000), Rodríguez (2000), López (2001), Casañas et al. (2002), Ríos (2002), and Barandalla et al. (2006) suggest that the Canary Island potatoes are diverse mixtures of Andean and Chilean landraces. The Canary Island component to an argument of an Andean origin of European potato is weakened, like the Indian argument (Spooner et al., 2005b). It is highly likely that some early introductions of potatoes to the Canary Islands and Spain were from the Andes and from Chile. Historical records of early introductions are so sparse and indefinite as to be meaningless (Salaman, 1949; Glendinning, 1983). There likely were multiple introductions of all

landrace groups from both the Andes and Chile after the value of potato became known, but Chilean introductions likely were better adapted and quickly became the dominant germplasm sources for early European varieties, long before the late blight epiphytotic of the 1840s. Particularly compelling are the chloroplast DNA data showing well over 99% of extant potatoes today to have Chilean germplasm. As pointed out by Plaisted and Hoopes (1989) and Grun (1990), modern advanced cultivars have germplasm from over 16 wild species and Andean germplasm in their pedigrees and is far removed from their original landrace progenitors. But an Andean origin for the early European potato is poorly supported, and we support a Chilean origin.

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