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Nuclear and chloroplast DNA reassessment of the origin of Indian potato varieties and its implications for the origin of the early European potato

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Abstract The modern cultivated potato was first recorded in Europe in 1562, but its area(s) of exportation has long been in dispute. Two competing hypotheses have proposed an "Andean" area (somewhere from upland Venezuela to northern Argentina) or a lowland south central "Chilean" area. Potato landraces from these two areas can be distinguished, although sometimes with difficulty, by (1) cytoplasmic sterility factors, (2) morphological traits, (3) daylength adaptation, (4) microsatellite markers, and (5) co-evolved chloroplast (cp) and mitochondria (mt) DNA. The Chilean introduction hypothesis originally was proposed because of similarities among Chilean landraces and modern "European" cultivars with respect to traits 2 and 3. Alternatively, the Andean introduction hypothesis suggests that (1) traits 2 and 3 of European potato evolved rapidly, in parallel, from Andean landraces to a Chilean type through selection following import to Europe, and (2) the worldwide late blight epidemics beginning in 1845 in the United Kingdom displaced most existing European cultivars and the potato was subsequently improved by importations of Chilean landraces. We reassess these two competing hypotheses with nuclear microsatellite and cpDNA analyses of (1) 32 Indian cultivars, some of which are thought to preserve putatively remnant populations of Andean landraces, (2) 12 Andean landraces, and (3) five Chilean landraces. Our microsatellite results cluster all Indian cultivars, including putatively remnant Andean landrace populations, with the Chilean landraces, and none with the "old Andigenum" landraces. Some of these Indian landraces, however, lack the cpDNA typical of Chilean landraces and advanced cultivars, indicating they likely are hybrids of Andean landraces with Chilean clones or more advanced cultivars. These results lead us to reexamine the hypothesis that early introductions of potato to Europe were solely from the Andes.

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Introduction

Solanum tuberosum, the cultivated potato, contains a highly variable set of modern cultivars grown worldwide. There has been a long controversy about the origin of potato out of its native home in South America, resulting in the proposal of two competing hypotheses—cultivated potato has an "Andean" origin (somewhere from upland Venezuela to northern Argentina) or a lowland south central "Chilean" origin. The taxonomy of cultivated potatoes used in this article follows the Group classification of Huamán and Spooner (2002). Of relevance to the present study are two of these eight Groups: (1) the Andigenum Group [= *S. tuberosum* subsp. *andigenum* (Juz. and Bukasov) Hawkes], which is composed of tetraploid clones, widely distributed in Andean South America from Venezuela south to northern Argentina, and (2) the Chilotanum Group (*S. tuberosum* subsp. *tuberosum*), also tetraploid, native to southern Chile. The two Groups are distinguished from each other by: (1) cytoplasmic sterility factors; hybrids of the Chilotanum Group, as a female, and Andigenum Group have male sterility, but the reciprocal cross is fertile (Grun 1990); (2) morphological data, with the Chilotanum Group having wider leaflets held more outward from the plant, and other minor differences (Huamán and Spooner 2002); (3) the Chilotanum Group

tuberizing under long days, and the Andigenum Group under short days; (4) microsatellite marker differences (Raker and Spooner 2002); (5) plastid differences of a 241-bp deletion in the chloroplast (cp)DNA molecule (Kawagoe and Kikuta 1991; Hosaka 1995), which is absent in the most accessions of the Andigenum Group (and indeed all other groups), and a co-evolved mitochondrial (mt)DNA type (Lössl et al. 1999). Differences with respect to traits 1–4 can overlap among accessions in both Groups, and there are exceptions among the accessions of the Andean and Chilean Groups with respect to trait 5.

Potato was first recorded in Europe in the Canary Islands in 1562 (Hawkes and Francisco-Ortega 1993) and spread throughout Europe and then worldwide (Hawkes 1990). There are two hypotheses for the origin of the first European introductions. Juzepczuk and Bukasov (1929) proposed Chile (Chilotanum Group) because of shared morphology and long daylength adaptation, while 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 (1) a convergent rapid selection of European potato to the morphology and daylength adaptation shown by members of the Chilotanum Group and (2) that the worldwide late blight epidemics beginning in 1845 in the United Kingdom and later spreading worldwide displaced most existing European cultivars by Chilean germplasm or hybrids with this germplasm.

In the investigation reported here we test these alternative hypotheses by means of a molecular identification to the Andigenum Group or Chilotanum Group using nuclear microsatellites and the 241-bp cpDNA deletion of Indian varieties that include putative Andigenum Group remnants of the early introductions to Europe. India has long been believed to contain remnant pure populations of Andigenum Group germplasm, which has supported the Andean introduction hypothesis (Swaminathan 1958). They are some of the few remaining clones suitable for such a test because extra-Andean Andigenum cultivars throughout much of the rest of the world have been thought to have been supplanted by Chilotanum Group germplasm subsequent to the late blight epidemics of the 1840s that swept across Europe and later the northern hemisphere (Butler 1903; Salaman 1949). Swaminathan (1958) characterized many of the materials we reexamine here with morphological data and daylength adaptation and concluded that these varieties matched Andigenum Group clones.

The earliest reference to potatoes in India is from Terry (1655; pp 91–92) who documented potato in northern India earlier than 1615. Further reports documented potatoes in India in 1771 (Johnson 1847) and 1838 (White 1838). These historical accounts provide ample evidence that by early in the nineteenth century the potato had established itself as an important vegetable crop in the hills and plains of India, well before the devastating late blight epidemic in the United Kingdom that began in 1845. Late blight was not recorded in India until 1870, where it was first recorded in the Nilgiri Hills (11°N, 76°E, 2,246 m altitude). By 1902, late blight was recorded throughout much of India, but in certain areas, such as the plains of Uttar Pradesh, it was not reported until 1943 when it appeared at Dehradun and Meerut (Butler 1903; Dastur 1917; Dutt 1979). This argues against a hypothesis of late blight very early displacing early introduced Andigenum Group varieties. India includes habitats appropriate for both modern long-day-adapted cultivars in the northern Indian hills at the base of the Himalayas and short-day-adapted Andigenum Group cultivars on the Indian plains. We place the present results in context of other facts bearing on these alternative hypothesis.

Materials and methods

Plant materials

The genotypes used in the present investigation consisted of the only putatively extant Group Andigenum clones (Darjeeling Red Round, Phulwa) and their four clonal selections (Darjeeling Red Round Purple, Kufri Red, Gulabia, Lalmutti) and 22 breeding materials to include their half sibs (one common parent), full sibs (two common parents) and unrelated varieties (no common parents) (Table 1). We also included four European cultivars (Craig's Defiance, released 1938; Great Scot, released 1919; Ultimus, released 1935; Up-to-Date, released 1894), 12 accessions of Group Andigenum clones, and five accessions of Group Chilotanum clones (Table 1). The Andigenum and Chilotanum clones are listed in Fig. 1 by their International Potato Center (CIP) accession number. We chose them from CIP's cultivated potato germplasm collection based on diverse morphological characteristics.

DNA extraction, microsatellite and chloroplast primers, and PCR conditions

Genomic DNA was obtained using standard protocols adopted at CIP (International Potato Center 1999). Genomic DNA concentration was estimated by visually comparing the staining intensity of 1 μg of λDNA (Gibco-BRL, Gaithersburg, Md.) digested with *Pst*I and subjected to electrophoresis on a 1% agarose gel. A set of 14 nuclear simple sequence repeats (SSRs) for cultivated potato were chosen from Ghislain et al. (2004). The primers and amplification conditions are listed in Table 2. The 241-bp cpDNA mutation characteristic of *S. tuberosum* Group Chilotanum and advanced cultivars was detected by the PCR-based assay of Hosaka (2003).

Table 1 Indian potato cultivars used in this study with date of release if known. The 12 Andigenum Group landraces from Guatemala to Bolivia and the five Chilotanum Group landraces southern Chile are not listed

Variety/genotype, with place and date of release, if known (from Hamester and Hils 2003)	Parentage (maternal parent first) or other comments
Putative early introductions of Andigenum Group clones to India	
Darjeeling Red Round (DRR)	Assumed to be an introduction of Group Andigenum from Europe
Phulwa	Assumed to be an introduction of Group Andigenum from Europe
Modern cultivars introduced from Europe to India	
Up-to-Date (UK, 1894)	Patterson's Victoria × Blue Don
Craig's Defiance (UK, 1938)	Epicure (Ireland, 1897) × Pepo-1
Ultimus (1935, The Netherlands)	Rode Star (The Netherlands, 1909) × Pepo-1
Great Scot (UK, 1919)	Imperator × Champion (UK, 1876)
Clonal selections from the above	
Darjeeling Red Round Purple (Central Potato Research Institute, CPRI)	May be a selection from DRR
Kufri Red (CPRI, 1958)	Clonal selection from DRR
Gulabia (CPRI)	May be a selection from Phulwa
Lalmutti (CPRI)	May be a selection from Phulwa
Burma Special (CPRI)	May be a selection from Up-to-Date (UK, 1894)
Ful-sibs; these and all below are modern varieties developed by CPRI	
Kufri Sheetman (CPRI, 1968)	Craig's Defiance (UK, 1838) × Phulwa
Kufri Dewa (CPRI, 1973)	Craig's Defiance (UK, 1838) × Phulwa
Half-sibs (only one parent in common)	
Kufri Red as a common parent	
Kufri Sindhuri (CPRI, 1967)	Kufri Red (CPRI, 1958) × Kufri Kundan (1958)
Kufri Bahar (CPRI, 1980)	Kufri Red (CPRI, 1958) × Geneke
Kufri Lalima (CPRI, 1982)	Kufri Red (CPRI, 1958) × AG 14 (Wis × 37)
Ekishirazu as a common parent	
Kufri Chamatkar (CPRI, 1958)	Ekishirazu × Phulwa
Kufri Kundan (CPRI, 1958)	Ekishirazu × Katahdin (1932)
Kufri Jyoti as a common parent	
Kufri Badshah (CPRI, 1979)	Kufri Jyoti (CPRI, 1968) × Kufri Alankar (CPRI, 1968)
Kufri Swarna (CPRI, 1958)	Kufri Jyoti (CPRI, 1968) × $(VTn)^2$ 62.33.3
Kufri Jawahar (CPRI, 1996)	Kufri Neelamani (CPRI, 1968) × Kufri Jyoti (CPRI, 1968)
M 109-3 (late blight-resistant clones from Scottish Crop Plant Breeding Station developed by W. Black) as a common parent	
Kufri Jeevan (CPRI, 1967)	M 109–3 × 696-D (includes *S. tuberosum* Andigenum Group and modern cultivars, and *S. demissum* in its pedigree)
Kufri Muthu (CPRI, 1971)	3046 (1) (late blight-resistant clone of complex origin developed at Scottish Plant Breeding Station) × M 109–3
Katahdin (USA, 1932) as a common parent	
Kufri Neela (CPRI, 1963)	Katahdin × Shamrock (1900)
Kufri Kumar (1958)	Lumbri × Katahdin
Unrelated varieties	
Kufri Alankar (CPRI, 1968)	Kennebec (USA, 1948) × ON 2090 (Majestic, UK, 1911 × Ekishirazu)
Kufri Naveen (CPRI, 1968)	3070 d (4) × 692-D (includes *S. tuberosum* Andigenum Group and modern cultivars, and *S. demissum* in its pedigree)
Kufri Jyoti (CPRI, 1968)	3069 d (4) × 2814 a(1) (both are late blight-resistant clones of complex hybrid origins, developed at the Scottish Plant Breeding Station)
Kufri Khasigaro (CPRI, 1968)	Taborky (Slovakia, 1946) × Sd 698-D (includes *S. tuberosum* and *S. demissum* in its pedigree)
Kufri Sherpa (CPRI, 1983)	Ultimus (The Netherlands, 1935) × Adina
Kufri Megha (CPRI, 1989)	SLB/K-37 × SLB/Z-73 (Indian hybrids of unknown origins)
Kufri Sutlej (CPRI, 1996)	Kufri Bahar (CPRI, 1980) × Kufri Alankar (CPRI, 1968)

Nuclear SSR allele detection and scoring

Amplification products were separated using a denaturing polyacrylamide gel (6% acrylamide, 7 *M* urea) stained with a silver staining protocol according to the manufacturer's directions (Promega, Madison, Wis.). The nuclear SSR alleles were determined for size in base pairs and scored as present (1) or absent (0) on a denaturing polyacrylamide gel. Each nuclear SSR allele was characterized by co-migration with a 1-bp ladder formed by a sequence of pUC18-forward primer. The scored band was either the upper band of each nuclear SSR allele when visible as a double band or the most intense one in the case of stutter bands.

Data analysis

We used a combination of infinite allele similarity models (NEI 72) and neighbor-joining to examine the phenetic structure in these three classes of *S. tuberosum* (Andigenum Group, Chilotanum Group, Indian varieties), based on results of Raker and Spooner (2002). Their results showed that these combinations of similarity and tree building algorithms grouped germplasm in *S. tuberosum* much better than did 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. All of the analyses used programs in NTSYS-PC VER. 2.02 K (Applied Biosystematics, Setauket, N.Y.). We searched for Andigenum Group or Chilotanum Group specific alleles in the Indian landraces.

Results

The 14 microsatellite primers produced 106 alleles (Table 2). Only four microsatellite sequences (STM0019a, STPAc58, STM2013, and STM0037) were needed to distinguish each genotype individually ("fingerprint"), with the exception of the varieties Darjeeling Red Round and Phulwa and their clonal selections Kufri Red and Gulabia, all of which could not be resolved.

The microsatellite results cluster all Indian cultivars, including the two putatively remnant Andigenum Group clones (Darjeeling Red Round, Phulwa), and their four clonal selections (Darjeeling Red Round Purple, Kufri Red, Gulabia, Lalmutti) with Chilean landraces and modern European cultivars—not with the landraces of the Andigenum Group from Central and South America. Five of these Indian cultivars that cluster with the Chilean landraces and modern European cultivars, however, show a discordance of expected combinations of Andigenum Group nuclear DNA (microsatellites) and cpDNA in that they lack the 241-bp cpDNA deletion typical of Chilean landraces and advanced cultivars (Fig. 1, accessions highlighted in ***bold italics***). All five clonal selections (Table 1) are tightly clustered or connected on the same branch of the phenogram to their putative progenitor based on microsatellite data (Fig. 1).

The average genetic distance among clones within the two gene pools, Indian versus Andean, was markedly different. On the whole, the mean genetic distance among Indian varieties is about 70% of that determined for the Andean cultivated potato germplasm. The Andigenum Group revealed 91 alleles in only 13 accessions, whereas the European and Indian cultivars revealed 67 alleles in 32 accessions (Table 3). There are several rare alleles for each group but markedly more for the Andigenum Group (35) than for the modern cultivars (ten) or the Chilotanum Group (one) (Table 3).

In order to assess if Andigenum-Group-specific alleles could be detected in the 106 SSR alleles, we identified 19 of the former as frequent alleles (arbitrarily set at above 0.2) belonging to either the Indian varieties or the Andigenum Groups. Consistent with the genetic distance analysis and the dendrogram, none except one (STPAc58-239) of the 11 Andigenum Group-specific alleles defined as not detected in the Chilotanum Group were observed in either the Chilotanum Group or the Indian remnant Andigena Group varieties. Similarly, all but one (STPAc58-249) of the eight Indian cultivar specific alleles (defined as not detected in the Andigenum Group) were found in the remnant Andigenum and Chilotanum Groups. These results coincide with our finding that the Indian putative remnant Andigenum Group varieties are actually more closely related to the Chilotanum Group than the Andigenum Group with the exception of three that show the absence of the 241-bp deletion typical of Chilotanum Group chloroplasts.

Discussion

Comparative microsatellite diversity among the potato Groups

The number of alleles per microsatellite was always higher for the Andigenum Group accessions than for the Indian cultivars. This is consistent with ideas of reduced genetic diversity in modern potato cultivars relative to landraces, and argues for the preservation of this germplasm for breeding programs. Rare alleles have been identified predominantly from the Andigenum Group.

Relationships of the Indian potato clones

The microsatellite grouping of the Indian "Andigenum Group" clones (Darjeeling Red Round, Phulwa) and their clonal selections (Darjeeling Red Round Purple, Kufri Red, Gulabia, Lalmutti) with Chilean landraces and modern European cultivars—and not with the Central and South American Andigenum Group landraces—was unexpected and refutes a long-accepted hypothesis that the former represent remnants of an

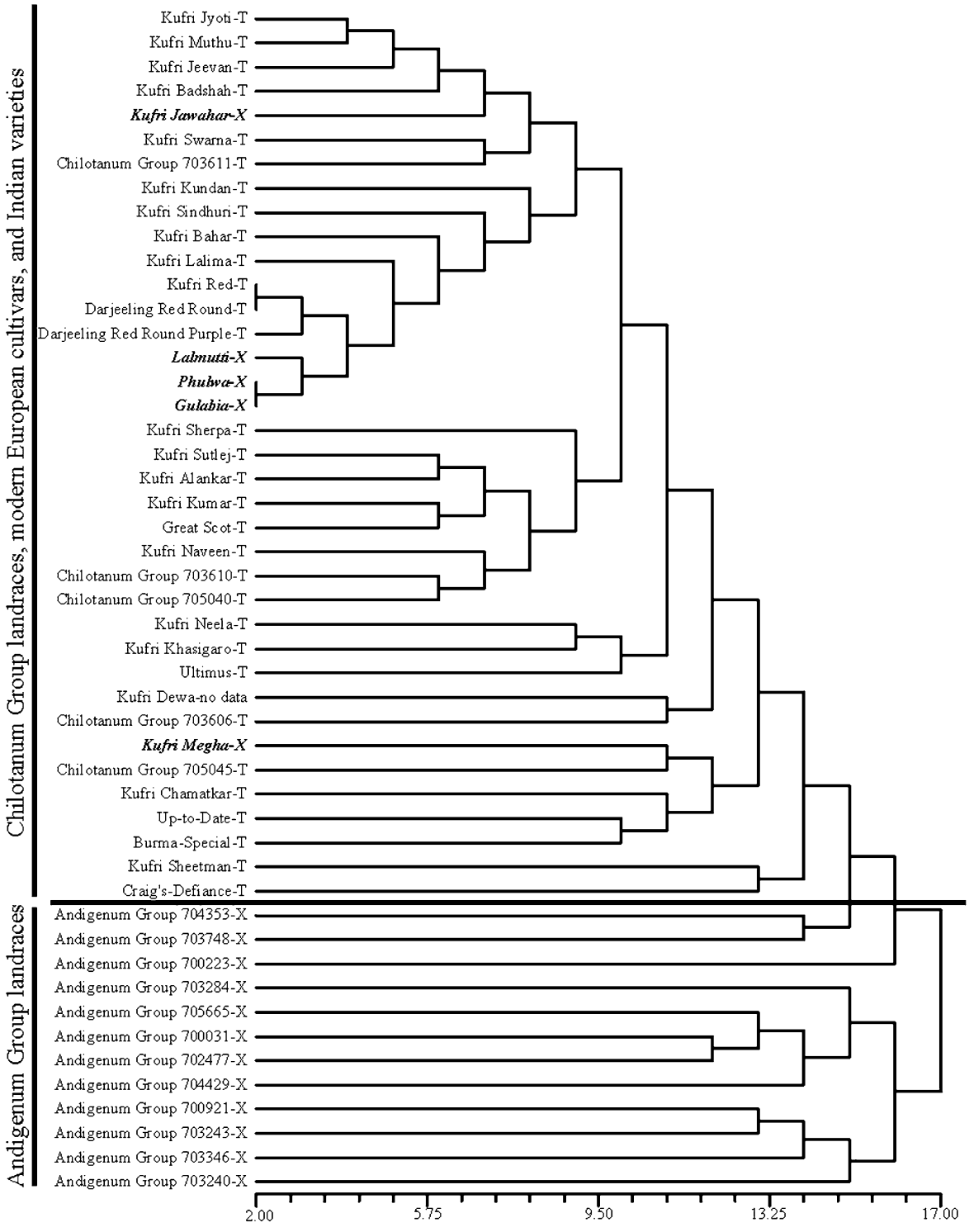

Fig. 1 Neighbor-joining tree generated from microsatellite data analyzed with the NEI 72 similarity coefficient. Included in the tree are: (1) 32 European or Indian potato cultivars, including putative early introductions of Andigenum Group clones to India (listed and described in Table 1); (2) five Chilotanum Group members (previously referred to as *S. tuberosum* subsp. *tuberosum* from Chile); (3) *below the thick horizontal line*, the 12 landrace Andigenum Group representatives from Guatemala to Bolivia. The putative origins of the Indian varieties and modern cultivars are listed in Table 1. The five Indian varieties possessing non-T-type cpDNA are highlighted in ***bold italics***. The T or X following the varieties refer to T-type cpDNA possessing the 241-bp deletion (Kawagoe and Kikuta 1991) or to cpDNA lacking this deletion, respectively

early introduction of Andigenum Group clones (Swaminathan 1958). Rather, the results suggest that the Indian Andigenum Group clones are: (1) hybrid derivatives of remnant Andigenum Group clones with

Table 2 Primers used for the amplification from microsatellite sequences (*ND* not determined)

Code	Repeat motif	Chromosome	T_m annealing	Number of alleles detected	Polymorphism information content (PIC)	Allele size (bp)
STM0019a[a]	$(AT)_7$ $(GT)_{10}$ $(AT)_4$ $(GT)_5$ $(GC)_4$ $(GT)_4$	VI	47	14	0.807	161–239
STM0019b[a]		ND	47	8	0.742	83–119
STM1031	$(AT)_{13}$	V	55	6	0.586	265–325
STM1017	$(ATT)_5$	IX	53	3	0.597	132–136
STM1064	$(TA)_{12}$ $(TG)_4$ GT $(TG)_5$	II	55	6	0.662	188–199
STPAc58	$(TA)_{13}$	V	57	11	0.758	231–277
STM0037	$(TC)_5$ $(AC)_6$ AA $(AC)_7$ $(AT)_4$	XI	53	10	0.810	75–99
STM0030	Compound (GT/GC) $(GT)_8$	XII	53	9	0.781	130–168
STM0031	$(AC)_5$... $(AC)_3$ (GCAC) $(AC)_2$ $(GCAC)_2$	VII	57	9	0.804	155–205
STM1049	$(ATA)_6$	I	57	7	0.658	184–254
STM3012	$(CT)_4$... $(CT)_8$	IX	57	6	0.660	168–213
STM2013	$(TCTA)_6$	VII	55	10	0.819	146–172
STM2022	$(CAA)_3$... $(CAA)_3$	II	53	4	0.652	184–241
STM2030	$(CA)_3$ $(TA)_5$	I	55	3	0.283	180–209

[a] STM00019 reveals two distinct loci using the same primer pairs, here labeled a, b

Chilotanum Group clones or modern cultivars, or (2) modern cultivars or Chilotanum Group clones that were selected for the morphological and daylength adaptation typical of Andigenum Group clones. The possibility for such a selection of a Andigenum Group type is inferred from selection in the opposite direction, where Andigenum Group landraces were selected for their greater flowering, shorter stolons, greater yield, earlier tuberization, and reduction of cytosterility (''Neo-tuberosum'' clones of Simmonds (1966), Glendinning (1975), Vilaro et al. (1989)).

The close microsatellite-based phenetic relationship of some Indian ''Andigenum Group'' clones (Fig. 1) suggests that they are all closely interbred or clonally selected derivatives from each other. The non-T-type cpDNA of five Indian varieties (Lalmutti, Phulwa, Gulabia, Kufri Jawahar, Kufri Megha) suggests that Andigenum Group germplasm was involved in their pedigrees as maternal parents. The historical record covering the introductions of potato as described above does not provide unambiguous data regarding the source of these introductions. Hosaka and Hanneman (1988) showed that 3 of 26 Chilean landraces lacked the 241-bp deletion, so alternatively, these could represent Chilean introductions lacking the deletion. We conclude that Indian germplasm consists of a diverse set of clones that contain both Andigenum Group and Chilotanum Group germplasm but not the original remnant landraces of Andigenum Group landraces as was previously thought.

Table 3 Allele distribution among three potato Groups: 32 samples of European or Indian (modern) cultivars; five samples of the Chilotanum Group; 13 samples of the Andigenum Group

	Unique	Shared	Total
Modern cultivar alleles	10	57	67
Chilotanum Group alleles	1	38	39
Andigenum Group alleles	35	56	91
All germplasm	46	60	106

Implications for the initial germplasm introductions of potato to Europe

The status of the Indian potato varieties Darjeeling Red Round, Phulwa, Darjeeling Red Round Purple, Kufri Red, Gulabia, and Lalmutti as remnant Andigenum Group introductions or their clonal selections has long been accepted. These assumptions have been used to help support the Andigenum Group introduction hypothesis (Swaminathan 1958). As pointed out by Spooner and Hetterscheid (2005), every argument advanced for the Andigenum Group hypothesis has inherent problems or alternative explanations. (1) The vast majority (over 99%) of extant modern potato cultivars 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 late blight epidemics (cv. Yam released in 1836; Powell et al. 1993). It is unlikely that if Andigenum Group clones were predominant before 1845 they would have so completely disappeared worldwide with late blight. (2) The sole Andean introduction proponents explain these facts by a wholesale elimination of Andigenum Group clones after the late blight epidemics and subsequent breeding with Chilotanum Group clones. This explanation overlooks the cytoplasmic male sterility of the Chilotanum Group, where their crosses as females (but not males) to members of the Andigenum Group are sterile and would be unlikely to serve as breeding stock (Grun 1990) and where only a cross with Chilotanum Group as female would confer the T-type cpDNA. (3) Chilotanum Group clones are not known for late blight resistance, and it is unclear how these would have rescued potato cultivation worldwide after the appearance of this disease, unless it is

through their earlier tuberization and escape from severe disease expression. (4) The historical evidence of early introductions of Andigenum Group clones to the Canary Islands (Hawkes and Francisco-Ortega 1993) and to continental Spain (Hawkes and Francisco-Ortega 1992), combined with extant putatively remnant populations in the Canary Islands (Gil González 1997; Casañas et al. 2002), make a strong case for early introductions of the Andigenum Group there. But historical records of early introductions are at best sparse and indefinite (Salaman 1949; Glendinning 1983). There were likely multiple early introductions of all landrace groups from both the Andes and Chile, after the value of the potato became known, that simply were not recorded. Juzepczuk and Bukasov's (1929) argument that Chilean landraces were pre-adapted to the long days of Europe are compelling, and early introductions from Chile would rapidly be selected over less-adapted Andean clones. Although Neo-tuberosum clones show the characteristic to select for long-day adaptation from Andigenum clones (Simmonds 1966; Glendinning 1975; Vilaro et al. 1989), Chilean introductions would not require such intentional selection.

In summary, our data on the Indian potato, in combination with other facts, suggest a very different scenario of early potato introductions to Europe. That is, we propose that it is much more likely that the early introductions of cultivated potatoes came from both the Andes and Chile and that the Chilean landraces became the predominant modern breeding stock long before the 1840s.

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References

Butler EJ (1903) Potato diseases (*Solanum tuberosum*) of India. Agric Ledger 10:87–124

Casañas R, González M, Rodríguez E, Marrero A, Díaz C (2002) Chemometric studies of chemical compounds in five cultivars of potatoes from Tenerife. J Agric Food Chem 50:2076–2082

Dastur JF (1917) Conditions influencing the distribution of potato blight in India. Agric J India 12:90–96

Dutt BL (1979) Bacterial and fungal diseases of potato. Indian Council of Agricultural Research, ICAR), New Delhi

Ghislain M, Spooner DM, Rodríguez F, Villamón F, Nuñez J, Vásquez C, Waugh R, Bonierbale M (2004) Selection of highly informative and user-friendly microsatellites (SSRs) for cultivated potato genotyping. Theor Appl Genet 108:881–890

Gil González J (1997) El cultivo tradicional de la papa en la isla de la Tenerife. Associación Granate, La Laguna

Glendinning DR (1975) Neo-Tuberosum: new potato breeding material 2. A comparison of Neo-tuberosum with selected Andigena and with Tuberosum. Potato Res 18:343–350

Glendinning DR (1983) Potato introductions and breeding up to the early 20th century. New Phytol 94:479–505

Grun P (1990) The evolution of cultivated potatoes. Econ Bot 44[Suppl 3]:39–55

Hamester W, Hils U (2003) World catalogue of potato varieties. Agrimedia, Bergen/Dumme

Hawkes JG (1990) The potato: evolution, biodiversity, and genetic resources. Belhaven Press, London

Hawkes JG, Francisco-Ortega J (1992) The potato in Spain during the late 16th century. Econ Bot 46:86–97

Hawkes JG, Francisco-Ortega J (1993) The early history of the potato in Europe. Euphytica 70:1–7

Hosaka K (1993) Similar introduction and incorporation of potato chloroplast DNA into Japan and Europe. Jpn J Genet 68:55–61

Hosaka K (1995) Successive domestication and evolution of the Andean potatoes as revealed by chloroplast DNA restriction endonuclease analysis. Theor Appl Genet 90:356–363

Hosaka K (2003) T-type chloroplast DNA in *Solanum tuberosum* L. ssp. *tuberosum* was conferred from some populations of *S tarijense* Hawkes. Am J Potato Res 80:21–32

Hosaka K, Hanneman Jr RE (1988) The origin of the cultivated tetraploid potato based on chloroplast DNA. Theor Appl Genet 76:172–176

Huamán Z, Spooner DM (2002) Reclassification of landrace populations of cultivated potatoes (*Solanum* sect. *Petota*). Am J Bot 89:947–965

International Potato Center (1999) Molecular biology laboratory protocols: plant genotyping. In: Ghislain M, Zhang D, Herrera R (eds) Genetic Resources Department, training manual, CIP, Lima

Johnson, GW (1847) Gardener 1:19

Juzepczuk SW, Bukasov SM (1929) A contribution to the question of the origin of the potato (in Russian). Proc USSR Congr Genet Plant Anim Breed 3:592–611

Kawagoe Y, Kikuta Y (1991) Chloroplast DNA evolution in potato (*Solanum tuberosum* L.). Theor Appl Genet 81:13–20

Lössl A, Adler N, Horn R, Frei U, Wenzel G (1999) Chondriome-type characterization of potato: mt α, β, γ, δ, ϵ and novel plastid-mitochondrial configurations in somatic hybrids. Theor Appl Genet 98:1–10

Powell W, Baird E, Duncan N, Waugh R (1993) Chloroplast DNA variability in old and recently introduced potato cultivars. Ann Appl Bot 123:403–410

Provan J, Powell W, Dewar H, Bryan G, Machray CG, Waugh R (1999) An extreme cytoplasmic bottleneck in the modern European cultivated potato (*Solanum tuberosum*) is not reflected in decreased levels of nuclear diversity. Proc R Soc London Ser B 266:633–639

Raker C, Spooner DM (2002) The Chilean tetraploid cultivated potato, *Solanum tuberosum*, is distinct from the Andean populations; microsatellite data. Crop Sci 42:1451–1458

Salaman RN (1937) The potato in its early home and its early introduction into Europe. J R Hortic Soc 62:61–77, 112–123, 153–162, 253–266

Salaman RN (1949) The history and social influence of the potato. Cambridge University Press, Cambridge

Salaman RN, Hawkes JG (1949) The character of the early European potato. Proc Linn Soc London 161:71–84

Simmonds NW (1966) Studies on the tetraploid potatoes II. Factors in the evolution of the Tuberosum Group. J Linn Soc Bot 59:43–56

Spooner DM, Hetterscheid WLA (2005) Origins, evolution, and Group classification of cultivated potatoes. In: Motley TJ, Aorega N, Cross H (eds) Darwin's harvest: new approaches to the origins, evolution, and conservation of crops. Columbia University Press, New York (in press)

Swaminathan MS (1958) The origin of the early European potato-evidence from Indian varieties. Indian J Genet Plant Breed 18:8–15

Terry E (1655) Voyage to East India. John Wilkie, London (reprinted in 1777 from the edition of 1655)

Vilaro FL, Plaisted RL, Hoopes RW (1989) Comparison of cytoplasmic male sterilities in progenies of Tuberosum × Andigena and Tuberosum × Neo-Tuberosum crosses. Am Potato J 66:13–24

White GF (1838) In: Roberts E (ed) Views in India, chiefly among the Himalayan Mountains. Fisher Sons and Co, London Paris