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Wild and Cultivated Potato Species Diversity, Taxonomy, and Conservation

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Abstract

In the present chapter, we summarize the knowledge of wild and cultivated potato species, diversity, a taxonomic update including group concept classification and description, species valid names, and a complete synonymy, distribution, and habitat. Likewise, the importance of reproductive characters, breeding barriers, interspecific hybridization, and gene flow, introgression, polyploidy in potato evolution and ecological adaptation, and conservation strategies is explained. Also a comprehensive taxonomy of all wild and cultivated potatoes, based on the integration of multiple evidences and phylogenetic relationships between taxa is discussed, providing a framework for further investigation of complex groups as well as rare endemic species. Hypothesis regarding patterns of species diversity and distributions, and adaptive mechanisms to different extreme environments are proposed. More recent genomic approaches are promissory not only to investigate wild potato genome evolution but also to detect alleles related to important agronomic traits. Germplasm of more wild species or potato landraces can be explored considering hypothesis of relationships. A taxonomic framework could be useful for harmonizing names and classification of potato collection among genebanks. The knowledge of species diversity and distribution patterns is fundamental for collecting strategies and the establishment of natural protected areas as well as agrobiodiversity zones, and for management and sustainable use of potato genetic resources.

4.1 Introduction

Ancient American farmers domesticated potato species on the high plateaus of Andean Punas, and also in the lowlands of Southern Chile. The temperament and capacity of these communities, their knowledge of natural diversity and environment, led to the development of a rich culture, reflected in the diversity of their food resources, farming practices, and traditions (Zhang and Rodríguez 2015; De Haan et al. 2019). Andean

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© Springer Nature Switzerland AG 2021
D. Carputo et al. (eds.), *The Wild Solanums Genomes*, Compendium of Plant Genomes,
https://doi.org/10.1007/978-3-030-30343-3_4

farmers not only domesticated potatoes, but also more than 40 species for their subsistence (Parodi 1966; Popenoe et al. 1990) and generated ingenious cultivation methods on the slopes of the high mountains, which still last to this day. This legacy is one of America's great treasures bequeathed to the world, and potatoes are essentials for human food subsistence.

Potatoes were introduced to Europe in the mid-sixteenth century and then its cultivation spread to the whole world (Hawkes 1990; Ames and Spooner 2008). Nowadays, potato is one of the most important crops for human nutrition and health (Burgos et al. 2020), and it is the first tuberous species cultivated worldwide, with an average production of 378,201,964 Ton and a harvested area of 19,062,653 Ha (http://www.fao.org/faostat).

Cultivated potatoes were domesticated from its indigenous relatives. Wild species are native of America distributed from Southwestern United States (latitude 38 °N), Central and South America to Argentina, and adjacent mainland Chile (latitude 41 °S) (Fig. 4.1), with greatest species richness at latitude 21 °S in South America and a secondary center of speciation around 20 °N in the Central Mexican highlands (Hijmans and Spooner 2001; Hijmans et al. 2002). Landraces of cultivated potatoes are grown throughout mid to high (about 3000–3500 m) elevations in the Andes from Northern South America to Northwestern Argentina, and in lowland South-Central Chile, concentrated in the Chonos Archipelago (Fig. 4.2).

Traditionally, potatoes have been included in the genus *Solanum* section *Petota* Dumort., which comprises all wild tuber bearing species and the cultivated potato (*S. tuberosum* L.). A closely related group, *Solanum* section *Etuberosum* (Bukazov & Kameraz.) A. Child, includes three wild non-tuber bearing species but morphologically similar to potatoes (Contreras and Spooner 1999; Spooner et al. 2016).

The taxonomy of potatoes have been difficult to elucidate due to their great diversity along a wide geographic range, ecological adaptation to different habitat, great phenotypic variation that made difficult the interpretation of morphological characters, and also complicated by reproductive features such as interspecific hybridization, introgression, allopolyploidy, prezygotic and postzygotic mechanisms, also a unique mixture of sexual and asexual reproduction, and possible recent species divergence (Ghislain et al. 2006; Rodríguez et al. 2009; Spooner et al. 2004, 2014, 2016, 2019).

Besides the biological processes involved in potatoes evolution and ecological adaptations, early taxonomists who have worked on section *Petota* applied different concepts in their treatments, fundamentally in the criteria to delimitate taxa and number of species, hypotheses of their interrelationships, and interpretations of the hybrid origins of various taxa (Spooner and Van den Berg 1992; Spooner and Salas 2006; Rodríguez et al. 2010; Spooner et al. 2014, 2016, 2019).

More recently comprehensive monographs of section *Petota* and section *Etuberosum* (Spooner et al. 2004, 2016, 2019; Ovchinnikova et al. 2011) revised initial taxonomic treatments, incorporating studies of numerous herbarium specimens, including types, and cultivated representatives of all recognized species. In these comprehensive monographs, it is important to highlight the application of common taxonomic concepts based on phylogeny to elucidate potato diversity. Furthermore, the results of recent morphological and molecular phylogenetic studies have driven us to continuously reduce the number of potato species relative to early taxonomic treatments (Spooner et al. 2004, 2016, 2019; Ovchinnikova et al. 2011).

In the present chapter, we summarize the knowledge of potato species diversity, a taxonomic update including group concept classification and description, species valid names and a complete synonymy, distribution and habitat, as well as the importance of reproductive characters, breeding barriers, interspecific hybridization, gene flow, introgression, polyploidy in potato evolution and ecological adaptation. Additionally, a discussion is included about difficult groups for further taxonomical studies, and possible approaches to clarify and solve taxonomical controversies. The methods and issues

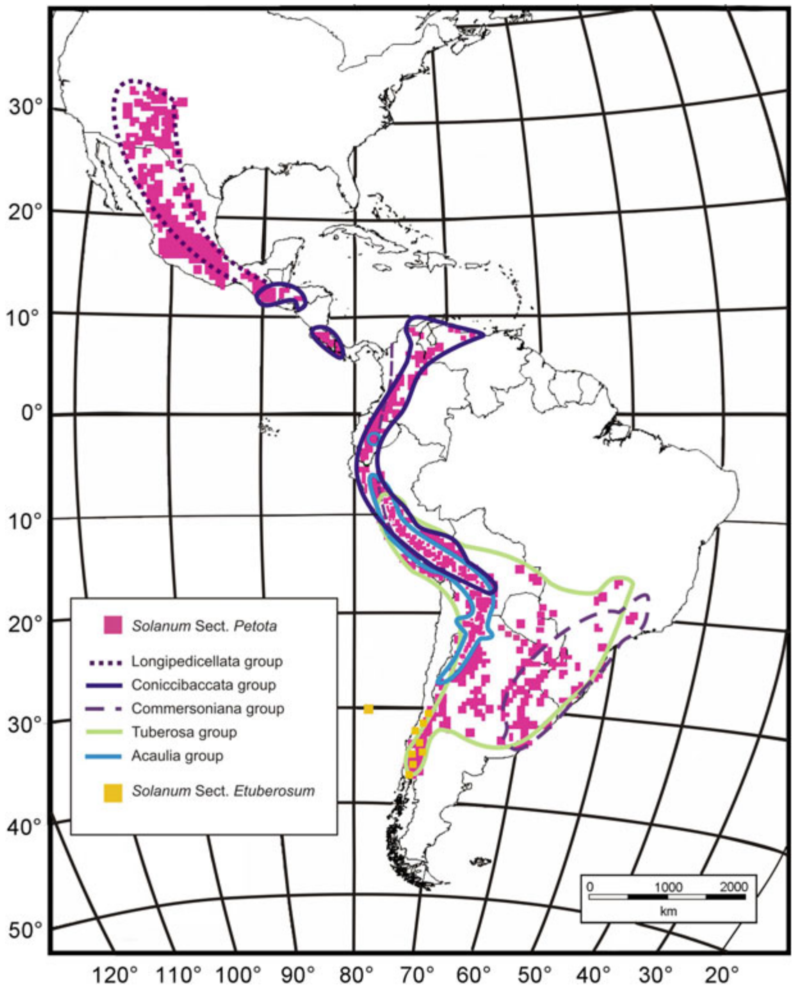

Fig. 4.1 Distribution of wild species of sect. *Etuberosum* and sect. *Petota*, delimited areas were drawn in five most widespread and diverse non-formal groups: Longipedicellata, Conicibaccata, Commersoniana, Tuberosa, and Acaulia

for ex-situ conservation of potato genetic resources are also considered. Finally, the strategies for in situ conservation in natural and agroecological areas are discussed.

4.2 Potato Reproductive Characteristics

The reproductive characteristics of wild potato species and the evidences of natural hybridization phenomena have led botanists to have different taxonomical interpretations that are sometimes conflicting (Spooner and Van den Berg 1992; Spooner and Salas 2006; Spooner et al. 2016, 2019).

All species of section *Etuberosum* and *Petota* have the same basic chromosome number of x = 12. Ploidy refers to the number of chromosome sets in the genome, and Rybin (1929, 1933) first described the polyploid series in wild potatoes (2*x*, 3*x*, 4*x*, 5*x*, 6*x*). Ploidy assessment, summarized in Table 4.1, revealed that the majority (66%) of wild species are diploids (2*x* = 24), but there is also variation in species ploidy (Gavrilenco 2011). Hijmans et al. (2007) determined the geographical and environmental correlations of ploidy for the wild taxa of *Solanum* sect. *Petota*, documented multiple cytotypes in 21 wild species, and found that diploids occupy a larger geographical area, at the northern and southern edges of distribution, than

Fig. 4.2 Distribution of cultivated species: *S. tuberosum* L. with two cultivar groups, the 'Andigenum Group' of upland Andean genotypes with diploid, triploid, and tetraploids, and the 'Chilotanum Group' of lowland tetraploid Chilean landraces, and other three Andean cultivated species *S. ajanhuiri* (diploid), *S. juzepzukii* (triploid) and *S. curtilobum* (pentaploid)

polyploids that most frequently occur in small areas at ecological extremes where higher-level polyploids species occur in colder habitats and triploids in warmer and drier sites than diploid. In Table 4.1, ten diploid species have additional triploid populations with 36 chromosomes ($3x$), and one diploid species also present tetraploid populations with 48 chromosomes ($4x$); two of hybrid origin were found exclusively triploids ($3x = 36$); eleven exclusively tetraploids ($4x = 48$); one exclusively pentaploid ($5x = 60$) and six exclusively hexaploids ($6x = 72$). In few species, populations of diploids and hexaploids, triploids and tetraploids and tetraploids and hexaploids have been detected. Four species have populations with more than one even ploidy level (S. *colombianum, S. andreanum, S. brevicaule* and *S. candolleanum*) (Table 4.1). Triploid and pentaploid populations are generally highly sterile. Ploidy in cultivated potatoes has been also investigated in the *S. tuberosum* Andigenum Group, where no ecogeographical association for the ploidy variants and different habitat was found, while in *S. tuberosum* Chilotanum Group ploidy was related with extreme northern and southern distribution (Spooner et al. 2010).

Genome structure has been analyzed by Matsubayashi (1991) and Gavrilenko (2007, 2011) through various cytological techniques (see also Chap. 2). Additional approaches, like the analysis of orthologous GBSSI genes sequences, showed the first molecular evidence of allopolyploidy in potato (Spooner et al. 2008). Analysis of single-copy genes have been useful to understand genomic complexity, revealing patterns of hybrid origins and allele losses in potato polyploids (Rodriguez and Spooner 2009; Cai et al. 2012). Genome rearrangements in *S. bulbocastanum*, a wild potato species with B genome, were uncovered for the first time when its linkage map was compared with potato and tomato physical maps, and provided a promissory approach for investigation of genome-specific structural chromosome rearrangements between *Solanum* A and B genomes as well as for mapping of agronomical traits (Iorizzo et al. 2014; Mann et al. 2011; Aversano et al. 2015).

Wild potatoes are distributed along a wide geographic range in America, where physical and ecological barriers can prevent gene flow among species. Nevertheless, Camadro et al. (2004) argued that these external factors are not sufficient to explain maintenance of potato species integrity. These authors, based on the evidences of little genome differentiation in potatoes, and also taking into account the lack of interspecific crossing in several sympatric populations, proposed that internal barriers to hybridization may have played a fundamental role in wild potatoes evolution. Interspecific pollen-pistil incompatibility, nuclear-cytoplasmic male sterility, and seed endosperm development are major forces that strengthen geographic and ecological barriers, even though a certain amount of gene exchange could be possible, species remain separate in an evolutionary context (Camadro et al. 2004).

Most diploid potato species are self-incompatible due to a multiallelic S-locus with gametophytic expression (Cipar et al. 1964; Goldberg et al. 2010). The style produces a ribonuclease codified by the S-locus that prevents the normal growth of genetically matching pollen tubes (Dodds et al. 1996; Luu et al. 2000). The S locus has been mapped to chromosome 1 in potato germplasm (Gebhardt et al. 1991) and S-RNase genes have also been mapped in the same chromosome (Rivard et al. 1996). A dominant self-incompatibility inhibitor gene that allows self-pollination has been reported in wild diploid species and mapped to the distal end of chromosome 12 (Hosaka and Hanneman 1998). Interspecific pollen-pistil interaction has been explained by a genetic system of cross incompatibility or incongruity (CI), in which genes interact on a one-to-one basis to allow or prevent hybridization (Hogenboom 1973, 1979). Camadro and Peloquin (1981) proposed a genetic model to explain the isolation in tuber-bearing *Solanum* species and the maintenance of their genetic integrity, with dominant CI genes in styles that prevent fertilization by pollen carrying specific dominant complementary genes. These genetic systems developed during the evolution

Table 4.1 Three species of sect. *Etuberosum*, and 108 epecies of sect. *Petota* are included in non-formal groups, information about countries and regions of occurrence, as well as altitude, ploidy levels, endosperm balance numbers (EBN), and phenology are indicated. Abbreviations are used for the countries: ARG Argentina, BOL Bolivia, BRA Brazil, CHI Chile, COL Colombia, CRI Costa Rica, ECU Ecuador, GUA Guatemala, HON Honduras, MEX México, PAN Panmá, PAR Paraguay, PER Perú, URU Uruguay, USA United States of America, VEN Venezuela, and numbers indicated species quantity

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
ETUBEROSUM	1	*S. etuberosum* Lindl.	CHI	V, VI, VII, VIII, IX Regions	430–2500	$2X$ (1)	December–March
	2	*S. palustre* Schltdl.	ARG CHI	ARG (Neuquén) CHI (V, VIII, IX, X)	40–1170	$2X$ (1)	January–March
	3	*S. fernandezianum* Phil.	CHI	Masatierra Island	100–610	$2X$ (1)	January–March
PETOTA	ACAULIA						
	1	*S. acaule* Bitter	ARG BOL CHI PER	ARG (Catamarca, Jujuy, La Rioja, Salta, San Juan, Tucumán) BOL (Chuquisaca, Cochabamba, La Paz, Oruro, Potosí, Tarija) CHI (II Región) PER (Cajamarca)	2000–4700	$4X$ (2)	December–April
	2	*S. albicans* (Ochoa) Ochoa	ECU PER	ECU (Chimborazo) PER (Cajamarca)	3340–4800	$6X$ (4)	January–May
	3	*S. demissum* Lindl.	GUA MEX	GUA (Huehuetenango, Sacatepequez, Totonicapán), MEX (Aguascalientes, Chiguagua, Distrito Federal, Durango, Hidalgo, México, Michoacán, Morelos, Oaxaca, Puebla, Sinaloa, Sonora, Tlaxcala, Veracruz)	[1900] 2100–3700	$6X$ (4)	August–October
	4	*S.* × *aemulans* Bitter & Wittm.	ARG	Jujuy, La Rioja, Salta, San Juan, Tucumán	2690–4020	$3X$ $4X$ (2)	January–April
	5	*S.* × *brucheri* Correll	ARG	Jujuy	3100–4000	$3X$	
	6	*S.* × *edinense* Berthault	MEX	Distrito Federal, Guanajuato, Hidalgo, México, Michoacán, Puebla, Tlaxcala, Veracruz	2050–3560	$5X$	August–October
	BULBOCASTANA						
	7	*S. bulbocastanum* Dunal	GUA, HON, MEX	GUA (Baja Verapaz, Guatemala, Huehuetenango, Quezaltenango, Sacatepequez, Sololá) HON (La Paz) MEX (Chiapas, Colima, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Tlaxcala, Veracruz)	1200–2300	$2X$ (1) $3X$	July–November
	8	*S. cardiophyllum* Lindl.	MEX	Aguascalientes, Chihuahua, Distrito Federal, Durango, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, Sinaloa, Tlaxcala, Zacatecas	1320–2800	$2X$ (1) $3X$	July–October
	COMMERSONIANA						
	9	*S. commersonii* Dunal	ARG BRA URU	ARG (Buenos Aires, Chaco, Corrientes, Entre Ríos, Misiones) BRA (Rio Grande do Sul, Santa Catarina) URU (Artigas, Canelones, Cerro Largo, Florida, Lavalleja,	0–400	$2X$ (1) $3X$	October–July

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
				Maldonado, Montevideo, Paysandú, Río Negro, Rocha, Salto, San José, Soriano, Tacuarembó)			
PETOTA	10	*S. malmeanum* Bitter	ARG BRA PAR URU	ARG (Buenos Aires, Chaco, Corrientes, Entre Ríos, Formosa, Misiones, Santa Fé) BRA (Rio Grande do Sul) PAR (Boquerón, Central, Cordillera, Itapuá, Presidente Hayes) URU (Colonia, Maldonado, Soriano)	0–330	2*X* (1)	October–July
	CONICIBACCATA						
	11	*S. agrimonifolium* Rydb.	GUA HON MEX	GUA (Chimaltenango, El Progreso, Huehuetenango, Quezaltenango, San Marcos, Sololá, Totonicapán) HON (Morazán) MEX (Chiapas)	1800–3400 [3800]	4*X* (2)	June–March
	12	*S. ayacuchense* Ochoa	PER	Ayacucho	2000–3200	2*X* (2)	February–April
	13	*S. bombycinum* Ochoa	BOL	La Paz	2000–2870	4*X*	February
	14	*S. buesii* Vargas	PER	Cuzco	2400–3700	2*X* (2)	February–September
	15	*S. burkartii* Ochoa	PER	Amazonas, Cajamarca	2600–3350	2*X*	March–July
	16	*S. colombianum* Dunal	COL ECU PER VEN	COL (Antioquia, Boyacá, Caldas, Caquetá, Cauca, Cesar, Cundinamarca, Huila, Nariño, Norte de Santander, Putumayo, Quindío, Risaralda, Santander, Tolima, Valle) ECU (Azuay, Cañar, Carchi, Chimborazo, Cotopaxi, El oro, Loja, Morona-Santiago, Napo, Orellana, Pichincha, Tungurahua, Zamora Chinchipe) PER (Piura) VEN (Apure, Carabobo, Falcón, Mérida, Portuguesa, Táchira, Trujillo)	[1200] 2000–3950	4*X* (2) 6*X* (4)	All year
	17	*S. flahaultii* Bitter	COL	Cundinamarca, Boyacá, Meta, Santander, Cauca	[2500] 3150–3610 [4310]	4*X*	April–August
	18	*S. garcia-barrigae* Ochoa	COL	Santander	3010–3900	4*X*	July–August
	19	*S. laxissimum* Bitter	PER	Ayacucho, Cuzco, Huánuco, Junín, Pasco	[670, 1200] 1700–3580	2*X* (2)	All year
	20	*S. limbaniense* Ochoa	PER	Puno	2900–3750	2*X* (2)	January–April
	21	*S. lobbianum* Bitter	COL	Caldas	3000–3570	4*X* (2)	July
	22	*S. longiconicum* Bitter	CRI, PAN	CRI (Alajuela, Cartago, Guanacaste, Heredia, Limón, Puntarenas, San José), PAN (Chiriquí, Bocas del Toro)	[1050] 1400–3300	4*X*	All year
	23	*S. nubicola* Ochoa	PER	Huánuco, La Libertad	3260–3600	4*X* (2)	April–May
	24	*S. oxycarpum* Schiede	MEX	Hidalgo, Oaxaca, Puebla, Veracruz		4*X* (2)	

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
					[1520] 1870–2870		July–November
	25	*S. pillahuatense* Vargas	PER	Apurímac, Cuzco	2700–3700	2*X* (2)	January–March
PETOTA	26	*S. rhomboideilanceolatum* Ochoa	PER	Ayacucho, Junín	2100–3100	2*X* (2)	January–April
	27	*S. salasianum* Ochoa	PER	Huánuco	2600–3000	2*X*	March–May
	28	*S. violaceimarmoratum* Bitter	BOL PER	BOL (Cochabamba, La Paz) PER (Cuzco)	1800–3800	2*X* (2)	January–October
	29	*S. woodsonii* Correll	PAN	Chiriquí	3000–3500		All year
	IOPETALA						
	30	*S. guerreroense* Correll	MEX	Guerrero	2800–3000	6*X* (4)	July–December
	31	*S. hougasii* Correll	MEX	Colima, Guerrero, Jalisco, Michoacan	1600–3135	6*X* (4)	August–December
	32	*S. iopetalum* (Bitter) Hawkes	MEX	Distrito Federal, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Querétaro, Tlaxcala, Veracruz	1700–3350	6*X* (4)	July–November
	33	*S. schenckii* Bitter	MEX	Oaxaca, Puebla, Querétaro, Veracruz	[1780] 2420–2900 [3700]	6*X* (4)	August–October
	LONGIPEDICELLATA						
	34	*S. hjertingii* Hawkes	MEX	Coahuila, Nuevo León, San Luis Potosí, Tamaulipas	[1230] 1650–3210	4*X* (2)	July–October
	35	*S. stoloniferum* Schltdl.	MEX USA	MEX (Aguascalientes, Baja California Sur, Chihuahua, Coahuila, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tlaxcala, Veracruz) USA (Arizona, Colorado, New Mexico, Texas)	[1040] 1440–3400 [3700]	4*X* (2)	USA: July–September MEX: July–November
	36	*S.* × *vallis-mexici* Juz.	MEX	Distrito Federal	2280–3000	3*X*	July–October
	MEGISTACROLOBA						
	37	*S. boliviense* Dunal	ARG BOL PER	ARG (Catamarca, Jujuy, Salta, Tucumán) BOL (Chuquisaca, Cochabamba, La Paz, Oruro, Potosí, Santa Cruz, Tarija) PER (Apurímac, Cusco)	1600–4270	2*X* (2)	
	38	*S. hastiforme* Correll	PER	Amazonas, La Libertad, Ancash	[2850] 3200–3900 [4700]	2*X* (2)	March–May

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
	39	*S. raphanifolium* Cárdenas & Hawkes	PER	Cuzco, Apurimac, Puno	[2000] 2700–4200 [4500]	2*X* (2)	January–April
	40	*S. sogarandinum* Ochoa	PER	Cajamarca, Lima	2800–4100	2*X* (2) 3*X*	January–March
PETOTA	*MORELLIFORME*						
	41	*S. clarum* Correll	GUA, MEX	GUA (Huehuetenango, Quezaltenango, Sacatepequez, San Marcos, Sololá, Totonicapán) MEX (Chiapas)	2740–3800	2*X*	July–November
	42	*S. morelliforme* Bitter & Muench	BOL GUA HON MEX	BOL (La Paz) GUA (Chimaltenango, Huehuetenalgo, Quetzaltenango, Quiché, San Marcos, Totonicapán) HON (Morazán) MEX (Chiapas, Guerrero, Hidalgo, México, Michoacán, Oaxaca, Puebla, Querétaro, Veracruz)	1600–3050	2*X*	July–October
	PINNATISECTA						
	43	*S. jamesii* Torr.	MEX, USA	MEX (Chihuahua, Querétaro, San Luis Potosí, Sonora) USA (Arizona, Colorado, Nebraska, New Mexico, Texas, Utah)	1370–2870	2*X* (1)	June–October
	44	*S. pinnatisectum* Dunal	MEX	Guanajuato, Jalisco, Michoacán, Querétaro	1500–2200	2*X* (1)	July–September
	45	*S.* × *michoacanum* (Bitter) Rydb.	MEX	Michoacán	1900–2100	2*X*	July–September
	46	*S.* × *sambucinum* Rydb.	MEX	Guanajuato, Querétaro	1720–2200	2*X*	August–October
	PIURANA						
	47	*S. acroglossum* Juz.	PER	Huánuco, Pasco	2025–3800	2*X* (2)	January–May
	48	*S. acroscopicum* Ochoa	PER	Arequipa, Ayacucho, Cajamarca, Tacna	2350–3900	2*X*	February–June
	49	*S. albornozii* Correll	ECU	Azuay, Loja	2350–3400	2*X* (2)	March–July
	50	*S. anamatophilum* Ochoa	PER	Ancash	1720–2800	2*X* (2)	March–May
	51	*S. andreanum* Baker	COL ECU	COL (Nariño, Putumayo) ECU (Azuay, Bolívar, Cañar, Carchi, Cayambe, Chimborazo, Cotopaxi, Imbabura, Loja, Morona Santiago, Napo, Orellana, Pichincha, Santiago-Zamora, Sucumbíos, Tungurahua)	Diploid populations: 1900–3700 Polyploid populations: 2200–4000	2*X* (2) 4*X* (4)	Mainly April–July but all year
	52	*S. augustii* Ochoa	PER	Ancash	3200–3800	2*X* (1)	April–May
	53	*S. cajamarquense* Ochoa	PER	Cajamarca	2200–3000	2*X* (1)	March–May

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
	54	*S. cantense* Ochoa	PER	Ancash, Lima	2350–3400	2*X* (2)	March–May
	55	*S. chilliasense* Ochoa	ECU	El Oro	3200–3450	2*X* (2)	April–May
	56	*S. chiquidenum* Ochoa	PER	Ancash, Cajamarca, Huánuco, La Libertad	[420] 2000–3500 [3700]	2*X* (2)	March–June
PETOTA	57	*S. chomatophilum* Bitter	ECU PER	ECU (Azuay, Pichincha) PER (Amazonas, Ancash, Cajamarca, Huánuco, La Libertad, Lima, Junín, Pasco, San Martín)	1950–4500 [4800]	2*X* (2)	Mainly March–June but all year
	58	*S. contumazaense* Ochoa	PER	Cajamarca	2150–2900	2*X* (2)	April–June
	59	*S. dolichocremastrum* Bitter	PER	Ancash, Huánuco	3400–4400	2*X* (1)	February–May
	60	*S. huancabambense* Ochoa	PER	Cajamarca, Lambayeque, Piura	1650–3000 [3460]	2*X* (2)	February–June
	61	*S. humectophilum* Ochoa	PER	Amazonas	2800–3200	2*X* (1)	March–May
	62	*S. hypacrarthrum* Bitter	PER	Ancash, Cajamarca, Lima	1800–3800	2*X* (1)	March–June
	63	*S. immite* Dunal	PER	Cajamarca, Lima	Lomas: 80–480 Mountains: 1650–3160	2*X* (1) 3*X*	Lomas: August–October Uplands: March–June
	64	*S. minutifoliolum* Correll	ECU	Napo, Cañar	1200–3400	2*X* (1)	December–August
	65	*S. mochiquense* Ochoa	PER	Piura, Lima	Lomas: 150–800 Mountains: 1170–3000	2*X* (1)	Lomas: August–October Uplands: March -May
	66	*S. multiinterruptum* Bitter	PER	Ancash, Huancavelica, Lima	2675–3900	2*X* (2)	March–May
	67	*S. olmosense* Ochoa	ECU PER	ECU (Loja) PER (Lambayeque)	1200–2650	2*X* (2)	March–May
	68	*S. paucissectum* Ochoa	PER	Cajamarca, Piura	2350–3360	2*X* (2)	February–May
	69	*S. piurae* Bitter	PER	Piura	2000–3360	2*X* (2)	April–June

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
	70	*S. raquialatum* Ochoa	PER	Piura	[1350] 1900–3100	2*X* (1)	March–June
	71	*S. scabrifolium* Ochoa	PER	Huánuco	2800–3340	2*X*	March–April
	72	*S. simplicissimum* Ochoa	PER	Lima	1600–2720	2*X* (1)	January–April
	73	*S. trinitense* Ochoa	PER	Cajamarca	2700–3450	2*X* (1)	April–June
PETOTA	74	*S. wittmackii* Bitter	PER	Lima	Lomas: 30–480 Mountains: 2200–3400	2*X* (1)	Lomas: July–October Uplands: March–May
	75	*S.* x*blanco-galdosii* Ochoa	PER	Ancash, Cajamarca, La Libertad	2700–3260	2*X* (2)	February–June
	POLYADENIA						
	76	*S. lesteri* Hawkes & Hjert.	MEX	Oaxaca	2100–2390	2*X*	September–October
	77	*S. polyadenium* Greenmam	MEX	Hidalgo, Jalisco, México, Michoacán, Oaxaca, Puebla, Querétaro, Veracruz	1900–2900	2*X*	August–October
	STENOPHYLLIDIA						
	78	*S. hintonii* Correll	MEX	Colima, Guanajuato, México, Querétaro	1700–2800	2*X* (1)	August–October
	79	*S. stenophyllidium* Bitter	MEX	Aguascalientes, Chihuahua, Durango, Jalisco, México, Michoacán, Nayarit, Sonora, Zacatecas	[1100] 1380–2500	2*X* (1)	July–September
	80	*S. ehrenbergii* (Bitter) Rydb.	MEX	Aguascalientes, Distrito Federal, Guanajuato, Hidalgo, Jalisco, México, Michoacán, Nayarit, Puebla, Queretaro, San Luis Potosí, Zacatecas	[800] 1450–2500	2*X* (1)	July–October
	STIPULOIDEA						
	81	*S. stipuloideum* Rusby	BOL	Chuquisaca, Cochabamba, La Paz, Santa Cruz	2000–4000	2*X* (1)	December–April
	82	*S. neocardenasii* Hawkes & Hjert.	BOL	Santa Cruz	1400–1700	2*X* (2)	January–February
	TRIFIDA						
	83	*S. tarnii* Hawkes & Hjert.	MEX	Hidalgo, Querétaro, Veracruz	2000–2600	2*X*	September–October

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
	84	*S. trifidum* Correll	MEX	Jalisco, Michoacán	[1800] 2000–2800 [3050]	2*X* (1)	July–October
	TUBEROSA						
	85	*S. amayanum* Ochoa	PER	Huancavelica	3000–3900	2*X* (2)	January–March
	86	*S. ancophilum* (Correll) Ochoa	PER	Ancash, La Libertad	[2600] 3000–3800	2*X* (2)	March–May
PETOTA	87	*S. berthaultii* Hawkes	ARG BOL	ARG (Jujuy, Salta) BOL (Chuquisaca, Cochabamba, La Paz, Potosí, Santa Cruz, Tarija)	1200–3950	2*X* (2) 3*X*	January–March
	88	*S. brevicaule* Bitter	ARG BOL	ARG (Catamarca, Jujuy, La Rioja, Salta, San Juan) BOL (Chuquisaca, Cochabamba, La Paz, Oruro, Potosí, Santa Cruz, Tarija)	1500–4180	2*X* (2) 4*X* (4) 6*X* (4)	January–April
	89	*S. candolleanum* Berthault	BOL PER	BOL (La Paz, Santa Cruz) PER (Ancash, Huánuco)	1600–4400	2*X* (2) 6X (4)	January–March
	90	*S. chacoense* Bitter	ARG BOL BRA PAR PER URU	ARG (Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Formosa, Jujuy, La Pampa, La Rioja, Misiones, Salta, San Luis, Santa Fé, Santiago del Estero, Tucumán) BOL (Chuquisaca, Cochabamba, La Paz, Potosí, Santa Cruz, Tarija) BRA (Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo) PAR (Alto Paraguay, Alto Paraná, Amambay, Boquerón, Caaguazú, Caazapá, Central, Concepción, Cordillera, Gran Chaco, Guairá, Itapuá, Paraguarí, Presidente Hayes, San Pedro) PER (Puno) URU (Montevideo, Canelones, Florida)	0–3700	2*X* (2) 3X 4*X*	All year
	91	*S. gandarillasii* Cárdenas	BOL	Chuquisaca, Cochabamba, Santa Cruz	1450–3000	2*X* (2)	February–March
	92	*S. gracilifrons* Bitter	PER	Huancavelica	1200–2700	2*X*	January–March
	93	*S. incasicum* Ochoa	PER	Cuzco	[2000] 3700–3800	2*X* (2)	February–March
	94	*S. infundibuliforme* Phil.	ARG BOL	ARG (Jujuy, Salta) BOL (Cochabamba, La Paz, Potosí, Tarija)	2350–4300	2*X* (2) 3*X*	January–April
	95	*S. kurtzianum* Bitter & Wittm.	ARG	Catamarca, La Rioja, Mendoza, San Juan	750–3000	2*X* (2) 3*X*	January–May
	96	*S. lignicaule* Vargas	PER	Cuzco	2510–3460	2*X* (1)	January–April
	97	*S. maglia* Schltdl.	ARG CHI	ARG (Mendoza) CHI (IV, V, VIII Regions)	1630–1820	2*X* 3*X*	

(continued)

Table 4.1 (continued)

Section		Wild Species	Distribution (Countries)	Distribution (Regions)	Altitude (m)	Ploidy (EBN)	Phenology (Flowering & Fruiting)
							CHI lowlands: all year ARG uplands: January–March
	98	*S. medians* Bitter	CHI PER	CHI (I, II Regions) PER (Ancash, Arequipa, Lima, Tacna)	200–3800	2*X* (2) 3*X*	Coast: May–October Andes: November–April
PETOTA	99	*S. microdontum* Bitter	ARG BOL	ARG (Catamarca, Jujuy, La Rioja, Tucumán, Salta) BOL (Chuquisaca, Cochabamba, La Paz, Tarija)	1400–3850	2*X* (2)	December–June
	100	*S. neorossii* Hawkes & Hjert.	ARG	Jujuy, Salta	2530–3800	2*X* (2) 3*X*	January–March
	101	*S. neoweberbaueri* Wittm.	PER	Lima	200–750	3*X*	October
	102	*S. okadae* Hawkes & Hjert.	BOL	Chuquisaca, Cochabamba, La Paz	2450–3200	2*X* (2)	February–March
	103	*S. velardei* Ochoa	PER	Apurimac, Cuzco	[1800] 2450–3400	2*X*	February–May
	104	*S. venturii* Hawkes & Hjert.	ARG	Catamarca, Jujuy, La Rioja, Salta, Tucumán	1900–3000	2*X* (2)	December–March
	105	*S. vernei* Bitter & Wittm.	ARG	Catamarca, Jujuy, Salta, Tucumán	2270–3600	2*X* (2)	December–April
	106	*S.* × *doddsii* Correll	BOL	Chuquisaca, Cochabamba, Santa Cruz	2050–2600	2*X* (2)	January–March
	107	*S.* × *rechei* Hawkes & Hjert.	ARG	La Rioja	1200–3950	2*X* (2) 3*X*	January–March
	VERRUCOSA						
	108	*S. verrucosum* Schltdl.	MEX	Coahuila, Distrito Federal, Gunajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nuevo Leon, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tamaulipas, Tlaxcala, Veracruz	[1870] 2100–3500 [4000]	2*X* (2)	June–November

of sympatric species at the pollen-pistil level. Polyploid species are self-compatible due to a "competition interaction" that either reduce or suppress the incompatibility reaction that occurs in pollen grains carrying different S-alleles (Frankel and Galun 1977). Tetraploid and hexaploid species (with the exception of tetraploid forms of *S. andreanum*) are capable of self-fertilization (Hawkes 1990). When diploid self-incompatible potato species are induced to chromosome doubling produces self-compatible tetraploids (Stout and Chandler 1941; Ross 1986). Interestingly, in these tetraploids, pollen tube growth is inhibited when pollen is homozygous for S alleles, but not when it is heterozygous (Lewis 1943, 1947).

Male sterility of hybrid plants is an important post-zygotic isolating mechanism in natural potato species populations. Cytoplasmic-genetic male sterility occurs when dominant nuclear genes from the male parent interact with sensitive cytoplasm from the female parent (Hermundstad and Peloquin 1985; Tucci et al. 1996). Male sterility has been reported in several F1 hybrids derived from crosses involving various wild and cultivated species (Lamm 1941, 1953; Brown 1984; Hermundstand and Peloquin 1985; Tucci et al. 1996, Santini et al. 2000; Carputo et al. 2003a) and between cultivated potatoes (Grun 1973; Hanneman and Peloquin 1981). Genetic and environmental conditions can influence the expression of cytoplasmic-genetic male sterility (Hanneman and Peloquin 1981). Hybrids lacking sensitive cytoplasm or nuclear male sterility genes are male-fertile (Iwanaga et al. 1991; Tucci et al. 1996).

In Angiosperms the development of viable seed depends on double fertilization that generates a diploid embryo and triploid endosperm. The endosperm contains two genomes of the maternal parent and one genome of the paternal parent. Intraspecific, intraploidy crosses in potato typically produce viable seeds containing well-developed endosperm, on the contrary, in most interploidy crosses, seeds are inviable due to endosperm failure (Friedman 1998). Normal endosperm development in potato requires a 2:1 maternal: paternal ratio of a set of genes called endosperm balance factors (Johnston and Hanneman 1980, 1982, 1996). Viable seeds could be generated from crosses between plants that produce gametes with the same endosperm balance number (EBN), resulting in a 2:1 maternal:paternal ratio of endosperm balance factors after male gamete fusion with two nuclei of the central cell to produce triploid endosperm, and consequently allowed further development of a normal embryo. The EBN is an arbitrary value, which is not necessarily a direct indication of species ploidy, assigned to each *Solanum* species based on its behavior in crosses with EBN standards and on the assumption that the 2:1 ratio is essential for normal endosperm development (Hanneman 1994). The ploidy and endosperm balance number combinations in potato are 6x (4EBN), 4x(4EBN), 4x(2EBN), 2x(2EBN) and 2x(1EBN) (Table 4.1). However, endosperm development may also fail in some intraploidy, interspecific crosses, while some interploidy crosses could succeed. The nature of these endosperm balance factors is not yet known, but nuclear genetic models have been proposed (Ehlenfeldt and Hanneman 1988; Camadro and Masuelli 1995).

Wild and cultivated potatoes have meiotic mutants that result in the production of unreduced (2n) gametes (Carputo et al. 2003b). Some meiotic mutations produce 2n eggs (Stelly and Peloquin 1986; Werner and Peloquin 1991), while others produce 2n pollen (Quinn et al. 1974). The fusion of unreduced (2n) gametes during fertilization explain the occurrence of spontaneous polyploidization in wild plant populations (Harlan and de Wet 1975; Veilleux 1985; Bretagnolle and Thompson 1995). Unreduced gametes can be detected microscopically, since diploid pollen grains are larger than monoploid pollen grains (Quinn et al. 1974) and 2n eggs can be identified with stain-clearing techniques (Stelly et al. 1984). Unreduced gametes facilitate the evolution of polyploids by allowing interspecific hybridization across ploidy levels (Mason and Pires 2015). Nevertheless, triploid seeds resulting from the union of an n and a 2n gamete are generally inviable due to endosperm failure (Kohler et al. 2009). Camadro et al. (2004) pointed out the complementary role of EBN and unreduced gametes, not only because it facilitates interspecific gene introgression but also because it maintains the ploidy integrity of the two parental species. Den Nijs and Peloquin (1977) and more recently by Carputo et al. (2003b) proposed an evolutionary scenario for potatoes where n and 2n gametes link together all ploidy and EBN levels, thereby providing an opportunity for gene flow throughout sympatric species with different EBN and chromosome numbers (Camadro et al. 2004). Hawkes (1962) considered that introgression and interspecific hybridization that not led to speciation seems to be a common phenomenon throughout the range of section *Petota*. The lack of strong biological isolating mechanisms, morphologically intermediate characteristics in natural populations, and sympatry of many species suggest that much of the taxonomic confusion in section *Petota* is due most probably to frequent gene flow among the species (Spooner et al. 2019). Interestingly, Rabinowitz et al. (1990) documented high levels of gene flow between wild and cultivated species in Peru, supporting Ugent's hypotheses who proposed that cultivated species were formed and genetically enriched by gene flow from the wild species (Ugent 1970). Traditional Andean farming systems incorporate natural hybrids between cultivated potatoes and the wild potato relatives growing in their surrounding fields (Brush et al. 1981). The unique reproductive characteristics of tuber-bearing potatoes allow to incorporate new genetic combinations by sexual reproduction, while asexual reproduction maintains adapted gene complexes (Spooner et al. 2019).

In natural potato populations, several biological internal barriers such us pollen-style interactions, male sterility, and endosperm failure, prevent the production of interspecific hybrids and maintain the integrity of sympatric species (Camadro et al. 2004). However, on the other side of an evolutionary perspective, the wide natural occurrence of unreduced gametes, self-incompatibility, and little genome differentiation among potato species favor hybridization between wild *Solanum* species (Erazzú et al. 2009; Masuelli et al. 2009; Ispizúa et al. 2015).

Potato wild relatives are critical natural resources that serve as a model system for genebank conservation (Jansky et al. 2013; Bethke et al. 2019). The understanding of several biological mechanisms allows the use of wild species in potato breeding. The introduction of diploid wild potato genes to the tetrahaploid cultivated species has been successfully carried out using various breeding methods and strategies such as haploid production (Peloquin et al. 1989a), the use of unreduced gametes (Mendiburu and Peloquin 1977, Peloquin et al. 1989b, 1996, 2008), the application of the balance of endosperm value to produce hybrids (Johnston and Hanneman 1980, 1982; Hanneman 1994), and the use of embryo rescue techniques and somatic fusion of protoplasts. Carputo and Frusciante (2011) highlighted the classical genetics and traditional approaches applied in potato crop improvement. New insights from genomic research provided promissory methods to explore a wide pool of genetic resources that include not only wild species but also landraces, and increase the efficiency of identifying and introgressing alleles rather than traits (Iorizzo et al. 2014; Mann et al. 2011; Potato Genome Sequencing Consortium 2011; Bethke et al. 2019; Ghislain and Douches 2020).

In the context of present knowledge, wild species have shown their enormous value as a source of traits of agronomic importance and resistances to biotic and abiotic factors for crop improvement (Ross 1986; Hanneman, 1999; Kuhl 2011; Watanabe 2015; Bonierbale et al. 2020; Ortiz 2020). Nevertheless, few wild species have been used in breeding. A better comprehension of wild potato diversity and ecological adaptation, taxonomy, and relationships, and the application of new promissory methods will also contribute to their utilization as models to understand genetic and genomic evolution as well as in cultivated potato improvement (Hardigan et al. 2017) (see other chapters).

4.3 Taxonomy of Potato Species (Section *Petota*) and Close Related Non Tuberous Species (Section *Etuberosum*)

Classical treatments of Bukasov (1978), Correll (1962), Gorbatenko (1989, 2006), Hawkes and Hjerting (1969, 1989), Ochoa (1990, 1999, 2001) and Hawkes (1990), proposed taxa delimitation mainly based on morphological species concept (Spooner and Van der Berg 1992). Hawkes (1990) also considered species intercrossability, and his taxonomic treatment of section *Petota* has been the most comprehensive and traditionally used, where he recognized 228 wild species and seven cultivated species, grouped into 21 Series. Taxonomic treatments differ in author's concepts and interpretation of taxonomic rank used to establish species, botanical varieties or subspecies, hypotheses about species hybrid origin and introgression with other species, as well as the criteria to define the arrangement and number of taxonomical series, the number of species in each series, and the different affiliation of species to these series (Spooner and Van den Berg 1992; Spooner and Hetterscheid 2005; Spooner and Salas 2006).

It is interesting to compare taxonomic interpretations of two sister phylogenetic lineages of genus *Solanum*, potatoes and tomatoes, that separated earlier about eight Ma and later section *Petota* started diversifying around seven Ma (Särkinen et al. 2013). Prevalent taxonomical interpretation (Hawkes 1990) considers more than 200 wild potato species in contrast with the 13 species of tomatoes (Sect. *Lycopersicon*) and four species in the most related groups (Sect. *Juglandifolia* and *Lycopersicoides*) (Peralta et al. 2008). This enormous differences in the interpretation of diversity in sister groups can be explained by the unique reproductive characteristics, genetic structure, and ecological adaptations of potatoes in a wide geographic area. However, another non biological explanation are the concepts to circumscribe species and a complex nomenclature system initially used by potato taxonomists that cause an overestimation of natural diversity (Peralta et al. 2008).

A different philosophy and consistent application of a comprehensive criteria have driven to continuously reduce the number of potato species relative to early taxonomic treatments (Hijmans and Spooner 2001; Spooner and Salas 2006; Ames and Spooner 2010; Fajardo and Spooner 2011; Spooner et al. 2004, 2014, 2016, 2019). More recently comprehensive treatments of section *Petota* and section *Etuberosum* (Spooner et al. 2004, 2016, 2019) not only revised early taxonomical contribution, but also applied a taxonomical integrative approach using different sources of evidences mainly based on phylogeny to propose new group classification. These 3 monographs treated the complete diversity of tuber bearing and stoloniferous wild species in America, based on the analysis of numerous herbarium specimens, including types, and field assessment of cultivated representatives of all recognized species. Other relevant evidences of recent morphological, reproductive and cladistics molecular studies were integrated into these comprehensive treatments. A similar approach has been used to describe wild potato diversity for regional or country Floras (Spooner et al. 2009; Clausen et al. 2013).

The classification of potatoes based on a phylogenetic approach clarified evolutionary relationships, and the recognition of close related cluster of organisms by a parental pattern of ancestry and descent, and diagnosable distinct from other clusters (Cracraft 1989). Most methods for studying cladistics have been based on models of strictly branching cladogeny, however, in complex groups with possible reticulate evolution at chromosomal, genomic and species levels inference of relationships could fail when modeled by a bifurcating tree. Classification of wild potatoes is a difficult goal, since interpretation of relationships is complicated by introgression, interspecific hybridization, auto- and allopolyploidy, sexual incompatibility among many species, a mixture of sexual and asexual reproduction, possible recent species divergence, phenotypic plasticity, and consequent great morphological similarity among species (Spooner and van den Berg 1992; Spooner et al. 2014; Camadro et al. 2004; Camadro 2012). Further phylogenetic analysis using models of reticulated evolution in potatoes, a complex group with hybridization and introgression phenomena, could elucidated their relationships.

The relationships between Sect. *Petota* and Sect. *Etuberosum* have been a subjet of debate. Initially Juzepczuk and Bukasov (1929) included non-tuber-bearing species in ser. Etuberosa within Sect. *Petota* [then referred to as Sect. Tuberarium (Dunal) Bitter]. Morphological similarities of *Solanum* species in Sect. *Petota* and Sect. *Etuberosum* led to considered them as closest relatives. Nevertheless, several concordant molecular studies have clarified relationships among these *Solanum* sections, supporting tomatoes (Sect. *Lycopersicon*) and close related species (sects. *Juglandifolia* and *Lycopersicoides*) as a monophyletic sister clade to Sect. *Petota*, with Sect. *Etuberosum* sister to all the above (Spooner et al. 2016, 2019). These relationships have been corroborated by plastid phylogenies (Spooner et al. 1993; Olmstead and Palmer 1992, 1997; Bohs and Olmstead 1997, 1999; Olmstead et al. 1999), nuclear genes and conserved orthologous sequences phylogenies (Peralta and Spooner 2001; Rodríguez and Spooner 2009; Rodríguez et al. 2009) and recently by seven regions (five plastids and two nuclear) used to generate the Solanaceae megaphylogeny (Särkinen et al. 2013). Further phylogenetic analysis of large data set could test the hypothesis of relationships between Sect. *Petota* and Sect. *Etuberosum*. Within genus *Solanum*, sects. *Etuberosum*, *Petota*, *Juglandifolia*, *Lycopersicoides*, and *Lycopersicon* are all members of a New World broader group of species informally named the Potato Clade (Tepe et al. 2016; Bohs 2005; Särkinen et al. 2013).

We summarized our actual comprehensive taxonomy of Sections *Petota* and *Etuberosum*, including species distributions and habitat, ploidy, and EBN numbers, and phenology (Table 4.1; Fig. 4.1), as well as a complete list of accepted names, synonyms (450), and the inclusion of species in non-formal groups (Tables 4.1 and 4.2). These provisional taxonomic groups are based on hypothesis of phylogenetic relationships among species that reflect the evolutionary history of potatoes, and pending from more data to elucidate interrelationships. Similar non-formal group systems of classification have been widely applied to *Solanum* by Whalen (1984), Bohs (1994, 2005), Knapp (1991, 2000, 2002, 2008, 2013), Peralta et al. (2008), and Spooner et al. (2004, 2016, 2019). These non-formal groups should not be confused with "Groups", which are category taxonomic names for groups of cultivated plants (ICNCP 2016). Non-formal groups in section *Petota* are detailed in Tables 4.1 and 4.2, and the most widespread ones are represented in Fig. 4.1. Detailed morphological description of the accepted wild species, synonyms, taxonomic keys, illustrations, locality distributions, habitat, phenology, uses, and taxonomic characteristics, as well as a detailed explanation of non-formal groups, are found in the three monographic treatments of Spooner and collaborators (2004, 2016, 2019), information that has been also incorporated in the Solanaceae Source website (http://www.solanaceaesource.org).

SECT. *ETUBEROSUM* (Bukasov & Kameraz) A. Child: comprises three species confined to southern South America, erect to ascending herbs that possess thickened rhizomes, from which arise thin stolons but lacking tubers (Tables 4.1 and 4.2; Fig. 4.1).

SECT. *PETOTA* Dumortier: comprises 108 wild herbaceous species (Tables 4.1 and 4.2), erect to ascending, sometimes forming a rosette or semi-rosette, bearing tubers at the ends of stolons. A large geographical distribution of wild potato species from the southwestern United States (latitude 38 °N), Central and South America to Argentina, and adjacent mainland in Chile (39 °S) (Fig. 4.1) indicates a varied range of ecological diversity as well as adaptations to extreme climatic conditions; these species can be found from sea level at both Atlantic and Pacific oceans, and from high altitude deserts to rainforests (Hawkes 1990; Spooner and Hijmans 2001; Hijmans et al. 2002; Spooner et al. 2004, 2016, 2019). Some are widespread such as *S. acaule*, *S. brevicaule* and *S. chacoense* while others, with a restricted range and an endemic nature, are found in areas with specific ecological conditions. *Solanum chacoense*, *S. palustre* and *S. commersonii* are found at very low altitudes, frequently at sea level, while *S. acaule*, *S.* × *aemulans*, *S. brevicaule* and *S. boliviense* and *S. candolleanum*, reach more than 4000 m in the Andes. *Solanum morelliforme* is mainly restricted to Central Mexico, Guatemala, and Honduras but a single population has been identified 4000 km south in Bolivia. This is the only species in sect. *Petota*, growing in both Central and South America (Simon et al. 2011). Cultivated species present a more restricted geographical distribution, from northern South America and down to southern Chile (Fig. 4.2).

Wild potatoes are classified into 16 non-formal species groups (Spooner et al. 2004, 2016, 2019).

ACAULIA GROUP: three species and three nothospecies species with rosette to semi-rosette habit, in some cases erect and taller, typical flower pedicel with articulation appearing toward the distal end or no articulated (*S. acaule*), all polysomic polyploids, distributed in Mexico and Central America, and in South America from Ecuador to Argentina reaching the high puna plateau and possessing high frost tolerance (Vega and Bamberg 1995).

BULBOCASTANA GROUP: *S. bulbocastanum* and *S. cardiophyllum* are characterized by cream to light yellow corollas, diploids and triploids with and EBN = 1, distributed in Guatemala, Honduras, and Mexico (Spooner et al. 2004).

COMMERSONIANA GROUP: *S. commersonii* and *S. malmeanum* possess characteristic stellate corollas, diploids and triploids (*S. commersonii*) with EBN = 1, distributed in Argentina, Brasil, Paraguay, and Uruguay. Both are partially sympatric and are likely sister taxa (Spooner et al. 2016).

CONICIBACCATA GROUP: 19 species characterized by non-glossy parallel shaped leaves, with the distal-most lateral leaflet pairs diminishing toward the leaf base, and typical conical fruits (Spooner et al. 2019; Fajardo and Spooner 2011), diploids, tetraploids, and hexaploids (S. *colombianum*) with EBN = 2 or 4, distributed in Central America and South America from Venezuela to Bolivia.

IOPETALA GROUP: four species distributed in Mexico, polysomic polyploids with 6x(4EBN) crossability, and with no clear morphological characters uniting them, probably because they could have multiple origins (Spooner et al. 2004).

LONGIPEDICELLATA GROUP: two species and one nothospecies, with 4x(2EBN) crossability, but there are no clear specific morphological characters defining them, distributed from the Southwestern U.S.A to South Mexico.

MEGISTACROLOBA GROUP: four species, herbaceous low-growing rosette plants, with terminal leaflets much larger than the lateral leaflets and with the proximal leaflets reduced in size and often broadly decurrent on the rachis, diploids, and also triploids with EBN = 2, distributed in Peru, Bolivia, and northern Argentina.

MORELLIFORME GROUP: *S. morelliforme* and *S. clarum*, small plants with stellate corollas. *Solanum clarum* is present in Guatemala and Mexico, and *S. morelliforme* in Mexico to Guatemala but with a disjunct population in Bolivia (Spooner and Sytsma 1992).

PINNATISECTA GROUP: two species and two nothospecies, characterized by the presence of pinnatifid pseudostipules, diploids, distributed from southern U.S.A. to Mexico (Lara Cabrera and Spooner 2004).

PIURANA GROUP: 29 species, the majority with moniliform tubers and coriaceous, glabrous to subglabrous shiny or glossy leaves (Ames and Spooner 2010), diploids, also triploids, and tetraploids with EBN = 1, 2, or rare 4, distributed in Colombia, Ecuador, and Peru.

POLYADENIA GROUP: two species identified by their glandular leaves (type A trichrome) and strong odor, diploids, distributed in México (Lara Cabrera and Spooner 2004, Spooner et al. 2004).

STENOPYLLIDIA GROUP: three species with typical lunate pseudostipules and with triangular to conical fruits, diploids with EBN = 1, restricted to Mexico (Spooner et al. 2004).

STIPULOIDEA GROUP: *S. stipuloideum* and *S. neocardenasii*, diploids endemic to Bolivia, with typical white corollas (Spooner et al. 2016).

TRIFIDA GROUP: two endemic, diploid, Mexican species supported by cpDNA data (Spooner and Sytsma 1992) and AFLP data (Lara Cabrera and Spooner 2004).

TUBEROSUM GROUP: 21 species and two nothospecies, with dissected leaves, round fruits, and rotate-pentagonal corollas, diploids, triploids, tetraploids, and hexaploids with EBN = 1, 2 or 4, widely distributed in South America (Spooner et al. 2007). Also includes the cultivated potatoes (Table 4.3).

VERRUCOSA GROUP: *S. verrucosum,* distinguished by the corollas with the edges inrolled dorsally and often with berries with raised white dots, diploid species with 2EBN, widely distributed throughout Mexico.

Although provisional taxonomic groups attempt to reflect phylogenetic relationships in sect P*etota*, they are hypothesis that needs further investigations. In South America some *taxa* have been difficult to understand, like *S. boliviense* Dunal initially considered in Acaulia group (Spooner et al. 2016) but recently included in Megastricoloba group (Spooner et al. 2019), provisionally accepted here. Further research including more accessions representative of larger areas could help to solve this taxonomic puzzle. Also, with in Tuberosa group, additional studies are needed in complex taxa, fundamentally in two morphologically very similar species, *S. candolleanum* and *S. brevicaule*, to elucidate relationships and current hypothesis of potato domestication and cultivation origin (Spooner et al. 2005; Rodríguez et al. 2017). The taxonomy of *S. brevicaule* and related species has long been controversial (Correll 1962; Ugent 1970; Grun 1990), and several studies using morphological phenetics (Van den Berg et al. 1998; Alvarez et al. 2008), molecular marker data of RFLPs and RAPDs (Miller and Spooner 1999), and with AFLPs (Spooner et al. 2005) have been focusing on this group. All datasets distinguished *S. candolleanum*, distributed from Central Peru to Northernmost Bolivia, and *S. brevicaule*, distributed from northern Bolivia to northern Argentina, but with little to no support for the many names that were placed in synonymy (Table 4.2). Although Conicibaccata group have been recently revised, further studies are needed in *S. colombianum* and related taxa. Likewise, within Piurana a revision will be necessary to better define the members included in this group. Regarding endemism, new methodologies such environmental niche modeling, could be helpful to define collecting strategies as well as to identify threatened environment and antropic factors that may affect natural populations, like in the case of *S. rhomboideilanceolatum* (Castañeda Álvarez et al. 2015). These approaches can be also applied to explore and define new areas of distributions, as in the case of *S. maglia*, a wild species found in Chile but only one population in the mountains of Mendoza, Argentina. In this case, it will be interesting to test the hypothesis of ploidy in relation of habitat adaptation.

4.4 Cultivated Potatoes Origin, Domestication, Diversity and Taxonomy

South American indigenous farmers domesticated potatoes in the high plateaus of the Andean Punas and also in the lowlands of south-central Chile, where landrace cultivars are still highly diverse with an enormous variety of tuber shapes, sizes, and different colors of skin and internal tissues (INIA 2012; Fonseca et al. 2014; INIAF VDRA and MDRyT 2014; SPDA CCTA and INIA 2015; CIP 2015; MINAGRI 2017; PRODERN 2018; MINAM 2019).

The scarcity of direct botanical evidence has made difficult archeological research focused on potato species used by early American inhabitants and evidences of domestication. Ancient remains of potato have been found in archeological sites in Southern Chile, revealing that potato species have been consumed for at least 13,000 years (Ugent et al. 1987). Similarly, archeological rest indicated that about 10,000 years ago potato species have been used as food supply by native communities of Perú

Table 4.2 Recognized valid wild species names of sect. *Etuberosum* and sect. *Petota* are included in non-formal groups, and a list of synomyms in each species is provided. Numbers indicated species quantity

SECTION	SPECIES		SYNONYMS
ETUBEROSUM	1	*Solanum etuberosum* Lindl.	*S. bustillosii* Phil., *S. etuberosum* var. *antucense* Bitter, *S. etuberosum* var. *bustillosii* (Phil.) Witasek, *S. etuberosum* var. *chillanense* Bitter, *S. kunzei* Phil., *S. looseri* Juz. ex Bukasov, *S. subandinum* F. Meigen, *S. subandinum* Phil., *S. tuberosum* var. *polemoniifolium* Hook.f.
	2	*Solanum palustre* Schltdl.	*S. brevidens* Phil., *S. brevidens* var. *glabrescens* (Dunal) Hawkes, *S. brevidens* var. *glabrescens* (Walp.) Hawkes, *S. bridgesii* A.DC., *S. caldasii* var. *glabrescens* (Walp.) Dunal, *S. palustre* Poepp., *S. palustre* Poepp. ex Walp., *S. palustre* var. *glabrescens* Poepp. ex Walp., *S. pearcei* Phil., *S. tuberosum* subsp. *brevidens* (Phil.) Reiche, *S. tuberosum* subsp. *pearcei* (Phil.) Reiche, *S. tuberosum* var. *brevidens* (Phil.) Reiche, S. *tuberosum* var. *pearcei* (Phil.) Reiche
	3	*Solanum fernandezianum* Phil.	*S. brevistylum* Wittm., *S. tuberosum* subsp. *fernandezianum* (Phil.) Reiche, S. *tuberosum* var. *fernandezianum* (Phil.) Reiche
PETOTA	*ACAULIA*		
	1	*Solanum acaule* Bitter	*S. acaule* subsp. *punae* (Juz.) Hawkes & Hjert., *S. acaule* var. *caulescens* Bitter, *S. acaule* var. *checcae* Hawkes, *S. acaule* var. *punae* (Juz.) Hawkes, *S. acaule* Bitter forma *incuyo* Ochoa, *S. acaule* var. *subexinterruptum* Bitter, *S. depexum* Juz., *S. depexum* var. *chorruense* Hawkes, *S. punae* Juz., *S. schreiteri* Bukasov, *S. uyunense* Cárdenas
	3	*Solanum albicans* (Ochoa) Ochoa	*S. acaule* subsp. *albicans* (Ochoa) Hawkes, *S. acaule* var. *albicans* Ochoa, *S. acaule* subsp. *palmirense* Kardolus
	5	*Solanum demissum* Lindl.	*S. alpicum* Standl. & Steyerm., *S. demissum* forma *adpressoacuminatum* Bukasov ex Rybin, *S. demissum* forma *atrocyaneum* Lechn., *S. demissum* forma *calycotrichum* Hawkes, *S. demissum* forma *microcalyx* Lechn. ex Bukasov, *S. demissum* forma *tlaxpehualcoense* Bukasov ex Rybin, *S. demissum* forma *xitlense* Bukasov ex Rybin, *S. demissum* var. *demissum* forma *calycotrichum* Hawkes, *S. demissum* var. *demissum* forma *longifilamentosum* Hawkes, *S. demissum* var. *demissum* forma *perotanum* Hawkes, *S. demissum* var. *demissum* forma *tolucense* Hawkes, *S. demissum* var. *mastoidostigma* Hawkes, *S. demissum* var. *orientale* Hawkes, *S. semidemissum* Juz. ex Bucasov, *S. stoloniferum* var. *pumilum* M.Martens & Galeotti, *S. utile* Klotzsch
	2	*Solanum* × *aemulans* Bitter & Wittm.	*S. acaule* subsp. *aemulans* (Bitter & Wittm.) Hawkes & Hjert., *S. acaule* var. *aemulans* (Bitter & L. Wittm.) Correll, *S.* × *indunii* K.A.Okada & A.M.Clausen
	4	*Solanum* × *brucheri* Correll	*S.* × *viirsooi* K.A. Okada & A. M. Clausen
PETOTA	6		

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
		Solanum × *edinense* Berthault	*S. edinense* subsp. *salamanii* (Hawkes) Hawkes, *S. salamanii* Hawkes
	BULBOCASTANA		
	7	*Solanum bulbocastanum* Dunal	*S. bulbocastanum* subsp. *dolichophyllum* (Bitter) Hawkes, *S. bulbocastanum* subsp. *partitum* (Correll) Hawkes, *S. bulbocastanum* var. *dolichophyllum* Bitter, *S. bulbocastanum* var. *glabrum* Correll, *S. bulbocastanum* var. *latifrons* Bitter, *S. bulbocastanum var. partitum* Correll, *S. longistylum* Correll, *S. mexicanum* Sessé & Moc., *S. symphysicaulis* Pav. ex Dunal
	8	*Solanum cardiophyllum* Lindl.	*S. cardiophyllum* subsp. *lanceolatum* (Berthold) Bitter, *S. cardiophyllum* var. *amphixanthandrum* Bitter, *S. cardiophyllum* var. *endoiodandrum* Bitter, *S. cardiophyllum* var. *oligozygum* Bitter, S. *cardiophyllum* var. *pliozygum* Bitter, *S. coyoacanum* Bukasov ex Rybin, *S. lanceolatum* Berthault, *S. lanciforme* Rydb.
	COMMERSONIANA		
	9	*Solanum commersonii* Dunal	*S. acroleucum* Bitter, *S. commersonii* forma *mechonguense* (Bukasov) Correll, *S. commersonii* var. *depauperatum* Bitter, *S. commersonii* var. *ellipticans* Bitter, *S. commersonii* var. *glabratum* Hook.f., *S. commersonii* var. *indigoticascens* Bitter, *S. commersonii* var. *pubescens* Sendtn., *S. commersonii* var. *raphanistrum* Bitter, *S. commersonii* var. *rosulans* Bitter, *S. commersonii* var. *violaceum* Herter, *S. debile* Dunal, *S. henryi* Bukasov & Lechn., *S. henryi* forma *laticalix* Lechn., S. *henryi* forma *pubescens* Lechn., *S. mechonguense* Bukasov, *S. mercedense* Bukasov, *S. nicaraguense* Rydb., *S. ohrondii* Carrière, *S. rionegrinum* Lechn., *S. sorianum* Bukasov, *S. tenue* Sendtn., *S. tenue* var. *pubescens* Sendtn. ex Dunal, *S. tenue* var. *raphanifolium* Dunal
	10	*Solanum malmeanum* Bitter	*S. chacoense* forma *pilosulum* (Hassl.) Hassl., *S. commersonii* forma *malmeanum* (Bitter) Correll, *S. commersonii* subsp. *malmeanum* (Bitter) Firbas & Ross, *S. commersonii* subsp. *malmeanum* (Bitter) Hawkes & Hjert., *S. commersonii* subsp. *pseudostipulatum* Hassl., *S. commersonii* var. *pseudostipulatum* Hassl., *S. commersonii* var. *pubescens* Chodat, *S. guaraniticum* forma *pilosulum* Hassl. *S. millanii* Bukasov & Lechn., *S. pseudostipulatum* (Hassl.) Bukasov
	CONICIBACCATA		
	11	*Solanum agrimonifolium* Rydb.	
	12	*Solanum ayacuchense* Ochoa	
	13	*Solanum bombycinum* Ochoa	

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
PETOTA	14	*Solanum buesii* Vargas	
	15	*Solanum burkartii* Ochoa	*S. irosinum* Ochoa, *S. irosinum* forma *tarrosum* Ochoa
	16	*Solanum colombianum* Dunal	*S. cacetanum* Ochoa, *S. calacalinum* Ochoa, *S. colombianum* var. *meridionale* Hawkes, *S. colombianum* var. *trianae* Bitter, *S. colombianum* forma *quindiuense* Bukasov, *S. colombianum* var. *zipaquiranum* Hawkes, *S. cuatrecasasii* Ochoa, *S. dolichocarpum* Bitter, *S. filamentum* Correll, *S. jaenense* Ochoa, *S. moscopanum* Hawkes, *S. nemorosum* Ochoa, *S. orocense* Ochoa, *S. otites* Dunal, *S. otites* forma *dizygum* Bitter, *S. otites* forma *trizygum* Bitter, *S. pamplonense* L.E.López, *S. papa* Valenz. ex Palacio, *S. subpanduratum* Ochoa, *S. sucubunense* Ochoa, *S. tundalomense* Ochoa, *S. valenzuelae* Palacio, *S. venezuelicum* Bukasov
	17	*Solanum flahaultii* Bitter	*S. neovalenzuelae* L.E.López
	18	*Solanum garcia-barrigae* Ochoa	*S. donachui* (Ochoa) Ochoa, *S. garcia-barrigae* var. *donachui* Ochoa
	19	*Solanum laxissimum* Bitter	*S. claviforme* Correll, *S. claviformum* Correll, *S. laxissimum* forma *rockefelleri* (Vargas) Correll, *S. neovargasii* Ochoa, *S. rockefelleri* Vargas, *S. santolallae* Vargas, *S. santolallae* var. *acutifolium* Vargas
	20	*Solanum limbaniense* Ochoa	
	21	*Solanum lobbianum* Bitter	
	22	*Solanum longiconicum* Bitter	*S. longiconicum* var. *quadrijugum* Bitter, *S. nanoteranthum* Bitter
	23	*Solanum nubicola* Ochoa	
	24	*Solanum oxycarpum* Schiede	*S. confusum* Correll, *S. nelsonii* Correll, *S. reconditum* Correll
	25	*Solanum pillahuatense* Vargas	
	26	*Solanum rhomboideilanceolatum* Ochoa	
	27	*Solanum salasianum* Ochoa	
	28	*Solanum violaceimarmoratum* Bitter	*S. multiflorum* Vargas, *S. neovavilovii* Ochoa, *S. santolallae* forma *velutinum* Correll, *S. urubambae* Juz., *S. urubambae* forma *chakchabambense* Ochoa, *S. urubambae* forma *velutinum* (Correll) Ochoa, *S. villuspetalum* Vargas, *S. violaceimarmoratum* var. *papillosum* Hawkes
	29	*Solanum woodsonii* Correll	
	IOPETALA		
	30	*Solanum guerreroense* Correll	
	31	*Solanum hougasii* Correll	*S. spectabile* (Correll) Hawkes, *S. verrucosum* var. *spectabile* Correll

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
PETOTA	32	*Solanum iopetalum* (Bitter) Hawkes	*S. brachycarpum* (Correll) Correll, *S. demissum* forma *longibaccatum* Bukasov ex Rybin, *S. demissum* forma *recurvoacuminatum* Bukasov ex Rybin, *S. demissum* forma *stenantherum* Lechn. ex Bukasov, *S. oxycarpum* var. *brachycarpum* Correll, *S. verrucosum* var. *iopetalum* Bitter
	33	*Solanum schenckii* Bitter	*S. demissum* var. *megalocalyx* Hawkes
	LONGIPEDICELLATA		
	34	*Solanum hjertingii* Hawkes	*S. fendleri* var. *physaloides* Correll, *S. hjertingii* var. *physaloides* (Correll) Hawkes, *S. leptosepalum* Correll, *S. matehualae* Hjert. & Tarn
	35	*Solanum stoloniferum* Schltdl.	*S. ajuscoense* Bukasov ex Rybin, *S. antipovichii* Bukasov ex Rybin, *S. antipovichi* var. *neoantipoviczii* (Bukasov) Hawkes, *S. antipoviczii* Bukasov ex Rybin, *S. boreale* (A.Gray) Bitter, *S. candelarianum* Bukasov, *S. fendleri* A. Gray, *S. fendleri* subsp. *arizonicum* Hawkes, *S. fendleri* var. *texense* Correll, *S. leptosepalum* Correll, *S. longipedicellatum* Bitter, *S. longipedicellatum* var. *longimucronatum* Hawkes, *S. longipedicellatum* var. *pseudoprophyllum* Bitter, *S. malinchense* Hawkes, *S. nannodes* Correll, *S. neoantipoviczii* Bukasov, *S. noctiflorum* Hort. Dunal, *S. orbiculatibaccatum* Lechn., *S. papita* Rydb., *S. polytrichon* Rydb., *S. schizostigma* Bitter, *S. stoloniferum* subsp. *moreliae* Hawkes, *S. tlaxcalense* Hawkes, *S. tuberosum* var. *boreale* A.Gray, *S. wightianum* Rydb.
	36	*Solanum* × *vallis-mexici* Juz.	*S. vallis-mexici* Juz. ex Bukasov
	MEGISTACROLOBA		
	37	*Solanum boliviense* Dunal	*S. alticola* Bitter, *S. alticola* var. *xanthotrichum* Hawkes, *S. astleyi* Hawkes & Hjert., *S. boliviense* subsp. *astleyi* (Hawkes & Hjert.) D.M.Spooner, M. Ugarte & P.W.Scroch, *S. catamarcae* Bitter ex Brücher, *S. decurrentilobum* Cárdenas & Hawkes, *S. ellipsifolium* Cárdenas & Hawkes, *S. megistacrolobum* Bitter, *S. megistacrolobum* forma *purpureum* Ochoa, *S. sanctae-rosae* Hawkes, *S. tilcarense* Hawkes, *S. toralapanum* Cárdenas & Hawkes, *S. toralapanum* var. *subintegrifolium* Cárdenas & Hawkes, *S. ureyi* Cárdenas
	38	*Solanum hastiforme* Correll	
	39	*Solanum raphanifolium* Cárdenas & Hawkes	*S. hawkesii* Cárdenas
	40	*Solanum sogarandinum* Ochoa	*S. sogarandae* Firbas & Ross

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
PETOTA	MORELLIFORME		
	41	*Solanum clarum* Correll	
	42	*Solanum morelliforme* Bitter & Münch	
	PINNATISECTA		
	43	*Solanum jamesii* Torr.	*S. jamesii* var. *heterotrichium* Bitter, *S. jamesii* var. *sinclairii* Bitter & Correvon, *S. jamesii* subsp. *septentrionale* Bitter
	44	*Solanum pinnatisectum* Dunal	*S. pinnatisectum* var. *heptazygum* Bitter, *S. pinnatisectum* var. *pentazygum* Bitter
	45	*Solanum* × *michoacanum* (Bitter) Rydb.	*Solanum jamesii* var. *michoacanum* Bitter
	46	*Solanum* × *sambucinum* Rydb.	
	PIURANA		
	47	*Solanum acroglossum* Juz.	
	48	*Solanum acroscopicum* Ochoa	*S. lopez-camarenae* Ochoa
	49	*Solanum albornozii* Correll	
	50	*Solanum anamatophilum* Ochoa	*S. peloquinianum* Ochoa
	51	*Solanum andreanum* Baker	*S. baezense* Ochoa, *S. burtonii* Ochoa, *S. cyanophyllum* Correll, *S. correllii* Ochoa, *S. paucijugum* Bitter, *S. pichinchense* Bitter & Sodiro, *S. regularifolium* Correll, *S. serratoris* Ochoa, *S. solisii* Hawkes, *S. suffrutescens* Correll, *S. tuquerrense* Hawkes
	52	*Solanum augustii* Ochoa	
	53	*Solanum cajamarquense* Ochoa	
	54	*Solanum cantense* Ochoa	
	55	*Solanum chilliasense* Ochoa	
	56	*Solanum chiquidenum* Ochoa	*S. ariduphilum* Ochoa, *S. chiquidenum* forma *amazonense* Ochoa, *S. chiquidenum* var. *cachicadense* Ochoa, *S. chiquidenum* var. *gracile* Ochoa, *S. chiquidenum* var. *porconense* Ochoa, *S. chiquidenum* var. *robustum* Ochoa
	57	*Solanum chomatophilum* Bitter	*S. chomatophilum* forma *angustifoliolum* Correll, *S. chomatophilum* forma *pilosum* Correll, *S. chomatophilum* forma *sausianense* Ochoa, *S. chomatophilum* var. *subnivale* Ochoa, *S. huarochiriense* Ochoa, *S. jalcae* Ochoa, *S. jalcae* var. *pubescens* Correll, *S. pascoense* Ochoa, *S. sinclairii* Hort. ex Bitter, *S. taulisense* Ochoa
	58	*Solanum contumazaense* Ochoa	
	59	*Solanum dolichocremastrum* Bitter	*S. chavinense* Correll, *S. huanucense* Ochoa

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
PETOTA	60	*Solanum huancabambense* Ochoa	
	61	*Solanum humectophilum* Ochoa	
	62	*Solanum hypacrarthrum* Bitter	*S. guzmanguense* Whalen & Sagást., *S. tuberosum* var. *puberulum* Hook.f.
	63	*Solanum immite* Dunal	*S. immite* Dunal var. *vernale* Correll, *S. mathewsii* Bitter, *S. tuberosum* L. var. *multijugum* Hook.f., *S. wittmackii* var. *glauciviride* Bitter, *S. yamobambense* Ochoa
	64	*Solanum minutifoliolum* Correll	
	65	*Solanum mochiquense* Ochoa	*S. chancayense* Ochoa, *S. earl-smithii* Correll, *S. incahuasinum* Ochoa, *S. mochicense* Ochoa
	66	*Solanum multiinterruptum* Bitter	*S. chrysoflorum* Ochoa, *S. moniliforme* Correll, *S. multiinterruptum* Bitter forma *albiflorum* Ochoa, *S. multiinterruptum* forma *longipilosum* Correll, *S. multiinterruptum* var. *machaytambinum* Ochoa
	67	*Solanum olmosense* Ochoa	
	68	*Solanum paucissectum* Ochoa	
	69	*Solanum piurae* Bitter	
	70	*Solanum raquialatum* Ochoa	*S. ingaefolium* Ochoa, *S. rachialatum* Ochoa,
	71	*Solanum scabrifolium* Ochoa	
	72	*Solanum simplicissimum* Ochoa	
	73	*Solanum trinitense* Ochoa	
	74	*Solanum wittmackii Bitter*	*S. vavilovii* Juz. & Bukasov, *S. tuberosum* var. *macranthum* Hook.f., *S. wittmackii* var. *glauciviride* Bitter
	75	*Solanum xblanco-galdosii* Ochoa	
	POLYADENIA		
	76	*Solanum lesteri* Hawkes & Hjert.	
	77	*Solanum polyadenium* Greenmam	*S. polyadenium* subsp. *orizabae* Bitter
	STENOPHYLLIDIA		
	78	*Solanum hintonii* Correll	
	79	*Solanum stenophyllidium* Bitter	*S. brachistotrichium* (Bitter) Rydb., *S. brachistotrichium* var. *ripicolum* (Bitter) Correll, *S. jamesii* var. *brachistotrichium* Bitter, *S. jamesii* subsp. *nayaritense* Bitter, *S. jamesii* var. *ripicolum* Bitter, *S. jamesii* subsp. *septentrionale* var. *ripicola* Bitter *S. nayaritense* (Bitter) Rydb.

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
PETOTA	80	*Solanum ehrenbergii* (Bitter) Rydb.	*S. cardiophyllum* subsp. *ehrenbergii* (Bitter) Correll
	STIPULOIDEA		
	81	*Solanum stipuloideum* Rusby	*S. capsicibaccatum* Cárdenas, *S. capsicibaccatum* var. *latifoliolatum* Ochoa, *S. circaeifolium* Bitter, *S. circaeifolium* forma *lobatum* Correll, *S. circaeifolium* subsp. *quimense* Hawkes & Hjert., *S. soestii* Hawkes & Hjert.
	82	*Solanum neocardenasii* Hawkes & Hjert.	
	TRIFIDA		
	83	*Solanum tarnii* Hawkes & Hjert.	
	84	*Solanum trifidum* Correll	
	TUBEROSA		
	85	*Solanum amayanum* Ochoa	
	86	*Solanum ancophilum* (Correll) Ochoa	*S. rhomboideilanceolatum* Ochoa var. *ancophilum* Correll
	87	*Solanum berthaultii* Hawkes	*S.* x*flavoviridens* Ochoa, *S. berthaultii* forma *zudanense* (Cárdenas) Correll, *S. litusinum* Ochoa, *S. tarijense* Hawkes, *S. tarijense* var. *pojoense* (Cárdenas) Correll, *S. trigalense* Cárdenas, *S. vallegrandense* Cárdenas, *S. vallegrandense* var. *pojoense* Cárdenas, *S. zudanense* Cárdenas
	88	*Solanum brevicaule* Bitter	*S. abancayense* Ochoa, *S. alandiae* Cárdenas, *S. anomalocalyx* Hawkes, *S. anomalocalyx* var. *brachystylum* Cárdenas & Hawkes, *S. anomalocalyx* var. *llallaguanianum* Cárdenas & Hawkes, *S.anomalocalyx* var. *murale* Cárdenas & Hawkes, *S. avilesii* Hawkes & Hjert., *S. aymaraesense* Ochoa, *S. bill-hookeri* Ochoa, *S. boliviense* subsp. *virgultorum* Bitter, *S. brevimucronatum* Hawkes, *S. calcense* Hawkes, *S. calcense* Hawkes var. *urubambense* Vargas, *S. candelarianum* Cárdenas, *S. coelestispetalum* Vargas, *S. colominense* Cárdenas, *S. famatinae* Bitter & Wittm., *S. gourlayi* Hawkes, *S. gourlayi* subsp. *saltense* A.M. Clausen & K.A.Okada, *S. huancavelicae* Ochoa, *S. hondelmannii* Hawkes & Hjert., *S. hoopesii* Hawkes & K.A.Okada, *S. incamayoense* K.A.Okada & A.M. Clausen, *S. lapazense* Hawkes, *S. leptophyes* Bitter, *S. liriunianum* Cárdenas & Hawkes, *S. membranaceum* Vargas, *S. mollepujroense* Cárdenas & Hawkes, *S. ochoae* Vargas, *S. oplocense* Hawkes, *S. pachytrichum* Hawkes, *S. pampasense* Hawkes, *S. puberulofructum* Correll, *S. ruiz-zeballosii* Cárdenas, *S. sawyeri* Ochoa, *S. setulosistylum* Bitter, *S. sleumeri* Correll, *S. spegazzinii* Bitter, *S. subandigenum* var. *camarguense* Cárdenas, *S. sucrense* Hawkes, *S. torrecillasense* Cárdenas, *S. sparsipilum* (Bitter) Juz. & Bukazov, *S. tuberosum*

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
			subsp. *sparsipilum* Bitter, *S. ugentii* Hawkes & K.A. Okada, *S. vidaurrei* Cárdenas, *S. virgultorum* (Bitter) Cárdenas & Hawkes
PETOTA	89	*Solanum candolleanum* Berthault	*S. abbottianum Juz., S. achacachense* Cárdenas, *S. amabile* Vargas, *S. ambosinum* Ochoa, *S. ancoripae* Ochoa, *S. antacochense* Ochoa, *S. bukasovii* Juz., *S. canasense* Hawkes, *S. canasense* Hawkes var. *album* Vargas, *S. canasense* Hawkes var. *calcense* Vargas, *S. canasense* Hawkes var. *intihuatanense* Vargas, *S. catarthrum* Juz., *S. chillonanum* Ochoa, *S. cuzcoense* Ochoa, *S. espinarense* Vargas, *S. fragariifructum* Hawkes, *S. hapalosum* Ochoa, *S. lechnoviczii* Hawkes, *S. lechnoviczii* Hawkes var. *latifolium* Vargas, *S. lechnoviczii* var. *xerophyllum* Vargas, *S. longimucronatum* Vargas, *S. longiusculus* Ochoa, *S. marinasense* Vargas, *S. marinasense* Vargas var. *dentifolium* Vargas, *S. multidissectum* Hawkes, *S. multiinterruptum* Bitter forma *longipilosum* Correll, *S. multiinterruptum* Bitter var. *machaytambinum* Ochoa, *S. neohawkesii* Ochoa, *S. orophilum* Correll, *S. pampasense* Hawkes, *S. puchupuchense* Ochoa, *S. punoense* Hawkes, *S. sarasarae* Ochoa, *S. saxatile* Ochoa, *S. sicuanum* Hawkes, *S. soukupii* Hawkes, *S. tapojense* Ochoa, *S. tarapatanum* Ochoa
	90	*Solanum chacoense* Bitter	*S. arnezii* Cárdenas, *S. boergeri* Bukasov, *S. caipipendense* Cárdenas, *S. calvescens* Bitter, *S. commersonii* var. *glabriusculum* Hook.f., *S. cuevoanum* Cárdenas, *S. chacoense* var. *latisectum* forma *plurijugum* Hassler, *S. emmeae* Juz. & Bukasov, *S. garciae* Juz. & Bukasov, *S. gibberulosum* Juz. & Bukasov, *S. guaraniticum* var. *latisectum* forma *glabrescens* Hassler, *S. horovitzii* Bukasov, *S. horovitzii* var. *multijugum* Hawkes, *S. jamesii* var. *grandifrons* Bitter, *S. jujuyense* Hawkes, *S. knappei* Juz. & Bukasov, *S. laplaticum* Bukasov, *S. limense* Correll, *S. muelleri* Bitter, *S. muelleri* forma *densipilosum* Correll, *S. parodii* Juz. & Bukasov, *S. saltense* Hawkes, *S. schickii* Juz. & Bukasov, *S. subtilius* Bitter, *S. tuberosum* var. *glabriusculum* Dunal, *S. tuberosum* subsp. *yanacochense* Ochoa, *S. yungasense* Hawkes
	91	*Solanum gandarillasii* Cárdenas	
	92	*Solanum gracilifrons* Bitter	
	93	*Solanum incasicum* Ochoa	
	94	*Solanum infundibuliforme* Phil.	*S. glanduliferum* Hawkes, *S. infundibuliforme* var. *albiflorum* Ochoa, *S. infundibuliforme* var. *angustepinnatum* Bitter, *S. microphyllum* Hawkes, *S. pinnatifidum* Cárdenas, *S. platypterum* Hawkes
PETOTA	95	*Solanum kurtzianum* Bitter & Wittm.	*S. commersonii* var. *glanduloso-pubescens* Hook.f., *S. commersonii* var. *pilosiusculum* Hook.f., *S. improvidum*

(continued)

Table 4.2 (continued)

SECTION	SPECIES		SYNONYMS
			Brücher, *S. macolae* Bukasov, *S. ruiz-lealii* Brücher, *S. velascanum* Bitter & Wittm.
	96	*Solanum lignicaule* Vargas	*Solanum lignicaule* var. *longistylum* Vargas
	97	*Solanum maglia* Schltdl.	*S. collinum* Dunal, *S. maglia* var. *witasekianum* Bitter, *S. tuberosum* var. *sabinii* A.DC
	98	*Solanum medians* Bitter	*S. arahuayum* Ochoa, *S. medians* var. *angustifoliolum* Ochoa, *S. medians* var. *autumnale* Correll, *S. medians* var. *majorifrons* Bitter, *S. medians* subvar. *protohypoleucum* Bitter, *S. sandemanii* Hawkes, *S. tacnaense* Ochoa, *S. weberbaueri* Bitter, *S. weberbaueri* var. *decurrentialatum* Ochoa, *S. weberbaueri* var. *poscoanum* Cárdenas & Hawkes
	99	*Solanum microdontum* Bitter	*S. bijugum* Bitter, *S. cevallos-tovari* Cárdenas, *S. gigantophyllum* Bitter, *S. higueranum* Cárdenas, *S. microdontum* var. *montepuncoense* Ochoa, *S. simplicifolium* Bitter, *S. simplicifolium* subsp. *gigantophyllum* var. *metriophyllum* Bitter, *S. simplicifolium* subsp. *gigantophyllum* var. *mollifrons* Bitter, *S. simplicifolium* subsp. *gigantophyllum* var. *trimerophyllum* Bitter, *S. simplicifolium* var. *variabile* Brücher & Ross
	100	*Solanum neorossii* Hawkes & Hjert.	
	101	*Solanum neoweberbaueri* Wittm.	
	102	*Solanum okadae* Hawkes & Hjert.	*S. venatoris* Ochoa
	103	*Solanum velardei* Ochoa	
	104	*Solanum venturii* Hawkes & Hjert.	
	105	*Solanum vernei* Bitter & Wittm.	*S. ballsii* Hawkes
	106	*Solanum* × *doddsii* Correll	
	107	*Solanum* × *rechei* Hawkes & Hjert.	
	VERRUCOSA		
	108	*Solanum verrucosum* Schltdl.	*S. macropilosum* Correll, *S. squamulosum* M.Martens & Galeotti

Table 4.3 Cultivated potato species of Section *Petota*, cultivar Group (ICNCP), distribution, ploidy, EBN number, and synonyms of the recognized valid species according to the current taxonomic treatment (Spooner et al. 2007). Complete synonyms, epithets and names not validly published in Ovchinnikova et al. 2011 and Solanaceae Source website (http://www.solanaceaesource.org)

Species	Cultivar Group	Distribution	Ploidy (EBN)	Synonyms
Solanum tuberosum L.	Chilotanum Group	Southern Chile Chonos and Guaitecas Arquipelagos	*4X* (4)	*S. tuberosum* subsp. *tuberosum*
	Andigenum Group	Western Venezuela, Colombia, Ecuador, Perú, Northern Argentina, mid to high Andean elevations (3000–3500 m)	*2X* (2) *3X 4X* (4)	*S. tuberosum* subsp. *andigenum* (Juz. & Bukasov) Hawkes, *S. chaucha* Juz. & Bukasov, *S. phureja* Juz. & Bukasov, *S. phureja* subsp. *estradae* (L. López) Hawkes, *S. phureja* subsp. *hygrothermicum* (Ochoa) Hawkes, *S. stenotomum* Juz. & Bukasov, *S. stenotomum* Juz. & Bukasov subsp. *goniocalyx* (Juz. & Bukasov) Hawkes
Solanum ajanhuiri Juz. & Bukasov		Bolivia and Perú Andean highlands (above 3500 m)	*2X* (2)	*S. ajanhuiri* Juz. & Bukasov forma *janckoajanhuiri* Ochoa, *S. ajanhuiri* Juz. & Bukasov var. *yari* Ochoa
Solanum curtilobum Juz. & Bukasov		Bolivia and Perú Andean highlands (above 3500 m)	*5X* (4)	
Solanum juzepczukii Bukasov		Bolivia, Perú, Northern Argentina Andean highlands (above 3500 m)	*3X* (2)	*S. juzepczukii* Bukasov var. *parco* Hawkes, *S. juzepczukii* Bukasov var. *roseum* Vargas, *S. juzepczukii* Bukasov forma *ckoyuckaisalla* Ochoa, *S. juzepczukii* Bukasov forma *janckock-aisalla* Ochoa, *S. juzepczukii* Bukasov forma *luckipechuma* Ochoa, *S. juzepczukii* Bukasov forma *luckipinkula* Ochoa, *S. juzepczukii* Bukasov forma *wilackaisalla* Ochoa, *S. juzepczukii* Bukasov var. *lucki* Ochoa

(Engel 1970). Fossilized tubers found in Casma Valley of Perú have been directly dated to 7800 cal B.P. (C^{14} calibrated date), and even though starch microremains resembled those of the domesticated potato may still represented a wild species (Ugent et al. 1982). Recently, an archeological study based on the microscopic analysis of starch granules found on ground stone tools in deposits dating between 10,900 and 10,100 cal B.P. at North Creek Shelter (Utah) documented the earliest use of wild potatoes in North America as important food source (Louderback and Pavlik 2017). These archeological findings evidence the early consumption of potato tubers at a time that precedes agriculture (Ugent et al. 1982; Hawkes 1990; Louderback and Pavlik 2017). The analysis of starch microremains recovered from groundstone tools found at Jiskairumoko, an ancient village in Perú, revealed an intensive exploitation of potatoes that took place between 3400 and 1600 B.P. during Late Archaic to Early Formative in the western

Titicaca Basin (Rumold and Aldenderfer 2016). These archeological evidences, based on the consistency of ancient starch remains with those of cultivated potato, documented a time of transition from nomadism to sedentism and food production, and may be related to potato domestication and early cultivation in southern Perú (Rumold and Aldenderfer 2016).

Prevalent hypothesis for cultivated potato's origins advocated multiple, independent domestications from a group of about 20 morphologically similar wild potato species, the "*Solanum brevicaule* complex" (Alvarez et al. 2008), distributed from southern Peru, northwestern Bolivia, and northern Argentina (Brücher 1964; Ugent 1970; Bukasov 1978; Hawkes 1990; Grun 1990; Ochoa 1990, 1999; Van den Berg et al. 1998; Huamán and Spooner 2002; Spooner et al. 2014). New insights from phylogenetic analysis that include a wide sampling of 362 representatives of landraces, putative progenitors, and outgroups, supported a reduction in the number of species in the *Solanum brevicaule* complex and a monophyletic origin of landrace cultivars from a single species in a broad area of southern Peru (Spooner et al. 2005). Landraces developed by early Andean farmers were dispersed from Peru both north and south. Nowadays, potato landraces reveal great morphological, physiological, and genetic diversity, and are distributed throughout the Andes, from western Venezuela to northern Argentina, and in southern Chile (Spooner et al. 2010). Landrace potato populations in Mexico and Central America are recent, post-Columbian introductions (Ugent 1968).

Cultivated potatoes were first introduced from America in the Canary Islands in 1567 (Hawkes and Francisco Ortega 1993; Spooner et al. 2005; Ríos et al. 2007), and soon arrived in Spain in 1573 (Hawkes 1990; Hawkes and Francisco Ortega 1993; Romans 2005). The first botanical description of potato in Europe was made by Caspar Bauhin in 1596, but the origin of the plant described was unknown (Hawkes 1990). In 1597 Gerard made the first description of the potato in English and a detailed illustration in The Herbals, although he mistakenly believed it came from Virginia in North America rather than South America. Later Carolus Clusius (1601) described potatoes and mentioned he received the tubers in 1588 from Phillippe de Sirvry who cultivated potatoes in Belgium and made the first drawing of potato in Europe indicating with his handwriting its common name and origin "*Taratoufli Vienae*, 26 *januarii* 1588*, Papas Peruam Petri Cieca*" (Parodi 1966). Evidences from early herbalist indicated that potatoes were cultivated since mid-XVI century in different European countries and rapidly disseminated worldwide. Regarding the origin of the first potatoes introduced in Europe, two hypotheses have been proposed: from lowland Chile (Juzepczuk and Bukasov 1929) or from the Andes (Salaman 1937; Salaman, and Hawkes 1949), being the Andean origin the most accepted. Ames and Spooner (2008) investigated these two competing hypothesis using historical herbarium potato specimens for a screening with a plastid DNA deletion marker. Interestingly, the first direct evidences from early preserved plants showed not only that potatoes of Andean origin predominated in Europe in the 1700s, but also that potatoes from Chile were introduced as early as 1811 in Europe, and became predominant long before the late blight epidemics begun in 1845 in potato crops causing high mortality and famine (Ames and Spooner 2008). Consequently, after the late blight epidemics, resistances from Chilean landraces were introduced into European potato cultivars.

Alphonse de Candolle, French-Swiss botanist, was a pioneer to investigate the origins of cultivated plants and crop geographic distribution. In his influential contribution, Origin of Cultivated Plants, De Candolle (1882) used evidences from different disciplines, presence of wild relatives, historical sources, linguistics (local names), archeology, and variation patterns, to determine the origin of cultivated plants. De Candolle (1882) was the first to name as distinct the Chilean populations of *S. tuberosum* as *var. chiloense* A.DC. Vavilov (1920, 1940), Russian geneticist and plant geographer, participated in over 100 collecting missions to explore the major agricultural centers worldwide, and built crop origin hypothesis. Vavilov and his Russian colleagues made several expeditions to Central and South America between 1925 and 1930, and generated a large potato collection that initiated the basic germplasm of the N. I. Vavilov Institute of Plant Industry in Saint Petersburg, Russia (Loskutov 1999). Some of the potato accessions are still maintained, as well as the herbarium specimens of the initial collections of high value to elucidate the taxonomy and nomenclature of cultivated potato (Ovchinnikova et al. 2011). Later, between 1938 and 1939 other important potato germplasm collections in South America were made by British Botanists Balls, Gourley and Hawkes (Hawkes 1944; 2004; Hawkes and Hjerting 1969, 1989). Germplasm derived from these initial collections is maintained at the Scottish Crop Research Institute (SCRI) in Dundee, United Kingdom, and specimens are mainly deposited at the Herbarium of Kew Botanical Gardens (KEW), and in many other collections worldwide (Ovchinnikova et al. 2011). Peruvian botanists C. Ochoa and A. Salas collected potatoes throughout South America that initiate the base of germplasm collections at the Universidad Nacional Agraria La Molina, Peru, and later the International Potato Center (Centro Internacional de la Papa, CIP). M. Cárdenas made early collections and descriptions of new potatoes from Bolivia (Cárdenas and Hawkes 1946), where National Agricultural and Forestry Institute (INIAF) maintains an important and diverse collection of cultivated potatoes (Cadima–Fuentes et al. 2013). In Argentina, several potato germplasm collections have been made by K. A. Okada, A. Clausen, and collaborators, which are maintained at INTA Potato Germplasm Bank in Balcarce (Clausen et al. 2010). In Chile, A. Contreras also collected and led germplasm collections that are maintained at the Chilean Germplasm Bank (Contreras 1987). David Spooner and collaborators from different countries also made important potato collections in North, Central and South America, which are maintained in CIP, US Potato Genebank, and other genebanks.

In order to organize large collections of cultivated potatoes, early Russian taxonomists applied a complex method to describe, named, and classified them, based on ploidy, ecogeography, and analysis of morphological and physiological characters. This system of nomenclature considered the homologous series of variation (Vavilov 1922), where geographical distribution and ecological types are major characters to define and name taxa (Juzepczuk and Bukasov 1929; Bukasov 1930; Juzepczuk 1937). Initially, Hawkes also applied this system to describe and name his potato collections, but later he simplified his classifications (Hawkes 2004). The application of this complex nomenclature system in initial cultivated potato collections, created numerous names, sometimes polynomials as well as many invalid names and a complicated classification by ranks. Recently, Ovchinnikova et al. (2011) clarified the nomenclature and taxonomy of cultivated potatoes, recognized 626 epithets associated with all taxa of cultivated potato and placed them in synonymy, and also made lectotype designations for names validly published (Ovchinnikova et al. 2011, Solanaceae Source website http://www.solanaceaesource.org). Four cultivated potato species are recognized: *S. tuberosum* L., *S. ajanhuiri* Juz. & Bukasov, *S. curtilobum* Juz. & Bukasov and *S. juzepczukii* Bukasov (Spooner et al. 2007), the three later species were formed by hybridization of *S. tuberosum* with more distantly related wild species of groups Acaulia and Megistacroloba (Rodríguez et al. 2010; Ovchinnikova et al. 2011) (Table 4.3).

The current taxonomical interpretation considers two main groups of landraces within *Solanum tuberosum* L, named according to the International Code of Nomenclature of Cultivated Plants (2016). The ‘Andigenum Group’ comprising diploid, triploid, or tetraploid, adapted to short-day flowering and tuberization. The ‘Chilotanum Group’ includes landraces from Southern Chile, mainly concentrated in the Chonos and Guaitecas Archipelagos, adapted to long-day flowering and tuberization (Huamán and Spooner 2002; Spooner et al. 2007; Ovchinnikova et al. 2011) (Table 4.3).

4.5 Methods and Issues for the Conservation of Potato Genetic Resources

The conservation of potato genetic resources implies two different strategies: the first one, ex situ conservation, is focused on the maintenance of potato genetic diversity outside its natural environment. The second, in situ strategy, comprise the conservation of ecosystems and natural habitats as well as the maintenance and recovery of viable populations of species in their natural surroundings, and in the case of domesticated or cultivated plant species conservation incorporate the surroundings where they have developed their distinctive properties (UNCED 1992; FAO 2009). These strategies have advantages and disadvantages, but the most remarkable characteristic is that both are complementary rather than exclusive. Nowadays it is accepted that a holistic approach is more effective in conservation programs of genetic resources.

The ex situ conservation of potato genetic resources is performed mainly in genebanks, and in a few cases in botanical gardens and museums. A fundamental goal of genebanks is to preserve germplasm and made it available for different purposes including research, breeding, agriculture production, industry, etc. (Ellis et al. 2020). The Second Report of the State of the Genetic Resources for Food and Agriculture (FAO 2010) registered 174 potato genebanks around the world and a total number 98,285 accessions, with possible material duplication, but it was estimated that 24,500–29,500 unique potato accessions are conserved worldwide. The same report showed that six genebanks hold 41% of the global potato accessions: The French National Institute for Agricultural Research (INRA) in France (11%), Vavilov Institute in Russia (9%), The International Potato Center (CIP) in Peru (8%), The Leibniz Institute of Plant Genetics and Crop Plant Research (IPK) in Germany (5%), USDA-ARS in the USA (5%), and The National Institute of Agrobiological Sciences (NIAS) in Japan (3%) and other 20 genebanks hold over 1000 potato accessions each. These genebanks collectively held collections of 15% wild relatives of potato, 20% cultivated potato accessions, 16% research, and breeding materials, 14% advanced breeding lines, and 35% uncategorized accessions (Ellis et al. 2020). According to the last report of the Global Strategy for Ex Situ Conservation of Potato, Latin American genebanks contain principally native cultivars while those in Europe and North America contain modern cultivars, breeding materials, and wild relatives (Ellis et al. 2020). Castañeda-Álvarez et al. (2015) determined that 43.8% of wild potato species are under-represented in genebanks, some of them with no accessions available such as *S. ayacuchense*, *S. neovavilovii*, *S. olmosense* and *S. salasianum*. To improve the worldwide representation of wild potatoes conserved ex situ in genebanks, Instituto Nacional de Innovación Agraria (INIA, Peru) and CIP joined to collect more than 300 new accessions in Peru; two of them belong to *S. ayacuchense* (Zorrilla et al. 2019a). The type of biological sample preserved in genebanks varies depending on the biological status of the accessions, if they come from wild or cultivated species. In genebanks seeds are the most common biological sample for conservation of potato wild relatives, to assure the preservation of genetic diversity of the original population instead of individual characteristics. The most important variables, taken into account for adequate seed conservation, are population size, storage temperature, seed humidity, and seed quality as these variables can affect the expected viability of the seed accession lot. The number of regenerations, sexual multiplication, should be the minimum in order to preserve the accessions identity. Genebanks follow standard conservation methods recommended by Biodiversity International and other institutions (FAO-IPGRI, Engels, and Visser 2003; FAO 2014; CGIAR 2020). Seeds of cultivated and wild potatoes are orthodox (Holle 1988), meaning that seeds can be dried to low moisture contents and stored at cold temperature without damage during different periods of time (Roberts and Ellis 1984). For instance, seeds are stored at −18 °C for the maintenance as base collections or safety copy in the genebank Svalbard Global Seed Vault which preserves potato duplicated seeds as a "black box" for long term conservation (Ellis et al. 2020). In this case, the depositors are responsible for processing, packing, and shipping the seeds before storage; subsequent seed multiplication when needed, and distributing these seeds from their stocks under conditions similar to the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA). The International Potato Center (CIP) in Perú stores potato seeds in the active collection at 4 °C, and in the base collection at −20 °C. The active collection is used for distributing germplasm and the base collection for the regeneration of new seed stocks. CIP has defined standard procedures for seed processing, packing, and storage of potato wild relatives, considering the extraction, cleaning of impurities, drying to 5% water seed content before entering the corresponding storage room (Salas et al. 2008). Similarly, the US potato genebank stores dried seeds with 5% of water content at −20 °C, while a subset of the most requested accessions is maintained at 4 °C, and another copy is sent to genebank Fort Collins Seed Vault for safety duplication (del Río A. pers. com.).

Seed regenerations are necessary to maintain seed stocks, and are performed when viability and/or the amount of seeds drop below the established minimum value. Indeed, regeneration is performed at CIP when viability drops below 85% and/or when the amount of seeds drops below 5000 units. The same criteria as in CIP, is taking into account for the regeneration of wild potato seeds at the Potato Genebank at Balcarce Agricultural Experimental Station of the National Institute of Agricultural Research (INTA) (Digilio A. pers. com.). At the US Potato Genebank, accessions are regenerated every 20 years (del Rio, pers.com.). Seed regeneration procedures define population size and type of crosses (open pollination, reciprocal sibling crosses, or mass pollination), depending on the species reproductive biology (cleistogamous, autogamous, exogamous, or alogamous). CIP has defined 25 plants as the minimum population size for regeneration; meanwhile, the US potato genebank uses 20 plants. Camadro (2012) recommended using 15–25 plants in controlled crosses during the multiplication process. The results of studies that assessed the effects of population size on genetic diversity during regeneration of the accessions, found that a sample of 25 to 30 plants is the optimal number to capture and maintain most of the alleles (Bamberg and del Río 2004), and similar criteria is used by the Potato Genebank at Balcarce. A concern in genebanks are the effects of accession multiplication, since populations derived from different regeneration events can differ significantly (Cadima-Fuentes 2014; Zorrilla et al. 2019b). Currently, the genetic diversity of Solanaceous crops from the principal genebanks is being studied within a similar objectives and approaches outlined in the G2PSOL initiative. As part of this project, the effects of sample size on the genetic diversity of conserved accessions in genebanks is an important issue expected to be solved.

A different strategy is used to preserve accessions of cultivated potatoes, botanical tubers named tuber-seeds are the main type of biological sample in genebanks for maintaining potato characteristics as a clone (asexually) where unique allelic combinations in the individual are preserved. Andean farmers traditionally have been used tuber-seeds as the principal method for conservation of their cultivated potatoes, since is the type of preservation that requires fewer resources in terms of equipment and supplies. Even though tubers conservation in genebanks is less demanding, only allows tuber conservation between 3 and 9 months at temperatures between 0 and 10 °C, depending of the dormancy and quality of the tuber before entering the storage room (JICA 2016). In the same way, the lowland tetraploid landraces, *S. tuberosum* L. Chilotanum Group, is conserved using botanical tubers at Institute of Agricultural Research of Chile and, Agricultural and Livestock Service of Chile (Muñoz et al. 2016).

Other methods, like in vitro slow growth have been used for the conservation of landraces, modern cultivars, and/or specific genotypes, and it eliminates the challenges of external biotic and abiotic factors. This procedure is based on tissue-culture conservation methodology, minimizing tissue growth so subcultures are reduced. Explants, under aseptic conditions, are introduced into glass tubes containing slow growth media and transferred into cultivated chamber where environmental variables, temperature, light intensity, and photoperiod, are regulated. In vitro conservation allows potato samples survive up to two years, depending on the composition of the media and environmental conditions. The culture media frequently used for potato in vitro conservation is Murashige and Skoog supplemented with sorbitol and sucrose, and samples are maintained at temperatures between 6 to 10 °C and low light intensity (Clausen et al. 2010; Bamberg et al. 2016; Muñoz et al. 2019). CIP's potato method (2019) is currently the most efficient in vitro method for conserving potato accessions, which prolonged transference periods from once every 6–8 weeks up to two years. CIP currently maintains the largest in vitro potato collection with 8354 potato in vitro accessions, the majority of which (89.8%) are landraces or "papas nativas" originating mainly from the Andean region, with the remaining accessions being improved varieties and breeding lines (Ellis et al. 2020). In vitro slow growth conservation has been used by farmers of highland communities at the Potato Park in Cusco, Peru, to maintain their native potatoes tuber-seed clean of pest and diseases.

Cryopreservation is another methodology for long-term germplasm preservation where different types of explants are maintained at ultra-low temperatures in liquid nitrogen or liquid nitrogen vapor (Wang et al. 2020), and using osmoprotectant solutions in order to dehydrate the tissues and decrease the formation of ice crystals that would be lethal for cells. Potato seeds and meristems can be preserved and maintain its genetic stability by cryopreservation for longer periods of time compared to any other method (Digilio et al. 2018). This conservation strategy allows the storage of large quantities of samples in reduced spaces and at low costs, and is being employed in the largest genebanks with adequate infrastructure, equipment, trained personnel, and a continuous supply of liquid nitrogen. At CIP, the droplet PVS2 vitrification method preceded by a pre-culture treatment at 6 °C is used for application of cryopreservation for the long-term conservation of a wide diversity of potato genotypes (Panta et al. 2014, 2015) and has a recovery rate of 55–61% (Vollmer et al. 2019). A high-quality management of cryopreservation systems includes periodical viability reassessment, clear recovery criteria and the monitoring of success and contamination rates has been implemented (Vollmer et al. 2016, 2017). Currently, CGIAR in vitro genebanks unite the in vitro slow growth conservation and cryopreservation as part of the clonal crop conservation strategy, where the first is implemented to maintain for a medium-term the active collection, and the latter for the long term conservation of the base collection (Benson et al. 2011).

Another fundamental objective of genebanks is the characterization of genetic resources, in potato different molecular markers have been used to assess genetic variability, population structure, and taxa relationships, but single nucleotide polymorphisms (SNPs) are most frequently used due to their affordable cost and data quality, SNP arrays allow to assess about one million genome-wide SNP's simultaneously in an individual assay, and because provide fundamental information not only for conservation but also for genetic analysis and breeding (Ellis et al. 2018).

DNA storage is another type of sample used for the conservation of genetic resources. However, only fragments of nucleic acids that can be later amplified, cloned, and inserted into another plant. This type of conservation is employed by a limited number of genebanks.

Herbarium specimens are another type of samples representative of potato genetic resources diversity. These collections kept voucher samples of the originally collected material and later regenerations. Herbarium specimens are important to document potato diversity and also permit the correct taxonomic characterization and identification of genebanks collections. Interestingly, DNA samples have been obtained from historical specimens using isolation techniques to determine potato species identity with molecular markers (Ames and Spooner 2008).

The maintenance of genetic resources in their natural environment where the species naturally evolved, is the strategy for in situ conservation. The main goal is to establish genetic reserves that guarantee the dynamic species evolutionary process, favoring the appearance of new allelic variants in natural populations that allow species adaptation in front of changing environments. The most effective method, in economic and political terms, is to implement Genetic Reserves inside existing Protected Areas (Maxted et al. 1997). In order to establish protected areas for in situ conservation, it is fundamental to know species taxonomy, distribution, phenology, genetic characteristics, plant demography, ecology, etc. as well as species diversity in the community of the Protected Areas (Dulloo et al. 2008). Clausen et al. (2018) identified 12 wild potato species growing in different Protected Areas of Argentina, and all these species were included in at least one protected area. More recently, studies of wild potato population species are in progress for the future establishment of a genetic reserves within Los Cardones National Park in Salta province (Kozub et al. 2019), in the Natural Reserve Villavicencio in Mendoza province (Marfil et al. 2015), and in the Natural Reserve Paititi in the southeast of Buenos Aires province (Garavano 2018). In the last area, the wild species *S. commersonii* could lose a high percentage of its distribution range due to agricultural activities. In Bolivia, Cadima-Fuentes et al. (2013), found that only 7 of the 21 Bolivian species were detected in parks and protected areas and recommended an increase in the inventories in these areas. In Peru, Sotomayor and Zorrilla (2019) are developing GIS-based studies for the identification of a network of areas with high diversity of wild potato species that need to be protected from threats such as urbanization, land-use change, mining, etc. One way to protect them is to become "Agrobiodiversity Zones", community-owned territories recognized by the government as prioritized for in situ conservation activities. The establishment of on farm conservation zones not only focused on the conservation of cultivated landraces but also in the fundamental role of local communities in the processes of crop evolution (De Haan et al. 2016a, b, c). One of these initiatives is "The Potato Park", recognized as Agrobiodiversity Zones by the Peruvian Minister of Agriculture and Irrigation (MINAGRI), based on their native, cultural and ecological wealth where indigenous peoples preserve their cultural traditions to manage and maintain genetic resources of their fields and ecosystems. The Potato Park located in the Cusco Inca Sacred valley in Calca province (Peru) comprise and extension of more than 7000 ha, where around 1330 potato landraces and other native Andean crops are cultivated and maintained in a local genebank, managed by four Quechua communities or "ayllus". This example of in situ conservation is characterized by strong interactions between the crops, their wild relatives, and the farmers, promoting different strategies for conservation and sustainable use of these genetic resources (MINAM 2019). Currently, different initiatives and efforts, such as the Papa Andina experience are focused on sustainable agriculture-food system development considering the needs for nutrition security while promoting better crop management and productivity, and the optimization of the potato value chain (Devaux et al. 2020). At present different projects in Andean countries are focused on the conservation of their potato genetic resources.

The in situ strategy could be essential for the conservation of genetic resources, and considering different scenarios of climatic change the distribution of wild potato species is likely to diminish at low altitudes and wild species population could be affected or became extinct (Jarvis et al. 2008). Different approaches, such as environmental niche modeling methods, have been used to evaluate the conservation status 73 wild potatoes maintained in genebanks, revealing high priority for collecting 32 species (43.8%), while 20 species have medium priority for collection and only three species have good representation in ex situ collections (Castañeda-Álvarez et al. 2015). These studies not only support collecting strategies but also help to define zones for in situ conservation through the detection of areas where species are potentially threatened by several factors (urbanization, agriculture expansion, overgrazing, etc.). In front of uncertain scenarios, could be possible to securely preserve diversity in potato, and predict what diversity has been lost or is in imminent danger of being lost, and also estimated the actual economic value, as well as, potential future value of the potato diversity that is not securely conserved (Ellis et al. 2020). The understanding of the diversity and distribution of wild and cultivated potato also contributes to the development of policies on biosafety as it has occurred in Peru (MINAM 2019).

4.6 Conclusions

At present, there is a better understanding of the diversity, distribution, and genetic diversity of potatoes. A recent comprehensive taxonomy of all wild and cultivated potatoes, based on the integration of multiple evidences and phylogenetic relationships between taxa, proposed a framework for further investigation of complex groups as well as endemic species in restricted areas, which have been poorly collected.

Integrative taxonomy also provides hypothesis to study patterns of species diversity and distributions, physical and ecological isolation factors, biological barriers and physiological plasticity, and in particular the role of ploidy, gene flow, and interspecific hybridization in the adaptation of species to different and extreme environment.

Genetic and genomic studies have contributed to understand potato evolution. Recent investigations provide promissory approaches to compare and differentiate potato species genomes that help not only to elucidate the process of evolution, but also to detect alleles related to important agronomic traits. Few wild species have been used to improve cultivated potatoes, and these valuable resources can be incorporate into breeding plans.

Results from different disciplines demonstrated the value of complementary evidences from archaeological remains and phylogeny to support the hypothesis of a single origin of domestication and culture of potatoes occurred in southern Peru, and encouraged to continue research to elucidate the sources and areas of initial cultivation.

Genebanks worldwide guarantee the conservation of valuable potato genetic resources for food security. In addition, advances in ex situ conservation techniques like in vitro and cryoconservation made more efficient sample preservation reducing costs and maintenance space. A stable taxonomic framework could be useful for harmonizing potato nomenclature used in global genebanks and to identify unique and redundant material to promote an efficient conservation through collection homologation.

A better understanding of potato diversity is fundamental for the establishment of protected areas, where populations could be monitored to ensure their persistence in natural habitat or in local communities. Agrobiodiversity Zones are also fundamentals for preservation and sustainable use of potato genetic resources and for local communities' alimentary subsistence.

Acknowledgements This work is dedicated to David Spooner, botanist, indefatigable explorer and passionate taxonomist who led research using new methods and analytical approaches to elucidate the phylogeny and diversity of crop species and wild relatives, fundamentally potatoes, and inspire people and students with his insights.The authors acknowledge Dr. Claudio Galmarini, for his critical revision of the present chapter. Iris Edith Peralta research supported by CONICET and SIIP UNCuyo projects.

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