DARWIN'S HARVEST

New Approaches to the Origins, Evolution, and Conservation of C...

Timothy J. Motley, Nyree Zerega, and Hugh C...

EDITORS

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New Approaches to the Origins,
Evolution, and Conservation of Crops

Edited by

TIMOTHY J. MOTLEY,
NYREE ZEREGA,
and **HUGH CROSS**

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Origins, Evolution, and Group Classification of Cultivated Potatoes

Potato is the world's most productive vegetable and provides a major source of nutrition and income to many societies. The story of the potato begins with wild potato species that look very similar to the cultivated potato today. Wild potatoes are widely distributed in the Americas from the southwestern United States to southern Chile, but the first cultivated potatoes probably were selected from populations in the central Andes of Peru and Bolivia sometime between 6000 and 10,000 years ago. These wild species and thousands of indigenous primitive cultivated landrace populations persist throughout the Andes, with a second set of landrace populations in Chiloé Island, the adjacent islands of the Chonos Archipelago, and mainland areas of lowland southern Chile. These Chilean populations probably arose from Andean populations that underwent hybridization with the wild species *Solanum tarijense*, found in southern Bolivia or northern Argentina. The first record of potato out of South America is from the Canary Islands in 1562, and the potato rapidly became cultivated in Europe and then worldwide. Selection and breeding transformed the potato into a set of modern cultivars with more uniform colors and shapes and with improved agronomic qualities such as greater disease resistance and yield. Current opinion invokes the earliest European introductions from Andean landraces, with the introduction of Chilean landraces only after late blight disease killed many potato

populations in Europe in the 1840s. We suggest early introductions of cultivated potatoes from both the Andes and Chile, with the Chilean landraces becoming the predominant modern breeding stock long before the 1840s. There is also a controversy about the classification of potato as Linnean species treated under the International Code of Botanical Nomenclature (ICBN) or as Groups under the International Code of Nomenclature of Cultivated Plants (ICNCP). We support a recent Group classification of the landrace populations and here propose the first Group classification of the modern cultivars, placing all under the single name (denomination class) of *Solanum tuberosum*.

Cultivated Potato in the Context of Tuber-Bearing Species in *Solanum* Section *Petota*

The cultivated potato and its tuber-bearing wild relatives, (*Solanum* L. sect. *Petota* Dumort.) are monophyletic (Spooner et al., 1993) and are distributed from the southwestern United States to central Argentina and adjacent Chile (Hijmans and Spooner, 2001). Indigenous primitive cultivated (landrace) potatoes are grown throughout middle to high (about 3000–3500 m) elevations in the Andes from western Venezuela to northern Argentina, and then in south-central Chile, concentrated in the Chonos Archipelago. Landrace populations in Mexico and Central America are recent, post-Columbian introductions (Hawkes, 1967; Ugent, 1968; Glendinning, 1983). Potatoes can be divided into three artificial groups based entirely on use: wild species, cultivated indigenous landrace populations growing in the Andes and southern Chile, and modern cultivars initially developed in Europe in the 1500s and later spread worldwide. The landrace populations are highly diverse, with a great variety of shapes and skin and tuber colors not often seen in modern varieties (figure 13.1). There are fewer than 200 wild species (Spooner and Hijmans, 2001).

Ploidy levels in *S. tuberosum* L. and in section *Petota* range from diploid $(2n = 2x = 24)$, to triploid $(2n = 3x = 36)$, to tetraploid $(2n = 4x = 48)$, to pentaploid $(2n = 5x = 60)$; the wild species also have hexaploids $(2n = 6x = 72)$. This chapter focuses on the origin and taxonomy of *S. tuberosum*, beginning with its selection from wild Andean species in the *S. brevicaule* complex, to the origin of Andean and Chilean landraces, to first introductions of Andean and Chilean landraces to Europe, to the current breeding efforts of modern cultivars.

Hawkes (1990) provided the last attempt to formally classify wild potatoes and recognized 21 series, which included tuber-bearing and

non–tuber-bearing species. Studies by Spooner and Sytsma (1992), Spooner et al. (1993), and Spooner and Castillo (1997) showed that the non–tuber-bearing species do not belong to section *Petota* and that not all Hawkes's series are monophyletic.

Origin of Cultivated Potatoes from the *S. brevicaule* Complex

We lack well-resolved multigene phylogenies to divide section *Petota* into formal taxonomic groups, but one phenetic group, the *S. brevicaule* complex, has long attracted the attention of biologists because of its similarity to cultivated potatoes (Correll, 1962; Ugent, 1970; Grun, 1990; Van den Berg et al., 1998; Miller and Spooner, 1999). Some members of this group, endemic to central Peru, Bolivia, and northern Argentina, probably were ancestors of the landraces. The species in the complex share the pinnately dissected leaves, round fruits, and rotate to rotate-pentagonal corollas of cultivated potato and are largely sexually compatible with each other and with cultivated potato (Hawkes, 1958; Hawkes and Hjerting 1969, 1989; Ochoa, 1990, 1999; Huamán and Spooner, 2002). The complex includes diploids, tetraploids, pentaploids, and hexaploids. Most are weedy plants, sometimes occurring in or near cultivated potato fields, from about 2500–3500 m. It is so hard to identify species in the group that experienced potato taxonomists Hawkes and Hjerting (1989) and Ochoa (1990) provide different identifications to identical collection numbers of the *S. brevicaule* complex in 38% of the cases (Spooner et al., 1994). Many species grow as weeds in or adjacent to cultivated potato fields and form crop–weed complexes (Ugent, 1970). Morphological data (Van den Berg et al., 1998) and single- to low-copy nuclear restriction fragment length polymorphism data (Miller and Spooner, 1999) failed to clearly differentiate wild species in the complex from each other or from most landraces, and the most liberal taxonomic interpretation of these studies was to recognize only three wild taxa: the Peruvian populations of the *S. brevicaule* complex, the Bolivian and Argentinean populations of the *S. brevicaule* complex, and *S. oplocense*. However, even these three groups could be distinguished only by computer-assisted use of widely overlapping character states, not by species-specific characters (a polythetic morphological species concept). Accordingly, it is difficult to designate species-specific progenitors of the landraces, as Hawkes (1990) has done by designating *S. leptophyes* Bitter and *S. sparsipilum* (Bitter) Juz. and Bukasov as progenitors of the cultivated diploid *S. stenotomum*.
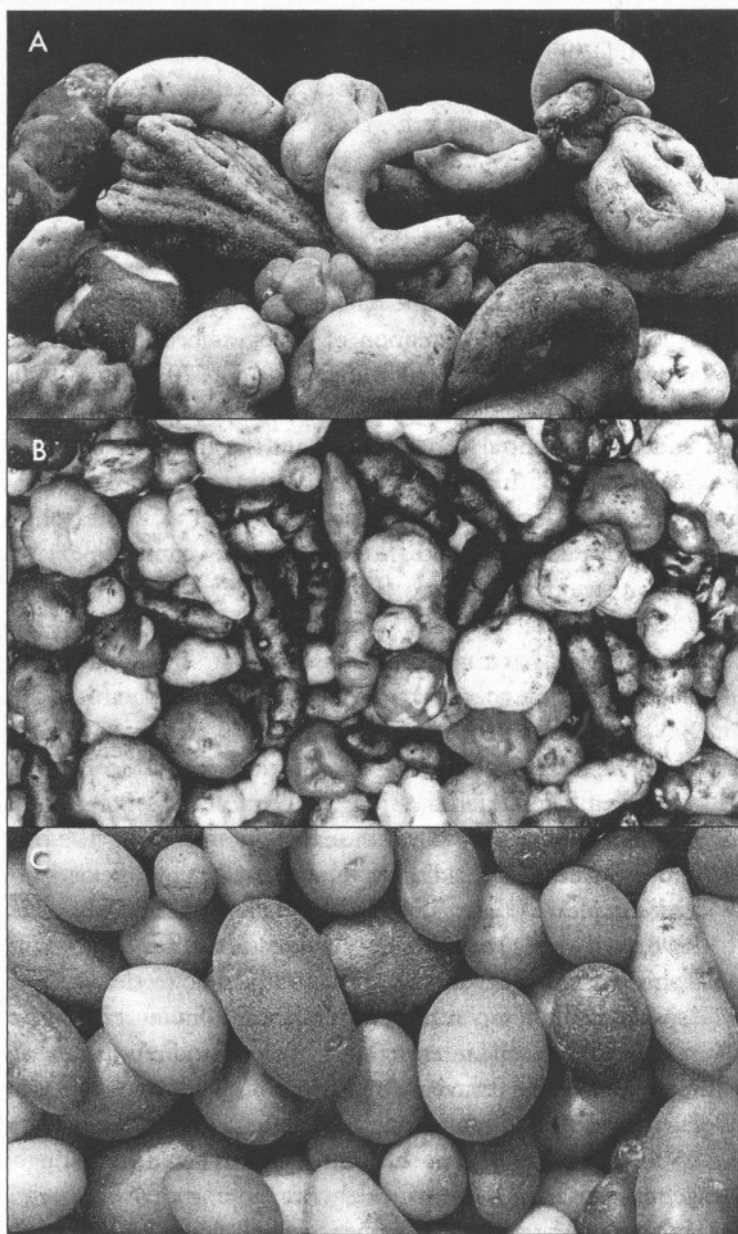
FIGURE 13.1 Representative landraces **(A)** from the Andes (from Graves, 2001) and **(B)** from Chile (courtesy of Andres Contreras, Universidad Austral de Chile) and **(C)** modern cultivars (USDA Agricultural Research Magazine image gallery, www.ars. usda.gov/is/graphics/photos/). (Full-color version of this figure follows page 230.)

Ploidy Level and Gene Flow Within and Between Cultivated and Wild Species

Bukasov (1939) was the first to count chromosomes of the cultivated potatoes and discovered diploids, triploids, tetraploids, and pentaploids. Ploidy level soon became a major character to distinguish one cultivated species from another. Cultivated potato fields in the Andes contain mixtures of landraces at all ploidy levels (Ochoa, 1958; Jackson et al., 1980; Brush et al., 1981; Johns and Keen, 1986; Quiros et al., 1990, 1992; Zimmerer, 1991), which often co-occur and hybridize with wild potato species (Ugent, 1970; Grun, 1990; Rabinowitz et al., 1990). Watanabe and Peloquin (1989, 1991) showed both diploid and unreduced gametes to be common in the wild and cultivated species, potentially allowing gene transfer between different ploidy levels. The boundary between cultivated and wild often is vague, and some putative wild species may be escapes from cultivation (Spooner et al. 1999).

Treatment of Cultivated Potatoes as Linnean Taxa

Cultivated potatoes have been classified as species under the ICBN (Greuter et al., 2000). The widely used species classification of Hawkes (1990) recognizes seven cultivated species (and subspecies): *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, *S. phureja* ssp. *phureja*, *S. phureja* ssp. *hygrothermicum*, *S. phureja* ssp. *estradae*, *S. stenotomum* ssp. *stenotomum*, *S. stenotomum* ssp. *goniocalyx*, *S. tuberosum* ssp. *andigenum* (as *andigena*), and *S. tuberosum* ssp. *tuberosum*. In contrast, Ochoa (1990, 1999) recognizes 9 species and 141 infraspecific taxa (subspecies, varieties, and forms, including his unlisted autonyms) for the Bolivian cultivated species alone, and Russian potato taxonomists Bukasov (1971) and Lechnovich (1971) recognize 21 cultivated species, including separate species status for *S. tuberosum* ssp. *andigenum* and ssp. *tuberosum* (as *S. tuberosum*) (Huamán and Spooner, 2002).

Treatment of Cultivated Potatoes as Groups

Dodds (1962) suggested that there was poor morphological support for most cultivated species, and he recognized only *S.* ×*curtilobum*, *S.* ×*juzepczukii*, and *S. tuberosum*, with five Groups recognized in the latter. The classifications of Dodds (1962) and Hawkes (1990) are regularly used today, creating confusion among users. Groups are classification categories used by the ICNCP (Brickell et al., 2004) to group cultivated plants with traits that are of use

to agriculturists. The term *Group* replaces *Cultivar Group* of the prior ICNCP (Trehane et al., 1995). The ICNCP associates cultivated plant names with denomination classes. A denomination class is a nomenclatural device found in the ICNCP, not the ICBN. It is defined (ICNCP Article 5) as a taxon, or a designated subdivision of a taxon, or a particular Group, within which cultivar epithets must be unique. The botanical genus is the denomination class by default. However, *S. tuberosum* is the denomination class recognized by the International Union for the Protection of New Varieties of Plants (UPOV) as a tool in naming potato cultivars in countries that signed the UPOV treaty and as such possess the mechanism of breeders' rights protection.

Huamán and Spooner (2002) studied the morphological distinction of the potato landraces with numerical phenetics and showed a gradation of support for the cultivated species of Hawkes (1990). For example, the best support was shown for *S. ajanhuiri, S. chaucha, S. curtilobum, S. juzepczukii,* and *S. tuberosum* ssp. *tuberosum,* but there was little or no support for the other six taxa. However, most characters, except tuber dormancy for *S. phureja* ssp. *phureja* and relative position of pedicel articulation for *S. ajanhuiri, S. curtilobum,* and *S. juzepczukii,* overlap extensively with those of other species. In other words, the only morphological support is provided by a complex of characters, all of which are shared with other taxa (polythetic support). Huamán and Spooner (2002) group all landrace populations of cultivated potatoes into the single denomination class, *S. tuberosum,* with eight Groups: Ajanhuiri Group, Andigenum Group, Chaucha Group, Chilotanum Group (*S. tuberosum* ssp. *tuberosum* from Chile), Curtilobum Group, Juzepczukii Group, Phureja Group, and Stenotomum Group.

This gradation of support (groups defined only by shared characters) makes a taxonomic decision of cultivated potatoes under the ICBN or ICNCP difficult. An argument could be made for *S. ajanhuiri, S. curtilobum, S. juzepczukii,* and *S. tuberosum* ssp. *tuberosum* to be recognized as species and the other taxa as Groups under a separate cultivated species *S. andigenum.* Support for the separate species treatment of *S. tuberosum* ssp. *tuberosum* is provided by Raker and Spooner (2002), who demonstrated that most of the landrace populations of the Chilotanum Group (from Chile) can be distinguished with microsatellite data from most populations of the Andigenum Group (from the Andes), and molecular support probably will be provided for the Ajanhuiri, Curtilobum, and Juzepczukii groups because of their independent hybrid origins involving other wild species. Despite these ambiguities, Huamán and Spooner (2002) classify

all cultivated landraces under the single denomination class *S. tuberosum* because of the following lack of monophyly, taxonomic difficulties, and classification philosophy:

- Polythetic morphological support predominates (Huamán and Spooner, 2002).
- Origins are reticulate (Hawkes, 1990; Huamán et al., 1982; Schmiediche et al., 1982; Cribb and Hawkes, 1986).
- Multiple origins are possible (Hosaka, 1995).
- There are evolutionarily dynamic populations with continuing hybridization of crops to weeds (Ugent, 1970).
- Some accessions of wild and cultivated species 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).
- ICNCP classification philosophy is more logical for cultivated species.

Chilean and Andean Hypotheses of the First Introductions of Potato to Europe

Juzepczuk and Bukasov (1929) proposed that Chilean potato landraces originated from indigenous primitive Chilean tetraploid wild species and that the first European modern cultivars were introductions of Chilean landraces. They argued that the Chilean landraces were already adapted to the long days of Europe (Andean landraces form tubers under short days) and have a leaf morphology more similar to that of European landraces than Andean landraces.

In contrast, Salaman (1949), Salaman and Hawkes (1949), Hosaka and Hanneman (1988b), Grun (1990), Hawkes (1990), and Hawkes and Francisco-Ortega (1993) collectively suggested the following:

- *S. tuberosum* ssp. *tuberosum* in Chile arose from ssp. *andigenum* from the Andes, either directly or through a cross with an unidentified wild species. Grun (1979, 1990) found that the cytoplasmic types of Chilean landraces of *S. tuberosum* and modern potatoes were identical. However, he identified nine cytoplasmic factors that separate ssp. *andigenum* from ssp. *tuberosum* that cause sterility in the presence of specific chromosomal genes, abnormal anthers and pollen, anthers fused to styles, and female sterility. These factors are expressed only when ssp. *tuberosum* is used as a female, and when it is used as a male the crosses are fertile; that is, there are reciprocal crossing differences that affect sterility. Hawkes (1990)

identified the putative wild progenitors of Chilean landraces proposed by Juzepczuk and Bukasov (1929) to be nothing more than other landraces, not wild species.

- The first modern potatoes were introduced from the Andes to Europe as *S. tuberosum* ssp. *andigenum*. The first record of potato in Europe is from the Canary Islands in 1562 (Hawkes and Francisco-Ortega, 1993) and the second record from Seville, Spain, in 1570 (Hawkes and Francisco-Ortega, 1992).

- *S. tuberosum* ssp. *andigenum* in Europe rapidly evolved into a wider leaf morphotype with long-day adaptation, a parallel event to long-day selection in Chile, and these evolved forms should be classified as ssp. *tuberosum,* just like the Chilean landraces.

- The fungal disease late blight (*Phytophthora infestans* (Mont.) De Bary) in Europe killed most *tuberosum*-evolved *andigenum* clones in the 1840s, but modern potato was rapidly mass selected and bred for blight resistance with ssp. *tuberosum,* purchased in Panama (as cultivar Rough Purple Chile) but believed to have come from Chile (Plaisted and Hoopes, 1989; Grun, 1990).

Chloroplast and Mitochondrial DNA Evidence

Chloroplast DNA (cpDNA) restriction site data have been used to investigate the wild species progenitors of the putative first cultivated potato *S. stenotomum* (a diploid) and subsequent origins of the other cultivated potatoes. Hosaka and Hanneman (1988a) and Hosaka (1995) documented five chloroplast genotypes (A, C, S, T, and W) in the Andean diploid and tetraploid landraces and in their putative progenitors in the *S. brevicaule* complex. The Chilean landraces had three of these genotypes (A, T, and W) but with a predominant T type cpDNA, characterized by a 241-bp deletion (Kawagoe and Kikuta, 1991), which is rare in the Andes. Hosaka (2002) showed that the only other wild potato species possessing T-type cpDNA were *S. berthaultii, S. neorossii,* and *S. tarijense* from Bolivia and Argentina. However, he also showed that that there were other chloroplast DNA restriction site markers shared only by some populations of *S. tarijense* and Chilean landraces of potato (Hosaka, 2003). He therefore concluded that these populations of *S. tarijense* were maternal parents to Chilean potato, perhaps after hybridization with Andean diploid or tetraploid landraces.

Both chloroplasts and mitochondria are extranuclear (cytoplasmic) organelles that contain their own DNA, but only mitochondria are known to condition the reciprocal crossing differences of male sterility that are

evidenced in crosses between Andean and Chilean potato. Lössl et al. (1999) detected five major mitochondrial DNA (mtDNA) types in potato that they designated with Greek symbols α, β, γ, δ, and ε. Interestingly, β-type mtDNA is associated with T-type cpDNA. Lössl et al. (1999) found β-type mtDNA in Chilean landraces and *S. berthaultii* that has T-type cpDNA (*S. tarijense* was not examined). This suggests that Hosaka's cpDNA types are good markers to infer origins of Chilean landraces but that the mtDNA is the actual causal agent conditioning cytoplasmic male sterility.

Our Challenge to the Andean Introduction Hypothesis

Most publications since Salaman (1949) and Salaman and Hawkes (1949) accept the Andean introduction hypothesis without question, and most suggest that Chilean landraces were an important cultivated germplasm source only after the late blight epidemics of the 1840s. Evidence supporting the Andigenum Group as the first European introductions includes the following:

- Early herbarium specimens of potato in Europe had the narrow-leaved phenotype thought to distinguish the Andigenum Group from the Chilotanum Group = *S. tuberosum* ssp. *tuberosum* in Chile (Salaman and Hawkes, 1949).
- The earliest records of cultivated potatoes from the Canary Islands (in 1567; Hawkes and Francisco-Ortega, 1993) and from Seville, Spain (in 1573; Salaman, 1949; Hawkes and Francisco-Ortega, 1992), apparently were harvested late in the year (November and December), suggesting that they were the short day–adapted Andigenum Group. Remnants of these early introductions of Andigenum Group and triploid clones of Andean Chaucha Group persist on the Canary Islands, with putatively more recent introductions of the Chilotanum Group (Gil González, 1997; Casañas et al., 2002).
- The trip from Chile to Europe took longer than from Peru (or Colombia) to Europe, and tubers from Chile would have less of chance to survive this long voyage.
- Artificial selection of Andigenum Group collectively produced some Chilotanum Group–like clones ("neo-*tuberosum*") having greater flowering, shorter stolons, greater yield, earlier tuberization, reduction of cytosterility, and greater late blight resistance (Simmonds, 1966; Glendinning, 1975; Huarte and Plaisted, 1984; Vilaro et al., 1989) that showed the possibility for rapid selection.

We challenge the sole Andean introduction hypothesis and suggest that early introductions to Europe were from the Andes *and* from Chile, and the Chilean introductions became the prominent type well before the 1840s. Our arguments follow:

- Huamán and Spooner (2002; character 13 of figure 3) quantified overlap of leaf shapes between Andigenum Group and Chilotanum Group landraces. Identification is problematic of a limited set (18) of early European introduction potato herbarium specimens to Andean or Chilean origins based on leaf shape alone (Salaman and Hawkes, 1949).

- The historical evidence, including late cultivation of potatoes in Spain and the Canary Islands (Salaman, 1949; Hawkes and Francisco-Ortega, 1992, 1993) combined with extant putatively remnant populations in the Canary Islands (Gil González, 1997; Casañas et al., 2002), makes 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 probably were multiple introductions of all landrace groups from both the Andes and Chile after the value of potato became known, but they simply were not recorded.

- The argument that Chilean tubers would not have survived the long trip from the Andes to Europe (Hawkes, 1967) ignores the simple possibility of transport of true seeds, potted plants, or even well-preserved tubers. Potatoes certainly were an item of ship's stores from Chile, and there are records as early as 1587 of potatoes crated for shipment to Europe (Glendinning, 1983).

- 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 be selected rapidly 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.

- More than 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 1836 (cultivar "Yam"; Powell et al., 1993). The Andean introduction proponents explain these facts by an elimination of Andigenum Group clones

after the late blight epidemics and breeding with Chilotanum Group clones. This explanation overlooks the cytoplasmic male sterility of the Chilotanum Group because many crosses as females (but not males) are sterile (Grun, 1979, 1990), and only a cross with Chilotanum Group as female would confer the T-type cpDNA. It also overlooks the fact that Chilotanum Group clones are not known for late blight resistance.

In summary, we consider it likely that both Andigenum Group and Chilotanum Group clones were part of multiple early introductions of potato to Europe and that Chilotanum Group clones quickly became the predominant modern cultivars in Europe, as their derivatives are today worldwide.

Group Classification Under the ICNCP

The most recent edition of the ICNCP (Brickell et al., 2004) lists currently accepted categories to classify and name cultivated plants. Hetterscheid (1994), Hetterscheid and Brandenburg (1995a, 1995b), Hetterscheid et al. (1996), and Spooner et al. (2003) argue for a modernization of the classification and nomenclature of cultivated plants. The use of Linnean categories to classify cultivated plants presents problems because their artificial selection often involves processes very different from the natural evolution of wild plants. These processes often include human-directed multiple origins, extensive interspecific and sometimes intergeneric hybridization, and rapid selection of traits (such as gigantism, lack of dispersability, increased variability of the selected organ, elimination of physical and chemical defenses, change of habit, habitat, and breeding mechanisms) that often obscure origins (Hawkes, 1983; Harlan, 1992). In addition to these biological complications, pedigree records often are lost or intentionally kept secret to guard the proprietary nature of these industrial products. Undoubtedly, parallels occur between artificial and natural selection, such as hybrid origins in wild plants. The difference can be viewed as the scale of intensity between wild plant origins and human-directed selection, with maintenance of cultivated plants that typically cannot survive in nature. These human-selected products require classification codes that are quite different by both necessity and design.

The divergence between the classification objectives for wild and cultivated plants has always been obscured by the use of one common language arising from the taxonomy of wild plants, with the term *taxon* being the main source of confusion (Hetterscheid et al., 1996; Spooner et al., 2003).

Hetterscheid and Brandenburg (1995a, 1995b) introduced an alternative term, *culton* (user-defined groups), to replace *taxon,* a term today used mostly for phylogenetically related organisms.

The name *S. tuberosum* ssp. *tuberosum* may be one of the best examples of the differences between the ICBN and the ICNCP because of its unnatural divisions into cultivated "species." Modern potato cultivars have resulted from crosses between other cultivars and wild species. Fully 16 wild species are documented in pedigrees of different cultivars (Ross, 1986; Plaisted and Hoopes, 1989). Although the pedigrees of many modern cultivars are known, some of them are lost or have always been proprietary (Świeżyński et al., 1997). *S. tuberosum* sensu stricto (as distinct from the other culti-vated species) is not a species in the modern concept of related individuals as used by modern evolutionary biologists. The evolutionary dynamics of cultivated plants are not the same as those of wild plants because domes-tication involves human-driven, special-purpose, artificial selection. The latter leads to a very different diversity of organisms ("industrial products") than what we call biodiversity for wild plants.

Past attempts to classify cultivated plants into the ICBN-based hierarchi-cal systems have problems. The complex and diverse origins of potato are typical of many crop cultivars. An ICBN-based taxonomy of cultivated plants stimulates an inflated number of taxonomic ranks. Ongoing breeding of new cultivars continuously challenge the utility of these ranks, and the clas-sifications become cumbersome. ICBN-based classifications of cultivated plants are plagued by complex typification, diagnosing, and nomenclatural discussions disputing relationships. Such classifications fail to serve the prac-tical needs of users of cultivated plants where cultivar protection, marketing, and useful divisions of plants demand nomenclatural stability.

Name inflation caused by ICBN-based classifications of cultivated plants has become extreme. Fully 55 subspecific ranks for cultivated plants existed (Jirasek, 1961). Jirasek (1966) proposed the following 12 ranks below the species, listed in decreasing order: *specioid, subspecioid, cultiplex, subcultiplex, convarietas, subconvarietas, provarietas, subprovarietas, conculta, subconculta, cultivar,* and *subcultivar.* In such a system, every rank must follow the nomen-clatural rules of ICBN; this results in an extreme vulnerability of such cumber-some names to frequent name changes. As impractical as this classification philosophy may seem, even today it is used by many taxonomists of crop plants. Recent classifications of *Brassica oleracea* (cabbage) illustrate this point. Although a much lower number of categories are used, they are still all embed-ded in nested classification systems for cultivar classification. Even ICBN-based

ranks such as *subspecies, varietas,* and *forma* are misused to encompass group-ings of plants of purely cultivated origin.

For example, the following is a complex and nested system of classifica-tion for vegetable kohlrabi in Mansfeld's World Database of Agricultural and Horticultural Crops (Mansfeld, 1986) that is a mixture of ICBN and ICNCP nomenclature: *Brassica oleracea* ssp. *oleracea* convar. *acephala* var. *gongylodes.*

To avoid this cumbersome and complex way of classifying cultivated plants, we propose that cultivated plants be classified solely by the one code that properly and exclusively deals with this subject, the ICNCP. The basis of this code lies with the very nature of the concept of the cultivar (Brickell et al., 2004, article 2). A few types of cultivars are as follows:

- Clones (several types)
- Graft chimeras
- Assemblages of plants grown from seed
- Inbred lines
- Multilines (assemblages of inbred lines)
- F_1 hybrids
- Hybrids of various complexity
- Genetically modified plants

To date the only ICBN-based systematic categories for cultivated plant clas-sification are the cultivar and the Group (Brickell et al., 2004; Greuter et al., 2000, article 3). Names of culta belonging to either category may be associ-ated loosely with ICBN-based taxa for reference based on a suggested phylo-genetic background but must be treated with restraint (see *Brassica oleracea*). The combination of genus name and cultivar epithet suffices to uniquely identify a cultivar, and the latter may subsequently be put in a Group.

The Group

In order to minimize instability resulting from name changes in a hierarchi-cal Linnean-based system, the Group is an appropriate device to eliminate Latin in a name below the generic level. It provides a means of creating clas-sifications purely based on user criteria, ignoring Linnean systems based on relationships that often disregard criteria essential to practical user-driven classifications. The generic name seems to be the one globally used, Latin part of a crop name, but new insights into relationships can change even the genus name. For example, recently an attempt was made to reclassify the garden strawberry from *Fragaria* to *Potentilla* (Mabberley, 2002), but a

subsequent DNA study of the Rosoideae (Eriksson et al., 2003), established the monophyly of *Fragaria*. Spooner et al. (1993) reclassified tomatoes from *Lycopersicon* to *Solanum* based on chloroplast DNA restriction site and morphological data, and subsequent molecular studies unequivocally support the nesting of tomato in *Solanum* (e.g., Olmstead and Palmer, 1997; Bohs and Olmstead, 1999).

Several successful attempts at Group classifications replacing the more cumbersome Linnean hierarchy and nomenclature have been made (e.g., Hetterscheid and van den Berg, 1996 [*Aster* L.]; Hoffman, 1996 [*Philadelphus* L.]; Hetterscheid et al., 1999 [onions]; Lange et al., 1999 [beet]; Huamán and Spooner, 2002 [potato landraces]). Van den Berg (1999) discusses the advantages of modern Group classifications over older, more cumbersome ones.

However, stability in names for Groups is not permanent, and they can change based on evolving needs. Contrary to such changes in Linnean classifications, the wishes of the user group at large is the decisive factor that leads to a new classifications rather than intricacies of the Botanical Code or decisions of individual taxonomists. One user group may be best served by a Group classification based on pest resistance, another by ornamental value. Accordingly, several coexisting special-purpose classifications are possible (Spooner et al., 2003). Pitfalls of Group names are that they carry no information on crop origins, and coexisting Group classifications could create confusion.

Names of Groups

Article 7 of the ICNCP (Brickell et al., 2004) lays down the fundamentals for naming Groups. It states that any word or words in a modern language, or even a Latin name, may form a Group name, provided it stabilizes historical reference. Such descriptive names as "Early Red Group" or "Sweet Yellow Group" are possible as Group names. Also, a group may be named after a widely known cultivar in the group to improve recognition. For example, one could imagine a "Bintje Group," based on a well-known Dutch potato cultivar "Bintje." This system also creates the possibility of using translations of Group names into other languages. Thus, a term such as Early Red Group would become *Frühe Rote Gruppe* in German. When a Group name is used in the full name of a cultivar, it reads like *Solanum tuberosum* (Early Red Group) "Mother's Finest."

Which Name for the Potato?

Vilmorin (1881, 1886, 1902), Kohler (1909, 1910), Milward (1912), and Stuart (1915) proposed early group classifications of cultivated potato; Stuart (1915) provides details on these classifications. In sum, the classifications were based on color, shape, and size of the tubers; tuber eye depth; color of the potato sprouts in the dark; color of the flowers; and vine type. None of the early group classifications (to 1915) were widely adopted or persist.

The following more recent publications have informally grouped potatoes: the Potato Association of America's North American Potato Variety Inventory (www.ume.maine.edu/PAA/PVI.htm, 498 cultivars from the United States), the Potato Association of America variety images and descriptions (www.ume.maine.edu/PAA/var.htm, 49 cultivars from the United States), the European Cultivated Potato Database (www. europotato.org/, 4000 cultivars from Europe), Świeżyński et al. (1997, 1998; 2000 and 130 cultivars, respectively, from the United States and Europe), and Hamester and Hils (2003; 3200 cultivars worldwide). We surveyed these publications and the potato Web sites listed in the next paragraph for characters currently in use to divide modern cultivars.

Tuber skin color and shape were the most common characters that grouped potatoes. For instance, the U.S. National Potato Board (www. potatohelp.com/potato101/varieties.asp) groups potatoes as russets (tan to brown-skinned tubers with netted skin), round whites, long whites, long reds, yellow flesh, and blue and purple flesh. Potato skin and flesh characters are not parallel descriptors, but potatoes commonly are divided into these classes using these two traits. Maturity is commonly used in descriptor lists, such as the Potato Association of America's variety images and descriptions. The British Potato Council Variety Handbook (www.potato. org.uk/seedSearch.asp?sec=446&con=458) divides potatoes by tuber size, skin color, flesh color, eye depth, tuber shape (short oval, oval, long oval, round), skin texture (smooth, rough, russet), and corolla traits (color, number, size, peduncle length). Similarly, Schneider and Douches (1997) divide potatoes into tuber skin color and shape classes in order to provide an additional discriminator, in combination with molecular marker data, for cultivar fingerprinting. All cultivar descriptions (e.g., the North American Potato Variety Inventory or the British Potato Council Variety Handbook) class potatoes, irrespective of morphology, into early and late varieties. One type of classification grades potatoes within market classes by tuber quality as it relates to compliance with specific tolerances for

tuber sizes, defects, diseases, and other factors; different countries provide different names for these quality classes. However, these are transient quality factors that vary by year and locality and are not suitable as potential Groups.

Hamester and Hils (2003) provide worldwide coverage and a wide range of morphological and disease characterization data, making this publication the most useful resource for quantifying distribution of traits in cultivated potato. We therefore use it for our analysis of use categories that we present here. We analyzed all 20 disease scores from this publication as a single proportion and combined the five general use categories of processing, French fries, chips, dried products, and starch into a processing category that we compared with table use. Most of the records are from Europe (79%), with lesser numbers from North America (8%), Central and South America (6%), Asia (4%), Africa (2%), and Oceania (1%). The dates of release begin at 1760 ("Red Icelandic") and 1836 ("Fortyfold"), with 953 cultivars released from 1990–2002. In our analysis figure 13.2 shows distributions of maturity, tuber shape, skin color, eye depth, flesh color, and disease resistance for all 3530 cultivars. Space constraints preclude displaying use data, but they are as follows: table stock, 1707 cultivars; processing, 779; either processing or table, 1567; and both processing and table, 459.

Clone-specific disease resistance data have use for breeders or growers, but the multitude of disease variants (20) and unknown traits (figure 13.2) make their use for Group classifications unmanageable. Similarly, the use data are of interest to growers and processors, but there are so many mixed use categories as to be impractical for classifications. Flesh color and eye depth are rarely used in classifications, except for blue-fleshed potatoes for specialty markets. The most commonly used potato cultivar classification traits are tuber skin color, skin texture (although this is not part of the Hamester and Hils database), tuber shape, and maturity. Fifteen of the 27 variants of tuber skin color are very rare, with percentages of less than 1%, with the predominant types as yellow (55%), red (12%), white (8%), light yellow, buff (8%), light yellow–white (3%), and light red, pink (3%). Skin texture is divided into two categories of russets and smooth-skinned potatoes.

Figure 13.2 is the first graphic presentation of the variation in worldwide modern potato cultivars. It demonstrates that any Group classification based on very simple categories will be subject to interpretation of intergrading categories of many similar traits. For example, it may be
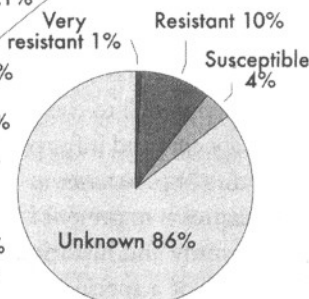
Skin Color

Less than 1%:
- Ochre with blue eyes 0.1%
- Light yellow w/red eyes 0.1%
- Light yellow, buff with red eyes 0.1%
- Deep ochre 0.1%
- Deep or dark 0.1%
- Deep blue-violet 0.1%
- Red-violet 0.1%

- White with blue eyes 0.1%
- Red-brown 0.1%
- Light pink 0.1%
- Yellow with violet eyes 0.1%
- Blue-violet 0.1%
- Violet, purple 0.1%
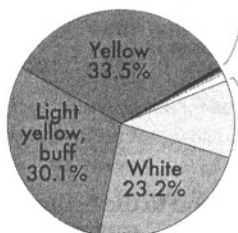- Yellow dotted pink 0.1%
- Deep red 0.1%
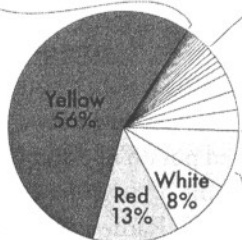
- White w/pink eyes 1%
- Light ochre 1%
- Yellow w/red eyes 1%
- Blue 1%
- Deep yellow 1%
- Ochre 2%
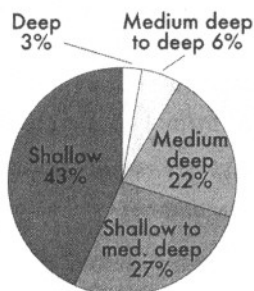- Light red, pink 3%
- Lght yellow-white 3%
- Light yellow-buff 8%

Yellow 56%
Red 13%
White 8%

Disease Resistance

Very resistant 1%
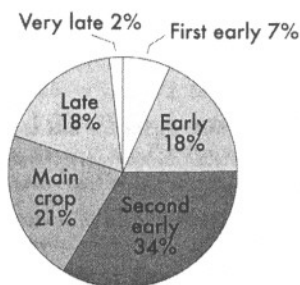Resistant 10%
Susceptible 4%
Unknown 86%

Flesh Color

- Light pink 0.03%
- White with pink eyes 0.03%
- Yellow with violet eyes 0.03%
- Blue 0.0%
- Light ochre 0.1%
- Red 0.1%
- Violet, purple 0.1%
- Violet, purple 0.1%
- Light blue 0.1%
- Ochre 0.1%
- Light blue-violet 0.1%
- Light red, pink 0.2%
- Yellow, dotted pink 0.3%
- Deep yellow 1.0%

Yellow 33.5%
Light yellow, buff 30.1%
White 23.2%

Light yellow-white 11.0%

Depth of Eyes

Deep 3%
Medium deep to deep 6%
Shallow 43%
Medium deep 22%
Shallow to med. deep 27%

Maturity

Very late 2%
First early 7%
Late 18%
Early 18%
Main crop 21%
Second early 34%

Tuber Shape

Kidney 1%
Round 0.2%
Long 3%
Long oval 19%
Short oval 44%
Oval 33%
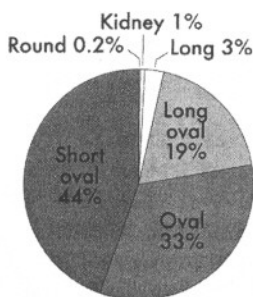
FIGURE 13.2 Distribution of selected modern potato cultivar traits on a worldwide basis as determined from data in Hamester and Hils (2003).

difficult to consistently distinguish skin colors of deep yellow, yellow, light yellow–buff, and light yellow–white (figure 13.2), and similar challenges would arise with tuber shape.

Conclusions

We propose to maintain the name *S. tuberosum* as the umbrella name (as a denomination class) for all potato Groups. Huamán and Spooner (2002) use this approach to classify potato landraces into Groups, thereby discarding all specific and infraspecific ICBN-based names and the catch-all subspecies name "ssp. *tuberosum*" for modern cultivated potatoes. The purpose of this chapter is to present a story of modern cultivated potato in the context of taxonomy and historical data to show that the name *S. tuberosum* sensu stricto is not a species in the proper sense of the word. Rather, this name has been applied to a diverse set of modern clones, of complex hybrid origins, involving other cultivars and wild species. We argue that it is better to classify modern cultivated potato into Groups that reflect actual use by breeders, growers, and processors. We present the first graphic presentation of tuber traits from Hamester and Hils (2003) that may be used to form a formal Group classification for user groups and potato scientists.

Acknowledgments

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