

GERMPLASM AVAILABILITY, SPECIES BOUNDARIES, AND
INTERRELATIONSHIPS OF WILD AND CULTIVATED POTATOES (*SOLANUM*
SECT. *PETOTA*)

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ABSTRACT

Solanum sect. *Petota*, the potato and its wild and cultivated relatives, contains 232 species, according to the latest taxonomic interpretation. Seven of these species are cultivated, and the rest are wild. The group is distributed from the southwestern United States to south central Chile, with a concentration of species in the Andes of Peru and Bolivia. There is much morphological and physiological diversity in the group. Many taxa are used in breeding programs to improve the disease resistances and agronomic traits of the world's cultivars. This diversity makes them challenging and fascinating subjects for systematic studies. Habitats range from seashore to alpine grasslands over 4500 m. Most species are diploid ($2n = 2x = 24$), but some are triploid, tetraploid, pentaploid, or hexaploid ($2n = 6x = 72$). There are some well-developed biological isolating mechanisms in the group, but many morphologically very dissimilar species placed in different taxonomic series can hybridize easily to produce fertile progeny. Many wild and cultivated species are believed to be of hybrid origin. Authors disagree regarding species boundaries, treatment of infraspecific taxa, species interrelationships, and the extent and evolutionary significance of natural interspecific hybridization.

Collecting expeditions continue to increase the germplasm resources of *Solanum* sect. *Petota*, and approximately 146 (160 taxa, including subspecies) of the 232 currently recognized species are available from genebanks. Recent morphological and molecular studies of these collections are continuing to refine our understanding of systematic relationships of the group. Integrated morphological and molecular studies are essential. Morphological studies are needed to test the taxonomic criteria and identifications of collections. Explicit morphological studies have revealed unexpected synonymy, and it is likely that the group contains fewer than 200 species. Molecular studies have used nuclear genes to address systematic questions of species boundaries, hypotheses of hybridization, and intrasectional relationships. Chloroplast DNA has been used for these types of studies, and to investigate intrasectional and intergeneric relationships. While many studies corroborate prior taxonomic interpretations, others are modifying our understanding of the group.

WILD POTATO DIVERSITY

Solanum L. sect. *Petota* Dumort., the potato and its wild and cultivated relatives, is a very diverse group. It is distributed entirely in the Americas, from the southwestern United States to south central Chile. Most species grow from 1500 m to 3500 m, but

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others grow at or near sea level, such as wild and landrace populations of *S. tuberosum* L. subsp. *tuberosum* at the southern range of the group in the Chonos and Guaitecas Archipelagos, Chile, and *S. chacoense* Bitter in eastern Argentina. Others, such as the Ecuadorian to Argentinian species *S. acaule* Bitter, can grow to elevations over 4500 m. Habitats of the group range from seashore, dry coastal desert lomas, humid tropics, dry scrub or semi-deserts, high-rainfall mountain forests, and high alpine grasslands (Hawkes, 1990).

Vegetatively, most wild species look much like the cultivated potato, with erect to ascending stems from 0.2 to 1 m tall; pinnately dissected leaves; lateral and pseudoterminal inflorescences with pentagonal to rotate, white to pink to violet to blue corollas; and globose fruits. Tubers vary in size from that of a pea to nearly the size of the cultivars. The tubers of the wild species usually are bitter, and sometimes toxic, with leaves and tubers containing medium to high levels of glycoalkaloids (Deahl et al., 1993). The wild species rarely are used as food.

Morphological diversity within sect. *Petota* includes many variations from this common form. Some species grow as low rosettes, while others are upright or recumbent with stems 2 m or more long; leaves vary from entire to narrowly dissected and eglandular or with two distinct types of glands; corollas stellate to rotate; and fruits globose to conical (Hawkes, 1990). Two species, *S. clarum* Correll and *S. morelliforme* Muench, can grow as epiphytes. This morphological diversity is paralleled by much physiological diversity of value for crop improvement. The cultivated potato is affected by many viral, bacterial, and fungal diseases, and is attacked by nematodes, insects, and affected by extremes of heat, cold, and drought. Fortunately, many wild species have moderate to extreme natural disease and stress resistances. In addition, they can impart improved agronomic traits such as increased yields and higher specific gravity of value for the potato chip industry (Hanneman, 1989; Hawkes, 1990; Hawkes & Hjerting, 1969; 1989; Plaisted & Hoopes, 1989; Ross, 1986; Spooner & Bamberg, 1994).

GERMPLASM AVAILABILITY

The economic value of sect. *Petota* has stimulated an international effort of collection and preservation of the wild species and indigenous cultivars. The major gene banks for potatoes (followed by their latest published accession-specific catalogues) include: Instituto Nacional de Tecnología Agropecuaria (INTA), Balcarce, Argentina (Okada, 1974); Universidad Austral de Chile, Valdivia, Chile (Contreras, 1980); Colección Central Colombiana, Bogotá, Colombia; Institut für Pflanzenbau und Pflanzenzüchtung, Germany (Hoekstra & Seidewitz, 1987); Landwirtschaftswissenschaften, Gross-Lüsewitz, Postleitzahl, Germany (Rothacker et al., 1991); Centro Internacional de Papa, Lima, Perú (Huamán, 1987; only the cultivated species listed); Commonwealth Potato Collection, Dundee, Scotland, United Kingdom (Wilkinson et al., 1994); The United States Potato Collection at the National Research Support Program-6 (NRSP-6, formerly known as the Inter-Regional Potato Introduction Project, IR-1 [Bamberg et al., 1993; Bamberg & Spooner, 1994]); and N. I. Vavilov Institute of Plant Industry, Leningrad, Russia (Budín et al., 1989). Recent collecting expeditions continue to increase the internationally available germplasm from Argentina (Okada, 1976; Spooner & Clausen, 1993); Bolivia (Hawkes & Hjerting, 1989; Ochoa, 1990; Spooner et al., 1994); Chile (Contreras et al., 1993; Spooner et al., 1991b); Colombia and Venezuela

(Spooner et al., 1995a); Ecuador (Spooner et al., 1992); and Mexico (Rodríguez et al., 1995; Spooner et al., 1991a). The United States Potato Collection cooperates with other genebanks in the collection, increase, and international distribution of germplasm of these species. It is the largest genebank for the wild species, and maintains 4308 accessions of 146 (160 taxa, including species) of the 232 species accepted by Hawkes (1990) (Bamberg & Spooner, 1994).

TAXONOMIC TREATMENTS

The widespread range and economic value of sect. *Petota* has stimulated much taxonomic interest in the group. Hawkes (1990) produced the latest of eight comprehensive taxonomic treatments of sect. *Petota*, and there are ten regional ones (see Spooner & van den Berg, 1992a, for a summary). In total, 72 taxonomists have described 531 validly published basionyms, plus 67 nomina dubia or nomina nuda, and subsequent transfers to other ranks raise the number of species, subspecies, and varietal names to 664 (Spooner & van den Berg, 1992a). Hawkes (1990) recognized 232 species.

These careful workers have employed various taxonomic philosophies and practices, and their treatments differ in the placement of species into series, species boundaries, rank of infraspecific taxa, and hypotheses of hybridization (Spooner & Sytsma, 1992; Spooner & van den Berg, 1992a). An example of the taxonomic difficulty can be shown from a comparison published by Spooner et al. (1994) of the two recent independent taxonomic treatments of the Bolivian potatoes by Hawkes and Hjerting (1989) and Ochoa (1990). The identifications of identical collection numbers cited in common between these two treatments, excluding types, differed in 20% of the cases. Some identifications differed more. For example, identifications differed 38% of the time among the similar species *S. brevicaulis* Bitter, *S. gourlayi* Hawkes, *S. hondelmannii* Hawkes & Hjert., *S. leptophyes* Bitter, *S. oplocense* Hawkes, *S. pachytrichum* Hawkes, *S. sucrensis* Hawkes, *S. sparsipilum* (Bitter) Juz. & Buk., and *S. vidaurrei* Cárdenas.

PLOIDY LEVELS

Solanum sect. *Petota* includes diploids ($2n = 2x = 24$), triploids, tetraploids, pentaploids, and hexaploids ($2n = 6x = 72$); natural aneuploidy is unknown. Seventy-three percent of the species with chromosome counts are diploid (Hawkes, 1990). Odd-ploidy cytotypes (diploids vs. triploids) are known for nine species, and even-ploidy cytotypes (diploids vs. tetraploids or hexaploids) are known for two species (Hawkes, 1990; Spooner et al., 1994). Many wild species produce $2n$ gametes that may have played a role in the origin of these cytotypes (Camadro & Peloquin, 1980; den Nijs & Peloquin, 1977; Ortiz & Ehlenfeldt, 1992; Watanabe & Peloquin, 1989, 1991).

ISOLATING MECHANISMS

Many species in sect. *Petota* can be easily hybridized artificially (Hawkes, 1958; Hawkes & Hjerting, 1969, 1989; Ochoa, 1990) and are believed to hybridize freely in nature. For example, Hawkes and Hjerting (1969) identified 9.5% of the specimens they examined for the potato flora of Argentina, Brazil, Paraguay, and Uruguay as hybrids,

and Hawkes and Hjerting (1989) identified 7% of the specimens examined for the potato flora of Bolivia as hybrids. Many species may be of hybrid origin (Grun, 1990; Hawkes, 1962, 1990; Ugent, 1970).

Despite this apparent ease of natural interspecific hybridization, most species boundaries are believed to be maintained by a combination of ecogeographical factors, advanced generation hybrid breakdown, genomic differences, and interspecific stylar incompatibilities (Fritz & Hanneman, 1989; Hawkes, 1990; Matsubayashi, 1991). In addition, some species are isolated by strong crossing barriers, governed by a process involving ratios of maternal/paternal effective ploidy in the endosperm, and evidenced by endosperm breakdown (the Endosperm Balance Number, or EBN hypothesis [Hanneman, 1994]). Under this hypothesis, normal seed development depends on a balance of genetic factors contributed to the endosperm from both parents. Within sect. *Petota*, species are 2x (1EBN), 2x (2EBN), 4x (2EBN), 4x (4EBN), and 6x (4EBN) (Hanneman, 1994; Hawkes & Jackson, 1992).

The predictive value of EBN has been useful to engineer interspecific crosses in potato breeding programs (Ehlenfeldt & Hanneman, 1984), and has been used to speculate on phylogenetic patterns in sect. *Petota* (Hawkes, 1994). Although EBN acts as an effective isolating mechanism between some sympatric species, the EBN barrier may have been bridged naturally by $2n$ gametes. Doubling ploidy level doubles EBN, and unilateral and bilateral sexual polyploidization may have been operative in the evolution of the polyploids (Ortiz & Ehlenfeldt, 1992).

RECENT SYSTEMATIC DISCOVERIES—MORPHOLOGICAL DATA

Most determinations of species boundaries in sect. *Petota* have been intuitive. Some have been tested by explicit morphological analyses (Clausen & Crisci, 1989; Giannattasio & Spooner, 1994a; Johns et al., 1987; Kardolus, in press; Spooner & van den Berg, 1992b; Spooner et al., 1995b; van den Berg et al., 1996; van den Berg & Spooner, 1992). Most of these studies have investigated difficult species complexes. Morphological support for taxa in these studies is usually only through multivariate approaches, and there are few, if any, species-specific morphological characters.

This lack of definitive characters poses problems for construction of keys and repeatability of identifications. This complex pattern of character state variability may be the cause of the lack of concordance of independent identifications of identical herbarium specimens mentioned above. It is unknown if such complex patterns of variability are caused by primary divergence, secondary hybridization and introgression, or a combination of both.

RECENT SYSTEMATIC DISCOVERIES—MOLECULAR DATA

The complex pattern of morphological variability in sect. *Petota* has made phylogenetic reconstructions difficult, and molecular characters are sought to provide additional insights. Hawkes (1994) and Spooner and van den Berg (1992a) review systematic studies using flavonoids, total protein electrophoresis, isozymes, immunology, chloroplast DNA (cpDNA), and single- to low-copy nuclear DNA restriction fragment length polymorphisms (nrFLPs). Flavonoid and immunological data have provided few, and often conflicting, insights into the evolution of the group. Total protein

electrophoresis (Desborough & Peloquin, 1968; Stegemann & Schick, 1985) and isozymes (Douches & Ludlum, 1991; Douches et al., 1991; Oliver & Martínez-Zapater, 1985) have helped resolve some low taxonomic-level questions of cultivar or species identity, hypotheses of hybridization, and genetic diversity. Random amplified polymorphic DNA (RAPDs) have been used for cultivar identification (Cribb & Hawkes, 1986; Demeke et al., 1993; Mori et al., 1993), and phylogeny of the cultivars (Hosaka et al., 1994).

Chloroplast DNA has resolved outgroup relationships (Spooner et al., 1993) to show that tomatoes [*Solanum* sect. *Lycopersicum* (Mill.) Wettst.] are nested within *Solanum* and are sister taxa to potatoes, and that the series *Etuberosa* Bukasov & Kameraz and series *Juglandifolia* (Rydb.) Hawkes do not belong in sect. *Petota*, as treated by Hawkes (1990). Chloroplast DNA also has helped resolve some major clades in sect. *Petota* (Hosaka et al., 1984; Spooner & Sytsma, 1992), but resolution within the clades is poor. Chloroplast DNA also has addressed questions of origin of the cultivated species (Hosaka & Hanneman, 1988a, b), and hypotheses of hybridization (Spooner et al., 1991c). Data from nRFLPs have been useful to resolve intrasectional relationships (Bonierbale et al., 1990; Debener et al., 1990), species boundaries, and hypotheses of hybridization (Debener et al., 1991; Hosaka & Spooner, 1992; Giannattasio & Spooner, 1994b), and cultivar identification (Görg et al., 1992).

It is crucial in these molecular studies to conduct parallel morphological studies to reevaluate species boundaries. Identifications in taxonomic treatments and germplasm catalogues have been provided by taxonomists with different taxonomic philosophies and practices, and some identifications will change. For example, the nRFLP study of Hosaka and Spooner (1992) used identifications in Hanneman and Bamberg (1986; superseded by Bamberg et al. [1993]). This nRFLP study distinguished all subspecies of *S. acaule* except subsp. *acaule* and subsp. *punae* (Juz.) Hawkes & Hjert. A later explicit morphological study showed misidentifications of some germplasm accessions of *S. acaule* (Kardolus, in press), and showed *S. acaule* subsp. *acaule* and subsp. *punae* to be distinguished by the nRFLP results.

DIRECTIONS FOR FUTURE SYSTEMATIC RESEARCH

Spooner and van den Berg (1992a) provided the latest suggestions for future research in sect. *Petota*. They stressed the need for explicit morphological studies of species boundaries, DNA studies to investigate species boundaries and interrelationships, a clearer use of terms to distinguish cladistic from phenetic concepts, and more controlled crossing studies with inter- and intraspecific crossing controls and statistical analyses. Additional ideas are provided below.

Solanum sect. *Petota* has been one of the most intensively studied groups of angiosperms, and therefore provides many independent data sets for comparison. An area of general systematic interest is the development of statistical methods for evaluating and comparing independent data sets (Olmstead & Sweere, 1994; Smith & Smith, 1992; Williams, 1994). Explicit morphological and molecular data sets are rapidly appearing in sect. *Petota*, and explicit comparisons of diverse results will be needed.

Chloroplast DNA, RAPDs, and nRFLPs have much potential to investigate hypotheses of hybridization (Rieseberg & Ellstrand, 1993). Such data have been used to support (Rabinowitz et al., 1990) and fail to support (Spooner et al., 1991c) such

hypotheses in sect. *Petota*. These studies need to be extended to the many other hypotheses of hybridization in sect. *Petota* (see Spooner & van den Berg [1992b] for a compilation of hybridization hypotheses in sect. *Petota*).

Comparative genome rearrangement (synteny) studies using mainly nRFLPs showed five paracentric inversions, but with conservation of gene order, in a comparison of tomato and potato (Bonierbale et al., 1988; Tanksley et al., 1992). Synteny studies are progressing within sect. *Petota*. The results will test hypotheses of genome evolution generated by cytogenetic data (Matsubayashi, 1991) and help to design successful interspecific crosses and breeding strategies.

The ranges of taxonomic applicability of various molecular data sets need to be explored in sect. *Petota*. For example, RAPDs provide a cheap and quick way to screen large numbers of accessions for diversity and systematics, and have only been used at low taxonomic levels in potatoes and other taxa. Molecular sequence data from cpDNA (Johnson & Soltis, 1994) and the internal non-transcribed spacer regions of nuclear ribosomal DNA (Baldwin, 1992) have potential systematic utility at the genus level (Sytsma & Hahn, 1994). To date, the sequence phylogenies in sect. *Petota* that are needed to test the existing molecular and non-molecular phylogenies in the group are lacking.

I suspect that future studies will quantify and clarify the following patterns and processes in sect. *Petota*: (1) common hybridization and introgression, (2) highly polymorphic polythetic taxa, and (3) genetic similarity between many species. These factors have been invoked by past workers (e.g., Hawkes, 1990; Ochoa, 1990), have bedeviled attempts at systematic interpretations, and are likely to provide continuing difficulties. Future taxonomies probably will recognize fewer species, and interpretations of intrasectional relationships (as series) will be very different.

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LITERATURE CITED

- BALDWIN, B. G. 1992. Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: An example from the Compositae. *Molec. Phylogen. Evol.* 1: 3–16.
- BAMBERG, J. B., M. W. MARTIN, J. J. SCHATNER & D. M. SPOONER. 1993. Inventory of Tuber-bearing *Solanum* Species. Potato Introduction Station, NRSP-6, Sturgeon Bay, Wisconsin.
- _____, & D. M. SPOONER. 1994. The United States Potato Introduction Station herbarium. *Taxon* 43: 489–496.
- BONIERBALE, M. W., R. L. PLAISTED & S. D. TANKSLEY. 1988. RFLP maps based on a common set of clones reveal modes of chromosomal evolution in potato and tomato. *Genetics* 120: 1095–1103.
- _____, M. W. GANAL & S. D. TANKSLEY. 1990. Applications of restriction fragment length polymorphisms and genetic mapping in potato breeding and molecular

- genetics. Pp. 13–24 in M. E. Vayda & W. D. Park (editors), *The Molecular and Cellular Biology of the Potato*. CAB International, Wallingford.
- BUDIN, K. Z., L. E. GORBATENKO & L. M. TUROLOVA. 1989. Catalogue Potato Collection VIR. St. Petersburg, Russia.
- CAMADRO, E. L. & S. J. PELOQUIN. 1980. The occurrence and frequency of $2n$ pollen in three diploid *Solanums* from northwest Argentina. *Theor. Appl. Genet.* 56: 11–15.
- CLAUSEN, A. M. & J. V. CRISCI. 1989. Análisis multivariado de la variación morfológica de poblaciones diploides y tetraploides de *Solanum gourlayi* (Solanaceae) y especies relacionadas. *Darwiniana* 29: 247–259.
- CONTRERAS, A. 1980. Chilean potato germplasm (*Solanum* sp.). Final report, 1980. Facultad de Ciencias Agrarias, Univ. Austral Chile.
- _____, L. CIAMPI, S. PADULOSI & D. M. SPOONER. 1993. Potato germplasm collecting expedition to the Guaitecas and Chonos Archipelagos, Chile, 1990. *Potato Res.* 36: 309–316.
- CRIBB, P. J. & J. G. HAWKES. 1986. Experimental evidence for the origin of *Solanum tuberosum* subsp. *andigena*. Pp. 383–404 in W. G. D'Arcy (editor), *Solanaceae: Biology and Systematics*, Columbia Univ. Press, New York.
- DEAHL, K. L., S. L. SINDEN & R. J. YOUNG. 1993. Evaluation of wild tuber-bearing *Solanum* accessions for foliar glycoalkaloid level and composition. *Amer. Potato J.* 70: 61–69.
- DEBENER, T., F. SALAMINI & C. GEBHARDT. 1990. Phylogeny of wild and cultivated *Solanum* species based on nuclear restriction fragment length polymorphisms (RFLPs). *Theor. Appl. Genet.* 79: 360–368.
- _____, _____ & _____. 1991. The use of RFLP's (restriction fragment length polymorphisms) detects germplasm introgressions from wild species into potato (*Solanum tuberosum* ssp. *tuberosum*) breeding lines. *Pl. Breed.* 106: 173–181.
- DEMEKE, T., L. M. KAWCHUK & D. R. LYNCH. 1993. Identification of potato cultivars and clonal variants by random amplified polymorphic DNA analysis. *Amer. Potato J.* 70: 561–570.
- DEN NIJS, T. P. M. & S. J. PELOQUIN. 1977. $2n$ gametes in potato species and their function in polyploidization. *Euphytica* 26: 585–600.
- DESBOROUGH, S. & S. J. PELOQUIN. 1968. Potato variety identification by use of electrophoretic patterns of tuber proteins and enzymes. *Amer. Potato J.* 45: 220–229.
- DOUCHES, D. S. & K. LUDLUM. 1991. Electrophoretic characterization of North American potato cultivars. *Amer. Potato J.* 68: 767–780.
- _____, _____ & R. FREYRE. 1991. Isozyme and plastid DNA assessment of pedigrees of nineteenth century potato cultivars. *Theor. Appl. Genet.* 82: 195–200.
- EHLENFELDT, M. K. & R. E. HANNEMAN, JR. 1984. The use of Endosperm Balance Number and $2n$ gametes to transfer exotic germplasm in potato. *Theor. Appl. Genet.* 68: 155–161.
- FRITZ, N. K. & R. E. HANNEMAN, JR. 1989. Interspecific incompatibility due to stylar barriers in tuber-bearing and closely related non-tuber-bearing *Solanums*. *Sexual Pl. Reprod.* 2: 184–192.
- GIANNATTASIO, R. B. & D. M. SPOONER. 1994a. A reexamination of species boundaries between *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): Morphological data. *Syst. Bot.* 19: 89–105.

- ____ & _____. 1994b. A reexamination of species boundaries and hypotheses of hybridization concerning *Solanum megistacrolobum* and *S. toralapanum* (*Solanum* sect. *Petota*, series *Megistacroloba*): Molecular data. *Syst. Bot.* 19: 106–115.
- GÖRG, R., U. SCHACHTSCHABEL, E. RITTER, F. SALAMINI & C. GEBHARDT. 1992. Discrimination among 136 tetraploid potato varieties by fingerprints using highly polymorphic DNA markers. *Crop Sci.* 32: 815–819.
- GRUN, P. 1990. The evolution of cultivated potatoes. In P. K. Bretting (editor), *New Perspectives on the Origin and Evolution of New World Domesticated Plants*. *Econ. Bot.* 44 (3 Suppl.): 39–55.
- HANNEMAN, R. E., JR. & J. B. BAMBERG. 1986. Inventory of tuber-bearing *Solanum* species. *Wisconsin Agric. Exp. Sta. Bull.* 533: 1–216.
- _____. 1989. The potato germplasm resource. *Amer. Potato J.* 66: 655–667.
- _____. 1994. Assignment of Endosperm Balance Numbers to the tuber-bearing *Solanums* and their close non-tuber-bearing relatives. *Euphytica* 74: 19–25.
- HAWKES, J. G. 1958. Kartoffel. I. Taxonomy, cytology and crossability. Pp. 26–35 in H. Kappert & W. Rudolf (editors), *Handb. Pflanzenzüch.*, ed. 2, vol. 3. Paul Parey, Berlin.
- _____. 1962. Introgression in certain wild potato species. *Euphytica* 11: 26–35.
- _____. 1994. Origins of cultivated potatoes and species relationships. Pp. 3–42 in J. E. Bradshaw & G. R. Mackay (editors), *Potato Genetics*. CAB International, Wallingford, England.
- _____ & J. P. HERTING. 1969. The potatoes of Argentina, Brazil, Paraguay, and Uruguay: A biosystematic study. *Ann. Bot. Mem.* 3: 1–525 + 150 pl.
- _____ & _____. 1989. The potatoes of Bolivia: Their breeding value and evolutionary relationships. Oxford Univ. Press, Oxford.
- _____. 1990. *The Potato: Evolution, Biodiversity and Genetic Resources*. Belhaven Press, London.
- _____ & M. T. JACKSON. 1992. Taxonomic and evolutionary implications of the Endosperm Balance Number hypothesis in potatoes. *Theor. Appl. Genet.* 84: 180–185.
- HOEKSTRA, R. & L. SEIDEWITZ. 1987. *Evaluation Data on Tuber-bearing Solanum Species* (second ed.). Dutch German Curatorium for Plant Genetic Resources, Braunschweig.
- HOSAKA, K., Y. OGIHARA, M. MATSUBAYASHI & K. TSUNEWAKI. 1984. Phylogenetic relationship between the tuberous *Solanum* species as revealed by restriction endonuclease analysis of chloroplast DNA. *Jap. J. Genet.* 59: 349–369.
- _____ & R. E. HANNEMAN, JR. 1988a. The origin of cultivated tetraploid potato based on chloroplast DNA. *Theor. Appl. Genet.* 76: 172–176.
- _____ & _____. 1988b. Origin of chloroplast DNA diversity in the Andean potatoes. *Theor. Appl. Genet.* 76: 333–340.
- _____ & D. M. SPOONER. 1992. RFLP analysis of the wild potato species, *Solanum acaule* Bitter (*Solanum* sect. *Petota*). *Theor. Appl. Genet.* 84: 851–858.
- _____, M. MORI & K. OGAWA. 1994. Genetic relationships of Japanese potato cultivars assessed by RAPD analysis. *Amer. Potato J.* 71: 535–546.
- HUAMÁM, Z. 1987. Inventory of Andean potato cultivars with resistance to some pests and diseases and other desirable traits. CIP, Lima, Peru.
- JOHNS, T., Z. HUAMÁM, C. OCHOA & P. E. SCHMIEDICHE. 1987. Relationships among wild, weed, and cultivated potatoes in the *Solanum* × *ajanhui* complex. *Syst. Bot.* 12: 541–552.

- JOHNSON, L. A. & D. E. SOLTIS. 1994. matK DNA sequences and phylogenetic reconstruction in Saxifragaceae s. str. *Syst. Bot.* 19: 143–156.
- KARDOLUS, J. in press. Morphological variation with series *Acaulia* (*Solanum* sect. *Petota*). In M. Nee, D. Simon & J. P. Jessup (editors), *Solanaceae IV: Taxonomy, Chemistry, Evolution*. Royal Botanic Gardens, Kew.
- MATSUBAYASHI, M. 1991. Phylogenetic relationships in the potato and its related species. Pp. 93–118 in T. Tsuchiya & P. K. Gupta (editors), *Chromosome Engineering in Plants: Genetics, Breeding, Evolution*, Part B. Elsevier, Amsterdam.
- MORI, M., K. HOSAKA, Y. UMEMURA & C. KANEDA. 1993. Rapid identification of Japanese potato cultivars by RAPDs. *Jap. J. Genet.* 68: 167–174.
- OCHOA, C. M. 1990. *The Potatoes of South America: Bolivia*. Cambridge Univ. Press, Cambridge.
- OKADA, K. A. 1974. Colección de *Solanum* tuberíferos de Argentina. Lista de semillas No. 3, Diciembre, 1974. Instituto Nacional de Tecnología Agropecuaria, Balcarce.
- _____. 1976. Exploration, conservation and evaluation of potato germplasm in Argentina. *Potato Res.* 19: 263–269.
- OLIVER, J. L. & J. M. MARTÍNEZ-ZAPATER. 1985. A genetic classification of potato cultivars based on allozyme patterns. *Theor. Appl. Genet.* 69: 305–311.
- OLMSTEAD, R. & J. A. SWEERE. 1994. Combining data in phylogenetic systematics: An approach using three molecular data sets in the Solanaceae. *Syst. Biol.* 43: 467–481.
- ORTIZ, R. & M. K. EHLENFELDT. 1992. The importance of Endosperm Balance Number in potato breeding and the evolution of tuber-bearing *Solanum* species. *Euphytica* 60: 105–113.
- PLAISTED, R. L. & R. W. HOOPES. 1989. The past record and future prospects for the use of exotic potato germplasm. *Amer. Potato J.* 66: 603–627.
- RABINOWITZ, D., C. R. LINDER, R. ORTEGA, D. BEGANO, H. MURGUIA, D. S. DOUCHES & C. F. QUIROS. 1990. High levels of interspecific hybridization between *Solanum sparsipilum* and *S. stenotomum* in experimental plots in the Andes. *Amer. Potato J.* 67: 73–81.
- RIESEBERG, L. H. & N. C. ELLSTRAND. 1993. What can molecular and morphological markers tell us about plant hybridization? *C. R. C. Crit. Rev. Pl. Sci.* 12: 213–241.
- RODRÍGUEZ, A., O. VARGAS, E. VILLEGAS & D. M. SPOONER. 1995. Wild potato (*Solanum* sect. *Petota*) germplasm collecting expedition to Mexico in 1993, with special reference to *Solanum bulbocastanum* Dunal and *S. cardiophyllum* Lindley. *Potato Res.* 38: 47–52.
- ROSS, H. 1986. *Potato Breeding—Problems and Perspectives*. Paul Parey, Berlin.
- ROTHACKER, D., E. HINZE & P. HUNGER. 1991. Sortiment wilder und kultivierter mittel- und südamerikanischer Kartoffelspezies (GLKS). Institut für Kartoffelforschung Gross Lüsewitz, Gross Lüsewitz.
- SMITH, O. S. & J. S. C. SMITH. 1992. Measurement of genetic diversity among maize hybrids; A comparison of isozymic, RFLP, pedigree, and heterosis data. *Maydica* 37: 53–60.
- SPOONER, D. M., J. B. BAMBERG, J. P. HJERTING & J. GÓMEZ. 1991a. Mexico, 1988 potato germplasm collecting expedition and utility of the Mexican potato species. *Amer. Potato J.* 68: 29–43.
- _____, A. CONTRERAS-M. & J. B. BAMBERG. 1991b. Potato germplasm collecting expedition to Chile, 1989, and utility of the Chilean species. *Amer. Potato J.* 68: 681–690.

- _____, K. J. SYTSMA & J. F. SMITH. 1991c. A molecular reexamination of diploid hybrid speciation of *Solanum raphanifolium*. *Evolution* 45: 757–764.
- _____, R. CASTILLO-T. & L. LÓPEZ-J. 1992. Ecuador, 1991 potato germplasm collecting expedition: Taxonomy and new germplasm resources. *Euphytica* 60: 159–169.
- _____ & K. J. SYTSMA. 1992. Reexamination of series relationships of Mexican and Central American wild potatoes (*Solanum* sect. *Petota*): Evidence from chloroplast DNA restriction site variation. *Syst. Bot.* 17: 432–448.
- _____ & R. G. VAN DER BERG. 1992a. An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*). *Gen. Res. Crop Evol.* 39: 23–37.
- _____ & _____. 1992b. Species limits and hypotheses of hybridization of *Solanum berthaultii* Hawkes and *S. tarijense* Hawkes: Morphological data. *Taxon* 41: 685–700.
- _____, G. J. ANDERSON & R. K. JANSEN. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepinos (Solanaceae). *Amer. J. Bot.* 80: 676–688.
- _____ & A. M. CLAUSEN. 1993. Wild potato (*Solanum* sect. *Petota*) germplasm collecting expedition to Argentina in 1990, and status of Argentinian potato germplasm resources. *Potato Res.* 36: 3–12.
- _____ & J. B. BAMBERG. 1994. Potato genetic resources: Sources of resistance and systematics. *Amer. Potato J.* 71: 325–337.
- _____, R. G. VAN DEN BERG, W. GARCÍA & M. L. UGARTE. 1994. Bolivia potato germplasm collecting expeditions 1993, 1994: Taxonomy and new germplasm resources. *Euphytica* 79: 137–148.
- _____, R. CASTILLO T., L. LÓPEZ J., R. PINEDA, R. LEÓN P., A. VARGAS, M. L. GARCÍA & J. B. BAMBERG. 1995a. Colombia and Venezuela 1992 wild potato (*Solanum* sect. *Petota*) germplasm collecting expedition: Taxonomy and new germplasm resources. *Euphytica* 81: 45–56.
- _____, R. G. VAN DEN BERG & J. B. BAMBERG. 1995b. Examination of species boundaries of *Solanum* series *Demissa* and potentially related species in series *Acaulia* and series *Tuberosa* (Solanaceae: sect. *Petota*). *Syst. Bot.* 20: 295–314.
- STEGEMANN, H. & D. SCHNICK. 1985. Index 1985 of Potato Varieties. Paul Parey, Berlin.
- SYTSMA, K. J. & W. J. HAHN. 1994. Molecular systematics: 1991–1993. *Prog. Bot.* 55: 307–333.
- TANSKLEY, S. D., M. W. GANAL, J. P. PRINCE, M. C. DE VICENTE, M. W. BONIERBIALE, P. BROUN, T. M. FULTON, J. J. GIOVANNONI, S. GRANDILLO, G. B. MARTIN, R. MESSEGUER, J. C. MILLER, L. MILLER, A. H. PATTERSON, O. PINEDA, M. S. RÖDER, R. A. WING, W. WU & N. D. YOUNG. 1992. High density molecular linkage maps of the tomato and potato genomes. *Genetics* 132: 1141–1160.
- UGENT, D. 1970. The potato: What is the botanical origin of this important crop plant, and how did it first become domesticated? *Science* 170: 1161–1166.
- VAN DEN BERG, R. G. & D. M. SPOONER. 1992. A reexamination of infraspecific taxa of a wild potato, *Solanum microdontum* Bitter (*Solanum* sect. *Petota*: Solanaceae). *Pl. Syst. Evol.* 182: 239–252.
- _____, N. GROENDIJK-WILDERS & J. P. KARDOLUS. 1996. The wild ancestors of the cultivated potato: The brevicaulis complex. *Acta Bot. Neerl.* 45: 157–171.
- WATANABE, K. & S. J. PELOQUIN. 1989. Occurrence of $2n$ pollen and ps gene frequencies in cultivated groups and their related wild species in tuber-bearing Solanums. *Theor. Appl. Genet.* 78: 329–336.

- ____ & _____. 1991. The occurrence and frequency of $2n$ pollen in $2x$, $4x$, and $6x$ wild, tuber-bearing *Solanum* species from Mexico, and Central America. *Theor. Appl. Genet.* 82: 621–626.
- WILKINSON, M. J., A. DONNELLY & I. BLACK. 1994. The Commonwealth Potato Collection, Inventory for 1994. Scottish Crop Research Institute, Invergowrie, Dundee, Scotland.
- WILLIAMS, D. M. 1994. Combining trees and combining data. *Taxon* 43: 449–453.