

Molecular Studies on the Origin of the Cultivated Potato: a Review

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Abstract

Molecular data have been used to address the origin of the crop potato, relationships with its wild relatives and the introduction of the cultivated potato from South America into Europe and the rest of the world.

Results from the chloroplast and nuclear genome conflict as to the role taxa such as *Solanum tarijense*, *S. stenotomum* and the Brevicaule complex have played in the origin of the crop. Different data sets give rise to different hypotheses on the single or multiple domestication event(s) that occurred, most probably in southern Peru.

Molecular studies focusing on the first introductions from South America to Europe show that introductions before the late blight epidemics were already a mixture of both Andean and Chilean *S. tuberosum* plant material.

INTRODUCTION

Solanum tuberosum L. (potato) is a very important staple crop, listing fourth worldwide in tons of production. It is an unusual crop in having an extremely large secondary genepool. This secondary genepool consists of around 180 to 200 species, the number depending on different taxonomic treatments. These wild species are an important source of novel resistances and quality traits for the improvement of existing cultivated potatoes.

The classical approach to the taxonomy of this crop is exemplified by the treatment of Hawkes (1990). All the tuber-bearing *Solanum* L. species are placed in section *Petota* Dumortier of subgenus *Potatoe* (G. Don) D'Arcy. Section *Petota* is divided into 19 series of tuber-bearing species plus two series accommodating non tuber-bearing species. Series *Tuberosa* (Rydb.) Hawkes contains all the cultivated material as well as a large group of wild species. Seven cultivated species were recognized by Hawkes (1990):

- three diploids: *S. stenotomum* Juz. et Buk. with two subspecies, subsp. *stenotomum* and subsp. *goniocalyx* (Juz. et Buk.) Hawkes, *S. phureja* Juz. et Buk., and *S. ajanhuiri* Juz. et Buk.
- two triploids: *S. juzepczukii* Buk. and *S. chaucha* Juz. et Buk.
- one tetraploid: *S. tuberosum* L. with two subspecies, subsp. *andigena* Hawkes and subsp. *tuberosum*
- one pentaploid: *S. curtilobum* Juz. et Buk.

As early as 1962, Dodds (in Correll, 1962) pointed out the poor morphological support for most cultivated species. He only recognized *S. curtilobum* and *S. juzepczukii* as separate species and considered the other taxa as groups within *S. tuberosum*, anticipating the use of cultivar-groups as defined in the International Code of Nomenclature for Cultivated Plants, ICNCP (Brickell et al., 2004). Huaman and Spooner (2002) proposed classifying all the landrace populations of cultivated potatoes as the single species, *S. tuberosum*, with eight cultivar-groups: Ajanhuiri, Andigenum, Chaucha, Chilotanum, Curtilobum, Juzepczukii, Phureja and Stenotomum group.

Although Hettterscheid and Van den Berg (in the present volume) reject the use of Linnean names for crops, it is necessary to refer to the species names used by the majority of previous authors in order to be able to discuss the most important papers on this subject.

THE ORIGIN OF THE CULTIVATED POTATO

Hawkes (1990) and Grun (1990) regarded the cultigenic species *S. stenotomum* as the most primitive and as the progenitor of all other cultivated material. Hawkes (1990) identified the wild species *S. leptophyes* Bitt. as the probable progenitor of *S. stenotomum*, based on morphological similarity. *S. stenotomum* itself was considered the ancestor of other cultivated species such as *S. phureja*, *S. ajanhuiri* and *S. chaucha*. Grun (1990) was less specific: he regarded the so-called Brevicaule complex as the genepool from which the first cultivated material, *S. stenotomum*, was domesticated.

Both authors regarded *S. stenotomum* (partly or wholly) as the progenitor of *S. tuberosum* subsp. *andigena*, which was seen as the progenitor of *S. tuberosum* subsp. *tuberosum*.

Newer hypotheses on this subject have been based on various molecular techniques, such as AFLP, chloroplast RFLP and nuclear RFLP. Since 1986 Hosaka and co-workers have published many papers on this subject, mainly based on chloroplast DNA haplotypes derived from RFLP patterns. Hosaka (1986), in a paper aptly called 'Who is the mother of the potato?' distinguished seven different chloroplast haplotypes in a selection of wild and cultivated species:

1. Type T, restricted to *S. tuberosum* subsp. *tuberosum*
2. Type A, characteristic of *S. tuberosum* subsp. *andigena* and *S. maglia*
3. Type S, found in *Solanum goniocalyx* (= *S. stenotomum* subsp. *goniocalyx*), *S. phureja*, *S. stenotomum*, *S. chaucha* and one accession of subsp. *andigena*
4. Type C, found in *S. acaule* Bitt., *S. bukasovii*, *S. canasense*, *S. multidissectum* and *S. × juzepczukii*
5. Type W', found in *S. chacoense* Bitter f. *gibberulosum* (Juz. et Buk.) Corr.
6. Type W'', found in *S. tarijense* Hawkes
7. Type W, found in other wild species.

He concluded that *S. goniocalyx*, *S. phureja*, *S. chaucha*, and *S. tuberosum* subsp. *andigena* were derived from *S. stenotomum*. A direct ancestry between *S. tuberosum* subsp. *andigena* and *S. tuberosum* subsp. *tuberosum* could not be confirmed. The results also showed that haplotype A is found in some accessions of *S. tuberosum* subsp. *andigena* and the authors suggested that *S. maglia* might be the female ancestor of *S. tuberosum* subsp. *andigena*.

However, these conclusions were followed by steadily changing opinions on the ancestry of the cultivated potato. Hosaka et al. (1988a) showed that the differences between types T and type W were in fact all caused by a single physical deletion in the chloroplast genome of the T type chloroplast; therefore the authors drew the conclusion that T type chloroplast could easily have evolved from the primitive W type. Because most of the South American tuber-bearing *Solanum* species have the W haplotype, they could all be considered as candidates for the female ancestor of *S. tuberosum* subsp. *tuberosum*.

Hosaka (1995) suggested that *S. bukasovii* Juz. seems the most likely ancestral species of *S. stenotomum*, although it was stated that other diploid wild species such as *S. canasense* Hawkes, *S. candolleanum* Berth., *S. leptophyes* Bitt. and *S. multidissectum* Hawkes also remained possible candidates.

Hosaka (2003) then suggested that populations of *S. tarijense* Hawkes could have acted as maternal ancestors of the cultivated potato, based on the presence of T type chloroplast in accessions of *S. tarijense*, and Hosaka (2004) showed that some accessions of *S. tuberosum* subsp. *andigena* possess the T type.

Sukhotu et al. (2004) presented results combining chloroplast haplotypes with nuclear DNA restriction fragment length polymorphisms (RFLP). The results showed that nuclear DNA RFLPs only supported the differentiation between the chloroplast haplotypes of the W type on one hand and the C, S, and A types on the other hand. The cultivated species belong to the group showing C, S and A types.

The most recent paper on this subject (Sukhotu and Hosaka, 2006) suggests that the initial *S. tuberosum* subsp. *andigena* populations arose by multiple origin from *S.*

stenotomum.

Other authors have also tried to solve the question which wild species could be the progenitor of the cultivated potato. Kardolus et al. (1998) showed in an amplified fragment length polymorphism (AFLP) tree that *S. tuberosum* subsp. *tuberosum* clusters with the Peruvian species *S. multidissectum* and *S. canasense* in the Brevicaule complex. Spooner et al. (2005a) concluded that the cultivated species are in the same clade as the northern Brevicaule clade, including the following species: *S. bukasovii*, *S. ambosinum* Ochoa, *S. canasense*, *S. leptophyes*, *S. achacachense* Card. and *S. multidissectum*.

Summarizing these studies, it can be concluded that the ancestor of the first diploid cultivated material (*S. stenotomum*) is probably one of the species in the Brevicaule complex. Material of *S. stenotomum* is ancestral to the primitive tetraploid landraces in South America (*S. tuberosum* subsp. *andigenum*), as a result of sexual polyploidization, accompanied by hybridization and human selection. It seems clear that molecular data, especially the RFLP data on cpDNA, are not sufficiently informative to point to one wild ancestral species in particular.

SINGLE OR SUCCESSIVE DOMESTICATION?

Potatoes have been cultivated in South America for a very long time; archeological evidence from graves and rubbish heaps puts the domestication of the potato somewhere around 4000 and 2000 BC. Food remains containing cultivated potato material were found in Peru, in Ancón-Chillón near Lima, in a site from the Chilca canyon in the Andes and from Casma on the northern Peruvian coast (Hawkes, 1990) but the location of the domestication event leading to the first diploid cultivated potatoes is unknown.

Diamond (2002) distinguished two different domestication scenarios:

1. a single domestication event within a restricted geographic area;
2. multiple independent domestications at different sites.

He also suggests that most New World crops have arisen by multiple domestication as opposed to the predominantly single domestications of Fertile Crescent founder crops. He explains this difference to the restricted geographic ranges of the wild ancestors of the Fertile Crescent founder crops plus a rapid spread of domesticates (domesticated plants). Crops domesticated in the New World on the other hand, would have slowly diffused along the north-south axis of the New World. Various examples are outlined, but potato is not one of them.

Hosaka and Hanneman (1988a,b) considered the polymorphic nature of the chloroplast DNA of *S. tuberosum* subsp. *andigena* and, to a lesser extent, that of *S. tuberosum* subsp. *tuberosum*, as an indication that the former may have arisen many times by hybridization and introgression from cultivated diploid populations. Hosaka (1995) showed that the chloroplast variety found in *S. tuberosum* subsp. *andigena* also exists in the possible progenitor *S. stenotomum*. All the chloroplast DNA haplotypes in *S. stenotomum* can be found in the wild species, except for the T type. To explain this parallel spectrum of the diversity of chloroplast DNA types in wild and cultivated species, Hosaka (1995) proposed a theory of successive domestication. Differentiation of the chloroplast DNA could have occurred in the 'ancestral species' complex from which several wild species, as well as cultivated species, evolved. Sukhotu et al. (2004) also claimed that the fact that many different haplotypes are found in wild species and in cultivated material suggested successive domestication events and parallel differentiation of wild species from the ancestral species complex.

In contrast to this, Spooner et al. (2005a) claimed a single domestication event for potato. Their AFLP data showed that the cultivated species are all in one clade, nested within the clade of the northern Brevicaule complex. However, support for these clades is low. They concluded that the cultivated potato originated from an unknown member of the Brevicaule complex, probably from the northern clade. Because, in their view, the Brevicaule complex can be reduced to one species, they consider this to be a single domestication event.

INTRODUCTION OF THE CULTIVATED POTATO INTO EUROPE AND THE REST OF THE WORLD

Hawkes (1990) stated that the first potato in Europe probably arrived in Spain somewhere between 1565 and 1573. There are two competing theories about the nature of the first material to be introduced into Europe. Grun (1990) and Hawkes (1990) proposed that the first potato material brought to Europe consisted of *S. tuberosum* subsp. *andigena* from the Andes, very probably from Colombia. Most of the potato stock from this original material would then have been wiped out during the late blight epidemic in Europe in the 1840s. After the epidemic, new introductions would have been mainly *S. tuberosum* subsp. *tuberosum*.

On the other hand, Juzepczuk and Bukasov (1929) suggested that the early European introductions already consisted of subsp. *tuberosum* germplasm from Chile. This was based on the similarity in morphology and growing conditions of the early European crop plants to those of Chilean material. Chilean potatoes were already adapted to form tubers under long-day conditions and as such, were suitable to grow in Europe.

Hosaka and Hanneman (1988b) also drew the conclusion that the first potato introduced in Europe before the late blight epidemic was subsp. *andigena*. They based this on the results of a cpDNA analysis in which the cpDNA of the cultivar 'Myatts' Ashleaf', seen as one of the relics of the first European potato material, was determined as type A. This A type chloroplast was relatively abundant in the potato accessions analysed from the northern Andes. Hosaka (1993) repeated this conclusion based on a study of Japanese varieties that were considered to have been introduced before the late blight epidemics. Four of these Japanese varieties had A type cpDNA while many modern varieties carried T or W type cpDNA.

However, three more recent publications seem to confirm the opposite theory. Spooner et al. (2005b) investigated the origin of potato cultivars (varieties) from India. Among these varieties were cultivars thought to be derived from *S. tuberosum* subsp. *andigena*. These accessions would not have been eliminated by the late blight epidemic because late blight did not occur in India until 1870. Nuclear microsatellites clustered all Indian varieties, including the early introductions of subsp. *andigena* (putative remnant populations of Andean landraces) with subsp. *tuberosum* landraces (from Chile) and European cultivars. The old subsp. *andigena* landraces (from Guatemala to Bolivia) clustered together and formed a separate group. The authors suggested that they might be hybrids of Andean landraces (from upland Venezuela to northern Argentina) with Chilean material (lowland south central Chile) or more advanced cultivars. Five varieties from India possessed non T type cpDNA which is typical of *S. tuberosum*. Therefore the authors suggest that subsp. *andigena* germplasm was involved in their ancestry as maternal parent. The general conclusion was that early introductions of cultivated potatoes to India and Europe came from both subsp. *tuberosum* and subsp. *andigena*.

Rios et al. (2007) treated the same issues but focused on Canary island landraces. The results from the nuclear DNA SSRs showed that these Canary Islands landraces were distributed over two clusters (although not strongly separated): one cluster associated with *S. tuberosum* subsp. *tuberosum* germplasm, and another associated with *S. tuberosum* subsp. *andigena* germplasm. All the landraces from Chile and the Canary Islands with subsp. *tuberosum* germplasm possessed a characteristic 241 bp deletion. This allowed the conclusion that potato material was introduced from both the Andes and Chile, before the late blight epidemics. The Canary Islands are believed to be one of the first regions where potatoes were introduced from South America, and the results for the Canary Islands can be extrapolated to the rest of Europe. Although the authors found that some cultivars were derived from subsp. *andigena*, they concluded that most of the potato material introduced before the late blight epidemic was derived from subsp. *tuberosum*, as these were better adapted to the long-day conditions in Europe.

Recently, Ames and Spooner (2008) used the same 241 bp deletion to study DNA from historical herbarium specimens and concluded that although the Andean potato (lacking the deletion) appeared in Europe first, the Chilean potato was already present

long before the late blight epidemics.

Literature Cited

- Ames, M. and Spooner, D.M. 2008. DNA from herbarium specimens settles a controversy about origins of the European potato. *American Journal of Botany* 95:252-257.
- Brickell, C.D., Baum, B.R., Hetterscheid, W.L.A., Leslie, A.C., McNeill, J. Trehane, P., Vrugtman, F. and Wiersema, J.H. (eds.). 2004. *International Code of Nomenclature for Cultivated Plants*, 7th edition. Acta Hort. 647.
- Diamond, J. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* 418:700-707.
- 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.
- 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.
- Hawkes, J.G. 1990. *The potato: evolution, biodiversity and genetic resources*. Belhaven Press, London, UK.
- Hetterscheid, W.L.A. and Van den Berg, R.G. (present volume). The crop-group and the inconsistent use of Linnean names in the taxonomy of domesticated plants.
- Hosaka, K. 1986. Who is the mother of the potato? Restriction endonuclease analysis of chloroplast DNA of cultivated potatoes. *Theoretical and Applied Genetics* 72:606-618.
- Hosaka, K. 1993. Similar introduction and incorporation of potato chloroplast DNA into Japan and Europe. *Japanese Journal of Genetics* 68:55-61.
- 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.
- Hosaka, K. 2003. T-type chloroplast DNA in *Solanum tuberosum* L. ssp. *tuberosum* was conferred from some populations of *S. tarijense* Hawkes. *American Journal of Potato Research* 80:21-32.
- Hosaka, K. 2004. Evolutionary pathway of T-type chloroplast DNA in potato. *American Journal of Potato Research* 81:153-158.
- Hosaka, K. and Hanneman Jr., R.A. 1988a. The origin of the cultivated tetraploid potato based on chloroplast DNA. *Theoretical and Applied Genetics* 76:172-176.
- Hosaka, K. and Hanneman Jr., R.A. 1988b. Origin of chloroplast DNA diversity in the Andean potatoes. *Theoretical and Applied Genetics* 76:333-340.
- Hosaka, K., De Zoeten, G.A. and Hanneman Jr., R.A. 1988. Cultivated potato chloroplast DNA differs from the wild type by one deletion-evidence and implications. *Theoretical and Applied Genetics* 75:741-745.
- Huaman, Z. and Spooner, D.M. 2002. Reclassification of landrace populations of cultivated potatoes (*Solanum* sect. *Petota*). *American Journal of Botany* 89:947-965.
- Juzepczuk, S.W. and Bukasov, S.M. 1929. A contribution to the question of the origin of the potato. *Proceedings of the USSR congress of Genetics* (in Russian). *Plant and Animal Breeding* 3:592-611.
- Kardolus, J.P., Van Eck, H.J. and Van den Berg, R.G. 1998. The potential of AFLPs in biosystematics: a first application in *Solanum* taxonomy (*Solanaceae*). *Plant Systematics and Evolution* 210:87-103.
- Rios, D., Ghislain, M., Rodriguez, F. and Spooner, D.M. 2007. What is the origin of the European potato? Evidence from Canary Island landraces. *Crop Science* 47:127-128.
- Spooner, D.M., McClean, K., Ramsay, G., Waugh, R. and Bryan, G.J. 2005a. A single domestication for potato based on multilocus AFLP genotyping. *Proceedings of the National Academy of Science, USA* 102:14694-14699.
- Spooner, D.M., Nunez, J., Rodriguez, F., Naik, P.S. and Ghislain, M. 2005b. Nuclear and

- chloroplast DNA reassessment of the origin of Indian potato varieties and its implications for the origin of the early European potato. *Theoretical and Applied Genetics* 110:1020-1026.
- Sukhotu, T., Kamijima, O. and Hosaka, K. 2004. Nuclear and chloroplast DNA differentiation in Andean potatoes. *Genome* 47:46-56.
- Sukhotu, T. and Hosaka, K. 2006. Origin and evolution of Andigena potatoes revealed by chloroplast and nuclear DNA markers. *Genome* 49:636-647.