

An analysis of recent taxonomic concepts in wild potatoes (*Solanum* sect. *Petota*)

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Summary

Solanum L. sect. *Petota* Dumort., the potato and its wild relatives, contains 232 species, according to the latest taxonomic interpretation of Hawkes (1990). Section *Petota* is distributed in the Americas from the southwestern United States to southern Chile. This economically important group has attracted the attention of numerous taxonomists with various taxonomic philosophies. There are 531 validly published basionyms in the group, plus 67 nomina nuda or nomina dubia, and subsequent transfers to other ranks raise the number of names to 664. The taxonomy of sect. *Petota* has been dominated in recent years by J. G. Hawkes & J. P. Hjerting (co-workers) and C. M. Ochoa. The near simultaneous and independent publication of three recent books by these workers, treating the Bolivian species of sect. *Petota*, provides a novel opportunity to compare their taxonomic philosophies. Additionally, a recent independent treatment of all of the South American species by L. E. Gorbatenko provides a new interpretation of affiliations of species to series that is compared to the recent treatment of Hawkes and earlier treatments of S. M. Bukasov and D. S. Correll. These treatments differ in the placement of species into series, species boundaries, rank of infraspecific taxa, and hypotheses of hybridization. Our analysis illustrates the wide differences of taxonomic interpretation possible when independent workers treat the same material. The comparison provides insights into unresolved taxonomic questions in sect. *Petota* and indicates the need for a practical taxonomic resolution that will benefit plant breeders and other researchers on wild potatoes. Reasons for the discrepancies are discussed and suggestions for future research are provided.

Introduction

“The inconsistencies and lack of agreement among taxonomists dealing with the same materials are remarkable, to say the least, and even more striking when the treatments of different crops are compared.” (Harlan & de Wet, 1971). Harlan & de Wet (1971) highlighted the conflicting taxonomic treatments of wild and cultivated potatoes (*Solanum* sect. *Petota*) as one of the four examples (along with corn, sorghum, and wheat)

of the lack of agreement among taxonomists and implied that traditional taxonomy had little to offer plant breeders. They argued for a more “rational classification” of crop plants that would circumvent the great confusion generated by conflicting taxonomies. They advanced the “gene pool” classification focused entirely on genetic compatibility and constructed a hierarchical system based on ease of crossability. Our paper analyzes the continuing taxonomic disagreement in *Solanum* sect. *Petota* with examples from historical

and recent treatments. We suggest that a revised traditional taxonomy of the group, in combination with the gene pool concept, can better serve breeders and other scientists by providing a more accurate interpretation of the morphological and genetic diversity in the group.

Solanum sect. *Petota*, the potato and its wild relatives, has been the subject of intensive taxonomic work since the description of the cultivated potato, *S. tuberosum* L. (Linnaeus, 1753). This great interest is the result of a number of factors. Its widespread range, from the southwestern United States to southcentral Chile, has led to many separate regional treatments. The wild relatives have generated curiosity because of their similarity to cultivated potatoes. Much work has been stimulated by the necessity to understand the crossing and taxonomic relationships of these species for plant breeding programs. Also, funding was available for extensive collecting and subsequent study.

Solanum sect. *Petota* has been studied by numerous taxonomists with various taxonomic philosophies. Walpers (1844) accepted only ten species in sect. *Petota*. The last attempt to monograph *Solanum* in its entirety was by Dunal (1852) who included 17 species in sect. *Petota*, while Baker (1884) and Wittmack (1909) recognized only six and four species, respectively, in sect. *Petota*. Bitter (1912–1914), in his monumental work on *Solanum*, described more than 50 new species, subspecies or varieties of wild potatoes.

The first regional treatment of sect. *Petota* was provided by Rydberg (1924), who monographed the Mexican and Central American species and described ten new taxa. Extensive taxonomic investigations were conducted by Vavilov's Russian associates Bukasov, Juzepczuk, and Kameraz, who worked on material gathered on Russian expeditions to Mexico, Central America, and South America in the 1920s and 1930s. They validly described 30 wild and 18 cultivated species, in addition to publishing a great number of invalid names (Bukasov, 1930, 1933, 1937, 1940; Juzepczuk & Bukasov, 1936; Juzepczuk, 1937; Bukasov & Kameraz, 1959). Hawkes (1944) treated collections from a series of British expeditions to Mexico and South America in the 1930s and described 52 new species, subspecies, or varieties, of which he accepted only ten in 1990

(Hawkes, 1990). Regional treatments have been provided for Argentina, Brazil, Paraguay, and Uruguay (Hawkes & Hjerting, 1969); Bolivia (Hawkes & Hjerting, 1989; Ochoa, 1990a); Chile (Montaldo & Sanz, 1962; Contreras-M., 1987); Mexico and Central America (Correll, 1952); Mexico (Flores-C., 1966; Hawkes, 1966; Rodriguez-C., 1991); and Peru (Vargas-C., 1949, 1956; Ochoa, 1962; Correll, 1967).

The first modern comprehensive treatment of *Solanum* sect. *Petota* was provided by Hawkes (1956) who synonymized many species. The treatment of Correll (1962) was similar in its taxonomy, and included extensive specimen citations and excellent illustrations. Other comprehensive treatments have been provided by Hawkes (1963, 1978, 1990), Bukasov (1978), and Gorbatenko (1989). Intensive taxonomic work continues to the present day. Since the work by Correll (1962), 176 new taxa have been described, 140 of these by Ochoa, including 77 new varietal and form names for the Bolivian cultivated species alone (Ochoa, 1988). In total, 72 taxonomists have described 531 validly published basionyms in *Solanum* sect. *Petota*, plus 67 nomina dubia or nomina nuda, and subsequent transfers to other ranks raise the number of species, subspecies, and varietal names to 664 (data obtained from Hawkes (1990), to which Ochoa (1990b) is added). Regional treatments are in preparation by Ochoa for Venezuela, Columbia, Ecuador and Peru (Ochoa, 1990a).

Bitter (1912, vol. 11: 349–394) was the first to recognize series in sect. *Petota*, and subsequent workers have recognized different numbers of series, sometimes informally (see Spooner & Sytma (1992) for a historical conspectus of series in sect. *Petota*). For example, Hawkes (1990) and Gorbatenko (1989) recognize 15 and 20 series, respectively, for the South American species, and Hawkes (1990) and Bukasov (1978) recognize 21 and 36 series, respectively, for the entire group. These series often are not well-defined morphologically, the affiliations of species to series vary widely among different authors.

Many of the taxa in *Solanum* sect. *Petota* are extremely similar morphologically. Most species possess pinnately dissected leaves, short to long hairs, but lack a conspicuous glandular pubescence, and have round to conical fruits. Some species are easily distinguished by various

combinations of entire leaves, glandular pubescence, or other unique features (e.g. *S. acaule* Bitter, *S. bulbocastanum* Dunal, *S. clarum* Correll, *S. minutifolium* Correll, *S. polyadenium* Greenman, *S. trifidum* Correll), but many others are very similar and are distinguished only by minor and often overlapping character states like differences in non-glandular pubescence, degree of dissection of leaves, position of the articulation of the pedicel, and/or color or shape of the corolla.

Identifications have been provided for living plantings at the Inter-Regional Potato Introduction Station (the sole genebank for *Solanum* sect. *Petota* in the United States) by visiting taxonomists over the past 37 years (Hanneman & Bamberg, 1986; Spooner & Bamberg, 1991). Currently, this station maintains 4200 accessions of 120 of the wild species. Despite conflicting opinions of different visiting taxonomists, the identifications of these accessions have remained relatively stable. However, these plantings for identification have been accompanied with former taxonomic determinations and data on the geographic origin and chromosome number of the collections.

The independent publication of the taxonomic treatments of Bolivian wild potatoes by Hawkes & Hjerting (1989) and Ochoa (1990a), the treatment of sect. *Petota* by Hawkes (1990), and a conspectus of the South American species by Gorbatenko (1989) provides a novel opportunity to analyze the recent taxonomic practices and philosophies of these authorities of sect. *Petota*. The treatments of Hawkes & Hjerting (1989), Hawkes (1990), and Ochoa (1990a) are compared at the species level, with species, varieties, and forms noted under each individual species (Fig. 1). Comparisons are made of the characters used to distinguish taxa, hypotheses of natural hybridization, hypotheses of species interrelationships, and taxonomic philosophies of the above authors, with references made in appropriate cases to the primary literature. Separately, the recent series treatments of Gorbatenko (1989) and Hawkes (1990) are compared, along with the earlier series treatments of Correll (1962) and Bukasov (1978) to provide a historical context for the development of series concepts (Fig. 2). Rarely has such an opportunity presented itself in systematics to compare the near simultaneous and independent treatments

of the same plant group. This comparison illustrates the wide differences of taxonomic interpretation possible when independent workers treat the same material. It highlights unresolved taxonomic problems in sect. *Petota* and indicates the need for a practical taxonomic resolution that will benefit plant breeders and other researchers on wild potatoes.

Comparison of Bolivian treatments

Figure 1 illustrates the agreements and conflicts of the taxonomic treatments of the Bolivian taxa of *Solanum* sect. *Petota* of Hawkes & Hjerting (1989) and Hawkes (1990) to Ochoa (1990a). Illustrative examples of these conflicts are highlighted below and grouped into the following classes: series affiliations, species boundaries, treatment of infraspecific taxa, characters used to separate taxa, and hypotheses of natural hybridization.

Series affiliations. The treatments compared here arrange the Bolivian species of sect. *Petota* into seven series and provide keys and descriptions for them. Ochoa (1990a) considers series to "probably have slight taxonomic value." Hawkes (1989) erects superseries *Rotata* Hawkes (containing, among others, the Bolivian series *Acaulia*, *Cuneolata*, *Megistacroloba*, and *Tuberosa*) and superseries *Stellata* Hawkes (containing, among others, the Bolivian series *Circaeifolia*, *Commersonianana* and *Yungasensia*) to separate groups of species with substellate to rotate corollas from those with stellate corollas. Hawkes (1989, 1990) changes his earlier concept of ser. *Commersonianana* (e.g. Hawkes, 1963, 1978), dividing it into ser. *Commersonianana*, containing 1EBN (Endosperm Balance Number (Johnston *et al.*, 1980), a phenomenon of sexual compatibility based on ratios of maternal/paternal genomes in the endosperm) species, and ser. *Yungasensia*, containing 2EBN species. Ochoa (1990a) does not comment on superser. *Rotata* or *Stellata*, and synonymizes ser. *Yungasensia* under ser. *Commersonianana*. A major difference resulting from these alternative hypotheses is Hawkes & Hjerting's (1989) separation of *S. berthaultii* and *S. tarijense* into ser. *Tuberosa* (superser. *Rotata*) and ser. *Yungasensia* (superser. *Stellata*), respectively, and their

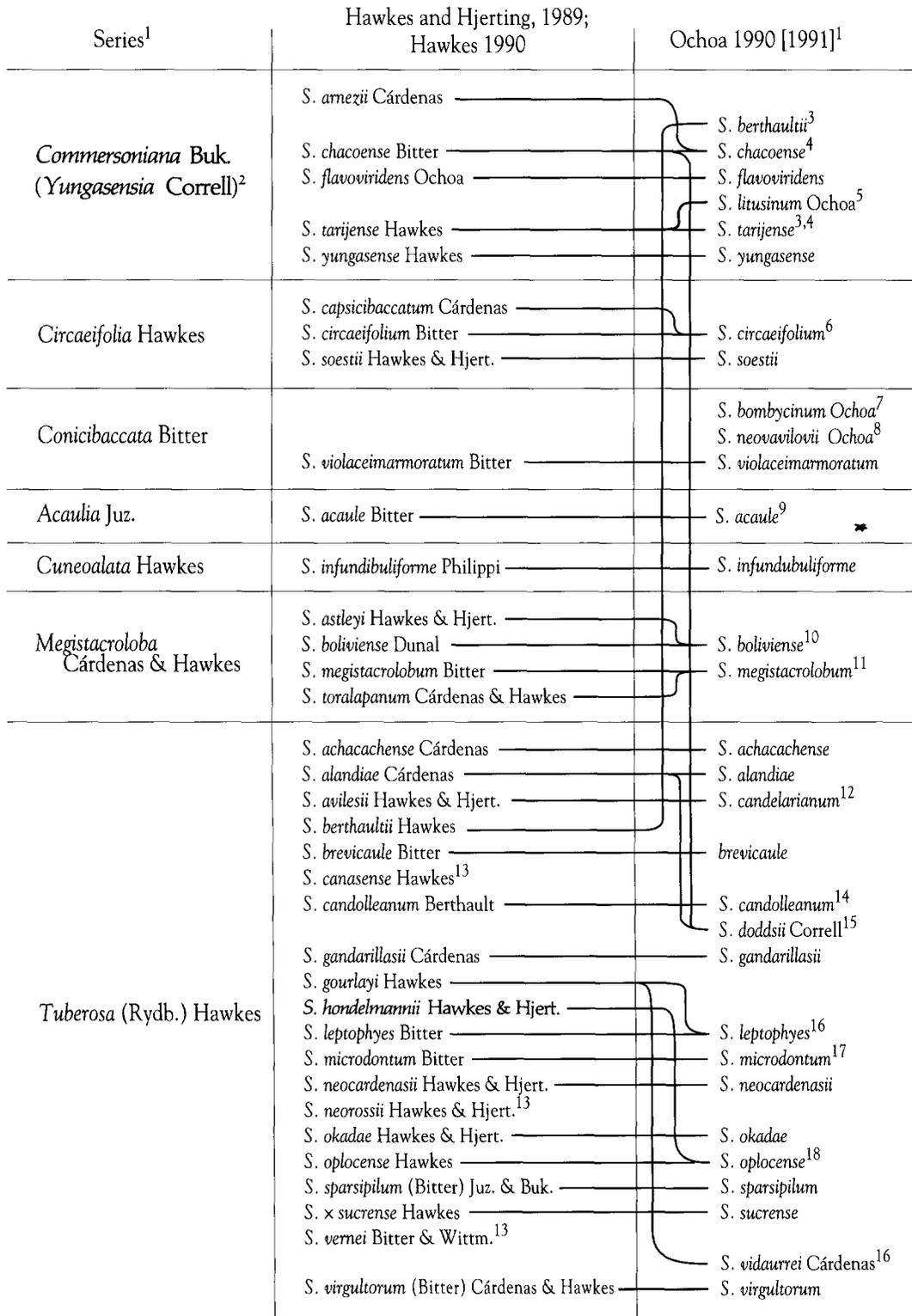


Fig. 1.

Fig. 1. A comparison of the hypotheses of species boundaries and series affiliations of the Bolivian wild species of *Solanum* sect. *Petota* of Hawkes & Hjerting (1989) and Hawkes (1990) to those of Ochoa (1990a)¹. This table traces synonymy, hypotheses of hybridization, and hypotheses of affiliations of species to series. Nomenclaturally designated hybrid species, subspecies, varieties, and forms are noted under the individual species. This table does not include *S. hoopesii* Hawkes & Okada and *S. ugentii* Hawkes & Okada (Hawkes & Okada, 1988) that were described too late to be included in Hawkes & Hjerting (1989) and Ochoa (1990a).

¹The actual release date (data obtained from publisher) was 13 June 1991.

²Hawkes (1989, 1990) changed his earlier interpretation (Hawkes, 1956, 1963, 1978) of series *Commersoniana* and placed 1EBN (see text) species in ser. *Commersoniana* and 2EBN species in ser. *Yungasensia*.

³Hawkes (1990) formally treats *S. x zudaniense* Cárdenas as a hybrid species formed by a natural cross between *S. berthaultii* and *S. tarijense*. Ochoa (1990a) synonymizes *S. zudaniense* under *S. tarijense*.

⁴Hawkes (1990) formally treats *S. x trigalense* Cárdenas as hybrid taxon formed by a natural cross between *S. chacoense* and *S. tarijense*. Ochoa (1990a) synonymizes *S. trigalense* under *S. tarijense*.

⁵Hawkes (1990) formally treats *S. x litusinum* as a hybrid species formed by a natural cross between *S. berthaultii* and *S. tarijense*. Ochoa (1990a) indicates that *S. x litusinum* may have resulted from this cross or possibly from a cross between *S. alandiae* and *S. chacoense*.

⁶Hawkes & Hjerting (1989) recognize *S. capsicibaccatum* and *S. circaeifolium* at the species level and divide *S. circaeifolium* into ssp. *circaeifolium* and ssp. *quimense* Hawkes & Hjert. Ochoa (1990a) divides *S. circaeifolium* into var. *capsicibaccatum* (Cárdenas) Ochoa (under which he synonymizes ssp. *quimense*) and var. *circaeifolium*.

⁷Hawkes & Hjerting (1989, in text) indicate that *S. bombycinum* may be synonymous with *S. villuspetalum* Vargas from Peru but later (Hawkes & Hjerting 1989, in postscript) note the tetraploid nature of *S. bombycinum* and suggest that it may be a good species. Hawkes (1990) relates *S. bombycinum* to *S. villuspetalum*, *S. multiflorum* Vargas and *S. urubambae* Juz. (all from Peru).

⁸Hawkes & Hjerting (1989) and Hawkes (1990) indicate that *S. neovavilovii* is probably synonymous with *S. violaceimarmoratum*.

⁹Hawkes & Hjerting (1989) recognize four subspecies within *S. acaule*: ssp. *acaule* (4x, distributed from southern Peru to northwestern Argentina), ssp. *aemulans* (Bitt. & Wittm.) Hawkes and Hjert. (4x, confined to northwestern Argentina), ssp. *punae* (Juz.) Hawkes & Hjert. (4x, distributed from central Peru to northern Argentina), and ssp. *albicans* (Ochoa) Hawkes (6x, confined to northern Peru). Hawkes (1990) recognizes all these taxa but elevates *S. albicans* (Ochoa) Ochoa to specific rank. Ochoa (1990a) recognizes two varieties of *S. acaule*: var. *acaule* (under which he synonymizes ssp. *punae*), and var. *aemulans* (Bitt. & Wittm.) Correll, and also recognizes *S. albicans*. Ochoa followed Brücher (1959), and Correll (1962), who also synonymized var. *punae* under var. *acaule*.

¹⁰Ochoa (1990a) suggests that *S. astleyi* may be an ecotype of *S. boliviense*.

¹¹Ochoa (1990a) divides *S. megistacrolobum* into var. *megistacrolobum* and var. *toralapanum* (Cárdenas & Hawkes) Ochoa.

¹²*Solanum avilesii* Hawkes & Hjerting, J. Linn. Soc., Bot. 86: 410. 1983 is the legitimate name for this taxon, not *S. candelarianum* Cárdenas, Bol. Soc. Peruana Bot. 5: 12. 1956, because of the earlier homonym, *S. candelarianum* Buk., Trudy Prikl. Bot. Suppl. 47: 218. 1930 (Hawkes, 1990).

¹³Hawkes & Hjerting (1989) include *S. canasense*, *S. neorossii*, and *S. vernei* for the flora of Bolivia. Although there are no records of these species there, populations are known from very near the border with Peru, Argentina, and Argentina, respectively. Ochoa (1990a) makes no mention of *S. neorossii* and *S. vernei*, and considers *S. canasense* a “mere variant” of *S. bukasovii* (from Peru). Hawkes (1990) maintains the latter two as distinct species, separating them (in the key) by differences in length and appression of hairs on the inflorescence.

¹⁴Ochoa (1990a) recognizes *S. candolleianum* f. *sihuampampinum* Ochoa but does not provide a Latin description.

¹⁵Hawkes & Hjerting (1989) treat *S. doddsii* as a natural interspecific hybrid between *S. alandiae* and *S. chacoense*. They also indicate that it was only known from a single site, and the species is now extinct. Ochoa (1990a) accepts *S. doddsii* at the species level and relates it to *S. alandiae*.

¹⁶Hawkes & Hjerting (1989) recognize *S. gourlayi* and *S. leptophyes* at the specific level and divide *S. gourlayi* into ssp. *gourlayi* (confined to Argentina), ssp. *pachytrichum* (Hawkes) Hawkes & Hjert. (confined to Bolivia), ssp. *vidaurrei* (Cárdenas) Hawkes & Hjert. (occurring in Bolivia and Argentina). Hawkes (1990) later accepts a fourth subspecies, ssp. *saltense* A. Clausen & K. Okada, from Argentina, in agreement with Clausen & Okada (1987). Ochoa (1990a) recognizes *S. leptophyes* but synonymizes ssp. *gourlayi* and ssp. *pachytrichum* under it. He treats *S. vidaurrei* as a distinct species.

¹⁷Hawkes & Hjerting (1989) divide *S. microdontum* into ssp. *microdontum* and ssp. *gigantophyllum* (Bitt.) Hawkes & Hjert., both occurring in Bolivia and Argentina. Ochoa (1990a) treats these taxa at the varietal level (valid name for ssp. *gigantophyllum* at the varietal level = var. *metriophyllum* [Bitt.] Ochoa), and in addition recognizes a third variety, var. *montepuncoense* Ochoa. Hawkes & Hjerting (1989) consider the latter as a natural hybrid between *S. microdontum* ssp. *gigantophyllum* and *S. violaceimarmoratum*. Hawkes (1990) accepts var. *montepuncoense*. Although he maintains the hybridization hypothesis of Hawkes & Hjerting (1989) he does not nomenclaturally designate it as a hybrid taxon (as in the case of 4, 5, 6, above).

¹⁸Hawkes & Hjerting (1989) recognize *S. oplocense* and *S. hondelmannii* as distinct species, but Ochoa (1990a) considers *S. hondelmannii* as a “hybrid variant” of *S. oplocense*, possibly involving *S. chacoense* or *S. x litusinum*.

placement together in ser. *Commersoniana* by Ochoa (1990a). This wide difference of interpretation begs the question as to the differences of these species and series. Hawkes & Hjerting (1989) and Hawkes (1990) separate ser. *Commersoniana* and *Yungasensia* on the basis of EBN and corolla shape, and ser. *Commersoniana* and *Tuberosa* on corolla shape. Our investigation of *S. berthaultii* and *S. tarijense* (Spooner & van den Berg, in press) demonstrates that both species have corollas varying in shape from rotate to stellate, sometimes even in the same population.

Species boundaries. Ochoa (1990a) generally recognizes fewer taxa for the Bolivian wild species. For example, he synonymizes *S. arnezii* to *S. chacoense*, treats *S. astleyi* as an “ecotype” of *S. boliviense*, and treats *S. hondelmannii* as a “hybrid variant” of *S. oplocense*. Hawkes (1990) follows Clausen & Okada (1987) and recognizes both *S. gourlayi* (with four subspecies: ssp. *gourlayi*, ssp. *pachytrichum* (Hawkes) Hawkes & Hjert., ssp. *saltense* A. Clausen & Okada, ssp. *vidaurrei* (Cárdenas) Hawkes & Hjert.), and *S. leptophyes*, while Ochoa (1990a) considers *S. gourlayi* (including ssp. *pachytrichum*) as a synonym of *S. leptophyes*. Ochoa (1990a), however, recognizes ssp. *vidaurrei* at the species level. Hawkes & Hjerting (1989) recognize *S. canasense*, but Ochoa (1990a) indicates that *S. canasense* should be considered as a “mere variant” of *S. bukasovii* Juz.

Treatment of infraspecific taxa. Hawkes & Hjerting (1989) and Hawkes (1990) use subspecies to designate infraspecific taxa of the wild species where Ochoa (1990a) uses varieties. In contrast to their usual practice, however, Hawkes (1990) recognizes a variety of *S. microdontum* (Fig. 1, footnote 17), and Ochoa (1990a) recognizes a form of *S. candolleianum* (Fig. 1, footnote 14). The use of subspecies and varieties for the same taxon has created many additional names in *Solanum* sect. *Petota*. For example, Hawkes & Hjerting (1989) and Ochoa (1990a) accept infraspecific taxa within *S. acaule* and *S. microdontum*, but Hawkes & Hjerting (1989) do so at the subspecific rank, while Ochoa (1990a) does so at the varietal rank. Similarly, Ochoa (1990a) treats *S. toralapanum* and *S. capsicibaccatum* as varieties of *S. megistacrolobum* and *S. circaeifolium*, respectively, while

Hawkes & Hjerting (1989) treat these taxa as distinct species.

Hawkes (1980; 1986a,b) and Hawkes & Hjerting (1989) discuss the problems of classification of variable taxa at length and conclude that wild potato species should be regarded as large units that contain a wide range of genetic diversity. Hawkes & Hjerting (1989) state that such a species concept makes it “inadvisable, if not impossible to divide potato species into the conventional infraspecific categories of varieties and forms. Nevertheless, in several instances regular geographical patterns of diversity [show] the need for subspecies grouping.” These authors thus indicate a preference for subspecies, defined by morphological and geographic criteria. They do not define their concepts of varieties vs. subspecies, however. Ochoa (1990a) provides no theoretical discussion of taxonomic classification or rank. Because of the lack of comparison of the concepts of varieties and subspecies from these authors, we are unable to compare the relative merits of these ranks in their treatments.

Characters used to separate taxa. The wild and cultivated species of *Solanum* sect. *Petota* in Bolivia and elsewhere contain groups of extremely similar taxa that often are distinguished by what on the surface appear to be minor characters with often overlapping character states like habit, pubescence, number of lateral or interjected leaflets, or colors or shapes of the calyx or corolla. To gain an appreciation of this similarity, compare the illustration of *S. leptophyes* to that of *S. sparsipilum* in Hawkes & Hjerting (1989), or the illustrations of *S. berthaultii*, *S. flavoviridens* and *S. tarijense* in Ochoa (1990a). These illustrations capture only a small window of the variability in these taxa. Many descriptive differences also appear very minor. For example, Hawkes & Hjerting (1989) distinguish *S. sparsipilum* from *S. leptophyes* by the broader leaflets and shorter pubescence of the former, and *S. okadae* from *S. venturii* Hawkes & Hjerting by its more robust habit and more well-defined lateral leaflets with clearly marked petioles. Ochoa (1990a) distinguishes *S. berthaultii*, *S. x litusunum* Ochoa and *S. tarijense* by differences in leaf pubescence, and corolla color and shape, although these characters vary tremendously within the species.

Hypotheses of natural hybridization. Hawkes & Hjerting (1989) continue the practice of hypothesizing extensive hybridization initiated in their earlier treatment of the potatoes of Argentina, Brazil, Paraguay, and Uruguay (Hawkes & Hjerting, 1969), where nine and one-half percent of the specimens examined were interpreted as natural hybrids. Although comparable percentages are not provided by the authors in these recent treatments, our counts indicate that 23 of the 32 (72%) wild species included by Hawkes & Hjerting (1989) as occurring in Bolivia are hypothesized to have undergone natural interspecific hybridization with one or more species, with an average of 1.5 interspecific hybrid combinations per hybridizing species. The figures in Ochoa (1990a) are much lower: 9 hybridizing species of a total of 31 species (32%), with an average of 1.1 interspecific combinations per hybridizing species. Additionally, the actual numbers of hypothesized hybrid populations are much lower in Ochoa (1990a). For example, 24% of the *S. berthaultii* and *S. tarijense* specimens examined in Hawkes & Hjerting (1989) are listed as interspecific hybrids between the two, but Ochoa hypothesizes hybridization in only 4% of the same combination.

Hawkes & Hjerting (1989) and Hawkes (1990) also hypothesize much more hybrid speciation than Ochoa (1990a): They designate *S. x zudaniense* Cárdenas, *S. x trigalense* Cárdenas, and *S. x litusinum* as hybrid taxa, treat *S. doddsii* as a rare chance hybrid, and indicate a hybrid origin for *S. microdontum* var. *montepuncoense* Ochoa (see Fig. 1, footnotes 3, 4, 5, 15, 17). Ochoa (1990a) recognizes the possibility of the hybrid origin of *S. x litusinum*, but does not taxonomically designate the above as hybrid taxa. Ochoa's (1990a) only hypothesis of a hybrid origin of a species is *S. hondelmannii* (Fig. 1, footnote 18).

Series treatments

The different hypotheses of the affiliations of species to series of the classifications of Correll (1962), Bukasov (1978), Gorbatenko (1989), and Hawkes (1990) are presented in Fig. 2. There have been extensive differences of interpretation of series. Some series are relatively well-defined phenetically by a unique character or a combi-

nation of character states rarely found in the rest of the group. Examples are the series *Acaulia*, *Circaeifolia*, *Etuberosa*, *Lignicaulia*, *Morelliformia*, *Olmosiana*, and *Polyadenia*, and little disagreement has occurred among authors about the affiliations of species in these series. Other series are only poorly (if at all) characterized by series-specific morphological character states and have formed the basis of extensive disagreement. For example, ser. *Tuberosa* is so poorly-characterized that Hawkes (1990) does not provide any diagnostic features for it beyond those in the series key that include character states of the corolla shape that are common in many other series. Other examples of morphologically poorly-characterized series include *Bulbocastana*, *Commersoniana*, *Demissa*, *Longipedicellata*, and *Yungasensia*.

The difficulty in distinguishing these series is not evident from their descriptions or keys for two reasons. First, the descriptions of series of Gorbatenko (1989) and Hawkes (1990) are not always parallel. Second, the variability within the series often exceeds that indicated in the series descriptions, although this variability is not clearly indicated in the treatments. For example, ser. *Yungasensia* (sensu Hawkes, 1990) is partially defined by stellate corollas, yet contains *S. tarijense*, that possesses both stellate and rotate corollas (Spooner & van den Berg, in press). Hawkes (1990) includes ser. *Polyadenia* in super-series *Stellata*, yet *S. polyadenium* has rotate-stellate corollas (Correll, 1962, p. 238; his Fig. 91), a shape that Hawkes (1990) includes for other species within ser. *Rotata*. Also, Hawkes (1989) credits Bukasov (1939) with the *Rotata*/*Stellata* superseries concept, and Bukasov (1939) included *S. polyadenium* in the "Rotata" group.

Discussion

A comparison of these modern taxonomic treatments illustrates the many unresolved questions of affiliations of species to series, species boundaries, concepts of infraspecific taxa, and hypotheses of natural hybridization in *Solanum* sect. *Petota*. Our analysis illustrates that: 1. The species are grouped in series in all treatments, but the differences among the series are often unclear. 2. Hawkes's (1989, 1990) superser. *Rotata*/*Stellata*

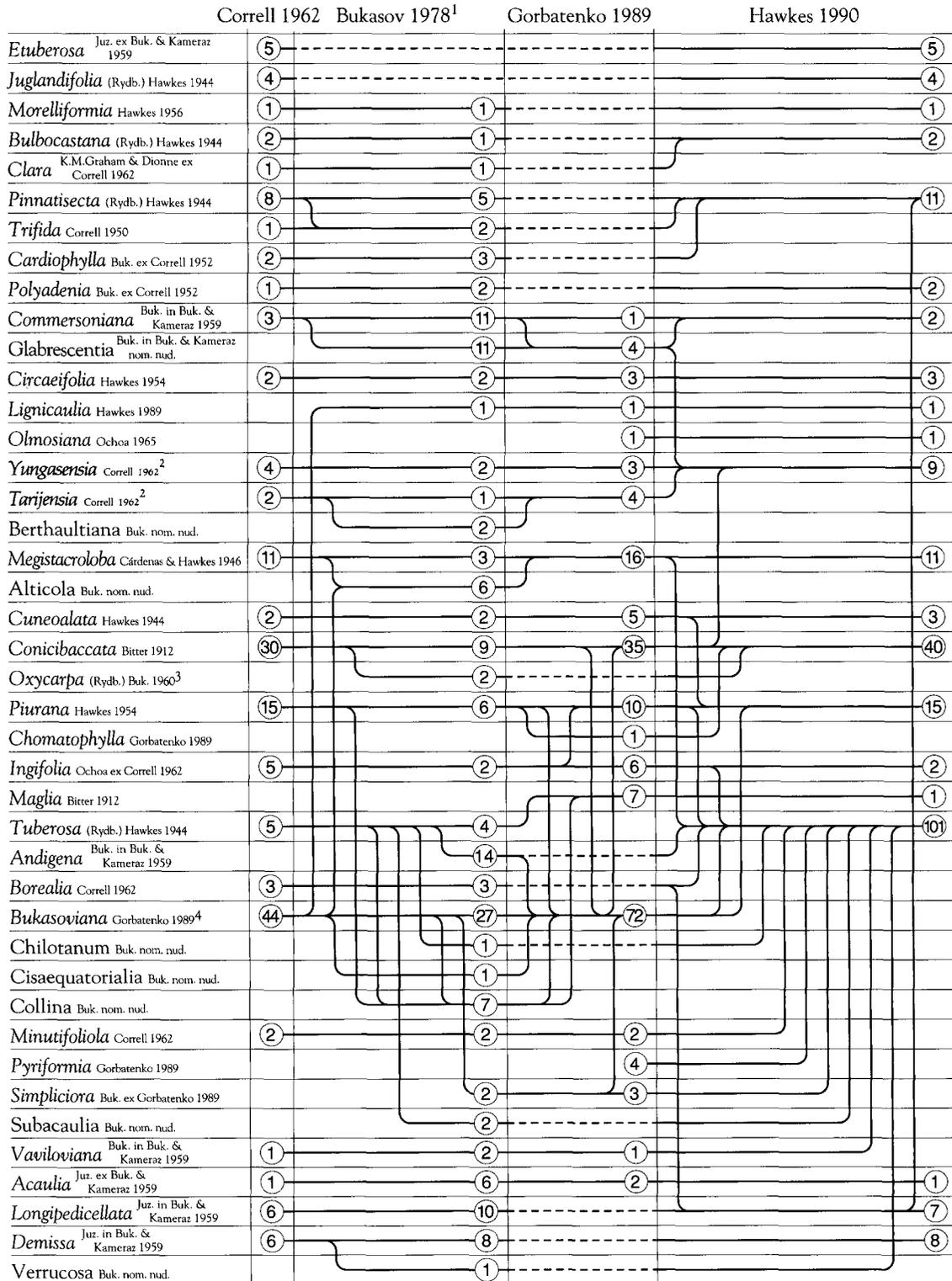


Fig. 2.

hypothesis overlooks variability of some of its component taxa. 3. Numerous differences of opinion exist about species boundaries and rank of infraspecific taxa. 4. Hawkes & Hjerting (1989) and Hawkes (1990) hypothesize much more natural hybridization than Ochoa (1990a). 5. Ochoa (1990a) provides a slightly more conservative treatment of the Bolivian wild species by his recognition of fewer taxa. 6. Many taxa are extremely similar morphologically.

The lack of exactly parallel treatments is expected in some groups because the reproductive strategies of different groups affect the degree and pattern of variation and the consequent ease of interpretation by Linnaean nomenclature (Grant, 1981). *Solanum* sect. *Petota* has been interpreted to be composed of morphologically similar species, partially isolated by ecogeographical factors. Hawkes (1990) applies the Andersonian concept of "hybridization of the habitat" (Anderson, 1949) to this group, and hypothesizes the vegetative persistence of hybrids as one possible cause of taxonomic confusion. Although many species can be freely crossed artificially to form F_1 and later-generation hybrids (Hawkes, 1958), Hawkes (1990) suggests that cryptic structural differentiation of the chromosomes and habitat specialization maintain the species as distinct.

An analysis of the history of the series concept sheds some light on the possible reasons for the problem of poorly defined series. When Bitter (1912, vol. 11: 349–394) first described ser. *Conicibaccata* and *Maglia*, the morphological distinction between the conical fruits of the former and the round to ovoid fruits of the latter

presented few problems taxonomically. Similarly, Rydberg's (1924) informal groups (*Bulbocastana*, *Juglandifolia*, *Oxycarpa*, *Pinnatisecta*, *Tuberosa*; these names were later validated as series by Hawkes (1944), and Bukasov (1960)), generally formed phenetically distinct groups. A later proliferation of series names produced some series that were morphologically indistinguishable. Many of these names were advanced by the Russian school (Bukasov, 1939, 1978; Bukasov & Kameraz, 1959; Gorbatenko, 1989) that followed the concepts of Vavilov (1940, 1957), who included a strong geographic component into systematic and phyto-geographic concepts. This geographic concept is embodied in the names of some of the series (e.g., *Borealia* = from the northern part of the range of the group in the United States, Mexico, and Central America; *Collina* = plants of the loma hills in Peru and Chile; *Cisaequatorialia* = plants north of the equator; *Transaequatorialia* = plants south of the equator). This geographic bias is evident even at the species level in Hawkes's (1990) treatment of the very similar species *S. colombianum* Dunal (4x, from Columbia) and *S. nemorosum* Ochoa (6x, from Peru). He states "In its general habit [*Solanum nemorosum*] resembles *S. colombianum* but is surely too far south to be related to it."

Hawkes (1990) argues for a morphological species concept and most decisions on species, subspecies, or varietal boundaries made by Gorbatenko, Hawkes, Ochoa, and others use morphological data to intuitively define taxa. Only a few of these taxonomic decisions have been tested by numerical methods. In our opinion, the main

Fig. 2. A chronological history of the hypotheses of placement of species into series by Correll (1962), Bukasov (1978), Gorbatenko (1989), and Hawkes (1990). The non-italicized names of Bukasov have been treated as series but are not validly published. Solid lines connecting series indicate the maintenance or transfer of species between series. Dotted lines indicate that an author did not treat these series. The numbers in circles are the number of species accepted for the series.

¹Bukasov (1978) groups his 36 series into 25 invalidly-published subsections.

²Correll (1962) described the series *Yungasensia* and *Tarijensia*. In order to conform to nomenclatural rules the spelling of these names must be changed to *Yungasensia* and *Tarijensia*. Gorbatenko (1989) subdivides ser. *Tarijensia* into two subseries: *Tarijensia* (cited as subser. *Tarijensia* [Corr.] Gorbatenko and *Berthaultiana* Buk. ex Gorbatenko (cited as *Berthaultiana* [Buk.] Gorbatenko).

³Rydberg (1924) treated *Oxycarpa* as an informal group and failed to provide a description and designation of rank, but the name was validly published because his dichotomous key serves as a diagnosis. The earliest publication that treats the name *Oxycarpa* at the rank of series validates the name. Bukasov's (1939, 1955) earlier taxonomic treatments referred to *Oxycarpa* as a "group", and the earliest publication we can find that treats the name as a series is Bukasov (1960).

⁴Gorbatenko (1989) subdivides ser. *Bukasoviana* into seven validly-published subseries: *Andreana* Hawkes ex Gorbatenko 1989 (cited as subser. *Andreana* [Hawkes] Gorbatenko), *Angustisecta* Buk. & Gorbatenko 1989, *Latisecta* Buk. & Gorbatenko 1989, *Regularifolia* Gorbatenko, 1989, *Multidissecta* Buk. & Gorbatenko, *Vigultoria* Buk. & Gorbatenko, and *Collina* (Buk.) Gorbatenko.

problem in many taxonomic interpretations in sect. *Petota* is the lack of documentation of morphological variability within taxa. Most authors (i.e., Correll, 1962; Hawkes, 1990; Ochoa, 1990a) indicate much phenotypic plasticity within taxa and the necessity to use a broad species concept. In practice, many taxa are narrowly defined by minor and often overlapping character states, and variability frequently either is not documented or ignored. Some of these taxa, however, later may prove to be supported by multivariate analyses, and their intuitive recognition by Gorbatenko, Hawkes, Hjerting, Ochoa, and others may indicate insightful judgement. Such a complex pattern of overlapping character states but with multivariate support for taxa occurs between *S. megistacrobium* and *S. toralapanum* (Giannattasio & Spooner, unpublished data), and such support may be found between other similar taxa. Future evaluation of the numerous opposing hypotheses of taxonomic boundaries will be greatly facilitated by explicit and repeatable techniques with a clear presentation of the populations examined and the analytic methods used.

Many taxa lack comparisons to similar or even conspecific taxa. This lack of comparison is due to four factors: First, new species descriptions frequently lack comparisons to similar taxa. Second, most treatments are regional (Ochoa, 1962; Hawkes & Hjerting, 1969, 1989; Ochoa, 1990a) and do not document variability of taxa throughout their entire ranges. Even the comprehensive treatments (Correll, 1962; Gorbatenko, 1989; Hawkes, 1990) rely heavily on geographic characters and fail to compare similar taxa from different regions. Hawkes (1990) divides the 94 wild taxa of ser. *Tuberosa* into three regional groups (1. Mexico south to Ecuador, 2. Peru, and 3. Bolivia, Argentina, and Chile), using distribution as the sole criterion, and does not compare very similar species from Peru (*S. bukasovii*, *S. canasense*, *S. multidissectum* Hawkes) with those from Bolivia (*S. achacachense*, *S. brevicaulis*, *S. leptophyes*). Occasionally, authors have synonymized many species (e.g., Brücher, 1974, 1985; Ugent, 1966) or have relied on the "species complex" designation for variable taxa (e.g. the "group" concept of cultivated taxa of Dodds (1962), or the "*S. brevicaulis* complex" or "*S. stenotomum* complex" of Grun (1990)), but

Gorbatenko, Hawkes, and Ochoa largely ignore or do not investigate these arguments for synonymy (except Ochoa's (1990a) treatment of *S. canasense* and *S. bukasovii*, see above). Third, most treatments only provide comparative data on morphologically similar species within series. Because of the vast differences of placement of species in series (Table 2; Spooner & Sytsma, 1992), a comparison of similar or possibly conspecific taxa from different series is ignored. Fourth, the cultivated species treated in Gorbatenko (1989), Hawkes & Hjerting (1989), Hawkes (1990), and Ochoa (1990a) are keyed separately from the wild relatives, avoiding the necessity to provide diagnostic characters separating the wild from the cultivated taxa.

Ploidy level is used to great extent within sect. *Petota* to help define species and series. Natural ploidy levels include diploids ($2n = 2x = 24$), triploids, tetraploids, pentaploids, and hexaploids ($2n = 6x = 72$); natural aneuploidy is unknown (Hawkes, 1990). Odd-ploidy cytotypes are recognized within the following species: *S. bulbocastanum*, *S. cardiophyllum* Lindley, *S. chacoense*, *S. jamesii* Torrey, *S. calvescens* Bitter, *S. commersonii* Dunal, *S. maglia* Schldl., *S. microdontum*, *S. venturii* (Tarn & Hawkes, 1986; Hawkes, 1990). Even-ploidy cytotypes are recognized within other species: *S. gourlayi*, *S. oplocense* (Hawkes, 1990). Some morphologically very similar or possibly conspecific species are distinguished by different ploidy levels, however. For example, *S. colombianum* and *S. moscopanum* Hawkes are extremely similar species that Hawkes (1990) distinguishes by minor differences of corolla shape, but *S. colombianum* is tetraploid and *S. moscopanum* is hexaploid. Our observations of the germplasm accessions of these two species at the Inter-Regional Potato Introduction Project (IR-1) indicate that corolla shape does not distinguish these species. Similarly, Hawkes & Okada (1988) distinguish *S. ugentii* Hawkes & Okada (4x) by a combination of leaf, peduncle, and corolla color character states that we have observed in other species (e.g., *S. tuberosum* ssp. *andigena* Hawkes, 4x). They focus on the tetraploid chromosome number of *S. ugentii* to help distinguish it from diploid wild species without a thorough examination of the range of morphological variability within similar wild and cultivated species at all ploidy levels. Our observations suggest that the

range of variability between morphologically similar "species" with different ploidy levels may equal that within cytotypes.

Directions for future research. Hawkes & Hjerting (1969, 1989) and Hawkes (1990) rely heavily on the observation of artificial interspecific hybrids to speculate on biological isolating mechanisms between similar taxa (their "F₂ breakdown hypothesis"), but these experiments lack control crosses and the data analyses lack statistical treatment. For example, many F₂ hybrids are simply listed as "unthrifty" or as showing "breakdown," without further data. The crossing tests should be redone with sufficient control crosses and a statistical presentation of the results to gain insights into biological isolating mechanisms in sect. *Petota*.

The treatments analyzed here often use vague terminology to advance hypotheses of taxonomic relationships that hinders their objective interpretation and comparison. For example, Hawkes & Hjerting (1969) or Hawkes (1990) use "may be related in some way," "possibly less-related" . . . "not too remote from," "features that link it to," "slight relationship." Ochoa (1990a) uses "affinity," "constitutes the closest link between," "shows some relationship to," "is somewhat related to." Hypotheses of similarity or relationship should be clearly stated as phenetic, cladistic, or phylogenetic (e.g. Stuessy, 1990) for objective evaluation. Phenetic studies are needed to help circumscribe taxa, as is done by Clausen & Crisci (1989) and van den Berg & Spooner (in press). Cladistic studies are needed to reinvestigate phylogeny. A synthesis of morphological and molecular data sets awaits a better understanding of the species boundaries and morphological diversity in the group.

New data addressing series concepts and cladistic relationships are evolving from chloroplast DNA restriction site investigations (Hosaka et al., 1984; Spooner & Sytsma, 1992). Genome maps are providing powerful new insights into outgroup relationships, such as the tomato-potato studies of Bonierbale et al. (1988). New data addressing questions of genetic diversity within and between populations and lower-level cladistic relationships are being provided by nuclear DNA data (Debener et al., 1990; Hosaka & Spooner,

in press), isozyme data (Zimmerer & Douches, 1991; Spooner & Douches, 1992), and multivariate analysis of morphological data (van den Berg & Spooner, in press).

Hybridization and introgression within sect. *Petota* have been investigated by numerous and detailed studies. These studies have involved the inference of hybridity from morphological, physiological, ecological, geographical, cytological, or secondary chemical data, using natural and synthetic hybrids (e.g. studies on *S. ajanhuiri* Juz. & Buk. (Huamán et al., 1980, 1982, 1983; Johns et al., 1987), *S. chacoense* (Hawkes, 1962a; Juned et al., 1988), *S. commersonii* (Tarn & Hawkes, 1986), *S. curtilobum* Juz. & Buk. and *S. juzepczukii* Buk. (Hawkes, 1962b; Jackson et al., 1977; Schmiediche et al., 1980, 1982), *S. x edinense* Berthault (Ugent, 1967), *S. x indunii* Okada & A. Clausen (Okada & Clausen, 1982), *S. raphanifolium* Cárdenas & Hawkes (Ugent, 1970), *S. x rechei* (Okada & Hawkes, 1978), *S. x sucrense* Hawkes (Astley & Hawkes, 1979), *S. tuberosum* ssp. *andigena* (Cribb & Hawkes, 1986) *S. x viirsooi* Okada & A. Clausen (Okada & Clausen, 1985), and various cultivated species (Jackson et al., 1978; Grun, 1990; Matsubayashi, 1991)). DNA and isozyme studies are extending the scope of these pioneering investigations by helping to distinguish between competing hypotheses of hybridization, convergent evolution, the retention of ancestral characters, and phenotypic plasticity (e.g., studies on *S. raphanifolium* (Spooner et al., 1991) and *S. tuberosum* (Oliver & Martinez Zapater, 1984; Hosaka, 1986; Hosaka & Hanneman, 1988a,b; Rabinowitz et al., 1990; Douches et al., 1991)).

The extreme similarity of many of the taxa in *Solanum* sect. *Petota*, combined with the 531 basionyms, necessitates that future descriptions of new taxa be accompanied with a key to similar species and documentation of infraspecific variability. Many taxa in *Solanum* sect. *Petota* have been described from single populations of non-fruiting material, despite the importance of fruit shape as a taxonomic character. For example, Ochoa (1990b) described *S. serratoris* Ochoa from two herbarium specimens of non-fruiting material and stated "no close affinities [of *S. serratoris*] have been found with any other known tuber-bearing species," although it

is synonymous with *S. andreanum* Baker, as are other species accepted by current taxonomists (Spooner et al., in press).

Despite our criticisms of the treatments analyzed above, they represent lifetimes of intensive work, impressive in volume, scope, and detail. We are fortunate to have such a wealth of taxonomic information to provide data and ideas for the continuing refinement of the systematic hypotheses in *Solanum* sect. *Petota*. Our goal is to build upon and refine these treatments, using traditional and modern techniques. We aim to produce a more practical, repeatable, and stable taxonomy, primarily applying the morphological species concept, based on clear discontinuities in morphological patterns, without a reliance on past identifications, place of origin, or chromosome numbers as has been the practice in sect. *Petota*. Section *Petota* has many phenetically distinct groups of populations (here viewed as species) that have the ability to freely exchange genes artificially to advanced generation hybrids. Lumping these species with an application of the biological species concept would reduce the species in sect. *Petota* to very few, but hide much potentially useful genetic and phylogenetic information. We would modify our application of the morphological species concept only with compelling information that groups of morphologically coherent populations with different geographical ranges were members of different clades or reproductively isolated biologically. Our revised taxonomy will reduce the number of names in the group, and will provide a better estimate of the range of morphological and genetic diversity to better serve all sciences using the wild species. Once potato species are more objectively defined, cladistic studies, comparisons of genetic partitioning within and among species, and of patterns of geographical partitioning of this variability can better proceed. The patterns to emerge within the larger morphologically coherent species are more appropriately treated as ecotypes or biotypes, similar to the treatment of the widespread and highly polymorphic Andean endemic *Lycopersicon peruvianum* (L.) Mill. (Rick, 1963; Taylor, 1986), or as ecotypes.

Considering the importance of taxonomy to plant breeding (Hawkes, 1980), and the increasing use of the wild species for practical breeding programs (Hanneman, 1989; Plaisted & Hoopes,

1989), these basic questions of taxonomic boundaries, evolution, and interrelationships of wild potatoes will continue to increase in importance. We agree with Harlan & de Wet (1971) that conflicting taxonomies greatly confuse breeders and that crossability is one of their most important data sets. A refined taxonomy of sect. *Petota* will complement the gene pool concept with additional information to help breeders by providing a more accurate interpretation of the morphological and genetic diversity within crossing groups. Better-planned extensions of breeding programs using the wild species will result by choosing or avoiding related or unrelated taxa based on prior breeding results. Because it takes 8–15 years from the initiation of a breeding program to a commercial variety release (Plucknett et al., 1987), a better-planned choice of initial breeding materials, based on more accurate estimates of species boundaries and cladistic relationships, will save much time and money.

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