Species Concepts and Relationships in Wild and Cultivated Potatoes

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Abstract

Wild and cultivated potatoes (*Solanum* section *Petota*) present challenges to taxonomists arising from lack of clearly defined morphological character differences among many species, phenotypic plasticity, a range of ploidy levels from diploid to hexaploid, and hybrid speciation and introgression. Taxonomic treatments of the group have differed greatly regarding numbers of species and hypotheses of their interrelationships at the series level. Recent morphological phenetic studies and molecular studies have confirmed the general lack of clearly defined species, have shown the need to use a number of character states with overlapping ranges for species delimitation (polythetic support), and have suggested the need for the reduction of species in section *Petota*. Molecular studies have sometimes confirmed hypotheses of hybridization and sometimes have failed to support them. Molecular studies have suggested the need for a reconsideration of the traditionally held series concepts. Currently, section *Petota* contains 196 wild species and a single cultivated species, *Solanum tuberosum*, with eight landrace cultivar groups, exclusive of the modern cultivars that are not yet classified into cultivar groups. The number of wild species likely will decrease with future study. These points are here illustrated by (1) a discussion of published species level studies in *Solanum* series *Longipedicellata*, the *Solanum brevicaule* complex, and the cultivated landrace populations of potatoes; (2) reinvestigations of hybridization in *S. chacoense*, *S. raphanifolium* and *S.* ×*rechei*; and (3) studies of ingroup and outgroup relationships of section *Petota*.

INTRODUCTION

Solanum L. section *Petota* Dumort., the potato and its wild relatives, is distributed from the southwestern United States to southern Chile, with a concentration of diversity in the Andes. Section *Petota* traditionally presents challenges to taxonomists arising from similarity among species, phenotypic plasticity, a range of ploidy levels from diploid to hexaploid, and hybrid speciation and introgression. Different taxonomists have recognized different numbers of species and have grouped these species quite differently into series. The latest comprehensive taxonomic treatment by Hawkes (1990) recognized 232 species, partitioned into 21 series. Spooner and Hijmans (2001) updated this to 196 wild species and seven cultivated species, considering taxonomic changes (new species descriptions and synonymized species) made since 1990.

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MORPHOLOGICAL PHENETIC STUDIES AT THE SPECIES LEVEL

Species Concepts

Species have a central place in taxonomy as they form the basic units of biological classification (Davis and Heywood, 1963; Greuter et al., 2000), but there is no consensus on how to define species. Species concepts have changed considerably with the development of new data and theory. Spooner et al. (2003) summarized six major classes of species concepts of which the morphological, interbreeding, cladistic, and eclectic species concepts are the most widely applied.

Morphology provided the first data type used to infer species boundaries. Such morphological data initially relied on subjective interpretation of the overall form of the plant, and these data frequently were used to make intuitive judgments on what constituted a species. Because of its utility for routine identifications of large numbers of germplasm samples in genebanks, the morphological species concept is still practical and widely applied. A potential problem was an intuitive (subjective) application of the concept, where taxonomists would make “judgments” of species based on impressions of overall form, precluding an objective evaluation by others.

The advent of computers, however, allowed the practical application of multivariate techniques to taxonomic data. In practice, morphological, anatomical, chemical, or any character type was appropriate for analyses. These methods opened up these classifications to scrutiny, as data and analytical techniques were open for evaluation by all and not hidden as inscrutable impressions of experts. In practice, a taxonomist scores quantitative or qualitative characters and enters them on rectangular data matrices (data entry cells with characters vs. individuals). Various algorithms then transform this matrix into a triangular similarity (or dissimilarity) matrix of individuals by individuals. Various data reduction techniques then convert the similarity matrix to a graphical display of phenetic trees (phenograms or dendrograms), ordination plots (as principal components analyses, principal coordinates analyses, or multidimensional scaling analyses). Decisions are made on species limits based on clustering of individuals, but there is no universally accepted objective criterion to determine the degree of clustering to define species or higher taxonomic levels.

Recently morphological phenetic studies, sometimes accompanied by parallel molecular studies of the same accessions using isozymes, Random Amplified Polymorphic DNA (RAPDs), Amplified Fragment Length Polymorphisms (AFLPs), and simple sequence repeats (SSRs or microsatellites) have been applied to potato. These include a study of species boundaries of *S. berthaultii* and *S. tarijense* (Spooner and van den Berg, 1992a), subspecies of *S. microdontum* (Van den Berg and Spooner, 1992), species boundaries of *S. megistacrolobum* and *S. toralapanum* (Giannattasio and Spooner, 1994a,b), species boundaries within. series *Demissa* (Spooner et al., 1995), species boundaries within series *Circaeifolia* (Van den Berg and Groendijk-Wilders, 1998; Van den Berg et al., 2001) species boundaries within the *Solanum brevicaule* complex (Van den Berg et al., 1996, 1998; Miller and Spooner, 1999), species boundaries within series *Longipedicellata* (Spooner et al., 2001; Van den Berg et al., 2002), species boundaries within the Mexican diploid species (Lara-Cabrera and Spooner, in press), and species boundaries of the cultivated potatoes (Huamán and Spooner, 2002). Three of these studies are highlighted below.

Solanum* Series *Longipedicellata

Hawkes (1990) recognized six species in series *Longipedicellata*. Morphological studies (Spooner et al., 2001) suggested that there were at best only three species in the series: 1) *S. polytrichon*, 2) *S. hjertingii* (including *S. matehualae*), and 3) *S. stoloniferum* (including *S. fendleri* and *S. papita*). That study showed these species to be supported only by many character states exhibiting overlapping ranges with other species (Fig. 1), a phenomenon termed polythetic support (Sokal and Sneath, 1963). This was especially true for *S. polytrichon*, supported only by a canonical variate analysis, but not by a principal components analyses that intermixed *S. polytrichon* with many other species. Putative *S. polytrichon* diagnostic characters of spreading pubescence, enlarged terminal leaflets, and white corollas varied tremendously in this species, and it is impossible to unambiguously identify many specimens.

Van den Berg et al. (2002) analyzed a subset of the species analyzed for morphology with AFLPs, RAPDs, and chloroplast microsatellites (cpSSRs). The cpSSR results were completely discordant with AFLP and RAPD results and greatly intermixed species. Different molecular results of the same taxa are rarely completely concordant (Wendel and Doyle, 1998), and microsatellite results are frequently very discordant with other molecular data (Milbourne et al., 1997; Russell et al., 1997). The great cpSSR discordance could be a function of the low numbers of markers (10 as scored as alleles in a locus, 44 when scored as separate characters, vs. 79 for RAPDs and 419 for AFLPs). Another possible cause for discordance of cpSSR results may be the predominantly maternal inheritance of cpDNA in *Solanum* (Corriveau and Coleman, 1988) and a separate history of chloroplasts because of hybrid origins (Wendel and Doyle, 1998). If these cpSSR data are providing true phylogenetic signal, it suggests a history of extensive separate and independent origins of members of series *Longipedicellata*, a hypothesis that needs further testing with genome-specific markers.

The RAPD and AFLP results were largely concordant to each other. An analysis of these combined data support the synonymy of *S. hjertingii* and *S. matehualae*, and intermix *S. papita* and *S. fendleri*. However, accessions of *S. stoloniferum* have a tendency to cluster but with exceptions, and *S. polytrichon* is intermixed with *S. fendleri* and *S. papita*. The cpSSRs fail to distinguish any of the species in series *Longipedicellata*. Van den Berg et al. (2002) interpreted the combined morphological and molecular data to support only two species in series *Longipedicellata*: *S. hjertingii* and *S. stoloniferum*.

Solanum hjertingii (to include *S. matehualae*) is embedded in other members of series *Longipedicellata*. Recently, Olmstead (1995) argued that geographically localized models of speciation typically produce a monophyletic daughter species and remnant paraphyletic progenitor species, and argue that a strict concept for monophyly fails for many species. Olmstead (1995) termed the former apospecies and the latter plesiospecies. The recognition of *S. hjertingii* is justified by its morphological distinctness (Spooner et al., 2001), distinct range (in northwestern Mexico) and an apospecies concept.

Solanum brevicaule Complex

The *Solanum brevicaule* complex is a group of approximately 30 morphologically very similar taxa within section *Petota*. This complex was first recognized, in part, by Ugent (1970) as a taxonomically confusing group of putative ancestors of the cultivated potato species endemic to central Peru, Bolivia, and northern Argentina. Wild members of the *S. brevicaule* complex are difficult to distinguish from each other and from the cultivated species. Like in *Solanum* series *Longipedicellata,* no qualitative characters distinguish these species, and they differ only by widely overlapping character states (Spooner and van den Berg, 1992b; Van den Berg et al., 1996; Van den Berg et al., 1998).

Van den Berg et al. (1998) examined 256 populations of 30 taxa. They concluded that only three groups could be distinguished with difficulty, and only by a widely overlapping series of morphological character states: 1) Peruvian and immediately adjacent northwestern Bolivian accessions (the “northern” populations), including wild species and all the cultigens, 2) northwestern Bolivian and Argentinean accessions (the “southern” populations) and *S. verrucosum* from Mexico (including only wild species), and 3) the Bolivian and Argentinean wild species *S. oplocense*. In practicable taxonomic application (i.e., without resorting to multivariate analyses), however, only *S. oplocense* can be distinguished with difficulty from these two geographic groups, and the geographic groups cannot be distinguished from each other. The morphological data (Van den Berg et al., 1998) suggested that many of these species should be relegated to synonymy.

Most of the taxa are widely interfertile, at least in early generations (Hawkes, 1958; Hawkes and Hjerting, 1969, 1989; Ochoa, 1990, 1999). Most taxa are diploid and interbreed where they overlap (Hawkes, 1990). This suggests that the species as currently recognized have recently evolved from a common ancestor, form a single gene pool, or are perhaps even conspecific.

A subset of these accessions was examined with RAPDs and single- to low-copy nuclear RFLPs. Cladistic analyses of both data sets are largely concordant with each other and with the morphological phenetic analyses. All three data sets separate members of the complex into the northern populations and the southern populations. The molecular results suggest that the complex is paraphyletic as currently circumscribed, as it contains not only representatives of the complex but phenetically distinctive species that were never placed in the complex (Fig. 2).

These combined morphological and molecular results suggest that many species of the *S. brevicaule* complex should be relegated to synonymy, but a practical taxonomic solution to this is unclear. The molecular data would suggest the “northern” and “southern” populations as two species, but as mentioned above these two “species” are so similar as to be impractical to distinguish from each other. An additional complication is the apparent intermixing of the southern members of the complex with phenetically distinctive species that have not previously been considered to be members of the complex (Fig. 2), making this possible southern species paraphyletic. Continuing studies are using additional molecular markers and a replicated morphological field trial in Peru for additional insights to this complex problem.

Landrace Cultivated Potatoes

The latest comprehensive taxonomic treatment of section *Petota* by Hawkes (1990) recognized seven cultivated species. However, as in the wild species, different taxonomists rarely agreed, with Dodds (1962) recognizing three species, Bukasov (1971) and Lechnovich (1971) together recognizing 21 species, and Ochoa (1990, 1999) recognizing nine species. Dodds (1962) classified cultivated potatoes as cultivar-groups under the International Code of Nomenclature of Cultivated Plants (ICNCP; Greuter et al., 2000), while the other taxonomists classified them as species under the International Code of Botanical Nomenclature (ICBN; Trehane et al., 1995). Cultivar-groups are taxonomic categories used by the ICNCP to associate cultivated plants with traits that are of use to agriculturists, but have no necessary “naturalness” in a biological sense.

Huamán and Spooner (2002) examined morphological support for the landrace populations of cultivated potatoes (i.e., all cultivated species except the modern cultivars bred in post-Colombian times) using representatives of all seven species and most subspecies as outlined in Hawkes (1990). These taxa are *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, *S. phureja* subsp. *phureja*, *S. stenotomum* subsp. *stenotomum*, *S. stenotomum* subsp. *goniocalyx*, *S. tuberosum* subsp. *andigena*, and *S. tuberosum* subsp. *tuberosum*. The results show some phenetic support for *S. ajanhuiri*, *S. chaucha*, *S. curtilobum*, *S. juzepczukii*, and *S. tuberosum* subsp. *tuberosum*, but little support for the other taxa. Like in the wild species described above, most morphological support for these “species” was only by a suite of characters with overlapping character states. They interpreted these results in light their likely hybrid origins, multiple origins, evolutionary dynamics of continuing hybridization, and their classification philosophy, to classify all landrace populations of cultivated potatoes as a single species, *S. tuberosum*. They divided *S. tuberosum* into eight cultivar-groups: Ajanhuiri Group, Andigena Group, Chaucha Group, Chilotanum Group, Curtilobum Group, Juzepczukii Group, Phureja Group, and Stenotomum Group. They deferred classification of modern cultivars, traditionally classified in Tuberosum Group, to a later study.

REINVESTIGATIONS OF HYBRID SPECIATION

Hybridization has been thought to be a major evolutionary force at both the diploid and polyploid levels (Rieseberg, 1995). Traditionally, additive morphological traits, sometimes supplemented with crossability data, or artificial reconstruction of the hybrids, were the main data used to infer hybridity. Nonetheless, Rieseberg and Ellstrand (1993) showed that hybrids are no more likely to display intermediate character states than parental traits, and can even express an array of transgressive or novel traits. Other long-held beliefs that hybrids are uniformly less fit than their parents, and that they exhibit character coherence (parental characteristics remain associated) have also been questioned (Rieseberg, 1995).

Molecular markers present powerful new tools to reinvestigate hypotheses of hybridization. One way to use these markers is to search for additivity of parental-specific molecular markers in the hybrids. The utility of this method depends on discovering species-specific markers, yet this may be difficult because many hybrids are between closely related taxa that have not diverged enough to have formed specific markers. Also, the utility of this method decreases with time of divergence, as markers from both parents can be disrupted through recombination, and both can mutate to new markers. This can happen very rapidly as was shown by Song et al. (1995) who showed extensive loss of markers and novel new markers to appear in just the F_5 generation of an artificial interspecific *Brassica* hybrid. This was constructed as a homozygous allopolyploid, demonstrating that at least on the polyploid level species can generate extensive genetic diversity in a very short period of time.

Over 20% of the approximately 200 wild potatoes are of putative diploid or polyploid hybrid origin (Spooner and van den Berg, 1992a). To date, three molecular studies of hybrid speciation have been conducted on diploid wild potatoes, using data from cpDNA and mitochondrial restriction site data, nRFLPs, and RAPDs. Two of these hypotheses were not supported: 1) *Solanum raphanifolium* by Spooner et al. (1991), and *Solanum chacoense* by Miller and Spooner (1997). One species was supported as a hybrid, *S. ×rechei* (Clausen and Spooner, 1998). In addition, one experimental study supported local introgressive hybridization between the wild species *S. sparsipilum* and the cultivated species *S. stenotomum* (Rabinowitz et al., 1990). Clearly, the many remaining hypotheses of hybrid speciation and introgression need corroboration with further studies before these phenomena can be unequivocally cited as widespread in section *Petota*.

INTERSPECIFIC RELATIONSHIPS

Outgroup Studies

Hawkes (1990) divided section *Petota* into subsection *Potatoe*, with 19 tuber-bearing series, and subsection *Estolonifera* with two non-tuber-bearing series: *Etuberosa* and *Juglandifolia*. He considered the close relatives of section *Petota* to be members of *Solanum* section *Basarthrum*.

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 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 section *Petota*, but the members of series *Etuberosa* and *Juglandifolia* as treated by Hawkes (1990) did not belong to *Petota* and were placed as outgroups (Fig. 3).

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) removed series *Etuberosum* from section *Petota*, recognizing it at the sectional level as section *Etuberosum*. Subsequent molecular studies are supporting these outgroup relationships of section *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). *Solanum* section *Etuberosum*, and then *Solanum* section *Basarthrum* are supported as sister to tomatoes and potatoes. 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 *rbc*L and *ndh*F. Peralta and Spooner (2001) supported all components of the cpDNA phylogeny of Fig. 3 with DNA sequences of the nuclear-encoded granule bound starch synthase ("waxy") gene.

The studies reviewed above all support section *Petota* as a monophyletic group, exclude series *Etuberosa* and series *Juglandifolia* from section *Petota*, and recognize the sister-group relationships of potatoes and tomatoes within *Solanum*. Some taxonomists, as Lester (1991), and Nee (1999), continue to maintain *Lycopersicon* as a distinct genus for nomenclatural stability, arguing adherence to convenience and a phenetic criteria for classification.

Ingroup Studies

The 21 series taxonomic series taxonomic classification by Hawkes (1990) is only one of many taxonomic treatments in section *Petota* (Spooner and van den Berg, 1992b) (Fig. 4). Discordant taxonomic treatments (e.g., Correll, 1962; Hawkes, 1990; Ochoa, 1999) differ greatly in their hypotheses of the number of species and affiliation to series. These generate confusion among users regarding the best taxonomy to use, and even the reliability of taxonomy to guide users at all. Chloroplast DNA restriction site data (Rodríguez and Spooner, 1997; Spooner and Castillo, 1997; Castillo and Spooner, 1997), have suggested that the 21 series of Hawkes (1990) are not natural groups, but rather support only four branches of a phylogenetic tree (clades) (Fig. 3). These results need corroboration from additional molecular markers, however, as any one molecular marker can give misleading phylogenetic results (Wendel and Doyle, 1998).

CONCLUSIONS

The taxonomy of wild and cultivated potatoes has changed considerably since Hawkes (1990) regarding numbers of species and their ingroup and outgroup relationships (Fig. 3). Despite the description of ten new species since Hawkes (1990), the placement of other species in synonymy has resulted in a net decrease of 34 wild species and six cultivated species, for a current total of 196 wild species and one cultivated species with eight cultivar groups (Spooner and Hijmans, 2001; Huamán and Spooner, 2002). Definition of species remains extremely difficult, for reasons outlined in Spooner and Van den Berg (1992b) and Spooner and Hijmans (2001), that include phenotypic plasticity in different environments, sexual compatibility among many species, and hybrid speciation and introgressive hybridization. Many wild species are supported only by a range of overlapping character states, with few if any species-specific characters (only polythetic support).

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 data 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 section *Petota*, not the many series of other authors. Future studies are likely to continue to reduce species and refine concepts of species interrelationships.

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Figures

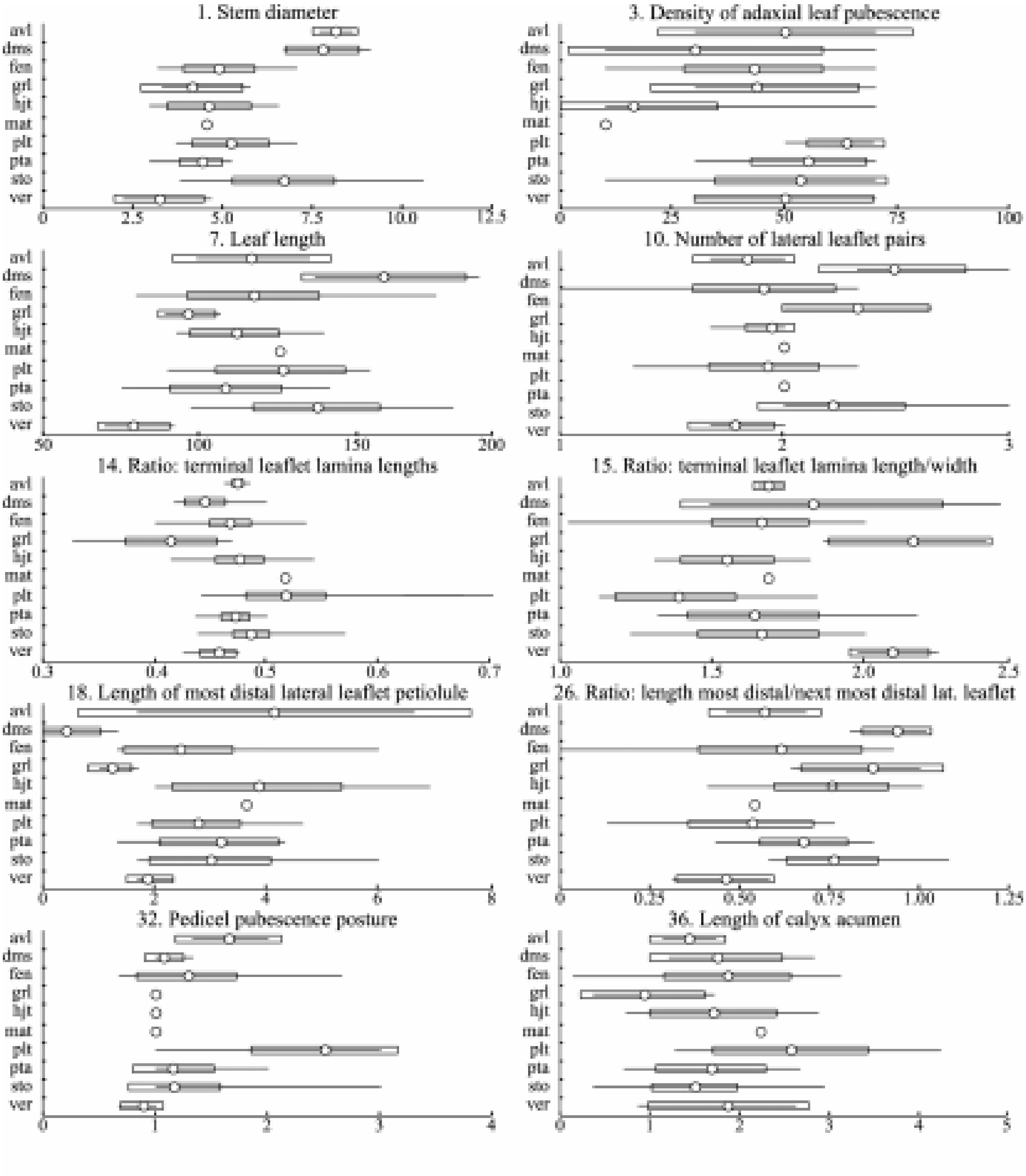

Fig. 1. A subset of ten of the 24 sets of means, ranges, and one standard deviation of the mean illustrated in Spooner et al. (2001) for the six species of *Solanum* series *Longipedicellata*, and other phenetically similar species for comparison, as recognized by Hawkes (1990). *Solanum avilesii* = avl; dms = *S. demissum*; fen = *S. fendleri*, grl = *S. gourlayi*, hjt = *S. hjertingii*, mat = *S. matehualae*; plt = *S. polytrichon*; pta = *S. papita*; sto = *S. stoloniferum*; ver = *S. verrucosum*.

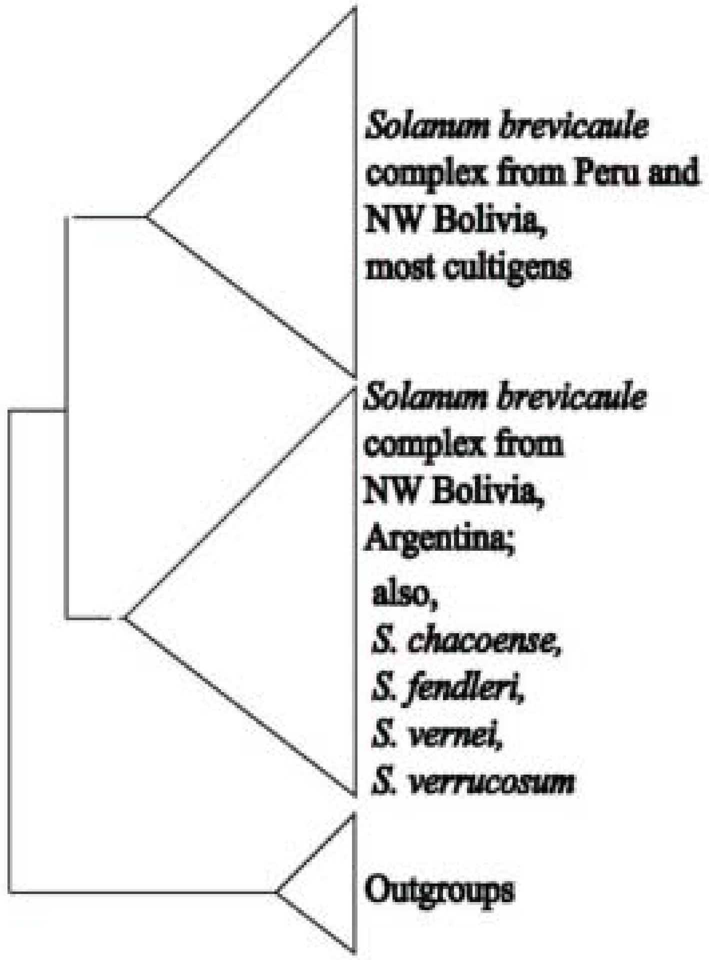

Fig. 2. A summary diagram showing the concordant results of the RAPD and nRFLP cladistic results of the *Solanum brevicaule* complex from Miller and Spooner (1999). There is little species-specific clustering of species within each expanded clade. This separation of species is concordant with the canonical variates analysis of these species using morphological data by van den Berg et al. (1998).

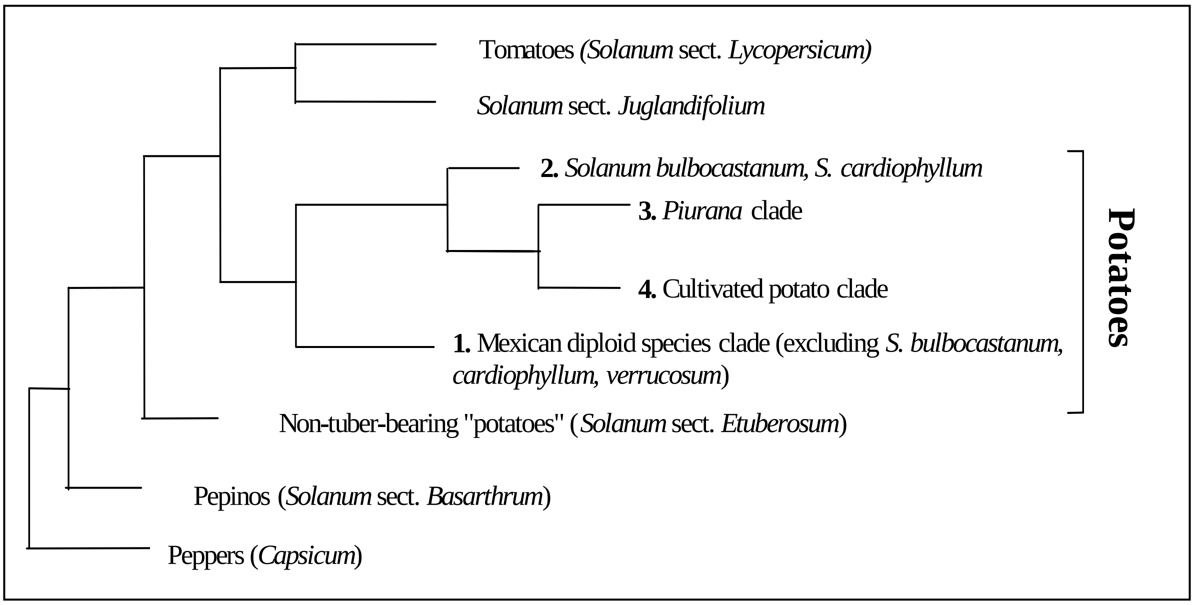

Fig. 3. Ingroup and outgroup relationships of potato, tomato, and further outgroups according to the chloroplast DNA restriction site studies of Spooner et al. (1993), Rodríguez and Spooner (1997), Spooner and Castillo (1997), and Castillo and Spooner (1997); and the "waxy" gene sequence phylogeny of Peralta and Spooner (2001).

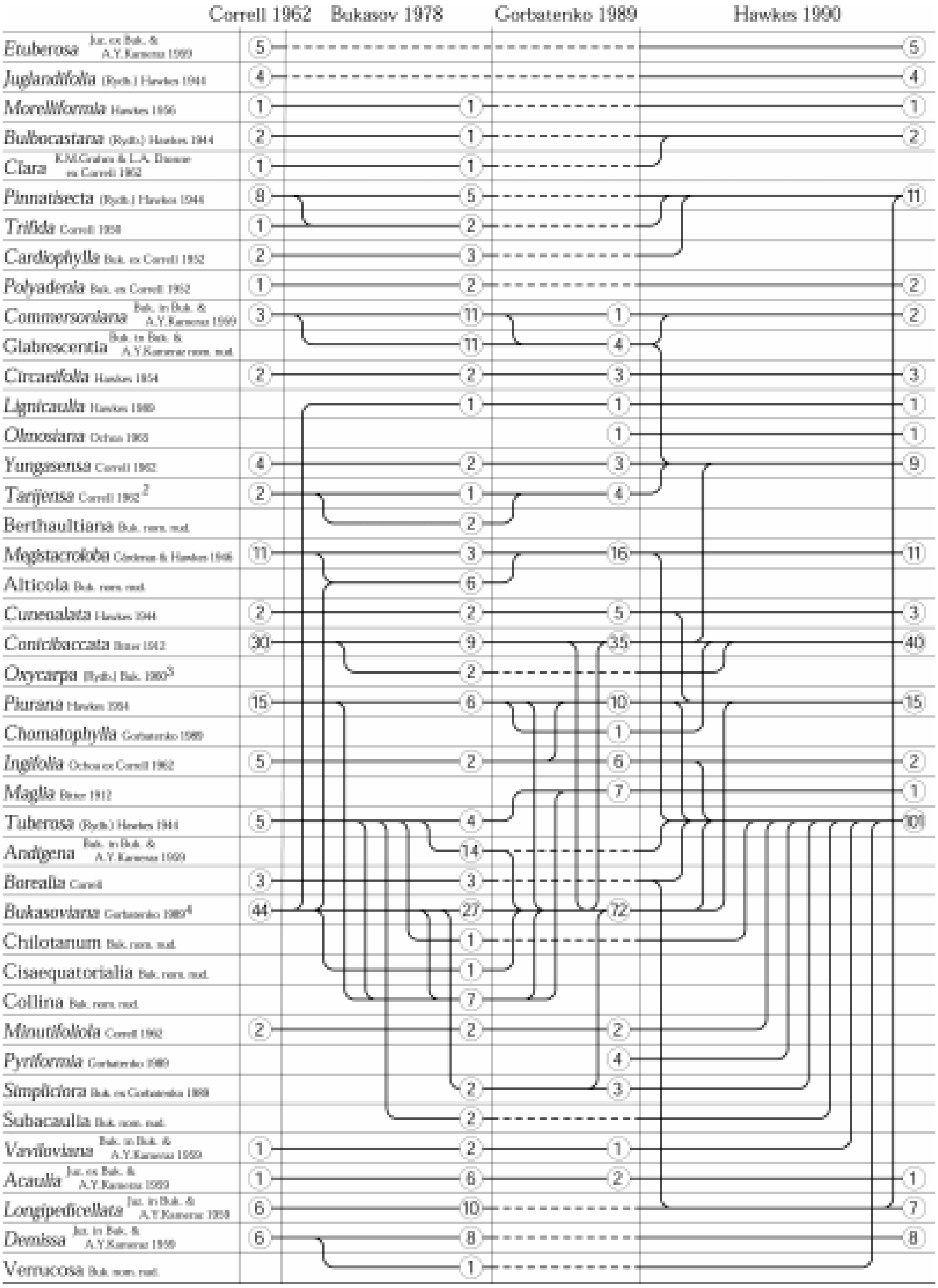

Fig. 4. A chronological history of the hypotheses of placement of species into series by Correll (1962), Bukasov (1978), Gorbatenko (1989), and Hawkes (1990). The non-italicized names of Bukasov (1978) have been treated as series but were not validly published. Solid lines connecting series indicates the maintenance or transfer of species among 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 (after Spooner and van den Berg, 1992b).