

Potato Systematics and Germplasm Collecting, 1989-2000

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ABSTRACT

This paper reviews the systematics of wild potatoes over the past 11 years, in reference to the latest comprehensive taxonomic treatment by Hawkes (1990. *The potato: evolution, biodiversity and genetic resources*. Belhaven Press, Washington, D.C.). Included here is information on monographs and floras, new germplasm collections made since 1988 compared to total potato distributional data, new taxonomic changes (including synonymy and new species descriptions), ingroup and outgroup relationships, intraspecific studies, diversity studies, and fingerprinting. In addition, data supporting taxonomic changes and phylogeny from ploidy levels, Endosperm Balance Numbers, and morphological studies of taxonomically important characters are reviewed. A revised list of 206 species is presented (from 232 in Hawkes) that incorporates recent synonymy of names, recognition of new names, and new species descriptions. New germplasm collections of 58 potato taxa were collected that did not occur in genebanks before 1988.

RESUMEN

En este artículo se resume el tratamiento sistemático de las papas silvestres durante los pasados 11 años, en referencia al más reciente tratado taxonómico de Hawkes (1990. *The potato: evolution, biodiversity and genetic resources*. Belhaven Press, Washington, D.C.) Aquí se incluye información sobre monografías, nuevas colecciones de germoplasma hechas desde 1988 y comparadas con la distribución geográfica completa de papas sil-

vestres, nuevos cambios taxónomicos (incluidas la descripción de sinónimas y de nuevas especies), parentesco filogenético dentro y fuera del grupo, estudios intraespecíficos, estudios diversos y tipificación del ADN. Adicionalmente, se revisan los datos que sustentan los cambios taxonómicos y en el parentesco filogenético: niveles de ploidia, Balance Numérico de Endosperma y estudios morfológicos de caracteres taxonómicamente importantes. Se presenta una lista revisada de 206 especies (de 232 de Hawkes) que incorpora la reciente sinonimia de nombres, el reconocimiento de nuevos nombres y la descripción de nuevas especies. Se colectaron 58 taxa de papa que no se encontraban en los bancos genéticos antes de 1988.

INTRODUCTION

The cultivated potato grown worldwide, *Solanum tuberosum* L., has six related cultivated species and 225 wild species relatives, according to the latest comprehensive taxonomic treatment by Hawkes (1990). The other cultivated species are grown in the Andes, and the wild species occur from the southwestern United States to central Argentina and Chile. Hawkes's treatment superseded his earlier treatments, and that of Correll (1962), and yet earlier taxonomists. Wild and cultivated potatoes are also treated in regional floras (e.g., Hawkes and Hjerting 1989; Ochoa 1990a, 1999). Cultivated and wild potato species are grouped in the genus *Solanum* L. sect. *Petota* Dumort. (Hawkes 1990). They are morphologically similar, and cross with difficulty to species in sect. *Etuberosum* (Buk. and Kamezay) A. Child (Valkonen *et al.* 1995; Contreras and Spooner 1999). Section *Petota* is a difficult group that has attracted the attention of many taxonomists. Unfortunately, many taxonomic treatments are highly discordant, due to morphological similarity of many species, hybrid speciation and introgression, and different taxonomic concepts and practices (Spooners and Van den Berg 1992a).

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ADDITIONAL KEY WORDS: Diversity, Endosperm Balance Number (EBN), genetic resources, molecular markers, phylogeny, *Solanum* sect. *Petota*.

Wild and cultivated potato genetic resources have proven value in breeding programs for disease resistance, environmental tolerances, and other agronomic traits of interest (Ross 1986; Hawkes 1990, 1994a; Spooner and Bamberg 1994; Ruiz de Galereta *et al.* 1998; Ochoa 1999; Jansky 2000). This economic value, the unresolved taxonomy, and the inherent scientific interest in this widespread group continue to stimulate research into the systematics of the group, as well as germplasm collecting expeditions.

Taxonomic changes are treated with reference to the latest comprehensive treatment of Hawkes (1990). This paper follows a continuing series of reviews attempting to keep pace with research in the taxonomy, genetic diversity, and germplasm collection of sect. *Etuberosum* and sect. *Petota* (Grun 1990; Hawkes 1991, 1992a,b, 1994b, 1997a; Spooner and Van den Berg 1992a; Brown 1993; Spooner 1994). The topics covered here are monographs and floras, new germplasm collections made since 1988 compared to total potato distributional data, new taxonomic changes (including synonymy and new species descriptions), ingroup and outgroup relationships, intraspecific studies, diversity studies, and fingerprinting. In addition, data supporting taxonomic changes and phylogeny from ploidy levels, Endosperm Balance Numbers, and morphological studies of taxonomically important characters are reviewed.

MATERIALS AND METHODS

Literature from 1989-2000 on the systematics of wild potatoes was surveyed using the bibliographic databases Agricola, Agris, Biological Abstracts, and CAB. The terms potato and *Petota* were individually searched in combination with the terms biogeography, diversity, evolution, fingerprint, germplasm, phylogeny, systematics, and taxonomy. This resulted in more than 5000 references that were imported and organized with the bibliographic database program ProCite (Institute for Scientific Information 1998). The total was reduced to 140 after inspection of the titles and abstracts, and deleting the references outside the scope of this paper. Some additional references were added based on personal knowledge or cross-referencing. This search strategy found many topics not reviewed here, including breeding technology, disease resistance, genebank characterization, and genetic characterization of artificial sexual or somatic hybrids or haploids. Additional references that were published prior the review period were added only as needed to place the topics in perspective.

Regarding terminology, various terms have been used for the cultivated species, including clone, genotype, cultivar, and landrace. All have specific meanings, but the term genotype is used here in most cases to facilitate comparison of studies. In the other cases we deemed it important to keep the authors' original terminology.

This review covers both sect. *Petota* (tuber-bearing) and sect. *Etuberosum* (non-tuber-bearing). The latter are treated because of their crossability and practical use in potato breeding, unlike members of Hawkes's series *Juglandifolia* (Rydb.) Hawkes, that are sister taxa to tomatoes (Figure 1, Outgroup Relationships), and not crossable to potatoes. This paper assumes basic knowledge of molecular techniques and terms. The reader is directed to Hillis *et al.* (1996), Staub *et al.* (1996), Godwin *et al.* (1997), Hamrick and Godt (1997), Karp *et al.* (1997), and Wolfe and Liston (1998) for the concepts, techniques, and terms of molecular systematics and diversity assessment.

A map of the area where wild potatoes occur was made using 6118 observations made previous to and during the 1988-2000 period. The most important sources were the Intergenebank potato database described by Huamán *et al.* (in press); additional observations made during collecting expeditions by D.M. Spooner and coworkers (see section 2, New Potato Germplasm Collections, for references); and the herbarium specimen database described by Hawkes (1997). Some additional observations were taken from regional floras such as Ochoa (1999). A circular area with a radius of 50 km was assigned to each observation. On the map we also identified the 1418 sites where wild potatoes were collected between 1988 and 2000.

RESULTS AND DISCUSSION

Taxonomic changes are listed in Tables 2 and 3, and summarized in Table 4. Table 4 is bibliographic in nature and should **not** be construed as our acceptance of names, except as they relate to publications of D. M. Spooner and coworkers in Table 3. However, we **will** use this list as the current potato taxonomy. Figure 1 presents a summary cladogram of outgroup relationships based on recent data. Table 1 and Figure 2 summarize collecting expeditions and new taxa collected in this review period. Taxonomic names in Table 1 are those used in planning the expedition. Some of these have been recently synonymized (Table 3), but are listed here to document germplasm of these names useful for tests of synonymy.

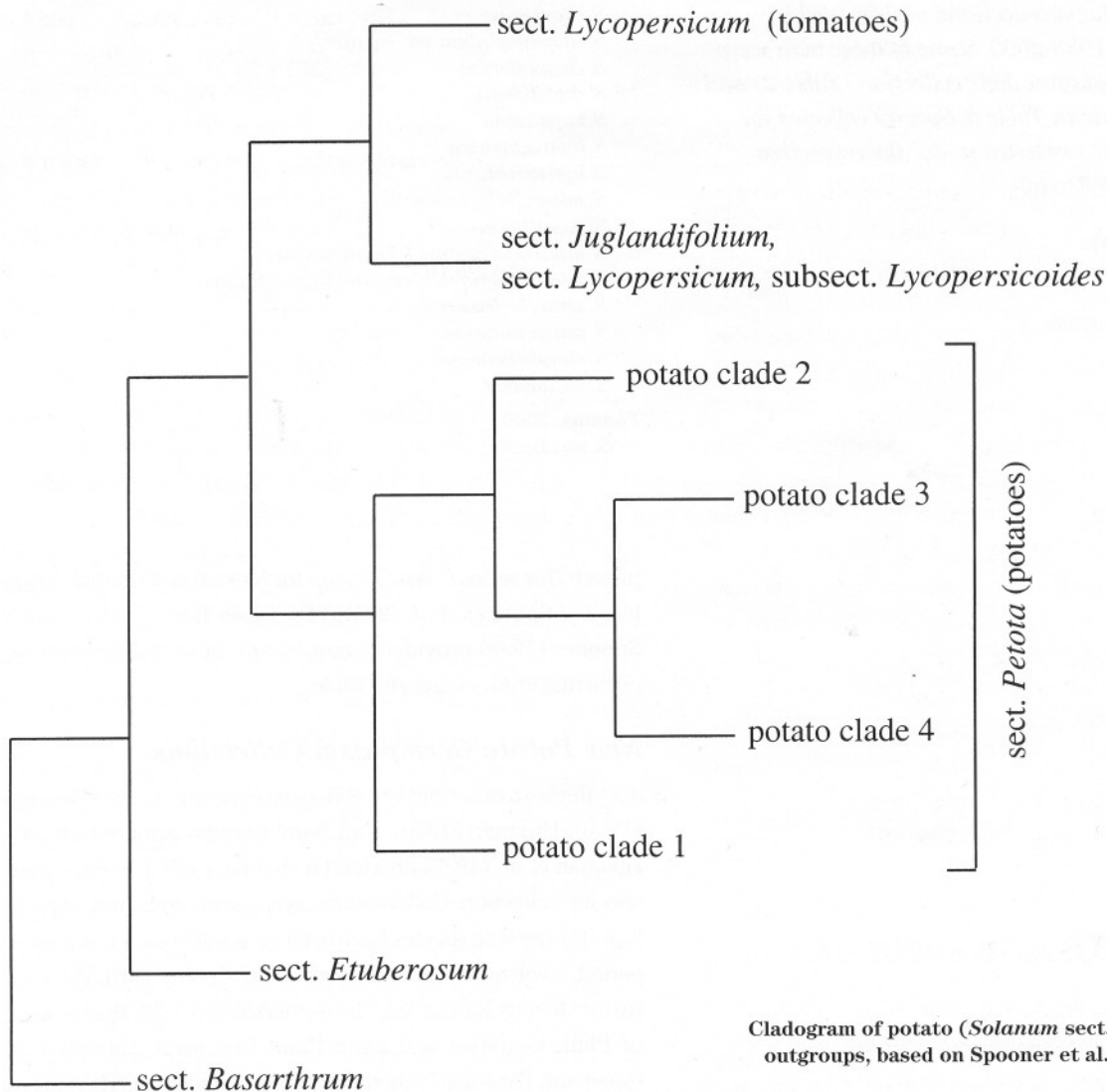


FIGURE 1.
Cladogram of potato (*Solanum* sect. *Petota*) and immediate
outgroups, based on Spooner et al. (1993) and Peralta and
Spooner (in press).

Monographs and Floras

Prior to this review period, Correll (1962) and Hawkes (1963) were the standard comprehensive taxonomic treatments for sect. *Petota*. Hawkes (1989) provided needed typification of series names. He also divided sect. *Petota* into new subsections *Estolonifera* Hawkes, containing the non-tuber-bearing series *Etuberosa* and series *Juglandifolia*, and subsect. *Potatoe* G. Don, with 19 tuber-bearing series. He also divided subsect. *Potatoe* into a primitive superseries *Stellata* Hawkes, containing nine of these 19 series, and a derived subsect. *Rotata* Hawkes, bearing the remaining 10 series. He also recognized a new series *Lignicaulia* Hawkes. Hawkes (1990) provided an update to his 1963 taxonomic treatment, incorporating these new subsections and

superseries, providing an update to new species names, and making some transfers of species among series.

Gorbatenko (1989) provided a series treatment of the South American species, which was very different from that of Hawkes (1990). She followed the taxonomic tradition of her Russian predecessor Bukasov (1971) in recognizing many series placed in synonymy by Correll (1962) and Hawkes (1990). For example, Gorbatenko (1989) recognized 20 South American series, compared to 13 South American series by Hawkes (1990).

Floristic treatments also were produced by Hawkes and Hjerting (1989) for Bolivia; Ochoa (1990a) for Bolivia; Ochoa (1999) for Peru; Rodríguez and Vargas (1994) for Jalisco State, Mexico; Spooner et al. (1998) for Guatemala; Spooner et al. (in

TABLE 1—New germplasm collections maintained in genebanks, 1988-2000. Some of these taxa were synonymized after their collection (Table 2) and do not appear in Table 3. Species collected for the first time are listed under the respective country of collection.

Mexico, 1988, 1993, 1997

Solanum cardiophyllum subsp. *lanceolatum*
S. hintonii
S. hjertingii var. *physaloides*
S. leptosepalum
S. lesteri
S. macropilosum
S. ×michoacanum
S. ×sambucinum

Chile, 1989, 1990

S. maglia

Ecuador, 1991

S. chilliasense
S. cyanophyllum
S. minutifolium
S. paucijugum
S. serratoris

Colombia, Venezuela, 1993

S. cacetanum
S. cuatrecasasii
S. lobbianum
S. orocense
S. paramoense
S. sucubunense

Bolivia, 1993, 1994

S. chacoense (from Bolivia)
S. soestii
S. vidaurrei
S. yungasense

Peru, 1998

S. aymaraesense
S. chillonanum
S. incasicum
S. megistacrolobum subsp. *megistacrolobum* f. *purpureum*
S. megistacrolobum subsp. *toralapanum* (from Peru)
S. longiusculus
S. multiflorum
S. pillahuatense
S. sawyeri
S. sandemanii
S. tacnaense
S. tarapatanum
S. urubambae
S. velardei
S. yungasense (from Peru)

Peru, 1999

S. anamatophilum
S. amayanum
S. augustii
S. bill-hookeri
S. cantense

S. chavinense
S. chomatophilum var. *subnivale*
S. chrysoflorum
S. gracilifrons
S. hapalosum
S. huarochiriense
S. hypacrarthrum
S. jalcae
S. moniliforme
S. multiinterruptum f. *longipilosum*
S. multiinterruptum var. *machaytambinum*
S. neoWEBERBAUERi
S. peloquinianum
S. simplicissimum
S. wittmackii

Panama, 2000

S. woodsonii

press b) for series *Conicibaccata* for Mexico and Central America, and Spooner *et al.* (2001a) for Costa Rica. Contreras and Spooner (1999) provided a monograph of sect. *Etuberosum*, occurring in Argentina and Chile.

New Potato Germplasm Collections

Reviews of germplasm collecting expeditions were Hawkes (1970), Huamán (1986), and Bamberg and Spooner (1994). Huamán *et al.* (1997) provided a summary of CIP's cultivated species collection. Collaborative germplasm collecting expeditions for the wild species have been very active over this review period, involving the International Potato Center (CIP), The Centre for Genetic Resources, The Netherlands (CGN), the Institute of Plant Genetics and Crop Plant Research Gatersleben, Genebank External Branch North, Germany (IPK), The United States Potato Genebank (National Research Support Project-6, NRSP-6), Wageningen University, and national programs in countries where potatoes were collected. These collections have been to Mexico in 1988, 1993, and 1997 (Spooner *et al.* 1991a; Rodríguez *et al.* 1995; Spooner *et al.* 2000), Guatemala in 1995 (Spooner *et al.* 1998), Honduras and Panama in 2000, Costa Rica in 1996 (Spooner *et al.* 2001a), Colombia and Venezuela in 1992 (Spooner *et al.* 1995a), Ecuador in 1991 (Spooner *et al.* 1992a), Peru in 1998 and 1999 (Spooner *et al.* 1999; Salas *et al.* in press), Bolivia in 1993 and 1994 (Spooner *et al.* 1994), Argentina in 1989 and 1990 (Clausen 1989; Spooner and Clausen 1993), and Chile in 1989 and 1990 (Spooner *et al.* 1991b; Contreras *et al.* 1993) (Table 1, Figure 1). In addition, a few germplasm samples have been donated from expeditions not devoted to potato collecting. Planning for the latter expeditions were greatly aided by

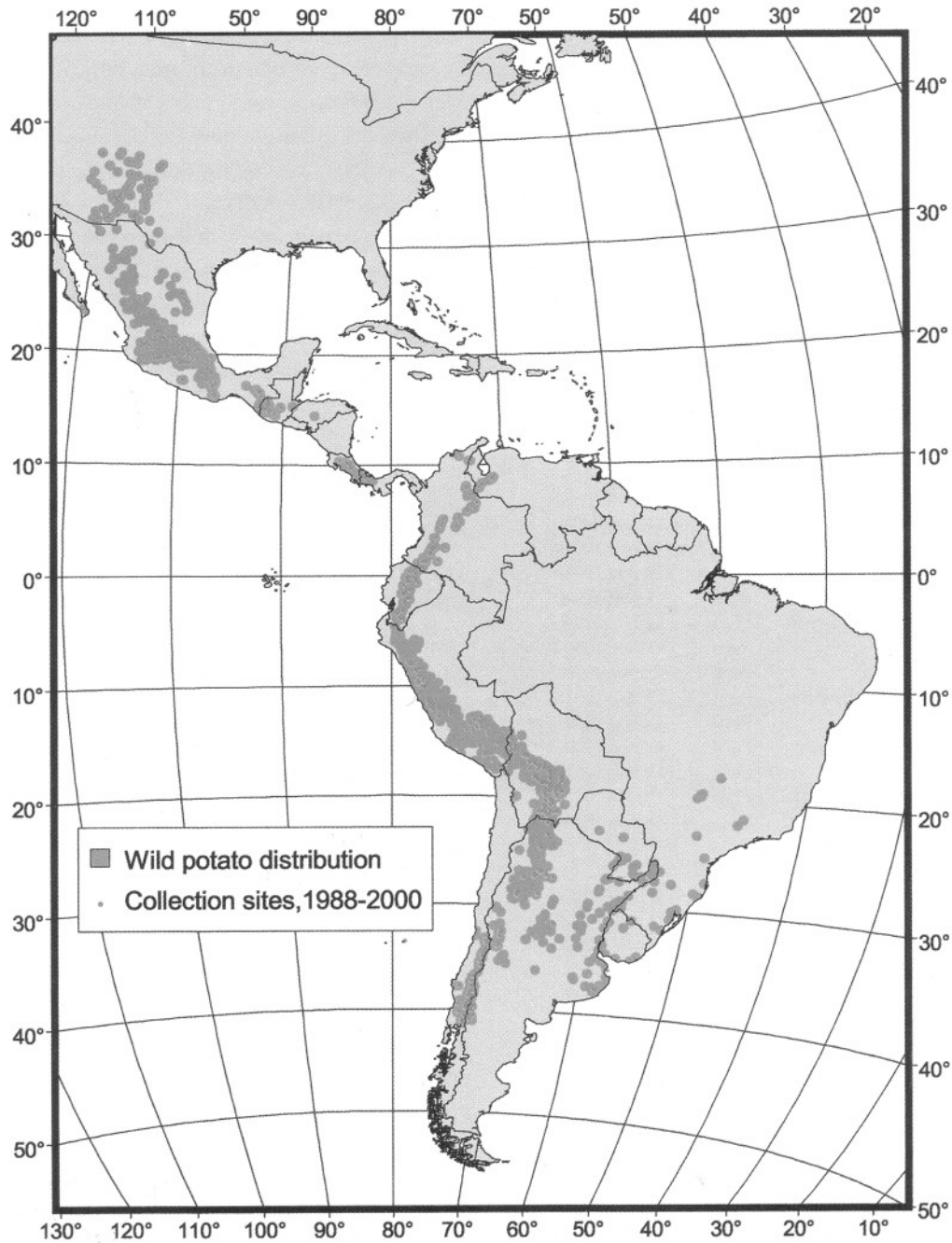


FIGURE 2.

Locations where wild potato are known to occur, and where they were collected between 1988-2000. Germplasm is not available from all 1988-2000 collecting sites because some of the collections were lost as live specimens.

a database of herbarium collections described by Hawkes (1997b).

Germplasm availability of these collections were given in Bamberg and Spooner (1994), Wilkinson *et al.* (1994), Bamberg *et al.* (1996), Kehoe (1986), Hoekstra and Seidewitz (1987),

Angeli *et al.* (2000a,b), Huamán (1998), United States Department of Agriculture, Agricultural Research Service (2000), and Huamán *et al.* (2000a). Major genebank data are listed at: www.plant.wageningen-ur.nl/about/Biodiversity/Cgn/collections/crops/potato/genbanks.htm. Huamán *et al.* (2000a)

TABLE 2—*New names in Solanum sect. Petota published between 1989 and 1999. Organized alphabetically first by series, then by species.*

Taxon	Country	Reference
<i>Solanum</i> series <i>Simplicissima</i> Ochoa.		
Monotypic, containing <i>Solanum simplicissimum</i> Ochoa.		
<i>S. acaule</i> f. <i>incuyo</i> Ochoa	Peru	Ochoa 1989c
<i>S. acaule</i> subsp. <i>palmirensis</i> J. Kardolus	Ecuador	Kardolus 1998a
<i>S. amayanum</i> Ochoa	Peru	Ochoa 1989a
<i>S. ancoripae</i> Ochoa	Peru	Ochoa 1999
<i>S. arahuayum</i> Ochoa	Peru	Ochoa 1994a
<i>S. candolleianum</i> f. <i>sihuanpampinum</i> Ochoa ¹	Bolivia	Ochoa 1999a
<i>S. chillonanum</i> Ochoa. A new name to replace for <i>S. tenellum</i> Ochoa, 1987, due to the earlier name <i>S. tenellum</i> Bitter, 1912.	Peru	Ochoa 1989d
<i>S. chiquidenum</i> var. <i>amazonense</i> Ochoa	Peru	Ochoa 1994b
<i>S. chiquidenum</i> var. <i>gracile</i> Ochoa	Peru	Ochoa 1994b
<i>S. chiquidenum</i> var. <i>robustum</i> Ochoa	Peru	Ochoa 1994b
<i>S. chomatophilum</i> f. <i>saussianense</i> Ochoa	Peru	Ochoa 1994b
<i>S. chomatophilum</i> var. <i>subnivale</i> Ochoa	Peru	Ochoa 1994b
<i>S. huancavelicae</i> Ochoa	Peru	Ochoa 1999
<i>S. irosinum</i> f. <i>tarosum</i> Ochoa	Peru	Ochoa 1999
<i>S. megistacrolobum</i> f. <i>purpureum</i> Ochoa	Peru	Ochoa 1994b
<i>S. ortegae</i> Ochoa	Peru	Ochoa 1998
<i>S. puchupuchense</i> Ochoa	Peru	Ochoa 1999
<i>S. saxatilis</i> Ochoa	Peru	Ochoa 1992d
<i>S. salasianum</i> Ochoa	Peru	Ochoa 1989b
<i>S. serratoris</i> Ochoa	Ecuador	Ochoa 1990b
<i>S. sicuanum</i> Hawkes. New name to replace <i>S. pumilum</i> Rojas, 1879, not <i>S. pumilum</i> Dunal, 1852.	Peru	Hawkes 1990
<i>S. simplicissimum</i> Ochoa	Peru	Ochoa 1989c
<i>S. stoloniferum</i> subsp. <i>moreliae</i> Hawkes	Mexico	Hawkes 1990
<i>S. tuberosum</i> subsp. <i>andigena</i> var. <i>qhuchi-aca</i> f. <i>qhuchi-chupa</i> Ochoa ¹	Bolivia	Ochoa 1990a
<i>S. tuberosum</i> subsp. <i>andigena</i> var. <i>runa</i> f. <i>abajeña</i> Ochoa ¹	Bolivia	Ochoa 1990a
<i>S. urubambae</i> f. <i>chakhabambense</i> Ochoa	Peru	Ochoa 1999

¹These names have not been validly published according to the International Code of Botanical Nomenclature (Greuter *et al.* 1999) because they lack Latin descriptions and types have not been designated. They are not listed in Table 3.

described a compilation of major potato genebank data available online at www.potgenebank.org.

Not all germplasm reported in the papers of expeditions (above) cleared quarantine or survived a germplasm increase. Table 1 lists new species collected on these expeditions that survived an increase, or in the case of recent collections from Peru and Panama, are expected to eventually be increased and to be made available as germplasm. Germplasm from the 1999 Peru-

vian expedition is not available for international distribution at the moment. Peru is in the process of finalizing its germplasm access regulation in conformity with the Convention on Biological Diversity and the Andean Pact Genetic Resources Decision 391. When the regulation is officially in place, Peru will make the materials available under the conditions of the official regulation in accord with international agreements.

Recently, genebank passport data have been linked to geographic information systems (GIS) to analyze results of past collections and to aid planning of new ones (Guarino *et al.* in press). Passport data often are incomplete (Greene and Hart 1996) and imprecise and need to be checked prior to analysis (Hijmans *et al.* 1999). Hijmans *et al.* (2000) showed, however, that genebank collections can consist of a geographically biased sample that may hamper analysis. Jones *et al.* (1997), Jones and Gladkov (1999), and Skov (2000) described GIS methods to assess the likelihood of finding wild species in areas where they have not been previously recorded.

Every country has unexplored areas that could harbor significant new germplasm collections. Relative coverage of germplasm collection is best for the United States, Mexico, Guatemala, Costa Rica, Ecuador, Bolivia, Argentina, and Chile. By virtue of its large number of wild species and missing germplasm collections, Peru clearly is the country where more collections are most warranted (Spooner *et al.* 1999; Salas *et al.* in press). Other countries warranting more collections are Panama, Brazil, Paraguay, and Uruguay.

New Potato Taxa

One new series, ten species, two subspecies, four varieties, four forms, three invalidly published forms, and three substitute names (new names resulting from a former name found to be invalid according to the International Code of Botanical Nomenclature, Greuter *et al.* 1999) were published in this review period (Ochoa 1989a,b,c,d, 1990a,b, 1992d, 1994a,b, 1998, 1999; Hawkes 1990; Kardolus 1998). One of these new taxa is from Mexico, two from Ecuador, 21 from Peru, and the three invalidly published names from Bolivia (Table 2). Many taxa also were synonymized, as described above, and summarized in Table 3.

Hawkes (1993) determined the proper authorship of the name *S. maglia*. Gorbatenko and Hawkes (1996) designated a lectotype specimen for *S. goniocalyx*.

Outgroup Relationships

Cladistic and phenetic classification procedures are widely used in taxonomy, but employ very different assumptions and

CORRECTION

A production error resulted in the incorrect publication of Table 3 of the D.M. Spooner and R.J. Hijman article "Potato systemics and germplasm collecting, 1989-2000" (Page 243, Volume 78, Number 4). This corrected version should be inserted into the July-August, 2001 issue.

TABLE 3—New determinations of synonymy, new combinations, and newly resurrected names in wild and cultivated potato species (*Solanum* sect. *Petota*) and close outgroup relatives in sect. *Etuberosa* (*S. etuberosum*, *S. fernandezianum*, *S. palustre*), subsequent to Hawkes (1990). The listed name is the new one proposed by the author in the heading, and the indented names are the old, superseded (synonymized) taxa. Additional synonyms that are not at variance with decisions in Hawkes (1990) are not listed here.

Ochoa, 1990 [1991]

- Solanum acaule* Bitter var. *acaule*
- S. acaule* var. *punae* (Juz.) Hawkes
- S. boliviense* Dunal
- S. astleyi* Hawkes and Hjert.
- S. brevicaule* Bitter
- S. mollepujroense* Cárdenas and Hawkes
- S. chacoense* Bitter
- S. arnezii* Cárdenas
- S. circaeifolium* Bitter var. *capsicibaccatum* (Cárdenas) Ochoa
- S. capsicibaccatum* Cárdenas
- S. circaeifolium* subsp. *quimense* Hawkes and Hjert.
- S. circaeifolium* var. *circaeifolium*
- S. circaeifolium* subsp. *circaeifolium*
- S. leptophyes* Bitter
- S. gourlayi* Hawkes (Hawkes 1990; as *S. gourlayi* subsp. *gourlayi*)
- S. pachytrichum* Hawkes (Hawkes 1990; as *S. gourlayi* subsp. *pachytrichum* (Hawkes) Hawkes and Hjert.). - Note: Ochoa (1990) did not comment on *S. gourlayi* subsp. *saltense* A. M. Clausen and K. A. Okada, accepted in Hawkes (1990).
- S. oplocense* Hawkes
- S. hondelmannii* Hawkes and Hjert.
- S. tarijense* Hawkes
- S. xtrigalense* Cárdenas
- S. xzudaniense* Cárdenas
- S. tuberosum* subsp. *andigena* (Juz. and Bukasov) Hawkes
- S. estradae* L. López, = *S. phureja* subsp. *estradae* (L. López) Hawkes
- S. xsubandigena* Hawkes

Ochoa, 1992

- S. bukasovii* Juz. var. *bukasovii*
- S. canasense* Hawkes
- S. hapalosum* Ochoa
- S. pampasense* Hawkes
- S. sicuanum* Hawkes
- S. bukasovii* var. *multidissectum* (Hawkes) Ochoa
- S. multidissectum* Hawkes
- S. colombianum* Dunal
- S. cacetanum* Ochoa
- S. marinasense* Vargas
- S. canasense* var. *xerophllum* (Vargas) Hawkes
- S. raphanifolium* Cárdenas and Hawkes
- S. hawkesii* Cárdenas
- S. tuberosum* subsp. *andigena* (Juz. and Bukasov) Hawkes
- S. paramoense* Bitter

Spooner et al., 1992

- S. regularifolium* Correll
- S. correllii* Ochoa, 1981

Van den Berg and Spooner, 1992

- S. microdontum* Bitter
- S. microdontum* var. *microdontum*
- S. microdontum* subsp. *microdontum*
- S. microdontum* var. *metriophyllum* (Bitter) Ochoa
- S. microdontum* subsp. *gigantophyllum* (Bitter) Hawkes and Hjert.

Ochoa, 1993

- S. chomatophilum* f. *angustifoliolum* Correll (Hawkes [1990, pgs. 108, 121] synonymized this form under both *S. colombianum* and *S. alborno-zii*).

Spooner et al., 1993

- S. andreanum* Baker
- S. cyanophyllum* Correll
- S. suffrutescens* Correll
- S. serratoris* Ochoa

Giannattasio and Spooner, 1994b

- S. megistacrolobum* Bitter subsp. *megistacrolobum*
- S. megistacrolobum*
- S. megistacrolobum* var. *megistacrolobum*
- S. megistacrolobum* subsp. *toralapanum* (Hawkes and Hjert.) R. B. Giannattasio and D. M. Spooner
- S. toralapanum* Cárdenas and Hawkes
- S. megistacrolobum* var. *toralapanum* (Cárdenas and Hawkes) Ochoa

Spooner et al., 1997

- S. boliviense* subsp. *astleyi* (Hawkes and Hjert.) D. M. Spooner, M. L. Ugarte, and P. W. Skroch
- S. astleyi* Hawkes and Hjert.

Contreras and Spooner, 1999

- S. palustre* Poepp.
- S. brevidens* Phil. var. *brevicens*
- S. brevidens* var. *glabrescens* (Poepp ex Schldl.) Hawkes
- S. etuberosum* Lindl.
- S. subandinum* Meigen

Ochoa, 1999

- S. acaule* Bitter subsp. *acaule*
- S. acaule* subsp. *punae* (Juz.) Hawkes and Hjert.
- S. ancophilum* (Correll) Ochoa
- S. rhomboideilanceolatum* var. *ancophilum* Correll
- S. bukasovii* Juz. (see Ochoa, 1992)
- S. abancayense* Ochoa
- S. antacochense* Ochoa
- S. hapalosum* Ochoa
- S. bukasovii* f. *multidissectum* (Hawkes) Ochoa (see Ochoa 1992)
- S. multidissectum* Hawkes
- S. bukasovii* var. *multidissectum* (Hawkes) Ochoa
- S. chomatophilum* Bitter
- S. pascoense* Ochoa
- S. dolichocremastrum* Bitter
- S. chavinense* Correll
- S. huanucense* Ochoa
- S. immite* var. *vernale* Correll. Hawkes (1990) synonymized under *S. immite*.
- S. jalcae* var. *pubescens* Correll. Hawkes (1990) synonymized under *S. jalcae*
- S. medians* var. *autumnale* Correll
- S. weberbaueri* Bitter
- S. multiinterruptum* Bitter var. *multiinterruptum*
- S. moniliforme* Correll
- S. multiinterruptum* f. *longipilosum* Correll
- S. multiinterruptum* var. *multiinterruptum* f. *albiflorum* Ochoa
- S. chrysoflorum* Correll
- S. pampasense* Hawkes. Ochoa (1999) recognized this species that he previously synonymized under *S. bukasovii* f. *bukasovii* (Ochoa 1992).
- S. sparsipilum* (Bitter) Juz. and Bukasov
- S. sparsipilum* subsp. *calcense* Hawkes
- S. tacnaense* f. *decurrentialatum* (Ochoa) Correll. Ochoa (1999) recognized this taxon that Hawkes (1990) synonymized under *S. weberbaueri*.
- S. urubambae* Juz.
- S. multiflorum* Vargas
- S. villuspetalum* Vargas
- S. urubambae* Juz. f. *velutinum* (Correll) Ochoa
- S. santolallae* Vargas f. *velutinum* Correll

TABLE 3—New determinations of synonymy, new combinations, and newly resurrected names in wild and cultivated potato species (*Solanum* sect. *Petota*) and close outgroup relatives in sect. *Etuberosa* (*S. etuberosum*, *S. fernandezianum*, *S. palustre*), subsequent to Hawkes (1990). The listed name is the new one proposed by the author in the heading, and the indented names are the old, superseded (synonymized) taxa. Additional synonyms that are not at variance with decisions in Hawkes (1990) are not listed here.

Ochoa, 1990 [1991]

- Solanum acaule* Bitter var. *acaule*
- S. acaule* var. *punae* (Juz.) Hawkes
- S. boliviense* Dunal
- S. astleyi* Hawkes and Hjert.
- S. brevicaule* Bitter
- S. mollepujroense* Cárdenas and Hawkes
- S. chacoense* Bitter
- S. arnezii* Cárdenas
- S. circaeifolium* Bitter var. *capsicibaccatum* (Cárdenas) Ochoa
- S. capsicibaccatum* Cárdenas
- S. circaeifolium* subsp. *quimense* Hawkes and Hjert.
- S. circaeifolium* var. *circaeifolium*
- S. circaeifolium* subsp. *circaeifolium*
- S. leptophyes* Bitter
- S. gourlayi* Hawkes (Hawkes 1990; as *S. gourlayi* subsp. *gourlayi*)
- S. pachytrichum* Hawkes (Hawkes 1990; as *S. gourlayi* subsp. *pachytrichum* (Hawkes) Hawkes and Hjert.). - Note: Ochoa (1990) did not comment on *S. gourlayi* subsp. *saltense* A. M. Clausen and K. A. Okada, accepted in Hawkes (1990).
- S. oplocense* Hawkes
- S. hondelmannii* Hawkes and Hjert.
- S. tarijense* Hawkes
- S. xtrigalense* Cárdenas
- S. xzudaniense* Cárdenas
- S. tuberosum* subsp. *andigena* (Juz. and Bukasov) Hawkes
- S. estradae* L. López, =*S. phureja* subsp. *estradae* (L. López) Hawkes
- S. xsubandigena* Hawkes

Ochoa, 1992

- S. bukasovii* Juz. var. *bukasovii*
- S. canasense* Hawkes
- S. hapalosum* Ochoa
- S. pampasense* Hawkes
- S. sicuanum* Hawkes
- S. bukasovii* var. *multidissectum* (Hawkes) Ochoa
- S. multidissectum* Hawkes
- S. colombianum* Dunal
- S. cacetanum* Ochoa
- S. marinasense* Vargas
- S. canasense* var. *xerophyllum* (Vargas) Hawkes
- S. raphanifolium* Cárdenas and Hawkes
- S. hawkesii* Cárdenas
- S. tuberosum* subsp. *andigena* (Juz. and Bukasov) Hawkes
- S. paramoense* Bitter

Spooner et al., 1992

- S. regularifolium* Correll
- S. correllii* Ochoa, 1981

Van den Berg and Spooner, 1992

- S. microdontum* Bitter
- S. microdontum* var. *microdontum*
- S. microdontum* subsp. *microdontum*
- S. microdontum* var. *metriophyllum* (Bitter) Ochoa
- S. microdontum* subsp. *gigantophyllum* (Bitter) Hawkes and Hjert.

Ochoa, 1993

- S. chomatophilum* f. *angustifolium* Correll (Hawkes [1990, pgs. 108, 121] synonymized this form under both *S. colombianum* and *S. albornozii*).

Spooner et al., 1993

- S. andreanum* Baker
- S. cyanophyllum* Correll
- S. suffrutescens* Correll
- S. serratoris* Ochoa

Giannattasio and Spooner, 1994b

- S. megistacrolobum* Bitter subsp. *megistacrolobum*
- S. megistacrolobum*
- S. megistacrolobum* var. *megistacrolobum*
- S. megistacrolobum* subsp. *toralapanum* (Hawkes and Hjerting) R. B. Giannattasio and D. M. Spooner
- S. toralapanum* Cárdenas and Hawkes
- S. megistacrolobum* var. *toralapanum* (Cárdenas and Hawkes) Ochoa

Spooner et al., 1997

- S. boliviense* subsp. *astleyi* (Hawkes and Hjert.) D. M. Spooner, M. L. Ugarte, and P. W. Skroch
- S. astleyi* Hawkes and Hjert.

Contreras and Spooner, 1999

- S. palustre* Poepp.
- S. brevidens* Phil. var. *brevidens*
- S. brevidens* var. *glabrescens* (Poepp ex Schtdl.) Hawkes
- S. etuberosum* Lindl.
- S. subandinum* Meigen

Ochoa, 1999

- S. acaule* Bitter subsp. *acaule*
- S. acaule* subsp. *punae* (Juz.) Hawkes and Hjert.
- S. ancophilum* (Correll) Ochoa
- S. rhomboideilanceolatum* var. *ancophilum* Correll
- S. bukasovii* Juz. (see Ochoa, 1992)
- S. abancayense* Ochoa
- S. antacochense* Ochoa
- S. hapalosum* Ochoa
- S. bukasovii* f. *multidissectum* (Hawkes) Ochoa (see Ochoa 1992)
- S. multidissectum* Hawkes
- S. bukasovii* var. *multidissectum* (Hawkes) Ochoa
- S. chomatophilum* Bitter
- S. pascoense* Ochoa
- S. dolichocremastrum* Bitter
- S. chavinense* Correll
- S. huanucense* Ochoa
- S. immite* var. *vernale* Correll. Hawkes (1990) synonymized under *S. immite*.
- S. jalcae* var. *pubescens* Correll. Hawkes (1990) synonymized under *S. jalcae*
- S. medians* var. *autumnale* Correll
- S. weberbaueri* Bitter
- S. multiinterruptum* Bitter var. *multiinterruptum*
- S. moniliforme* Correll
- S. multiinterruptum* f. *longipilosum* Correll
- S. multiinterruptum* var. *multiinterruptum* f. *albiflorum* Ochoa
- S. chrysoflorum* Correll
- S. pampasense* Hawkes. Ochoa (1999) recognized this species that he previously synonymized under *S. bukasovii* f. *bukasovii* (Ochoa 1992).
- S. sparsipilum* (Bitter) Juz. and Bukasov
- S. sparsipilum* subsp. *calcense* Hawkes
- S. tacnaense* f. *decurrentialatum* (Ochoa) Correll. Ochoa (1999) recognized this taxon that Hawkes (1990) synonymized under *S. weberbaueri*.
- S. urubambae* Juz.
- S. multiflorum* Vargas
- S. villuspetalum* Vargas
- S. urubambae* Juz. f. *velutinum* (Correll) Ochoa
- S. santolallae* Vargas f. *velutinum* Correll

methods. Cladistic classifications use common ancestry as the sole criterion for grouping taxa. The phenetic method, in contrast, classifies organisms based on overall similarity, without regard to evolutionary history (except insofar as that similarity reflects phylogeny). Most classifications of sect. *Petota* have employed phenetic methods, both to delimit species and to produce an intrasectional classification. Cladistic methods use techniques that produce branching trees, and inter-specific hybridization disrupts neatly bifurcating phylogenies. Hybridization is known to be common in sect. *Petota*. Many taxonomists consider that cladistic classifications maximize information content and represent an ideal classification philosophy, but hybridization is a serious problem in phylogenetic reconstruction and cannot be ignored.

The terms monophyletic, ingroup, outgroup, clade, and sister taxa are basic cladistic terms needed for effective communication. A monophyletic group encompasses all descendants of an ancestral taxon. An ingroup refers to a putatively monophyletic group, such as "tuber-bearing Solanums." An outgroup is a putatively monophyletic group related to the ingroup, and a sister group is the most closely related monophyletic group to the ingroup. A clade is any monophyletic group.

Hawkes (1990) divided sect. *Petota* into subsection *Potatoes* Hawkes, with 19 tuber-bearing series, and subsection *Estolonifera* Hawkes with two non-tuber-bearing series: *Etuberosa* Juz. and *Juglandifolia* (Rydb.) Hawkes. He considered the close relatives of sect. *Petota* to be members of *Solanum* sect. *Basartherum* (Bitter) Bitter.

Spooner *et al.* (1993) used chloroplast DNA (cpDNA) restriction site data and morphological data to reinvestigate the relationships of all of these groups, along with the tomatoes (genus *Lycopersicon*), farther outgroups in *Solanum*, and other genera of the Solanaceae. Their results confirmed placement of all members of Hawkes's (1990) tuber-bearing species into sect. *Petota*, but the members of series *Etuberosa* and *Juglandifolia* as treated by Hawkes (1990) did not belong to *Petota* and were placed as outgroups (Figure 1).

Based on cpDNA and morphological data and cladistic classification theory, Spooner *et al.* (1993) placed tomatoes in the genus *Solanum* (not *Lycopersicon*), and Contreras and Spooner (1999) recognized series *Etuberosa* in a monograph of this group. Child (1990) foresaw many components of this phylogeny. He likewise included tomatoes in *Solanum*, as sect. *Lycopersicum* (Mill.) Wettst. He also treated some of Hawkes's (1990) series *Juglandifolia* at the sectional rank, as sect. *Juglandifolium* (Rydb.) Child, and other members of this series as

sect. *Lycopersicum*, subsect. *Lycopersicoides* Child. Like Hawkes (1990), he treated potatoes at the sectional rank (sect. *Petota* Dumort.).

Subsequent molecular studies are supporting these outgroup relationships of sect. *Petota*. For example, tomatoes and potatoes were shown to be sister taxa by separate phylogenetic studies using cpDNA restriction site variation (Olmstead and Palmer 1992, 1997) and DNA sequences of the chloroplast-encoded *ndhF* gene (Bohs and Olmstead 1997, 1999). The latter study supported *Solanum* sect. *Basartherum* as sister to tomatoes and potatoes as suggested by Hawkes (1990; sect. *Etuberosum* was not examined). Olmstead *et al.* (1999) supported tomatoes and potatoes as sister taxa by cpDNA restriction site data, and DNA sequence data of the cpDNA encoded genes *rbcl* and *ndhF*. Peralta and Spooner (in press) supported all components of the cpDNA phylogeny of Figure 1 with DNA sequences of the nuclear-encoded "waxy" gene.

Other non-cladistic studies also suggested the outgroup relationships outlined in Figure 1. Restriction enzyme mapping of the 18S, 5.8S, and 25S nuclear ribosomal DNA (nrDNA) showed tomatoes to be more similar to potatoes than other Solanaceae, and for the Mexican potato species clade (clade 1, Figure 1) to be similar to members of *Solanum* sect. *Etuberosum* (Borisjuk *et al.* 1994). Repetitive DNA showed a high similarity of *Lycopersicon* to potatoes (Schweitzer *et al.* 1993; Stadler *et al.* 1995; Malkamaki *et al.* 1996). They also showed tomatoes, potatoes, and sect. *Etuberosum* to be more similar to each other than to other Solanaceae.

The studies reviewed above all support sect. *Petota* as a monophyletic group, exclude series *Etuberosa* and series *Juglandifolia*, and recognize the sister-group relationships of potatoes and tomatoes within *Solanum*. Others, however, continue to maintain *Lycopersicon* as a distinct genus for nomenclatural stability, arguing adherence to phenetic criteria. For example, Lester (1991) and Nee (1999) concluded that tomatoes, potatoes, and pepinos formed a monophyletic group, but did not make nomenclatural changes. Both treatments remain in use today, based on differing classification philosophies and desire for nomenclatural stability.

Comparative genomic rearrangements have not yet conclusively addressed questions of outgroup relationships, but a growing body of data have the potential to do so. The first comparative genomic study was conducted by Bonierbale *et al.* (1988) who discovered three paracentric inversions distinguishing the sister taxa potato and tomato. Construction of a higher-density map (Tanksley *et al.* 1992) discovered an additional two

paracentric inversions differentiating these taxa. Three other potato maps have been constructed and integrated by use of common markers (Gebhardt *et al.* 1994; Jacobs *et al.* 1995; van Eck *et al.* 1995). Rouppe van der Voort *et al.* (1998) published 733 mapped Amplified Fragment Length Polymorphism (AFLP) markers useful for saturated AFLP linkage mapping. Maps of crosses within tomato (Fulton *et al.* 1997), and of tomato to sister taxon *S. lycopersicoides* (Chetelat *et al.* 2000) also have been constructed, that show overall genome conservation within this group. Comparative genetic linkage maps in *Capsicum* (Livingston *et al.* 1999) and in sect. *Etuberosum* (Perez *et al.* 1999) show genome rearrangements, but with conservation of substantial linkage blocks, making it possible for genome rearrangements to address outgroup relationships.

Ingroup Relationships

Chloroplast DNA Restriction Site Data—Hosaka (1995) extended his prior studies (Hosaka 1986; Hosaka and Hanneman 1988) on the origin of the cultivated tetraploid potato species with cpDNA restriction site data of entire cpDNA digest patterns. He studied 132 accessions of the diploid cultivated species *S. stenotomum* and of six related diploid wild species. He showed extensive cpDNA polymorphism in all taxa except *S. brevicaulis*, and concluded that Andean diploid cultivated potatoes were domesticated many times from the wild species, followed by sexual polyploidization to form Andean tetraploid potatoes. He also concluded that Chilean native cultigens of tetraploid *S. tuberosum* were selected from a limited subset of the germplasm of Andean tetraploid potatoes somewhere near the Bolivian and Argentinean border. Hosaka *et al.* (1988) earlier showed that Chilean *S. tuberosum* was primarily distinguished from most populations of Andean *S. tuberosum* and other cultivated and wild species by an approximately 400 base pair deletion in cpDNA. Kawagoe and Kihuta (1991) determined this to be 241 base pairs in size through comparative sequence analysis and mapped it downstream to the cpDNA trnV-UAC gene.

The origin of the European (and from there worldwide) *S. tuberosum* genotypes have long been held in dispute, with competing hypotheses suggesting genotypes from Chiloé Island and adjacent southern Chile, or from the Andes (Hawkes 1990). Ugent *et al.* (1987) contended, through analysis of starch grains of a 13,000-year-old tuber skin fossil from southern Chile, and recent collections of *S. maglia* from southern Chile, that the origin of Chilean genotypes was from the wild species *S. maglia*. Ugent *et al.* (1987) made no voucher specimens of these southern populations of *S. maglia* (otherwise known from 1000 km

north in coastal central Chile) to support their hypothesis, casting doubt on their argument of Chilean *S. tuberosum* arising from this species. Brücher (1990) also questioned their hypothesis by extensive and unsuccessful searches for *S. maglia* in southern Chile.

The cpDNA studies of Hosaka and collaborators were extended by cpDNA restriction site data using cloned probes, more restriction endonucleases, and more species. Three studies investigated the United States, Mexican and Central American species (Spooner *et al.* 1991c; Spooner and Sytsma 1992) and the South American species (Spooner and Castillo 1997). In total, these three studies examined 90 accessions of 86 species of 17 of the 19 tuber-bearing series of Hawkes (1990; germplasm of series *Cuneolata* and *Olmosense* were not available), and a representative of sect. *Etuberosum* as the outgroup. These studies defined four clades in sect. *Petota*: (1) the United States, Mexican, and Central American diploid species, exclusive of *S. bulbocastanum*, *S. cardiophyllum*, and *S. verrucosum*; (2) *S. bulbocastanum* and *S. cardiophyllum*; (3) all examined members of the South American series *Piurana* and some South American species classified to other series; (4) all remaining South American species and the United States, Mexican, and Central American polyploid species (Figure 1).

Other cpDNA restriction site studies were in-depth extensions of the above three with greater intraspecific sampling of clades 2 and 4. The cladistic separation of *S. bulbocastanum* and *S. cardiophyllum* (clade 2) from the other species of clade 1 was discordant with prior phylogenetic interpretations. These results, however, were from only two accessions of *S. bulbocastanum* (two of the three subspecies) and two accessions of *S. cardiophyllum* (one of the three subspecies). Rodríguez and Spooner (1997) reexamined these unexpected results with cpDNA analysis of 48 accessions of all six subspecies of these two species. The results confirmed the prior cpDNA results except for *S. cardiophyllum* subsp. *ehrenbergii* that fell in clade 1. These results suggested misclassification of this subspecies or introgressive hybridization with members of this clade.

Castillo and Spooner (1997) examined cpDNA phylogenetic relationships of 114 accessions of 23 out of 40 available species of series *Conicibaccata* using cpDNA restriction site variation and morphology. The results defined three main groups within the series: (1) polyploids from central Mexico to southern Ecuador; (2) diploids from northern Peru to Bolivia; (3) diploids and tetraploids cladistically related to members of series *Piurana* and suggesting misclassification in series *Conicibaccata*. Chloroplast DNA is predominately or entirely maternally inher-

ited in *Solanum* (Corriveau and Coleman 1988). Hosaka *et al.* (1984) showed maternal inheritance of cpDNA through an interspecific cross in sect. *Petota*, but Simmonds (1969) showed a possible case a biparental inheritance in *S. tuberosum*. The interpretation of these maternal gene trees into true species phylogenies, therefore, awaits conformation of data from nuclear markers (Wendel and Doyle 1998).

Nuclear Restriction Fragment Length Polymorphisms—Bonierbale *et al.* (1990) used single- to low-copy nuclear restriction fragment polymorphisms (nRFLPs) to study the interspecific relationships of 12 wild and four cultivated members of sect. *Petota*, encompassing seven series of Hawkes (1990), and sections *Etuberosum* and *Lycopersicum* as outgroups. The results grouped Mexican primitive diploid species next to *S. capsibaccatum*, grouped *S. acaule* (series *Acaulia*) with *S. demissum* (series *Demissa*), and intermixed members of two other series with members of series *Tuberosa*. This close similarity of *S. capsibaccatum* to the Mexican primitive (basal on the cladogram; potato clade 1, Figure 1) diploid species was discordant with cpDNA results of Spooner and Castillo (1997), who supported it as derived (more terminal on the cladogram; potato clade 4). As well, the intermixing of members of different series did not match Hawkes's (1990) series classifications.

Debener *et al.* (1990) used nRFLPs to study the interspecific relationships of 14 wild and three cultivated members of sect. *Petota*, encompassing eight series of Hawkes (1990), and sect. *Etuberosum* as the outgroup. The results grouped members of the Mexican diploid series next to sect. *Etuberosum*, and similar to Bonierbale *et al.* (1990) grouped *S. acaule* (series *Acaulia*) with *S. demissum* (series *Demissa*), and intermixed members of two other series with members of series *Tuberosa*.

Amplified Fragment Length Polymorphisms—Kardolus (1998) studied the potential of AFLPs to examine interspecific relationships of 19 species of four series in sect. *Petota*, and three species of sect. *Lycopersicum* (outgroups). Their data supported prior phylogenetic interpretations of Mexican diploid species as a primitive clade. Like the cpDNA studies and nRFLP studies (above), some series were poorly supported. For example, like the Debener *et al.* (1990) results, AFLP data united *S. demissum* (series *Demissa*) and *S. acaule* and *S. albicans* (series *Acaulia*), and failed to separate members of series *Cuneolata* and series *Megistacroloba* from members of series *Tuberosa*. Like Bonierbale *et al.* (1990), their results showed members of series *Circaeifolia* to be primitive. The discordance in cpDNA and nRFLP and AFLP data in series *Circaeifolia* likely is caused by a history of hybridization in this series, and shows

the necessity of using corroborative data from other molecular markers before translating molecular data into a taxonomy (Wendel and Doyle 1998).

Genomes—Within section *Petota* and the closest non-tuber-bearing relatives in section *Etuberosum*, chromosome pairing relationships have been interpreted with genome formulae (Marks 1955; Hawkes 1958; Irikura 1976; Matsubayashi 1991). The genome concept has been developed extensively, to the point that minor differences in pairing between genomes of different species have been recognized by giving the common genome a superscript to identify each of the subcategories. Most authors agree on a five genome hypothesis for sect. *Etuberosum* and sect. *Petota*, although they do not use standard letter designations. Matsubayashi (1991) presented the latest review of genome hypotheses and designated genomes as A, B, C, D, and E. The 'A' genome and its superscripted minor variants are part of the genomes of all species except for the non-tuber-bearing species of *Solanum* section *Etuberosum*; these are designated as 'E' genome species. The 'B' genome is a separate genome associated with the Mexican tetraploid wild species of series *Longipedicellata* (genome AABB); the 'C' genome is associated with the Mexican, Central and South American tetraploid and hexaploid wild species of series *Conicibaccata* (diploids with genomes AA, tetraploids AACC, the hexaploid genomes were not postulated); and the 'D' genome with the Mexican hexaploid wild species of series *Demissa* (AADDDD). López and Hawkes (1991a,b) speculated on crossing relationships and genome formulae of diploid, tetraploid, and hexaploid members of series *Conicibaccata* that provided hypotheses of species evolution in the group, and suggested a close relationship with members of series *Piurana*.

Secondary Chemistry—Petersen *et al.* (1993) studied interspecific relationships of 75 species of sect. *Petota* encompassing 14 series of Hawkes (1990) with steroidal sapogenins; lack of data from sect. *Etuberosum* precluded outgroup analysis. Although most wild members of series *Tuberosa* clustered, they did so with members of putatively unrelated series, and other clusters also grouped putatively advanced and primitive species. The results suggested limited use of these chemical markers for phylogenetic reconstruction in wild potatoes.

Intra- and Interspecific Studies

The former section discussed relationships among taxa and this one discusses criteria to define taxa. The validity of species and subspecies and varieties have been reexamined by morphological phenetics, intuitive judgements based on herbarium

and fieldwork, and molecular methods. Those studies that led to formal taxonomic decisions are listed in Table 3.

Solanum section Etuberosum—Spooner *et al.* (1992b) examined isozyme variability of three species of sect. *Etuberosum* (*S. etuberosum*, *S. fernandezianum*, and *S. palustre*). They showed that all three species have very low levels of heterozygosity, and that *S. fernandezianum*, endemic to the Juan Fernandez Islands (Chile) differs from the two continental species in adjacent Chile and Argentina by two unique alleles. Spooner *et al.* (1996) additionally examined these species with nRFLPs Random Amplified Polymorphic DNA (RAPD), and cpDNA. The nRFLP and RAPD and isozyme markers were generally concordant in showing equal genetic distance of all three taxa from each other, but cpDNA showed the insular endemic *S. fernandezianum* to be divergent from the two continental taxa. Based on morphological data, including comparison with type specimens, Contreras and Spooner (1999) synonymized the five species of sect. *Etuberosa* of Hawkes (1990) into three taxa (*S. etuberosum*, *S. fernandezianum*, and *S. palustre*).

Solanum Series Acaulia—Hosaka and Spooner (1992) used 94 probe-enzyme combinations of nRFLPs to examine 105 accessions of all four subspecies of *S. acaule*, throughout its distribution area, from northern Peru to northern Argentina. They were able to support all subspecies except subsp. *acaule* and subsp. *punae*. This corresponded with taxonomic treatments of Ochoa (1990a, 1999), that united these two subspecies (as subsp. *acaule*). However, Kardolus (1999) used phenetic analysis of morphological data to distinguish most accessions of the two subspecies, and he ascribed the mixture of the two in the study of Hosaka and Spooner (1992) to be due to misidentifications. Yet, both AFLP and morphological data of Kardolus (1998) were unable to consistently distinguish subsp. *acaule* and subsp. *punae*. Based on morphological and AFLP data, Kardolus (1998) recognized a new subspecies of *S. acaule*, subsp. *palmirensis*. Although it has the hexaploid chromosome number and overall morphological similarity to *S. albicans*, AFLP data influenced him to classify it in *S. acaule* (typically tetraploid).

Solanum Series Circaeifolia—Van den Berg and Groen-dijk-Wilders (1999) analyzed the four taxa of series *Circaeifolia*. Phenetic analysis of morphological data showed difficulty to distinguish *S. capsicibaccatum* and *S. circaeifolium* subsp. *quimense*, and character states of all taxa overlapped in range. Van den Berg *et al.* (in press), however, showed that all four taxa of this series were well-distinguished by AFLP data, suggesting that the taxa were good at some rank (species or subspecies), and that polythetic morphological support for species is com-

mon in sect. *Petota*. A polythetic morphological species concept is one where species are defined where they have the greatest number of shared features, no single feature of which is essential for group membership or is sufficient to make an organism a member of a group (Sokal and Sneath 1963; Stuessy 1990). Stated otherwise, species are distinguished only by a complex of features, all of which overlap in range.

Solanum Series Demissa—Spooner *et al.* (1995b) examined six taxa of the hexaploid species of series *Demissa* by phenetic analysis of morphological data, and the morphologically similar species *S. albicans* (series *Acaulia*) and *S. verrucosum* (series *Tuberosa*). The results showed that *S. demissum* was closer to *S. albicans* than to any other species in series *Demissa* and questioned series affiliations. Results also showed the difficulty in distinguishing three other species of series *Demissa*, and that all taxa were distinguished only by polythetic support. Kardolus (1999) studied phenetic relationships of all taxa in series *Acaulia* and members of five other series. Like Spooner *et al.* (1995b), they showed *S. demissum* (series *Demissa*) to group with *S. albicans* of series *Acaulia*. Note similar results linking *S. demissum* and series *Acaulia*, discussed above, in the nRFLP and AFLP results of Bonierbale *et al.* (1990), Debener *et al.* (1990), and Kardolus (1998).

Solanum Series Longipedicellata—Spooner *et al.* (2001b) examined six taxa of the Mexican tetraploid species of series *Longipedicellata*, and morphologically similar species in series *Demissa* (*S. demissum*) and series *Tuberosa* (*S. avilesii*, *S. gourlayi*, and *S. verrucosum*), by phenetic analysis of morphological data. The results supported only three species in series *Longipedicellata* (*S. fendleri* + *S. papita* + *S. stoloniferum*, *S. polytrichon*, *S. hjertingii* + *S. matehualae*) and showed that *S. gourlayi* and to a lesser extent *S. demissum* and *S. verrucosum* are very similar to members of series *Longipedicellata* and are difficult to distinguish morphologically, despite differences in chromosome numbers and crossability relationships.

Solanum andreanum—Spooner *et al.* (1993b) synonymized *S. andreanum*, *S. baezense*, *S. cyanophyllum*, *S. pichinchense*, *S. serratoris*, and *S. suffrutescens* under the earliest name, *S. andreanum*, based on an examination of type specimens and field work throughout their range in Colombia and Ecuador. Prior authors had placed these species in five separate taxonomic series.

Solanum astleyi, *S. boliviense*—Spooner *et al.* (1997) used RAPDs to study the species boundaries and relationships of the morphologically very similar species *S. astleyi* and *S. boliviense*.

By comparison with RAPD differentiation of other taxa classified as subspecies, they recognized these at the subspecies level under *S. boliviense* (Table 3).

Solanum berthaultii, *S. tarijense*—Spooner and Van den Berg (1992b) studied the species status of *S. berthaultii*, *S. tarijense*, and putative interspecific hybrids between them. They concluded that the taxa likely belonged to one species, despite the fact that Hawkes (1990) placed them in different superseries. They withheld formal taxonomic decisions awaiting further molecular data of the same accessions.

Solanum brevicaulle Complex—Included here are studies of species and subspecies included by Van den Berg *et al.* (1998) and Miller and Spooner (1999) in the broad term "*Solanum brevicaulle* complex," but all authors did not use this term. Clausen and Crisci (1989) studied the morphological phenetics among diploid and tetraploid populations of *S. gourlayi*, and morphologically similar *S. incamayoense* and *S. vidaurrei*. They concluded that the diploid and tetraploid populations of *S. gourlayi* were sufficiently distinct to be considered distinct subspecies, but made no formal taxonomic decision to effect this. They showed that *S. vidaurrei* resembled diploid *S. gourlayi*, and *S. incamayoense* was a distinct species. Hawkes and Hjerting (1989) formally transferred *S. vidaurrei* to subspecies status under *S. gourlayi*. Clausen and Okada (1990) continued these studies with a phenetic analysis of the diploid and tetraploid populations of *S. gourlayi*, *S. incamayoense*, *S. infundibuliforme*, and *S. vidaurrei*, using tuber proteins. The results distinguished all species, but showed only partial separation of the populations of *S. gourlayi*.

Van den Berg *et al.* (1996, 1998) studied competing hypotheses of the validity of species in the *Solanum brevicaulle* complex, a group of about 30 morphologically very similar diploid, tetraploid, and hexaploid taxa believed to be related to the cultivated potato. Miller and Spooner (1999) studied the same accessions, but with nRFLPs and RAPDs. All data were concordant in showing that (1) there were no species-specific morphological characters that distinguished species, and any species that may be valid would be distinguished only by use of a complex of widely overlapping traits (polythetic morphological support); (2) at best, two species were defined with a north-south geographical partitioning, one from Peru and northwestern Bolivia, and another from northwestern Bolivia to northern Argentina. They withheld formal taxonomic decisions awaiting further molecular data of the same accessions. AFLP data (Kardolus 1998) confirmed the north-south split of the two groups of the *S. brevicaulle* complex.

Solanum lobbianum—The original collection site of the wild potato species *S. lobbianum* has long been a source of confusion. The type specimen is immature (it lacks fruits), the place name 'Columbia' is ambiguous because of changing political boundaries and name changes involving Venezuela, Colombia, and Ecuador when it was collected in the mid-1880s, and 'Columbia' may have been a mislabeling or later addition by another person after collection (Spooner *et al.* 1995a). Hawkes (1992c) identified recent collections from Ecuador as *S. lobbianum*, while Spooner *et al.* (1992a) identified these as *S. paucijugum*. Ochoa (1992c), and Spooner *et al.* (1995a), however, identified *S. lobbianum* as a separate species from central Colombia (Manizales Department), based on comparison of the type specimen with their recent collections there.

Solanum megistacrolobum, *S. toralapanum*—Giannattasio and Spooner (1994a,b) investigated competing hypotheses of *S. megistacrolobum* and *S. toralapanum* as distinct species, the same species, or as different varieties. Concordant data from morphology and nRFLPs supported their distinction as varieties or subspecies of *S. megistacrolobum*. These included contiguous but largely non-overlapping distributions and very close morphological and molecular similarity. Varieties and subspecies have been used frequently in potatoes and in flowering plants in general to refer to ranks below species, amplifying the number of names and creating confusion among users (Hamilton and Reichard 1992). To bring uniformity to names below the species level, Giannattasio and Spooner (1994b) followed recommendations of Hamilton and Reichard (1992) to use the subspecies rank (*S. megistacrolobum* subsp. *megistacrolobum* and *S. megistacrolobum* subsp. *toralapanum*).

Solanum microdontum—Van den Berg and Spooner (1992) conducted a phenetic analysis of the varieties and subspecies of *S. microdontum*, concluded that none of these were valid, and made a formal taxonomic decision to group all under *S. microdontum*.

General Synonymy Papers—Judgements based on morphology and distributional data also have been used to effect many changes in taxonomy of sect. *Petota* and sect. *Etuberosum*. Ochoa (1990a) synonymized 11 taxa and changed rank for three taxa from Bolivia. Ochoa (1992a) synonymized eight taxa and changed rank on one taxon from Colombia, Peru, and Venezuela. Ochoa (1993) resurrected one variety from Ecuador. Spooner *et al.* (1992a) synonymized one species from Ecuador. Ochoa (1999) synonymized 14 taxa, changed rank for three, and resurrected three previously synonymized names for the flora of Peru.

Morphological Evaluations as They Relate to Taxonomy

The former section focused on studies examining intra- and interspecific relationships. This section discusses studies focused on an examination of characters used to define these relationships and relationships at higher taxonomic levels.

Anthoclades—Recent studies have clarified structure and variation of morphological traits that have provided major taxonomic characters in sect. *Petota* and outgroups. Child and Lester (1991) studied anthoclades (patterns of branching and associated inflorescences) in potatoes, tomatoes, and outgroups. Their data supported tomatoes and potatoes as sister taxa. Spooner *et al.* (1993a) used anthoclades for a morphology-based cladistic analysis that corroborated the molecular-based outgroup relationships outlined in Figure 1.

Pedicle Articulation Position and Degree of Abscission—Kardolus and Bezem (1998) studied the presence and position of pedicle articulation and abscission zone. They showed that articulation and abscission was not a constant or clearly distinct character in all members of series *Acaulia*. Relative position of pedicle articulation was of reduced taxonomic value except for those species where articulation was extremely high, in some members of series *Acaulia* and series *Megistacroloba*, or low (sect. *Etuberosum*).

Inflorescence Architecture—Kardolus and Groendijk-Wilders (1998) studied the inflorescence architecture of members of series *Acaulia*, series *Demissa*, and series *Megistacroloba*. They described five types of inflorescence architecture, including a type not recognized previously of a monochasium with an "extra" flower at its base. None of these were species-specific and even they varied on individual plants, but they showed species-specific tendencies towards one type. Their results showed many cases of both concordance and discordance with the series classification of Hawkes (1990). For example, series *Acaulia*, *Megistacroloba* and *Pinnatisecta* generally were well supported, but series *Bulbocastana*, *Tuberosa*, *Piurana* less so.

Light Sprouts—Van den Berg and Groendijk-Wilders (1993) studied the taxonomic value of light sprouts of representatives of 14 series of sect. *Petota*. Light sprouts are stunted plants with leaves and sometimes flowers, arising from tubers grown under low light intensity. They traditionally have been used for varietal identification. Based on striking similarities and dissimilarities the affiliation of certain species to series was questioned. For example, light sprouts of *S. boliviense* were very different from those of all other species of series *Megistacroloba*, while differ-

ences between *S. bulbocastanum* and *S. clarum* contradicted their close alliance. On the other hand, *S. berthaultii* and *S. tarijense* proved to be very similar in light sprouts, despite their treatment as different series (Hawkes 1990).

Corolla Shape—Van der Heijden and Van den Berg (1997) studied corolla shape variation of 10 species of sect. *Petota* belonging to different superseries *Stellata* and *Rotata* (Hawkes 1990), by computer image analysis. They found a continuous range of variation between representatives of these two superseries, showing the difficulty of using this character alone taxonomically. In agreement with Spooner and Van den Berg (1992b), they were unable to distinguish *S. berthaultii* and *S. tarijense*, representatives of two superseries. Spooner and Van den Berg (in press) found statistically significant differences between species in radius of the corolla that distinguished series *Longipedicellata* from series *Demissa*. They excluded *S. demissum* from series *Demissa* in their analysis, that they grouped with members of the South American series *Acaulia*. There was, however, wide overlap in ranges of character states of the corolla that greatly reduced its utility as a practical taxonomic character in these series.

Endosperm Balance Number Determinations and Chromosome Counts

The Endosperm Balance Number (EBN) relates to a strong isolating mechanism in sect. *Petota* and has been used to speculate on major evolutionary trends in the group. The EBN hypothesis was first published by Johnston *et al.* (1980) to explain success or failure of intra- and interspecific crosses, due to the functioning or breakdown of the endosperm after fertilization. The EBNs are hypothetical genetic factors independent of ploidy and empirically determined relative to other EBNs. They are based on crossability with standard test EBN crosses or species of known EBN, and are published with the actual ploidy of the species. In potato, these are 2x(1EBN), 2x(2EBN), 4x(2EBN), 4x(4EBN), and 6x(4EBN). The standards first used were *S. cardiophyllum* (PI 279272, PI 347759) and *S. commersonii* subsp. *commersonii* (PI 320266, PI 458317) for 2x(1EBN); *S. chacoense* (PI 209411, PI 217451) and *S. phureja* (PI 225707, PI 243469, PI 275110) for 2x(2EBN); and two colchicine doubled genotypes of *S. chacoense* (PI 230582) and *S. tuberosum* subsp. *andigena* (PI 232045, PI 255507, PI 255508) for 4x(4EBN) and 6x(4EBN) (Hanneman 1994).

Crosses between species with differing EBNs are almost always unsuccessful, and crosses between species with the same EBN number are frequently successful, even if they differ

by ploidy. The EBN is increased or reduced as a direct multiple of ploidy manipulations, via colchicine doubling of parents, or 2n gametes, to introduce germplasm from normally EBN-incompatible species. EBN forms a major biological isolating mechanism in potato, along with failure of the pollen grain to germinate on the style, failure of the pollen tube to grow through the style, or seed abortion in crosses between EBN-compatible species (Fritz and Hanneman 1989; Hawkes and Jackson 1992).

Ehlenfeldt and Hanneman (1988) proposed the genetic control of EBN to be regulated by three unlinked loci with additive effects. Johnston and Hanneman (1996) provided evidence, through trisomics and induced mutations of pollen grains, that EBN in *Nicotiana* and *Solanum* is controlled by more than one gene on more than one chromosome. Johnston and Hanneman (1999) provided evidence, through aneuploid analysis, that only two chromosomes change EBN in *Datura*. Bamberg (1994) studies the inheritance of EBN in *S. acaule*, through crosses with artificially doubled 4x(2EBN) *S. commersonii*. They concluded that each of these two species carry genomes in a genetically similar way, and that inheritance of EBN throughout sect. *Petota* was similar. Alternatively, Camadro and Masuelli (1995) proposed two independent loci in each genome, carrying alleles 1/2 and 0 in homozygosity, to explain interspecific crossing with 4x *S. acaule*, 2x *S. commersonii*, 2x *S. gourlayi*, and 4x *S. gourlayi*. Katsiotis *et al.* (1995) show that the EBN concept in the Solanaceae likely is the same as the polar-nucleation activation (PNA) concept in the Gramineae, first worked out in *Avena* (Nishiyama and Yabuno 1978).

Hawkes and Jackson (1992), Ortiz and Ehlenfeldt (1992), Hanneman (1994), Johnston and Hanneman (1996), and Hanneman (1999) provided a history of the development of the EBN concept relative to related theories on the role, functioning, and evolutionary implications of endosperm. Regarding systematics and evolution, Hawkes and Jackson (1992) use EBN to support the phylogenetic hypothesis of sect. *Petota* advanced by Hawkes (1989, 1990) that divides potatoes into a primitive subsect. *Stelata* and an advanced subsect. *Rotata* (see Outgroup Relationships, above). Ortiz and Ehlenfeldt (1992) stress the role of EBN as an isolating mechanism driving speciation for sympatric progenitor-derivative species pairs. Watanabe and Peloquin (1989, 1991) document the widespread occurrence of 2n pollen in wild and cultivated species that allow for changes in ploidy and EBN in evolution.

Most of the initial EBN determinations were published in Hanneman and Bamberg (1986), and this publication provided the majority of the EBN data for the evolutionary interpretations

of Hawkes and Jackson (1992) and Ortiz and Ehlenfeldt (1992). Hanneman (1994) republished most, but not all, of these numbers and the materials, methods, and data that supported them. Hawkes (1990) and Ochoa (1992b, 1993, 1999) published additional EBN numbers that are providing the data needed for a more complete synthesis of EBNs and phylogeny.

Ochoa (1999:37-38) first published his materials and methods for his EBN determinations, listing the standard testers *S. commersonii* and *S. mochiuense* for 2x(1EBN), but not testers for other EBN levels. In individual species treatments he lists extensive crossing data (see notes 10, 11, 13, 14, 17, 18, 20, 23, of Table 4). The biggest EBN discrepancy (note 11, occurring in 29 species) is that crosses are reported as successful (as determined by fruit and seed set in F_1 's) that do not match expectations. This could be a result of 2n gametes in these crosses. Ploidies were not determined in progeny of crosses. His new EBN determinations, therefore, should be considered as provisional until repeated with tests of determination of seed quality, seed set, occurrence of fertilization, and ploidy of the offspring (Johnston and Hanneman 1980).

Determinations of EBN are independent of ploidy. Ploidy determinations often have been used to help determine identities of morphologically similar species (Spooner and Van den Berg 1992a; Van den Berg *et al.* 1998) and therefore are important in potato taxonomy. New determinations of ploidy have been published by Sangowama (1989), Hawkes (1990), Moscone (1992), Ochoa (1992b, 1993, 1999), Kardolus (1998), Valkonen (1994), Spooner *et al.* (1994, 1995b, 1999), Castillo and Spooner (1997), and Salas *et al.* (in press). Those determinations after the publication of Hawkes (1990) are listed in Table 4. In addition, NRSP-6 has determined hundreds of counts in this review period that were published in Bamberg *et al.* (1996), with updates present in the United States Germplasm Resources Information (GRIN) system (United States Department of Agriculture, Agricultural Research Service 2000).

Interspecific Hybridization

Approximately 12% (26) of the 225 wild tuber-bearing *Solanums* as recognized by Hawkes (1990) have been hypothesized to have arisen by hybrid speciation (listed in Spooner and Van den Berg 1992b). In addition, hybridization not leading to widespread introgression or speciation is believed to be common (Hawkes and Hjerting 1969, 1989). Most of these hypotheses have been generated by intermediate morphology, inference from distributional data, and/or artificial reconstruction of the hybrids and comparison with putative natural hybrids, and assessment

TABLE 4—Wild and cultivated potato species (*Solanum* sect. *Petota*) and wild species of close outgroup relatives in sect. *Etuberosa* (*S. etuberosum*, *S. fernandezianum*, *S. palustre*), based on Hawkes (1990), with subsequent changes as outlined in Tables 2, 3. This list is bibliographic in nature to update Hawkes (1990), and most EBN determinations listed under that reference originally were published in Hanneman and Bamberg (1986). We accept only those taxonomic changes under authorship of Spooner and collaborators in Table 3. This list does not include the 141 subspecies, varieties, and forms, including unlisted autonyms, of the Bolivian cultigens recognized by Ochoa (1988, 1990; see text). It adds the autonyms not included in Hawkes (1990) or Ochoa (1999), as needed to fill these mandatory taxonomic ranks (see text). The country code, EBN and ploidy, and reference data are listed only at the species level in the case of autonyms.

Taxon (putative hybrid origins) ¹	Code ²	Country ³	Ploidy and (EBN) ⁴	Reference for ploidy and EBN
Wild Species				
<i>Solanum acaule</i> Bitter	acl	ARG, BOL, PER	4x(2EBN)	Hawkes 1990
subsp. <i>acaule</i> ⁵	acl			
f. <i>acaule</i>	acl			
f. <i>incuyo</i> Ochoa	inc	PER	4x	Ochoa 1999
subsp. <i>aemulans</i> (Bitter and Wittm.)				
Hawkes and Hjert.	aem	ARG	4x(2EBN)	Hawkes 1990
subsp. <i>palmirensis</i> J. Kardolus	pal	ECU	6x	Spooner <i>et al.</i> 1995 (as <i>S. albicans</i>); Kardolus 1998
subsp. <i>punae</i> (Juz.)				
Hawkes and Hjert.) ⁶	pne	PER	4x(2EBN)	Hawkes 1990
<i>S. achacachense</i> Cárdenas	ach	BOL	2x	Hawkes 1990
<i>S. acroglossum</i> Juz.	acg	PER	2x(2EBN)	Ochoa 1992
<i>S. acroscopicum</i> Ochoa	acs	PER	2x	Hawkes 1990
<i>S. agrimonifolium</i> Rydb.	agf	GUA, HON, MEX	4x(2EBN)	Hawkes 1990
<i>S. alandiae</i> Cárdenas	aln	BOL	2x ⁷	Hawkes 1990
<i>S. albicans</i> (Ochoa) Ochoa	alb	ECU, PER	6x(4EBN)	Hawkes 1990
<i>S. albornozi</i> Correll	abz	ECU	2x(2EBN)	Ochoa 1992
<i>S. amayanum</i> Ochoa	amy	PER	2x(2EBN)	Ochoa 1992
<i>S. ambosinum</i> Ochoa	amb	PER	2x(2EBN)	Hawkes 1990
<i>S. anamophilum</i> Ochoa	amp	PER	2x(2EBN)	Ochoa 1992
<i>S. ancophilum</i> (Correll) Ochoa	acp	PER	2x(2EBN)	Ochoa 1999
<i>S. ancoripae</i> Ochoa	anp	PER	2n	Ochoa 1999
<i>S. andreanum</i> Baker	adr	COL, ECU	2x(2EBN)	Ochoa 1993 (as <i>S. suffrutescens</i>)
<i>S. xarahuayum</i> Ochoa (med × wtm)	ara	PER	2x	Ochoa 1994a
<i>S. aridophilum</i> Ochoa	adp	PER	2x(2EBN)	Ochoa 1999
<i>S. arnezii</i> Cárdenas ⁸	arz	BOL		
<i>S. augustii</i> Ochoa	agu	PER	2x(1EBN)	Hawkes 1990
<i>S. avilesii</i> Hawkes and Hjert. ⁹	avl	BOL	2x	Hawkes 1990
<i>S. ayacuchense</i> Ochoa	ayc	PER	2x(2EBN)	Ochoa 1992
<i>S. aymaraesense</i> Ochoa	aym	PER	2x	Hawkes 1990
<i>S. berthaultii</i> Hawkes	ber	BOL	2x(2EBN)	Hawkes 1990
<i>S. bill-hookeri</i> Ochoa	bhk	PER	2x ¹⁰	Hawkes 1990
<i>S. xblanco-galdosii</i> Ochoa (amp × plq)	blg	PER	2x(2EBN)	Ochoa 1992
<i>S. boliviense</i> Dunal	blv	BOL	2x(2EBN)	Hawkes 1990
subsp. <i>astleyi</i> (Hawkes and Hjert.) D.M. Spooner, M. Ugarte, and P. M. Skroch	ast			
subsp. <i>boliviense</i>	ast	BOL	2x(2EBN)	Hawkes 1990
<i>S. bombycinum</i> Ochoa	bmb	BOL	4x	Hawkes 1990
<i>S. brachistotrichum</i> (Bitter) Rydb.	bst	MEX	2x(1EBN)	Hawkes 1990
<i>S. brachycarpum</i> Correll	bcp	MEX	6x(4EBN)	Hawkes 1990
<i>S. brevicaule</i> Bitter	brc	BOL	2x(2EBN)	Hawkes 1990
<i>S. xbruecheri</i> Correll (<i>S. gourlayi</i> [=lph by Ochoa 1990] × inf)	bru	ARG		
<i>S. buesii</i> Vargas	bue	PER	2x(2EBN)	Ochoa 1992
<i>S. bukasovii</i> Juz.	buk	PER	2x(2EBN) ¹¹	Hawkes 1990
f. <i>bukasovii</i>	buk			
f. <i>multidissectum</i> (Hawkes) Ochoa	mlt	PER	2x(2EBN)	Hawkes 1999

TABLE 4—Cont.

Taxon (putative hybrid origins) ¹	Code ²	Country ³	Ploidy and (EBN) ⁴	Reference for ploidy and EBN
Wild Species				
<i>S. bulbocastanum</i> Dunal	blb	MEX	2x(1EBN)	Hawkes 1990
subsp. <i>bulbocastanum</i>	blb			
subsp. <i>dolichophyllum</i> (Bitter) Hawkes	dph	MEX	2x(1EBN)	Hawkes 1990
subsp. <i>partitum</i> (Correll) Hawkes	ptt	GUA, MEX	2x(1EBN)	Hawkes 1990
<i>S. burkartii</i> Ochoa	brk	PER	2x	Ochoa 1999
<i>S. burtonii</i> Ochoa	brt	ECU	3x	Ochoa 1993
<i>S. cajamarquense</i> Ochoa	cjm	PER	2x(1EBN)	Ochoa 1999
<i>S. calacalinum</i> Ochoa	cln	ECU	2x	Ochoa 1993
<i>S. calvescens</i> Bitter	clv	BRA	3x	Hawkes 1990
<i>S. candolleianum</i> P. Berthault	cnd	BOL, PER	2x(2EBN) ¹¹	Ochoa 1992
<i>S. cantense</i> Ochoa	cnt	PER	2x(2EBN)	Ochoa 1992
<i>S. cardiophyllum</i> Lindl.	cph	MEX	2x(1EBN), 3x	Hawkes 1990
subsp. <i>cardiophyllum</i>	cph			
subsp. <i>ehrenbergii</i> Bitter	ehr	MEX	2x(1EBN)	Hawkes 1990
subsp. <i>lancoletum</i> (P. Berthault) Bitter	lcl	MEX	2x(1EBN)	Hawkes 1990
<i>S. chacoense</i> Bitter	che	ARG, BOL, PAR, URU	2x(2EBN)	Moscone 1992; Hawkes 1990
subsp. <i>chacoense</i>	che			
subsp. <i>muelleri</i> (Bitter) Hawkes and Hjert.	mue	ARG, BRA	2x(2EBN)	Moscone 1992; Hawkes 1990
<i>S. chancayense</i> Ochoa	chn	PER	2x(1EBN) ¹¹	Hawkes 1990
<i>S. chilliasense</i> Ochoa	chl	ECU	2x(2EBN)	Ochoa 1992, 1993
<i>S. chillonanum</i> Ochoa ¹²	chi	PER	2x	Ochoa 1999
<i>S. chiquidenum</i> Ochoa	chq	PER	2x(2EBN)	Ochoa 1992
var. <i>amazonense</i> Ochoa	ama	PER	2x	Ochoa 1999
var. <i>chiquidenum</i>	chq			
var. <i>gracile</i> Ochoa	gra	PER	2x	Ochoa 1999
var. <i>robustum</i> Ochoa	rob	PER	2x	Ochoa 1999
<i>S. chomatophilum</i> Bitter	chm			
var. <i>chomatophilum</i>	chm	ECU, PER	2x(2EBN)	Hawkes 1990
f. <i>angustifolium</i> Correll	ang	ECU		
f. <i>chomatophilum</i>	chm	PER		
f. <i>sausianense</i> Ochoa	sau	PER		
var. <i>subnivale</i> Ochoa	sbv	PER	2x	Salas <i>et al.</i> in press
<i>S. circaeifolium</i> Bitter	crc	BOL	2x(1EBN)	Hawkes 1990
var. <i>capsicibaccatum</i> (Cárdenas) Ochoa	cap	BOL	2x(1EBN)	Hawkes 1990
var. <i>circaeifolium</i>	crc			
<i>S. clarum</i> Correll	clr	MEX, GUA	2x	Hawkes 1990
<i>S. coelestipetalum</i> Vargas	cop	PER	2x(2EBN) ¹¹	Ochoa 1999
<i>S. colombianum</i> Bitter	col	COL, ECU, VEN	4x(2EBN)	Hawkes 1990
<i>S. commersonii</i> Dunal	cmm	ARG, BRA, URU	2x(1EBN)	Hawkes 1990
subsp. <i>commersonii</i>	cmm			
subsp. <i>malmeanum</i> (Bitter) Hawkes and Hjert.	mlm	ARG, BRA, PAR, URU	2x(1EBN)	Hawkes 1990
<i>S. contumazaense</i> Ochoa	ctz		2x(2EBN) ¹³	Ochoa 1992
<i>S. demissum</i> Lindl.	dms	GUA, MEX	6x(4EBN)	Hawkes 1990
<i>S. ×doddsii</i> Correll (aln × chc)	dds	BOL	2x(2EBN)	Hawkes 1990
<i>S. dolichocremastrum</i> Bitter	dcm	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. donachui</i> (Ochoa) Ochoa	dnc	COL		
<i>S. ×edinense</i> P. Berthault	edn			
subsp. <i>edinense</i> (dms × tub)	edn	MEX	5x	Hawkes 1990
subsp. <i>salamanii</i> (Hawkes) Hawkes (dms × adg)	slm	MEX	5x	Hawkes 1990
<i>S. etuberosum</i> Lindl.	etb	CHL	2x(1EBN)	Hawkes 1990; Valkonen 1994
<i>S. fendleri</i> A. Gray	fen	MEX, USA	4x(2EBN)	Hawkes 1990
subsp. <i>arizonicum</i> Hawkes	azn	MEX, USA	4x(2EBN)	Hawkes 1990
subsp. <i>fendleri</i>	fen			
<i>S. fernandezianum</i> Phil.	frn	CHL	2x(1EBN)	Hawkes 1990; Valkonen 1994
<i>S. flahaultii</i> Bitter	flh	COL	4x	Hawkes 1990
<i>S. flavoviridens</i> Ochoa	flv	BOL		
<i>S. gandarillasii</i> Cárdenas	gnl	BOL	2x(2EBN)	Hawkes 1990
<i>S. garcia-barrigae</i> Ochoa	gab	COL		
<i>S. gracilifrons</i> Bitter	grc	PER	2x	Hawkes 1990
<i>S. guerreroense</i> Correll	grr	MEX	6x(4EBN)	Hawkes 1990
<i>S. guzmanguense</i> Whalen and Sagást	gzm	PER	2x(1EBN) ¹⁴	Ochoa 1992
<i>S. hastiforme</i> Correll	hsf	PER	2x(2EBN)	Ochoa 1999

TABLE 4—Cont.

Taxon (putative hybrid origins) ¹	Code ²	Country ³	Ploidy and (EBN) ⁴	Reference for ploidy and EBN
Wild Species				
<i>S. hintonii</i> Correll	hnt	MEX		
<i>S. hjertingii</i> Hawkes	hjt	MEX	4x(2EBN)	Sangowawa 1989; Hawkes 1990
var. <i>hjertingii</i>	hjt			
var. <i>physaloides</i> (Correll) Hawkes	phy	MEX		
<i>S. hoopesii</i> Hawkes and K. A. Okada	hps	BOL	4x	Hawkes 1990
<i>S. hougasii</i> Correll	hou	MEX	6x(4EBN)	Hawkes 1990
<i>S. huancabambense</i> Ochoa	hcb	PER	2x(2EBN)	Hawkes 1990
<i>S. huancavelicae</i> Ochoa	hcv	PER	2x(2EBN) ¹¹	Ochoa 1999
<i>S. huarochiriense</i> Ochoa	hro	PER	2x(2EBN)	Ochoa 1999
<i>S. humectophilum</i> Ochoa	hmp	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. hypacarthrum</i> Bitter	hcr	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. immite</i> Dunal	imt	PER	2x(1EBN), 3x	Ochoa 1992, Salas <i>et al.</i> 1999 (for triploid count)
var. <i>immite</i>	imt			
var. <i>vernale</i> Correll	vrl	PER		
<i>S. incahuasinum</i> Ochoa	inh	PER	2x(1EBN) ¹¹	Ochoa 1999
<i>S. incamayoense</i> K. A. Okada and A. M. Clausen	inm	ARG	2x	Hawkes 1990
<i>S. incasicum</i> Ochoa	ins	PER	2x(2EBN)	Ochoa 1999
<i>S. xindumii</i> K. A. Okada and A. M. Clausen (acl × mga)	ind	ARG	3x	Hawkes 1990
<i>S. infundibuliforme</i> Phil.	ifd	ARG, BOL	2x(2EBN)	Hawkes 1990
<i>S. ingifolium</i> Ochoa ¹⁵	igf	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. iopetalum</i> (Bitter) Hawkes	iop	MEX	6x(4EBN)	Hawkes 1990
<i>S. irosinum</i> Ochoa	irs	PER	2x(2EBN)	Ochoa 1992
var. <i>irosinum</i>	irs			
var. <i>tarrosom</i> Ochoa	trr	PER	2x	Ochoa 1999
<i>S. jaenense</i> Ochoa	jnn	PER	6x(4EBN) ¹⁶	Ochoa 1999
<i>S. jalcae</i> Ochoa	jlc	PER	2x(2EBN) ¹¹	Ochoa 1992
var. <i>jalcae</i>	jlc			
var. <i>pubescens</i> Correll	pub	PER		
<i>S. jamesii</i> Torr.	jam	MEX, USA	2x(1EBN)	Hawkes 1990
<i>S. kurtzianum</i> Bitter and Wittm.	ktz	ARG	2x(2EBN)	Hawkes 1990
<i>S. lacissimum</i> Bitter	lxs	PER	2x(2EBN) ¹¹	Hawkes 1990
<i>S. leptophyes</i> Bitter	lph	BOL, PER	2x(2EBN)/4x(4EBN) ¹⁷	Hawkes 1990
<i>S. leptosepalum</i> Correll	lps	MEX, USA		
<i>S. lesteri</i> Hawkes and Hjert.	les	MEX	2x	Hawkes 1990
<i>S. lignicaule</i> Vargas	lgl	PER	2x(1EBN) ¹¹	Hawkes 1990
<i>S. limbaniense</i> Ochoa	lmb	PER	2x(2EBN) ¹¹	Ochoa 1999
<i>S. xlitusinum</i> Ochoa (ber × tar)	lit	BOL	2x(2EBN)	Ochoa 1992
<i>S. lobbianum</i> Bitter	lbb	COL	4x(2EBN)	Ochoa 1992
<i>S. longiconicum</i> Bitter	lgc	CRI, PAN	4x	Hawkes 1990
<i>S. longiusculus</i> Ochoa	lgs	PER	2x	Ochoa 1999
<i>S. lopez-camarenae</i> Ochoa	lpc	PER	2x(1EBN)	Ochoa 1999
<i>S. macropilosum</i> Correll	mcp	MEX		
<i>S. maglia</i> Schltdl.	mag	CHL	2x, 3x	Hawkes 1990
<i>S. marinasense</i> Vargas	mrn	PER	2x(2EBN) ¹¹	Hawkes 1990
<i>S. matehualae</i> Hjert. and T. R. Tarn	mat	MEX	4x	Hawkes 1990
<i>S. medians</i> Bitter	med	PER	2x(2EBN), 3x	Hawkes 1990
var. <i>autumnale</i> Correll	aut	PER	2x(2EBN) ¹¹	Hawkes 1999
var. <i>medians</i>	med	PER		
<i>S. megistacrolobum</i> Bitter	mga	ARG, PER, BOL	2x(2EBN)	Hawkes 1990
subsp. <i>megistacrolobum</i>	mga			
f. <i>megistacrolobum</i>	mga			
f. <i>purpureum</i> Ochoa	prp	PER	2x	Salas <i>et al.</i> in press
subsp. <i>toralapanum</i> (Cárdenas and Hawkes) R. B. Giannattasio and D. M. Spooner	tor	ARG, PER, BOL	2x(2EBN) ¹¹	Hawkes 1990
<i>S. xmihoacanum</i> (Bitter) Rydb. (blb × pnt)	mch	MEX	2x	Hawkes 1990
<i>S. microdontum</i> Bitter	mcd	ARG, BOL	2x(2EBN), 3x	Moscone 1992; Hawkes 1990
var. <i>microdontum</i>	mcd			
var. <i>montepuncoense</i> Ochoa (mcd × vio)	mon	BOL	2x	Hawkes 1990
<i>S. minutifolium</i> Correll	min	ECU	2x(1EBN)	Ochoa 1992

TABLE 4—Cont.

Taxon (putative hybrid origins) ¹	Code ²	Country ³	Ploidy and (EBN) ⁴	Reference for ploidy and EBN
Wild Species				
<i>S. mochiquirense</i> Ochoa	mcq	PER	2x(1EBN)	Hawkes 1990
<i>S. morelliforme</i> Bitter and G. Muench	mrl	MEX, GUA, HON	2x	Hawkes 1990
<i>S. moscopanum</i> Hawkes	msp	COL	6x(4EBN)	Hawkes 1990
<i>S. multiinterruptum</i> Bitter	mtp	PER	2x(2EBN) ¹¹	Hanneman 1994
var. <i>machaytambinum</i> Ochoa	mac	PER	2x(2EBN)	Hawkes 1990
var. <i>multiinterruptum</i>	mtp			
f. <i>albiflorum</i> Ochoa	alf	PER	2x	Salas <i>et al.</i> in press
f. <i>multiinterruptum</i>	mtp			
<i>S. nayaritense</i> (Bitter) Rydb.	nyr	MEX		
<i>S. nemorosum</i> Ochoa	nmr	PER	6x(4EBN) ¹⁸	Ochoa 1992
<i>S. neocardenasii</i> Hawkes and Hjert. ncd	BOL	2x	Hawkes 1990	
<i>S. neorosii</i> Hawkes and Hjert.	nrs	ARG	2x	Hawkes 1990
<i>S. neovalenzuelae</i> L. López	nvz	COL	4x	Hawkes 1990
<i>S. neovargasii</i> Ochoa	nvg	PER	2x	Ochoa 1999
<i>S. neovavilovii</i> Ochoa	nvv	PER	2x(2EBN)	Ochoa 1992
<i>S. ×neoweberbaueri</i> Wittm. ¹⁰ (med × chn)	nwb	PER	3x ²⁰	Hawkes 1990
<i>S. nubicola</i> Ochoa	nub	PER	4x(2EBN)	Ochoa 1992
<i>S. okadae</i> Hawkes and Hjert.	oka	ARG, BOL	2x	Hawkes 1990
<i>S. olmosense</i> Ochoa	olm	ECU, PER	2x(2EBN) ¹¹	Ochoa (1992b, 1999) cited this species as 2x(1EBN) but Ochoa (1993) as 2x(2ENB)
<i>S. oplocense</i> Hawkes	opl	ARG, BOL	2x(2EBN), 4x(4EBN), 6x(4EBN)	Hawkes 1990
<i>S. orocense</i> Ochoa	oro	COL		
<i>S. orophilum</i> Correll	orp	PER	2x(2EBN) ¹¹	Ochoa 1992
<i>S. ortegae</i> Ochoa	ort	PER	2x	Ochoa 1998
<i>S. otites</i> Dunal	oti	COL, VEN		
<i>S. oxycarpum</i> Schiede	oxc	MEX	4x(2EBN)	Hawkes 1990
<i>S. palustre</i> Poepp.	pls	ARG, CHL	2x(1EBN)	Moscone 1992; Hawkes 1990; Valkonen 1994
<i>S. pampasense</i> Hawkes	pam	PER	2x(2EBN)	Hawkes 1990
<i>S. pamplonense</i> L. López	ppl	COL	4x	Hawkes 1990
<i>S. papita</i> Rydb.	pta	MEX	4x(2EBN)	Hawkes 1990
<i>S. paucijugum</i> Bitter	pcj	ECU	4x(2EBN)	Ochoa 1993
<i>S. paucissectum</i> Ochoa	pcs	PER	2x(2EBN)	Hawkes 1990
<i>S. peloquinianum</i> Ochoa	plq	PER	2x(2EBN) ¹¹	Ochoa 1992
<i>S. pillahuatense</i> Vargas	pll	PER	2x(2EBN)	Ochoa 1992
<i>S. pinmatisectum</i> Dunal	pnt	MEX	2x(1EBN)	Hawkes 1990
<i>S. piurae</i> Bitter	pur	PER	2x(2EBN)	Ochoa 1992
<i>S. polyadenium</i> Greenm.	pld	MEX	2x	Hawkes 1990
<i>S. polytrichon</i> Rydb.	plt	MEX	4x(2EBN)	Hawkes 1990
<i>S. puchupuchense</i> Ochoa	pch	BOL, PER	2x	Ochoa 1999
<i>S. raphanifolium</i> Cárdenas and Hawkes	rap	PER	2x(2EBN) ¹¹	Hawkes 1990
<i>S. raquialatum</i> Ochoa	raq	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. ×rechei</i> Hawkes and Hjert. (ktz × mcd)	rch	ARG	2x, 3x	Clausen and Spooner 1998
<i>S. regularifolium</i> Correll	rgf	ECU	2x	Ochoa 1993
<i>S. rhomboideilanceolatum</i> Ochoa ²¹	rhl	PER	2x(2EBN)	Ochoa 1999
<i>S. ×ruiz-lealii</i> Brücher (che × ktz)	rzl	ARG		
<i>S. salasianum</i> Ochoa	sls	PER	2x	Ochoa 1989b
<i>S. ×sambucinum</i> Rydb. (ehr × pnt)	smb	MEX	2x	Hawkes 1990
<i>S. sanctae-rosae</i> Hawkes	sct	ARG	2x(2EBN)	Hawkes 1990
<i>S. sandemanii</i> Hawkes	snd	PER	2x(2EBN)	Hawkes 1990
<i>S. santolallae</i> Vargas	san	PER	2x(2EBN)	Ochoa 1999
<i>S. sarasarae</i> Ochoa	srs	PER	2x(2EBN)	Ochoa 1999
<i>S. sawyeri</i> Ochoa	swy	PER	2x(2EBN)	Ochoa 1999
<i>S. saxatilis</i> Ochoa	sax	PER	2x(2EBN)	Ochoa 1999
<i>S. scabrifolium</i> Ochoa	scb	PER	2x	Ochoa 1999
<i>S. schenckii</i> Bitter	snk	MEX	6x(4EBN) ²²	Hawkes 1990
<i>S. ×semidissimulatum</i> Juz. (dms × ver)	sem	MEX	6x	Hawkes 1990
<i>S. ×setulosistylum</i> Bitter (che × spg)	stl	ARG	2x	Hawkes 1990
<i>S. simplicissimum</i> Ochoa	smp	PER	2x(1EBN)	Ochoa 1999
<i>S. soestii</i> Hawkes and Hjert.	sst	BOL	2x	Hawkes 1990

TABLE 4—Cont.

Taxon (putative hybrid origins) ¹	Code ²	Country ³	Ploidy and (EBN) ⁴	Reference for ploidy and EBN
Wild Species				
<i>S. sogarandinum</i> Ochoa	sgr	PER	2x(2EBN) ¹¹ , 2n = 36	Hawkes 1990; Ochoa 1999
<i>S. solisii</i> Hawkes	sol	ECU		
<i>S. sparsipilum</i> (Bitter) Juz. and Bukasov	spl	BOL, PER	2x(2EBN) ¹¹	Hawkes 1990
<i>S. spegazzinii</i> Bitter	spg	ARG	2x(2EBN)	Hawkes 1990
<i>S. stenophyllidium</i> Bitter	sph	MEX	2x(1EBN)	Hanneman 1994
<i>S. stoloniferum</i> Schtdl. and Bouchet	sto	MEX	4x(2EBN)	Hawkes 1990
subsp. <i>moreliae</i> Hawkes	mia	MEX		
subsp. <i>stoloniferum</i>	sto			
<i>S. subpanduratum</i> Ochoa	sup	VEN	4x	Hawkes 1990
<i>S. xsucrense</i> Hawkes (adg × opl)	scr	BOL	4x(4EBN)	Hawkes 1990
<i>S. sucubunense</i> Ochoa	suc	COL		
<i>S. tacnaense</i> Ochoa	tcn	PER	2x(2EBN) ¹¹	Ochoa 1992
f. <i>decurrentialanum</i> (Ochoa) Correll	dec	PER	2x	Ochoa 1999
f. <i>tacnaense</i>	tcn			
<i>S. tapojense</i> Ochoa	tpj	PER	2x(2EBN)	Ochoa 1999
<i>S. tarapatunum</i> Ochoa	trp	PER	2x ²³	Ochoa 1999
<i>S. tarijense</i> Hawkes	tar	ARG, BOL	2x(2EBN)	Hawkes 1990
<i>S. tarnii</i> Hawkes and Hjert.	trn	MEX	2x	Hawkes 1990
<i>S. taulisense</i> Ochoa	tau	PER	2x(2EBN) ²⁴	Ochoa 1992
<i>S. trifidum</i> Correll	trf	MEX	2x(1EBN)	Hawkes 1990
<i>S. trinitense</i> Ochoa	trt	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. tundalomense</i> Ochoa	tnd	ECU	6x(4EBN)	Ochoa 1993
<i>S. tuquerrense</i> Hawkes	tuq	COL, ECU	4x(2EBN)	Hawkes 1990
<i>S. ugentii</i> Hawkes and K. A. Okada	ugt	BOL	4x	Hawkes 1990
<i>S. urubambae</i> Juz.	uru	PER	2x(2EBN)	Ochoa 1992
f. <i>chakchabambense</i> Ochoa	chk	PER	2x	Ochoa 1999
f. <i>urubambae</i>	uru			
f. <i>velutinum</i> (Correll) Ochoa	vel	PER		
<i>S. xvallis-mexici</i> Juz. (sto × ver)	vll	MEX	3x	Hawkes 1990
<i>S. velardei</i> Ochoa	vlr	PER	2x	Ochoa 1999
<i>S. venturii</i> Hawkes and Hjert.	vnt	ARG	2x(2EBN)	Hawkes 1990
<i>S. vernei</i> Bitter and Wittm.	vrn			
subsp. <i>ballsii</i> (Hawkes) Hawkes and Hjert.	bal	ARG	2x(2EBN)	Hawkes 1990
subsp. <i>vernei</i>	vrn	ARG	2x(2EBN)	Hawkes 1990
<i>S. verrucosum</i> Schtdl.	ver		2x(2EBN)	Hawkes 1990
<i>S. vidaurrei</i> Cárdenas	vid	ARG, BOL	2x(2EBN)	Hawkes 1990 (as <i>S. gourtayi</i> subsp. <i>vidaurrei</i> (Cárdenas) Hawkes and Hjert.)
<i>S. xviirsoii</i> K. A. Okada and A. M. Clausen (acl × ifd)	vrs	ARG	3x	Hawkes 1990
<i>S. violaceimarmoratum</i> Bitter	vio	BOL	2x(2EBN)	Hawkes 1990
<i>S. virgultorum</i> (Bitter) Cárdenas and Hawkes	vrg	BOL	2x	Hawkes 1990
<i>S. wittmackii</i> Bitter	wtm	PER	2x(1EBN) ¹¹	Ochoa 1992
<i>S. woodsonii</i> Correll	wds	PAN		
<i>S. yamobambense</i> Ochoa	ymb	PER	2x	Ochoa 1999
<i>S. yungasense</i> Hawkes	yun	BOL, PER	2x(2EBN) ¹¹	Ochoa 1999
Cultivated Species²⁵				
<i>S. ajanhuiri</i> Juz. and Bukasov (mga × stn)	ajh	BOL, PER	2x	Hawkes 1990
<i>S. chaucha</i> Juz. and Bukasov (stn × adg)	cha	BOL, PER	3x	Hawkes 1990
<i>S. curtilobum</i> Juz. and Bukasov (juz × adg)	cur	BOL, PER	4x(4EBN), most 5x	Hawkes 1990; Hawkes 1990
<i>S. juzepczukii</i> Bukasov (acl × stn)	juz	BOL, PER	3x	Hawkes 1990
<i>S. phureja</i> Juz. and Bukasov	phu			Hawkes 1990
subsp. <i>hygrothermicum</i> (Ochoa) Hawkes	hyg	PER	4x	Hawkes 1990
subsp. <i>phureja</i>	phu	widespread Andes	2x(2EBN)	
<i>S. stenotomum</i> Juz. and Bukasov	stn			
subsp. <i>goniocalyx</i> (Juz. and Bukasov) Hawkes	gon	PER	2x(2EBN)	Hawkes 1990
subsp. <i>stenotomum</i>	stn	BOL, PER	2x(2EBN)	Hawkes 1990
<i>S. tuberosum</i> L.	tbr			
subsp. <i>andigena</i> (Juz. and Bukasov) Hawkes subsp. <i>tuberosum</i>	adg	widespread in the Andes	4x(4EBN)	Hawkes 1990
	tbr	CHL (native), introduced worldwide and/or evolved from adg in Europe	4x(4EBN)	Hawkes 1990

¹Author abbreviations are standardized by Brummitt and Powell (1992). Putative hybrid origins are from Hawkes (1990), or by Ochoa (1999) for *S. xarahuayum*, *S. xblanco-galdosii*, and *S. xneoweberbaueri*. The proper form of hybrid taxa designated by a single epithet is to place a multiplication sign against the initial letter of the specific epithet, without change in authorship if the name originally was described as a non-hybrid taxon (International Code of Botanical Nomenclature, Recommendation H.3A.1 [Greuter *et al.* 1999]). See also note 19.

²Species and subspecies codes follow Simmonds (1963), Huamán (1985), Hawkes (1990), or authors of new taxa in the original descriptions. Codes in **bold italic** are first provided here.

³Country abbreviations are: ARG, Argentina; BOL, Bolivia; BRA, Brazil; CHL, Chile; COL, Colombia; CRI, Costa Rica; ECU, Ecuador; GTM, Guatemala; HON, Honduras; MEX, Mexico; PAN, Panama; PER, Peru; USA, United States of America; VEN, Venezuela.

⁴New ploidy and EBN determinations are listed from the compilation of Hawkes (1990) who compiled them mainly from Hanneman and Bamberg (1986; later published in Hanneman 1994), with later additions provided by Ochoa (1992, 1993, 1999). If a prior count of ploidy was followed by a ploidy and EBN combination, the latter reference is listed.

⁵Taxonomic authorities are not needed for autonyms.

⁶Ochoa (1990) synonymized *S. acaule* var. *punae* (Juz.) Hawkes under *S. acaule* var. *acaule*. Kardolus (1998) recognized *S. acaule* subsp. *punae* and the other subspecies listed above based on Amplified Fragment Length Polymorphism (AFLP) data.

⁷An EBN has not been published for this species, but Ochoa (1990) showed it to be compatible with other 2x(2EBN) species.

⁸In agreement with Hawkes (1990) we maintain this species despite its synonymy under *S. chacoense* by Ochoa (1990) because our experience in Bolivia (Spooner *et al.* 1993) and the NRSP-6 genebank suggests that its yellowish corollas distinguish it from *S. chacoense* (with pure white corollas).

⁹Ochoa (1990) lists this species as *S. candelarianum* Cárdenas, but this is an invalid name because of the earlier homonym *S. candelarianum* Bukasov.

¹⁰Ochoa (1999) did not designate an EBN of this species but showed successful crosses with other 2x(2EBN) species.

¹¹Ochoa (1999) reported crosses matching EBN expectations and crosses not matching EBN expectations, as based on the formation of seeds produced in the F₁.

¹²Listed in Hawkes invalidly as *S. quillonanum* Ochoa.

¹³Ochoa (1992, 1999) reported this species as 2x(2EBN) but Ochoa (1999) reported crosses with this species and other 2x(2EBN) species to be incompatible. The only successful cross he reported was with *S. incahuasinum*, 2x(1EBN).

¹⁴Ochoa reported this species as 2x(1EBN) despite the fact that no crosses could be made with any other species.

¹⁵Hawkes (1989) provides the correct orthographic correction of this species, and the associated series, originally incorrectly spelled as *S. ingaeifolium* (Ochoa 1959) and series *Ingaeifolium* (Ochoa 1962) to series *Ingifolia* and *S. ingifolium* (Article 60.8, International Code of Botanical Nomenclature [Greuter *et al.* 1999]). Ochoa (1999, p. 262) maintains the incorrect original spellings for reasons not in conformance with the code.

¹⁶Hawkes (1990) reported the ploidy as 2x, conflicting with 6x(4EBN) for Ochoa. We could not find reference to Hawkes's ploidy in any publication and it possibly is in error.

¹⁷Ochoa (1990) synonymized *S. gourlayi* (and *S. pachytrichum*) under *S. leptophyes*, yet listed only a diploid count for this species. Both 2x(2EBN) and 4x(4EBN) are known for *S. gourlayi* and are listed here.

¹⁸Ochoa reported this species as 6x(4EBN) despite the fact that no crosses could be made with any other species.

¹⁹The correct authorship of this species is as above, not *S. xneoweberbaueri* (Wittm.) Ochoa (International Code of Botanical Nomenclature, Article H.3.3 [Greuter *et al.* 1999]).

²⁰Ochoa (1999) demonstrated that despite its triploid ploidy, crosses were successful with other 2x(2EBN) species.

²¹Ochoa (1999) provided an invalid orthographic correction of this name to *S. rhombilanceolatum* Ochoa, without explanation. Recommendation 60G.1 of the International Code of Botanical Nomenclature (Greuter *et al.* 1999) explains proper orthography of names, and it is converted to the status of a mandatory article by Article 60.8. The original spelling was valid and cannot be changed.

²²Neither Hawkes (1990) nor Hanneman (1994) designates an EBN for this species, but its designation as 6x(4EBN) appears in Bamberg and Martin (1993) and Bamberg *et al.* (1996). Hanneman indicates (per S. comm.) that his unpublished data support 6x(4EBN).

²³Ochoa (1999) did not designate a chromosome count or EBN for this species, and demonstrated unilateral compatibility with the 2x(2EBN) species *S. phureja*. We checked a germplasm collection at NRSP-6 identified by Ochoa (1999) as *S. tarapatanum* (Ochoa 2064). It is not this species but *S. sparsipitum* (PI 230502).

²⁴Ochoa (1992) designated this species as 2x(2EBN) but Ochoa (1999) only as 2x.

²⁵Our list excludes *S. parvicorollatum* Lechn., included by Hawkes (1990) in the list of wild Peruvian species, but as a possible escape of a cultivated species. Ochoa (1999) does not list *S. parvicorollatum* and it likely is a cultivated escape. Following Hawkes (1990) our list also maintains *S. hygrothermicum* as a subspecies of *S. phureja*. Ochoa (2000) lists this little known taxon as a good species, but we await his forthcoming treatment of the Peruvian cultigens (see Ochoa 1999).

of reduction of fertility. An understanding of the nature and extent of hybridization and introgression is useful taxonomically to explain patterns of variation that may lead to the difficult taxonomy of the group.

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

Solanum raphanifolium. Spooner *et al.* (1991d) reexamined, with cpDNA and nrDNA restriction site data, the hypothe-

ses of Ugent (1970b) that the Peruvian diploid species *S. raphanifolium* was of recent and ongoing hybrid origin between diploid *S. canasense* and *S. megistacrolobum*. The species is morphologically intermediate between the putative parents and occurs where the two species overlap in distribution. The expectation of a recent hybrid was for it to have identical or similar cpDNA (maternally inherited) of the maternal parent and to have an additive profile of nrDNA (biparentally-inherited). *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. Giannattasio and Spooner (1994b) examined these species with

nRFLPs and lack of an additive profile in *S. raphanifolium* likewise failed to support hybridization.

Solanum ×rechei—Clausen and Spooner (1998) reexamined the putative hybrid origin of *S. ×rechei* (with diploid and triploid populations), hypothesized by Hawkes and Hjerting (1969) and Okada and Hawkes (1978) to be of hybrid origin between diploid *S. kurtzianum* and *S. microdontum*. Like *S. raphanifolium*, it occurred at the overlap zone of its two parents. In addition, it had reduced fertility in comparison to natural and artificially constructed hybrids. Additive profiles of nRFLPs gave strong support to its hybrid origin. Its hybrid origin also was noted by Brücher (1989), who criticized the creation of a formal taxonomic name for this hybrid.

Solanum sparsipilum, *S. stenotomum*—Rabinowitz *et al.* (1990) tested hypotheses of gene flow between the diploid wild species, *S. sparsipilum*, and the diploid cultivated species *S. stenotomum*. By use of isozyme markers specific to these populations, they were able to document high levels of natural gene flow in experimental field plots in the Andes. They used these data to speculate extensive gene flow among other cultivated and wild species. 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) regarding the effect of gene flow on cultivated species evolution. Similarly, Debener *et al.* (1991) used phenetic analyses of nRFLPs to support incorporation of wild species germplasm into cultivated species.

Fingerprinting and Diversity Studies

Over this review period there has been rapid progress in molecular technologies that have been tested and applied to questions of potato intraspecific diversity and fingerprinting. Fingerprinting is the use of hypervariable markers to generate DNA patterns unique to individuals, with applications of unambiguous genotype identifications and plant variety protection. Most studies have addressed the cultivated species and, unlike many of the above, generally did not lead to taxonomic changes, but rather to an understanding of morphological or genetic diversity. They have potential application in genetic resources conservation and variety identification and protection.

Nuclear Restriction Fragment Length Polymorphisms—Nuclear RFLPs were one of the first DNA techniques developed, and continue to provide useful data at the species and intraspecific levels. Probes used vary from genomic to cDNA (complementary DNA) probes, and from single- to multiple-copy. Gebhardt *et al.* (1989) showed the ability to fingerprint 20

tetraploid potato varieties and 38 diploid potato lines with only two probe-enzyme combinations, and one system was sufficient to distinguish all of these except for six varieties that showed identical patterns. Estimated heterozygosity was much greater in diploid than in tetraploid genotypes. Görg *et al.* (1992) showed that 130 of the 136 potato genotypes could be fingerprinted with four probe-enzyme combinations, and one probe-enzyme combination fingerprinted 128 of them. Douches *et al.* (1991) was able to fingerprint 40 *S. tuberosum* genotypes with a minimum of two probe-enzyme combinations. Powell *et al.* (1991) distinguished 27 *S. tuberosum* genotypes with two probe-enzyme combinations.

Amplified Fragment Length Polymorphisms—Kim *et al.* (1998) evaluated seven AFLP primer combinations to fingerprint and classify 12 *S. tuberosum* genotypes. Any one of these primer combinations distinguished all genotypes. Phenetic analysis of these data, however, did not always reflect known genetic relationships of the genotypes, suggesting that although fingerprinting was efficient, their use at this taxonomic level to elucidate pedigrees was limited.

Random Amplified Polymorphic DNAs—All the RAPD studies described below used decamer primers. Mori *et al.* (1993) distinguished 36 *S. tuberosum* genotypes released in Japan and three introduced genotypes with five RAPD primers. Hosaka and Ogawa (1994) assessed genetic diversity of eight Japanese and eight North American potato processing genotypes with 14 RAPD primers. Similar levels of diversity were shown among these two geographic samples. Quiros *et al.* (1993) demonstrated Mendelian segregation ratios and mapped RAPD loci in diploid (12 loci) and tetraploid (18 loci) crosses of cultivated potato, demonstrating their use in potato genetics, breeding, and diversity studies. Hosaka *et al.* (1994) were able to distinguish 67 of 73 examined Japanese *S. tuberosum* breeding lines and cultivars with 31 polymorphic and scoreable RAPD primers. Phenetic analyses of their data generally grouped genotypes that are related based on pedigree. Oganisyan *et al.* (1996) fingerprinted eight *S. tuberosum* genotypes from Armenia with eight RAPD primers. Demeke *et al.* (1996) examined 28 *S. tuberosum* genotypes and three parental species of six progeny, using 12 RAPD primers. Results of phenetic analyses generally reflected relationships based on pedigree data, but with notable exceptions. They suggested that RAPDs provided additional data in such cases to select genetically divergent parents to maximize heterozygosity in breeding programs.

Sosinski and Douches (1996) examined 46 North American *S. tuberosum* genotypes, both sexually and clonally derived,

with 16 RAPD primers. Ten primers distinguished all 46 genotypes, but when these were grouped by tuber type, only three to four primers were needed for discrimination. As in the above studies, phenetic relationships based on RAPDs were not always concordant with pedigree relationships. Ghislain *et al.* (1999) examined the entire CIP collection of *S. phureja* (128 accessions) with RAPDs. Their results showed no clear geographic pattern of variability. They used their results to select a provisional core subset of 20 accessions to be later compared with other molecular markers and agronomic traits.

Del Rio *et al.* (1997a) used RAPDs to measure the loss of diversity in genebank samples of wild potatoes after one to four cycles of seed increase. The majority of the populations showed no significant or only very little loss, and they suggested that the seed increase methodology they used (using 20 individuals and pollinating from bulked pollen) was an appropriate seed increase strategy. Del Rio *et al.* (1997b) used RAPDs to measure genetic differences between genebank samples subjected to one cycle of seed increase and recollections from the original site of collections in the wild. These collections showed significant differences that could be due to genetic drift, gene flow from adjacent populations, or differences in sampling in the wild. Del Rio *et al.* (2001) examined ecogeographical correlates (altitude, geographic distance, soil type, temperature, rainfall) to two wild potato species (*S. fendleri*, *S. jamesii*) in the United States. They found that no single factor was correlated with genetic distance. In *S. fendleri*, however, there was a very low correlation of genetic diversity to both geographic distance and temperature.

Microsatellites—Simple sequence repeats (SSRs or microsatellites) are hypervariable markers of great potential use to distinguish genetically similar material. They typically produce fewer bands per primer than AFLPs or RAPDs. As discussed below, more primer pairs are being developed and mapped that are increasing their availability and use. Schneider and Douches (1997) used seven primer pairs flanking di- and trinucleotide SSR repeats in 39 *S. tuberosum* genotypes released between 1861 and 1988 and one diploid *S. phureja* breeding line. One primer pair yielded no fragments and the other was monomorphic. The remaining five pairs produced one to two bands per genotype, but up to four within the whole germplasm set. These five primers distinguished 24 of the 40 genotypes, but with additional data from tuber morphology, only five pairs of genotypes remained indistinguishable.

Provan *et al.* (1996a) developed 19 primer pairs that successfully amplified bands in a set of 18 *S. tuberosum* genotypes, and four sets developed for tomato were used. Seven of these

22 primer pairs were monomorphic within the 18 genotypes, and the remaining 15 revealed from two to 19 alleles at a locus. Phenetic analysis of the data resulted in groupings not consistent with co-ancestry, and the authors concluded that microsatellites had greater utility for fingerprinting than for deducing relationships. Milbourne *et al.* (1998) greatly extended the microsatellite markers available in potato by developing and mapping 65 primer pairs in *S. tuberosum*. They showed that 52 of them were clearly single locus markers. They assigned them quality scores based on ease and clarity of generation and scoring.

Bryan *et al.* (1999) developed 36 mononucleotide chloroplast SSR primers of the Solanaceae by inspection of the published sequence of tobacco. Of these 36, 26 showed polymorphism in 30 *S. tuberosum* genotypes and additional wild species. A single cpDNA haplotype was prevalent in some of the genotypes, suggesting widespread use of a limited gene pool of female genotypes for breeding. Other more divergent genotypes grouped with wild species, suggesting introgression of these species in breeding.

Inter-simple Sequence Repeats—Provan *et al.* (1996b) examined 12 *S. tuberosum* genotypes with two 5' anchored repeat Inter-Simple Sequence Repeat (ISSR) primers. These generated 24 polymorphic bands (eight with one set, 16 with the other set). One primer was sufficient to differentiate all 12 genotypes. A phenetic analysis of these data showed areas of concordance and discordance based on pedigree data. Prevost and Wilkinson (1999) showed two of four ISSR primers distinguish all 34 *S. tuberosum* genotypes.

Nuclear Ribosomal RFLPs—Harding (1991) examined two *S. tuberosum* genotypes with nrDNA RFLPs, using a probe from wheat, using radioactive techniques. The genotypes differed by the length of the intergenic spacer, the most variable region of the ribosomal repeat motif. Harding (1992) speculated that this technique would be useful for genotype identification. Harding (1992) examined the same two genotypes for nrDNA RFLPs, but developed a chemiluminescence technique for fragment detection that matched the radioactive technique patterns. We are not aware of any later studies that used nrDNA RFLPs for characterization of a wider cultivated potato germplasm base.

Chloroplast DNA—Chloroplast DNA has too little variation for fingerprinting, but it has been examined within *S. tuberosum* collections. Waugh *et al.* (1990) discovered four cpDNA restriction site phenotypes in 27 *S. tuberosum* genotypes using cloned probes covering the entire cpDNA molecule, using four restriction enzymes. Hosaka (1993) discovered three cpDNA types (that he labeled as A, T, W) among 68 Japanese genotypes. Many

named and unnamed genotypes had T type, common to old European introductions and to native genotypes in southern Chile (Hosaka and Hanneman 1988). Others had W type and that derived from *S. demissum*, and four old varieties had a putatively ancestral A type. Powell *et al.* (1993) studied 56 European *S. tuberosum* genotypes, and likewise identified three cpDNA types, of which T type was the most common.

Enzymes—Huamán and Stegemann (1989) used isozymes (esterases, peroxidases), tuber proteins, and morphological data to characterize a collection of 15,000 accessions of all cultivated potato species at CIP. Combined data sets allowed a reduction of duplicates to 3500 genotypes. Macias-M. *et al.* (1989) examined a collection of 231 genotypes of Chilean *S. tuberosum* with esterases and tuber proteins to identify 42 unique genotypes. Douches and Ludlam (1991) assayed 112 named *S. tuberosum* genotypes and advanced breeding lines with 13 enzyme systems. All genotypes generated by hybridization could be distinguished by electrophoretic patterns, but clonally derived sports or line selections could not be distinguished.

Huamán *et al.* (2000c) compared isozyme diversity of the entire non-duplicate CIP collection of 2379 accessions of Andean *S. tuberosum* with that of a core subset of 306 of these accessions, chosen by morphological, geographical, disease, and pest-resistance criteria (Huamán *et al.* 2000b). The core subset contained all 38 allozymes of the entire collection except two rare ones, and there was a similar distribution of allozyme frequencies in both collections. In other words, their core collection was as good as a random sample of the entire collection.

Quiros *et al.* (1992) surveyed isozymes of 542 tubers from diploid, triploid, and tetraploid potatoes obtained from markets in southern Peru, and identified 229 unique isozyme patterns. Cluster analysis grouped them into four major groups and six minor groups, but these did not correlate with groups based on flesh and skin color. They concluded that genotypes at all ploidy levels belonged to one gene pool with considerable gene flow within and among ploidy levels.

Zimmerer and Douches (1991) studied six landraces of diploid (*S. stenotomum*) and tetraploid (*S. tuberosum*) potato genotypes from three micro-regions to assess partitioning of genetic diversity by geographic locations and within landraces. They discovered that 99% of the diversity was found within single microregions, and 75% of the diversity occurred within individual landraces. High rates of tuber exchange explained weak geographical partitioning.

Brush *et al.* (1995) studied the diversity and population structure of cultivated potato landraces of different species and

ploidy levels. They examined 610 tubers from eight fields in southern Peru and 503 tubers from nearby markets. They identified 30 genotypes in the field samples and 82 in the market samples. They found that genotypes were unevenly distributed, with most diversity between, rather than within fields. They used these data to design germplasm collecting strategies.

Seed Proteins—Hosaka and Hanneman (1991) examined the relationship between ploidy level and breeding system and genetic variation within wild and cultivated potatoes, including an inbred population of the wild species *S. chacoense*, through an analysis of soluble seed proteins. They showed that self-compatible species had less heterozygosity than self-incompatible species, and that natural diploids possess less heterozygosity than natural tetraploids. Artificially inbred *S. chacoense* had greatly reduced diversity relative its natural parental population.

Multiple Marker Studies—Different data sets frequently give incongruent results (Wendel and Doyle 1998), and some studies in potato have used a combination of markers for analysis. Quiros *et al.* (1990) examined the relationship between isozyme phenotypes and putatively unique cultigens in southern Peru as determined by indigenous Andean farmer names. They discovered that an electrophoretic phenotype predicted names, but that names could have a variety of electrophoretic phenotypes, resulting in an underestimation of diversity if names were used as a proxy for diversity. In addition, their study showed greater isozyme variability in Andean genotypes than in North American and European phenotypes.

Cisneros and Quiros (1995) grouped 94 accessions of the cultivated triploid genotype *S. chaucha* with isozymes and RAPDs, which they compared to morphological groups of Ochoa (1975) and Jackson *et al.* (1977). A total of eight groups could be distinguished by isozymes, and ten groups by a combination of both datasets, and a single RAPD primer was sufficient to distinguish all ten groups. Isozyme and RAPD groups were largely concordant among each other, but much less so to the morphological classifications. RAPDs were judged to be more reliable than isozymes or morphology to classify these accessions.

Mandolino *et al.* (1996) examined eight *S. tuberosum* cultivars and breeding clones and in-vitro cultures from two cultivars of *S. tuberosum* with nRFLPs and RAPDs. Two probe-enzyme RFLP combinations and three RAPDs were able to distinguish all germplasm. Cultivars and their in-vitro derived cultures were identical with nRFLPs, but showed some variation with RAPDs.

Milbourne *et al.* (1997) examined heterozygosity (polymorphism of individual bands), multiplex ratios (number of mark-

ers per probe or primer combination), and concordance of phenetic results for AFLPs, RAPDs, and nSSRs, for 16 *S. tuberosum* genotypes. The multiplex ratios were calculated from the number of bands simultaneously analyzed per experiment, i.e., the number of bands resolved on a particular gel. The marker index was the product of a heterozygosity and multiplex ratio and was an overall measure of efficiency of any system to detect heterozygosity. The average heterozygosity increased from AFLP and RAPD (similar in magnitude) <nRFLP<nSSR. The effective multiplex ratio increased from nRFLP<nSSR<RAPD<AFLP. The marker index in this study increased from nSSR<RAPD<AFLP. All three markers showed low correlation, but the best was between AFLP and RAPD.

Spooner *et al.* (1996) examined cpDNA, isozymes, nRFLPs, and RAPDs in all three species of *Solanum* sect. *Etuberosum*, for concordance, as a function of the number of markers per marker type. They showed that at the interspecific level there was a gradation of resolution from isozymes (low)<RAPD<nRFLP, while at the intraspecific level it was nRFLP<RAPDs.

McGregor *et al.* (2000) examined mean number of fragments per individual marker system reaction (assay unit), mean number of fragments per genotype, number of polymorphic fragments per assay unit, frequency of polymorphic fragments, mean number of polymorphic fragments per assay unit, and mean number of genetic profiles, for RAPDs, ISSRs, AFLPs, multi-locus SSRs, and single-locus SSRs, for 39 genotypes of *S. tuberosum*. Efficiency of marker system was assessed by a genotype index, or the mean number of profiles generated by primer. All marker systems could successfully distinguish the 39 genotypes, but their relative order of merit as assessed by the genotype index was AFLPs (1.0), multi-locus SSR (0.77), RAPDs (0.53), ISSRs (0.47) and single-locus SSRs (0.36).

CONCLUSIONS

The taxonomy of wild and cultivated potatoes has changed considerably in the last 12 years (Tables 2, 3). Knowledge of immediate outgroup relationships (Figure 1) also has changed considerably, is relatively well resolved, and likely will remain stable. The biggest future changes will come from definition of species (and subspecies and varieties), and ingroup relationships.

The series classification of Hawkes (1990) and others has received little support in any molecular marker data set used to date. Currently, only the research using cpDNA restriction sites have used representatives from most series (Spooner and

Sytsma 1992; Spooner and Castillo 1997), and the results are supporting only four clades within sect. *Petota*, not the 19 series (of 21) that have been examined. Other nuclear molecular markers also fail to provide full support for the 21 series. Corroboration of cpDNA results clearly needs support from non-chloroplast markers from a wider range of species before new taxonomic interpretations of series can be made.

Definition of species remains extremely difficult, for reasons outlined in Spooner and Van den Berg (1992b). These include great morphological similarity among species, phenotypic plasticity in different environments, sexual compatibility among many species, and hybrid speciation and introgressive hybridization. Phenetic analyses of large germplasm collections, using the very characters used to define species and other characters, often fail to support recognized species. Those that are supported are defined only by a range of overlapping character states, with few if any species-specific characters (only polythetic support).

An example of these problems was shown by Spooner and Van den Berg (1992a), who showed that Hawkes and Hjerting (1989) and Ochoa (1990a) provided different identifications for identical collection numbers of Bolivian members of the *Solanum brevicaulis* complex 36% of the time. Morphological phenetics of the group by Van den Berg *et al.* (1998) and nRFLP and RAPD results of the same accessions (Miller and Spooner 1999) likewise showed difficulty to support these species. These results, and wide disagreement among different taxonomists working on the same group, suggested a need for a reduction of the number of different potato species.

Despite these problems, some difficult taxa may be well defined by taxonomic experts who were able to see differences that had escaped others. The conflicting morphological phenetics of the species in *Solanum* series *Circaeifolia* by Van den Berg and Groendijk-Wilders (1999) and RAPD and AFLP studies of the group by Van den Berg *et al.* (in press) illustrate this very clearly. The former suggested a need for reduction in taxa, and the latter supported species well. Therefore, despite cases of different identifications by different taxonomists, they have done a wonderful job of circumscription and identification of taxa.

The application of a wide range of molecular markers has addressed many questions of diversity and suitability for fingerprinting. Many markers suitable for closely related germplasm sources (i.e., AFLPs, RAPDs, SSRs) have proven utility to fingerprint varieties. Most studies of diversity and interrelationships of closely related taxa, however, have used single markers,

and corroborative data from other markers is needed for better supported phylogenetic conclusions. Cultivated species diversity does not appear to show broad-scale geographic patterns, except for differences in Chilean genotypes of *S. tuberosum*, relative to Andean genotypes of this species.

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