Taxonomy of cultivated potatoes (Solanum section Petota: Solanaceae)

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Solanum tuberosum, the cultivated potato of world commerce, is a primary food crop worldwide. Wild and cultivated potatoes form the germplasm base for international breeding efforts to improve potato in the face of a variety of disease, environmental and agronomic constraints. A series of national and international genebanks collect, characterize and distribute germplasm to stimulate and aid potato improvement. A knowledge of potato taxonomy and evolution guides collecting efforts, genebank operations and breeding. Past taxonomic treatments of wild and cultivated potato have differed tremendously among authors with regard to both the number of species recognized and the hypotheses of their interrelationships. In total, there are 494 epithets for wild and 626 epithets for cultivated taxa, including names not validly published. Recent classifications, however, recognize only about 100 wild species and four cultivated species. This paper compiles, for the first time, the epithets associated with all taxa of cultivated potato (many of which have appeared only in the Russian literature), places them in synonymy and provides lectotype designations for all names validly published where possible. We also summarize the history of differing taxonomic concepts in cultivated potato, and provide keys and descriptions for the four cultivated species. ©2010 The Linnean Society of London, Botanical Journal of the Linnean Society, 2011, 165, 107–155.


INTRODUCTION

The cultivated potato of world commerce, Solanum tuberosum L., is a primary food crop grown and consumed worldwide, forming a basic food and source of primary income for many societies. Indigenous primitive cultivated (landrace) and wild (Solanum section Petota) potatoes form the raw germplasm base used for breeding advanced potato varieties. Landrace potatoes are grown throughout mid to high (mainly about 3000–4000 m) elevations in the Andes from western Venezuela to northern Argentina, with a break in distribution of about 560 km in lowland south-central Chile, where they are concentrated in the Chonos and Guaitecas Archipelagos (Spooner et al., 2010). Landrace populations in Mexico and Central America are recent, post-Columbian introductions (Ugent, 1968). The landraces are highly diverse, with a great variety of shapes and skin and tuber colours not often seen in modern improved varieties. Potatoes were domesticated in the Andes of southern Peru about 10 000 years ago. Solanum tuberosum arose from wild species in the Solanum brevicaule Bitter complex (Ugent, 1970; Van den Berg et al., 1998; Miller & Spooner, 1999) in southern Peru (Spooner et al., 2005); three rarer domesticates (S. ajanhuiri Juz. & Bukasov, S. curtilobum Juz. & Bukasov and S. juzepczukii Bukasov) were later
formed by hybridization of *S. tuberosum* with more distantly related wild species of series *Acaulia* Juz. and *Megistacroloba* Cárdenas & Hawkes.

The taxonomy of section *Petota* is complicated by introgression, interspecific hybridization, auto- and allopolyploidy, sexual compatibility among many species, a mixture of sexual and asexual reproduction, possible recent species’ divergence, phenotypic plasticity and consequent great morphological similarity among species (Spooner, 2009). These biological complications have led to the description of many taxa now placed in synonymy and great discordance among treatments by different authors (Spooner & Van den Berg, 1992). Recent taxonomic research has greatly altered the knowledge of species’ boundaries and interrelationships of section *Petota*. In total, section *Petota* contains 494 epithets corresponding to wild taxa (including *nomen nudum* and illegitimate names) and 626 epithets corresponding to taxa that have arisen in cultivation, including names not validly published. Recent estimates are of about 100 wild species (Spooner et al., 2009) and four cultivated species (Spooner et al., 2007). The purpose of this article is to provide a brief history of cultivated potato taxonomy to explain how so many names came to be coined, to publish, for the first time, all of these names and place them in synonymy with the four taxa coined, to publish, for the first time, all of these names and place them in synonymy with the four currently recognized species, designate lectotypes for all validly published names, to provide keys and descriptions to the taxa we recognize and to provide a comprehensive list of all names not validly published in the group. In this article, we treat all epithets coined for cultivated potatoes under the *International Code of Botanical Nomenclature* (ICBN, McNeill et al., 2006), except for two groups of *S. tuberosum* (the *Andigenum* and *Chilotanum* groups), which we treat according to the *International Code for Nomenclature for Cultivated Plants* (ICNCP, Brickell et al., 2009).

**Cultivated potato in Chile**

All of the landrace cultivated potatoes occur in the Andes from western Venezuela to northern Argentina, except for the single entity *S. tuberosum* subsp. *tuberosum* using the Hawkes (1990) system of nomenclature, or *S. tuberosum* ‘Chilotanum group’ using the system of Spooner et al. (2007) (see below). The origin of the Chilean landraces is controversial. Juzepczuk & Bukasov (1929) proposed that they evolved from the indigenous tetraploid species *S. fonckii* Phil. ex Reiche (*nomen nudum* from a herbarium annotation made by R.A. Philippi in SGO), *S. leptostigma* Juz. ex Bukasov (*nomen nudum* from tubers collected in Chiloé Island, but never properly described) and *S. molinae* Juz. (a validly published name based on tubers collected on Chiloé Island). We recognize these three taxa as names not validly published associated with *S. tuberosum* and as plants of the ‘Chilotanum group’, not as wild species’ progenitors. Hawkes (1990) proposed that subsp. *andigenum* (Juz. & Bukasov) Hawkes evolved into subsp. *tuberosum* after transport to Chile. On the basis of starch grains, Ugent, Dillehay & Ramirez (1987) proposed the wild species *S. maglia* Schltdl. as a progenitor of the Chilean cultivated potatoes. Grun (1990) hypothesized that subsp. *tuberosum* evolved from a cross between subsp. *andigenum* and an unidentified wild species.

Raker & Spooner (2002) investigated the differentiation of the Andean and Chilean tetraploid landraces with nuclear microsatellites. They included in their analysis several wild potato species, including *S. maglia*. The nuclear microsatellite data separated most populations of Andean and Chilean tetraploid potato, and clustered *S. maglia* with the Chilean populations. This result could be interpreted to support *S. maglia* as a progenitor of the Chilean cultivated populations, but, in agreement with Cribb & Hawkes (1986), they considered this to be unlikely. Most populations of tetraploid potatoes in southern South America grow in isolated moist habitats along or near the coast of Chile, and in Argentina in a single valley in Mendoza Province, Quebrada de Alvarado, at the base of the Andes Mountains at 1500 m (Spooner, Contreras & Bamberg, 1991; Spooner & Clausen, 1993). Reports of extant populations of *S. maglia* in southern Chile by Ugent et al. (1987) are not backed up by voucher specimens and are probably misidentifications of *S. tuberosum*, based on voucher specimens of others who have collected potatoes extensively in Chile (Contreras, 1987; Spooner et al., 1991). It is possible that *S. maglia* is a divergent escaped population of *S. tuberosum*. Hosaka (2002) demonstrated that *S. tuberosum* from Chile (but not *S. maglia*) shares a 241-bp plastid deletion with some accessions of the wild species *S. berthaultii* Hawkes and *S. neorossii* Hawkes & Hjert. of Bolivia and northern Argentina, and it is unclear whether there has been plastid introgression between *S. tuberosum* from Chile and these species.

Potato expeditions to Chile (Contreras, 1987; Spooner et al., 1991; Contreras et al., 1993) have documented that the majority of the potato landraces in the Chonos and Guaitecas Archipelagos grow along the western chain of the islands near the Pacific shore. Most of these collections are relatively uniform in morphology. In the majority of the accessions, the tubers are ovoid, small (up to 3 cm in diameter), with blue to purple to light reddish skin and flesh. All have long stolons, some of which extend more than 2 m from the base of the plant. Many populations lack
flowers and fruits, and seedlings are rare. Sprouts of discarded modern cultivars can easily be found at abandoned fishing encampments, showing the apparently ideal climate for potato growth in these islands. On Chiloé Island, modern potato cultivars are commonly cultivated. However, farmers maintain small plots of older, native varieties as curiosities, which show a great variety of colours and shapes (Spooner et al., 1991), unlike the persistent populations of a uniform genotype on the many islands of the Chonos and Guaitecas Archipelagos further to the south (Contreras et al., 1993).

MODERN POTATO VARIETIES

Potato first appeared outside South America in Europe in 1567 and rapidly diffused worldwide. Two competing hypotheses suggested the origin of the ‘European’ potato from lowland Chile (Juzepczuk & Bukasov, 1929) or from the Andes from western Venezuela to northern Argentina (Salaman, 1937; Salaman & Hawkes, 1949), but the hypothesis of an Andean origin has been widely accepted over the last 60 years. All modern potato cultivars are based on Chilean germplasm, explained as originating from breeding with Chilean landraces subsequent to the late blight epidemics that began in 1845 in the UK. Ames & Spooner (2008) documented, through a plastid DNA deletion marker nearly specific to Andean or Chilean populations, that Andean potato predominated in the 1700s, but the Chilean potato was introduced into Europe as early as 1811 and became predominant long before the late blight epidemics in the UK. Modern cultivars of potato are the products of intensive breeding using germplasm of landraces of \textit{S. tuberosum} and 15 wild species members of section Petota (Ross, 1986; Plaisted & Hoopes, 1989). Only old potato varieties that were bred before the 1930s could be considered within the botanical species, \textit{S. tuberosum}, in the context of this article. After this time, crosses with closely related wild species and more distantly related species, such as \textit{S. stoloniferum} Schltldl., were widely used to breed new potato cultivars. Therefore, modern varieties have a clear hybrid (interspecific) nature. However, not more than 10\% of wild potato species have actually been used in potato breeding (Ross, 1986; Plaisted & Hoopes, 1989; Budin & Gavrilenko, 1994).

COLLECTING EXPEDITIONS

Germplasm collection of potato on an international scale was initiated by Russian scientists in a series of expeditions to Central and South America led by Yuri Voronov (including the noted potato taxonomist Sergei Bukasov) in 1925–26, by Sergei Juzepczuk from 1926 to 1928 and by Nikolai Vavilov in 1930–33 (Loskutov, 1999). These collections form the base of the potato germplasm collection of the N. I. Vavilov Institute of Plant Industry in St. Petersburg (in Soviet times known as the All-Union Institute of Plant Industry in Leningrad). In 1938–39, the Imperial Agricultural Bureaux (UK) sent the botanists Edward K. Balls, William Balfour Gourlay and John G. [Jack] Hawkes on what was called the British Empire Expedition (also known as the Empire Potato Expedition) to collect potatoes in South America (Hawkes, 1944, 2004; Hawkes & Hjerting, 1969, 1989). Duplicates of the herbarium specimens they made are today deposited in many collections worldwide (see below), and tuber collections were grown out at first in the Empire Potato Collection in Cambridge [later this material was transferred to the Commonwealth Potato Collection now held at the Scottish Crop Research Institute (SCRI) in Dundee, UK]. Carlos Ochoa and Alberto Salas collected potatoes throughout South America for the Universidad Nacional Agraria La Molina, Peru, and later the International Potato Center (Centro Internacional de la Papa, CIP), also in Peru, that form the base of the CIP collection. Many others added to these collections and germplasm collections of other genebanks worldwide (Ochoa, 1990, 1999). Cultivated potato taxonomy relies principally on an examination of these germplasm collections studied in experimental stations, sometimes supplemented by an examination of original specimens collected in South America, mainly those collected by Bukasov, Dodds, Juzepczuk, Ochoa and Hawkes and his collaborators as described below.

CULTIVATED POTATO TAXONOMY

Linnaeus (1753) recognized cultivated potatoes, known to him from both Europe and Peru, as a single species, \textit{S. tuberosum}. He did not mention any great variability, as he had for other species (e.g. \textit{S. dulcamara} L., see Linnaeus, 1753). Most 18th and 19th century taxonomists followed him in not formally naming any infraspecific variation in \textit{S. tuberosum}, until the German botanist Alefeld named many morphological variants of European cultivated potato in his \textit{Landwirthschaftliche Flora} (Alefeld, 1866) in a system that was based on tuber skin colour, flesh colour and texture and flower colour. Dunal, the last monographer of the genus \textit{Solanum} (Dunal, 1852), recognized a single species, \textit{S. tuberosum}, with a variety he suggested might in fact be a different species (now recognized as a synonym of \textit{S. chacoense} Bitter). De Candolle (1886) was the first to name as distinct the Chilean populations of \textit{S. tuberosum}, as var. \textit{chiloense} A.DC.; he did not, however, name the variation existing in Andean potatoes at the infraspe-
cific level. Juzepczuk & Bukasov (1929) first attempted to describe and name the morphological and taxonomic diversity of cultivated potatoes using the many accessions grown in the Leningrad (now St. Petersburg) region from their South American expedition in 1926–28. Rybin (1929, 1933) first demonstrated the existence of a polyploid series in cultivated potato from 2x, 3x, 4x and 5x, and in wild potatoes all these levels in addition to 6x. Ploidy became an important taxonomic and evolutionary character in potato. When describing these many potato species, Russian taxonomists applied a complex approach based on ploidy, ecogeography and analysis of morphological and physiological characters (see below). Ecogeography was a major taxonomic character in most Russian crop taxonomic systems, including potato (Juzepczuk & Bukasov, 1929; Bukasov, 1930; Juzepczuk, 1937). This is clearly evident from the nature of the taxonomic categories used in both their wild and cultivated taxa. For example, in the treatment of potato for the Cultivated Flora of the USSR, Lekhnovich (1972), a colleague of Juzepczuk and Bukasov, grouped S. andigenum Juz. & Bukasov [S. tuberosum subsp. andigenum (Juz. & Bukasov) Hawkes in the system of Hawkes 1990] into subspecies (none of which was validly published, see Appendix): mediamericum (Bukasov) Lechn. (from Mexico and Guatemala), colombianum Bukasov (from Colombia), rimbachii and ecuatorianum Lechn. (from Ecuador), tarmense Bukasov & Lechn. and centraliperuvianum Lechn. (from central Peru), australiperuvianum Lechn. (from southern Peru), bolivianum Bukasov & Lechn. (from Bolivia) and argentinicum Lechn. (from Argentina). Bukasov (1978) extended this geographical concept even to the higher taxonomic rank of series, e.g. series Andigena Bukasov (from the Andes), series Chilotana Bukasov (from Chile) and series Cisaequatorialia Bukasov (from the Andes around the equator). The Russian monographers first recognized 12 cultivated species (Juzepczuk & Bukasov, 1929), then 18 (Bukasov, 1937) and, finally, 17 (Bukasov, 1978). In addition to these species there are descriptions of hundreds of subspecies, ‘convarieties’, varieties and forms (Lekhnovich, 1972).

Working in Germany, Danert (1956) classified the European cultivated potatoes into a set of five convarieties, defined by their tuber skin colour, each of which was composed of a set of varieties based on a combination of flower and tuber flesh colour. He cited cultivars by name (e.g. ‘Capelle’, ‘Stärkeragis’) for some of his varietal names, but not all (seven of 17). He based his system on that of Alefeld (1866).

Bukasov (1978) grouped cultivated potatoes into ‘superspecies’ complexes based not only on their geographical origin, but also on their presumed relationships: (1) series Chilotana (S. chilotanum = Chilean subsp. tuberosum); (2) series Andigena (di-, tri- and tetraploid Andean potatoes exclusive of S. juzepczukii); and (3) series Subacaulia Bukasov (S. curtibolum and S. juzepczukii). The taxonomy of cultivated potatoes developed by Russian botanists was also based on a consideration of the hypothesized auto- and/or allopolyploid origin of cultivated forms (Bukasov, 1937, 1978; Lekhnovich, 1972).

Hawkes (1956a, 1963, 1990) divided cultivated potato into seven species and seven subspecies. Ochoa (1990, 1999) recognized nine species and 141 infraspecific taxa for the Bolivian cultivated potatoes alone. Dodds (1962) recognized three species, S. curtibolum, S. juzepczukii and S. tuberosum, with five groups recognized in S. tuberosum, largely defined by ploidy. Juzepczuk & Bukasov (1929), Bukasov (1937, 1978), Hawkes (1956a, 1963, 1990), Hawkes & Hjerting (1969, 1989), Lekhnovich (1972) and Ochoa (1990, 1999) classified potatoes as distinct species under ICBN (McNeill et al., 2006). Dodds (1962), in contrast, treated the cultivated species under ICNCP (Brickell et al., 2009). His five groups within S. tuberosum were categories used by ICNCP (both of his day and the eighth edition of Brickell et al., 2009) to associate cultivated plants that share specific traits that are of importance to users. Dodds (1962) used the multiplication sign (×) to indicate the hybrid nature of two of his species, but not the third, although it contained taxa he felt were of hybrid origin.

Dodds & Paxman (1962) contended that the morphological characters used by Hawkes (1956a) to separate species exaggerated the consistency of qualitative and quantitative characters. They showed that Andean farmers grow landraces of all ploidy levels together in the same field and that these can all potentially hybridize. They showed no genetic differentiation of the cultivated diploids (Dodds & Paxman, 1962). In the systems of Bukasov, Juzepczuk, Hawkes, Lekhnovich and Ochoa, each cultivated species had a single ploidy. Identifications were frequently made only after chromosome counts were determined, and re-identifications made after chromosome counts did not match that expected for the species. The strong reliance on ploidy was clearly stated by Hawkes & Hjerting (1989: 389): ‘The chromosome number of 2n = 36 largely helps to identify S. chaucha, but morphological characters can also be used’. This differs from the system of Dodds (1962) in which many of these species’ names were synonymized under S. tuberosum, which in this broader sense contains diploid, triploid and tetraploid cytotypes.

Huamán & Spooner (2002) examined the morphological support for the classification of landrace...
populations of cultivated potatoes, using representatives of all seven species and most subspecies as outlined in the taxonomic treatment of Hawkes (1990). The results showed some phenetic support for S. ajanhuiri, S. chaucha Juz. & Bukasov, S. curtloobum, S. juzepczukii and S. tuberosum subsp. tuberosum, but little support for the other taxa. Most morphological support was based on a suite of characters, all of which were shared with other taxa. These results, combined with their probable hybrid origins, multiple origins and evolutionary dynamics of continuing hybridization, led Huamán & Spooner (2002) to recognize all landrace populations of cultivated potatoes as a single botanical species, S. tuberosum, with the eight cultivar groups (recognized under ICNCP): Ajanhuiri, Andigena, Chaucha, Chilotanum, Curtloobum, Juzepczukii, Phureja and Stenotomum.

Ghislain et al. (2006) questioned the taxonomic recognition of the S. tuberosum Phureja group (sensu Dodds, 1962; Huamán & Spooner, 2002), as defined by Hawkes (1990) and Ochoa (1990, 1999), by its short-day adaptation, low tuber dormancy and its diploid (2n = 2x = 24) nature, although none of these characters was mentioned in the Latin diagnosis of S. phureja in the original publication (Juzepczuk & Bukasov, 1929) (see also http://vir.nw.ru/herbar/types/phureja_eng.php). Solanum phureja was believed to consist of a range of landraces widely grown in the Andes from western Venezuela to central Bolivia and to have excellent culinary properties and other traits for developing modern varieties. They examined the entire CIP collection of the Phureja group with nuclear simple sequence repeats (SSRs or microsatellites) to complement a previous random amplification of polymorphic DNA (RAPD) study. The initial goal was to explore the use of SSRs and RAPDs to form a core collection of cultivar groups of potatoes. The nuclear SSR data showed an unexpected result in that it uncovered 25 triploid and tetraploid accessions. Chromosome counts of the 102 accessions confirmed these results and highlighted seven more triploids or tetraploids. Thus, the SSR markers were good indicators of ploidy for diploid potatoes in 92% of cases. Because the Phureja group was defined on the basis of its diploid nature (Dodds, 1962; Huamán & Spooner, 2002), and because the SSR study showed over 30% of the CIP germplasm collection identified as belonging to the Phureja group to be polyploid, Ghislain et al. (2006) questioned the validity not only of the Phureja group, but of all previously recognized cultivar groups of potato.

Spooners et al. (2007) expanded the SSR study of Ghislain et al. (2006) through an investigation of 742 landraces of all cultivated potatoes, and eight closely related wild species’ progenitors, with 50 SSRs and the 241-bp plastid deletion marker generally distinguishing Andean from Chilean potato landraces. The data highlighted a tendency to separate three groups [(i) putative diploids; (ii) putative tetraploids; and (iii) the cultivated species of hybrid origin S. ajanhuiri (diploid), S. juzepczukii (triploid) and S. curtloobum (pentaploid)], but there were many exceptions to grouping by ploidy. Strong statistical support for this tree occurred only for S. ajanhuiri, S. juzepczukii and S. curtloobum, and supported previous ideas of S. curtloobum and S. juzepczukii having S. acaule Bitter as one of the parental species (Bukasov, 1933; Hawkes, 1962; Schmiediche, Hawkes & Ochoa, 1980, 1982). In combination with the morphological analyses of Huamán & Spooner (2002) and an examination of the identification history of these collections at CIP, Spooners et al. (2007) proposed a reclassification of the cultivated potatoes into four species: (i) S. tuberosum, with two cultivar groups (the Andigenum group of upland Andean genotypes containing diploids, triploids and tetraploids, and the Chilotanum group of lowland tetraploid Chilean landraces); (ii) S. ajanhuiri (diploid); (iii) S. juzepczukii (triploid); and (iv) S. curtloobum (pentaploid). Spooners et al. (2007) did not use the multiplication sign (∗) to indicate the hybrid origin of any of these taxa because they are stable in nature and have a long history of use (Dodds, 1962 excepted) as species.

Gavrilenko et al. (2010) examined the morphological and SSR support for the Russian National Cultivated Potato Collections at the N. I. Vavilov Institute for Plant Industry. The morphological taxonomic results are similar to those of Huamán & Spooner (2002) in recognizing entities corresponding to S. tuberosum, S. curtloobum and S. juzepczukii, despite using a different germplasm base, a different evaluation environment (upland central Peru versus lowland northern Russia) and different scoring methods for some of the traits. The main difference between these two studies is that Gavrilenko et al. (2010) failed to distinguish S. ajanhuiri from other taxa.

Spooners et al. (2010) tested the ecological differences in traditionally recognized taxa of landrace cultivated potatoes using a database of over 2000 georeferenced localities, analysed with a maximum entropy method. Except for the S. tuberosum Chilotanum group and extreme northern and southern range extensions of the Andigenum group, it was impossible to find distinct habitats for the ploidy variants of the S. tuberosum Andigenum group. These distributional and ecological data, in combination with previous results from morphology, microsatellites and crossing data, provided additional data to support their reclassification of cultivated potato species.
Names of cultivated potatoes

The plethora of Latin names (ICBN) for cultivated potatoes reflects not only the great genetic and morphological variability in these plants, but also a system of nomenclature based on the principles established by Vavilov from homologous series (Vavilov, 1922). He named parallel variation in crops and their relatives in different geographical regions in detail, often using the terminal same names for similar ecological variants. Vavilov (1940) conceived the Linnaean species as ‘a definite, discrete dynamic system differentiated into geographical and ecological types and comprising sometimes an enormous number of varieties’. This approach led to the sorts of names described above, based on geography and, secondarily, on either ecological characteristics or local common names. The complex polynomials used in the publications of potatoes (e.g. Lekhnovich, 1972; Bukasov, 1978) had up to four variously nested ranks, and occasionally the ranks were not nested consistently, i.e. the ranks variety and form were apparently used in the same way. In addition, the use of this nested system, in which the entire string of ranks was considered as the name, meant that a particular epithet was often used at the same rank in different subspecies or varieties, creating many unintentional homonyms.

Before he set out on his first collecting expedition to South America in 1938, Hawkes visited the All-Union Institute of Plant Industry in Leningrad, where he met Russian scientists who had been describing and documenting potato diversity using these systems. He classified the potatoes from the Empire Expedition using this complex system (see Hawkes, 1944) with which he had become familiarized during his trip to the Soviet Union: ‘when I later described and classified my own collections of potatoes I followed Vavilov in establishing far too complex a system. Much later I had to simplify this drastically’ (Hawkes, 2004). He later regarded this approach to classification, and thus to naming, as a ‘tedious way of building up an understanding of the diversity and promoting the use of the material in plant breeding’ (Hawkes, 2004). For these names, we have indicated on the Solanaceae Source website (http://www.solanaceasource.org) the nested set of epithets where this is possible to ascertain. Similar to the systems established by Bukasov and Juzepczuk, Hawkes (1944) system of names for potatoes used many Quechua and Aymará common names for local cultivars from South America as formal taxonomic names, e.g. forma orcco-amajaya from Peru or forma koso-ñahui from Bolivia (neither validly published, see below). For the potatoes of Peru and Bolivia, Ochoa (1990, 1999) also used local common names as formal taxonomic names, but recognized these differently from Hawkes (1944). The combination of over-description of variation in an attempt to create a classification in a name and the elevation of the many landraces native to the Andes to formal taxonomic ranks has led to the large numbers of names reduced here to synonymy in the cultivated potatoes.

Material and Methods

Lectotypification

We have lectotypified as many of the validly published names for cultivated potatoes as possible using material cited by the original authors. For names coined by European botanists of the 19th century, specimens often exist in herbaria, but, for the 55 varietal names coined by the German botanist Alefeld (1866), specimens (if they ever existed) were held in B and are now lost (see Hiepko, 1987). Alefeld cultivated the potato varieties he described in Darmstadt, but did not cite any specimens. He did, however, cite illustrations in Putsch (1819) for some of his infraspecific epithets; we have used these illustrations as lectotypes when possible. We do not designate neotypes for these names. Although validly published, these names are better regarded as cultivar names and treated under ICNCP. His varietal names were grouped into ‘var.-gr.’, or variety groups; we have not considered these as formal taxonomic names, although they are trinomials.

Danert (1956) did not cite specimens for any of his names, but they are validly published with a short diagnosis in Latin; specific cultivars (often as many as 10) are cited for only seven of his 17 varietal names. In the collections of the Liebniz Institute of Plant Genetics and Crop Plant Research (IPK Gatersleben, GAT), there are herbarium specimens of flowering branches and tuber collections in alcohol (K. Pistrick, 26.x.2010) of 17 of the cultivar names cited by Danert, sometimes of the same accession number, but often not. We have lectotypified only those epithets for which material exists; they are of European and relatively modern origin and, as for the names coined by Alefeld (1866) a century earlier, are better treated under ICNCP (Brickell et al., 2009). Danert (1956) treated Alefeld’s (1866) ‘var.-gr.’ as formal taxonomic names at the convarsity level; they are not accompanied by descriptions, and we consider them as not validly published.

Specimens for taxa named by Bukasov, Juzepczuk and Lekhnovich are generally held in the St. Petersburg herbaria (LE, WIR, see Ovchinnikova et al., 2009) (see http://vir.nw.ru/herbar/types/bukasov_eng.php); these were prepared from material grown out in Russia from tuber collections made in South
America and can be related to specific accession numbers, some of which are still maintained in the Russian National Potato Collection at the Vavilov Institute. We have lectotypified all names based on this material, even if a single sheet was found, as the authors did not cite herbaria or specimen sheets in descriptions, but instead cited tuber accession numbers (often several per new taxon). Illustrations of new taxa in many of these publications (e.g. Bukasov, 1930, 1933) are of freshly dissected flowers and fruits, not of herbarium specimens, and they are not usually associated with particular tuber accession numbers. For this reason, we have not assumed the numbers cited to be specimens, but instead accessions, thus necessitating lectotypification in all cases.

In several cases, we have not found herbarium material at either of the St. Petersburg herbaria, but rather than designate neotypes for all of these synonyms, we have left these names without types. Most of these names are forms of Chilean potatoes from Chiloé Island and its vicinity described by Bukasov & Lekhnovich in 1933 (Bukasov, 1933), e.g. forma barmacota, forma camota (see synonymy of S. tuberosum, below). Material may be found in the future.

On a few occasions (mainly Lekhnovich, 1983), the same tuber accessions were used by Russian potato taxonomists to describe different taxa at different times; for example, the tuber accession 4479/3481 based on the field collection Juzepczuk 1352 was used to describe both S. andigenum forma competillo Bukasov & Lechn. (Bukasov, 1933) and S. andigenum convar. curtibulum Lechn. (Lekhnovich, 1983), and tuber accession 4355/3291 based on field collection Juzepczuk 1348 was used to describe both S. andigenum var. cuzcoense Bukasov & Lechn. (Bukasov, 1930) and S. andigenum convar. longiacuminatum Lechn. (Lekhnovich, 1983). Where the collection dates on specimens are identical, we have treated these names as homotypic, and, where they are different, we have assumed that the specimens are the result of distinct collections and thus the names are not homotypic.

Hawkes made collections of plants grown in the field in Russia when he visited in 1938 (see above), and material taken from ‘type’ tuber accessions has been used here to neotypify two of Hawkes’ Andigenum group names (forma huallata and var. cuzcoense, see S. tuberosum, below). Names coined by Hawkes (1944, and later publications) were based on specimens collected in the field and on material grown in what was then the Empire Potato Collection. Most of the herbarium specimens from this expedition are now integrated into the herbarium at the Royal Botanic Gardens, Kew (K), to which most of Hawkes’ herbarium material was donated after his retirement. Duplicates of the collections of the Empire Potato Expedition (usually under the collection numbers of E.K. Balls or the Peruvian agronomist Luis Angel Yabar) can be found in other herbaria, but we have lectotypified these names with material now held at Kew as we are certain Hawkes used this. Spooner et al. (2004) found that herbarium material of wild species from this collection was widely distributed to A, B, BH, BM, BR, C, DS, E, F, G, GH, K, LL, MEXU, MICH, MPU, NY, P, UC, US, WAG and WIS. Many of the collections of cultivated potatoes, however, were collected as tubers in markets, and specimens were not always taken of plants in the field. Ochoa cited specimens in his personal herbarium as holotype material in almost all of his publications. He distributed his herbarium to many institutions prior to his death in 2008 (see http://agro.biodiver.se/2008/12/carlos-ochoa/), and much of the material of cultivated potatoes was donated to CUZ, with some duplicates to be found at CIP. We have indicated the original citation together with the current location of the holotype sheets (usually annotated as ‘holotype’ by Ochoa). Many names coined by Ochoa with holotypes cited from ‘herb. Ochoa’, however, have not been found at CUZ or any other of the herbaria in which his material was deposited (e.g. MOL, LPB, US, F). The residue of Ochoa’s herbarium was apparently donated to the Universidad Nacional Mayor de San Marcos in Lima, Peru (USM), and eventually the ‘lost’ holotypes may be found. We have therefore not neotypified any of these (many) names in the hope that specimens may eventually be found.

Because potatoes can be propagated year after year from the same tuber stock, the original accessions of many of these collections were re-collected as herbarium specimens several times over a number of years (see above). Thus, ascertaining which material was actually used by the taxonomists describing the taxa is sometimes difficult. Collections made from the ‘type’ tuber accession can be viewed as ‘clonotype’ material, but care should be taken with its identity, as accessions are occasionally confused and mislabelled from one season to the next. A ‘clonotype’ is not type material in the true sense, as it does not satisfy Article 8.2 of ICBN, which states that a type specimen is defined as a gathering at one time. In three cases, we have used specimens from later plantings of ‘type’ tuber accessions to neotypify taxa where no original material has been found (see above and S. rybinii var. pastoense; see S. tuberosum, below). Clonotype material is identified as such on the Solanaceae Source website (http://www.solanaceasource.org) and in the synonymy.

Many of the names and combinations published for cultivated potatoes were not validly published under
ICBN for a variety of reasons, most commonly because a Latin diagnosis was not provided for those published after 1935 (Article 36.1), a type specimen was not designated for those published after 1958 (Article 37.1) or for new combinations made after 1953, and full and direct reference to the basionym, including its author and place of publication, was not provided (Article 33.4). Individual details can be found on the Solanaceae Source website (http://www.solanaceaesource.org), and all of the names not validly published are listed in the Appendix.

Landraces and modern improved varieties of cultivated potatoes are widely grown throughout the world and are common in herbaria worldwide, and we do not cite specimens in our treatment. We do not list the thousands of cultivar names for landraces (e.g. Castronovo, 1949) or modern varieties (Pieterse & Hils, 2010), best treated under ICNCP.

Key to Cultivated Potato Landraces
The following key and descriptions, modified from Huamán & Spooner (2002), highlight typical traits. The qualifier terms 'mostly' or 'usually' could be employed throughout the key, but are not used for simplicity.

1. Plants semi-rosette to semi-erect; pedicel articulation indistinct to only slightly distinct, located in the upper one-fifth of the pedicel; frost tolerant (of putative hybrid origin with the frost-tolerant species S. acaule or S. megiastaurolosum).................................2
1. Plants ascending to erect; pedicel articulation evident, located below the upper one-fifth of the pedicel; generally not frost tolerant.................................................................4
2. Most distal lateral leaflets broadly decurrent; plants diploid.................................................................1. S. ajanhuiri (Fig. 1)
2. Most distal lateral leaflets not or only slightly decurrent; plants triploid or pentaploid................................................3
3. Plants low growing, 62–98 cm tall; triploid.................................................................3. S. juzepczuki (Fig. 3)
3. Plants of medium height, 96–125 cm tall; pentaploid.................................................................2. S. curtibulum (Fig. 2)
4. Plants adapted to short-day flowering and tuberization; upper leaves diverged from stem at 40°–50°; diploid, triploid or tetraploid.................................................................4. S. tuberosum Andigenum group (Fig. 4)
4. Plants adapted to long-day flowering and tuberization; upper leaves diverged from stem at angle of 50°–90°.................................................................5
5. Landrace populations native to south-central Chile..............................4. S. tuberosum Chilotanum group (Fig. 5)
5. Modern varieties originally derived from breeding populations in the Northern Hemisphere, now grown worldwide; of many complex hybrid origins from the Chilotanum and Andigenum groups and other cultivar groups bred up to the earlier 20th century..........................4. S. tuberosum relatively modern varieties

Note: There is a huge variation in morphology in the thousands of cultivars of landrace populations of cultivated potatoes. The following descriptions are modified from the phenetic study of Huamán & Spooner (2002) based on representative germplasm accessions planted in a field plot in upland central Peru. Many of the taxa treated in synonymy here, especially the Russian names pertaining to the S. tuberosum Andigenum group, were based on plants grown from germplasm accessions planted in northern Russia and experiencing long days atypical of the native habitat of these landraces (see Figs 1–3). For each name treated in synonymy, we have indicated whether it corresponds to the Andigenum group [A] or the Chilotanum group [C] as defined by Spooner et al. (2007). We have followed more common usage in the literature and Article H.3 Note 1 (‘Taxa which are believed to be of hybrid origin need not be designated as nothotaxa’) of ICBN and have not used the multiplication sign (×) to indicate the hybrid origins of cultivated potatoes we recognize at the species level; this preserves common usage in both the botanical and agricultural literature, and is in accordance with these taxa being stabilized products of hybridization.


Figure 1.
Figure 1. Lectotype specimen of *Solanum ajanhuiri* Juz. & Bukasov held in WIR (note spelling of specific epithet on this sheet, see text). Reproduced with permission of the N. I. Vavilov Institute of Plant Industry.
**Description:** Herbs 0.4–0.7 m tall, semi-rosette when young, developing to sub-rosette or to semi-erect. Stems 8–10 mm in diameter at base of plant, with narrow wings, densely pubescent, green to green and purple mottled. Sympodial units tri- to plurifoliate, not geminate. Leaves odd-pinnate, the blades 7–10 × 3.5–6.0 cm, dark green, membranous to chartaceous, densely pubescent adaxially and abaxially, with hairs like those of the stems; lateral leaflet pairs five or six, often subequal except for the most proximal one or two pairs that are greatly reduced in size; most distal lateral leaflets 4.5–7.0 × 2.0–3.5 cm, elliptic lanceolate, broadly decurrent onto the rachis on the basiscopic side, the apex distinctly acute, the base oblique to rounded; terminal leaflet 5–9 × 2.5–4.0 cm, elliptic lanceolate, the apex distinctly acute, the base oblique to rounded; intergraded leaflets three to five, sessile to short petiolulate, elliptic lanceolate; petioles 1–3 cm, pubescent as the stems. Pseudostipules minute to 5 mm long, auriculate, pubescent with hairs like those of the stem. Inflorescences 5–10 cm, terminal with a subtending axillary bud, generally in distal half of the plant, usually forked, with 9–12 flowers, with all flowers apparently perfect, the axes pubescent with hairs like those of the stem; peduncle 10–15 cm long; pedicels 21–28 mm long in flower and fruit, spaced 1–10 mm apart, articulation indistinct or only slightly distinct, articulated high in the distal half. Flowers homostylous, pentamerous. Calyx 4–12 mm long, the tube 1–2 mm, the lobes 2–11 mm, narrowly elliptic, shortly acuminate, the acumen 1–4 mm long, with hairs like those of the stem. Corolla 2.5–3.5 cm in diameter, rotate-pentagonal, white to white with mauve streaks to blue–mauve or blue–purple, the tube 1–2 mm long, the acumen 3–4 mm long, the corolla edges flat, not folded dorsally, glabrous abaxially, minutely puberulent adaxially, especially along the midribs, ciliate at the margins, especially at the tips of the corollas. Stamens with the filaments 1–2 mm long; anthers 4–6 mm long, lanceolate, connivent, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style 7.5–8.0 × 1 mm, exceeding stamens by 3–4 mm, straight, papilllose on the proximal half; stigma capitate. Fruit a globose to ovoid berry, 2–3 cm in diameter, green or green tinged with purple when ripe, glabrous. Seeds from living specimens ovoid and c. 2 mm long, whitish to greenish in fresh condition and drying brownish, with a thick covering of ‘hair-like’ lateral walls of the testal cells that make the seeds mucilaginous when wet, green–white throughout; testal cells honeycomb-shaped when lateral walls removed by enzyme digestion. Chromosome number: \(2n = 2x = 24\) (Ochoa 10527, Herbarium of the International Potato Center, Lima, Peru).

**Phenology:** Flowering and fruiting from January to May.

**Distribution:** In cultivated fields in the high Andean altiplano between southern Peru and central Bolivia, at elevations between 3600 and 4100 m.

*Solanum ajanhuiri* is of hybrid origin from diploid forms of *S. tuberosum* (formerly classified as *S. stenotonum Juz. & Bukasov*) and the wild species *S. boliviense* Dunal (including *S. megistacrolobum*; see Solanaceae Source, http://www.solanaceaesource.org). Some landraces of *S. ajanhuiri* are probably the result of backcrossing to *S. tuberosum*. Those named ‘Sisu’ are believed to be triploid hybrids with the tetraploid wild species *S. acaule* (Huamán et al., 1980; Johns et al., 1987). Landraces of *S. ajanhuiri* were distributed originally in the high Andean altiplano between southern Peru and central Bolivia at elevations between 3700 and 4100 m. However, in Peru, only the purple-skinned ‘Ajawiri’ is grown. In the International Potato Center genebank, there are 10 named landraces of *S. ajanhuiri*. These include ‘Janco Ajawiri’, ‘Laram Ajawiri’, ‘Janco Yari’, ‘Wila Yari’, ‘Chañu Yari’, ‘Alka Yari’ and ‘Janco Sisu Yari’ reported in Huamán et al. (1980). Others from Bolivia are ‘Chañu Ajawiri’, ‘Wila Palsa Yari’ and ‘Wila Ancanche’ (Huamán & Spooner, 2002).

The spelling of the epithet for *S. ajanhuiri* has been inconsistent in various treatments. In general, European taxonomists (Hawkes & Hjerting, 1989; Hawkes, 1990) used the spelling *ajanhuiri*, whereas Ochoa (1990) used the spelling *ahanhuiri*. In the original publication of *S. ajanhuiri*, Juzepczuk & Bukasov (1929) used the spelling ‘ahanhuiri’, and also cited the Aymará common name of this potato as ‘Ahanhuiri’, with an ‘h’ as the latinized spelling of ‘j’ from Aymará/ Spanish. Bukasov’s type specimen in WIR is annotated ‘Ahanhuiri’ (see Fig. 1), and in all later treatments the Russian taxonomists used the spelling with the j (‘ajanhuiri’) rather than the h (‘ahanhuiri’). We follow the intention of the original authors (as evidenced by all of their subsequent treatments using this name) and treat this as a substantive name (noun) correctable to the intended original spelling as indicated by usage of the original describers.

Hawkes & Hjerting (1989: 384) lectotypified *S. ajanhuiri* from the many tuber accessions cited (Juzepczuk 1518, 1661, 1699, 1744 & 1800, all from the region of La Paz, Bolivia) with a specimen of Juzepczuk 1661 in LE. The only sheet of Juzepczuk 1661 in LE, however, was collected after the 1929 publication date of the epithet, and so is not the material used in the original description (Ovchinnikova et al., 2009) and thus incorrect. Ochoa (1990) correctly lectotypified *S. ajanhuiri* with a sheet of...
another of the tuber accessions (Juzepczuk 1744) that had been made into herbarium material in 1929, but did not notice Hawkes & Hjerting’s (1989) error.

*Solanum ajanhuiri* is occasionally listed in indices as being published in 1930 (Bukasov, 1930), rather than 1929. This is probably a result of the unavailability of the original 1929 publication (Juzepczuk & Bukasov, 1929) in western libraries (see discussion under *S. curtilobum* below). The listing of *S. ajanhuiri* in Bukasov (1930) was not, in our view, an intentional publishing of a new name, but a use of one already published, but not widely known outside the former Soviet Union.


**Description:** Herbs 0.5–0.9 m tall, semi-rosette when young, developing to semi-erect. Stems 10–16 mm in diameter at base of plant, with narrow wings, sparsely pubescent, green splotched with purple. Sympodial units tri- to plurifoliate, not gaminate. Leaves odd-pinnate, the blades 7–18 × 3.5–9.0 cm, dark green, membranous to chartaceous, sparsely pubescent adaxially and abaxially, with hairs like those of the stems; lateral leaflet pairs five or six, decreasing in size from the apex to the base; most distal lateral leaflets 2.5–4.5 × 1.5–2.7 cm, ovate to elliptic, the apex shortly acuminate, the base truncate to rounded to cordate; terminal leaflet 2.7–4.5 × 1.5–2.7 cm, ovate to elliptic, the apex shortly acuminate, the base truncate to rounded to cordate; interjected leaves four to six, sessile to short petiolulate, ovate to elliptic; petioles 2–4 cm, pubescent as the stems. Pseudostipules absent to minute, auriculate, pubescent with hairs like those of the stem. Inflorescences 5–11 cm, terminal with a subtending axillary bud, generally in distal half of the plant, usually forked, with 8–14 flowers, with all flowers apparently perfect, the axes pubescent with hairs like those of the stem; peduncle 7–8 cm long; pedicels 16–22 mm long in flower and fruit, spaced 1–10 mm apart, articulation indistinct or only slightly distinct, articulated high in the distal half. Flowers homostylos, pentameros. Calyx 6.0–8.5 mm long, the tube 1–2 mm, the lobes 4.0–7.5 mm, elliptic lanceolate, abruptly narrowed at apex to short pointed acumens, the acumens 2.0–3.5 mm long, with hairs like those of the stem. Corolla 3.5–5 cm in diameter, rotate, lilac–purple, the tube 1–2 mm long, the acumens 1–3 mm long, the corolla edges flat, not folded dorsally, glabrous abaxially, minutely puberulent adaxially, especially along the midribs, ciliate at the margins, especially at the tips of the corollas. Stamens with the filaments 1–2 mm long; anthers 5–6 mm long, lanceolate, connivent, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style 8.0–9.5 mm × 1 mm, exceeding stamens by 3–4 mm, straight, papillose in the distal half; stigma capitate. Fruit a globose to ovoid berry, 2–3 cm in diameter, green to green tinged with purple when ripe, glabrous. Seeds from living specimens ovoid and c. 2 mm long, whitish to greenish in fresh condition and drying brownish, with a thick covering of ‘hair-like’ lateral walls of the testal cells that make the seeds mucilaginous when wet, green–white throughout; testal cells honeycomb-shaped when lateral walls removed by enzyme digestion. Chromosome number: 2n = 5x = 60 (Huamán 60, Herbarium of the International Potato Center, Lima, Peru).

**Phenology:** Flowering and fruiting from January to May.

**Distribution:** Throughout the highlands of northern Peru to central Bolivia and rarely in northern Argentina, in cultivated fields, at elevations between 3600–4300 m.

*Solanum curtilobum* is of hybrid origin, resulting from a cross between *S. juzepczukii* Bukasov and tetraploid cultivars of *S. tuberosum* (Hawkes, 1962; Schmiediche et al., 1980, 1982). In the CIP genebank are landraces mainly differentiated by the tuber skin colour and sprout colour. These have many different names, including ‘Shiri’, ‘Luki’, ‘Waña’, ‘Choquepito’, ‘Maliku’ and ‘Ococuri’, alone or in combination with names describing the tuber skin colour, such as ‘Yuracc’ or ‘Jancko’ (white), ‘Yana’, ‘Laram’ or ‘Azul’ (purple), or ‘Pinta’ (two-coloured) (Huamán & Spooner, 2002).

*Solanum curtilobum* was first described by Juzepczuk & Bukasov in Volume III of the Proceedings of the USSR Congress of Genetics, Plant- and Animal Breeding held in Leningrad in January 1929 (Juzepczuk & Bukasov, 1929), which was not available in the West. Therefore, in indices such as Index Kewensis (and, later, IPNI and the Gray Card Index), the place of first publication of this name and others coined in that 1929 publication was given as Bukasov’s (1930) treatment of the cultivated plants of Mexico, Guatemala and Colombia, in which the epithets validly described with Latin diagnoses previously were listed in the text, but not formally described. The use of *S. curtilobum* and other names (see *S. tuberosum* below) in Bukasov (1930) was clearly not intended as a new publication of these epithets.
Figure 2. Lectotype specimen of *Solanum curtilobum* Juz. & Bukasov held in LE. Reproduced with permission of the V. L. Komarov Botanical Institute.
Ovchinnikova et al. (2009: 584) confirmed Hawkes & Hjerting’s (1989: 403) lectotypification of *S. curtilobum* with a specimen in LE, but did not find the isotype cited by Hawkes & Hjerting as being in WIR; subsequent searches have also failed to reveal this specimen.

3. **Solanum juzepczukii** Bukasov, Trudy Vse-
Zhivotnov. 3: 603. 1929. Type: cultivated in Lenin-
grad from tuber accession 3355 collected in Peru 
(Cusco: prov. Acomayo, Pomacanchi, *S. Juzepczuk 
1166*, 1.ix.1928, V.S. Lekhnovich [3355] (lectotype 
WIR! [WIR-36897], designated here; isolectotype, 
K! [K000585544]). Figure 3.

*Solanum juzepczukii* Bukasov var. *parco* Hawkes, 
Classific. Collect. 73, 131. 1944. Type: cultivated in 
Cambridge (UK) from tuber accession EPC-1106 
collected in Peru (Puno, *J. Soukup* s.n.), 1940, 
Anon. *[J.G. Hawkes]* s.n. (lectotype, K! 
[K000658001], designated here).

*Solanum juzepczukii* Bukasov var. roseum Vargas, 
Papas Sudper. 2: 20, fig. 2. 1956 ['1954']. Type: 
Peru. Puno: Prov. Carabayla, Macusani, 4300 m, 
C. Vargas 1145 (holotype, CUZ!).

*Solanum juzepczukii* Bukasov forma *ekoyuchaisalla* 
Oruro: Prov. Carangas, Jango Cala, Z. Huamán 821 
(holotype, herb. Ochoa, not found).

*Solanum juzepczukii* Bukasov forma *jancock-aisalla* 
Oruro: Prov. Poopo, Toledo, 3700 m, Z. Huamán 809 
(holotype, CUZ! [original citation as herb. Ochoa]).

*Solanum juzepczukii* Bukasov forma *luckipechuma* 
Oruro: Challa, CIP-702631 (holotype, CIP!).

*Solanum juzepczukii* Bukasov forma *luckipinkula* 
Potosí: Prov. Frias, Callactiri, 3900 m, C. Ochoa 10571 
(holotype, CUZ! [original citation as herb. 
Ochoa]).

*Solanum juzepczukii* Bukasov forma *wilackaisalla* 
Oruro: Prov. Poopo, Saucaari-Toledo, Z. Huamán 815 
(holotype, herb. Ochoa, not found).

*Solanum juzepczukii* Bukasov var. *lucky* Ochoa, Phy-
Ingavi, Ingavi, Z. Huamán 789 (holotype, CUZ! 
[original citation as herb. Ochoa]).

Description: Herbs 0.4–0.8 m tall, semi-roseate when 
young, developing to semi-erect. Stems 10–15 mm in 
diameter at base of plant, unwinged to narrowly 
winged, sparsely pubescent, green to green splotched 
with purple. Sympodial units tri- to plurifoliate, not 
geminate. Leaves odd-pinnate, the blades 14–28 × 6– 
10 cm, dark green, membranous to chartaceous, 
rugose, sparsely pubescent adaxially and abaxially, 
with hairs like those of the stems; lateral leaflet pairs 
five to seven, decreasing in size from the apex to the 
base; most distal lateral leaflets 2.5–6.5 × 1.0–3.5 cm, 
slightly decurrent onto the rachis on the basiscopic 
side, broadly ovate to broadly elliptic, the apex obtuse 
to acute, the base cuneate or rounded; terminal leaflet 
3–7 × 2–4 cm, broadly ovate to broadly elliptic, the 
apex obtuse to acute, the base cuneate or rounded; 
interjected leaflets one to four, sessile to short petiolu-
ate, broadly ovate to broadly elliptic; petioles 2–4 cm, 
pubescent as the stems. Pseudostipules 1–5 mm, auri-
culate, pubescent with hairs like those of the stem. 
Inflorescences 5–6 cm, terminal with a subtending 
axillary bud, generally in distal half of the plant, 
usually forked, with 10–15 flowers, with all flowers 
apparently perfect, the axes pubescent with hairs like 
those of the stem; peduncle 7–16 cm long; pedicels 
22–35 mm in length and fruited, 1–10 mm apart, 
articulation indistinct or only slightly distinct, articu-
lated high in the distal half. Flowers homostylous, 
pentamorus. Calyx 4–10 mm long, the tube 1–2 mm, 
the lobes 2–9 mm, triangular-lanceolate or elliptic-
lanceolate, terminated in pointed acumen, the acu-
mens 2.0–4.5 mm long, with hairs like those of the 
stem. Corolla 3–4 cm in diameter, rotate, lilac–purple 
or dark red–purple or medium to dark purple, the tube 
1–2 mm long, the acumen c. 2 mm long, the corolla 
edges flat, not folded dorsally, glabrous abaxially, 
minutely puberulent adaxially, especially along the 
midribs, ciliate at the margins, especially at the tips of 
the corollas. Stamens with the filaments 1–2 mm long; 
anthers 3–5 mm long, lanceolate, connivent, yellow, 
poricidal at the tips, the pores lengthening to slits with 
age. Ovary glabrous; style 6–8 × 1 mm, exceeding 
stamens by 1–2 mm, straight, papillose in the distal 
halv; stigma capitate. Fruit a globose to ovoid berry, 
0.5–1.0 cm in diameter, green to green tinged with pur-
ple when ripe, glabrous. Seeds from living specimens 
ovid and c. 2 mm long, whitish to greenish in fresh 
condition and drying brownish, with a thick covering of 
‘hair-like’ lateral walls of the testal cells that make the 
seeds mucilaginous when wet, green–white through-
out; testal cells honeycomb-shaped when lateral walls 
removed by enzyme digestion. Chromosome number: 
2n = 3x = 36 (Huamán 815, Herbarium of the Interna-
tional Potato Center, Lima, Peru).

Phenology: Flowering and fruiting from January to 
May.

Distribution: In the high Andean altiplano between 
southern Peru and central Bolivia, in cultivated 
fields, at elevations between 3600 and 4400 m.

The name *S. juzepczukii* was validly published in 
1929 with a complete Latin description and a single
Figure 3. Lectotype specimen of *Solanum juzepczukii* Bukasov held in WIR (WIR-36897). Reproduced with permission of the N. I. Vavilov Institute of Plant Industry.

accession cited as the type (Juzepczuk & Bukasov, 1929, see discussion under *S. curtilibum* above), but is often cited as having been coined later (in Bukasov, 1930) in indices.


*Solanum tuberosum* L. var. *lentenanum* Alef., *Landw. Fl.* 137. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

*Solanum tuberosum* L. var. *helenanum* Alef., *Landw. Fl.* 140. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].


*Solanum tuberosum* L. var. *putescheanum* Alef., *Landw. Fl.* 140. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

*Solanum tuberosum* L. var. *sesquimensale* Alef., *Landw. Fl.* 140. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

*Solanum tuberosum* L. var. *xanthoceras* Alef., *Landw. Fl.* 140. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].


*Solanum tuberosum* L. var. *saccharatum* Alef., *Landw. Fl.* 141. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].


*Solanum tuberosum* L. var. *schnittspahnii* Alef., *Landw. Fl.* 141. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].


*Solanum tuberosum* L. var. *album* Alef., *Landw. Fl.* 143. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

*Solanum tuberosum* L. var. *batatinum* Alef., *Landw. Fl.* 143. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].
Figure 4. Lectotype specimen of *Solanum tuberosum* L. (*Chilotanum* group) held in LINN (LINN 248.12). Reproduced with permission of the Linnean Society of London.
Solanum tuberosum L. var. nucinum Alef., Landw. Fl. 143. 1866. Type: no specimens found (lectotype, Putsch, 1819, Monographie der Kartoffel, f. 21, designated here). [C].

Solanum tuberosum L. var. peruvianum Alef., Landw. Fl. 143. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 23, designated here). [C].

Solanum tuberosum L. var. alaudinum Alef., Landw. Fl. 144. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. anglicum Alef., Landw. Fl. 144. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. bufoninum Alef., Landw. Fl. 144. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. hispanicum Alef., Landw. Fl. 144. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. pecorum Alef., Landw. Fl. 144. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. praecox Alef., Landw. Fl. 145. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 31, designated here). [C].

Solanum tuberosum L. var. rugiorum Alef., Landw. Fl. 145. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. aethiopicum Alef., Landw. Fl. 145. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. concarpum Alef., Landw. Fl. 145. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. praeceps Alef., Landw. Fl. 145. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 5, designated here). [C].

Solanum tuberosum L. var. praedicandum Alef., Landw. Fl. 145. 1866. Type: no specimens found (lectotype, Putsch, 1819, Monographie der Kartoffel, f. 26, designated here).

Solanum tuberosum L. var. rokitii Alef., Landw. Fl. 145. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 9, designated here). [C].

Solanum tuberosum L. var. drakeanum Alef., Landw. Fl. 146. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. elongatum Alef., Landw. Fl. 146. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. tinctorum Alef., Landw. Fl. 146. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. vuchefeldicum Alef., Landw. Fl. 146. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 27, designated here). [C].

Solanum tuberosum L. var. aethiopicum Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. hassicum Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. kaunitzii Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. merceri Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. norfolcicum Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. rossicum Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. ulmense Alef., Landw. Fl. 147. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. cepinum Alef., Landw. Fl. 148. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].


Solanum tuberosum L. var. palatinatum Alef., Landw. Fl. 148. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 5, designated here). [C].

Solanum tuberosum L. var. versicolor Alef., Landw. Fl. 148. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 7, designated here). [C].

Solanum tuberosum L. var. corsicanum Alef., Landw. Fl. 149. 1866. Type: cultivated in Darmstadt, Germany (no specimens found). [C].

Solanum tuberosum L. var. salamandrinum Alef., Landw. Fl. 149. 1866. Type: cultivated in Darmstadt, Germany (no specimens found, lectotype, Putsch, 1819, Monographie der Kartoffel, f. 8, designated here). [C].


Solanum andigenum Juz. & Bukasov forma chalcoense Bukasov, Trudy Prikl. Bot. Suppl. 47: 204, 517. 1930. Type: cultivated in Leningrad from tuber accession collected in Mexico (Toluca: Cuautzingo (near Chalco), S. Bukasov 3 & 4; DF: Cocayan and Ajusco, M.C. Antipovich s.n. (no specimens found)). [A].


Figure 5. Lectotype specimen of *Solanum andigenum* Juz. & Bukasov (Solanum tuberosum L. Andigenum group) held in LE. Reproduced with permission of the V. L. Komarov Botanical Institute.

Solanum stenotomum Juz. & Bukasov var.

Solanum andigenum Juz. & Bukasov var.


Solanum andigenum Juz. & Bukasov forma

Solanum andigenum Juz. & Bukasov var. Solanum andigenum

Solanum andigenum Juz. & Bukasov forma

Solanum andigenum Juz. & Bukasov var. Solanum andigenum

Solanum andigenum Juz. & Bukasov forma

Solanum andigenum Juz. & Bukasov var. Solanum andigenum

S. Juzepczuk [1256] (lectotype, WIR! [WIR-3749], designated here). [A].


Type: cultivated in Leningrad from tuber accession collected in Chile (Yutuy, Aguatao, S. Juzepczuk 2002) (no specimens found). [C].


accession collected in Chile (Yutuy, Juezepczuk 1970) (no specimens found). [C].


**Solanum andigenum** Juz. & Bukasov var. *carhua* Vargas, Papas Sudper. 2: 49, fig. 5. 1956 ['1954']. Type: Peru. Apurimac: Prov. Grau, Maras, 3600 m, C. Vargas 842, 848 (no specimens found). [A].

**Solanum andigenum** Juz. & Bukasov var. *digitotuberosum* Vargas, Papas Sudper. 2: 49, fig. 4. 1956 ['1954'] as *'digitotuberosum'*. Type: Peru. Apurimac: Prov. Andahuaylas, 3050 m, C. Vargas 77 (no specimens found). [A].


**Solanum tuberosum** L. var. *rubrum* Danert, Kulturpflanze 4: 124. 1956. Type: ‘Sickingen’ cultivated in Gatersleben Nr. 20970/55, origin Groß Lüsewitz...


Solanum phureja Juz. & Bukasov var. caeruleum Ochoa, Phytologia 65: 103. 1988. as 'caeruleus'. Type: Bolivia. La Paz: Prov. Franz Tamayo, Queara, 3350 m, C. Ochoa & A. Salas 14973 (holotype, CUZ! [original citation herb. Ochoa]; isotypes, CIP!, F!). [A].


Solanum stenotomum Juz. & Bukasov forma

Solanum phureja Juz. & Bukasov var. rubro-roseum

Solanum phureja Juz. & Bukasov forma timus

Solanum phureja Juz. & Bukasov forma janckophureja

Solanum sterotomum Juz. & Bukasov forma chiaerkati

Solanum sterotomum Juz. & Bukasov forma chiaiphipi

Solanum sterotomum Juz. & Bukasov forma akkappi-tiquina

Solanum sterotomum Juz. & Bukasov forma jankchojilu

Solanum sterotomum Juz. & Bukasov forma pulu-waysyu

Solanum sterotomum Juz. & Bukasov forma wila-chojilu

Solanum sterotomum Juz. & Bukasov var. arichuwa

Solanum sterotomum Juz. & Bukasov var. chojilu

Solanum sterotomum Juz. & Bukasov var. kkmara

Solanum sterotomum Juz. & Bukasov var. luru

Solanum sterotomum Juz. & Bukasov var. pikipquina

Solanum sterotomum Juz. & Bukasov forma azure-oekati
Ochoa, Phytologia 65: 106. 1988. Type: Bolivia. La Paz: Prov. Inquisivi, Quime, 3200 m, C. Ochoa & A. Salas 15514 (holotype, herb. Ochoa, not found; isotype, CIP!). [A].

Solanum sterotomum Juz. & Bukasov forma chu-rupuya

Solanum sterotomum Juz. & Bukasov forma kkar-chipampa

Solanum sterotomum Juz. & Bukasov forma laram

Solanum sterotomum Juz. & Bukasov forma pitikalla

Solanum sterotomum Juz. & Bukasov forma quime

Solanum sterotomum Juz. & Bukasov var. zapallo

Solanum chaucha Juz. & Bukasov var. ccoesullu


Solanum tuberosum L. var. sicha Ochoa, Phytologia 65: 112. 1988. Type: Bolivia. La Paz: Prov. Inquisivi, Quime, 2700 m, C. Ochoa & A. Salas 15517 (holotype, herb. Ochoa, not found; isotype, CIP!). [A].


Solanum tuberosum L. forma wilakoyu Ochoa, Phytologia 65: 112. 1988. Type: cultivated in Lima, Peru from collection made in Bolivia [?], CIP-702691 (holotype, herb. Ochoa, not found; isotype, CIP!).


Description: Herbs 0.4–1.4 m tall, ascending to erect or semi-erect, decumbent or prostrate. Stems 5–19 mm in diameter at base of plant, unwinged or with wings to 5 mm, nearly glabrous to densely pubescent, green or purple to green and purple mottled. Sympodial units tri- to plurifoliolate, not geminate. Leaves odd-pinnate, with all flowers apparently perfect, the axes pubescent as the stems. Pseudostipules 4–25 mm long, leaflet pairs 3–8, only slightly decreasing in size from the apex to the base; most distal lateral leaflets 3–8 × 1.5–5.5 cm, ovate to elliptic to broadly elliptic-lanceolate, the apex acute to acuminate or shortly acuminate, the base generally oblique, rounded to cuneate to cordate, rarely truncate; terminal leaflet 3.5–9.0 × 1.0–5.5 cm, ovate to elliptic to broadly elliptic-lanceolate, the apex acute to acuminate or shortly acuminate, the base generally oblique, rounded to cuneate to cordate, rarely truncate; leaflet pairs 3–8, only slightly decreasing in size from the apex to the base, most distal lateral leaflets 3–8 × 1.5–5.5 cm, ovate to elliptic to broadly elliptic-lanceolate, the apex acute to acuminate or shortly acuminate, the base generally oblique, rounded to cuneate to cordate, rarely truncate; intermediate leaflets 0–45, sessile to short petiolulate, ovate to elliptic to broadly elliptic-lanceolate; petioles 2–6 cm, pubescent as the stems. Pseudostipules 4–25 mm long, auriculate to semi-elliptic, falcate, pubescent with hairs like those of the stem. Inflorescences 5–11 cm, terminal with a subtending axillary bud, generally in distal half of the plant, usually forked, with 0–25 flowers, with all flowers apparently perfect, the axes pubescent with hairs like those of the stem; peduncle 0–22 cm long; pedicels 10–35 mm long in flower and fruit, spaced 1–10 mm apart, articulated in approximatively the middle third. Flowers homostylous, pentamorous. Calyx 0–10 mm long, the tube 1–2 mm, the lobes 0–9 mm, short and acute to long attenuate, the acumens 1–8 mm long, with hairs like those of the stem. Corolla 2–6 cm in diameter, rotate to rotate-pentagonal, white to pink to lilac to blue to purple to red–purple, uniform or with white acumens or with a secondary colour stippled, in bands, or in the star, adaxially or abaxially or both, the tube 1–2 mm long, the acumens 3–5 mm long, often prominent, the corolla...
edges flat, not folded dorsally, glabrous abaxially, minutely puberulent adaxially, especially along the midribs, ciliate at the margins, especially at the tips of the corollas. Stamens with the filaments 1–2 mm long; anthers 3–8 mm long, cordate at the base, lanceolate, connivent, yellow, poricidal at the tips, the pores lengthening to slits with age. Ovary glabrous; style 9–13 × 1 mm, exceeding stamens by 7 mm, straight, papillose in the distal half; stigma capitate. Fruit a globose to ovoid berry, 1–4 cm in diameter, green to green tinged with white or purple spots or bands when ripe, glabrous. Seeds from living specimens ovoid and c. 2 mm long, whitish to greenish in fresh condition and drying brownish, with a thick covering of ‘hair-like’ lateral walls of the testal cells that make the seeds mucilaginous when wet, green–white throughout; testal cells honeycomb-shaped when lateral walls removed by enzyme digestion. Chromosome number: 2n = 2x = 24 (Ochoa & Salas 14973), 2n = 3x = 36 (Ochoa 2202), 2n = 4x = 48 (Ochoa 2159); all vouchers at the Herbarium of the International Potato Center, Lima, Peru.

**Phenology:** Flowering and fruiting from January to May.

**Distribution:** Landrace populations of *S. tuberosum* grow from western Venezuela south to northern Argentina (Andean populations), and then, with a gap of distribution in south-central Chile, in the islands of the Chonos and Guaiíceas Archipelagos and adjacent mainland Chile (lowland Chilean populations), with the Andean populations growing mainly from 2000 to 4600 m in elevation and the lowland Chilean populations at or near sea level to 500 m. Landrace populations are still maintained out of their natural range, introduced in post-Colombian times, in Mexico and Central America, the Shimla Hills of India and the Canary Islands. The modern cultivated potato (also classified as *S. tuberosum*) is cultivated worldwide.

The spelling of the epithet ‘andigenum’, as originally used by Juzepczuk & Bukasov (1929), has often been changed by subsequent authors to ‘andigena’, and it occasionally appears as ‘andigena’ in indices. In this article and on the Solanaceae Source website, all these have been corrected to the original spelling. The name *S. andigenum* was validly published in 1929 (see discussion under *S. curtilobum* above), but is often cited as having been coined later (in Bukasov, 1930). Together with *S. andigenum*, other names treated by us as synonyms of *S. tuberosum* which were validly published in 1929 and cited in various indices as having been published in 1930 are *S. boyacense* Juz. & Bukasov, *S. chaucha* Juz. & Bukasov, *S. goniocalyx* Juz. & Bukasov, *S. mamiliferum* Juz. & Bukasov, *S. phureja* Juz. & Bukasov, *S. rybinii* Juz. & Bukasov, *S. stenotonum* Juz. & Bukasov and *S. tenuifilamentum* Juz. & Bukasov. Descriptions in Latin accompanied these names and new species’ rank epithets in Bukasov (1930), but not those of taxa described at varietal and form rank. It may be that Juzepczuk and Bukasov did not really intend the many names coined at these lower ranks to be of the same sort or equivalent to the species’ level names, but, under the nomenclatural rules of the day, they must be treated as validly published in the absence of evidence to the contrary.

Hawkes & Hjerting (1989: 378) superfluously lectotypified *S. phureja* with *Juzepczuk 1654* at WIR; this lectotypification had already been carried out by Korovina et al. (1985). Hawkes & Hjerting (1989: 388) lectotypified *S. chaucha* with a specimen of *Juzepczuk 1010* said to be collected in Peru in ‘herb. Vavilov Institute’ (WIR), but Ovchininnkova et al. (2009: 583) failed to encounter any such specimen in the WIR herbarium. They did find three sheets of this collection (grown from *Juzepczuk 1010* in Russia) at LE, and designated one of these as the lectotype: (Ovchininnkova et al., 2009). Several isotypes with labels in Bukasov's handwriting with the tuber accession number *Juzepczuk 1010* and the same date of collection as the specimens in LE, which were presumably given to Hawkes by Russian potato taxonomists during his Russian trip in 1938 (see Hawkes, 2004), are today held at K. Hawkes & Hjerting (1989) also cite other specimens in ‘herb. JGH’ that were obtained from Russian potato taxonomists during Hawkes’ visit (e.g. a sheet of *Juzepczuk 1166*, isotype of *S. juzepczukii*, now at K [K000585544]).

Gorbatenko & Hawkes (1996) lectotypified *S. goniocalyx* with a specimen taken from the accession *Juzepczuk 571* from Cerro de Pasco (Peru) that was cited in the original description, because they were unable to locate any specimens of the number cited in the original publication as the type for this name (*Juzepczuk 587*) in either LE or WIR. A sheet of the type was apparently loaned to C. Ochoa, but has not been located. Should this sheet be located, it would be the obligate lectotype for *S. goniocalyx*, which would have to be re-lectotypified. Given the uncertain location of much of Ochoa’s herbarium (see synonymy above), we cite Gorbatenko & Hawkes’ (1996) lectotypification here. In describing *S. andigenum* var. mexicanum and var. colombianum, Bukasov (1930) did not specify material for these taxa, but instead described them in reference to their component forms. We have followed them in assuming forma *tolucanum* to be homotypic (and thus probably an illegitimate name for forma *mexicanum*); they state ‘the typical form’ in reference to forma *tolucanum*. The same principle has been used for var. colombianum and forma *tocanum*.
We have neotypified several of the names coined by Bukasov and Lekhnovich (Bukasov, 1933) with material collected in Leningrad by Hawkes in 1938 (see discussion above), as no original material was found in any of the St. Petersburg herbaria.

We have used specimens made of flowering stems of one of the many cultivars cited by Danert in his original description, which were cultivated in Gatersleben in 1955, as lectotypes for five of these names; these are the only names for which material has been found in GAT (K. Pistrick, 26.x.2010).

No original material of S. rybinii var. pastoense has been found in the Hawkes’ material held at K, and so this name has been neotypified with material of the type accession (collected in the market in Pasto, Colombia by E. K. Balls as tubers and grown as EPC accession 979) grown at the John Innes Institute in Norwich (UK), near the original cultivation site of Cambridge. Solanum subandigenum is not represented in the Hawkes’ herbarial material at K, but a specimen collected in the field is held in BM; this sheet, consisting of several sterile seedlings, has been designated the lectotype in the absence of other herbarial material. The only herbarial material we have found of the type collection of S. cardenasii (Balls 6299) is a flower dissection (prepared in the manner usually undertaken by Hawkes) at K; this has been designated the lectotype, although material with leaves would have been preferable. No specimens were cited by Hawkes (1944) in his description of S. yabari, but specimens were cited as belonging to the two varieties (neither validly published because of a lack of Latin diagnoses, Article 36.1, see above). Two of these were cited in the Latin diagnosis (but not in the English description) of S. yabari: Yabar 44 (EPC-698) and EPC-1077 without a collector. We have selected a sheet of Yabar 44 at K, collected from plants grown at Cambridge from EPC-698, as the lectotype for this species.

In his 1983 paper describing infraspecific variation in Andean potatoes, V. S. Lekhnovich used the infraspecific rank ‘coconvarietas’, a rank not explicitly recognized in ICBN (Article 4.1), but Article 4.3 states that additional ranks may be added provided that confusion may be added provided that confusion is not introduced. Lekhnovich (1983) appears to have deliberately used the rank convar. to indicate ‘groups of varietatis’, thus positioning it between subspecies and variety. We are treating these epithets as validly published despite the rank being nonstandard, as no confusion is apparent in Lekhnovich’s formulation of them.

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APPENDIX: NAMES NOT VALIDLY PUBLISHED

Dodds (1962) provided a list of names excluded from his treatment for various reasons. In it, he included many of the epithets coined by Bukasov in the 1930s, which he excluded because they were not accompanied by Latin descriptions. ICBN, however, only requires Latin diagnoses for names published after 1935, and so many names rejected by Dodds were in fact validly published.

Solanum ajanhuiri Juz. & Bukasov

Solanum ajanhuiri Juz. & Bukasov var. azul Lechn. in Bukasov, Kult. Fl. SSSR 10: 70. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1).

Solanum ajanhuiri Juz. & Bukasov var. jancho Lechn. in Bukasov, Kult. Fl. SSSR 10: 71. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1).
Solanum curtilobum Juz. & Bukasov
Solanum curtilobum Juz. & Bukasov forma chino-malko Lechn. in Bukasov, Kult. Fl. SSSR 10: 74. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1).

Solanum juzepczukii Bukasov
Solanum juzepczukii Bukasov forma orcco-malko Lechn. in Bukasov, Kult. Fl. SSSR 10: 73. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1).

Solanum stenotomum Juz. & Bukasov forma

Solanum tuberosum L.

Solanum tuberosum L. forma brachystylum Bukasov, Trudy Prikl. Bot. Suppl. 58: 80. 1933. 'Roode Star', nomen nudum, in list, name only. [C].


Solanum tuberosum


Solanum chaucha L. var. Solanum tuberosum convar. Solanum tuberosum


Solanum kessellbrenneri Juz. & Bukasov var. nudulum Lechn., in Bukasov, Kult. Fl. SSSR 10: 55. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum goonicalyx Juz. & Bukasov var. papa-amarilla Lechn., in Bukasov, Kult. Fl. SSSR 10: 64. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum phureja Juz. & Bukasov var. ruutu-papa Lechn., in Bukasov, Kult. Fl. SSSR 10: 59. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum phureja Juz. & Bukasov var. coloratum Lechn., in Bukasov, Kult. Fl. SSSR 10: 64. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1); later homonym of Solanum tuberosum L. var. coloratum Danert. [A].

Solanum phureja Juz. & Bukasov var. flaviarictulatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 64. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum phureja Juz. & Bukasov var. nigriarticulatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 64. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. laram Lechn., in Bukasov, Kult. Fl. SSSR 10: 68. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. rosada Lechn., in Bukasov, Kult. Fl. SSSR 10: 68. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. phinhu Lechn., in Bukasov, Kult. Fl. SSSR 10: 68. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma laram Lechn., in Bukasov, Kult. Fl. SSSR 10: 68. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma rosada Lechn., in Bukasov, Kult. Fl. SSSR 10: 68. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. iodes Lechn., in Bukasov, Kult. Fl. SSSR 10: 82. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. viridicu- tocanum Lechn., in Bukasov, Kult. Fl. SSSR 10: 84. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. funzanum (Bukasov) Lechn., in Bukasov, Kult. Fl. SSSR 10: 89. 1972 ['1971']. No full and direct reference to basionym author and valid place of publication provided (Art. 33.4). [A].


Solanum andigenum Juz. & Bukasov var. pigmen-tatulum Lechn., in Bukasov, Kult. Fl. SSSR 10: 88. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1); it is possible that Lekhnovich was referring to forma guatemalense of Bukasov (1933), but no full and direct reference to basionym author and valid place of publication provided (Art. 33.4). [A].


Solanum andigenum Juz. & Bukasov var. latiaccumatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 112. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. huarasii Lechn., in Bukasov, Kult. Fl. SSSR 10: 123. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. atroviolaceum Lechn., in Bukasov, Kult. Fl. SSSR 10: 125. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. alboascicum Lechn., in Bukasov, Kult. Fl. SSSR 10: 125. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. recurvatulum Lechn., in Bukasov, Kult. Fl. SSSR 10: 129. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. cerrodescente Lechn., in Bukasov, Kult. Fl. SSSR 10: 130. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov convar. breviceptatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 133. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma blanca Lechn., in Bukasov, Kult. Fl. SSSR 10: 133. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma pucanahui Lechn., in Bukasov, Kult. Fl. SSSR 10: 133. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. titicaense Lechn., in Bukasov, Kult. Fl. SSSR 10: 133. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. carguamayense Lechn., in Bukasov, Kult. Fl. SSSR 10: 139. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. pinha-cerro Lechn., in Bukasov, Kult. Fl. SSSR 10: 139. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. pipinilla Lechn., in Bukasov, Kult. Fl. SSSR 10: 140. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. platytherum Lechn., in Bukasov, Kult. Fl. SSSR 10: 140. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. dissecticollatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 141. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. chatablanca Lechn., in Bukasov, Kult. Fl. SSSR 10: 142. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. rubrica-neum Lechn., in Bukasov, Kult. Fl. SSSR 10: 152. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma viride Lechn., in Bukasov, Kult. Fl. SSSR 10: 152. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. cecompetillo (Bukasov & Lechn.) Lechn., in Bukasov, Kult. Fl. SSSR 10: 160. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. competillo (Bukasov & Lechn.) Lechn., in Bukasov, Kult. Fl. SSSR 10: 162. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov forma nahui Lechn., in Bukasov, Kult. Fl. SSSR 10: 164. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma aconoyoanum Lechn., in Bukasov, Kult. Fl. SSSR 10: 166. 1972 [’1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma pucapapa Lechn., in Bukasov, Kult. Fl. SSSR 10: 166. 1972 [’1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. pucapapa Lechn., in Bukasov, Kult. Fl. SSSR 10: 166. 1972 [’1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. chiar-imilla Lechn., in Bukasov, Kult. Fl. SSSR 10: 188. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); it is possible that Lekhnovich was referring to forma chiar-imilla of Bukasov & Lechn. (Bukasov, 1933) as some of the same tuber accessions were cited, but no full and direct reference to basionym author and valid place of publication provided (Art. 33.4). [A].

Solanum andigenum Juz. & Bukasov forma mixtum Lechn., in Bukasov, Kult. Fl. SSSR 10: 188. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. curtipedi-cellatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 188. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. magnicalyx Lechn., in Bukasov, Kult. Fl. SSSR 10: 190. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. pomacanchicum Lechn., in Bukasov, Kult. Fl. SSSR 10: 191. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1); it is possible that Lekhnovich was referring to forma pomacanchicum of Bukasov & Lechn. (Bukasov, 1933) as the same tuber accession was cited, but no full and direct reference to basionym author and valid place of publication provided (Art. 33.4). [A].


Solanum andigenum Juz. & Bukasov forma ckehuillo Lechn., in Bukasov, Kult. Fl. SSSR 10: 194. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. flavifolium Lechn., in Bukasov, Kult. Fl. SSSR 10: 204. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov var. brachystylum Lechn., in Bukasov, Kult. Fl. SSSR 10: 205. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov var. elongatibaccatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 208. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum andigenum Juz. & Bukasov forma hua-calaira Lechn., in Bukasov, Kult. Fl. SSSR 10: 211. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum andigenum Juz. & Bukasov forma huarisalla Lechn., in Bukasov, Kult. Fl. SSSR 10: 212. 1972 ['1971']. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].


Solanum tuberosum L. var. [1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].
Solanum tuberosum L. forma corniforme Lechn., in Bukasov, Kult. Fl. SSSR 10: 239. 1972 [1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].
Solanum tuberosum L. var. pehuenchense Lechn., in Bukasov, Kult. Fl. SSSR 10: 240. 1972 [1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].
Solanum tuberosum L. forma humile Lechn., in Bukasov, Kult. Fl. SSSR 10: 259. 1972 [1971]. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].
Solanum tuberosum L. forma violaceum Danert. [C].
Solanum tuberosum L. convar. pyriconicum Lechn., in Bukasov, Kult. Fl. SSSR 10: 264. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma costa Lechn., in Bukasov, Kult. Fl. SSSR 10: 265. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma murta Lechn., in Bukasov, Kult. Fl. SSSR 10: 266. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma montanara Lechn., in Bukasov, Kult. Fl. SSSR 10: 271. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma cabra Lechn., in Bukasov, Kult. Fl. SSSR 10: 274. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma olgae (Bukasov & Lechn.) Lechn., in Bukasov, Kult. Fl. SSSR 10: 277. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].


Solanum tuberosum L. var. infectum (Bukasov & Lechn.) Lechn., in Bukasov, Kult. Fl. SSSR 10: 286. 1972 ['1971'). No full and direct reference to basionym author and valid place of publication provided (Art. 33.4). [C].

Solanum tuberosum L. forma elongatipetiolatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 287. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma sebastianum Lechn., in Bukasov, Kult. Fl. SSSR 10: 288. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. var. yutuense Lechn., in Bukasov, Kult. Fl. SSSR 10: 288. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma mago Lechn., in Bukasov, Kult. Fl. SSSR 10: 289. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. var. grandifoliolatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 295. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma crassipedicellatum Lechn., in Bukasov, Kult. Fl. SSSR 10: 295. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].

Solanum tuberosum L. forma elvira Lechn., in Bukasov, Kult. Fl. SSSR 10: 300. 1972 ['1971'). No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [C].


Solanum stenotomum Juz. & Bukasov forma alkkaphinu Ochoa, Phytologia 65: 104. 1988. No Latin diagnosis or description (Art. 36.1); no type designated (Art. 37.1). [A].

Solanum phureja Juz. & Bukasov forma macmillanii (Bukasov) Ochoa, Phytologia 65: 104. 1988. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

Solanum phureja Juz. & Bukasov forma erlansonii (Bukasov) Ochoa, Potatoes of S. Amer: Bolivia 363. 1990. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

Solanum phureja Juz. & Bukasov forma chochlo (Bukasov & Lechn.) Gorbat., Potato Sp. S. Amer. 386. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].
**Solanum rybinii** Juz. & Bukasov forma *boyacense* (Juz. & Bukasov) Gorbat., Potato Sp. S. Amer. 388. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

**Solanum rybinii** Juz. & Bukasov forma *caniarense* (Bukasov & Lechn.) Gorbat., Potato Sp. S. Amer. 388. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

**Solanum rybinii** Juz. & Bukasov forma *ciezae* (Bukasov & Lechn.) Gorbat., Potato Sp. S. Amer. 388. 2006. As 'ciecae'. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

**Solanum rybinii** Juz. & Bukasov forma *cuencanum* (Bukasov & Lechn.) Gorbat., Potato Sp. S. Amer. 390. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

**Solanum rybinii** Juz. & Bukasov forma *kesselbrenneri* (Bukasov & Lechn.) Gorbat., Potato Sp. S. Amer. 390. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

**Solanum rybinii** Juz. & Bukasov forma *riobambaense* (Bukasov & Lechn.) Gorbat., Potato Sp. S. Amer. 391. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].

**Solanum stenotomum** Juz. & Bukasov forma *macmillanii* (Bukasov) Gorbat., Potato Sp. S. Amer. 392. 2006. Based on a name not validly published; no Latin diagnosis or description (Art. 36.1); no type specimen designated (Art. 37.1). [A].