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Systematics, Diversity, Genetics, and Evolution of Wild and Cultivated Potatoes

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Abstract The common potato, *Solanum tuberosum* L., is the third most important food crop and is grown and consumed worldwide. Indigenous cultivated (landrace) potatoes and wild potato species, all classified as *Solanum* section *Petota*, are widely used for potato improvement. Members of section *Petota* are broadly distributed in the Americas from the southwestern United States to the Southern Cone of South America. The latest comprehensive taxonomic treatment of section *Petota* was published by John (Jack) Hawkes in 1990; it recognized seven cultivated species and 228 wild species, divided into 21 taxonomic series. Since 1990, intensive field collections from throughout the range of the group, coupled with morphological and molecular studies, have halved the number of species and elucidated new ingroup and outgroup relationships. The recent sequencing of the potato genome has greatly accelerated investigation of all aspects of potato biology and allows us to address new questions not conceivable before. The purpose of this review is to provide a historical overview and update since 1990 of the systematics, diversity, genetics, domestication, evolution, and breeding of *Solanum* section *Petota* that will serve as a reference for the next generation of studies in the potato.

Keywords Domestication · Evolution · Genetics · Germplasm · Potato · Systematics · Taxonomy

Table of Contents

- Where do we go From Here? New Discoveries From Whole-Genome DNA Sequencing Data

Literature Cited

Introduction

The common potato, *Solanum tuberosum* L., is grown and consumed worldwide. It is the third most important food crop (FAO, 2013), and has remained so for at least 190 years (Sabine, 1824). *Solanum tuberosum* is the name traditionally used for landrace (indigenous cultivated) populations grown in lowland Chile and in the high Andes. The name *S. tuberosum* is also used for the world's potato cultivars grown since the end of the sixteenth century outside of South America. The modern cultivars are the products of extensive breeding between different cultivar groups and wild species. Landrace potatoes and wild potato species, all classified as *Solanum* section *Petota*, are widely used for potato improvement. Members of section *Petota* are broadly distributed in the Americas from the southwestern United States to the Southern Cone of South America (Hawkes & Hjerting, 1969, 1989; Ochoa, 1990a, 1999; Spooner et al., 2004, 2014). The last comprehensive taxonomic treatment of section *Petota* was published by John (Jack) Hawkes in 1990; it recognized seven cultivated species and 228 wild species, divided into 21 taxonomic series, including 19 series for tuber-bearing species and two series of non-tuberous species. Here we consider section *Petota* to include only the tuber-bearing species. Since 1990, intensive field collections from throughout the range of the group, coupled with morphological and molecular studies, have halved the number of species and elucidated new ingroup and outgroup relationships. The recent sequencing of the potato genome (The Potato Genome Sequencing Consortium, 2011) has greatly accelerated investigation of all aspects of potato biology.

The purpose of our review is to provide a historical overview and update since 1990 of the systematics, diversity, genetics, domestication, evolution, and breeding of *Solanum* section *Petota* that serves as a reference to aid the next generation of studies in the group. It updates reviews of Spooner and Hijmans (2001) and Spooner and Salas (2006) that were bibliographic summaries of taxonomic changes by many authors. This review is intended to provide our current and thoroughly independent taxonomic decisions regarding the number of species and the interrelationships among species in section *Petota*. We begin with a presentation of the genetics of the group because this has historically provided key concepts used to form taxonomic decisions and to choose species for breeding programs. Species names serve many purposes, one of which is to link studies across different publications. Because of the large reduction in species adopted here (Table 1), we use both the names in the original publications, followed by our concept of these species in parentheses, for example: *S. fendleri* (=*S. stoloniferum*).

Table 1 Accepted species (bold Roman type) of *Solanum* section *Petota* with our decisions on synonyms (indented italic text) that were accepted by Hawkes (1990) or subsequent authors, with three-letter standard abbreviations, countries of occurrence, ploidy (and EBN), and nuclear-marker-based cladistic relationships as explained in the text. These taxonomic decisions appear in more detailed monographs for North and Central America (Spooner et al., 2004), southern South America (Spooner et al., in press), northern South America (in preparation), and online on Solanaceae Source (www.http://solanaceaesource.org/)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
Wild species				
Solanum acaule Bitter	acl	ARG, BOL, PER	4*x* (2EBN), 6*x*	Complex[4]
S. acaule f. *incuyo* Ochoa (1994b)				
S. acaule var. *punae* (Juz.) Hawkes				
Solanum acroglossum Juz.	acg	PER	2*x* (2EBN)	3
Solanum acroscopicum Ochoa	acs	PER	2*x*	[4]
S. lopez-camarenae Ochoa				
Solanum ×aemulans Bitter & Wittm.	aem	ARG	3*x*, 4*x* (2EBN)	[4]
S. acaule subsp. *aemulans* (Bitter & Wittm.) Hawkes & Hjert.				
S. ×indunii K.A. Okada & A.M. Clausen				
Solanum agrimonifolium Rydb.	agf	GUA, HON, MEX	4*x* (2EBN)	3+4
Solanum albicans (Ochoa) Ochoa	alb	ECU, PER	6*x* (4EBN)	3+4
S. acaule subsp. *palmirense* Kardolus (1998)				
Solanum albornozii Correll	abz	ECU	2*x* (2EBN)	3
Solanum amayanum Ochoa	amy	PER	2x (2EBN)	4
Solanum anamatophilum Ochoa	amp	PER	2*x* (2EBN)	3
S. peloquinianum Ochoa				
Solanum andreanum Baker	adr	COL, ECU	2*x* (2EBN) 4*x* (4EBN)	3
S. burtonii Ochoa				
S. correllii Ochoa				
S. cyanophyllum Correll				
S. paucijugum Bitter				
S. regularifolium Correll				
S. serratoris Ochoa (1990b).				
S. solisii Hawkes				
S. suffrutescens Correll				
S. tuquerrense Hawkes				
Solanum augustii Ochoa	agu	PER	2*x* (1EBN)	3
Solanum ayacuchense Ochoa	ayc	PER	2*x* (2EBN)	4
Solanum berthaultii Hawkes	ber	ARG, BOL	2*x* (2EBN), 3x	4
S. flavoviridens Ochoa				
S. tarijense Hawkes				

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
S. ×*litusinum* Ochoa				
S. ×*trigalense* Cárdenas				
S. ×*zudaniense* Cárdenas				
Solanum×blanco-galdosii Ochoa	blg	PER	2*x* (2EBN)	3
Solanum boliviense Dunal in DC.	blv	ARG, BOL, PER	2*x* (2EBN)	4
S. astleyi Hawkes & Hjert.				
S. megistacrolobum Bitter				
S. megistacrolobum f. *purpureum* Ochoa (1994b)				
S. sanctae-rosae Hawkes				
S. toralapanum Cárdenas & Hawkes				
Solanum bombycinum Ochoa	bmb	BOL	4*x*	[3+4]
Solanum brevicaule Bitter	brc	ARG, BOL, PER	2*x* (2EBN) 4*x* (4EBN) 6*x* (4EBN)	4
S. alandiae Cárdenas				
S. avilesii Hawkes & Hjert.				
S. gourlayi Hawkes				
S. gourlayi subsp. *pachytrichum* (Hawkes) Hawkes & Hjert.				
S. gourlayi subsp. *saltense* A.M. Clausen & K.A. Okada				
S. gourlayi subsp. *vidaurrei* (Cárdenas) Hawkes & Hjert.				
S. hondelmannii Hawkes & Hjert.				
S. hoopesii Hawkes & K.A. Okada				
S. incamayoense K.A. Okada & A.M. Clausen				
S. leptophyes Bitter				
S. oplocense Hawkes				
S. setulosistylum Bitter				
S. sparsipilum (Bitter) Juz. & Bukasov				
S. spegazzinii Bitter				
S. sucrense Hawkes				
S. ugentii Hawkes & K.A. Okada				
S. virgultorum (Bitter) Cárdenas & Hawkes				
S. ×*subandigena* Hawkes				
Solanum ×brucheri Correll	bru	ARG	3x	[4]
S. ×*viirsoii* K.A. Okada & A.M. Clausen				
Solanum buesii Vargas	bue	PER	2*x* (2EBN)	4

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
Solanum bulbocastanum Dunal in Poir.	blb	GUA, HON, MEX	2*x* (1EBN), 3x	1
S. bulbocastanum subsp. *dolichophyllum* (Bitter) Hawkes				
S. bulbocastanum subsp. *partitum* (Correll) Hawkes				
Solanum burkartii Ochoa	brk	PER	2*x*	4
S. irosinum Ochoa				
S. irosinum forma *tarrosum* Ochoa (1999)				
Solanum cajamarquense Ochoa	cjm	PER	2*x* (1EBN)	3
Solanum candolleanum Berthault	buk	PER	2*x* (2EBN), 3x	4
S. abancayense Ochoa				
S. achacachense Cárdenas				
S. ambosinum Ochoa				
S. ancoripae Ochoa (1999)				
S. antacochense Ochoa				
S. aymaraesense Ochoa				
S. bill-hookeri Ochoa				
S. bukasovii Juz.				
S. bukasovii var. *multidissectum* (Hawkes) Ochoa (1992a)				
S. bukasovii forma *multidissectum* (Hawkes) Ochoa (1999)				
S. canasense Hawkes				
S. canasense var. *xerophilum* (Vargas) Hawkes				
S. chillonanum Ochoa (1989a)				
S. coelestispetalum Vargas				
S. hapalosum Ochoa				
S. huancavelicae Ochoa (1999)				
S. longiusculus Ochoa				
S. marinasense Vargas				
S. multidissectum Hawkes				
S. orophilum Correll				
S. ortegae Ochoa (1998)				
S. pampasense Hawkes				
S. puchupuchense Ochoa (1999)				
S. sarasarae Ochoa				
S. sawyeri Ochoa				
S. saxatile Ochoa (1992b), as 'saxatilis'				

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
S. sicuanum Hawkes (1990)				
S. sparsipilum subsp. *calcense* (Hawkes) Hawkes				
S. tapojense Ochoa				
S. tarapatanum Ochoa				
S. ×*mollepujroense* Cárdenas & Hawkes				
Solanum cantense Ochoa	cnt	PER	2*x* (2EBN)	3
Solanum cardiophyllum Lindl.	cph	MEX	2*x* (1EBN), 3*x*	1
S. cardiophyllum subsp. *lanceolatum* (Berthault) Bitter				
Solanum chacoense Bitter	chc	ARG, BOL, BRA, PAR, PER, URU	2*x* (2EBN), 3x	4
S. arnezii Cárdenas				
S. calvescens Bitter				
S. chacoense subsp. *chacoense*				
S. chacoense subsp. *muelleri* (Bitter) Hawkes				
S. tuberosum subsp. *yanacochense* Ochoa (2001); (=*S. yanacochense* (Ochoa) Gorbatenko (2006))				
S. yungasense Hawkes				
Solanum chilliasense Ochoa	chl	ECU	2*x* (2EBN)	3
Solanum chiquidenum Ochoa	chq	PER	2*x* (2EBN)	3
S. ariduphilum Ochoa				
S. chiquidenum forma *amazonense* Ochoa (1994b)				
S. chiquidenum var. *gracile* Ochoa (1994b)				
S. chiquidenum var. *robustum* Ochoa (1994b)				
Solanum chomatophilum Bitter	chm	ECU, PER	2*x* (2EBN)	3
S. chomatophilum forma *sausianense* Ochoa (1994b)				
S. chomatophilum var. *subnivale* Ochoa (1994b)				
S. huarochiriense Ochoa				
S. jalcae Ochoa				
S. pascoense Ochoa				
S. taulisense Ochoa				
Solanum clarum Correll	clr	GUA, MEX	2*x*	1
Solanum colombianum Dunal	col	COL, ECU, PER, VEN	4*x* (2EBN)	3+4
S. cacetanum Ochoa				
S. calacalinum Ochoa				

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
S. jaenense Ochoa				
S. moscopanum Hawkes				
S. nemorosum Ochoa				
S. orocense Ochoa				
S. otites Dunal				
S. pamplonense L.E. López				
S. subpanduratum Ochoa				
S. paramoense Bitter				
S. sucubunense Ochoa				
Solanum commersonii Dunal	cmm	ARG, BRA, URU	2*x* (1EBN), 3*x*	
Solanum contumazaense Ochoa	ctz	PER	2*x* (2EBN)	3
Solanum demissum Lindl.	dms	GUA, MEX	6*x* (4EBN)	Complex[3]
S. ×*semidemissum* Juz.				
Solanum ×doddsii Correll	dds	BOL	2*x* (2EBN)	4
Solanum dolichocremastrum Bitter	dcm	PER	2*x* (1EBN)	3
S. chavinense Correll				
S. huanuchense Ochoa				
Solanum ×edinense Berthault	edn	MEX	5*x*	[4]
S. ×*edinense* subsp. *salamanii* (Hawkes) Hawkes				
Solanum ehrenbergii (Bitter) Rydb.	ehr	MEX	2*x* (1EBN)	1
S. cardiophyllum subsp. *ehrenbergii* Bitter				
Solanum flahaultii Bitter	flh	COL	4*x*	3+4
S. neovalenzuelae L.E.López				
Solanum gandarillasii Cárdenas	gnd	BOL	2*x* (2EBN)	4
Solanum garcia-barrigae Ochoa	gab	COL	4*x*	3+4
S. donachui (Ochoa) Ochoa				
Solanum gracilifrons Bitter	grc	PER	2*x*	4
Solanum guerreroense Correll	grr	MEX	6*x* (4EBN)	[Complex[3]]
Solanum hastiforme Correll	hsf	PER	2*x* (2EBN)	4
Solanum hintonii Correll	hnt	MEX	2*x*	1
Solanum hjertingii Hawkes	hjt	MEX	4*x* (2EBN)	1+4
S. hjertingii var. *physaloides* (Correll) Hawkes				
S. leptosepalum Correll[5]				
S. matehualae Hjert. & T.R. Tarn				
Solanum hougasii Correll	hou	MEX	6*x* (4EBN)	Complex[3]

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
Solanum huancabambense Ochoa	hcb	PER	2*x* (2EBN)	3
Solanum humectophilum Ochoa	hmp	PER	2*x* (1EBN)	3
Solanum hypacrarthrum Bitter	hcr	PER	2*x* (1EBN)	3
S. guzmanguense Whalen & Sagást.				
Solanum immite Dunal	imt	PER	2*x* (1EBN), 3*x*	3
S. yamobambense Ochoa				
Solanum incasicum Ochoa	ins	PER	2*x* (2EBN)	
Solanum infundibuliforme Phil.	inf	ARG, BOL	2*x* (2EBN)	4
Solanum iopetalum (Bitter) Hawkes	iop	MEX	6*x* (4EBN)	3+4
S. brachycarpum (Correll) Correll				
Solanum jamesii Torr.	jam	MEX, USA	2*x* (1EBN)	1
Solanum kurtzianum Bitter & Wittm.	ktz	ARG	2*x* (2EBN)	4
S. ruiz-lealii Brücher				
Solanum laxissimum Bitter	lxs	PER	2*x* (2EBN)	4
S. neovargasii Ochoa				
S. santolallae Vargas				
Solanum lesteri Hawkes & Hjert.	les	MEX	2*x*	1
Solanum lignicaule Vargas	lgl	PER	2*x* (1EBN)	4
Solanum limbaniense Ochoa	lmb	PER	2*x* (2EBN)	4
Solanum lobbianum Bitter[6]	lbb	COL	4*x* (2EBN)	3+4
Solanum longiconicum Bitter	lgc	CRI, PAN	4*x*	3+4
Solanum maglia Schltdl.	mag	ARG, CHL	2*x*, 3*x*	
Solanum malmeanum Bitter		ARG, BRA, PAR, URU	2*x* (1EBN) 3*x*	
Solanum medians Bitter	med	CHL, PER	2*x* (2EBN), 3*x*	4
S. arahuayum Ochoa (1994a)				
S. sandemanii Hawkes				
S. tacnaense Ochoa				
S. weberbaueri Bitter				
Solanum ×michoacanum (Bitter) Rydb.	mch	MEX	2*x*	[1]
Solanum microdontum Bitter	mcd	ARG, BOL	2*x* (2EBN), 3*x*	4
S. microdontum subsp. *gigantophyllum* (Bitter) Hawkes & Hjert.				
S. microdontum var. *montepuncoense* Ochoa				
Solanum minutifoliolum Correll	min	ECU	2*x* (1EBN)	3
Solanum mochiquense Ochoa	mcq	PER	2*x* (1EBN)	3
S. chancayense Ochoa				
S. incahuasinum Ochoa				

Table 1 (continued)

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Solanum morelliforme Bitter & Muench	mrl	BOL, GUA, MEX, HON	2*x*	1
Solanum multiinterruptum Bitter	mtp	PER	2*x* (2EBN), 3x	4
S. chrysoflorum Ochoa				
S. moniliforme Correll				
S. multiinterruptum forma *albiflorum* Ochoa				
S. multiinterruptum forma *longipilosum* Correll				
S. multiinterruptum var. *machaytambinum* Ochoa (1999b)				
Solanum neocardenasii Hawkes & Hjert.	ncd	BOL	2x	
Solanum neorossii Hawkes & Hjert.	nrs	ARG	2x	4
Solanum neovavilovii Ochoa	nvv	BOL	2*x* (2EBN)	4
Solanum ×neoweberbaueri Wittm.	nwb	PER	3*x*	[4]
Solanum nubicola Ochoa	nub	PER	4*x* (2EBN)	4
Solanum okadae Hawkes & Hjert.	oka	BOL	2x	[4]
Solanum olmosense Ochoa	olm	ECU, PER	2*x* (2EBN)	3
Solanum oxycarpum Schiede	oxc	MEX	4*x* (2EBN)	3+4
Solanum paucissectum Ochoa	pcs	PER	2*x* (2EBN)	3
Solanum pillahuatense Vargas	pll	PER	2*x* (2EBN)	4
Solanum pinnatisectum Dunal	pnt	MEX	2*x* (1EBN)	1
Solanum piurae Bitter	pur	PER	2*x* (2EBN)	3
Solanum polyadenium Greenm.	pld	MEX	2*x*	1
Solanum raphanifolium Cárdenas & Hawkes	rap	PER	2*x* (2EBN)	4
S. hawkesii Cárdenas				
Solanum raquialatum Ochoa	raq	PER	2*x* (1EBN)	3
S. ingaefolium Ochoa				
Solanum ×rechei Hawkes & Hjert.	rch	ARG	2x, 3x	[4]
Solanum rhomboideilanceolatum Ochoa	rhl	PER	2*x* (2EBN)	3
Solanum salasianum Ochoa	sls	PER	2*x*	4
Solanum ×sambucinum Rydb.	smb	MEX	2x	[1]
Solanum scabrifolium Ochoa	scb	PER	2*x*	3
Solanum schenckii Bitter	snk	MEX	6*x* (4EBN)	Complex[3]
Solanum simplicissimum Ochoa (1989b)	smp	PER	2*x* (1EBN)	3
Solanum sogarandinum Ochoa	sgr	PER	2*x* (2EBN), 3x	4
Solanum stenophyllidium Bitter	sph	MEX	2*x* (1EBN)	1
S. brachistotrichium (Bitter) Rydb.				
S. nayaritense (Bitter) Rydb.				
Solanum stipuloideum Rusby[7]	stp	BOL	2*x* (1EBN)	

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
S. circaeifolium Bitter				
S. circaeifolium subsp. *quimense* Hawkes & Hjert.				
S. capsicibaccatum Cárdenas				
S. soestii Hawkes & Hjert.				
Solanum stoloniferum Schltdl.	sto	MEX, USA	4*x* (2EBN)	Complex[3]
S. fendleri A. Gray				
S. fendleri subsp. *arizonicum* Hawkes				
S. papita Rydb.				
S. polytrichon Rydb.				
S. stoloniferum subsp. *moreliae* Hawkes				
Solanum tarnii Hawkes & Hjert.	trn	MEX	2*x*	1
Solanum trifidum Correll	trf	MEX	2*x* (1EBN)	1
Solanum trinitense Ochoa	trt	PER	2*x* (1EBN)	3
Solanum ×vallis-mexici Juz.	vll	MEX	3*x*	
Solanum venturii Hawkes & Hjert.	vnt	ARG	2*x* (2EBN)	4
Solanum vernei Bitter & Wittm.	vrn	ARG	2*x* (2EBN)	4
S. vernei subsp. *ballsii* (Hawkes) Hawkes & Hjert.				
Solanum verrucosum Schltdl.	ver	MEX	2*x* (2EBN), 3x, 4x	4
S. macropilosum Correll				
Solanum violaceimarmoratum Bitter	vio	BOL, PER	2*x* (2EBN)	4
S. multiflorum Vargas				
S. neovavilovii Ochoa				
S. urubambae Juz.				
S. villuspetalum Vargas				
Solanum wittmackii Bitter	wtm	PER	2*x* (1EBN)	[3]
***S*olanum woodsonii** Correll	wds	PAN	4*x*	4
Cultivated species[8]				
Solanum tuberosum L. Chilotanum group	tub	CHL (Chilean landraces	4*x* (4EBN)	4
S. tuberosum subsp. *tuberosum*				
Solanum tuberosum Andigenum group	tub	Landraces from W Venezuela south to N Argentina	2*x* (2EBN), 3*x* 4*x* (4EBN)	4
S. chaucha Juz. & Bukasov				
S. phureja Juz. & Bukasov				
S. phureja subsp. *estradae* (L. López) Hawkes				
S. phureja subsp. *hygrothermicum* (Ochoa) Hawkes				

Table 1 (continued)

Taxon (Synonyms from Hawkes 1990 or later descriptions indented). Taxa published subsequent to Hawkes (1990) are referenced in this column and in the Literature Cited.	Code	Countries[1]	Ploidy and (EBN) [2]	Nuclear clade[3]
S. stenotomum Juz. & Bukasov				
S. stenotomum Juz. & Bukasov subsp. *goniocalyx* (Juz. & Bukasov) Hawkes				
S. tuberosum subsp. *andigenum* Hawkes				
Solanum ajanhuiri Juz. & Bukasov	ahj	BOL, PER	2*x* (2EBN)	4
Solanum curtilobum Juz. & Bukasov	cur	BOL, PER	5*x*	4
Solanum juzepczukii Juz.	juz	ARG, BOL, PER	3*x*	4

[1] County codes are *ARG* Argentina, *BOL* Bolivia, *BRA* Brazil, *CHL* Chile, *COL* Colombia, *CRI* Costa Rica, *ECU* Ecuador, *GUA* Guatemala, *HON* Honduras, *MEX* Mexico, *PAN* Panama, *PAR* Paraguay, *PER* Peru, *URU* Uruguay, *USA* United States of America, *VEN* Venezuela

[2] Spooner & Hijmans (2001) present references to ploidy and EBN determinations

[3] Cladistic relationships are based on plastid or nuclear clade investigations as described in the text; designations in brackets represent our hypotheses of relationships of species not yet investigated based on morphological similarity to investigated species. Nuclear clade 1 here includes species placed in both clades 1 and 2 of the plastid results

[4] Cai et al. (2012) document the complex multi-clade hybrid origins of these species

[5] *Solanum leptosepalum* changed from its synonymy under *S. stoloniferum* by Spooner et al. (2004)

[6] Hawkes (1992) identified *S. lobbianum* as *S. paucijugum* (=*S. andreanum*), but we recognize it (Spooner et al., 1995a) as a distinct species

[7] Spooner & Knapp (2013) provide the rationale for the adoption of *S. stipuloideum*

[8] Ovchinnikova et al. (2011) present a monograph of the cultivated potato species

Genetic Basis of Species Boundaries in Potatoes

Self-Incompatibility

Most diploid tuber-bearing *Solanum* species are self-incompatible due to a genetically-based gametophytic self-incompatibility system (Pushkarnath, 1942; Pandey, 1962). The style produces an S-RNase that inhibits the growth of genetically matching pollen tubes (Luu et al., 2000). The S locus and S-RNase genes have been localized on chromosome 1 (Tanksley & Loaiza-Figueroa, 1985; Rivard et al., 1996). Within wild species populations, self-compatible plants have occasionally been reported (Pushkarnath, 1942; Pandey, 1962; Cipar et al., 1964; De Jong et al., 1971; Oldster & Hermsen, 1976; De Jong & Tai, 1977; Hermsen, 1978; Birhman & Hosaka, 2000; Phumichai et al., 2005). In some plants of the wild species *S. chacoense*, self-compatibility is controlled by the dominant allele of an S-locus inhibitor gene (*Sli*) (Hosaka & Hanneman, 1998a) that is independent of the S locus. Unlike the S locus, which is expressed in the gametophyte, the *Sli* gene is expressed in the sporophyte. The *Sli* gene has been mapped to the distal end of chromosome 12 (Hosaka & Hanneman,

1998b). In addition to *Sli* in *S. chacoense*, a diploid *S. tuberosum* clone (US-W4) expresses a dominant self-incompatibility inhibitor (De Jong et al., 1971). The genetic basis of self-compatibility in US-W4 is not known.

In contrast to diploid potatoes, tetraploid potatoes (both wild and cultivated) are self-compatible. The breakdown of the gametophytic self-incompatibility mechanism in polyploid species is a common phenomenon in angiosperms (Frankel & Galun, 1977; Levin, 1983). In tetraploids, the pistil is still functional in the incompatibility reaction. However, since the pollen is diploid rather than monoploid, it does not elicit an incompatibility response. The molecular basis for the loss of self-incompatibility in polyploids is not understood (Comai, 2005).

When the cultivated potato or its *Sli*-bearing wild relatives are self-pollinated, a high degree of inbreeding depression is observed in the form of flower bud abortion, lack of flower bud formation, and sterility (De Jong et al., 1971; Birhman & Hosaka, 2000). In addition, selfing causes reductions in vigor and yield, presumably because these traits are controlled largely by heterotic genetic effects (Krantz, 1924, 1929; De Jong et al. 1971; Mendiburu & Peloquin, 1977; Ross, 1986; Golmirzaie et al., 1998). After several generations of self-pollination of the diploid wild species *S. chacoense*, however, vigorous, fertile clones were produced (Phumichai et al., 2005). In fact, recent SNP analyses of ten wild potato relatives previously used in cultivar development by potato breeders have revealed unexpectedly high levels of homozygosity (Hirsch et al., 2013). Assumptions about abundant heterozygosity within wild populations are called into question as a result of these initial findings. Perhaps wild and cultivated potatoes are actually somewhat tolerant of inbreeding.

Unilateral Incompatibility

Unilateral incompatibility is a phenomenon in which self-compatible species can be crossed as a female, but not as a male, to self-incompatible species (Abdalla & Hermsen, 1972). Pollen tubes fail to penetrate stylar tissue in self-incompatible (female) × self-compatible (male) crosses. Although most diploid potato species are self-incompatible, the Mexican diploid species *S. verrucosum* is self-compatible. *Solanum verrucosum* can be crossed as a female, but not as a male, to self-incompatible species (Dinu et al., 2005; Jansky & Hamernik, 2009). The stylar tissue of *S. verrucosum* does not produce the S-RNases that inhibit pollen tube growth in incompatible crosses (Eijlander, 1998). This is likely why it can be used as a female parent in crosses to species in section *Petota* (Hermsen & Ramanna, 1976; Jansky & Hamernik, 2009).

It is sometimes possible to find exceptional plants that do not exhibit unilateral incompatibility in self-incompatible × self-compatible interspecific crosses (Pandey, 1962). The identification of such plants allows a breeder to overcome the unilateral incompatibility crossing barrier. For example, exceptional plants ("acceptors") that accept *S. verrucosum* pollen and produce fertile hybrids have been reported (Eijlander et al., 2000). Apparently some "acceptor" plants will accept pollen of any other plant of *S. verrucosum*, while others only accept pollen from certain *S. verrucosum* plants (Hermsen, 1978).

Male Sterility

Male sterility is common in potato cultivars (Krantz, 1924; Howard, 1970). Because the marketable product in potato is not botanical seed, there is no selection pressure for fertility in cultivars. In fact, fruit development may partition resources away from tuber yield, so breeders may inadvertently select against high fertility (Jansky & Thompson, 1990). In addition, recessive sterility alleles can accumulate in tetraploid potato cultivars because they are easily masked by the additional chromosomal sets and are rarely found in a homozygous condition (Krantz, 1924; Lindhout et al., 2011).

Interactions between cytoplasmic and nuclear genes commonly lead to male sterility in potato interspecific hybrids. Cytoplasmic-genetic male sterility has been reported in a number of cultivated × wild potato species hybrids (Grun & Aubertin, 1966; Sanford and Hanneman 1979; Hanneman & Peloquin, 1981; Masuelli & Camadro, 1997; Camadro et al., 1998; Carputo et al., 2000b, 2003b; Jansky & Peloquin, 2006; Caruso et al., 2008; Masuelli et al., 2009; Jansky, 2010; Weber et al., 2012; Larrosa et al., 2012). For example, crosses between Chilotanum group (see "Cultivated Potato Taxonomy and Phylogeny" below for cultivated species group nomenclature) haploids and Andigenum group clones produce male fertile hybrids when the haploids are the male parent, but male sterile hybrids when the haploids are the female parent (Grun et al., 1962; Ross et al., 1964; Carroll, 1975). Nuclear genes that restore fertility to interspecific hybrids have been reported (Iwanaga et al., 1991; Tucci et al., 1996). Cytoplasmic-genetic male sterility provides an isolating mechanism to help maintain the integrity of sympatric species (Hosaka & Sanetomo, 2012, 2013).

2n Gametes

Numerically unreduced (2n) gametes are believed to have been responsible for polyploidization in potato (Den Nijs & Peloquin, 1977a; Camadro & Peloquin, 1980; Camadro et al., 2004). 2n gametes are typically produced by recessive alleles of genes that control meiosis. When homozygous, these mutations interrupt meiosis so that gametes contain the parental (sporophytic) chromosome number rather than half that number. Meiotic mutations occur naturally and frequently in cultivated and wild potatoes (Peloquin et al., 1999; Carputo et al., 2000a). Some meiotic mutations result in the production of 2n eggs (Stelly & Peloquin, 1986b; Werner & Peloquin, 1991a), while others produce 2n pollen (Quinn et al., 1974; Mok & Peloquin, 1975; Den Nijs & Peloquin, 1977a; Masuelli et al.,1992; Iwanaga & Peloquin,1982; Watanabe & Peloquin, 1991; Masuelli et al., 1992; Hanneman, 1999; Camadro et al., 2008). Meiotic mutations typically exhibit variable expressivity, so homozygous recessive plants produce both 2n and n gametes (Mok & Peloquin, 1975; Ortiz & Peloquin, 1992; Carputo et al., 2000a, 2003a; Carputo, 2003). However, as discussed below, a cross between a tetraploid and a 2n gamete-producing diploid will produce only tetraploid offspring. The union of an n (2x) gamete from a tetraploid and an n (x) gamete from a diploid will produce a seed with a triploid embryo but inviable endosperm. 2n pollen is easily detected microscopically because diploid (2x) pollen grains are larger than monoploid (1x) pollen grains (Quinn et al., 1974). 2n eggs can also be detected microscopically via a stain clearing technique (Stelly et al., 1984), but this is a laborious procedure and not practical for large-scale screening. Diploid clones

that produce 2n eggs can be identified by simply crossing them as females to tetraploids (Erazzú & Camadro, 2006). If seeds are produced, then the diploid parent produces 2n eggs.

The mechanism of 2n gamete production determines the genetic composition of the gametes. Normally, in anthers, the four products of meiosis are separated so that their poles define a tetrahedron and cytokinesis produces four haploid microspores. In contrast, a "parallel spindles" mutation produces two microspores, each with an unreduced (sporophytic) chromosome number. The first division is normal, but in the second division, the spindles are parallel and cytokinesis produces two diploid microspores. Even though the first meiotic division occurs in this mutant, the genetic result of parallel spindles is equivalent to a first division restitution (FDR) genetic mechanism because gametes contain non-sister chromatids from the centromere to the first crossover. Consequently, all loci in this region have the same genetic constitution in the gamete as that of the parent (Park et al., 2007; Peloquin et al., 2008). In the chromosomal region beyond the first crossover, half of the loci that were heterozygous in the parent will remain so in 2n gametes. There is typically only one crossover per chromosome in potato (Yeh et al. 1964; Park et al., 2007). Consequently, FDR 2n gametes transmit approximately 80 % of the diploid parent heterozygosity to tetraploid offspring. They provide a unique and powerful method of transmitting blocks of advantageous dominance (intralocus) and epistatic (interlocus) interactions to polyploid offspring even following meiosis, which usually breaks up such interactions.

While the genetic consequence of 2n pollen formation in potatoes is typically FDR, 2n eggs are formed by a second division restitution (SDR) mechanism (Stelly & Peloquin, 1986a; Werner & Peloquin, 1990). The SDR gametes contain sister chromatids from the centromere to the first crossover. SDR 2n gametes transmit less than 40 % of heterozygosity to offspring (Peloquin, 1983; Peloquin et al., 2008).

Chromosomal regions near the centromere carry major genes that contribute to yield in potatoes (Buso et al., 1999b). These regions are transmitted intact to the tetraploid level via FDR 2n gametes such as the products of the parallel spindles mutant. An ortholog of the parallel spindles gene (*AtPS1*) has been isolated and characterized in *Arabidopsis* (d'Erfurth et al., 2008). The AtPS1 protein appears to have a regulatory function and is conserved throughout the plant kingdom. The combination of a common mutation that produces FDR 2n gametes, a high rate of transmission of allelic interactions via FDR 2n gametes, a strong heterotic yield response in potatoes, and the positioning of yield enhancing genes near the centromere provide an advantageous set of circumstances to realize high productivity in the evolution of tetraploid potato.

Endosperm Balance Numbers

Endosperm development is critical for viable seed production in potatoes. Intraspecific, intraploidy crosses in potatoes typically produce viable seeds containing well-developed endosperm. Conversely, in most interploidy crosses, inviable seeds are produced due to endosperm failure (Brink & Cooper, 1947). However, endosperm failure is observed in some intraploidy, interspecific crosses. Conversely, sometimes interploidy, interspecific crosses succeed. The endosperm balance number (EBN) hypothesis proposes that a 2 maternal:1 paternal ratio of genes, rather than genomes, is necessary for normal endosperm development in potatoes (Johnston et al., 1980).

The genetic basis of these endosperm balance factors has yet to be elucidated, although genetic models have been proposed (Ehlenfeldt & Hanneman, 1988a; Camadro & Masuelli, 1995). Genes on more than one chromosome appear to control EBN (Johnston & Hanneman, 1996). Species in section *Petota* have been assigned endosperm balance numbers (EBN) based on their ability to hybridize with each other (Hanneman, 1994). Viable seeds will be produced from crosses between plants with matching EBN values, as long as other hybridization barriers are absent. Ploidy and EBN combinations in potatoes include 6x (4EBN), 4x (4EBN), 4x (2EBN), 2x (2EBN) and 2x (1EBN).

Hawkes (1988, 1990) proposed that wild potato species arose in Mexico and then spread to South America. Most of the diploid Mexican species are 1EBN (with the exception of *S. verrucosum*, which is 2EBN), while most of the diploid South American species are 2EBN (Table 1). Hence, the South American diploid 2EBN species may have evolved from the 1EBN Mexican species (Hawkes & Jackson, 1992). Hawkes proposed a reasonable hypothesis that *S. verrucosum* in Mexico today could be explained by the migration of the diploid 2EBN South American species back north.

Breeders use EBN values to predict crossing success. If two species differ in EBN by a factor of two, then doubling the genome of the species with the lower chromosome number will double its EBN value and increase the probability of hybridization success. Doubling can be achieved via somatic genome duplication (Ross et al., 1967; Johnston & Hanneman, 1982; Sonnino et al., 1988; Carputo et al., 1997, 2000c) or by selecting individuals that produce 2n gametes (Johnston & Hanneman, 1980, 1982; Carputo et al., 1997, 2000c; Hayes & Thill, 2002). Endosperm balance number can be reduced through anther culture or parthenogenesis, as discussed below. It is important to note that, while knowledge of EBN and 2n gamete production often allows for successful cross prediction, there are exceptions. Sometimes intra-EBN crosses fail and, at other times, inter-EBN crosses succeed even without the presence of 2n gametes. Endosperm balance number, therefore, is only one component of a complex system of pre-and post-zygotic interspecific crossing barriers (Masuelli & Camadro, 1997; Chen et al., 2004).

Endosperm balance number and 2n gametes have played a pivotal role in the evolution of both auto- and allopolyploidy in *Solanum* species (Den Nijs & Peloquin, 1977a, b; Camadro & Peloquin, 1980; Iwanaga & Peloquin, 1982; Carputo et al., 2003a). Because 2n gametes are common in wild *Solanum* species, they likely contributed to the production of spontaneous tetraploids (Marks, 1966; Quinn et al., 1974; Den Nijs & Peloquin, 1977a; Werner & Peloquin, 1991a). Unilateral sexual polyploidization occurs when hybrids between 4x (4EBN) species and 2n gamete-producing 2x (2EBN) species produce only tetraploid offspring. Triploid seeds are inviable due to endosperm failure, as discussed above. Bilateral sexual polyploidization is also possible when 2n gametes from two diploid species unite to produce tetraploid offspring. In contrast to somatic doubling, sexual polyploidization minimizes the level of inbreeding in a new tetraploid (Den Nijs & Peloquin, 1977a). Disomic polyploid wild potato species are likely the product of bilateral sexual polyploidization (Ortiz & Ehlenfeldt, 1992).

In addition to contributing to recurrent polyploidization, EBN may also serve a valuable function as an isolating mechanism (Ortiz & Ehlenfeldt, 1992). Sympatric species with matching ploidy levels may be sexually incompatible due to differences in EBN values. For example, *S. chacoense* (2x, 2EBN) and *S. commersonnii* (2x, 1EBN)

have overlapping ranges in Argentina. However, species integrity may be maintained by EBN incompatibility (Ortiz & Ehlenfeldt, 1992). The genes governing EBN have not been identified, so this biological factor governing species integrity is speculative.

Another evolutionary advantage of sexual polyploidization is that it allows for recurrent production of new tetraploids with different combinations of species and clones involved. It is interesting to note that a self-incompatible diploid will produce exclusively tetraploid offspring when self-pollinated, if it produces both 2n pollen and 2n eggs. As described above, self-incompatibility breaks down due to competitive interaction of S-alleles when heteroallelic pollen tubes interact with the style (Mok et al., 1976). The high frequency of the parallel spindles allele for 2n pollen production in potato cultivars supports the idea that tetraploid cultivated potatoes arose via sexual polyploidization (Iwanaga & Peloquin, 1982; Carputo et al., 2003a).

Stylar Barriers

Knowledge of EBN values helps to predict post-zygotic hybridization barriers in potatoes. However, other hybridization barriers are common among species of *Solanum* section *Petota* (Camadro et al., 2004; Jansky, 2006). Consequently, while matching EBN values are necessary for successful hybridization, they are not always sufficient. An important and common pre-zygotic hybridization barrier is the inhibition of pollen tube elongation by stylar tissue. It has been reported in many inter- and intra-EBN crosses (Camadro & Peloquin, 1981; Fritz & Hanneman, 1989; Novy & Hanneman, 1991; Erazzú et al., 1999; Peloquin et al., 1999; Raimondi & Camadro, 2003; Jansky & Hamernik, 2009; Masuelli et al., 2009; Weber et al., 2012). Pollen tube growth may be impeded in the top, middle or bottom of the style (Camadro et al., 2004). A few seeds are sometimes produced in incompatible crosses, indicating that stylar barriers are incomplete in some cases. A gene-for-gene interaction between stylar tissue and pollen has been proposed (Camadro et al., 2004). This hybridization barrier helps to maintain the identity of sympatric species with identical EBN values. Camadro et al. (2004) argue that genetic cross-incompatibility systems, such as that resulting from pollen-style interactions, are necessary for sympatric species to maintain their integrity.

Dihaploids

Haploids are sporophytes with the gametophytic chromosome number. In potatoes, haploids derived from tetraploids are commonly called dihaploids to indicate that they contain two sets of chromosomes. Dihaploids provide a mechanism for direct gene transfer from most of the wild diploid potato relatives and allow breeders to work at the diploid level. Dihaploids can also be used to measure the genetic load in the tetraploids from which they are derived, since they reveal deleterious alleles that were hidden in the tetraploids (De Jong et al. 1971).

Dihaploids are easily produced from female fertile tetraploid clones via parthenogenesis (Hougas et al., 1958; von Wangenheim et al., 1960). Selected diploid *S. tuberosum* Andigenum group (in literature these clones formerly referred to as cultivar group Phureja) ‘pollinator’ clones produce diploid offspring when crossed to tetraploids. In these crosses, both sperm cells from the pollinator enter the central cell,

allowing normal endosperm to develop. This stimulates the division of the egg cell in the absence of fertilization, resulting in the production of a dihaploid (2x) embryo (Von Wangenheim et al., 1960; Montelongo-Escobedo & Rowe, 1969). Sometimes, functional 2n pollen in the pollinator produces tetraploid offspring. It is important to distinguish between seeds that resulted from fertilization of the egg cell by 2n pollen (which would be tetraploid) and those that were not (and are therefore dihaploid). 'Pollinators' have been selected for homozygosity of a dominant gene that produces a small dark spot on seeds. Seeds expressing the marker are hybrids and are therefore discarded; seeds lacking the marker are retained with the expectation that they are dihaploids (Peloquin & Hougas, 1959; Hermsen & Verdenius, 1973).

Populations of dihaploids provide unique opportunities for the genetic analysis of polygenic traits (Hougas et al., 1958; Kotch et al., 1992). A population of dihaploids from a single heterozygous tetraploid clone represents a random pool of female gametes. Genetic analyses can be carried out on this population without the confounding effects of fertilization. In addition, genetic variability hidden in polyploids can be revealed in populations of dihaploids (Peloquin et al., 1991). As a result of segregation, dihaploids may express traits that were not found in their tetraploid parents. Genetic variation among dihaploids for plant and tuber traits is common and has been widely reported (Peloquin & Hougas, 1960; Matsubayashi, 1979; De Maine, 1984a, b; Rousselle-Bourgeois & Rousselle, 1992; Hutton, 1994). Disease resistance traits are also variable among dihaploids, with some dihaploid clones exhibiting better resistance than their parents. Dihaploids with resistance to late blight, Verticillium wilt, soft rot, common scab, blackleg, potato virus X, and potato cyst nematode have been reported (Hutten et al., 1995b; Carputo et al., 1996; Jansky et al., 2003; Ercolano et al., 2004; Bradshaw et al., 2006b). Dihaploid populations have been used to characterize the genetic basis of total tuber yield, average tuber weight, tuber number, dry matter content, tuber dormancy, vine maturity, and tuber glucose levels (Kotch et al., 1992). Because dihaploids form spontaneously from crosses with certain 'pollinator' clones, they may provide an opportunity to reduce ploidy in natural systems.

Tetraploid potatoes are typically more vigorous and higher-yielding than their dihaploid offspring (Peloquin & Hougas, 1960; De Maine, 1984a; Kotch et al., 1992). The lower vigor and yield in dihaploids is likely due to ploidy reduction and inbreeding depression. The magnitude of this loss at the diploid level varies depending on the tetraploid clone from which the dihaploids were derived (Kotch et al., 1992).

Potato monoploids (1x) can be produced from diploids via anther culture (Veilleux et al., 1985) or pollination (Uijtewaal et al., 1987). While the production of monoploids through anther culture is possible, it can be difficult because it requires the presence of genes for androgenic competence ("tissue culturability"), which are not found in all potato cultivars (Sonnino et al., 1989). A "monoploid sieve" selects against deleterious recessive alleles, allowing only the genotypes with high fitness values to develop into monoploid plants. These monoploids can be somatically doubled to produce homozygous diploids for heterosis breeding (Lightbourn & Veilleux, 2007). The first published potato genome sequence was based on the homozygous doubled monoploid DM1-3 (The Potato Genome Consortium, 2011). This has provided the structural framework for the sequencing of heterozygous genomes.

Dihaploid-Wild Species Hybrids

Wild relatives of potatoes are commonly used in breeding programs as sources of genes not found in cultivated potatoes (Leue, 1983; Hermundstad & Peloquin, 1986; Yerk & Peloquin, 1989, 1990; Jansky et al., 1990; Watanabe et al., 1995; Serquen & Peloquin, 1996; Tucci et al., 1996; Oltmans & Novy, 2002; Weber & Jansky, 2012). One strategy to access wild *Solanum* germplasm is through hybridization with dihaploids of tetraploid potato cultivars. Dihaploid-wild species hybrids allow breeders to capture valuable genes from wild species in an adapted form that can be maintained clonally as tubers.

Yield heterosis often is observed in dihaploid-wild species hybrids (Leue, 1983; Hermundstad & Peloquin, 1986; Santini et al., 2000). The high yield and large tuber size in hybrids allows breeders to determine the contributions of wild species to tuber traits such as dry matter content, dormancy, starch composition, nutritional components, and processing quality (Yerk & Peloquin, 1989, 1990; Jansky et al., 1990; Rousselle-Bourgeois & Rousselle, 1992; Serquen & Peloquin, 1996; Santini et al., 2000; Oltmans & Novy, 2002; Ortega et al., 2005). Many dihaploid-wild species hybrids produce edible tubers with acceptable appearance, even though they contain 50 % wild species germplasm. In addition to variation for tuber traits, dihaploid-wild species hybrids exhibit useful variation for disease resistance and stress tolerance (Carputo et al., 1996, 2000c; Tucci et al., 1996; Jansky & Rouse, 2000; Ortega et al., 2005; Hamernik et al., 2009; Weber & Jansky, 2012).

Tetraploid Genetics

Tetraploid potatoes, 2n=4x=48, contain four sets of chromosomes (4x) in the sporophyte (2n) generation with 48 chromosomes in each somatic cell. Gametes (n) from a cultivar are 2x=24. The cultivated potato is considered to be an autopolyploid and, as such, exhibits tetrasomic inheritance (Howard, 1970; Ross, 1986; Hawkes, 1990). In autotetraploids, three types of gene segregation are possible, depending on the proximity of the gene of interest to the centromere (Little, 1952; Burnham, 1962). If the gene is close to the centromere, then a crossover between that gene and the centromere is unlikely to occur during meiosis and that gene will experience chromosome segregation. That is, the gene segregates with the chromosome on which it resides. Consequently, a triplex (AAAa) genotype will produce 50 % AA and 50 % Aa gametes; no aa gametes are produced. In the other two types of segregation, called random chromatid segregation and maximum equational segregation, the gene is far enough from the centromere that a crossover is likely to occur during meiosis. Consequently, it is possible for the sister chromatids carrying the recessive allele to be transmitted to the same gamete (aa) through a process called double reduction. Four requirements must be met to achieve double reduction: 1) A quadrivalent must form. That is, all four homologous chromosomes must associate with each other through crossing-over at meiosis; 2) Crossing-over must occur between the gene of interest and the centromere; 3) The two pairs of chromosomes that were involved in the crossover must end up at the same pole after the first meiotic division; and 4) Chromatids must separate randomly during the second meiotic division. If these criteria are always met, then maximal equational separation occurs and the frequency of double reduction is

1/6. A less extreme type of segregation occurs when chromatids segregate randomly, resulting in 4/28 or 1/7 gametes carrying sister chromatids. Consequently, random chromatid segregation results in a frequency of double reduction of 1/7. It does not require a crossover between the gene and the centromere in every meiotic cell. Since both types of chromatid segregation produce similar results, very large segregating populations are needed to distinguish between them. With either type of chromatid segregation, all combinations of chromatids must be considered when determining gametic ratios. The gametes produced by a triplex (AAAa) individual would be all pairwise combinations of AAAAAAaa, which would be 15 AA, 12 Aa, and 1 aa, or 27 with the dominant phenotype and one with the recessive phenotype.

Tetrasomic genetic analyses differ from those of diploids in two critical ways. First, the segregation ratio of any gene depends on its location on the chromosome. This is in contrast to diploid segregation ratios, which do not depend on a gene's chromosomal position. Fixed ratios can be predicted from chromosome and random chromatid segregation models, but they represent extremes. In reality, these extremes are rarely attained and ratios fall between them. Exact ratios cannot be predicted because they are determined by crossover events, which differ in every meiotic cell. Second, large samples of segregating populations must be evaluated in order to characterize genetic ratios and to identify clones carrying genes for traits of commercial interest. For example, it is necessary to evaluate at least 1700 plants to distinguish between chromosome segregation and random chromatid segregation when self-pollinating a duplex (AAaa) clone (Little, 1952). In addition, epistatic (interlocus) interactions are magnified in tetrasomic tetraploids, gene dosage effects are often important, and interactions with the environment can be complex. All of these complications result in a loss of resolution at the tetraploid level, so that qualitative traits are difficult to identify. For example, early studies of potato eye depth using tetraploid potato breeding lines were unable to resolve the genetic basis of this trait. However, when a genetic study was carried out at the diploid level, a major gene for eye depth (*Eyd*) was discovered (Li et al., 2005).

In another study carried out at the tetraploid level, high heritability estimates were found for potato leaf roll virus resistance, indicating that a few major genes are likely to be mainly responsible for resistance. However, it was not possible to identify individual genes and their effects (Brown et al., 1997). In contrast, when inheritance studies were carried out at the diploid level using the wild species *S. chacoense*, a single dominant resistance gene was identified and parental genotypes were determined based on Mendelian diploid segregation ratios (Brown & Thomas, 1994).

Even highly selected tetraploid potato clones contain undesirable alleles along with desirable ones. The proportion of deleterious alleles in a plant is called the genetic load. Most deleterious alleles are recessive, so they are only expressed when homozygous. Consequently, the genetic load is high in tetraploids where homozygous recessive genotypes are less common than in diploids. These deleterious alleles are hidden by dominant alleles in tetraploid clones and do not typically have a negative effect. However, when tetraploid clones are self-pollinated or crossed to related clones, some of their offspring will be homozygous for deleterious recessive alleles and will exhibit reduced vigor and/or fertility (Krantz, 1929; Phumichai & Hosaka, 2006). These clones are discarded as seedlings in breeding programs. Therefore, one method to measure the genetic load in parents used in breeding programs is to self-pollinate them and measure

the proportion of non-vigorous offspring. It may be beneficial to select parents, in part, based on low genetic load.

Gene expression was studied in a 1x, 2x, 4x polyploid series created by somatic doubling (Stupar et al., 2007). It is interesting that a linear correlation between gene expression and ploidy was rarely found. That is, the diploid and tetraploid clones exhibited similar gene expression patterns. The diploid plants created by Stuper et al. (2007) were actually more vigorous than the tetraploid ones produced by somatic doubling, and thus not able to exploit the heterozygosity necessary for enhanced fitness in polyploids. The cost to maintain more DNA and larger cells was apparently not compensated by higher vigor. This provides evidence that polyploidy per se is not evolutionarily advantageous in potatoes. Instead, polyploidy must be accompanied by an increase in allelic diversity.

The Genetic Basis of Species Boundaries in Potatoes

Hundreds of successful artificial interspecific hybrids have been reported in the literature (for example, Bukasov, 1933; Bukasov & Kameraz, 1959; Hawkes, 1958; Hawkes & Hjerting, 1969, 1989; Kamaraz, 1971; Ochoa, 1990a, 1999). It is likely, then, that natural hybridization between species is common in the wild as well (Bedonni & Camadro, 2009; Masuelli et al., 2009; Camadro et al., 2012). Even the most universal barrier to interspecific hybridization in potatoes, endosperm balance number (EBN), is not expected to provide an impenetrable barrier between sympatric species. For example, the diploid species *S. chacoense* and *S. commersonii* are sympatric, but since the former is 2EBN and the latter is 1EBN, they would not be expected to hybridize. These hybrids have been generated in the lab (Ehlenfeldt & Hanneman, 1988b). Since 2n gametes are common in wild potatoes, they would allow inter-EBN crosses to occur spontaneously. The resulting progeny are typically odd-ploidy. This might be considered a reproductive dead-end, but 2n gametes, asexual reproduction, and perenniality allow gene flow even through triploid and pentaploid plants.

In addition to EBN, unilateral incompatibility may present a barrier to interspecific hybridization in wild potato populations. Sometimes, unilateral incompatibility results when pollen tube growth is inhibited in the style, but the reciprocal cross is successful. This is especially apparent with crosses between self-compatible and self-incompatible species, where hybridization is successful if the self-compatible species is the female, but not when it is the male. Reciprocal cross differences in hybridization success may also be due to cytoplasmic-genetic male sterility. Since wild species populations are typically both male and female fertile, stylar barriers and male sterility likely inhibit, but do not prevent, interspecific hybridization.

The continuous flow of genes across and within ploidy levels in sexually reproducing perennial populations results in a complex aggregation of related genotypes. According to Camadro et al. (2012) "Hybridization and subsequent gene flow and introgression in sympatric populations, within and between ploidy levels, often results in exceedingly complicated patterns of variation." Consequently, the biological concept of a species is difficult to apply to potatoes, as in all plants (Knapp, 2008). Breeders have proposed the concept of crossability groups to aid in utilization of wild and cultivated germplasm (Harlan & De Wet, 1971). Based on EBN and self-compatible/self-incompatible systems, Fig. 1 proposes five crossability groups in potatoes. First of

all, EBN divides the collection of species into three groups. Those groups may be crossed, though, if 2n gametes are present. Consequently, double-headed arrows connect the EBN groups. Within the 1EBN and 2EBN groups, the self-compatible species may be separated from the self-incompatible ones. All 4EBN species are self-compatible. At the 1EBN and 2EBN levels, self-compatible (female) by self-incompatible (male) crosses are typically successful, while reciprocal crosses fail. Hence, single-headed arrows connect these groups. Hybridization within each of the five groups is expected to be successful, although failures have occasionally been reported (see Hawkes, 1958). As discussed above, while hybridization across groups is less likely to be successful than that within groups, no barrier is complete.

Wild Potato Taxonomy and Phylogeny

History of Taxonomic Treatments of *Solanum* Section *Petota*

As detailed by Spooner & van den Berg (1992a), section *Petota* has been the subject of intensive taxonomic work since the description of the cultivated potato, *S. tuberosum* (Linnaeus, 1753). Different taxonomists applied various taxonomic philosophies and species concepts to the section, but mainly have used morphology to define species. Walpers (1844) accepted only ten species in section *Petota*. The last attempt to monograph *Solanum* in its entirety was by Dunal (1852) who included 17 species in section *Petota*, while Baker (1884) recognized only six species in the section. Bitter (1912–1913), in his monumental work on *Solanum*, described more than 50 new species, subspecies or varieties of wild potatoes.

The first regional treatment of section *Petota* was provided by Rydberg (1924), who monographed the Mexican and Central American species and described ten new taxa. Extensive taxonomic investigations were conducted by Nikolai Vavilov's Russian associates Sergei Bukasov and Sergei Juzepczuk, who worked on material gathered on Russian expeditions to Mexico, Central America, and South America in the 1920s and 1930s. They effectively and validly described 30 wild and 18 cultivated species, in addition to publishing a great number of names that were not validly published

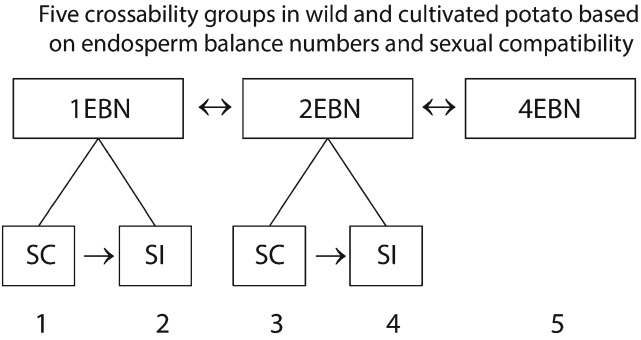

Fig. 1 Crossability groups in *Solanum* section *Petota* based on endosperm balance numbers (EBN) and sexual compatibility

(Bukasov, 1930, 1933, 1937). This first potato germplasm collection was widely used to study potato cytogenetics by Vladimir Rybin (Rybin, 1929, 1933) and interspecific hybridization by Abram Kameraz (Bukasov and Kameraz, 1959) whose results were used for developing potato taxonomy and phylogeny. Hawkes (1944) treated collections from a series of British expeditions to Mexico and South America in the 1930s and described 52 new species, subspecies, or varieties, of which he accepted only ten in 1990 (Hawkes, 1990). Regional treatments have been provided for North and Central America (Correll, 1952; Spooner et al., 2004); Mexico (Flores Crespo, 1966; Hawkes, 1966; Rodríguez & Vargas, 1994); Peru (Vargas, 1949, 1956; Ochoa, 1962, 1999; Correll, 1967); Bolivia (Hawkes & Hjerting, 1989; Ochoa, 1990a); Argentina, Brazil, Paraguay, and Uruguay (Hawkes & Hjerting, 1969); Bolivia, Argentina, Chile, Paraguay, and Uruguay (Spooner et al., in press), and Chile (Montaldo & Sanz, 1962; Contreras, 1987).

The first modern comprehensive (from throughout the entire range of the group) taxonomic treatment of section *Petota* was provided by Hawkes (1956b) who synonymized many species. The treatment of Correll (1962) was similar in its taxonomy, and included extensive specimen citations and excellent illustrations. Other comprehensive treatments have been provided by Hawkes (1956b, 1963, 1990), Bukasov (1978), and Gorbatenko (2006). Since the work by Correll (1962), 176 new taxa have been described, 140 of these by Carlos Ochoa, including 77 new varietal and form names for the Bolivian cultivated species alone (Ochoa, 1988). In total, there are 494 epithets for wild and 626 epithets for cultivated taxa, including names not validly published (Ovchinnikova et al., 2011).

Series Treatments in *Solanum* Section *Petota*

As detailed by Hawkes (1989), Bitter (1912) was the first to describe series in section *Petota* (series *Conicibaccata* and series *Maglia*), although he failed to designate series affiliations for many species. Rydberg (1924) divided the Mexican and Central American potatoes into five informal groups (Bulbocastana, Juglandifolia, Oxycarpa, Pinnatisecta, Tuberosa) but failed to designate rank. Hawkes (1944) validated these names as series (except Oxycarpa, which he equated to series *Conicibaccata*) and described series *Cuneoalata*. Since that time, 26 additional series have been validly published: series *Megistacroloba* (Cárdenas & Hawkes, 1946); *Trifida* (Correll, 1950); *Cardiophylla*, *Polyadenia* (Correll, 1952); *Circaeifolia*, *Piurana* (Hawkes, 1954b); *Morelliformia* (Hawkes, 1956b); *Acaulia*, *Andigena*, *Commersoniana*, *Demissa*, *Etuberosa*, *Longipedicellata*, *Vaviloviana* (Bukasov & Kameraz, 1959); *Ingifolia* (Ochoa, 1962); *Clara*, *Minutifoliola*, *Tarijensa*, *Yungasensa* (Correll, 1962); *Olmosiana* (Ochoa, 1965); *Lignicaulia* (Hawkes, 1989); *Bukasoviana*, *Chomatophylla*, *Pyriformia*, *Simpliciora* (Gorbatenko, 1989), *Simplicissima* (Ochoa, 1989b). Gorbatenko (1989) published series *Lignicaulia* as a later homonym. The date of publication on Gorbatenko (1989) is ambiguous, because the latest date listed on the volume is August 9, after the words (transliterated) "Podpisano v petsat"=signed off for printing. This was not the publication date, however, which was 21 Sep 1989 (letter from Ludmilla Gorbatenko to Jack Hawkes). Hawkes (1989) was released on 29 Aug 1989, giving his *Lignicaulia* priority at the sectional rank. The following names have been treated as series but were not validly published: Looseriana (Bukasov, 1939);

Andreana (Hawkes, 1944); Glabrescentia, Transaequatorialia (Bukasov & Kameraz, 1959); Borealia (Correll, 1962); Alticola, Berthaultiana, Chilotana, Cisaequatorialia, Collina, Subacaulia, and Verrucosa (Bukasov, 1978). Hawkes (1990) and Gorbatenko (1989) recognized 15 and 20 series, respectively, for the South American species, and Hawkes (1990) and Bukasov (1978) recognize 21 and 36 series, respectively, for section *Petota*. Spooner and van den Berg (1992a) provided a graphic chronological comparison of these varying concepts of series. These series often are not well-defined morphologically, and the affiliations of species to series vary widely among different authors.

Morphological Studies of Species Boundaries Subsequent to Hawkes (1990)

Recent reinvestigations of species boundaries, origins, and phylogeny in sect. *Petota* have employed extensive field work throughout the range of the group (summarized in Spooner & Salas, 2006) and numerical taxonomic investigations of morphological data gathered from field studies, herbarium specimens, or germplasm grown in field plots (Table 2) (Clausen & Crisci, 1989; Child & Lester, 1991; Lester, 1991; Spooner & van den Berg, 1992b, 2001; van den Berg & Spooner, 1992; Spooner et al., 1993b, 1995b, 2001a, b, 2008a; van den Berg & Groendijk-Wilders, 1993, 1999; Giannattasio & Spooner, 1994a; Miller & Spooner, 1996; van den Berg et al., 1996, 1998; Castillo & Spooner, 1997; Clausen & Spooner, 1998; Kardolus & Bezem, 1998; Kardolus & Groendijk-Wilders, 1998; Kardolus, 1999; Rodríguez & Spooner, 2002; Lara-Cabrera & Spooner, 2005; Alvarez et al., 2008; Ames et al., 2008; Fajardo et al., 2008; Bedonni & Camadro, 2009). These morphological studies documented wide character state variation within species and overlap of character states among closely related species. They were often conducted in parallel with molecular studies of the same accessions, as described below.

Molecular Studies of Species Boundaries Subsequent to Hawkes (1990)

Studies of species boundaries, origins, and phylogeny frequently have involved a wide range of molecular marker and DNA sequence data, sometimes in combination with morphological data (Table 2). These have included isozymes, protein electrophoresis, single- to low-copy nuclear DNA restriction sites, nuclear microsatellites, plastid microsatellites, plastid deletion markers, highly repeated nuclear DNA, mitochondrial DNA RFLPs, DNA sequences from the internal nontranscribed spacer of nuclear ribosomal DNA, and DNA sequences from orthologous nuclear genes, with the polyploid studies (summarized in Polyploidy – DNA Sequence data, below). Similar to the morphological studies (above) these studies frequently documented wide character state variation within species and overlap of character states among closely related species.

Introgression and Interspecific Hybridization

Natural interspecific hybridization has been hypothesized to be a major evolutionary mechanism in section *Petota* (Ugent, 1970a; Hawkes, 1990). Spooner & van den Berg (1992b) summarized literature proposing 26 potato species (then accepted) to have

Table 2 Molecular and morphological studies of species boundaries, diversity, and phylogeny in *Solanum* sections *Petota* and *Etuberosum* subsequent to Hawkes (1990); the species names are those used in the publication, but with currently accepted names of the wild species (Table 1) in parentheses. When studies involved both cultivated and related wild and species, they are listed under the cultivated species

Taxon[1]	Data type[2]	Aim of study[3]	Publication
Wild species			
Solanum gourlayi (=*S. brevicaule*)	M	A	Clausen & Crisci, 1989
S. sparsipilum (=*S. brevicaule*), *S. stenotomum* (=S. *tuberosum* Andigenum group)	Iso	G	Rabinowitz et al., 1990
Diverse wild species	M	D	Lester, 1991
Diverse wild species	M	D	Child & Lester, 1991
Diverse wild species	pRFLP	D	Spooner et al., 1991a
S. canasense (=S. *brevicaule*), *S. megistacrolobum* (=*S. boliviense*), *S. raphanifolium*	pRFLP	D	Spooner et al., 1991b
S. chacoense	pElec	D	Hosaka & Hanneman, 1991
S. acaule	nRFLP	A	Hosaka & Spooner, 1992
Diverse wild species	pRFLP	D	Spooner & Sytsma, 1992
Series *Etuberosa*	Iso	A	Spooner et al., 1992
S. berthaultii, *S. tarijense* (=*S. berthaultii*)	M	A	Spooner & van den Berg, 1992b
S. microdontum	M	A	Van den Berg & Spooner, 1992
Diverse wild species	pRFLP	D	Spooner et al., 1993a
S. andreanum	M	A	Spooner et al., 1993b
Diverse wild species	nDNA repeats	D	Schweitzer et al., 1993
Diverse wild species	M	A	van den Berg & Groendijk-Wilders, 1993
Diverse wild species	nDNA repeats	D	Borisjuk et al., 1994
S. megistacrolobum, *S. toralapanum* (both = *S. boliviense*)	M	A	Giannattasio & Spooner, 1994a
S. megistacrolobum, *S. toralapanum* (both = *S. boliviense*)	nRFLP	A	Giannattasio & Spooner, 1994b
Solanum series *Demissa*	M	A	Spooner et al., 1995b
S. chacoense	M, nSSR, RAPD	D	Miller & Spooner, 1996
Solanum brevicaule complex	M	A	van den Berg et al., 1996
S. fendleri (=*S. stoloniferum*), *S. jamesii*	RAPD	F	Del Rio et al., 1997a
S. fendleri (=*S. stoloniferum*), *S. jamesii*	RAPD	F	Del Rio et al., 1997b
Solanum series *Conicibaccata*	M, pRFLP	A, D	Castillo & Spooner, 1997
S. bulbocastanum, *S. cardiophyllum*	pRFLP	A	Rodríguez & Spooner, 1997

Table 2 (continued)

Taxon[1]	Data type[2]	Aim of study[3]	Publication
Diverse wild species	pRFLP	D	Spooner & Castillo, 1997
S. astleyi (=*S. boliviense*), *S. boliviense*	RAPD	A	Spooner et al., 1997
Solanum ×*rechei*	M, nRFLP	D	Clausen & Spooner, 1998
Diverse wild species	AFLP	D	Kardolus et al., 1998
Diverse wild species	M	A	Kardolus & Bezem, 1998
Diverse wild species	M	A	Kardolus & Groendijk-Wilders, 1998
Solanum brevicaule complex	M	A	van den Berg et al., 1998
Diverse wild species	M	A	Kardolus, 1999
Solanum brevicaule complex	nRFLP, RAPD	A	Miller & Spooner, 1999
Series *Circaeifolia*	M	A	van den Berg & Groendijk-Wilders, 1999
S. fendleri (=*S. stoloniferum*), *S. jamesii*	RAPD	E	Del Rio et al., 2001
Diverse wild species	M	A	Spooner & van den Berg, 2001
Solanum series *Longipedicellata*	M	A	Spooner et al., 2001a
Solanum series *Conicibaccata*	M, RAPD	A	Spooner et al., 2001b
Solanum series *Circaeifolia*	AFLP, RAPD	A	van den Berg et al., 2001
S. sucrense (=*S. brevicaule*)	RAPD	E	Del Rio & Bamberg, 2002
Diverse wild species	pdel	D	Hosaka, 2002
S. bulbocastanum, *S. cardiophyllum*	M, nRFLP	A	Rodríguez & Spooner, 2002
Solanum series *Longipedicellata*	AFLP, pSSR, RAPD	A	van den Berg et al., 2002
S. acaule, *S. albicans*	AFLP	A	McGregor et al., 2002
S. fendleri (=*S. stoloniferum*) *S. jamesii*	RAPD	F	Del Rio & Bamberg, 2003
S. jamesii, *S. sucrense* (=*S. brevicaule*)	RAPD	F	Bamberg & del Rio, 2003
Diverse wild species	RAPD	B	Bamberg & del Rio, 2004
Diverse wild species, *S. tuberosum*	AFLP	G	Celis et al., 2004
S. verrucosum	RAPD	E	Del Rio & Bamberg, 2004
Diverse wild species	AFLP	A	Lara-Cabrera & Spooner, 2004
Diverse wild species	M, nSSR	A	Lara-Cabrera & Spooner, 2005
S. ×*ruiz-lealii* (=*S. kurtzianum*)	M, nSSR, pSSR	D	Raimondi et al., 2005
Diverse wild species	RAPD	F	Del Rio et al., 2006
Diverse wild species	pdel	D	Ames et al., 2007
	AFLP, pDel, pRFLP	A	Spooner et al., 2007a

Table 2 (continued)

Taxon[1]	Data type[2]	Aim of study[3]	Publication
S. berthaultii, *S. tarijense* (=*S. berthaultii*)			
Diverse wild species	Mit	D	Scotti et al., 2007
S. verrucosum	RAPD	E	Bamberg & del Rio, 2008
Solanum brevicaule complex	M	A	Alvarez et al., 2008
Solanum series *Piurana*	M	A	Ames et al., 2008
Solanum series *Conicibaccata*	M	A	Fajardo et al., 2008
Solanum series *Conicibaccata*	AFLP	A	Jiménez et al., 2008
S. medians	M	A	Spooner et al., 2008a
Diverse wild species	nSeq	D	Spooner et al., 2008b
Diverse wild species	AFLP	D	Jacobs et al., 2008
Solanum series *Longipedicellata*	GISH	D	Pendinen et al., 2008a
S. jamesii, *S. stoloniferum*	RAPD	F	Bamberg et al., 2009
Diverse wild species	nSeq	D	Rodríguez & Spooner, 2009
Diverse wild species	nSeq	D	Rodríguez et al., 2009
S. kurtzianum and six related sympatric species	M, nSSR	A	Bedonni & Camadro, 2009
Diverse wild species	ITS	D	Spooner, 2009
S. fendleri (=*S. stoloniferum*)	AFLP	F	Bamberg et al., 2010
Solanum series *Piurana*	nSeq	A, D	Ames & Spooner, 2010
S. stoloniferum	AFLP	E	Bamberg & del Rio, 2011
S. stoloniferum	AFLP	E	Bamberg et al., 2011
Solanum series *Conicibaccata*	nSeq	A, D	Fajardo & Spooner, 2011
Diverse wild species	AFLP	D	Jacobs et al., 2011
Diverse wild species	nSeq	D	Cai et al., 2012
Solanum series *Acaulia*, *Demissa*	GISH	D	Pendinen et al., 2012
S. chacoense, *S. tuberosum*	RAPD	G	Capurro et al., 2013
Diverse wild species	Mit	D	Sanetomo & Hosaka, 2013
Solanum bulbocastanum, *S. fendleri* (=*S. stoloniferum*), *S. hougasii*	CAPS, STS	D	Brown et al., 2014
Diverse wild species	Mit, pDel, pRFLP	D	Hosaka & Sanetomo, 2014
Cultivated species			
Andean landraces	I, M, P	B	Huamán & Stegemann, 1989
S. tuberosum	nRFLP	C	Gebhardt et al., 1989

Table 2 (continued)

Taxon[1]	Data type[2]	Aim of study[3]	Publication
Diverse wild species	nRFLP		Bonierbale et al., 1990
S. tuberosum	pRFLP	B	Waugh et al., 1990
Andean landraces	Iso	B	Quiros et al., 1990
Andean landraces	PElec	A	Clausen & Okada, 1990
S. stenotomum, *S. sparsipilum* (=*S. brevicaule*)	Iso	D	Rabinowitz et al., 1990
S. tuberosum and various wild species	nRFLP	D	Debener et al., 1990
S. tuberosum and various wild species	nRFLP	D	Debener et al., 1991
S. tuberosum	I	C	Douches & Ludlam, 1991
S. tuberosum	nRFLP	C	Douches et al., 1991
S. tuberosum	pdel	D	Kawagoe & Kikuta, 1991
S. tuberosum	nRFLP	C	Powell et al., 1991
S. stenotomum, *S. tuberosum*	Iso	E	Zimmerer & Douches, 1991
S. tuberosum	nRFLP	C	Görg et al., 1992
Andean landraces	Iso	B	Quiros et al., 1992
S. tuberosum	pRFLP	D	Hosaka, 1993
S. tuberosum	RAPD	C	Mori et al., 1993
S. tuberosum	pRFLP	B	Powell et al., 1993
S. tuberosum	RAPD	D	Hosaka & Ogawa, 1994
S. tuberosum	RAPD	C	Hosaka et al., 1994
Andean landraces	I	B	Brush et al., 1995
S. chaucha	I, RAPD	C	Cisneros & Quiros, 1995
S. stenotomum, *S. brevicaule* complex	pRFLP	D	Hosaka, 1995
S. tuberosum	RAPD	B	Demeke et al., 1996
S. tuberosum	RAPD	C	Sosinski & Douches, 1996
S. tuberosum	nSSR	C	Provan et al., 1996a
S. tuberosum	ISSR	C	Provan et al., 1996b
S. tuberosum	RAPD	C	Oganisyan et al., 1996
S. tuberosum	nSSR	C	Kawchuk et al., 1996
S. tuberosum	RAPD	C	Ford et al., 1997
S. tuberosum	AFLP, RAPD	C	Milbourne et al., 1997
S. tuberosum	M, nSSR	C	Schneider & Douches, 1997
S. tuberosum	AFLP	C	Kim et al., 1998
S. tuberosum	pSSR	B	Bryan et al., 1999

Table 2 (continued)

Taxon[1]	Data type[2]	Aim of study[3]	Publication
S. phureja	RAPD	B	Ghislain et al., 1999
S. tuberosum	ISSR	C	Prevost & Wilkinson, 1999
S. tuberosum subsp. *andigenum*	I	B	Huamán et al., 2000c
S. tuberosum subsp. *andigenum*	M	B	Huamán et al., 2000b
S. tuberosum	AFLP, ISSR, nSSR, RAPD	C	McGregor et al., 2000
S. tuberosum	nSSR	B	Ashkenazi et al., 2001
Andean landraces and diverse wild species	RAPD	F	Bamberg et al., 2001
S. tuberosum	RAPD	C	Isenegger et al., 2001
S. tuberosum	ISSR	C	Bornet et al., 2002
Andean and Chilean landraces	M	A	Huamán & Spooner, 2002
S. tuberosum	nSSR, pDel	D	Raker & Spooner, 2002
Andean and Chilean landraces, *S. berthaultii*, *S. chacoense*, *S. neorossii*, *S. tarijense* (=*S. berthaultii*)	pDel	D	Hosaka, 2003
S. tuberosum	nSSR	C	Coombs et al., 2004
Andean and Chilean landraces, diverse wild species	nRFLP, pDel, pSSR,	D	Sukhotu et al., 2004
S. tuberosum	AFLP, nSSR	C	Braun & Wenzel, 2005
Andean and Chilean landraces, diverse wild species	AFLP	D	Spooner et al., 2005a
Andean and Chilean landraces	AFLP, pDel	D	Spooner et al., 2005b
S. tuberosum subsp. *andigenum*, subsp. *tuberosum*	nRFLP, pSSR	D	Sukhotu et al., 2005
S. tuberosum	AFLP, nSSR	C	Hale et al., 2005
S. tuberosum	nSSR	C	Barandalla et al., 2006
S. phureja	nSSR, RAPD	B	Ghislain et al., 2006
S. tuberosum	AFLP	B	Hong et al., 2006
Andean and Chilean landraces, diverse wild species	nRFLP, pDel, pRFLP, pSSR	D	Sukhotu & Hosaka, 2006
Andean landraces, wild species	nRFLP, pRFLP	D	Sukhotu et al., 2006
S. tuberosum	nSSR	C	Mathias et al., 2007
S. tuberosum	nSSR, pDel	D	Rios et al., 2007
Andean and Chilean landraces	nSSR, pDel	A	Spooner et al., 2007b
S. tuberosum	nSSR	C	Reid & Keer, 2007
S. tuberosum	pdel	D	Ames & Spooner, 2008
S. tuberosum subsp. *andigenum*	RAPD	F	Bamberg & del Rio, 2009

Table 2 (continued)

Taxon[1]	Data type[2]	Aim of study[3]	Publication
S. tuberosum	nSSR	C	Fu et al., 2009
S. tuberosum	nSSR, pdel	B	Ghislain et al., 2009b
Andean and Chilean landraces, diverse wild species	Mit	D	Hosaka & Sanetomo 2009
Cultivated species and related wild species	M, nSSR	A, D	Gavrilenko et al., 2010
S. tuberosum	nSSR	C	Karaagac et al., 2010
Andean and Chilean landraces	nSeq	D	Rodríguez et al., 2010
S. tuberosum	M, nSSR	C	Reid et al., 2011
S. tuberosum	nSSR	A	Ruiz de Galarreta et al., 2011
S. tuberosum, Andean and Chilean landraces, diverse wild species	Mit	D	Sanetomo & Hosaka, 2011
S. tuberosum	AFLP	B	Wang et al., 2011
Chilean landraces	nSSR, pRFLP	D	Spooner et al., 2012
S. tuberosum, Andean and Chilean landraces, diverse wild species	Mit	D	Hosaka & Sanetomo, 2012
S. tuberosum	ISAP	C	Seibt et al., 2012
S. tuberosum and *S. maglia*	nSSR, pRFLP	D	Spooner et al., 2012
Cultivated species and related wild species	pDel, pSSR	A, D	Gavrilenko et al., 2013
S. tuberosum	nSSR	C	Karaagac et al., 2014

[1] This columm lists only the primary species studied

[2] *AFLP* Amplified fragment length polymorphisms; *CAPS* cleaved amplified polymorphic sites; *GISH* genomic in-situ hybridization; *ISAP* Inter-Sine (Short interspersed nuclear elements) amplified polymorphism; *Iso* isozymes; *ISSR* inter simple sequence repeats; *ITS* internal nontranscribed spacer of nuclear ribosomal DNA; *M* morphology; *Mit*, mitochondrial DNA RFLPs; *nDNA* repeats, highly repeated nuclear DNA RFLPs; *nRFLP* single- to low-copy nuclear RFLPs; *nSeq* single- to low-copy nuclear DNA sequences; *nSSR* nuclear microsatellites; *pDel* plastid deletion markers; *pRFLP* plastid RFLPs; *PElec* protein electrophoresis; *pSSR* plastid microsatellites; *RAPD* random amplified polymorphic DNA; *STS* sequence tagged sites; *X* multiplex PCR with plastid and mitochonddrial probes, followed by *Bam*HI digestion

[3] *A* Species boundaries; *B* diversity assessments/core collections; *C* fingerprinting; *D* taxonomy/species origins/phylogeny; *E* Geographic partitioning of diversity; *F* genetic identity of genebank samples over increase cycles or recollections; *G* gene flow

resulted from hybrid speciation. Five of these were cultivated species and 21 wild species (12 diploid and nine polyploid). Most of these hypotheses have been generated by intermediate morphology, inference from distributional data, artificial reconstruction of the hybrids and comparison with putative natural hybrids, and assessment of reduction of fertility. We here discuss reinvestigations of putative diploid wild species; hypotheses of the cultivated and wild polyploid species are discussed below.

Spooner et al. (1991b) reexamined, with plastid DNA and nuclear ribosomal DNA restriction site data, the hypothesis of Ugent (1970b) that the Peruvian diploid species *S. raphanifolium* was of recent and ongoing hybrid origin between diploid *S. canasense* (=*S. candolleanum*) and *S. megistacrolobum* (=*S. boliviense*). *Solanum raphanifolium* is morphologically intermediate between the putative parents and occurs where the two species overlap in distribution. *Solanum raphanifolium*, however, was divergent from either putative parent regarding both markers. The putative parents were similar, and no support was provided for the hybrid origin.

Miller and Spooner (1996) reexamined the putative origin of mountain populations of *S. chacoense* (diploid), hypothesized by Hawkes (1962a) to have arisen from introgression with *S. microdontum* and lowland populations of *S. chacoense*. Its hybrid origin was not supported, however, with data from morphology, RAPDs, or nuclear RFLPs.

Clausen and Spooner (1998) reexamined the putative hybrid origin of *S.* ×*rechei*, hypothesized by Hawkes & Hjerting (1969) and Okada & Hawkes (1978) to be of hybrid origin between *S. kurtzianum* and *S. microdontum*. Like *S. raphanifolium*, *S.* ×*rechei* occurred at the overlap zone of its two parents. In addition, it had reduced fertility in comparison to natural and artificially constructed hybrids. In contrast to the two studies mentioned above, additive profiles of nRFLPs gave strong support to its hybrid origin.

Additionally, introgression and interspecific hybridization not leading to speciation has been believed to be common in section *Petota* (Hawkes, 1962a). For example, Hawkes & Hjerting (1969) interpreted 9.5 % of the wild potato specimens they examined for the flora of Argentina, Brazil, Paraguay, and Uruguay to be interspecific hybrids, and Hawkes and Hjerting (1989) and Ochoa (1999) provided extensive lists of natural and artificial interspecific hybrids. Spooner & van den Berg (1992b) and Spooner et al. (2007a) investigated, with morphological and molecular marker data, respectively, hypotheses by Hawkes & Hjerting (1989) that 9.5 % of the natural populations of *S. berthaultii* and *S. tarijense* were interspecific hybrids. While both studies showed extremes that could be recognized as variants identified as these two species, there was a near continuum of variation that Spooner et al. (2007a) interpreted as variation in the highly variable species *S. berthaultii*. This variation included three diploid hybrid species accepted by Hawkes (1990), *S.* ×*litusinum*, *S.* ×*trigalense*, and *S.* ×*zudaniense*.

A putative natural hybrid between *S. chacoense* and *S. kurtzianum* was described by Brücher (1962) as *S. ruiz-lealii*, and accepted by Hawkes & Hjerting (1969) and Hawkes (1990). Raimondi et al. (2005) examined the hypothesis of hybridization by phenetic analyses of morphological and molecular data and cytological analyses of interspecific hybrids. They concluded that *S. ruiz-lealii* is not a recent natural hybrid of *S. kurtzianum*×*S. chacoense* but originated by divergence of *S. chacoense* or by hybridization between *S. chacoense* and another unnamed taxon. They proposed maintaining the species status of *S. ruiz-lealii*.

Rabinowitz et al. (1990) tested hypotheses of gene flow between the diploid wild species *S. sparsipilum* (=*S. candolleanum*) and the cultivated diploid *S. stenotomum* (=*S. tuberosum* Andigenum group). By use of isozyme markers specific to these populations, they were able to document high levels of gene flow in experimental field plots in the Andes. They used these data to speculate that extensive gene flow occurs

among other cultivated and wild species. Similarly, Debener et al. (1991) used phenetic analyses of nuclear RFLPs to support incorporation of wild species germplasm into cultivated species. In addition, Celis et al. (2004) documented, with AFLP markers, the possibility of gene flow from cultivated species to diverse wild species occurring in the Andes. These results would need to be tested in natural situations to see if such hybrid populations would survive in the wild, but if so, they provide support to hypotheses of Ugent (1970a) who proposed that the cultivated species were formed and genetically enriched subsequent to formation by gene flow from the wild species.

Taxonomic Changes Subsequent to Hawkes (1990)

The combined molecular and morphological studies mentioned above and observations of species during collecting expeditions have often failed to support many of the traditionally recognized species of wild potatoes, and form the rationale for our reduction of species (Table 1). This has occurred in almost every group studied. An account of post-1990 taxonomic decisions in section *Petota* by many workers published in Spooner & Salas (2006) reduced the 235 species of Hawkes (1990) to 190, but our independent taxonomic decisions presented here result in a greatly reduced number of 107 wild and four cultivated species (Table 1).

This is perhaps best illustrated by studies of species boundaries in the wild potato *S. brevicaule* complex. This complex contains about 20 taxa and has long attracted the attention of biologists because of its similarity to cultivated potatoes (Correll, 1962; Ugent, 1970a; Grun, 1990). Some members of this complex, endemic to central Peru, Bolivia, and northern Argentina, were considered ancestors of the landraces (Ugent, 1970a). The species in the complex share pinnately dissected leaves, round fruits, rotate to rotate-pentagonal corollas, and are largely sexually compatible with each other and with the cultivated potato (Hawkes, 1958; Hawkes & Hjerting, 1969, 1989; Ochoa, 1990a, 1999; van den Berg & Spooner, 1992a). They include diploids, tetraploids, and hexaploids, with traditionally recognized species possessing multiple ploidy levels (*S. gourlayi* [=*S. brevicaule*] with diploids and tetraploids; and *S. oplocense* [=*S. brevicaule*] with diploids, tetraploids, and hexaploids). Members of the complex have been so difficult to distinguish from each other that even experienced potato taxonomists Hawkes & Hjerting (1989) and Ochoa (1990a) provided different identifications for identical collection numbers of the *Solanum brevicaule* complex in fully 38 % of the cases (Spooner & van den Berg, 1992a). Field collections in Peru (Spooner et al., 1999; Salas et al., 2001), Bolivia (Spooner et al., 1994), and Argentina (Spooner & Clausen, 1993); phenetic analyses of morphological data in the Netherlands (van den Berg et al., 1996) the United States (van den Berg et al., 1998) and Peru (Alvarez et al., 2008); single- to low-copy nuclear restriction fragment length polymorphism (nRFLPs) and random amplified fragment length (RAPD) data (Miller & Spooner, 1999); and amplified fragment length polymorphism (AFLP) data (Spooner et al., 2005a) failed to clearly differentiate many wild species in the complex, but defined two geographic subsets: (1) the Peruvian populations, (2) the Bolivian and Argentinean populations. However, even these two groups could only be distinguished by computer-assisted statistical analyses of widely overlapping character states, and not by species-specific characters. We here recognize two morphologically very similar species,

S. candolleanum from Peru (and extreme northern Bolivia), and *S. brevicaule* from Bolivia and Argentina.

There are many other similar examples of difficult species complexes in wild potatoes. For example, an examination by Spooner et al., (in press) of independent identifications of *S. megistacrolobum* and *S. toralapanum* by Hawkes & Hjerting (1989) and Ochoa (1990a) showed that they gave different identifications to identical collection numbers of these species 17 % of the time. Further identifications by Spooner et al. (in press) of all specimens from southern South America found that species variation in these species extended even to the long-accepted names *S. astleyi*, *S. boliviense*, and *S. sanctae-rosae*, necessitating their synonymy under the earliest name *S. boliviense* as shown in Table 1. Combined morphological and molecular studies show similar patterns failing to support traditionally recognized species in formerly recognized *Solanum* series *Conicibaccata* (Castillo & Spooner, 1997; Spooner et al., 2001b; Fajardo et al., 2008; Jiménez et al., 2008; Fajardo & Spooner, 2011); series *Demissa* (Spooner et al., 1995b); series *Longipedicellata* (Spooner et al., 2001a; van den Berg et al., 2002); and series *Piurana* (Spooner et al., 1995b; Ames et al., 2008; Ames & Spooner, 2010), as well as in the cultivated species (below).

Ingroup and Outgroup Relationships

Phylogenetic studies in section *Petota*, including plastid DNA restriction site data (Spooner et al. 1991a, 1993a; Spooner & Sytsma, 1992; Castillo & Spooner, 1997; Rodríguez & Spooner, 1997; Spooner & Castillo, 1997) and nuclear DNA sequencing data (Spooner et al., 2008b; Rodríguez & Spooner, 2009; Rodríguez et al., 2009; Ames & Spooner, 2010; Fajardo & Spooner, 2011; Cai et al., 2012) have greatly changed our understanding of ingroup and outgroup relationships. *Solanum* section *Petota* now excludes two non-tuber-bearing series Hawkes (1990) placed in section *Petota*, now reclassified in near outgroup section *Etuberosum* (Bukasov & Kameraz) A. Child,

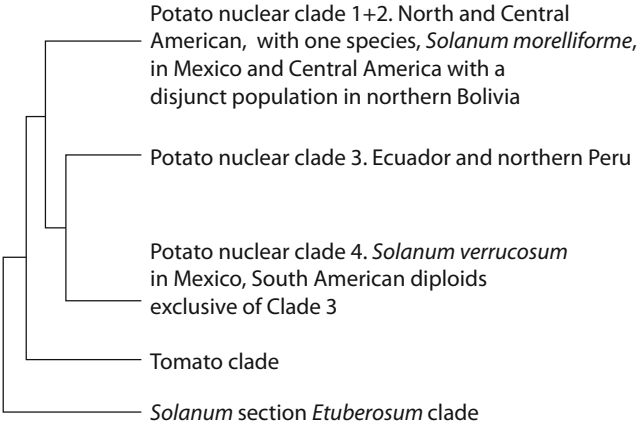

Fig. 2 Cladistic relationships of the diploid species of *Solanum* section *Petota* showing three nuclear clades (combining clades 1 and 2 of the plastid clade) and immediate outgroups. Most of the polyploid species are allopolyploids combining genomes of these three clades as discussed in the text and highlighted in Table 1

Fig. 3 *Solanum bulbocastanum* (*Solanum mexicanum* Sessé & Mociño, Pl. nov. hisp. 35. 1888), a representative of nuclear clade 1 (see text and Table 1). Photograph of original color plate, *Torner Collection 0621*. Reproduced by courtesy of Torner Collection of Sessé and Mociño Biological Illustrations, Hunt Institute for Biological Documentation, Carnegie Mellon University, Pittsburgh

section *Juglandifolia* (Rydberg) A. Child, and section *Lycopersicoides* A. Child (Peralta) (Contreras & Spooner, 1999; Peralta et al., 2008).

The remaining 19 series of Hawkes (1990) are all tuber-bearing, but we do not recognize series as many of them are not supported by recent studies. Rather, they are divided into four clades (1–4) based on plastid restriction site data or three clades based on nuclear DNA sequencing data (Fig. 2), with both results similar except that the nuclear DNA sequencing data combines species in plastid clades 1+2 (Fig. 2). In addition, many allopolyploid species combine alleles from different clades (Table 1) as outlined in the sections "Polyploidy—DNA Sequence Data," and "Genome Differentiation in section *Petota* Identified by Genomic in situ Hybridization" (below).

Figures 3, 4, and 5 illustrate species in these three nuclear clades: *S. bulbocastanum* (clade 1+2; Fig. 3), *S. chiquidenum* (clade 3; Fig. 4), and *S. verrucosum* (clade 4; Fig. 5). The diploid species within these clades possess trends in morphological character states, but there are many exceptions. For example, most species in clade 1+2 (Fig. 3) possess non-shiny leaves, white stellate corollas, and single tubers at the end of stolons; species in clade 3 (Fig. 4) possess shiny leaves, blue to purple (occasionally white) pentagonal corollas and moniliform (arranged like beads on a string) tubers (Fig. 4), and species in clade 4 have non-shiny leaves, variously colored pentagonal to rotate corollas, and single tubers at the end of stolons. The polyploids are mostly allopolyploids as discussed below in "Polyploidy—DNA Sequence Data" and it is more difficult to assign morphological character states to them. For example, some,

Fig. 4 *Solanum chiquidenum*, a representative of nuclear clade 3 (see text and Table 1), showing the moniliform tubers characteristic of most members of this clade

but not all of the allopolyploids in species formerly assigned to series *Conicibaccata* (possessing alleles from both clades 3 and 4) possess moniliform tubers (Fajardo et al., 2008), likely inherited from their diploid parents in clade 3 (Table 1).

As a result of these many variants within species and clades, our assignment to groups within section *Petota* relies mainly on molecular data that divides the diploid species into three nuclear clades, with allopolyploid derivatives that combine genomes of these three clades. Within these three main clades some species are clearly

Fig. 5 *Solanum verrucosum*, a representative of nuclear clade 4. Photograph of t. 2, Hortis Halensis, 1841. Reproduced by courtesy of Royal Botanic Gardens, Kew

interrelated. Spooner et al. (2004) summarized these relationships as 11 informal "species groups" for the North and Central American species, and Spooner et al., (in press) as six informal species groups for the southern South American species. Three groups (Morelliforme, Conicibaccata, and Acaulia groups) have representatives shared in both North and Central America and in South America.

Polyploidy—Occurrence, Taxonomy, Biogeography, Habitats

All species of the section *Petota* have the same basic chromosome number x=12. The first indications of the existence of different ploidy levels in the wild potatoes were provided by Salaman (1926), Smith (1927) and Vilmorin and Simonet (1927) for *S. chacoense, S. jamesii, S. fendleri* (=*S. stoloniferum), S. ×edinense* and *S. demissum*. Rybin (1929, 1933) first described the polyploid series in wild potatoes (2x, 3x, 4x, 5x, 6x) and a polyploid series in cultivated species (2x, 3x, 4x, 5x). Using the classical taxonomic system of Hawkes (1990), four taxonomic series (Hawkes, 1990) of wild potatoes were wholly or predominantly polyploid: series *Acaulia* (4x, 6x), *Conicibaccata* (2x, 4x, 6x), *Demissa* (6x), and *Longipedicellata* (4x). Other series of Hawkes (1990) were predominately diploid: *Bulbocastana* (2x, 3x), *Commersoniana* (2x, 3x), *Maglia* (2x, 3x), *Pinnatisecta* (2x, 3x), *Piurana* (2x, 4x), and *Tuberosa* (2x, 3x, 4x, 6x) (Hijmans et al., 2007).

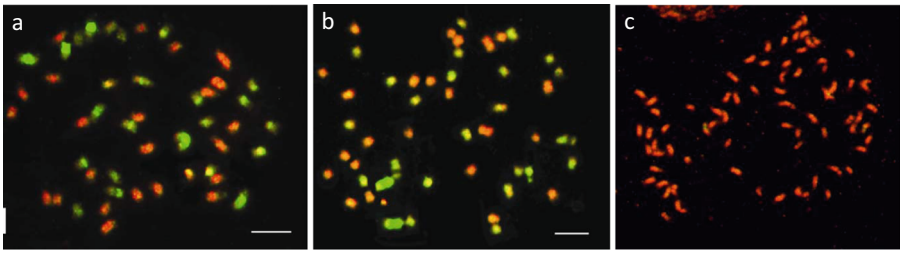

Fig. 6 GISH analysis of polyploid Mexican species *S. hjertingii*, *S. stoloniferum*, *S. demissum* using labeled DNA from diploid (2*n*=2x=24) putative A genome progenitor - *S. verrucosum*, and B genome progenitor - *S. cardiophyllum*, *S. jamesii*. Bars=5 μm. **a** Somatic chromosomes of tetraploid (2*n*=4x=48) species *S. hjertingii* using labeled DNA from *S. verrucosum* (*red*) and *S. jamesii* (*green*). **b** Somatic chromosomes of tetraploid (2*n*=4x=48) species *S. stoloniferum* probed with labeled DNA from *S. verrucosum* (*red*) and *S. cardiophyllum* (*green*). **c** Somatic chromosomes of hexaploid (2*n*=6x=72) species *S. demissum* using labeled DNA from *S. verrucosum* (*red*) and *S. jamesii* (*green*)

Of the 107 wild potato species we here accept with known chromosome numbers (Table 1), 19 (18 %) have multiple cytotypes. Sixty-four (60 %) are exclusively diploid, 14 (13 %) have diploid and triploid cytotypes, and three (3 %) have diploid and polyploid cytotypes exclusive of triploids. Eighteen (17 %) are exclusively polyploid at the tetraploid or hexaploid levels; one of these has tetraploid and hexaploid cytotypes, three (3 %) are exclusively triploid, one (1 %) is exclusively pentaploid, and one (1 %) has triploid and tetraploid cytotypes.

Hijmans et al. (2007) analyzed ploidy data with geographic information system (GIS) tools to elucidate the possible relationship of polyploidy to geographical and environmental range expansion in wild potatoes. Through an analysis of 5447 reports of chromosome counts of wild species, they found that the diploids occupy a larger area than the polyploids, but diploid and tetraploid species have similar range sizes, and the two species with by far the largest range sizes are tetraploids. The fraction of the plants that are polyploids is much higher from Mexico to Ecuador than farther south in the center of the sectional range. Compared with diploids, triploids tend to occur in warmer and drier areas, whereas higher-level polyploids tend to occur in relatively cold areas. Diploids are absent from Costa Rica to southern Colombia, the wettest part of the group's range. They concluded that polyploidy played an important role in this group's environmental differentiation and range expansion.

Genome Differentiation in Section *Petota* Identified by Genomic in situ Hybridization

As noted by Matsubayashi (1991) and Gavrilenko (2007, 2011), there is little karyotype variation among potato species. Traditionally, identification of the type of polyploidy (auto- or allopolyploid) is based on the analysis of meiosis of species and interspecific hybrids (Table 3). Multiple cytotypes of predominantly diploid potato species represent autopolyploids, or presumed autopolyploids (Gavrilenko, 2007). Segmental allopolyploidy has been proposed by Matsubayashi (1991) for tetraploid species of Hawkes's (1990) series *Acaulia* and for wild and cultivated polyploids of series *Tuberosa* (Hawkes, 1990), including *S. tuberosum*. Polyploid species of Hawkes's (1990) series *Conicibaccata*, *Demissa*, *Longipedicellata*, and *Piurana* have been considered as strict allopolyploids based on their regular bivalent pairing (Marks, 1955, 1965; Irikura,

1976; Matsubayashi, 1991). There are frequent contradictions in the hypotheses of the origin and genome composition of allopolyploids (Table 3). Matsubayashi (1991) proposed a five-genome concept that suggested that all diploid potato species comprised one major genomic group 'A' with minor variants designated by superscripts, corresponding to each taxonomic series of Hawkes (1990). Matsubayashi (1991) proposed that allopolyploid species share one common component genome 'A' (or its very similar genomic variants) and differed from each other by their second genome B, C, D or P (Table 3). The diploid North and Central American species *S. verrucosum* was suggested as the contributor of the 'A' component genome to Mexican allopolyploids based on traditional analysis of chromosome pairing in species and their hybrids (Bains, 1951; Marks, 1955, 1965; Irikura, 1976; Matsubayashi, 1991). However, Matsubayashi (1991) proposed that there are no extant diploid species with the B, C, D and P genomes.

Genomic in situ hybridization (GISH) and fluorescence in situ hybridization (FISH) techniques have been used extensively to investigate polyploid potato species (Pendinen et al., 2008a,b, 2012; Gavrilenko, 2011). These studies support allopolyploid origins of North and Central American tetraploid species *S. hjertingii* and *S. stoloniferum*, and Mexican hexaploid species *S. hougasii*, *S. iopetalum* and *S. schenckii*. GISH results support *S. verrucosum* (or its ancestral species) as an 'A' genome contributor in all North and Central American allopolyploids, confirming the prior hypothesis of classical cytogenetic analysis (Marks, 1965) and DNA sequence data (Spooner et al., 2008b; Rodríguez & Spooner, 2009). GISH supports *S. hjertingii* and *S. stoloniferum* to have originated through merging two divergent genomes (A and B) (Pendinen et al., 2008a; Table 3; Fig. 6). Symbol 'B' (rather than $A^{pi}A^{pi}$, as used by Matsubayashi, 1991) has been subsequently adopted to denote the genomes of Mexican diploid species (2n=2x=24, BB) *S. cardiophyllum*, *S. ehrenbergii*, and *S. jamesii*, reflecting their homology to the second component genome B of the allotetraploid Mexican species *S. hjertingii* and *S. stoloniferum* (Pendinen et al., 2008a) (Table 3). Genome B may also be homologous to the genome of Mexican diploid species *S. bulbocastanum* based on similar GISH results (unpublished data).

The genome formula PP (not equivalent to A^pA^p of Matsubayashi, 1991) was proposed by Spooner et al. (2008b) for South American diploid species in clade 3 (Fig. 2), largely consisting of species Hawkes placed in series *Piurana* (*S. andreanum*, *S. chomatophilum* and *S. piurae*) based on DNA sequence data. GISH data indicated that the 'P' genome diverged from both the A genome of *S. verrucosum* and the B genome of diploid Mexican species (*S. cardiophyllum*, *S. ehrenbergii*, *S. jamesii*). GISH results suggest that the P genome of diploid South American species of clade 3 and the genomes of *S. hjertingii* and *S. stoloniferum* (2n=4x=48, AABB) have homologous segments on only two chromosome pairs of allotetraploids (Pendinen et al., 2008a).

GISH analysis was also used to investigate the genome composition of Mexican hexaploid species of Hawkes's series *Demissa*, using labeled DNA of diploid species with AA, BB, or PP genomes (Pendinen et al., 2012). The results support *S. hougasii*, *S. iopetalum*, and *S. schenckii* as allopolyploids, suggesting the involvement of A, B, and P genome species as genome contributors (Pendinen et al., 2012). Differences between these allohexaploid species were revealed in the extent of presence of the B

Table 3 Genomic composition of potato species and putative progenitors of the polyploids based on different genomic concepts and methods; a dash indicates the species were not investigated with that method

Series according to Hawkes (1990)	Ploidy	Genome composition according to				
		Traditional and molecular (GISH) cytogenetics		Molecular markers		
		Matsubayashi (1991)	Pendinen et al. (2008a,b; 2011) Gavrilenko (2011)	DNA sequences of GBSSI (Spooner et al., 2008), nitrate reductase (Rodríguez & Spooner, 2009)	Nuclear clades[a]; COS markers, Cai et al. (2012)	Plastid clades[b]
Cuneoalata	2x	–	–	–	4	–
Megistacroloba	2x	AA	–	AA	–	4
Commersoniana	2x	–	–	–	4	–
Yungasensa	2x	–	–	AA	–	4
Ingaefolia	2x	A^iA^i,	–	–	3	3
Olmosiana	2x	A^oA^o	–	–	–	–
Morelliformia	2x	A^mA^m	–	BB	1	1
Polyadenia	2x	$A^{po}A^{po}$	–	BB	1	1
Bulbocastana	2x	A^bA^b	BB	BB	1	2
Pinnatisecta	2x	$A^{pi}A^{pi}$	BB	BB	1	1 (=*S. cardiophyllum*-2)
Tuberosa	2x	AA, AA	AA	AA	4	4
	3x	AAA^t,AAA^a	–	–	–	4
	4x	AAA^tA^t, AAA^sA^s	–	AAAA	4	4
	5x	$AAAAA^aA^t$				
Acaulia				Acaulia group:	Acaulia group:	
	4x	AAA^aA^a	AAAA	*S. acaule*-AAAA	*S. acaule*-3+4	4
	6x	AAA^aA^aXX	AAAAAA	*S. albicans*-AAAAAA	*S. albicans*-3+4	
Conicibaccata	2x	$A^{c1}A^{c1}$, $A^{c2}A^{c2}$ $A^{c1}A^{c1}C'C'$	A^CA^C	AA	4	4
	4x		$A^CA^CA^CA^C$ (or A^CA^CPP)	AAPP (or AACC)	3+4	4

Table 3 (continued)

Series according to Hawkes (1990)	Ploidy	Genome composition according to				
		Traditional and molecular (GISH) cytogenetics		Molecular markers		
		Matsubayashi (1991)	Pendinen et al. (2008a,b; 2011) Gavrilenko (2011)	DNA sequences of GBSSI (Spooner et al., 2008), nitrate reductase (Rodríguez & Spooner, 2009)	Nuclear clades[a]; COS markers, Cai et al. (2012)	Plastid clades[b]
Piurana	2x	A^pA^p	PP	PP (or CC, or A^pA^p)	3	3
	4x	A^pA^pPP	–	PPPP, or CCCC, or $A^pA^pA^pA^p$)	3+4	3
Longipedicellata	4x	AABB	*S. hjertingii*-AABB	AABB	*S. hjertingii*-1+4	4
	4x		*S. stoloniferum*-AABB		*S. stoloniferum*-1+4; (1+3; 3+4)	4
Demissa			Iopetala group:	Iopetala group:	Iopetala group:	-
	6x	ADDD`D`[c]	*S. hougasii*-AABB(PP) [d]	*S. hougasii*-AAPPPP	*S. hougasii*-3+4	4
	6x		*S. iopetalum*-AA(BB) [d](PP) [d]	*S. iopetalum*-AAPPPP	*S. iopetalum*-1+3+4	4
	6x		*S. schenckii*–AA(BB) [d](PP) [d]	*S. schenckii*-ABBPP	*S. schenckii*-1+3+4	4
			Acaulia group:	Acaulia group:		
	6x	$AADDD^dD^d$	*S. demissum*–AAAAAA	*S. demissum*-AAAAAA	Acaulia group:	4
					S. demissum-1+4	

[a] Indicates the nuclear clades for the majority of accessions with the minority of species in parentheses, using the clade numbering system of Cai et al. (2012)

[b] Plastid clades according to Spooner & Sytsma (1992) and Spooner & Castillo (1997)

[c] We combine different variants of the D subgenomes of Matsubayashi (1991) in allohexaploid species of series *Demissa* under the common genome formulae ADDD` D'

[d] For *S. iopetalum and S. schenckii* GISH data (Pendinen et al., 2012) support their allopolyploid nature. The presence of the complete component genome in allohexaploids is designated with corresponding letters BB, or PP; the presence of the incomplete component genome in allohexaploids (only part of the chromosomes of component genome shows an enhanced hybridization to the B, or to the P genome probe) is designated in parentheses as (BB) or (PP) correspondingly

and the P genomes (Table 3) that may be the result of genome restructuring subsequent to their formation.

However, the fourth Mexican hexaploid species *S. demissum* was supported as an autopolyploid A-genome species (Pendinen et al., 2012) (Table 3, Fig. 6). These results suggest that *S. demissum* may be derived from the related A-genome species or from the same A-genome ancestral species. GISH results support the recent reclassification by Spooner et al. (2004) of the Mexican hexaploid species into the Iopetala group containing *S. hougasii*, *S. iopetalum*, and *S. schenckii*, and the Acaulia group containing *S. demissum*. A similar autopolyploid nature (A genome polyploids) was revealed by GISH for other members of the Acaulia group South American polyploid species, *S. acaule* and *S. albicans,* of Hawkes's series *Acaulia* (Pendinen et al., 2012; Table 3).

GISH was unable to differentiate the component genomes in South American tetraploid species of Hawkes's series *Conicibaccata*, *S. colombianum* (A^cA^cCC genome according to Matsubayashi, 1991) (Table 3) indicating that the A^c and C genomes are closely related (Pendinen et al, 2008b). GISH analysis of *S. colombianum* also revealed high homology between the genome of *S. colombianum* and genomes of diploid species of the related species *S. violaceimarmoratum* and clade 3 species *S. andreanum* an *S. pascoense* (Pendinen et al., 2008b).

In summary, GISH supports traditional hypotheses of the allopolyploid origin of Mexican tetraploids and hexaploids (except *S. demissum*), confirms the genome composition of Mexican tetraploids, contradicts classical hypotheses of genome composition of all Mexican hexaploids as well as the South American hexaploid species *S. albicans*, supports recent DNA sequence results (see below), and provides new data on parental genome contributors in species of the Iopetala group.

Polyploidy—DNA Sequence Data

Hawkes (1990) proposed that section *Petota* arose in North and Central America from indigenous but unidentified ancestral species, possessed white stellate corollas, B genomes, and endosperm balance numbers of 1. He speculated that some of the North and Central American 2x (1EBN) species migrated to South America, evolving A genomes, rotate corollas, and EBN numbers of 2 or 4, then followed by a return migration of A genome species back to Mexico and Central America around 3.5 MA, followed by polyploid events leading to species he placed in series *Conicibaccata*, *Demissa*, and *Longipedicellata* with rotate to rotate-pentagonal corollas. Later genome 'B' was identified in Mexican diploid species *S. cardiophyllum*, *S. ehrenbergii*, and *S. jamesii*, (2n=2x=24, genome BB) based on the GISH analysis of Mexican allotetraploids (Pendinen et al. 2008).

DNA sequence data have the potential to infer allopolyploid origins if the parental genomes are divergent and if there has been little change in the homeologs subsequent to hybridization. Spooner et al. (2008b) used DNA sequence data from the GBSSI (*waxy*) gene and Rodríguez & Spooner (2009) used DNA sequences from the nitrate reductase gene to study polyploid origins in wild potatoes. Both studies gave similar results. Concordant with prior hypotheses based on classical cytogenetics and GISH data of Pendinen et al. (2008a), *S. hjertingii* and *S. stoloniferum* were strongly supported as combining genomes of the B-genome North and Central American

diploids (i.e., any of the diploids in this region exclusive of *S. verrucosum*), and A-genome species (likely *S. verrucosum*, the only A-genome species from this region). Also concordant with prior cytogenetic hypotheses, *S. albicans* and *S. demissum* (Acaulia group) had all alleles in the A-genome clade containing most South American species. These studies showed new allopolyploid origins, however, of *S. hougasii*, *S. iopetalum*, and *S. schenckii* (Iopetala group) and *S. colombianum* and *S. moscopanum* (Conicibaccata group) in that they combined genomes of the A-genome South American species (as expected) but also with genomes of the P-genome Piurana group (unexpected). Nitrate reductase also showed new alleles in *S. schenckii* the B-genome North and Central American clade. Fajardo & Spooner (2011) showed these A and P genome allopolyploid origins to be characteristic of a much wider range of species in the Conicibaccata group.

One problem with using orthologous DNA sequences to infer phylogeny of the allopolyploids is the occurrence of PCR recombination and heteroduplex fixation. Rodríguez et al. (2011) optimized an asymmetric single-strand conformation polymorphism technique to isolate allelic variants of highly heterozygous individuals, providing data of greater accuracy, speed, and reduced costs relative to prior procedures using cloning.

Lindqvist-Kreuze et al. (2013) tested the orthology of putative nuclear orthologs by aligning them with a whole genome sequence of potato. They showed that these markers are mostly single- or low-copy by comparison to the potato whole genome sequence (The Potato Genome Sequencing Consortium, 2011) and that there are several breaks in colinearity between the species analyzed. However, they found some nuclear orthologs to be present in multiple copies and these mapped to unexpected locations. Sequence comparisons between species show that some of these markers may be paralogs.

Both the GBSSI and nitrate reductase results were from single genes/regions, but Cai et al. (2012) examined 54 accessions of 11 polyploid species and 34 accessions of 29 diploid species with six nuclear orthologs. The results increased phylogenetic resolution within clades, giving better ideas of diploid progenitors, and showed unexpected complexity of allele sharing within clades. While some polyploid species have little diversity among accessions and concurred with the GBSSI and nitrate reductase results (e.g., *S. agrimonifolium*, *S. colombianum*, *S. hjertingii*, *and S. moscopanum*), the results gave much better resolution of species-specific progenitors. Seven other polyploid species showed variant patterns of allele distributions suggesting multiple origins and allele loss. Complex three-genome origins were supported for *S. hougasii*, *S. schenckii*, and one of the ten examined accessions of *S. stoloniferum* (the other nine accessions having only two genomes). It was unexpected that six Central American polyploid species (*S. demissum*, *S. hjertingii*, *S. hougasii*, *S. iopetalum*, *S. schenckii*, *and S. stoloniferum*) shared alleles from the South American diploid species *S. berthaultii*, as well as from the Central American diploid species *S. verrucosum*. These results, showing genomic complexity of some wild potato polyploids, could be explained by multiple hybrid origins and allele losses, similar to what is found in many allopolyploid groups (Wendel, 2000; Soltis et al., 2009).

Brown et al. (2014) associated cleaved amplified polymorphic site (CAPS) DNA markers and sequence tagged site (STS) DNA markers co-segregating with resistance phenotypes of Columbia root-knot nematode with resistant populations of

S. bulbocastanum, artificial hybrids of *S. bulbocastanum* and *S. tuberosum*, and plant introductions of *S. hougasii* and *S. stoloniferum*. These results support the findings of Cai et al. (2012), showing a B genome (clade 1+2) in some populations of *S. hougasii* and *S. stoloniferum*, demonstrating the utility of phylogeny to guide the search for useful allelic variants. Similarly, Sanetomo & Hosaka (2013) documented the exclusive presence of a mitochondrial DNA marker present only in some accessions of North and Central American polyploid members of the Longipedicellata group (tetraploid) and Iopetala group (groups sensu Spooner et al., 2004) and *S. demissum* (both hexaploid), and in their putative maternal ancestor *S. verrucosum* (diploid). These results support *S. verrucosum* as the maternal ancestor of these species, as well as illustrate the genomic complexity these polyploids. They also help to explain the difficulty of delimiting clearly defined species in polyploid potatoes.

Wild Potato Taxonomy: Our New Taxonomy Adopted Here

We summarize above the extensive studies using a variety of morphological, molecular, crossing, and field observation data that have been used to reinvestigate the species boundaries and interrelationships of wild potatoes. Table 1 provides our revised taxonomic decisions relative to Hawkes (1990), recognizing 107 wild species and four cultivated species, and provides hypotheses of interspecific relationships based on the three clade designations. This taxonomy is considerably changed relative to Hawkes (1990) who recognized 228 wild and seven cultivated species divided into 21 taxonomic series (19 tuber-bearing and two non-tuber-bearing).

While these changes since 1990 are extensive, they simply demonstrate that taxonomy of section *Petota* is inherently complicated by a "perfect storm" of biological factors that hinder the simple partitioning of populations into discrete species. These include the lack of strong biological isolating mechanisms and the resulting interspecific hybridization and introgression, allopolyploidy, a mixture of sexual and asexual reproduction, and recent species divergence (as supported by Särkinen et al., 2013) (Spooner & van den Berg, 1992a; Spooner, 2009). Recent workers have benefited by the collections of prior workers, personal opportunities to collect germplasm and observe variation in natural settings, access to experimental field plots to grow out and measure problematic groups in replicated field trials, and access to the majority of the type specimens that for a variety of reasons were not shared among previous workers.

The very nature of the complicating biological factors in section *Petota* makes it difficult to define species. The many problems in the recognition of species in section *Petota* have been discussed at length from literature reviews (e.g., Masuelli et al., 2009; Spooner, 2009; Camadro et al., 2012), and large scale molecular marker analyses (e.g., Jacobs et al., 2008, 2011). We consider our taxonomy (Table 1) to be subject to critique and modification, but to greatly improve the highly splintered and unworkable recognition of the many species recognized by Hawkes (1990). While the interspecific relationships are largely well-supported, our decisions of species boundaries are based primarily on results of morphological and molecular marker analyses (Table 2), combined with a practical ability to distinguish species, following a phylogenetic species concept, i.e., the recognition of an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent (Cracraft 1989).

Clearly, within our more broadly-defined species there exist distinct variants, sometimes distributed in small localized areas, that on first examination appear worthy of taxonomic recognition. Also, there are apparent wider clines of variation as described by Spooner et al. (2004) for *S. stoloniferum*, where smaller northern plants were previously called *S. fendleri*, taller southern ones *S. stoloniferum*, and softly pubescent more southern plants *S. papita*. The monographic studies leading to our decisions of species boundaries in section *Petota* (Table 1) rely, on necessity, from an examination of the thousands of living plantings of germplasm accessions in field plots and herbarium specimens. Previous decisions in Spooner's group relied partly on molecular marker analysis to distinguish species, for example, separation of *S. megistacrolobum* and *S. toralapanum* (both=*S. boliviense*; Spooner et al., 1997), or separation of *S. astleyi* and *S. boliviense* (both=*S. boliviense* (Giannattasio et al., 1994a,b). While both studies could discriminate these taxon pairs, it was only with the use of many morphological characters that overlapped in range. Field and herbarium studies, however, showed these to be imprecise and impractical, and to extend to yet other similar species (Table 1). We conclude that their maintenance as distinct species, as in many other examples in section *Petota*, will only perpetuate a taxonomy that is unnatural, unworkable, and continue to perpetuate variant identifications by future worders.

Cultivated Potato Taxonomy and Phylogeny

Early Classifications of Cultivated Potatoes

Landraces refer to indigenous cultivated crops. There are perhaps 3000 landraces of potato still grown by indigenous farmers in South America. Linnaeus (1753) recognized a single cultivated potato species, *S. tuberosum*. Dunal (1852) also recognized this single species, but with a separate variety that is now recognized as the wild potato *S. chacoense* (Ovchinnikova et al., 2011). De Candolle (1886) was the first to name the Chilean landraces as a distinct taxon (*S. tuberosum* var. *chiloense* A.DC. [=*S. tuberosum* Chilotanum group]). Here we use both formal Linnean nomenclature and non-Linnean group nomenclature. Table 4 lists a comparison of taxonomic treatments of cultivated potatoes at the Linnean ranks of series, species, and subspecies, and at the non-Linnean rank of groups and subgroups as discussed below.

Sergei Juzepczuk, Sergei Bukasov. The Russian taxonomists Juzepczuk & Bukasov (1929) were the next to describe the diversity of landrace potatoes. They expanded the concept of cultivated potato species, based on examination of germplasm collections and their observations in expeditions to South America by Bukasov (Colombia in 1926), Juzepczuk (Peru, Bolivia, Chile, 1927–1928), and Nicolai Vavilov (Ecuador, Peru, Bolivia, Argentina, Chile, Brazil, 1932–1933) (Juzepczuk & Bukasov, 1929; Bukasov, 1933; Juzepczuk, 1937). Most of their taxonomic descriptions were made from living plantings of germplasm collections at the experimental stations of the All-Union Institute of Plant Industry, now the Vavilov Institute of Plant Industry (VIR), Russia. The extensive diversity of these collections led Juzepczuk & Bukasov (1929) to at first consider *S. tuberosum* as a 'collective species' (*S. tuberosum* sensu lato). They further subdivided *S. tuberosum* into 13 species (named using the Linnaeus's binomial

Table 4 Comparison of taxonomic treatments of cultivated potatoes at the Linnean ranks of series, species, and subspecies, and at the non-Linnean rank of groups and subgroups

Ploidy	Bukasov (1978)	Dodds (1962)	Hawkes (1990)	Ochoa (1990, 1999)	Spooner et al. (2007); Ovchinnikova et al. (2011)
2x	series *Andigena* Bukasov	series *Tuberosa* (Rydb.) Hawkes	series *Tuberosa* (Rydb.) Hawkes	series *Tuberosa* (Rydb.) Hawkes	
		S. tuberosum			
	Solanum ajanhuiri Juz. & Bukasov	–	*S. ajanhuiri*	*S. ajanhuiri*	*S. ajanhuiri*
	S. stenotomum Juz. & Bukasov	Group Stenotomum	*S. stenotomum* subsp. *stenotomum* subsp. *goniocalyx*	*S. stenotomum*	*S. tuberosum* Andigenum group
	S. goniocalyx Juz. & Bukasov	Subgroup Goniocalyx			
	S. phureja Juz. & Bukasov	Group Phureja	*S. phureja*	*S. phureja*	
	S. rybinii Juz. & Bukasov				
	S. boyacense Juz. & Bukasov				
	S. canarense Bukasov				
	S. kesselbrenneri Juz. & Bukasov				
	S. multijugum Bukasov & Bavyko				
		Subgroup Amarilla			
3x	*S. chaucha* Juz. & Bukasov	Group Chaucha	*S. chaucha*	*S. chaucha*	
	S. chocclo Bukasov				
	S. cuencanum Juz. & Bukasov				
	S. mammilliferum Juz. & Bukasov				
	S. tenuifilamentum Juz. & Bukasov				
	series *Subacaulia* Bukasov				
	S. juzepczukii Bukasov	*S. ×juzepczukii*	*S. juzepczukii*	*S. ×juzepczukii*	*S. juzepczukii*

Table 4 (continued)

Ploidy	Bukasov (1978)	Dodds (1962)	Hawkes (1990)	Ochoa (1990, 1999)	Spooner et al. (2007); Ovchinnikova et al. (2011)
4x	series *Andigena* Bukasov				*S. tuberosum* Andigenum group
	S. andigenum	Group Andigenum[a]	*S. tuberosum* subsp. *andigenum*[a]	*S. tuberosum* subsp. *andigenum*[a] subsp. *yanacochense*[b]	
			S. phureja subsp. *hygrothermicum* (Ochoa) Hawkes subsp. *estradae*	*S. hygrothermicum*	
	series *Chilotana* Bukasov				*S. tuberosum* Chilotanum group
	S. chilotanum Hawkes	Group Tuberosum	*S. tuberosum*	*S. tuberosum*	
			subsp. *tuberosum*	subsp. *tuberosum*	
5x	series *Subacaulia* Bukasov				
	S. curtilobum Juz. & Bukasov	*S.* ×*curtilobum*	*S. curtilobum*	*S.* ×*curtilobum*	*S. curtilobum*

[a] Correcting the orthographic error "*andigena*"

[b] We consider *S. tuberosum* subsp. *yanacochense* as a synonym of the wild species *S. chacoense*

system) and defined *S. tuberosum* in a narrow sense (sensu stricto) as restricted to native Chilean landraces (Juzepczuk & Bukasov, 1929; Bukasov, 1933).

The taxonomic treatment of Juzepczuk & Bukasov (1929) was based mainly on a morphological species concept, but they indicated that these species were supported by distinctive ploidy levels and ecogeographical criteria. Rybin (1929, 1933), Bukasov (1933, 1937, 1960, 1971, 1978) and Lekhnovich (1971) published karyological, geographical, ecological, physiological, biochemical and anatomical information about the landrace species they accepted, using a complex approach that was novel for section *Petota*. Rybin (1929, 1933) first determined that landrace potatoes exist in a polyploid series from diploid (2n=2x=24), triploid (2n=3x=36), tetraploid (2n=4x=48), to pentaploid (2n=5x=60), and proposed to use ploidy levels to distinguish species. In many cases, ploidy levels were needed to discriminate morphologically similar cultivated species (e.g., triploid *S. chaucha* from Andean diploid and tetraploid landraces). However, even this criterion was not absolute for taxonomic recognition, as Lekhnovich (1971) and Bukasov (1978) later indicated the existence of autotriploid forms (cytotypes) in diploid *S. goniocalyx* and *S. stenotomum*.

Ecogeography was an important criterion in the taxonomic system of Juzepczuk & Bukasov (1929) and Bukasov (1930, 1933, 1938, 1978). Potato landraces were originally restricted to South America, distributed from western Venezuela to northern Argentina, and also in south-central Chile with a disjunction of 560 km due to the Atacama Desert separating the upland Andean and lowland Chilean potatoes. Based on an informal ecogeographic classification of the cultivated species (Bukasov, 1938) some (but not all) named landraces possessed distinct geographic or/and ecological characters. For example, *S. tuberosum* sensu stricto was endemic to the lowlands of south-central Chile and to neighboring islands growing at or near sea level, and able to produce tubers under the long days of central coastal Chile. Most of the cultivated diploids and triploids were relatively narrow endemics. However, these characters often relied on minor and overlapping morphological characters, and some of the cultivated species had the same ploidy level or/and occupied common habitats.

The 13 cultivated species (Juzepczuk & Bukasov, 1929) were later modified to 14 (Bukasov, 1933), then 18 (Bukasov, 1937), then 21 (Lekhnovich, 1971), and finally to 17 (Bukasov, 1978), 16 of these from the Andes of western Venezuela to northern Argentina, and one from south-central Chile (*S. tuberosum* s. str. in system of Juzepczuk & Bukasov (1929) and Bukasov (1933) or *S. chilotanum* in the latest treatment of Bukasov (1978) (Table 4). In addition, Russian taxonomists recognized hundreds of intraspecific taxa at various taxonomic ranks (subspecies, convarieties, varieties and forms) in order to characterize the tremendous variation (Bukasov, 1933; Lekhnovich, 1971). Many of these names were not validly published, most commonly because a Latin diagnosis was not provided (Lechnovich, 1971) or a type specimen was not designated, as reviewed in Ovchinnikova et al. (2011).

Bukasov (1933, 1938, 1939) attempted to classify these species into natural informal ecogeographical subgroups, and in his latest treatment (Bukasov, 1978) divided them into the three Linnean series *Andigena* Bukasov, *Chilotana* Bukasov, and *Subacaulia* Bukasov (Table 4). An ecogeographical pattern is evident in this classification, with 1) series *Subacaulia* composed of upland natural hybrids from the altiplano of Bolivia and Peru, 2) series *Andigena* in a wide range of latitudes and altitudes but generally in lower elevations than members of *Subacaulia*, and 3)

series *Chilotana* of lowland central Chilean landraces (Bukasov, 1978). Physiological characters reflecting the ecological conditions also were used. For example, Chilean landraces are able to produce tubers under the long days of central coastal Chile, whereas the Andean landraces form tubers under the shorter day length (Bukasov, 1933). Upland landraces of series *Subacaulia* are frost resistant (Bukasov, 1933, 1938) with bitter-tasting tubers that need special processing to remove high level of glycoalkaloids (Juzepczuk & Bukasov, 1929; Bukasov, 1933). Landraces of series *Subacaulia* can be readily distinguished from members of other series by the distinctive morphological character of high pedicel articulation (Juzepczuk & Bukasov, 1929).

John G. [Jack] Hawkes

The English taxonomist Jack Hawkes (1944) originally recognized 18 cultivated species with many formally named varieties and forms, informally grouped into geographic regions. This classification was very similar to the 13-species system of Juzepczuk & Bukasov (1929) but with the addition of five new species described by Hawkes. Hawkes (1944) subsequently named many varieties and forms, grouped into geographic regions similar to Bukasov (1933). Before he set out on his first collecting expedition to South America in 1938, Hawkes visited the All-Union Institute of Plant Industry in Leningrad, where he met Russian scientists who had been describing and documenting potato diversity using their system. Hawkes developed reservations about this system, however, saying: "when I later described and classified my own collections of potatoes I followed Vavilov in establishing far too complex a system. Much later I had to simplify this drastically" (Hawkes, 2004). Hawkes's subsequent classifications (Hawkes 1956a, b, 1963, 1990) greatly reduced his landrace taxa, converging on seven species and seven subspecies (Hawkes, 1990; Table 4). Much of Hawkes's (and colleagues) research was devoted to the biology (Hawkes, 1949), crossability (Jackson et al., 1978), ecology (Hawkes, 1954a), taxonomy (Hawkes 1956a, b), chemotaxonomy (Schmiediche et al., 1980; Huamán et al., 1983; Cribb & Hawkes, 1986) cytology (Hawkes, 1958), history (Hawkes & Francisco-Ortega, 1992, 1993), breeding value (Hawkes, 1958), classification theory (Hawkes, 1986), artificial resynthesis of putative hybrids (Hawkes, 1962b; Astley & Hawkes, 1979; Schmiediche et al., 1982; Cribb & Hawkes, 1986), and ethnobotany (Hawkes, 1947; Jackson et al., 1980) of cultivated potatoes.

Carlos M. Ochoa

Carlos Ochoa spent his entire career working on the collection, systematics, and breeding of potato, first at the Universidad Nacional Agraria in La Molina, Peru and later at the International Potato Center (http://agro.biodiver.se/2008/12/carlos-ochoa/). Most of his research was on the systematics of wild potatoes, where he used data from morphology of herbarium specimens and living plants grown in greenhouses, ploidy levels, and crossability to delimit taxa. His early monograph on the wild potatoes of Peru (Ochoa, 1962) was followed by much more complete treatments of the wild and cultivated potatoes of Bolivia (Ochoa,

1990a) and wild potatoes of Peru (Ochoa, 1999), in which he summarized his many new wild potato species from South America. His only taxonomic treatment of cultivated landraces is in his monograph of the wild and cultivated potatoes of Bolivia (Ochoa, 1990a), summarizing 77 new varietal and form names for the Bolivian cultivated landraces. This intraspecific classification was a complex inter-nested series of subspecies, varieties and forms, similar to that used by the Russian taxonomists. Ochoa never completed a planned treatment of the Peruvian cultivated potatoes. In total (including landrace taxa he mentioned as accepted in his Peruvian treatment; Ochoa, 1999), he recognized eight species and three subspecies of cultivated potatoes, similar to Hawkes (1990) (Table 4).

César Vargas

César Vargas was a lecturer at the National University of Cusco, Peru. He described new wild Peruvian potato species and treated the cultivated potatoes of Peru (Vargas, 1949, 1956) using the species names proposed by Juzepczuk & Bukasov (see above) and Hawkes (1944). He recognized 14 cultivated species (7 diploid, 5 triploid, 1 tetraploid [as *S. andigenum*], and 1 cultivated pentaploid species).

Alfonso Castronovo, Ludmila Kostina, Andrés Contreras and Ingrid Castro (Chilean Potatoes)

The Chilean taxonomist Alfonso Castronovo (1949) collected and provided cultivar names for 113 landrace potatoes in Chile as "papas Chilotas". The Russian taxonomist Ludmila Kostina (1978) provided a treatment of 360 landrace potatoes of Chile (as *S. chilotanum* Hawkes), classified into about 50 "varietal types". The Chilean agronomists Andrés Contreras & Ingrid Castro (2008) described and provided photographs of many of the 289 accessions of *S. tuberosum* subsp. *tuberosum* (=*S. tuberosum* Chilotanum group) in Chile maintained at the Universidad Austral de Chile in Valdivia.

Vladimir Lekhnovich

The Russian taxonomist Vladimir Lekhnovich (1971) described hundreds of Andean and Chilean landraces using different taxonomic ranks (subspecies, convarieties, varieties and forms).

John Dodds

All of the taxonomic treatments above classified the group of landraces as distinct Linnaean taxa (e.g., species, subspecies, varieties; the current Linnaean taxonomic code is the *International code of nomenclature for algae, fungi, and plants*, ICN; McNeill et al., 2012). The English taxonomist John Dodds (1962), in contrast, treated the landraces under the *International Code of Nomenclature of Cultivated Plants* (ICNCP; the latest version is Brickell et al., 2009) using the group nomenclature. "Cultivar-groups"(the current terminology) are taxonomic categories used by the ICNCP to associate cultivated plants with

traits that are of use to agriculturists (Spooner et al., 2003). Dodds suggested that there was poor morphological support for most cultivated species, and recognized only *S.* ×*curtilobum*, *S.* ×*juzepczukii*, and *S. tuberosum*, with five "groups" present in the latter (Table 4). The cultivar-group classification of Dodds (1962) was based on comparative morphology, reproductive biology, cytological and genetic data, and cultural practices. He contended that the morphological characters used by Hawkes (1956a) to separate cultivated species exaggerated the consistency of qualitative and quantitative characters. He showed that Andean farmers grow landraces of all ploidy levels together in the same field and that these can all potentially hybridize. He showed no genetic differentiation of the cultivated diploids existed (Dodds & Paxman, 1962) and contended that his classification was conservative in that it "provides a genetically reasonable classification that disturbs the established usage of words [taxonomic names] as little as possible" (Dodds, 1962, p. 530).

Later data supported Dodds's (1962) hypothesis of poor morphological separation of the cultivated species and suggested that they form a genetically diverse assemblage of genotypes of multiple and complex hybrid origins. Some "escaped" and persistent cultivated tetraploids in the Andes ("Araq" potatoes) and some putative "wild" species may be revertants from cultivation (Spooner et al. 1999; De Haan et al., 2012). Biological factors support gene flow among wild and cultivated potatoes. For example, Watanabe & Peloquin (1989, 1991) showed both diploid and unreduced gametes to be common in the South American wild and cultivated species, allowing gene transfer among different ploidy levels. Huamán (1975) showed evidence of natural crosses between the diploid wild species *S. megistacrolobum* (=*S. boliviense*) and the diploid cultivated species *S. stenotomum* (=*S. tuberosum* Andigenum group). Open pollinated hybrid fruits were found in all experimental plots containing 10, 25, 50, and 90 % of *S. megistacrolobum* plants within isolated plots of *S. stenotomum* grown in Huancayo, Peru. Rabinowitz et al. (1990) documented high levels of natural gene flow between the diploid wild taxon *S. sparsipilum* (=*S. brevicaule*) and *S. stenotomum*.

Cultivated Potato Taxonomy: Our Recent Potato Landrace Classification

Huamán & Spooner (2002) examined morphological support for the classification of potato landraces, using 267 accessions of representatives of all seven species and most subspecies as outlined in Hawkes (1990) (Table 4). The results showed some phenetic support for *S. ajanhuiri*, *S. chaucha* (=*S. tuberosum* Andigenum group) *S. curtilobum*, *S. juzepczukii*, and *S. tuberosum* subsp. *tuberosum* (=*S. tuberosum* Chilotanum group) but little support for the other taxa. However, most of this morphological support relied on a suite of characters, all of which are shared with other taxa (polythetic support).

Spooner et al. (2007b) examined 742 accessions of the same cultivated taxa and eight closely related wild species progenitors with 50 nuclear microsatellites and a plastid DNA deletion marker that distinguishes most lowland Chilean from upland Andean landraces (Hosaka et al., 1988). The results highlighted a tendency to separate three groups: 1) putative diploids, 2) putative tetraploids, and 3) the hybrid cultivated species *S. ajanhuiri* (diploid), *S. juzepczukii* (triploid), and *S. curtilobum* (pentaploid). However, there are many exceptions to grouping by ploidy. Strong statistical support occurred only for the species *S. ajanhuiri*, *S. curtilobum*, and *S. juzepczukii*. In combination with the morphological results of Huamán & Spooner (2002) and an examination of the identification history of these collections, Spooner et al. (2007b)

classifed the cultivated potatoes into four species: 1) *S. tuberosum*, with two cultivar groups (the Andigenum group of upland Andean genotypes containing diploids, triploids [except triploid *S. juzepczukii*]), and tetraploids, and the Chilotanum group of lowland tetraploid Chilean landraces), 2) *S. ajanhuiri* (diploid), 3) *S. juzepczukii* (triploid), and 4) *S. curtilobum* (pentaploid). Gavrilenko et al. (2010) used phenetic analysis of morphological data from an experimental field in the Saint Petersburg Region of Russia and 19 nuclear microsatellites, to study 238 landraces of all cultivated species from the VIR germplasm collection. This study had similar results of Huamán & Spooner (2002) for the morphological data and Spooner et al. (2007b) for the nuclear microsatellite data. The main difference between these two studies was that the VIR study failed to distinguish *S. ajanhuiri* (five accessions) from the majority of the other landraces.

Gavrilenko et al. (2013) studied 237 accessions of all of Hawkes's (1990) cultivated species and 155 accessions of closely related wild species using 15 plastid microsatellites. All 15 loci were polymorphic and identified a total of 127 haplotypes. As is typical for most cultivated plants, large decreases in genetic diversity were revealed in landraces in comparison with wild ancestral species. Phylogenetic analysis revealed two distinct groups: 1) the majority of accessions of the *Solanum tuberosum* Andigenum group and the majority of accessions of northern members of the wild progenitor *S. brevicaule* complex, 2) most of the wild species accessions and almost exclusively hybrid landraces which have introgressed plastid genomes from the other wild gene pools. Lack of clustering of traditionally recognized cultivated species (e.g., Hawkes, 1990) supported the revised four-species classification of cultivated potatoes of Spooner et al. (2007b) and Ovchinnikova et al. (2011; Table 4).

This new classification of cultivated potatoes was incomplete, however, because it failed to account for the many taxonomic names, many published in the Russian literature and not readily available to a non-Russian audience. Ovchinnikova et al. (2011) compiled all 602 basionyms of cultivated taxa, located their type specimens, designated lectotypes when possible, and placed these names (including names not validly published) in synonymy with this new classification.

In summary, landrace potatoes are grown throughout mid to high (about 3000–3500 m) elevations in the Andes from western Venezuela to northern Argentina, and then in lowland south-central Chile, concentrated in the Chonos Archipelago. The widely used classification of Hawkes (1990) divided cultivated potatoes into seven species and seven subspecies, but Bukasov (1978) and Lechnovich (1971) recognized 17 and 21 species respectively, and Ochoa (1990a, 1999) recognized nine species and 141 intraspecific taxa for the Bolivian cultivated species alone. Like the *S. brevicaule* complex, the *S. tuberosum* Andigenum group is characterized by ploidy variation and contains diploids, triploids, and tetraploids. Investigation of species boundaries in this group used data from morphological phenetics from a field plots in Peru (Huamán & Spooner, 2002) and the Saint Petersburg Region, Russia (Gavrilenko et al., 2010), nuclear microsatellites (Raker & Spooner, 2002; Ghislain et al., 2006; Spooner et al., 2007b; Gavrilenko et al., 2010), DNA sequence data of nuclear orthologs (Rodríguez et al., 2010), plastid microsatellites (Sukhotu et al., 2004, 2005, 2006; Gavrilenko et al., 2013) and plastid DNA deletion data (Hosaka, 2003; Sukhotu et al., 2004; Ames & Spooner, 2008; Gavrilenko et al., 2013). These results supported a classification of the cultivated potatoes into four species: (1) *S. tuberosum*, with two cultivar groups (the Andigenum group of upland Andean

genotypes containing diploids, triploids, and tetraploids and the Chilotanum group of lowland tetraploid Chilean landraces), (2) *S. ajanhuiri* (diploid), (3) *S. juzepczukii* (triploid), and (4) *S. curtilobum* (pentaploid) (Table 4).

Origin of Cultivated Potatoes

Two classes of hypotheses have long competed concerning the origin(s) of cultivated potatoes: (1) a multiple origin hypothesis developed by Russian scientists, and (2) a restricted origin hypothesis developed by English scientists.

Multiple Origin Hypotheses

Russian scientists (Juzepczuk & Bukasov, 1929; Bukasov, 1933; Vavilov, 1935, 1939; Juzepczuk 1937; Bukasov, 1938, 1939) first developed the multiple origin hypotheses. They followed Vavilov's (1926, 1928) idea that the center of origin of crop plants corresponded to geographic areas(s) containing the greatest diversity of cultivated species and their wild relatives, and Vavilov's ideas concerning the role of weedy wild crop relatives in crop domestication (Vavilov, 1962, 1965, 1989). Juzepczuk & Bukasov (1929) postulated that the greatest diversity in potato landraces was concentrated in two different centers corresponding to independent domestication events: 1) the Peruvian and Bolivian plateau, and 2) southern Chile, in the region of Chiloé Island and the adjoining islands.

Their observations were based on expeditions by Bukasov to Mexico, Guatemala, and Colombia from 1925 to 1926, and by Juzepczuk to Peru, Bolivia, and Chile from 1927 to 1928, supplemented by examination of living collections at the experimental stations of All-Union Institute of Plant Industry, Leningrad (now the Vavilov Institute of Plant Industry in Saint Petersburg, Russia (Juzepczuk & Bukasov, 1929; Bukasov, 1930, 1933; Juzepczuk, 1937). These studies documented extensive polymorphism in landrace morphology (Juzepczuk & Bukasov, 1929; Bukasov, 1930, 1933), chromosome numbers (Rybin, 1929, 1933), and physiological characters of frost tolerance, photoperiodic response, earliness, and dormancy (Bukasov, 1932, 1933; Razumov, 1931), reflecting adaptations to diverse ecogeographic conditions. As amplified below, these scientists proposed potato landraces to have two main separate origins, derived from different wild species in different geographic areas.

Solanum Tuberosum Andigenum Group

Andean Diploid Landraces. Juzepczuk and Bukasov (1929) hypothesized that Andean landraces evolved from wild species endemic to the Peruvian and Bolivian plateau, often growing in indigenous resident's fields, with ongoing hybridization after domestication. They proposed the Peruvian diploid wild species *S. multiinterruptum* and the Bolivian diploid wild species *S. sparsipilum* (=*S. brevicaule*) as wild species progenitors. Bukasov (1966, 1968, 1970, 1978) extended the list of putative wild species progenitors and postulated that each diploid cultivated species had an independent origin from separate diploid wild species. He suggested that the current distribution of cultivated species reflected their geographic origins. In agreement with Hawkes (1958), Bukasov (1966, 1978) indicated that the wild species

S. canasense (=*S. candolleanum*) and *S. leptophyes* (=*S. brevicaule*) both from Peru may have been involved in the origin of the polymorphic cultivated diploid *S. stenotomum* (=*S. tuberosum* Andigenum group). Bukasov (1966) agreed with Cárdenas (1950) that the Peruvian wild species *S. candolleanum* was involved in the origin of *S. phureja* (=*S. tuberosum* Andigenum group) and suggested that *S. phureja* was a result of crosses between the Peruvian wild species *S. candolleanum* and *S. leptophyes* (=*S. brevicaule*).

Bukasov (1966, 1978) proposed independent endemic origins of diploid landraces from Ecuador and Columbia (*S. canarense*, *S. kesselbrenneri*, *S. rybinii* [all =*S. tuberosum* Andigenum group], Table 4). The following northern Andean wild species were suggested as likely progenitors: *S. flahaultii*, *S. paucijugum*, *S. regularifolium* (=*S. andreanum*), and *S. solisii* (=*S. andreanum*); however, this suggestion was not supported by further studies (see below). Ugent (1970a) also proposed multiple origin hypotheses for the cultivated species, followed by continued hybridization with the wild species.

Andean Triploid Landraces (Exclusive of S. juzepczukii). Bukasov (1939, 1966, 1978) proposed that natural crosses of diploid and tetraploid landraces in various ecogeographic regions produced the cultivated triploids *S. chocclo*, *S. mamilliferum*, and *S. tenuifilamentum* (Table 4; all now classified as *S. tuberosum* Andigenum group). Bukasov (1939) postulated that *S. chaucha* (=*S. tuberosum* Andigenum group) a hybrid triploid species lacking tuber dormancy, formed from a cross between *S. phureja* (2x) and *S. andigenum* (4x) (both *S. tuberosum* Andigenum group). Lekhnovich (1971) and Bukasov (1978) later recognized *S. chaucha* as an autotriploid of *S. phureja*.

Andean Tetraploid Landraces. Bukasov (1939) suggested that Andean tetraploid landraces are of multiple origins arising through meiotic polyploidization (fusion of unreduced gametes of different cultivated diploids). Later, Bukasov (1966, 1978) proposed origins of Andean tetraploid landraces through interspecific hybridization between cultivated diploids and various diploid wild species with subsequent polyploidization of these interspecific hybrids.

Bitter Potatoes: S. juzepczukii (3x) and S. curtilobum (5x). Bukasov (1978) classified *S. juzepczukii* and *S. curtilobum* in series *Subacaulia*. They share frost resistance encountered at the high altitudes of Peru and Bolivia. The morphological similarity of *S. juzepczukii* and *S. curtilobum* to the sympatric wild species *S. acaule* was earlier noted by Juzepczuk & Bukasov (1929). Juzepczuk (1937) later proposed that *S. juzepczukii* and *S. curtilobum* were of hybrid origin involving species in series *Acaulia* (*S. acaule*, *S. punae*, *S. depexum* Juz. [all =*S. acaule*]; all tetraploids). Bukasov (1939) proposed that *S. juzepczukii* was derived from natural crosses between an unknown cultivated diploid and the wild tetraploid species *S. acaule*, and that *S. curtilobum* was derived from natural crosses between *S. juzepczukii* and Andean cultivated tetraploids (*S. andigenum* [=*S. tuberosum* Andigenum group]), matching their placement into series *Acaulia* together with *S. acaule* (Bukasov, 1955, 1966; Lekhnovich, 1971). Bukasov (1939) indicated that *S. juzepczukii* is similar to experimental interspecific hybrids produced in different combinations including *S. acaule* and

cultivated diploids that were then recognized as *S. canarense*, *S. gonicalyx*, and *S. rybinii* (=*S. tuberosum* Andigenum group). Further evidence as to the hybrid origins of *S. juzepczukii* and *S. curtilobum* was provided by morphological and cytological data generated by experimental resynthesis (Hawkes, 1962b; Schmiediche et al., 1982). All later taxonomists recognized *S. juzepczukii* and *S. curtilobum* at the species rank (Table 4), and agreed with the hybrid origin hypothesis involving *S. acaule*.

Solanum Tuberosum Chilotanum Group

Chilean Landraces. Following Darwin (1845), de Candolle (1912), and Bitter (1913), Juzepczuk & Bukasov believed that Chilean landraces evolved in the lowland region of southern Chile and adjoining islands independently from upland Andean potatoes (Juzepczuk & Bukasov, 1929; Juzepczuk, 1937; Bukasov, 1933, 1939, 1978), and as a result classified them into series *Chilotana* and series *Andigena* respectively (Table 4). Russian taxonomists hypothesized that Chilean landraces evolved from the wild Chilean tetraploid species *S. fonckii* (a *nomen nudum* from a herbarium annotation made by R.A. Philippi in SGO), *S. leptostigma*, and *S. molinae*. Hawkes (1956a) suggested that all these taxa represent naturalized escapes from cultivation and treated them as *S. tuberosum* subsp. *tuberosum* (=*S. tuberosum* Chilotanum Group).

Ugent et al. (1987) proposed a Chilean origin of tetraploid Chilean landraces but from another ancestor, the wild species *S. maglia*, today known from coastal Chile and a single valley in Argentina, but with all locations 1000 km north of Chiloé Island where *S. tuberosum* Chilotanum group landraces are today grown. This hypothesis was based mainly on starch grain analysis from the fossil tuber skins found in archaeological sites of south-central Chile compared to starch grains from extant *S. maglia* and Chilean landraces.

Restricted Origin Hypothesis

The restricted origin hypothesis was developed by Salaman (1946), Hawkes (1956a, 1990, 1999), and Simmonds (1964, 1995) who proposed that potato domestication took place in South America somewhere between Colombia and Bolivia from diploid wild species, followed by polyploidization. They then suggested a subsequent expansion of those short-day adapted landraces into new ecological conditions north to Colombia and Venezuela and south to coastal Chile.

Solanum Tuberosum Andigenum Group

Diploid Andean Landraces. Hawkes (1990) considered *S. stenotomum* (=diploid, *S. tuberosum* Andigenum group) to be the most primitive diploid cultivated species. Hawkes (1958) proposed the origin of *S. stenotomum* from wild ancestors related to the present day wild species *S. canasense* (=*S. candolleanum*) *S. leptophyes* (=*S. brevicaule*) and *S. soukupii* (=*S. candolleanum*) but later narrowed this to just *S. leptophyes* (Hawkes, 1994). He considered *S. phureja* to be selected from *S. stenotomum* (both =*S. tuberosum* Andigenum group) for quick maturity and lack of tuber dormancy (Hawkes & Hjerting, 1989).

According to Ugent (1970a), the cultivated diploids originated from a group of morphologically similar wild species distributed from central Peru to northern Argentina: *S. abbottianum*, *S. brevicaule*, *S. bukasovii*, *S. canasense*, *S. leptophyes*, *S. liriunianum*, *S. multidissectum*, *S. multiinterruptum*, *S. ochoae*, *S. soukupii*, *S. spegazzinii*, *S. vidaurrei*. Ugent (1970a) grouped all these 'microspecies' into the '*Solanum brevicaule* complex' and proposed continuing hybridization of cultivated species with yet another wild species outside the complex (*S. acaule*, *S. megistacrolobum* [=*S. boliviense*], *S. raphanifolium*) that continued to enrich the cultivated gene pool. Brücher (1975) hypothesized the wild Argentinian species *S. vernei* (not a member of *S. brevicaule* complex) as the ancestor of cultivated diploids; but this was not supported by recent molecular data (below).

Andean Triploid Landraces, Exclusive of S. juzepczukii. Hawkes (1963) synonymized all triploid cultivated species recognized by Bukasov (1978) with *S. chaucha* (=*S. tuberosum* Andigenum group) except *S. juzepczukii* (Table 4) and suggested that this cultivated triploid originated from natural crosses between the cultivated tetraploid *S. tuberosum* subsp. *andigenum* and cultivated diploid species *S. stenotomum* (both =*S. tuberosum* Andigenum group).

Tetraploid Andean Landraces. Hawkes (1956a) proposed two scenarios for the origin of tetraploid Andean landraces, both in the region of southern Peru and northern Bolivia. The first was from somatic chromosome doubling of widely distributed diploid landrace *S. stenotomum*, the second from natural crosses of *S. stenotomum* with wild diploid *S. sparsipilum* (=*S. brevicaule*). Ugent (1970a) reported the existence of natural interspecific hybridization between *S. stenotomum* and *S. sparsipilum*. Cribb & Hawkes (1986) synthesized this interspecific combination and analyzed its morphology and tuber proteins; their results did not contradict a hypothesis of the hybrid origin of subsp. *andigenum*. Rabinowitz et al. (1990) demonstrated, with isozyme markers, high levels of interspecific hybridization between *S. sparsipilum* and *S. stenotomum* in experimental plots in the Andes. Matsubayashi (1991) hypothesized that tetraploid Andean landraces originated from crosses of the two diploid cultivated species *S. phureja* and *S. stenotomum* (both =*S. tuberosum* Andigenum group) followed by chromosome doubling.

Cultivated Bitter Species, S. ajanhuiri, S. curtilobum, and S. juzepczukii. All taxonomists recognized *S. juzepczukii* and *S. curtilobum* at the species rank (Table 4) and agreed that they were hybrids involving the tetraploid wild species *S. acaule*. Hawkes (1962b) and Schmiediche et al. (1982) synthesized artificial triploids which were morphologically similar to the natural species *S. juzepczukii* in crosses between *S. acaule* (maternal parent) and cultivated diploid species. Schmiediche et al. (1982) could not resynthesize pentaploid hybrids in crosses of *S. juzepczukii* (maternal parent) with tetraploids of subsp. *andigenum*, although Hawkes (1962b) reported success in such crosses.

Ugent (1970a) suggested that the gene pool of cultivated diploids was enriched by natural hybridization with the wild diploid species *S. megistacrolobum* (=*S. boliviense*) and *S. raphanifolium* but did not mention cultivated diploid *S. ajanhuiri*. Huamán et al. (1982) resynthesized *S. ajanhuiri* with crosses of diploid cultivated *S. stenotomum*

(=*S. tuberosum* Andigenum Group) as the maternal parent and wild diploid *S. megistacrolobum* (=*S. boliviense*) as the male. Reciprocal combinations with *S. megistacrolobum* as the female parent produced only a few seeds with very poor germination (Huamán et al., 1982). Johns & Keen (1986) presented field data supporting a hybrid origin of *S. ajanhuiri* from *S. stenotomum* and *S. megistacrolobum*.

Solanum Tuberosum Chilotanum Group

Chilean Landraces. The main contradiction between the multiple and restricted origin hypotheses concerns the origin and taxonomic status of tetraploid Chilean landraces. As outlined above, Russian taxonomists proposed independent origins of tetraploid Chilean and Andean landraces in separate regions from separate indigenous ancestors, and hence treated them as different taxa: 1) *S. tuberosum* s. stricto (*S. tuberosum* var. *chilotanum* Bukasov & Lechn., later as *S. chilotanum* [both =*S. tuberosum* Chilotanum group]) (Bukasov, 1978)], and 2) *S. andigenum* Juz. & Bukasov, respectively.

Based on the restricted origin hypothesis, Chilean landraces initially were of Andean origin and then introduced into Chile after the potato was already domesticated in the central Andes. Thus, Andean tetraploids somehow appeared in Chile and evolved to the Chilean type including the ability to produce tubers under the long day conditions of Chile (Salaman, 1946; Hawkes, 1944, 1956a, 1990, 1999; Simmonds, 1964). This restricted origin hypothesis is based on two facts: 1) presently in the region of southern and central Chile there have been no diploid cultivated potatoes (except scattered reports) or of wild species from which *S. tuberosum* could have originated (Hawkes, 1944, 1956a), and 2) long-term selection experiments were reported to have adapted Andean tetraploids to a Chilotanum-like form (referred to as Neo-Tuberosum), especially regarding long day length adaptation (Salaman, 1946; Simmonds, 1966, 1969). This artificial selection to create Neo-Tuberosum was subsequently used by many authors as the model for the evolution of Andigenum germplasm to Chilotanum germplasm in south-central Chile. Using these two ideas, Hawkes (1956a) grouped all tetraploid potatoes (Chilean and Andean) under *S. tuberosum* L., considering this species as a complex of polymorphic forms that initially evolved in the Andes of southern Peru and northern Bolivia and subsequently spread north to Venezuela and Colombia and south to coastal Chile (*S. tuberosum* subsp. *tuberosum* [=*S. tuberosum* Chilotanum group]). Dodds (1962) and Brücher (1998) concurred with this idea. Grun (1990) proposed a modified scenario where the Chilean landraces originated from hybridizations of Andean landraces with a wild species, possibly *S. chacoense*, or an unidentified wild species. However, the restricted origin hypothesis lacks supporting evidence of movement from the Andes to southern Chile.

Recent Studies of Cultivated Potato Species Origins

Solanum tuberosum Chilotanum Group. The *S. tuberosum* Chilotanum and Andigenum groups can be separated by morphology, nuclear-cytoplasmic interactions, and day length responses (Grun, 1990). Data from nuclear and plastid microsatellites and morphology show that these groups often intergrade (Huamán & Spooner, 2002;

Table 5 Frequency distribution of plastid DNA haplotypes in cultivated potatoes and their putative wild progenitors. Solid lines in the table separate rank of species. Frequency of plastid DNA haplotypes is indicated in parentheses. If some species were represented by only one accession or some plastid haplotypes were represented only by one accession of some species parentheses are absent. The predominant plastid DNA haplotype of wild and cultivated species is indicated by bold letters.

Name of species according to Hawkes (1990)	Plastid DNA RFLP type (Hosaka & Sanetomo, 2009)	Name of species according to Spooner et al. (2007) and Ovchinnikova et al. (2011)	Plastid SSR haplotype (Gavrilenko et al., 2013)
CULTIVATED SPECIES			
Series Tuberosa cultivated		*S. tuberosum* Andigenum Group	
S. stenotomum	A(0.25), C(0.01), **S(0.73)**[a], W(0.01)	*S. tuberosum* Andigenum Group diploids	**I(0.83)**[a]**,** II(0.13),
S. phureja	**S(0.86)**[a], A(0.14)	A(0.24), C(0.01), **S(0.74)**[a], W(0.01)	Unique haplotypes(0.04)
S. chaucha	**A(0.70),** S(0.30)[a]	*S. tuberosum* Andigenum Group triploids	**I(0.51)**[a]**,** II(0.41), VI(0.04), Unique haplotypes(0.04)
S. tuberosum subsp. *andigenum*	**A(0.59)**, C(0.23), S(0.09)[a], T(0.01)[b], W(0.08)	*S. tuberosum* Andigenum Group tetraploids	I(0.15)[a], **II(0.40),** III(0.06)[b], V(0.06), VI(0.09), VIII(0.09), Unique haplotypes(0.15)
S. tuberosum subsp. *tuberosum*	A(0.12), **T(0.88)**[b]	*S. tuberosum* Chilotanum Group (tetraploids)	II(0.03), **III(0.88)**[b], V(0.06), Unique haplotypes(0.03)
S. ajanhuiri	**C**	*S. ajanhuiri*	I(0.333)[a], IV(0.333), Unique haplotypes(0.333)
S. juzepczukii	**C(1.0)**	*S. juzepczukii*	I(0.08)[a], **IV(0.92)**
S. curtilobum	**S**[a]	*S. curtilobum*	**I(1.00)**[a]
WILD SPECIES			
Series Acaulia	**C(1.00)**		IV(0.13), VII(0.06), X(0.24), XIX(0.13), Unique haplotypes(0.44)
S. acaule		*S. acaule*	
Series Maglia	-	*S. maglia*	**II(1.00)**
S. maglia			

Table 5 (Continued)

Name of species according to Hawkes (1990)	Plastid DNA RFLP type (Hosaka & Sanetomo, 2009)	Name of species according to Spooner et al. (2007) and Ovchinnikova et al. (2011)	Plastid SSR haplotype (Gavrilenko et al., 2013)
Series Megistacroloba		*S. boliviense*	Unique haplotypes(1.00)
S. boliviense	W, W2		
S. megistacrolobum	**C(1.00)**		
S. toralapanum	-	C(0.75), W(0.125), W2(0.125)	
S. raphanifolium	**C(1.00)**		
Series Tuberosa wild			
S. brevicaule	**W(1.00)**	*S. brevicaule* s.l. (Southern members of the *S. brevicaule* complex) A(0.02), C(0.05), W(0.88),W2(0.05)	I(0.01)[a], IX(0.05), XI(0.05), XII(0.04), XIII(0.04), XIV(0.04), XV(0.04), XVI(0.01), XXIII(0.03), XXIV(0.01), XXVII(0.03), XXVIII(0.03), Unique haplotypes(0.62)
S. gourlayi	–		
S. hondelmannii	–		
S. leptophyes	C(0.13), **W(0.79)**, W2(0.08)		
S. oplocense	**W(0.86)**, W2(0.14)		
S. sparsipilum	**W(1.00)**		
S. spegazzinii	-		
S. sucrense	A, W		
S. ambosinum	**C**	*S. candolleanum* s.l. (Northern members of the *S. brevicaule* complex) A(0.04), C(0.72), S(0.20)[a], W(0.04)	I(0.05)[a], XXII(0.05), XVIII(0.15), XX(0.11), XXI(0.11), XXII(0.11), Unique haplotypes(0.42)
S. bukasovii	A(0.09), **C(0.80)**, S(0.09)[a], W(0.02)		
S. canasense	**C(0.63)**, S(0.37)[a]		
S. candolleanum	**C(1.00)**		
S. coelestispetalum	**C(1.00)**		
S. multidissectum	C(0.44), **S(0.56)**[a]		
S. marinasense	**C(1.00)**		
S. pampasense	**W(1.00)**		

Table 5 (Continued)

Name of species according to Hawkes (1990)	Plastid DNA RFLP type (Hosaka & Sanetomo, 2009)	Name of species according to Spooner et al. (2007) and Ovchinnikova et al. (2011)	Plastid SSR haplotype (Gavrilenko et al., 2013)
S. multiinterruptum	C, W	-	
S. vernei	**W(1.00)**	*S. vernei*	XVI(0.25), XXIV(0.12),XXV(0.25), Unique haplotypes(0.38)
S. berthaultii[c]	T(0.00)[b] and others without 241 bp deletion (1.00)	*S. berthaultii* s.l. T(0.18)[b] and others without 241 bp deletion(0.82)	I(0.07)[a], III(0.20)[b], XVII(0.20), XXVI(0.13), Unique haplotypes(0.4)
Series Yungasensa			
S. tarijense[c]	T(0.27)[b] and others without 241 bp deletion(0.73)		
S. chacoense	**W(1.00)**		-

[a]The major plastid DNA type 'S', or plastid SSR haplotype 'I' of diploid landraces could be distinguished by the presence of the allele NTCP6_127 described earlier by Hosaka (2003) as having a 48 bp deletion in *rps16/trnQ* region of plastid DNA

[b]The major plastid DNA type 'T', or plastid SSR haplotype 'III' of tetraploid Chilean landraces could be distinguished by using H1 marker detecting the 241 bp deletion in the ?*ndhC/trnV* region of plastid DNA (Hosaka, 2003)

[c]Data from Hosaka (2003)

Raker & Spooner, 2002; Spooner, et al. 2007b; Gavrilenko et al. 2010, 2013). One of the arguments of the restricted origin hypothesis (proposing an Andean origin of Chilean landraces) was based on the results of Simmonds (1966) who worked with "Neo-Tuberosum" clones. Neo-Tuberosum refers to cultivated potato adapted to long-day tuberization and a syndrome of related morphological and physiological traits developed by intercrossing and selection of short-day adapted potatoes of the Andigenum group. The putative rapid selection of Neo-Tuberosum suggested that this process could occur naturally to produce Chilotanum group germplasm.

Ghislain et al. (2009b) demonstrated with nuclear microsatellites, however, that Neo-Tuberosum germplasm is related to the Chilotanum group, not the Andigenum group. They interpreted this unexpected result to be caused by strong rapid selection against the original Andigenum clones after unintended hybridization with Chilotanum group germplasm that occurred in nearby experimental fields. This result questioned a separate hypothesis that the European potato was derived from the Andigenum group (Salaman, 1937), and supported an earlier hypothesis that the European potato was derived from the Chilotanum group (Juzepczuk & Bukasov, 1929).

As was mentioned above, Grun (1990) proposed a modification of the restricted origin hypothesis and suggested that Chilean landraces originated from crosses between tetraploid Andigenum group and an unidentified wild species. Hosaka's group proposed an evolutionary pathway where hybrids of the wild species *S. tarijense* (=*S. berthaultii*; as a maternal ancestor) and tetraploid Andigenum group species were transferred to the southern regions to Chile. This view was based on plastid RFLPs, dividing cultivated species into five main "types:" A, C, S, T, W (Hosaka et al., 1984; Hosaka, 1986, 1995; Hosaka & Hanneman, 1988) or according to new nomenclature based on multiplex PCR and using an additional mitochondrial marker: A, M, P, T, W types (Sanetomo & Hosaka, 2011; Hosaka & Sanetomo 2012) (Table 5).

None of these plastid types were species-specific (Table 5). Thus, the T-type plastid DNA was predominantly found in the Chilotanum group (88 %), and rarely (about 1 %) in tetraploid Andigenum group, mainly from Argentina and southern Bolivia (Hosaka, 2002; Hosaka and Sanetomo, 2009). Similar frequencies of the T-type plastid DNA in tetraploid landraces was detected by Spooner et al. (2007b) and by Gavrilenko et al. (2013). Further screening of 566 accessions of 35 wild species including putative wild ancestors of the Chilotanum group revealed T-type plastid DNA in about 18 % of *S. berthaultii* (including *S. tarijense*) and *S. neorossii* (Table 5) but not any other examined wild species (Hosaka, 2002, 2003). The T-type plastid DNA could be distinguished by the presence of a 241 bp deletion in the *ndhC/trnV* intergenic spacer region (Kawagoe & Kikuta, 1991); this deletion is easily detected by PCR marker H1 (Hosaka 2002). Gavrilenko et al. (2013) demonstrated with plastid microsatellites that the T-type plastid DNA is distinct not only by the presence of the 241 bp deletion, but also by the combination of many plastid simple sequence repeat SSR (microsatellite) alleles which were not detected in the other haplotypes of cultivated species. All accessions with the 241 bp deletion (representatives of the T-type plastid DNA) share the same plastid SSR haplotype 'III' which was detected only in Chilean landraces and in a few *S. berthaultii* accessions (Table 5, Fig. 7). Other representatives of *S. berthaultii* without the 241 bp deletion having different plastid SSR haplotypes were close to haplotype III in the plastid SSR tree (Gavrilenko et al. 2013). All the results of molecular studies mentioned above support *S. berthaultii* sensu lato from southern

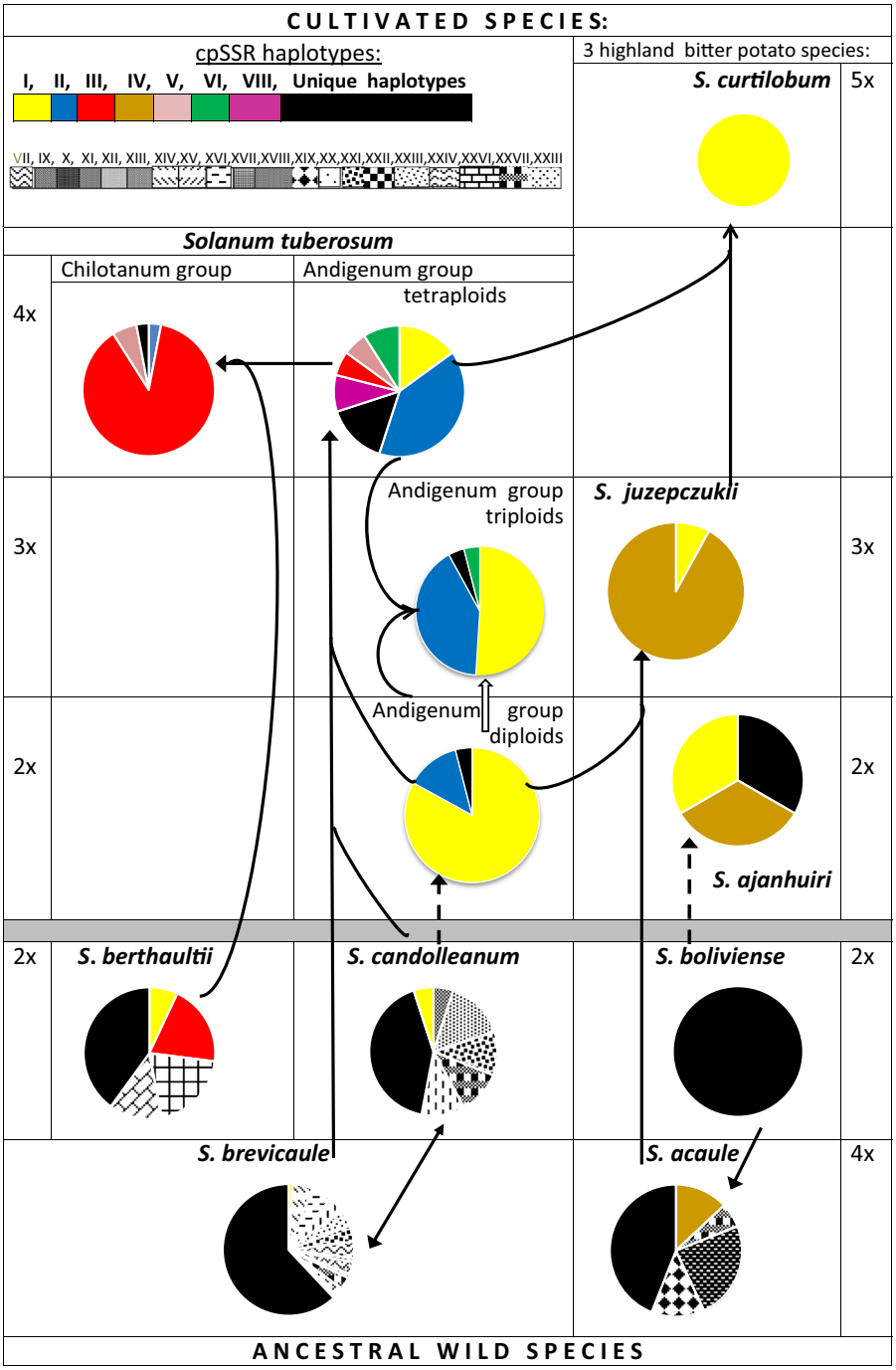

Fig. 7 Evolution of cultivated potatoes. Frequency of plastid SSR haplotypes in cultivated and wild species are according to Gavrilenko et al. 2013. *Solid arrows* indicate hybridization events; *dotted arrows* indicate domestication through natural variation and selection; *double arrows* indicate doubling events including unreduced gamete formation. Species names correspond to our revised taxonomy (Table 1)

Bolivia to northern Argentina as the maternal ancestor (cytoplasm donor) of Chilean landraces with the T-type of plastid DNA.

The hypothesis of Ugent et al. (1987) about the origin of the Chilotanum group from the wild species *S. maglia* found support from nuclear microsatellites (Spooner et al. 2012), which grouped *S. maglia* with the Chilotanum group. Rodríguez et al. (2010) using DNA sequence data of the waxy gene, also found that two of three examined accessions of the Chilotanum group had alleles grouping with *S. maglia* and in a clade containing the Andigenum group and related wild species, supporting *S. maglia* as a hybrid contributor to the Chilotanum group. However, the results were ambiguous because the two *S. maglia* accessions lack the 241 bp plastid deletion that is shared by most accessions of the Chilotanum group. Only one of 34 accessions of Chilean landraces had the same plastid SSR haplotype ('II') as all three examined accessions of *S. maglia* and as the majority of tetraploid Andean landraces in the plastid microsatellite study of Gavrilenko et al. (2013), whereas 88 % of Chilean landraces had another plastid SSR haplotype ('III') and all shared a 241 bp deletion in the *ndhC/trnV* region (Table 5). Two accessions of *S. maglia* analyzed for plastid DNA type (Hosaka, 1986) also showed haplotypes common with majority of tetraploid Andean cultivated potatoes. Based on results of Spooner et al. (2012) and the results of plastid DNA studies, Gavrilenko et al. (2013) proposed *S. maglia* as a possible paternal contributor to Chilean tetraploid landraces. In conclusion, the origin of the Chilotanum group remains unresolved.

Rodríguez et al. (2010) studied the hybrid origins of *S. ajanhuiri* from the Andigenum group diploids × *S. boliviense*, *S. juzepczukii* from the Andigenum group diploids × *S. acaule*, and *S. curtilobum* from the Andigenum group tetraploids × *S. juzepczukii*. For the tetraploid Cultivar groups of *S. tuberosum*, hybrid origins are suggested entirely within much more closely related species, except for two of three examined accessions of the Chilotanum group that appear to have alleles from the wild species *S. maglia*. Two hybrid origins proposed by others received no support, that is, the crop/weed species *S. sucrense* (from Andigenum group tetraploids and *S. oplocense*), and *S. vernei* as a wild species progenitor of the Andigenum group.

Solanum tuberosum Andigenum Group. The first plastid DNA RFLP studies supported the multiple origin hypotheses for diploid landraces of the Andigenum group (Table 5). Hosaka (1995) detected four "types" of plastid genomes (W, A, S, C) within *S. stenotomum* that he interpreted to support multiple origins of the diploid Andigenum group from different closely related wild species. However, further analyses of additional landrace and wild species accessions revealed restricted plastid DNA polymorphism within diploids of the Andigenum group. It showed a predominance of two major plastid DNA types 'S' (74 %) and 'A' (24 %) in the diploid Andigenum group, (Table 5); these two types were also found in many representatives of wild species progenitors in the *S. brevicaule* complex (Sukhotu and Hosaka, 2006; Sukhotu et al. 2004, 2005, 2006; Hosaka & Sanetomo, 2009) (Table 5). These results suggested that diploid landraces either 1) had dual origins from two different wild species or 2) had introgression with haplotype A (Sukhotu & Hosaka, 2006; Sukhotu et al. 2006).

Gavrilenko et al. (2013) used another set of plastid SSR markers and detected only two haplotypes among 100 diploid landraces (*S. phureja* and *S. stenotomum* [both

=*S. tuberosum* Andigenum group]), 83 % had predominant haplotype 'I' and 13 % had haplotype 'II' (Fig. 7). Plastid diversity in the ancestral *S. brevicaule* complex exhibited much higher diversity, with 93 wild species accessions having 69 haplotypes; most of them were unique. The predominant haplotype 'I' of diploid landraces was found also in two accessions (2 %) of representatives both northern and southern members of the *S. brevicaule* complex (Gavrilenko et al., 2013).

These data, together with the results of Sukhotu et al. (2006) and Sukhotu & Hosaka 2006), support the domestication of Andigenum group diploids from members of the *S. brevicaule* complex having the predominant in cultivated diploids 'S' type plastid DNA (or plastid SSR haplotype 'I'); which could be easily distinguished by the presence of the allele NTCP6 127 described earlier by Hosaka (2003) as having a 48 bp deletion in *rps16/trnQ* region of plastid DNA.

Results of plastid DNA studies of Hosaka's group (Hosaka, 2003; Sukhotu et al. 2004, 2005, 2006; Sukhotu & Hosaka 2006) and Gavrilenko et al. (2013) in general are in agreement, although the results are obtained with different germplasm collections and different plastid DNA markers. Species differentiation based on plastid DNA studies demonstrate that all accessions of the diploid and triploid Andigenum groups were grouped together with representatives of wild species accessions of '*S. brevicaule* complex'—mostly of northern members (*S. bukasovii*, *S. canasense*, *S. multidissectum* [all =*S. candolleanum*]), but also with a few representatives of the southern members of '*S. brevicaule* complex' and with a few accessions of wild species from other gene pools (as *S. boliviense*, *S. maglia*, *S. tarijense* [=*S. berthaultii*]). These results could reflect subsequent hybridization of landrace and wild species as proposed by Ugent (1970a).

Within the landraces, the Andigenum group tetraploids have the highest level of plastid DNA polymorphism (Hosaka, 1995; Sukhotu et al. 2004, 2005; Sukhotu & Hosaka, 2006; Gavrilenko et al., 2013) (Table 5, Fig. 7). This supports earlier hypotheses that they arose both from cultivated diploids by sexual polyploidization and from hybridization with wild species (as maternal parents). Some of the plastid microsatellite haplotypes specific only to Andean tetraploid landraces were detected in the samples from the southern Andes and were absent farther north (Gavrilenko et al., 2013). In contrast, some haplotypes detected in the northern Andes were not found in tetraploid landraces from the southern Andes, supporting possible independent introgression events with representatives of different wild species (Gavrilenko et al., 2013).

AFLP analysis (Spooner et al., 2005a) supported a hypothesis of a single origin of Andean landraces from the northern members of the *Solanum brevicaule* complex indigenous to southern Peru and northern Bolivia. These northern members of the *S. brevicaule* complex are here combined into the single highly polymorphic species *S. candolleanum* sensu lato (Table 1). Thus, disagreement between two hypotheses of origin of diploid members of the Andigenum group (multiple origins vs. a single origin) is simply a result of differing taxonomic circumscriptions of wild species belonging to members of the northern *S. brevicaule* complex.

One of the arguments of a multiple origin of the *Solanum tuberosum* Andigenum group was based on the putative distinct ecogeographical habitats of landraces that exist in the polyploid series forming this group. In addition, ploidy level has been a major character

helping to classify cultivated potatoes under previous taxonomic systems. Spooner et al. (2010) examined associations of environments to ploidy levels (2x, 3x, 4x, 5x) of all landrace populations in South America using a database of 2048 georeferenced accessions examined with random-Forest library (Liaw and Wiener, 2002) (in R; R Development Core Team, 2010). Except for the Chilotanum group and extreme northern and southern range extensions of the Andigenum group, it was impossible to find distinct habitats for the ploidy variants of the *S. tuberosum* Andigenum group.

Solanum ajanhuiri, *S. curtilobum*, and *S. juzepczukii*. *Solanum ajanhuiri*, *S. curtilobum*, and *S. juzepczukii* have long been proposed to be of hybrid origin from members of the Andigenum group and the wild species *S. acaule* and *S. boliviense* sensu lato (Juzepczuk & Bukasov, 1929; Juzepczuk, 1937; Bukasov, 1939; Hawkes, 1944, 1958). Nuclear DNA sequence data (Rodríguez et al., 2010) have supported their origins by showing additivity of alleles from their proposed parents; plastid SSRs (Gavrilenko et al., 2013) have supported the wild species parents as the maternal ancestors for *S. juzepczukii* and *S. ajanhuiri*. However, there are rare exceptions to classically proposed hybrid origins as seen with plastid microsatellite data, suggesting possible multiple origins of *S. ajanhuiri* and *S. juzepczukii* from reciprocal crosses (Gavrilenko et al., 2013) (Table 5, Fig. 7).

Contradiction between nuclear SSR and plastid SSR results in relation to *S. curtilobum* supports an alternative lineage in its maternal origin related to the Andigenum group (Gavrilenko et al., 2013), and not to *S. juzepczukii* as was proposed before. All ten examined accessions of *S. curtilobum* have the plastid SSR haplotype 'I' common with members of the Andigenum group, grouping *S. curtilobum* separately from *S. acaule* and *S. juzepczukii* (Table 5, Fig. 7). Accordingly, different scenarios for the origin of the pentaploid cultivated species *S. curtilobum* were proposed, such as Andigenum group tetraploids × *S. juzepczukii* (unreduced gametes) and Andigenum group triploids (unreduced gametes) × *S. acaule* (Gavrilenko et al., 2013). These assumptions correlate with observations of Hawkes (1962b) that mixed fields of representatives of the cultivated species *S. curtilobum*, *S. juzepczukii*, and members of Andigenum group frequently co-occur with the wild species *S. acaule*.

Summary of Cultivated Potato Origins

Two hypotheses have been advanced for the origin of cultivated potatoes, 1) a multiple origin hypothesis, and 2) a restricted origin hypothesis. Much of the disagreement between these two hypotheses stems from the taxonomic circumscription of the putative progenitor species, mainly proposed to be members of the taxonomically difficult *S. brevicaule* complex. However, there remain gaps in archaeological and genome sequence data that need to be filled in to delineate these origins. For example, we have no knowledge of possible human transport of domesticated potatoes from the Andes to southern Chile. There may have been a (now extinct) widespread tuber-bearing wild species progenitor in southern Chile. Molecular data from accessions currently residing in genebanks may not truly represent the genetics of the original accessions. Finally, many wild species are represented by very few accessions, which may introduce a bias in these studies.

Recent investigations gave support to some points of both hypotheses of potato domestication and proposed the following scenarios. The Andigenum group originated in a single domestication event from diploid wild species in the *S. brevicaule* complex in southern Peru and immediately adjacent northern Bolivia (Spooner et al., 2005a). The ancestral diploid population(s) and domesticated diploids probably had the same plastid DNA haplotype that is predominant in the present day diploid landraces (plastid DNA type 'S' or plastid SSR haplotype 'I'). The origin of the triploid and tetraploid forms of the Andigenum group could have multiple origins both through meiotic polyploidization events (unreduced gametes) of diploid landraces and through interspecific hybridization.

Later differentiation of the Andigenum group likely involved nuclear and organellar introgression from wild species other than members of the *S. brevicaule* complex, allowing cultivated species to spread to broader ecological conditions and wider geographical areas, with yet more rounds of hybridization (Gavrilenko et al., 2013). Thus, the origin of the frost resistant species *S. juzepczukii*, *S. curtilobum*, *S. ajanhuiri* involved *S. acaule* and *S. boliviense* in the highland Andes of southern Peru and Bolivia. Introgression from *S. berthaultii* (as a maternal ancestor) and possibly *S. maglia* led to the formation Chilean landraces in lowland southern coastal Chile. In conclusion, the question of the origin of the cultivated potato is not fully resolved and may need additional data from a wider sample of in situ collections and further investigations in genomics and archeology.

From Landraces to Modern Potatoes

Landrace potatoes are today widely distributed from western Venezuela to northern Argentina, with another group of landraces in coastal Chile (Spooner et al., 2010). Fossil evidence (as preserved tubers) document potatoes in various sites along the dry coast of Peru as early as 8000 BC (Engel, 1970; Ugent et al., 1982; Ugent & Peterson, 1988) and in south-central Chile at the Monte Verde archaeological site (as potato skins) at 11,500 BC. The primary domestication of potatoes in the Andean uplands likely occurred around Lake Titicaca at the boundary of Peru and Bolivia (Hawkes, 1944; Ugent, 1970a; Spooner et al., 2005a). Potatoes were first observed in South America by outsiders by Spanish explorers in 1536 in the tropical lowlands of the Magdalena River Valley in present-day Colombia (Castellanos, 1886) [1601].

Potato germplasm has a huge reservoir of genetic and morphological diversity. This implies that predictions based on one or a few clones are not representative of the potato crop. This has implications for properly assessing the potential of potatoes for food security under climate change; predictions of global yields, adaptation to climate, or influence of climate change are only true for that particular clone or set of clones. For example, it is possible to make crosses in northern Ireland and select progeny in the Negev desert resistant to heat stress up to 40° Celsius as well as resistant to Verticillium wilt and early blight (Susnoschi et al., 1987). In summary, the potential of potatoes as a crop may have a much better range of adaptability to climate change than previously predicted through modeling (Hijmans, 2003; Schafleitner et al., 2011).

Domestication Traits

An obvious and major domestication trait in potatoes is the shortening of stolons and a corresponding increase in tuber size. Wild potato species typically produce small tubers on the ends of stolons which may be a meter or more in length. This is an adaptive feature that allows for the production of asexual propagules over a large area. Domesticated potatoes, in contrast, require short stolons for commercial production systems and large tuber size for high marketable yield.

Members of the Solanaceae produce glycoalkaloids, which are toxic and can cause DNA damage when consumed (Korpan et al., 2004). Glycoalkaloids are found in both leaves and tubers, where they impart a bitter taste (Camire et al., 2009). Wild potato species contain varying levels of a wide array of glycoalkaloids (Friedman, 2006). However, the cultivated potato contains low glycoalkaloid levels, typically only solanine and chaconine, suggesting these bitter compounds were selected against during domestication (Johns & Alonso, 1990).

Cultivated potatoes likely originated in a broad band of the equatorial regions of South America, where photoperiod remains near 12 h throughout the year. However, potatoes grown in the major production areas in Europe, North America and Asia must be able to tuberize under the long photoperiods of temperate zone summers. One of the most important traits required for the adaptation of South American potatoes to Europe was the ability to tuberize under a long photoperiod. Genetic models for the tuberization response to photoperiod have been proposed. In diploid cultivated × wild species hybrids, tuber production under a 14-h photoperiod appears to be dominant over that for the inability to tuberize (Hermundstad & Peloquin, 1985; Jacobsen & Jansky, 1989; Yerk, 1989; Jansky et al., 2004; Kittipadakul et al., 2012). Wild species do not produce tubers when grown under the photoperiods of the summer production season at temperate latitudes. Cultivated potatoes segregate for this trait and, when crossed to wild species, produce some hybrid offspring that tuberize under long days (Hermundstad & Peloquin, 1985; Kittipadakul et al. 2012).

The physiological basis for tuberization under long photoperiods involves biochemical and molecular signals that link photoperiod perception in leaves to changes in cellular growth patterns in stolons (Rodriguez-Falcon et al., 2006; Sarkar, 2008, 2010). The tuberization stimulus is perceived in above-ground stems and transmitted to underground stolons (Gregory, 1956). Some of the essential players in this long-distance signaling pathway have been identified and include phytochrome B (Batutis & Ewing, 1982; Hannapel et al., 2004), phloem transmissible StBel5 mRNA (Banerjee et al., 2006; Hannapel, 2010), miR172 microRNA (Martin et al., 2009), gibberellins (Krauss & Marschner, 1982; Carrera et al., 1999; Martínez-García et al., 2002), POTH1 (Chen et al., 2003), StSP6A (Navarro et al., 2011), CO (Rodriguez-Falcon et al., 2006; Navarro et al., 2011), sucrose (Chincinska et al., 2008) and temperature (Krauss & Marschner, 1982). Gibberellins, cytokinins, and jasmonate-like compounds are important in regulating tuberization that is activated in the stolon apex (Hannapel et al., 2004). In temperate zone cultivars, short photoperiods, cool temperatures, and low levels of available nitrogen promote early tuberization (Ewing & Wareing, 1978; Krauss, 1985; Sarkar, 2008). Recently, a major effect quantitative trait locus for plant maturity and tuber initiation was found to be controlled by a transcription factor

that acts as a mediator between the circadian clock and StSP6A (Kloosterman et al., 2013). Consequently, even though the pathway for the perception of photoperiod and the response to it is complex, it appears that a major regulatory factor controls tuberization under long days. We can speculate that it would have been easy to select for this simply inherited, dominant genetic system during potato domestication and adaptation to worldwide production systems. In fact, it would be self-selecting. In segregating populations, any genotypes that did not tuberize would not have been maintained.

Geographic Correlates of Potato Systematics and Diversity

The 107 wild potato species can be found between 38 °N to 41 °S, between 0 and 5000 m altitude, within habitats from −1 °C to 26 °C annual average temperature, and with mean annual rainfall from less than 100 mm (*S.* ×*neoweberbaueri*) to more than 3700 mm (*S. acaule*, *S. boliviense*). Most wild potato species can be found between 35 °N and 35 °S, between 1500 m and 4000 m altitude, 7.5 to 20 °C mean annual temperature, and 250 to 1250 mm annual rainfall (Hawkes, 1994; Hijmans & Spooner, 2001). These ranges of ecological parameters of wild potato species are paralleled by high morphological polymorphism within and among the species (Spooner et al., 2004), making it difficult to delineate species.

Geographic information systems (GIS) have played a major role in improving the accuracy of accession locations since the late 1990's (Hijmans et al., 1999) and spatial methods are increasingly applied to the analysis of the ecology of crop wild relatives, including potatoes. While earlier analyses were largely descriptive (Hijmans & Spooner, 2001), later ones frequently used specialized Bayesian approaches (e.g. Simon et al., 2010). Though spatial methods have made significant contributions there are still some caveats to consider: a) the temporal and spatial resolution of the underlying datasets may be insufficient (e.g. some databases for current climate often refer to a climate scenario before climate change based on average data from the 1960's to 1990's, and spatial data are mostly based on interpolations that may not be representative of micro-climates) and b) the bias introduced by the selection of standard sets of variables, i.e., some elements of environment may not be included, like soil data and ground-water level. Notwithstanding, spatial or GIS analytical tools have made many contributions to the analysis of the distribution and ecology of potatoes, including improved distribution maps (Hijmans et al., 1999, 2001), genebank management (Hijmans et al., 2000; Jansky et al., 2013), the compatibility of climatic niches (Simon et al., 2010, 2011; Spooner et al., 2010), the confirmation of the role of ploidy in range expansion (Hijmans et al., 2007), or in the analysis of species-level traits, such as disease resistance (Spooner et al., 2009).

In some species, such as *S. jamesii*, *S. stoloniferum*, and *S. sucrense* (=*S. brevicaule*) there are no associations of genetic variation and ecogeographical variation (del Rio et al., 2001; del Rio & Bamberg, 2002; Bamberg & del Rio, 2008). However, an association of geography and genetic variation was found within *S. verrucosum* (del Rio & Bamberg, 2004). This was not explained by introgression with other nearby species (Bamberg & del Rio, 2008). A variety of confounding factors that influence the association have been identified including a) sampling bias due to ease of access near

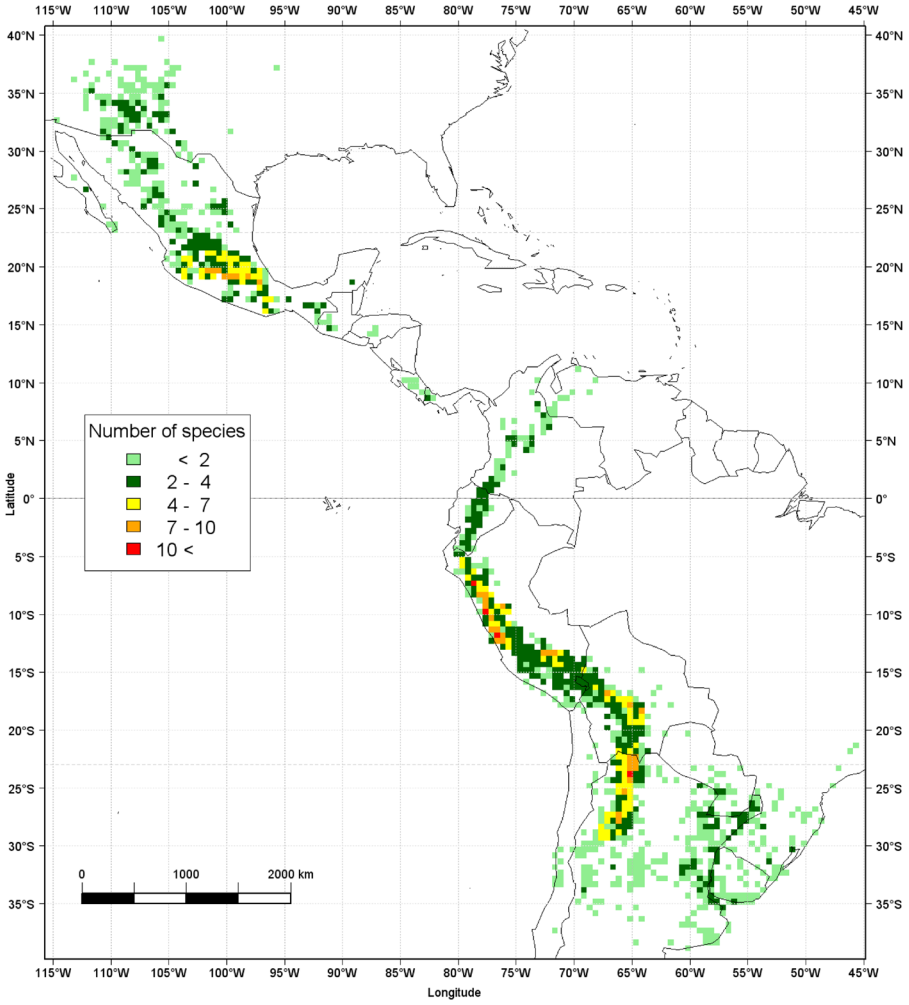

Fig. 8 Number of wild potato species per half degree grid cell in the Americas. The map shows five centers of species richness (from South to North): **a** northern Argentina, **b** Bolivia, **c** southern Peru, **d** northern Peru, and **e**) central Mexico. Highest numbers of species richness are in northern Peru and northern Argentina. Large areas formed of one to two potato species can be found from eastern Argentina to the south-eastern coast of Brazil including Paraguay and Uruguay as well as from Colombia to southern Mexico and from northern Mexico to the south-eastern United States

roads (Hijmans et al., 2000); b) differential dispersion (Bamberg et al., 2010; Bamberg & del Rio, 2011); c) mis-identification of wild materials after introduction into genebanks (del Rio & Bamberg, 2003; Bamberg et al., 2009); and d) considerable genetic change over time at sampling locations (del Rio et al., 1997b; Bamberg & del Rio, 2003).

The fate of germplasm in situ and the efficiency of its collection, preservation, and evaluation in the genebank are all influenced by the interaction of population structure and population sampling techniques. When multiple generations of seed propagation in the genebank were compared with RAPDs by del Rio et al. (1997a), those generations

showed small, insignificant differentiation compared to the distinction of different populations.

Bamberg & del Rio (2004) showed that RAPD markers segregated in accord with reputed population structures of four model potato species. Bamberg & del Rio (2006) also devised experiments to test for techniques that could promote genetic shifts during the genebank's propagation of populations. They tested germplasm expected to be most vulnerable to genetic drift from selecting the most vigorous seedlings for parents and unbalanced maternal seed bulks (Bamberg & del Rio, 2009), and found that neither introduces opportunity for large genetic changes. This is because more robust seedlings typically result from random early sprouting, and even when parents have a high degree of heterozygosity, few loci have low frequency alleles. Furthermore, few loci fail to fix both alleles in at least one population in the genebank (Bamberg & del Rio, 2003), so even if an individual population would lose an allele in the next generation, no alleles would be lost overall from the genebank.

Hijmans & Spooner (2001) mapped 6073 locality records of wild potatoes using the 196 species then recognized in Spooner and Hijmans (2001). For comparative purposes in this review, we re-assessed the effect of both the revised potato taxonomy (Table 1) and increased numbers of observation records. We qualitatively contrasted these latest data with those reported in Hijmans and Spooner (2001) to look for general trends. In comparison to the data underlying Hijmans and Spooner (2001) our database contains 13,117 records. Of those, 11,485 are georeferenced (87.5 %) and used to compile Table 6, Fig. 8 (corresponding to Table 1 and Fig. 6 in Spooner & Hijmans, 2001).

The overall number of observation records more than doubled (from 6073 to 13,115) while the number of species was reduced from 199 to 107 (Table 6). Consequently, the average observations per species quadrupled (from 30 to 125). The biggest increase in observations came from Argentina (from 1688 to 4547). In terms of number of species, Peru remains the country with the most species (reduced from 93 to 51) and also remains the country with most rare species (from 42 to 13). Rare species are defined following Hijmans (2001) as species with overall observations less than five. However, Peru's share of rare species increased from 58 to 65 %. Peru is followed in terms of number of species by Mexico, Argentina, and Bolivia as in Hijmans and Spooner (2001). Mexico as before occupies a middle range between Peru and Argentina/Bolivia (from 36 to 27). Despite the absolute reduction, Mexico represents a much bigger share of the species genepool (7.6 % more; from 18.1 to 25.2 %). Yet the biggest increase in relative terms is Honduras that has three species as opposed to only one reported in 2001 (from 0.5 to 2.8 % of the species genepool).

Species richness can be represented by spatial explicit counts of wild potato species per half degree grid cell (Fig. 8). The resulting map shows an overall similar pattern of hot spots to the one published in Hijmans and Spooner (2001). The main differences are in the relative changes in the number of species at the hot spots: the most species-rich areas are now distributed from central to northern Peru, whereas the relative number of hot spots in Bolivia and Argentina decreased overall. The hot spot in central Mexico remains roughly the same with perhaps a more even distribution of species richness. Peru still contains almost half of total number of species (48 %) and has an increased share of rare species. Mexico's importance as a secondary center of species richness increased while Bolivia's importance in the share of the wild potato genepool decreased. As mentioned above, these hot spot patterns and changes probably bear little

Table 6 Wild potato distribution by country, indicating the number of observations, number of species, number of rare species (those containing 5 or fewer records), and the ratio of observations to species. The last row contains the total number of unique localities from the above. In the case of observations this is the same total as the sum of the above; whereas in the case of columns 'Species' and 'Rare species' it is less since there are overlaps

Country	Observations	Total species	Endemic species	Rare species
Argentina	4547	17	6	0
Bolivia	1740	16	7	1
Brazil	111	3	0	0
Chile	85	3	0	0
Colombia	165	5	3	2
Costa Rica	143	1	0	0
Ecuador	226	8	3	2
Guatemala	135	5	0	0
Honduras	10	3	0	0
Mexico	2562	27	20	1
Panama	12	2	1	1
Paraguay	121	2	0	0
Peru	2440	51	41	13
USA	608	2	0	0
Uruguay	187	3	0	0
Venezuela	23	1	0	0
Total unique	13,115	107	81	20

relevance for trait screening purposes but may be of interest for national or regional management of biodiversity.

Conclusions about genetic changes due to one genebank's techniques may not apply to all genebanks. For example, del Rio et al. (2006) compared the germplasm samples in genebanks in the USA and Peru which had been propagated from the same original source population. Differences were usually small and insignificant, but illustrated that evaluation data generated in one genebank may not be completely transferable to the reputed identical germplasm in another genebank.

A number of studies have investigated the relationship between disease and pest resistance diversity with geography, taxonomy, ploidy, and breeding system (Jansky, et al. 2006, 2008, 2009; Spooner et al., 2009; Cai et al., 2011; Chung et al., 2011; Khiutti et al., 2012; Uribe et al., 2013; Pérez et al., 2014; Limantseva et al., 2014). All of these studies found high intra-accession and intraspecific variation of disease and pest resistance, but none of them found conclusive association with geography alone. Hence, the current way to find genetic variation for such traits is still through broad screening studies of large populations until a more efficient strategy using taxonomic, molecular, or biogeographic parameters can predict discovery of such useful traits.

Jackson (1990) proposed use of Nikolai Vavilov's (1922) law of homologous variation for predictivity. Basically, Vavilov proposed that knowledge of traits in one species can be used to predict the presence of similar traits in related species. However,

as can be inferred from above, this is not a generally promising strategy in wild potatoes, in contrast to other crops such as wheat (Endresen, 2010).

Germplasm Collections and Molecular Characterization

Wild and cultivated potatoes have been collected extensively and intensively throughout their entire range and are maintained by national and international genebanks. These include the International Potato Center (CIP), The Centre for Genetic Resources and Wageningen University, The Netherlands (CGN), the Institute of Plant Genetics and Crop Plant Research Gatersleben, Genebank External Branch North, Germany (IPK), the Vavilov Institute of Plant Industry (VIR), the United States Potato Genebank (National Research Support Project-6, NRSP-6), and national programs in countries where potatoes were collected. Huamán et al. (2000a) constructed a database of germplasm collections of major genebanks that show collections held in common; this is available by writing to the US genebank (NRSP-6). The ready availability of these genetic resources and associated laboratories, greenhouses, and field stations, has proven invaluable for the study of the genetics and taxonomy of section *Petota*.

The study and management of ex situ germplasm collections and the study of in situ genetic diversity required new technologies not available to plant taxonomists before the 1990s. The advent of DNA markers led to the development of rapid and reliable methods to uniquely identify potato samples. This can be difficult because they are generally closely related. Common methods use morphological and physiological traits to compare cultivated varieties (Reid et al., 2011), but there are many inherent problems with these techniques, leading to a search for molecular methods for discrimination (Morell et al. 1995; Cooke, 1999). DNA fingerprinting refers to a DNA-based assay to uniquely identify individual accessions. Many fingerprinting markers have been applied, including AFLPs, isozymes, ISAPs, ISSRs, RAPDs, nuclear microsatellites, and nuclear RFLPs (Table 2; Gebhardt et al., 1989; Douches & Ludlam, 1991; Douches et al., 1991; Powell et al., 1991; Görg et al., 1992; Mori et al., 1993; Hosaka et al., 1994; Cisneros & Quiros, 1995; Kawchuk et al., 1996; Oganisyan et al., 1996; Provan et al., 1996a; Sosinski & Douches, 1996; Ford and Taylor 1997; Milbourne et al., 1997; Schneider & Douches, 1997; Kim et al., 1998; Prevost & Wilkerson, 1999; McGregor et al., 2000; Isenegger et al., 2001; Bornet et al., 2002; Coombs et al., 2004; Braun & Wenzel, 2005; Hale et al., 2005; Barandalla et al. 2006; Mathias et al., 2007; Reid & Kerr 2007; Fu et al., 2009; Gavrilenko et al., 2010; Karaagac et al., 2010; Reid et al., 2011; Seibt et al., 2012; Karaagac et al., 2014). When used in combination with easily scored morphological traits of market classes of tubers (e.g., Schneider & Douches, 1997), many of these markers serve as effective discriminators of most cultivated varieties. Currently, the hypervariability and well-screened database of nuclear microsatellites (e.g., Ghislain et al., 2009a) make these ideal markers for fingerprinting applications. However, the continuous drop of sequencing cost is leading to the development of sequence-based markers.

Germplasm Utilization and Contributions to Cultivar Improvement

Even though potato breeders have been experimenting with the introduction of wild relatives into their programs for 150 years, the genetic diversity within and among

major cultivars remains low (Mendoza & Haynes, 1974a; Wang et al., 2011). While the introgression of a few specific genes from wild species has had a significant impact on cultivar development, only a handful of species have been used extensively (Bradshaw et al., 2006a). These include *S. acaule*, *S. chacoense*, *S. demissum*, *S. spegazzinii* (=*S. brevicaule*), *S. stoloniferum*, and *S. vernei*, mainly as sources of major genes for resistance to late blight, viruses, and potato cyst nematodes. Although not developed as a processing cultivar, 'Lenape' containing genes from *S. chacoense*, is in the pedigree of many modern chip cultivars and is credited with contributing to major advances in breeding for chip quality in the late twentieth century (Love et al., 1998). 'Lenape' was removed from the market, however, due to excessive levels of glycoalkaloids in its tubers, likely coming from *S. chacoense* (Zitnak & Johnston, 1970). This example illustrates the need for germplasm enhancement programs to carry out comprehensive evaluations of their products to avoid the inclusion of undesirable properties in eventual varieties.

To broaden the genetic base of the common potato gene pool and to combine different resistance genes introgressed from wild potato species, various methods have been used, including ploidy manipulations and bridge crosses, embryo rescue, hormone treatments, reciprocal crosses and protoplast fusion (Jansky, 2006). The range of sexual hybridization has been broadened using biotechnological methods that allowed the use of new species that have never been used before in breeding programs such as species outside of section *Petota* (*S. etuberosum, S. palustre*, *S. nigrum*), and species in section *Petota* but in a clade distantly related to cultivated potatoes (*S. tarnii*, *S. cardiophyllum*, *S. bulbocastanum* (review in Gavrilenko, 2007).

Direct genetic transfer of genes from wild potatoes into existing widely-adopted varieties is another tool available to breeders. The current development of late blight resistant varieties using genes from *S. bulbocastanum* is an example of the shortcut breeders can use instead of the 45 years it took from the original bridge crosses between cultivated and wild species to introduce useful traits (Haverkort et al., 2009). However, public resistance to genetically modified organisms is still delaying full exploitation of such direct transfer.

Breeding tetraploid potatoes is a challenge due to the heterozygous nature of parents used in breeding. Selfing produces severe inbreeding depression in potatoes and has impeded the elimination of unfavorable alleles and the fixation of alleles responsible for important traits after 150 years of potato breeding. Wild potatoes can be a genetic source of a self-compatible breeding system that can revolutionize potato breeding through the development of hybrid potatoes from diploid inbred lines (Lindhout et al., 2011).

Breeding Potential of Polyploids

Fifty years ago, a sexual polyploidization breeding strategy was proposed to increase yield in tetraploid potatoes by maximizing heterozygosity (Chase, 1963b). Since then, a number of studies have revealed the contributions of inter- and intra-allelic interactions to yield in potatoes (Rowe, 1967b; Mendoza & Haynes, 1974b; Mendiburu & Peloquin, 1977; Peloquin, 1983; Carputo et al., 2000a). Because an autotetraploid can theoretically carry four alleles per locus, the number of combinations within a gene and in epistatic interactions among genes is much higher than can be achieved in diploids. However, recent genomic studies have revealed that tri-allelic and tetra-allelic

loci are rare in potato cultivars (Hirsch et al., 2013). In addition, evidence for a heterosis threshold has been published (Sanford & Hanneman, 1982). Three-way hybrids were never superior to two-way hybrids for vigor or yield. Rather than overall heterozygosity, the presence of certain alleles may be more important for high yield (Bonierbale et al., 1993). In addition, genes that contribute to yield are predominantly located near centromeres, where recombination is limited (Buso et al., 1999b). This likely limits advances through conventional breeding methods. So, despite optimism that yield gains from maximizing heterozygosity would be realized via new tetraploid breeding strategies, yield has remained steady for the past century (Douches et al., 1996; Jansky et al., 2013). However, improvements in market traits, such as processing quality and disease resistance have been realized. Consequently, a major concept in potato breeding, that intra-locus interactions in general are required in competitive cultivars, must be reevaluated.

Polyploidy offers a strategy to maximize hybrid vigor (Chen, 2010) and is a major mechanism in potato evolution. Two options are available to bring diploids to the tetraploid level. First, they can be somatically doubled through chemical means such as colchicine (Ross et al., 1967) or through tissue culture (Sonnino et al., 1988). However, somatically doubled diploids exhibit slower growth rates, later maturity, reduced vigor, lower yield, and lower fertility than their diploid counterparts. In one study, yield of the diploid clones was nearly twice that of the tetraploids, mainly due to high tuber number (Rowe, 1967a). In another study, when diploids were crossed with each other and then their somatically doubled counterparts were intercrossed, the highest yielding clones included 27 tetraploid and 13 diploid individuals (Rowe, 1967b).

An alternative method to double chromosome number is through sexual polyploidization using 2n gametes (Chase, 1963a). Unilateral sexual polyploidization results from polyploidization of one parent, while the other parent is already at the polyploid level (4x female×2x male, or 2x female×4x male to produce 4x offspring). Bilateral sexual polyploidization results from polyploidization of both parents (2x×2x to produce 4x offspring). Triploid offspring are not produced from these crosses due to endosperm failure. Sexual polyploidization can produce three types of heterozygotes (simplex-Aaaa, duplex-AAaa, and triplex-AAAa) and up to four alleles per locus. Complex combinations of triallelic ($A_1A_2A_3A_3$) and tetraallelic ($A_1A_2A_3A_4$) loci also can be produced. In addition, sexual polyploidization produces a wide array of complex epistatic (interlocus) interactions.

Initial studies of sexual polyploidization in potatoes focused on tuber yield and quality. Yield heterosis is common following unilateral sexual polyploidization in which the tetraploid female parent is typically a potato cultivar or advanced breeding selection and the diploid male parent is a dihaploid × wild species hybrid or a cultivated diploid × dihaploid hybrid (De Jong et al., 1981; Bani-Aameur et al., 1991; De Jong & Tai, 1991; Buso et al., 1999a; Alberino et al., 2004). Unlike somatic doubling, sexual polyploidization transmits a large proportion of heterozygous loci and epistatic interactions to the tetraploid offspring (Peloquin et al., 2008). This allelic diversity likely buffers against environmental variability, leading to yield stability (Darmo & Peloquin, 1990; Ortiz et al., 1991). Sexual polyploidization has been used to transfer many additional traits to tetraploid offspring, including abiotic stress tolerance (Sterrett et al., 2003), processing quality (De Jong & Tai, 1991; Hutten et al., 1996; Hayes &

Thill, 2002; Jansky et al., 2011) and disease resistance (DeMaine et al. 1986; Herriott et al., 1990; Watanabe et al., 1992; Carputo et al., 2000b; Capo et al., 2002; Frost et al., 2006).

Bilateral sexual polyploidization provides an alternative sexual polyploidization mechanism. In this scenario, both parents are diploid and produce 2n gametes. The potential advantage of bilateral sexual polyploidization is that highly heterotic offspring can be produced by hybridization between diverse diploid parents. The disadvantage is that both parents must produce 2n gametes. Tetraploid progeny from bilateral sexual polyploidization are highly heterotic and typically out-yield their diploid full-sibs (Mendiburu & Peloquin, 1977; Sanford & Hanneman, 1982; Hutten et al., 1995a) and even tetraploid commercial cultivars (Werner & Peloquin, 1991b). The yield gains from bilateral sexual polyploidization are typically higher than those from unilateral sexual polyploidization, presumably due to the contributions of heterozygosity from both parents (Werner & Peloquin, 1991b).

Where do we go from Here? New Discoveries from Whole-Genome DNA Sequencing Data

Tetraploid cultivated potatoes are believed to be autotetraploid with a chromosome base number of 12 and a genome size estimated at 840 million base pairs. The potato genome sequencing consortium (PGSC) started from a collaborative effort of various potato researchers developing genetic linkage maps from diploid and tetraploid potatoes (Visser et al., 2009). A consortium of European institutions led by the University of Wageningen, The Netherlands, developed an ultra-high density (UHD) genetic linkage map with more than 10,000 unique AFLP markers (van Os et al., 2006). At that time, 16 research groups from Argentina, Brazil, China, Chile, India, Ireland, The Netherlands, New Zealand, Peru, Poland, Russia, the United Kingdom and the United States agreed to sequence the potato genome using a bacterial artificial chromosome (BAC)-by-BAC sequencing strategy from RH89-039-16 (RH), a diploid potato line used as male parent of the mapping population used to develop the ultra high density (UHD) genetic linkage map. A BAC library equivalent to 10 genomes from the RH clone was fingerprinted with AFLPs to assemble the first physical map of the potato genome made of contiguous overlapping BAC clones (De Boer et al., 2011). Fluorescent in situ hybridization with selected BAC clones was used to anchor some of the BAC contigs. The resulting hybrid physical map was shown to be 1.64 times longer than the estimated potato genome sequence (De Boer et al., 2011). In parallel, whole-genome shotgun sequencing of the heterozygous potato line RH was performed. Assembly of the reads from the RH BAC sequences and the whole-genome shotgun sequencing effort was more difficult than expected, due to extensive heterozygosity, duplicated regions, and the lack of a reference genome.

The PGSC then turned to another genetic stock presumed to be fully homozygous because it was generated by spontaneous chromosome doubling of a monoploid plant, selected from anther culture of a diploid potato clone in the Andigenum group (*S. phureja*) (Paz & Veilleux 1999). This doubled monoploid clone (DM1-3 516R44, or DM) was used for a whole-genome sequencing strategy using a genetic linkage map to anchor the large assembly of contigs, and super-scaffolds (The Potato Genome Sequencing Consortium 2011). In total, 96.6 Gb of raw sequences were assembled

into 776 Mb of genome sequences with a total length estimated to 844 Mb. Using high density genetic markers, super-scaffolds and genetic and physical maps, 623 Mb were aligned into pseudomolecules corresponding to each of the 12 chromosomes. This represented 86 % of the assembled genome, with the remainder believed to be mostly highly repetitive DNA sequences with little gene content. Genetic maps using DM as a female parent helped further the correct assembly of scaffolds, the resolution of discordances usually attributed to paralogs, and the testing of order and orientation of the superscaffolds in the pseudomolecules (Felcher et al., 2012; Sharma et al., 2013). Interestingly, the relationship between physical and linkage distances displays relatively large regions around the centromere without recombination, which may explain the transmission block of major genes contributing to yield as well as difficulties in breaking genetic linkages for many traits (David Douches, pers. comm.). Regions with distorted segregations were also identified as blocks on several chromosomes, depending on the populations.

Gene content was assessed by transcript sequence analyses and prediction searches. The DM genome sequence assembled in super-scaffolds contained 90.3 % of the 39,031 predicted genes. Transcriptome analysis revealed that 25.3 % of the sequences have alternative splicing, which represents higher functional variation than originally assumed. The potato transcriptome of DM was assembled from 32 tissues and growth conditions leading to the identification of 22,074 protein-coding genes, roughly 60 % of the predicted genes (Massa et al., 2011). In addition, gene co-expression pattern analyses led to the identification of 18 modules containing 5400 genes with highly correlated expression profiles to either organ(s) or developmental stage(s). These transcriptome data sets are pioneering ongoing studies of exploitation of gene expression in potato breeding.

The genome sequences from RH and DM allowed an estimate of haplotype diversity in potatoes from much larger regions than was possible before. For example, a previous study using sequencing of 78 genomic DNA fragments corresponding to 14 loci with an overall length of 31 kb from a panel of 11 diploid and 17 tetraploid potato genotypes identified, on average, one SNP every 21 base pairs and one InDel every 243 base pairs (Rickert et al., 2003). Another study using 47 diverse potato accessions and 66 fragments distributed across all potato chromosomes confirmed these frequencies: one single nucleotide polymorphism (SNP) every 23 bp and one insertion deletion (indel) every 441 bp (Simko et al., 2006). The comparison of DM and the two RH genome sequences was possible for 99 Mb with the DM genome where one SNP was found every 40 bp and one InDel every 394 bp. The two RH genomes were aligned for 6.6 Mb with one SNP every 29 bp and one InDel every 253 bp (The Potato Genome Sequencing Consortium 2011). A more recent study using 83 tetraploid potato cultivars representing the global gene pool of commercial potatoes, re-sequencing using next-generation sequencing with an in-solution hybridization enrichment for 807 targeted nuclear genes distributed across the genome resulted in detection of one SNP every 24 bp in exons and 15 bp in introns (Uitdewilligen et al., 2013). Hence, the potato genome has an extraordinary high polymorphism manifested by high frequency of SNPs, InDels, duplications, and rearrangements. Maize and soybean, for example, have one SNP every 104 and 1030 bp respectively (Tenaillon et al., 2001; Zhu et al., 2003). This means that close to 100 DNA markers (SNPs, InDels) potentially exploitable by breeders are expected to cover every single allele of the potato crop.

Linkage disequilibrium (LD: non-random association of alleles at linked genomic loci) is influenced by the number of meiotic divisions that have occurred among the individuals of a population. Potato LD has been first reported at the R1 locus using 600 potato accessions from the German potato gene bank to be relatively quickly lost after less than 1 cM whereas the analysis of 66 DNA fragment in only 47 potato accession revealed a LD decay of ~10 cM for a disequilibrium coefficient $r^2<0.10$ which is close to linkage equilibrium (Gebhardt et al., 2004; Simko et al., 2006). More recently, a genome-wide estimate of LD was around 5 cM for $r^2<0.10$ (D'Hoop et al., 2010). This is a relatively high value for LD compared to another outbreeder, maize, for which LD falls within 2 kb for $r^2<0.10$ (Remington et al., 2001). Hence, at one SNP every 25 bp and LD between ~10 cM for $r^2<0.10$, the precise identification of the gene of interest by genetic or association mapping remains a serious challenge in potatoes. However, a more recent study has shown LD decay after only 275 bp for $r^2<0.10$ (Stich et al., 2013). Although done on a small sample of 36 tetraploid varieties of similar origin than prior other studies, the marked difference in LD decay is attributed to a much more diverse germplasm sample used and the SNP marker in trait-coding loci. Hence, more genome-wide studies need to be conducted to improve our understanding of LD decay in potato. Studies of SNPs in potato landraces and breeding populations have indicated that large numbers of SNPs are inherited together, referred to as haplotype blocks. Their identification is needed to use haplotyping mapping methods that increase the power of detecting associations as opposed to using single marker association mapping. For diploid crops, haplotypes can be inferred from homozygous individuals and their use greatly facilitated by the availability of a genome sequence, but polyploid crops present numerous challenges (reviewed by Edwards et al., 2013). SNPs are bi-allelic markers and pose two difficulties in tetraploid organisms: 1) genotype calling in one of the five genotypic classes and 2) determining the phase between adjacent SNPs. Until recently, bioinformatic tools were not available for calling and phasing SNP markers in polyploids (Simko, 2004). Using a GoldenGate dataset consisting of 384 SNPs scored on 224 tetraploid potatoes, a new software program can assign the correct genotypic class for about half of the SNP markers on 90 % of the genotypes (Voorrips et al., 2011). This first success in genotype calling for tetraploid potatoes will need to be followed by more bioinformatic developments before large SNP data sets can be fully utilized for haplotype mapping in autotetraploid potatoes. However, SNPs can readily be used in potatoes by reducing autotetraploid potatoes to dihaploid families (Simko, 2004; Velásquez et al. 2007). Alternatively, reducing the number of loci is achievable either by transcriptome mapping (Ritter et al., 2008) or by in-solution hybridization methods (Uidewilligen et al., 2013).

Despite these complications, a number of discoveries have already been produced thanks to the potato genome sequence. Breeding for disease resistance, a permanent global threat to potato production, has new tools for rapid identification of alleles of interest. Using nucleotide binding (NB) and leucine-rich repeat (LRR) conserved domains, the search for resistance genes identified 438 NB-LRR type genes which were among the 39,000 predicted genes from DM (Jupe et al., 2012). The physical map position was identified for most of them and was organized into 63 clusters of which 50 consisted of *R* genes derived from a recent common ancestor. The potato genome sequence also helped elucidate the genes for maturity and the initiation of tuber development, with the identification of the gene underlying a major QTL for tuberization under long-day conditions (Kloosterman et al., 2013). The tomato genome sequence, published a year

later than the potato sequence, confirmed remarkable synteny with the potato genome (8.7 % sequence divergence between homologous euchromatic regions) with nine large and several smaller inversions (The Tomato Genome Consortium, 2012), providing evolutionary data relating to these two sister clades.

The availability of a first potato genome sequence and several transcriptomes from a diverse set of potato genotypes, organs and developmental conditions, have already produced genomic tools useful to study genetic diversity and gene networks underlying important traits (Rensink & Buell, 2005; Kloosterman et al., 2008; Hamilton et al., 2011). As mentioned above, the autotetraploid potato genome is characterized by relatively large haplotype blocks encompassing large numbers of SNPs compared to other crops. This is due to fewer meiotic generations and clonal selections from an original diverse pool of ancestral wild species. The understanding of the domestication process will require many more genome sequences from a wide sample of potato germplasm including wild relatives. The impact of polyploidization from diploid cultivated potatoes will give new insights into the evolutionary process of polyploidization. Bioinformatic tools for autotetraploid organisms are still needed but will eventually revolutionize breeding methods. Predictive breeding methods in potatoes rely heavily on understanding both the advantageous alleles as well as the hidden deleterious alleles in the genetic code of its four genomes. Diploid inbred lines are under development thanks to the introgression of a self-compatibility gene which may eventually lead to the production of F_1 hybrid seed potato (Phumichai et al., 2005; Lindhout et al., 2011).

In addition to nucleotide sequence polymorphism, methylation of nucleotides and other changes not encrypted by the base of each nucleotide constitute the epigenome, which is becoming accessible by next-generation sequencing technologies. The epigenome may vary during the individual development, be altered by environmental stimuli, and transmitted unevenly across generations. Such genetic variability has often been observed in potatoes of hybrid origin and those regenerated from tissue culture or in inbred lines (Law & Suttle, 2005; Marfil et al., 2009; Nakamura & Hosaka, 2010). Methylation-sensitive sequencing technologies are now available to study at least partially the potato epigenome. Using these new tools and genetic stocks, fundamental questions in potato genetics such as the identification of domestication genes and the molecular basis of heterosis will be addressed and will improve the selection of progenitors for desirable traits of the next generation of potato varieties. Many more genome sequences need to be assembled from distinct potato taxonomic groups and wild relatives to contribute to the development of new and more efficient breeding methods as well as answering the fascinating questions of the multiple or restrictive origin of the cultivated potato which have puzzled potato taxonomists for over a century.

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