The wild ancestors of cultivated potato: the brevicaule-complex

R. G. VAN DEN BERG, N. GROENDIJK-WILDERS and J. P. KARDOLUS

Department of Plant Taxonomy, Agricultural University Wageningen, PO Box 8010, 6700 ED Wageningen, The Netherlands

SUMMARY

The closest relatives of the cultivated potato comprise a group of morphologically very similar species, which have been designated as the brevicaule-complex. The interrelationships among these species and their relationships to the cultivated species are unclear. The influences of the domestication process on these weedy plants may have determined their pattern of variation, making it difficult to assess the nature and delimitations of the entities to be recognized within this group. Multivariate methods were applied to analyse the taxonomic situation and the status of several of the involved species was evaluated.

Key-words: brevicaule, cultivated potato, multivariate analysis, *Solanum*, species complex, wild potato.

INTRODUCTION

Correll (1962: 434), in discussing relationships among a number of species of tuber-bearing Solanums (*S. canasense* Hawkes, *S. leptophyes* Bitter, *S. brevicaule* Bitter, *S. bukasovii* Juz. and others) rendered the following interesting comment: 'If all of these were placed together as one highly variable species it would probably be in the best interest of science.' Users of his book *The Potato and its Wild Relatives* (Correll 1962) have noted the extreme similarity among this group of potato species, which all belong to the series *Tuberosa*. According to Hawkes (1990), the most primitive cultivated potato, the cultigen *S. stenotomum* Juz. et Buk., is closely related to this group of species. Ugent (1966) circumscribed this group and suggested their merging into one species, *S. brevicaule* (the oldest name), which he divided into three subspecies, accommodating a total of 17 species names (Table 1). In his revision of the whole group of tuber-bearing Solanums (*Solanum* sect. *Petota*), Hawkes (1990) maintains many of these species as separate, while acknowledging their close relationship. His revision also differs from Correll's treatment in distinguishing *S. gourlayi* Hawkes from *S. leptophyes*, while assigning subspecific status to *S. vidaurrei* Cárdenas and *S. pachytrichum* Hawkes (Table 1).

Unfortunately, the keys in both Correll (1962) and Hawkes (1990) rely on geographic data to subdivide the species of series *Tuberosa*. Consequently, many of these species are not compared to each other and their extreme similarity remains unnoticed (Spooner & Van den Berg 1992). When species of this group from the same area are keyed out,

Table 1. Alternative classifications of taxa of the brevicaule-complex. Synonyms in small print

Correll 1962	Ugent 1966	Hawkes 1990
S. abbottianum	*S. brevicaule*	*S. bukasovii*
S. brevicaule	ssp. *brevicaule*	*S. abbottianum*
S. achacachense	*S. leptophyes*	*S. neohawkesii*
S. liriunianum	*S. pachytrichum*	*S. canasense*
S. colominense	*S. gourlayi*	*S. lechnoviczii*
S. bukasovii	*S. punoense*	*S. punoense*
S. canasense	*S. soukupii*	*S. soukupii*
S. lechnoviczii	*S. colominense*	*S. multidissectum*
S. fragariaefructum	*S. achacachense*	*S. fragariaefructum*
S. punoense	*S. liriunianum*	*S. achacachense*
S. neohawkesii	*S. espiranense*	*S. brevicaule*
S. lobbianum	ssp. *bukasovii*	*S. liriunianum*
S. multidissectum	*S. bukasovii*	*S. colominense*
S. soukupii	*S. abbottianum*	*S. gourlayi*
S. vidaurrei	*S. multidissectum*	ssp. *gourlayi*
S. leptophyes	*S. neohawkesii*	ssp. *saltense*
S. gourlayi	ssp. *cananense*	ssp. *vidaurrei*
S. spegazzinii	*S. canasense*	ssp. *pachytrichum*
S. pachytrichum	*S. lechnoviczii*	*S. leptophyes*
	S. fragariaefructum	*S. spegazzinii*
	S. ochoae	*S. incamayoense*

the key characters are mainly leaf dissection and pubescence, notably variable characteristics in sect. *Petota*.

Both the circumscription of the group and the distinction of its components are unclear. A number of species names is involved, referring to species which show subsequent distribution areas from north to south roughly in the following order: *S. bukasovii*, *S. canasense*, *S. multidissectum* Hawkes, *S. soukupii* Hawkes, *S. achacachense* Cárdenas, *S. leptophyes*, *S. brevicaule*, *S. gourlayi*, *S. incamayoense* Okada et Clausen, and *S. spegazzinii* Bitter (Fig. 1). Many more names are linked to this group through synonymy. Brücher (1985) designates seven species names as synonyms of *S. leptophyes*, including *S. spegazzinii* and *S. vidaurrei*. Ochoa (1990), in his treatment of the wild potato species of Bolivia, comments upon the similarity between *S. leptophyes*, *S. bukasovii* (including *S. multidissectum* and *S. canasense*), *S. brevicaule* and *S. spegazzinii*. An earlier edition of Hawkes' treatment of the tuber-bearing Solanums (Hawkes 1956) synonymized *S. spegazzinii* and *S. pachytrichum* under *S. leptophyes*.

The many conflicting treatments of these species illustrate the problematic species boundaries in this group. The group is of interest because of its putative relationship to the cultivated potato. Grun (1990) proposes a scheme to describe the origin of the cultivated potato through selection from a brevicaule-complex and subsequent hybridization events involving a number of unknown diploid species. Hawkes (1990) identifies *S. leptophyes* as the progenitor of *S. stenotomum*, the species he designated as the most primitive of the cultivated species. Thus, the cultivated potato seems to have originated from a group of wild tuber-bearing *Solanum* species such as *S. brevicaule*, *S. leptophyes*, *S. canasense* and others. The present paper reports on a morphological
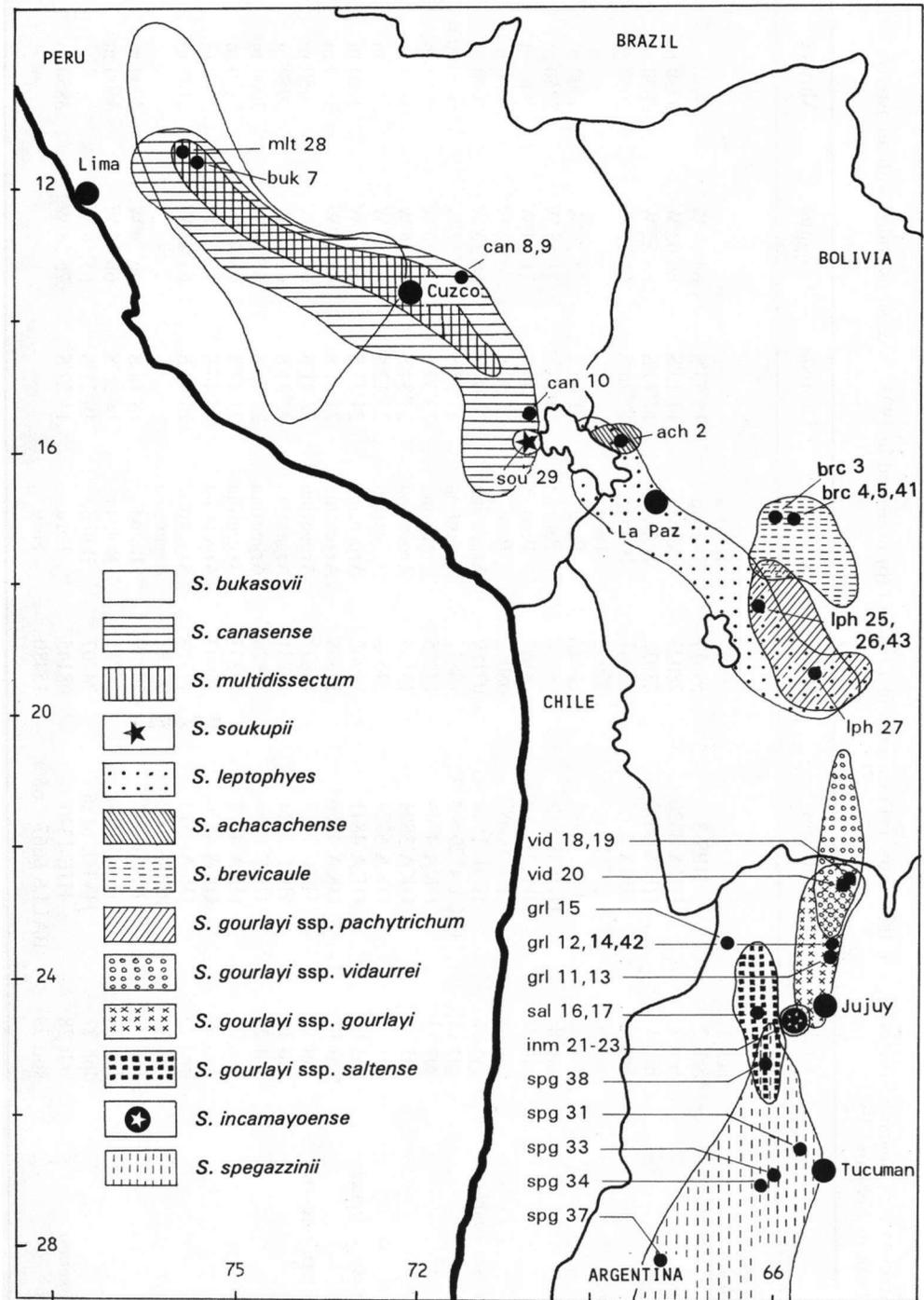
Fig. 1. Distribution areas of the studied taxa (Correll 1962; Hawkes & Hjerting 1969, 1989; Bamberg & Martin 1993) and locality data of the accessions in this study. Taxon abbreviations as in Table 2.

Table 2. Accessions of *Solanum* species used in this study, (a) measured in 1990 and (b) measured in 1993. Accessions coded with an asterisk were measured both in 1990 and 1993

Taxon	Code	Collector	BGRC	Country	Latitude	Longitude	Altitude
(a)							
S. achacachense	*ach 1	?	29617	Bolivia	—	—	—
	*ach 2	HPS 3	53017	Bolivia	15°55′S	68°40′W	3730 m
S. brevicaule	*brc 3	HHA 6620	28023	Bolivia	17°13′S	66°03′W	3850 m
	*brc 4	HHA 6690	28038	Bolivia	17°19′S	66°22′W	3650 m
	*brc 5	HHA 6701	28041	Bolivia	17°20′S	66°21′W	—
S. bukasovii	buk 6	OCH s.n.	07992	Peru	—	—	—
	buk 7	HJE 1366	15424	Peru	11°45′S	75°28′W	4000 m
S. canasense	can 8	HHCH 5126	08110	Peru	13°28′S	71°55′W	3350 m
	can 9	HHCH 5107	08105	Peru	13°23′S	71°54′W	3000 m
	can 10	RR 0668	08012	Peru	15°50′S	70°02′W	4000 m
S. gourlayi ssp. *gourlayi*	grl 11	HOF 1800	07180	Argentina	23°47′S	65°33′W	1900 m
	grl 12	OKA 4320 × 4332	16837	Argentina	23°37′S	65°32′W	3200–3300 m
	grl 13	OKA 4346	17305	Argentina	23°39′S	65°36′W	3200 m
	grl 14	OKA 3801	18529	Argentina	23°34′S	65°26′W	2850 m
	grl 15	OKA 6724	24534	Argentina	23°12′S	67°17′W	3500 m
S. gourlayi ssp. *saltense*	sal 16	OKA 4841	16902	Argentina	24°33′S	66°12′W	3900 m
	*sal 17	OKA 4866	17338	Argentina	24°31′S	66°12′W	3880 m
S. gourlayi ssp. *vidaurrei*	vid 18	HOF 1727	16832	Argentina	22°31′S	65°07′W	3050 m
	vid 19	HOF 1724	16831	Argentina	22°31′S	65°06′W	3050 m
	vid 20	HOF 1704	16828	Argentina	22°43′S	65°12′W	3000 m
S. incamayoense	inm 21	OKA 4853	17333	Argentina	24°43′S	65°45′W	2320 m
	inm 22	OKA 4850	16903	Argentina	24°46′S	65°44′W	2200 m
	inm 23	OKA 4893	17350	Argentina	24°47′S	65°43′W	2100 m
S. leptophyes	lph 24	ROSS 0145	07184	Argentina	—	—	—
	lph 25	HAM 007	27209	Bolivia	18°14′S	66°29′W	3200 m
	*lph 26	HAM 014	27215	Bolivia	18°26′S	66°26′W	3600 m
	lph 27	HVHL 6126	24707	Bolivia	19°28′S	65°50′W	—
S. multidissectum	mlt 28	HJE 1340	08145	Peru	11°27′S	75°58′W	3850 m
S. soukupii	sou 29	BALLS 6667 × 6668	15480	Peru	—	—	—

Table 2. *(Continued)*

S. spegazzinii	spg 30	RR 0054	18326	Argentina	—	—	2000 m
	spg 31	HOHH 6079	24694	Argentina	26°40'S	65°49'W	2700 m
	spg 32	HJE 0332 × HAW 2464	15458	Argentina	—	—	—
	spg 33	OKA 6155	16973	Argentina	27°25'S	66°39'W	2200 m
	spg 34	OKA 6137	16970	Argentina	27°35'S	67°07'W	1900 m
	spg 35	OKA 4071 × 4070	16943	Argentina	—	—	—
	spg 36	OKA 4063 × 4065	16929	Argentina	—	—	—
	spg 37	HOF 1754	16905	Argentina	28°35'S	68°09'W	2850 m
	spg 38	OKA 4056	16915	Argentina	25°02'S	66°14'W	2640 m
(b)							
S. brevicaule	brc 39	OCHK s.n.	15461	Bolivia	—	—	—
	brc 40	OCHK s.n.	18291	Bolivia	—	—	—
	brc 41	HVHL 5654	24571	Bolivia	17°20'S	66°13'W	—
S. gourlayi ssp. *gourlayi*	grl 42	OKA 4435 × 4437	17311	Argentina	23°34'S	65°16'W	3900 m
S. leptophyes	lph 43	HAM 009	27211	Bolivia	18°14'S	66°29'W	3250 m
S. stenotomum	stn 44	SAH 184	27165	Bolivia	—	—	—
	stn 45	SAH 185	27166	Bolivia	—	—	—
	stn 46	?	53633	—	—	—	—
	stn 47	OCH S-46	53667	Peru	12°04'S	75°14'W	—
	stn 48	ROSS 0104	07227	Peru	—	—	—
	stn 49	BALLS 6755 × 6757	07478	Peru	—	—	—
	stn 50	TOX 204 × 693	07485	Peru	—	—	—
	stn 51	?	53645	—	—	—	—

Collector: BALLS, Balls; HAM, Hondelmann, Astley and Moreira; HAW, Hawkes; HHA, Hawkes, Hjerting and Aviles; HHCH, Hawkes, Hjerting, Cribb and Huaman; HJE, Hjerting; HOF, Hoffman; HOHH, Hawkes, Okada, Van Harten and Hermsen; HPS, Hoopes; HVHL, Hawkes, Van Harten and Landeo; OCH, Ochoa; OCHK, Ochoa and Kemp; OKA, Okada; ROSS, Ross; RR, Rimpau and Ross; SAH, Van Soest, Alarcon and Huaman; TOX, Toxopeus. BGRC: Braunschweig Genetic Resources Collection number.

investigation into the species boundaries among a number of the representatives of this group, including observations on the cultivated 'species' *S. stenotomum*, in order to investigate the morphological similarity between wild and cultivated potatoes.

MATERIALS AND METHODS

Plant material

Thirty-eight gene bank accessions of 12 (sub)species belonging to the brevicaule-complex (all members of series *Tuberosa*) were examined in 1990 (Table 2). These accessions represented all the material of these species that was available from the gene bank at Braunschweig (Germany), namely all material that was tested for quarantine diseases at that time. Their localities were plotted on a map (Fig. 1). The identities of the accessions were obtained from the gene bank catalogue based on identifications given by visiting taxonomists, especially Hawkes. In using these names we follow the most recent revision of the tuber-bearing *Solanum* species (Hawkes 1990). The seeds were sown in a greenhouse in March 1990 and 20 individuals per accession were transferred to pots in April. Seven of these accessions (belonging to *S. achacachense*, *S. brevicaule*, *S. gourlayi* ssp. *saltense*, and *S. leptophyes*) were re-examined in 1993, together with five additional accessions of three species (*S. brevicaule*, *S. gourlayi*, and *S. leptophyes*) and eight accessions of *S. stenotomum*.

Character measurement

In total 30 characters (Table 3) were measured for each specimen. Leaf measurements were based on five leaves per plant. Means of the measurements of 10 plants were used to represent each accession in 1990. In the 1993 trial, only three plants per accession were measured.

Data analysis

Each character was analysed per taxon for its mean, standard deviation and range. A one-way analysis was performed with SPSS-PC, version 5.01, using Duncan's multiple range test, to determine whether characters differed significantly between pairs of taxa (Norusis 1990).

Principal components analysis (PCA) of all accessions was performed with NTSYS-pc, version 1.80 (Rohlf 1993). Product–moment correlation among variables was generated with procedure SIMINT on standardized data. Projections of the OTUs were plotted on the PCA-axes extracted with the EIGEN procedure. Figure 2a and b show the first and second principle component (PC) and the first and third PC of the analysis of the 1990 dataset. In Fig. 3a and b the 20 accessions studied in 1993 are also plotted on the first and second, and first and third PC, respectively. A minimum spanning tree (MST) was superimposed on the PCA plots to help detect local distortions.

RESULTS

Geographical distribution

Figure 1 shows the distribution of the collections of the 12 taxa studied here, and—for the sake of completeness—the distribution area of a thirteenth taxon (*S. gourlayi* ssp.

Table 3. Characters and character states measured in this study

Plant
PH:	Plant height (mm)
SW:	Stem width (mm)
WW:	Stem wing width (mm)
PUS:	Pubescence density on stem (number of hairs/cm^2)
PUSL:	Pubescence length on stem (mm)

Leaf
LL	Leaf length (mm)
LF:	Ratio: leaf length/leaf width
DA:	Ratio: distance from apex to widest part of leaf/leaf length
PUU:	Pubescence density on upper side of leaf (number of hairs/cm^2)
PUUL:	Pubescence length on upper side of leaf (mm)
PUL:	Pubescence density on lower side of leaf (number of hairs/cm^2)
PULL:	Pubescence length on lower side of leaf (mm)
PEL:	Petiolule length (mm)
LLP:	Number of lateral leaflet pairs
TLL:	Terminal leaflet length (mm)
TLF:	Ratio: terminal leaflet length/terminal leaflet width
TDA:	Ratio: distance from apex to widest part of terminal leaflet/terminal leaflet length
LLL:	Largest lateral leaflet length (mm)
LLF:	Ratio: largest lateral leaflet length/largest lateral leaflet width
LDA:	Ratio: distance from apex to widest part of lateral leaflet/lateral leaflet length
ILR:	Number of interjected leaflets on rachis
ILJ:	Maximum number of interjected leaflets between pairs of lateral leaflets

Inflorescence
PDL:	Peduncle length (mm)
FN:	Number of flowers per inflorescence
PEDL:	Pedicel length (mm)
ART:	Length from base of calyx to articulation point (mm)
CL:	Calyx length (mm)
COR:	Corolla diameter (mm)
AL:	Anther length (mm)
STL:	Style length (mm)

pachytrichum (Hawkes) Hawkes et Hjerting) of which no material was available. On this map the locality data of the studied accessions and the distribution of the taxa deduced from literature data are shown together. Most of the accessions of *S. stenotomum*, a widely cultivated crop plant, lack distribution data and were not plotted. The distribution areas of the members of the brevicaule-complex form a continuous range from southern Peru to northern Argentina. There are no obvious geographical barriers present, and the species succeed each other from north to south. Some overlap is present, especially in Peru where *S. bukasovii*, *S. canasense* and *S. multidissectum* occupy large areas. Some species possess a large distribution area, others such as *S. soukupii* and *S. achacachense* are restricted in their distribution. The range in altitude (data in Hawkes 1990) is mostly between 3000 and 4000 m, but *S. achacachense* reaches up to 4250 m, while the southernmost species *S. spegazzinii* also occurs at lower altitudes (1900–3100 m).
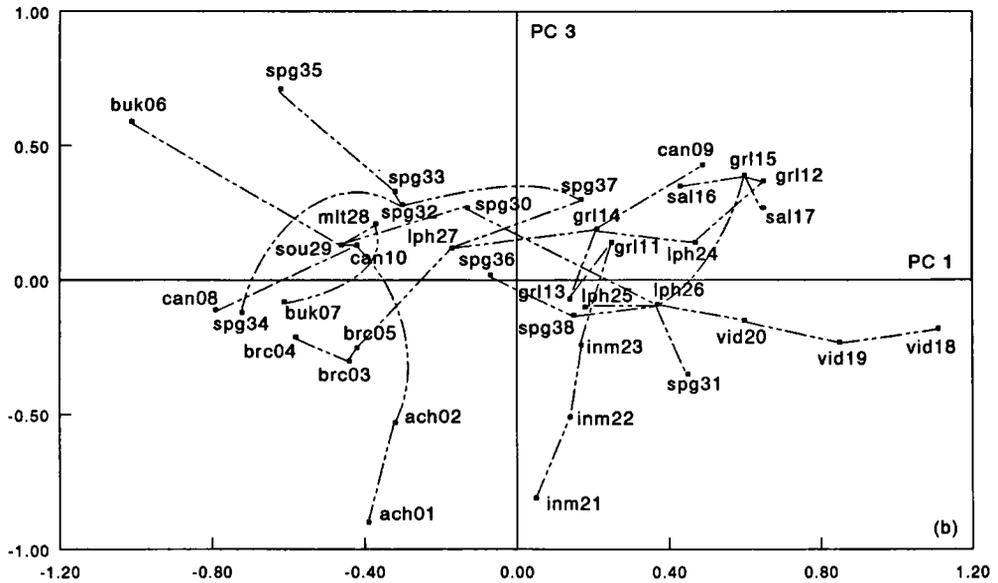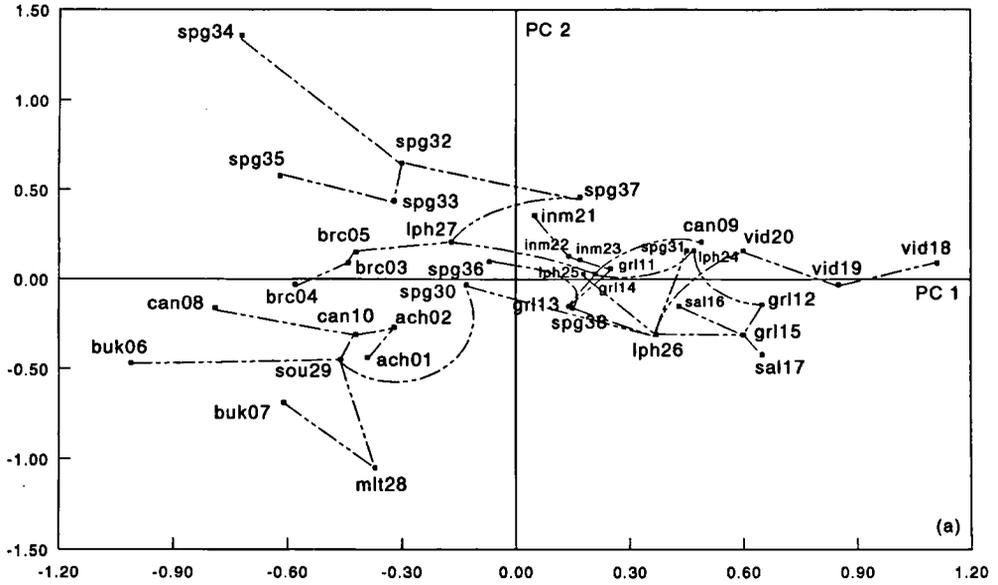
Fig. 2. Projection of the accessions studied in 1990 on the first two principal components (a) and the first and third principal component (b). Taxon abbreviations as in Table 2. The network connecting the accessions is the minimum spanning tree.
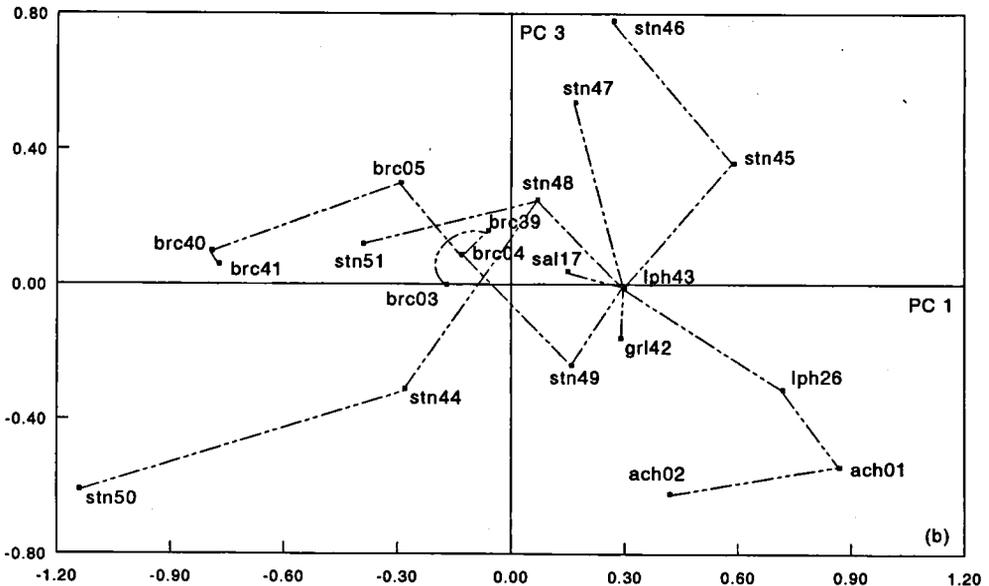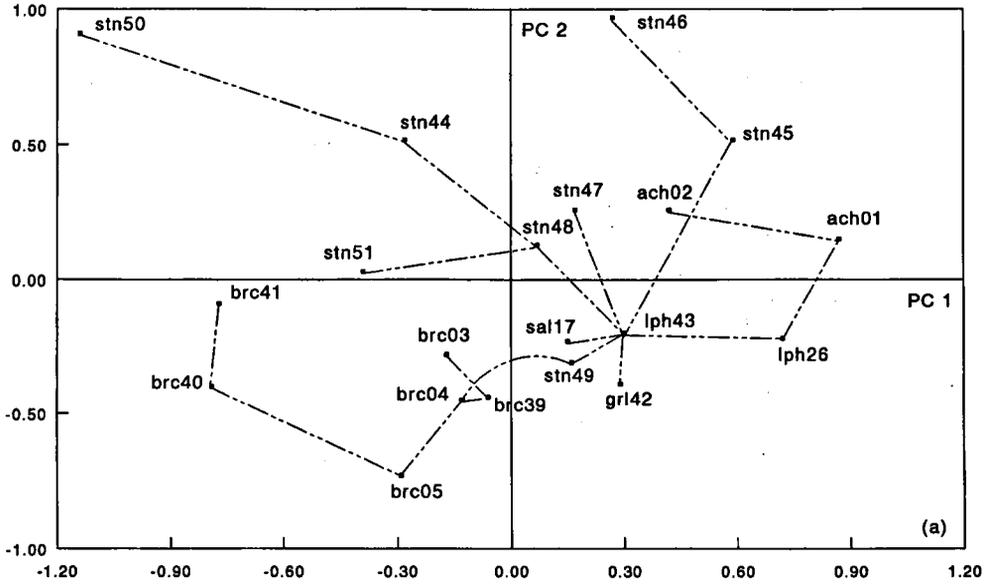
Fig. 3. Projection of the accessions studied in 1993 on the first two principal components (a) and the first and third principal component (b). Taxon abbreviations as in Table 2. The network connecting the accessions is the minimum spanning tree.

Character analysis

All characters show statistically significant differences between at least certain pairs of taxa in the one-way analysis of variance ($P<0.05$), but in most cases there is considerable overlap of the ranges. Table 4 gives a summary of a number of the characters that were given in the original descriptions, combined with data from recent literature and from our own measurements. Generally, since the first publication, the range of variation in many of these characters has enlarged substantially, diminishing the number of 'species specific' character states. This has resulted in increasing overlap between the taxa, for example LL in *S. leptophyes* and *S. spegazzinii*. Figure 4 shows this overlap for four of these characters.

Three characters (LLL, LLF, ILJ) were removed from the analysis due to their high correlation ($\geqslant 0.85$) with the characters TLL, TLF and ILR, respectively. In the PCA of the material studied in 1990 (Fig. 2a and b) the first three factors accounted for 25·5, 17·0 and 12·7% of the variation, for a total of 55·2%. Factor 1 had high negative loadings of the characters SW, LL, ILR and PDL. Character TLF had a high positive loading on factor 1. Factor 2 had high negative loading of character LF and high positive loadings of characters TLL, ART and DA. Factor 3 had high positive loadings of characters PEDL and STL.

OTUs of some taxa cluster together in the periphery of the plot, for example *S. gourlayi* ssp. *vidaurrei* (Cárdenas) Hawkes et Hjerting and part of the accessions of *S. spegazzinii* (Fig. 2a and b), *S. achacachense* and *S. incamayoense* (Fig. 2b). Accessions of *S. gourlayi* ssp. *gourlayi* and ssp. *saltense* Clausen et Okada, *S. leptophyes* and *S. canasense* are scattered throughout the centre of the plot.

The first three factors in the PCA of the trial conducted in 1993 accounted for 26·3, 21·4, and 13·5% of the variation, for a total of 61·2%. Factor 1 had high negative loadings of the characters LL, SW, TLL, COR, and PDL. Factor 2 had a high positive loading of PH and a high negative loading of PULL.

The plot of the first and second PC (Fig. 3a) shows some clustering of the accessions of *S. brevicaule*, *S. achacachense* and a mixed group composed of accessions of *S. gourlayi*, *S. leptophyes* and one accession of *S. stenotomum*. The other accessions of *S. stenotomum* do not group closely together but occupy a large area in the upper quadrants of the plot. The separate accessions seem to display more similarity to the other species than among themselves. It is also noteworthy that in the plot of the first and third PC (Fig. 3b) the *S. stenotomum* accessions form two separate branches radiating from the centre group.

DISCUSSION

From the PCA plots (Fig. 2a and b) it is evident that the representatives of the accessions of wild material studied in 1990 form one cloud of points in the multidimensional character space. There are no clear gaps that would help distinguish species in the absence of the predetermined names. This indicates an overall similarity among these taxa: they are morphologically very much alike and hard to distinguish (Correll 1962; Brucher 1985; Spooner & Van den Berg 1992; Spooner *et al.* 1994). The characters measured by us, although most of them are statistically significantly different between at least certain combinations of species, display substantial overlap (Fig. 4, Table 4). Similar situations are reported in other groups within sect. *Petota*, namely: the species

Table 4. Ranges of nine characters

Character		Taxon ach	brc	buk	can	grl	sal	vid	inm	lph	mlt	sou	spg
LL	org	—	—	—	80–130	70–130	70–130	—	170	65–73	90–160	60–80	55–90
	lit	30–170	40–230	<250	80–280	35–180	—	50–220	—	50–220	80–170	60–100	35–300
	obs	81–165	93–199	87–222	73–207	69–195	68–169	60–168	102–192	80–192	74–155	104–176	74–239
LW	org	—	—	—	30–60	—	—	—	—	—	30–65	—	—
	lit	20–30	15–120	25–117	30–230	20–100	—	30–150	—	20–140	30–70	—	20–160
	obs	41–80	35–113	27–97	42–99	39–118	36–82	34–101	45–105	44–106	30–68	48–84	11–169
LLP	org	—	3–4	—	6	4–5	8	—	2–4	4–5	6–8	4–6	4–5
	lit	1–8	1–6	3–6	3–8	2–6	—	3–5	2–4	2–8	6–8	4–8	3–7
	obs	4–7	3–6	4–7	4–8	3–5	3–5	3–5	3–5	3–5	5–7	5–8	3–7
TLL	org	—	45–50	—	22–30	25–32	25–32	—	40–56	18–22	20–35	17–24	17–23
	lit	12–45	28–70	<80	20–90	15–45	—	20–50	—	18–55	<35	<30	10–85
	obs	21–46	26–58	13–50	24–46	22–46	22–35	20–41	23–52	20–61	16–34	27–45	31–87
TLW	org	—	30–35	—	7–13	9–16	7–14	—	20–36	6–8	15–19	8–10	6
	lit	5–30	16–40	<40	7–40	5–25	—	5–18	—	6–35	<20	<20	4–25
	obs	13–29	17–35	10–30	11–21	9–29	7–16	7–17	11–34	10–45	11–23	16–31	13–46
ILR	org	—	0–5	—	7–19	0–2	—	—	0–2	4–8	20–40	2–20	0–2
	lit	0–20	3–30	4–20	6–40	0–24	—	0–6	0–4	0–32	20–40	6–40	0–36
	obs	7–15	3–13	7–16	2–22	0–7	2–7	0–8	0–7	2–17	4–12	2–16	2–19
PDL	org	—	20	—	35–65	10–20	—	—	30–65	40–45	50–110	20–50	20–33
	lit	15–100	50–150	150–200	35–90	20–50	10–39	30–50	—	15–70	50–100	20–90	10–100
	obs	20–110	15–120	50–155	12–120	9–72	—	8–63	17–72	5–93	63–131	25–160	12–119
ART	org	—	10–15	—	6–7	5–6	—	—	4–8	5–7	4–5	7–9	4–12
	lit	2–7	5–20	<6	4–10	5–10	—	5–8	—	5–10	4–10	5–9	5–13
	obs	2–7	4–12	3–8	4–9	2–8	3–9	3–9	2–7	3–11	2–5	3–7	2–17
COR	org	—	25	—	25–35	20–30	—	—	25–30	18	20–25	40	20–23
	lit	15–35	25–40	28–45	25–50	15–30	—	10–25	25–30	18–30	20–25	25–50	10–35
	obs	16–36	24–38	24–40	20–38	19–35	18–32	15–28	20–32	18–36	26–30	27–38	16–38

org: data from the original descriptions; lit: data from later publications (Correll 1962; Hawkes 1990; Hawkes & Hjerting 1969); obs: our 1990 observations; —: data not available.
Taxon abbreviations as in Table 2, character abbreviations as in Table 3.
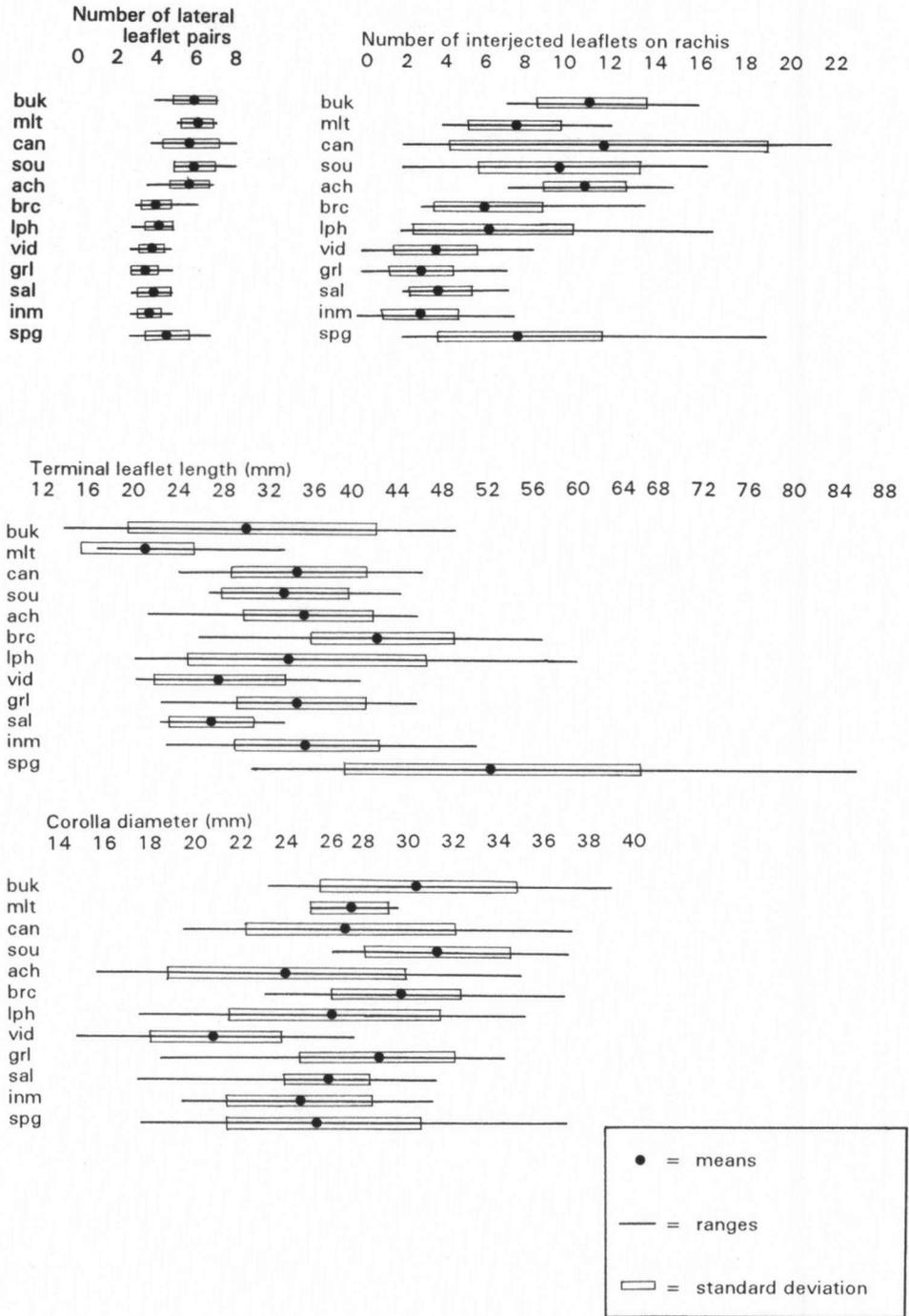
Fig. 4. Means, ranges and standard deviations of four characters. Taxon abbreviations as in Table 2.

S. megistacrolobum Bitter and *S. toralapanum* Cárdenas et Hawkes (Giannattasio & Spooner 1994) and taxa within series *Circaeifolia* (Van den Berg & Groendijk-Wilders 1996) and series *Demissa* (Spooner et al. 1995).

Accessions of some of the taxa in the 1990 study do show a tendency to cluster in more or less distinct subgroups, branching away from the central group (Fig. 2a and b): for example, *S. gourlayi* ssp. *vidaurrei*, *S. brevicaule*, *S. achacachense*, *S. incamayoense* and (part of) *S. spegazzinii*. On the other hand, the accessions of *S. leptophyes* and of the other subspecies of *S. gourlayi* form a mixed assemblage. This would argue against the treatment proposed by Hawkes (1990), separating *S. leptophyes* and *S. gourlayi* from each other.

Clausen & Okada (1987) propose to recognize two subspecies within *S. gourlayi* based on minor morphological characters (rapid decrease of the size of the primary lateral leaflets towards the leaf base, size of the terminal leaflet, length of style and anthers) and difference in chromosome number. *Solanum gourlayi* ssp. *gourlayi* comprises the tetraploid cytotype with some rare diploids from Argentina, Province of Jujuy, and ssp. *saltense* encompasses the diploid cytotype from Argentina, Province of Salta. Clausen & Crisci (1989) give a multivariate analysis of these diploid and tetraploid cytotypes of *S. gourlayi*, together with representatives of *S. gourlayi* ssp. *vidaurrei*, which they recognize as *S. vidaurrei*, and *S. incamayoense*. They conclude that the subspecies of *S. gourlayi* are distinct, that *S. vidaurrei* resembles *S. gourlayi*, and that *S. incamayoense* is clearly distinct.

According to the present results, *S. gourlayi* ssp. *vidaurrei* seems to be one of the more clearly distinguishable taxa, which might merit species status conform Ochoa's treatment (Ochoa 1990). However, the accessions of *S. gourlayi* ssp. *gourlayi* (both tetraploids and diploids) and ssp. *saltense* and *S. leptophyes* are very similar to each other.

Two accessions of *S. canasense* associate with the accessions of *S. bukasovii* and *S. multidissectum* (Fig. 2a), conform Ochoa's opinion that *S. canasense* and *S. multidissectum* are variants of *S. bukavosii* (Ochoa 1990). The third *S. canasense* accession clusters with *S. spegazzinii* and *S. leptophyes* and may have been misidentified. The MST connects the accession of *S. soukupii* to *S. canasense*, corroborating their synonymy as indicated by Hawkes (1990) (see Table 1). In Fig. 2a the lower left quadrant contains all the Peruvian material.

Ugent (1966) proposed combining most of the studied taxa in one species, *S. brevicaule*. This would mean recognizing many of the studied taxa at the infraspecific level. We did not find a clear division in the three subspecies established by Ugent (see Table 1).

The differences found in the 1993 trial between the accessions of *S. stenotomum* and their putative parental group of species (*S. stenotomum* has generally larger dimensions and higher number of interjected leaflets) are likely to be the result of the influence of domestication. Hawkes (1990) designated *S. leptophyes* as the probable progenitor of *S. stenotomum*. From a phenetic analysis like the present study it is not possible to conclude which member of the brevicaule-complex was ancestral to the cultivated potato. The MSTs in Fig. 3a and b connect the accessions of *S. stenotomum* to an accession of *S. leptophyes*, conform Hawkes' opinion, but their positions in the plot indicate an appreciable variation within this cultigen, presumably reflecting the results of differential selection. This is an example of the difficulties arising from applying the taxon concept (namely the

species category) to cultivated material. If the cultigenic nature of *S. stenotomum* is not taken into account, the PC analysis could be interpreted to indicate the need to subdivide *S. stenotomum*. We prefer the approach of Dodds (in Correll 1962), who proposed to treat *S. stenotomum* as a group within *S. tuberosum*, anticipating the development of the culton concept (Hetterscheid & Brandenburg 1995; Hetterscheid *et al.* 1996) and the use of the category 'cultivar group' as being more appropriate for cultivated plants.

Ochoa (1990) discusses the high polymorphism found in *S. stenotomum* and suggests a polyphyletic origin of this cultigen 'in more than one place and at more than one time from such commonly distributed wild potato species as *S. bukasovii*, *S. soukupii*, and *S. brevicaule*' (Ochoa 1990: 338–339). This would also strongly suggest the need to treat this kind of entity as culta rather than as taxa.

It is clear that the species associated in the brevicaule-complex exhibit a complex pattern of variation, with boundaries between some of its entities difficult to draw satisfactorily. There are four possible causes for this complex pattern.

1. 'Phylogenetic sorting': a widely distributed ancestral species locally developed into more or less recognizable species, intermediate forms indicating this ongoing speciation process, resulting in the present geographical distribution pattern.
2. 'Phenotypic plasticity': morphological characteristics are influenced by environmental factors, inducing, for example, leaf shape polymorphism in several of the taxa concerned, depending on their habitat. Lack of appreciation of morphological variability within taxa leads to the application of a too narrow species concept, and thus to the distinction of too many taxa.
3. 'Hybridization': most of the diploid wild potato species classified in series *Tuberosa* cross readily with each other and this hybridization produced extensive hybrid swarms, parts of which have been recognized as taxa.
4. 'Weediness': many of the representatives of this group display a preference for disturbed habitats (roadsides, at the base of walls, boundaries of cultivated fields). Interaction with potato crop plants through hybridization probably takes place (Ugent 1970) and will have influenced the morphological characters. The taxonomic difficulties of this group might be partly due to its close relationship to cultivated potatoes.

Taking these potential sources of taxonomic problems into account, it is doubtful whether a detailed classification of this group in many clearly distinct entities is feasible. A very broad species concept, accommodating variants caused by any of the factors mentioned above, may be the only practical taxonomic solution.

Which factor has been most important in producing the described pattern of variation cannot be deduced at the present time. A large-scale research project including many more accessions of representatives of the brevicaule-complex, advanced statistical analysis techniques and additional molecular work is in preparation.

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