

# Light sprout morphology of wild tuberiferous *Solanum* species

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## SUMMARY

The morphology of light sprouts produced by tubers of the wild relatives of the cultivated potato was studied in order to determine its usefulness for the classification of wild tuberiferous *Solanum* species. Light sprout morphology is routinely used in tests to distinguish potato cultivars but it has not yet been applied to wild species. An advantage of this method is that the influence of environmental factors on the morphological characters of these phenotypically plastic plants is avoided. The results indicate that light sprout morphology can be used to characterize species and species groups. The implications for the current taxonomic system of the wild tuberiferous *Solanum* species are discussed.

*Key-words:* light sprouts, morphology, potato, *Solanum*.

## INTRODUCTION

Light sprouts of potatoes can be generated by exposing tubers to reduced light intensity. The result is a complete but stunted plant with leaves, and even (sometimes) flowers. Light of low frequency (near infra-red) inhibits elongation and excessive chlorophyll production, allowing anthocyanin coloration to be observed unimpaired. Pubescence, number of root tips, presence or absence of lenticels, number and development of lateral shoots, etc. are characters that can be used in identification and classification of tuberiferous species. The production of light sprouts under controlled laboratory circumstances avoids environmental influences on the morphological features of the adult plants in their natural habitat. This is especially important when studying groups of plants adapted to short day conditions (like the relatives of the potato) away from their natural distribution area.

The value of light sprouts for the identification of cultivars of potato has been recognized for a long time (Snell 1932). The method has been standardized and is routinely applied for cultivar registration purposes. All extant potato cultivars in the Dutch reference collection can be distinguished by means of light sprout morphology (Houwing *et al.* 1986).

In this paper the method is applied to light sprouts of wild *Solanum* species. Due to extensive breeding in potatoes and the vegetative reproduction system an astounding variation can be found in the light sprout morphology of the clonal cultivars within *Solanum tuberosum* (van Hoogen 1989). Within most of the wild species, light sprouts are much more homogeneous, offering reliable, constant, specific features which can be used as additional characters in the classification of these often variable species. The range of

variability of characters in the light sprouts of the wild species is larger than that of cultivars. Variation among light sprouts originating from several tubers of the same plant is negligible and comparable to the uniformity one expects in a potato cultivar (i.e. the members of a clonal group); variation between tubers from different plants of the same accession is also low and different accessions of most species show a constant morphology.

## MATERIALS AND METHODS

### *Plant material*

The tubers used in this investigation were obtained from the gene banks of Braunschweig, Germany (BGRC-numbers) and Sturgeon Bay, USA (PI-numbers). A list of the species studied is given in Table 1.

### *Methods*

If potato tubers are allowed to sprout in light with low intensity, light sprouts develop that differ in elongation and colour characteristics from sprouts generated in the absence of light. Elongation is inhibited by near infra-red radiation. The development of chlorophyll is not stimulated at these low frequencies, allowing anthocyanin patterns to be studied. However, a certain amount of chlorophyll development is necessary and this can be induced by adding some red light. Houwing *et al.* (1986) describe a simple method using small light bulbs at low intensity producing the desired light composition.

Five tubers of each accession were mounted on foam plastic laths provided with pins. These were placed on shelves 35 cm apart in a cabinet which was closed off by a non-translucent curtain. Four small light bulbs (6 V) were mounted on the lower surface of each shelf. The cabinet was placed in a dark room where the temperature was maintained at a constant level (21°C). Humidity was  $\pm 50\%$  rH.

The tubers were regularly checked for sprouts which were removed, leaving only the top one. The sprouts were measured and described at regular intervals.

## RESULTS

### *Morphological characters of light sprouts*

The 'eyes' of the potato are buds located in the axils of bracts capable of producing lateral sprouts. Initially, a single sprout will be produced at the terminal growing point of the tuber, governed by apical dominance. Subsequently, each eye may produce up to three sprouts, one main and two subsidiary sprouts. The first internodes remain extremely compact and a globular, conical or cylindrical base is formed. In time this may elongate and produce lateral shoots in its turn. These arise from buds in the axils of the spirally arranged leaves which will develop along the length of the sprout. The surface of the base of the sprout is covered by usually slightly protruding lenticels. Pubescence and intensity of anthocyanin coloration may vary. Root tips develop around the base of the leaves. At low humidity their growth is inhibited (Danert 1961). The tip of the sprout is surrounded by an accumulation of leaves which results in either a closed or open habit of the tip, depending on the position (imbricate or spreading) of the leaves. The first leaves of the sprout are simple. Later they become compound, and the leaves are usually pinnate at the tip of the sprout.

In tests for distinctness of potato cultivars a number of characters of light sprouts can be used (UPOV 1986): e.g. size and shape of the base, distribution and intensity of anthocyanin, intensity of the pubescence, habit of the tip, number of root tips around the leaves, protrusion of lenticels, and length of the lateral shoots.

The range of variation of these characters in the light sprouts of wild species differs distinctly from, and often is wider than that of the cultivars. On the other hand, not all characters used for cultivar distinction can be employed for the identification of wild species. The characters that are useful for the distinction of wild species are discussed here.

#### *Length of the sprouts*

Elongation of the sprouts is initially inhibited by the near infra-red component of the light (see Methods). However, most sprouts will start growing after a certain length of time that differs for different species. By measuring the length of the sprouts at regular time intervals, growth curves can be plotted (Fig. 1). Most species reach a length between 20 and 100 mm after  $\pm 100$  days. Some species (e.g. a number of species in series *Megistacroloba*) remain very small, reaching only a few millimetres, while others (e.g. *S. bulbocastanum*) become very long, up to 380 mm.

#### *Colour*

The colour of the base of the light sprouts of cultivars is usually either reddish purple or bluish purple. In wild species it is mostly bluish purple but complete absence of anthocyanin also occurs (*S. acaule*). The intensity of anthocyanin coloration usually diminishes from the bottom to the tip of the sprout. Often the distribution of anthocyanin is not homogeneous and concentrations around leaves, root tips, or lenticels may occur.

#### *Pubescence*

All species have short-stalked glandular hairs with a multicellular head (as in the full-grown plants). The pubescence proper (called 'cover-hairs' by Seithe 1979) can vary from nearly absent (*S. acaule*) to very dense (*S. berthaultii*)—more dense than in any cultivar—and from very short, less than 0.5 mm (*S. pinnatisectum*) to very long, about 4 mm (*S. polytrichon*). Both glandular and non-glandular hairs occur (Fig. 3).

#### *Root tips*

The number of root tips around the leaves can vary from (0–)2 (*S. berthaultii*) to 6–7 (*S. brevicaulle*, *S. guerreroense*). This number decreases towards the tip of the sprout. Usually the root tips are glabrous, but in a few species they are pubescent, e.g. *S. pinnatisectum* (Fig. 2), *S. jamesii*, *S. tarnii*, *S. hypocrarthrum*.

#### *Habit of tip*

In cultivars the degree of openness of the tip is a useful character. Although differences in this feature are present among species, it seems to depend on the stage of development of the sprout. In some species the tip remains curved back towards the tuber, but the usual habit is erect. Colour and pubescence of the tip are often somewhat less in intensity than the rest of the light sprout.

#### *Leaf type along the sprout and at the tip*

Species with entire leaves also show this type of leaf in the light sprouts (*S. boliviense*). The first leaves of the sprouts of species with pinnate leaves are also entire, however. Individual

**Table 1.** Gene bank accessions used. Identification of the species according to Hoekstra & Seidewitz (1987) for BGRC-numbers and Hanneman & Bamberg (1986) for PI-numbers

Series	Species	Accession number
<i>Acaulia</i> Juz.	<i>acaule</i> Bitter	BGRC 17128; PI 320277, 210029, 365305, 500008
<i>Bulbocastana</i> (Rydb.) Hawkes	<i>bulbocastanum</i> Dunal <i>clarum</i> Correll	BGRC 53641, 8008 PI 283099
<i>Circaeifolia</i> Hawkes	<i>capsicibaccatum</i> Cárdenas <i>circaeifolium</i> Bitter	BGRC 53010 BGRC 27036
<i>Commersoniana</i> Buk.	<i>commersonii</i> Dunal	BGRC 17655, 17660
<i>Cuneolata</i> Hawkes	<i>infundibuliforme</i> Philippi	PI 458321, 472858
<i>Demissa</i> Buk.	<i>brachycarpum</i> Correll <i>demissum</i> Lindley <i>guerreroense</i> Correll <i>hougasii</i> Correll <i>iopetalum</i> (Bitter) Hawkes <i>verrucosum</i> Schldl.	BGRC 8100 BGRC 9983, 9981, 53631 BGRC 7186, 53009 PI 161174 PI 275181 BGRC 8254
<i>Longipedicellata</i> Buk.	<i>fendleri</i> Asa Gray <i>hjertingii</i> Hawkes <i>papita</i> Rydb. <i>polytrichon</i> Rydb. <i>stoloniferum</i> Schldl. et Bouché	BGRC 8088, 23568 BGRC 32671 BGRC 15444 BGRC 53650 BGRC 7229, 7230
<i>Megistacroloba</i> Dunal	<i>boliviense</i> Dunal <i>megistacrolobum</i> Bitter <i>raphanifolium</i> Cárdenas et Hawkes <i>sanctae-rosae</i> Hawkes <i>toralapanum</i> Cárdenas et Hawkes	BGRC 7985, 27385, 17049 BGRC 8113, 17456 BGRC 7207, 24668 BGRC 15454 BGRC 28020
<i>Pinnatisecta</i> (Rydb.) Hawkes	<i>brachistotrichum</i> (Bitter) Rydb. <i>cardiophyllum</i> Lindley <i>jamesii</i> Torrey × <i>michoacanum</i> (Bitter) Rydb. <i>pinnatisectum</i> Dunal <i>tarnii</i> Hawkes et Hjert.	BGRC 7986 BGRC 8024, 10052 PI 458428, 498407 BGRC 8128 BGRC 8175, 8168, 8169 PI 498046
<i>Piurana</i> Hawkes	<i>blanco-galdosii</i> Ochoa <i>hypacrarthrum</i> Bitter <i>piurae</i> Bitter	PI 442702 PI 473477 PI 473501
<i>Polyadenia</i> Buk. ex Correll	<i>lesteri</i> Hawkes et Hjert. <i>polyadenium</i> Greenman	PI 442694 BGRC 8182
<i>Tuberosa</i> (Rydb.) Hawkes	<i>tuberosum</i> ssp. <i>andigena</i> Hawkes <i>berthaultii</i> Hawkes <i>brevicaule</i> Bitter <i>bukasovii</i> Juz.	BGRC 7632 BGRC 18548, 28033 PI 473378, 498113, 498114 PI 498221, 473452

**Table 1.** (Cont'd)

Series	Species	Accession number
<i>Tuberosa</i> (Rydb.) Hawkes (continued)	<i>canasense</i> Hawkes	PI 283080, 210035, 458376
	<i>gourlayi</i> Hawkes	PI 442668, 473003; BGRC 16951, 16953, 16955
	<i>incamayoense</i> Okada et A.M. Clausen	BGRC 16903, 17333, 17350
	<i>leptophyes</i> Bitter	PI 320340, 473451
	<i>microdontum</i> Bitter	BGRC 24981
	<i>phureja</i> Juz. et Buk.	BGRC 53646
	<i>sparsipilum</i> (Bitter) Juz. et Buk.	BGRC 28015
	<i>spgazzinii</i> Bitter	PI 458336, 458398
	<i>stenotomum</i> Juz. et Buk.	BGRC 18478
	× <i>sucrensis</i> Hawkes	BGRC 27365, 27370
	<i>Yungasensia</i> Correll	<i>chacoense</i> Bitter
<i>huancabambense</i> Ochoa		PI 458400, 498244
<i>tarijense</i> Hawkes		BGRC 24717, 27350, 16853, 17412

species differ in where and how soon pinnate leaves are formed. Most species have pinnate leaves at the tip.

#### *Formation of lateral shoots*

In some species many long lateral shoots are formed very early (*S. commersonii*, *S. gourlayi*). Other species elongate to appreciable length without forming any lateral shoots (*S. bulbocastanum*).

#### *Light sprout morphology and taxonomy*

The morphology of light sprouts produced by the tubers of wild *Solanum* species provides means to distinguish individual species, to group related species together or to evaluate such groups. The implications for the taxonomy of the investigated species are discussed here. The species are arranged in the series accepted by Hawkes (1990). No material was investigated of the series *Conicibaccata*, *Ingifolia*, *Lignicaulia*, *Maglia*, *Morelliformia*, and *Olmosiana*.

## ACAULIA

The species *S. acaule* produces light sprouts (Fig. 3d) which are readily distinguished by their green colour. Anthocyanin intensity, if at all present, is very low, particularly at the base. Also the pubescence is almost absent. If present, the hairs are very short to short, spreading, and non-glandular. The absence or low intensity of the pubescence causes the many lenticels on the base to be clearly visible. The number of root tips is two or three. The type of leaf varies from simple to pinnate. The light sprouts of *S. acaule* do not resemble those of any other species, except those of *S. demissum* and *S. brachycarpum* to some extent, and this would support the rather isolated position of the series.

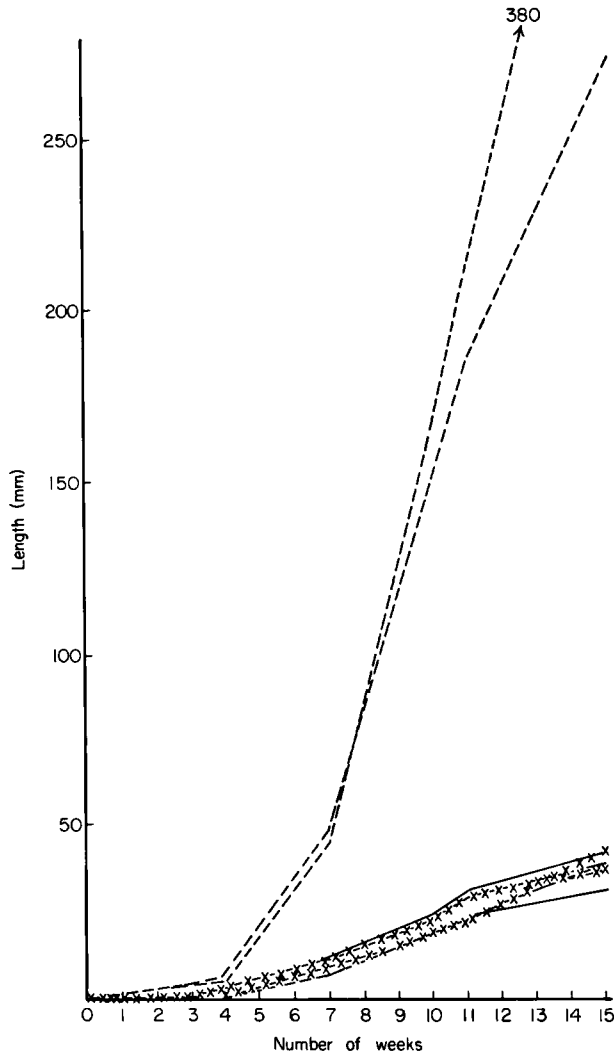


Fig. 1. Growth curves of the light sprouts of (---) *S. bulbocastanum*, (—) *S. pinnatisectum*, and (x—x) *S. x michoacanum*.

## BULBOCASTANA

The light sprouts of *S. bulbocastanum* are particularly striking due to their extreme elongation. They reach up to 380 mm after about 100 days (Fig. 1). They are covered by a medium to dense pubescence of often glandular hairs, and always have two root tips adjacent to the simple leaves. *S. clarum* produces light sprouts reluctantly. They reach up to 12 mm in length, possess a non-glandular pubescence of long spreading hairs and show only one root tip at the simple leaves. This species was placed in series *Bulbocastana* by Hawkes (1963, 1990) although Correll (1962) placed it in a series of its own, series *Clara*. It would be of interest to compare *S. clarum* with *S. morelliforme* as cpDNA data indicate a

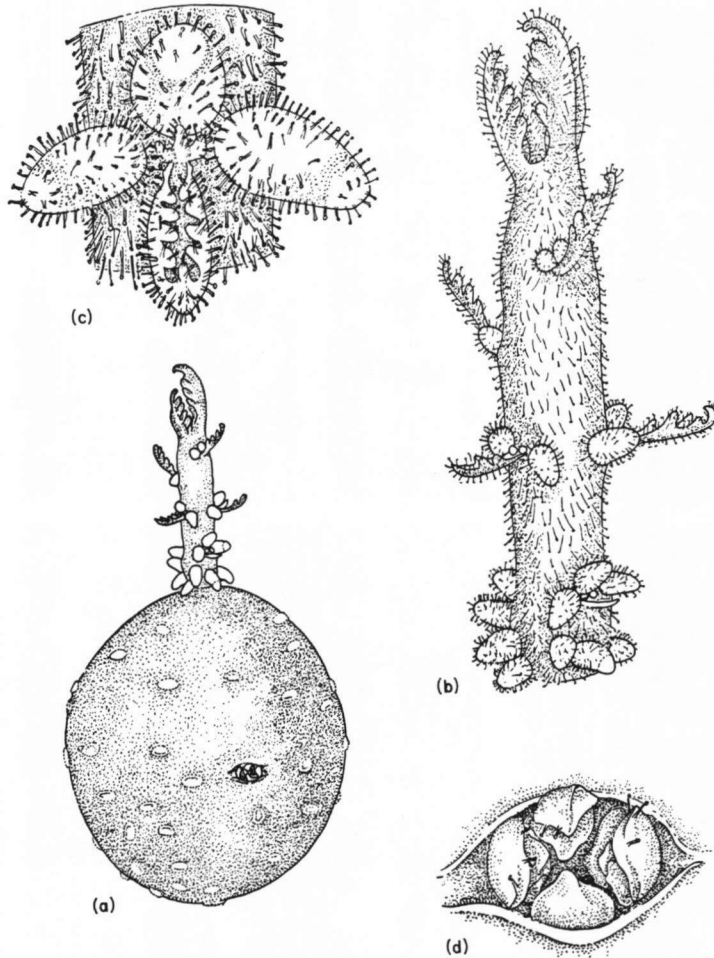
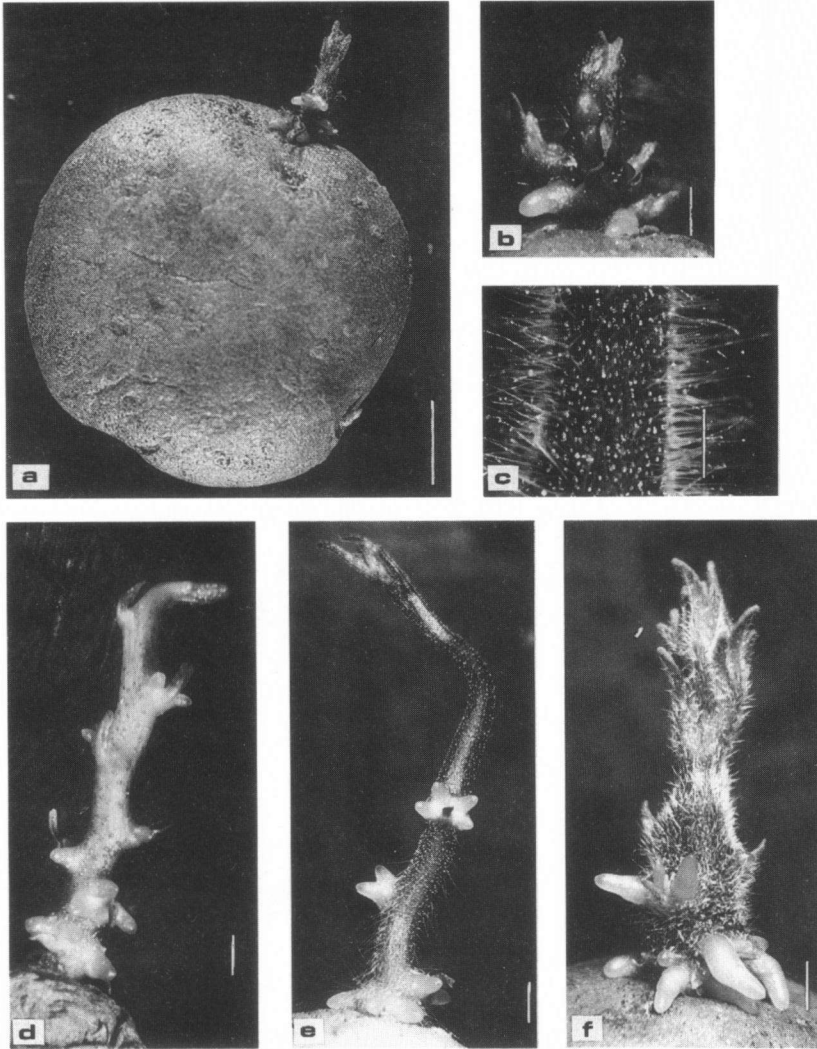


Fig. 2. Light sprout of *S. pinnatisectum* (BGRC 8168). (a) Tuber with sprout (3 ×). (b) Light sprout (9 ×). (c) Detail of root tips (18 ×). (d) Detail of eye (15 ×).

close relationship with this species, rather than with *S. bulbocastanum* (Spooner & Sytsma 1992).

### CIRCAEIFOLIA

The species of this series, *S. circaeifolium* and *S. capsicibaccatum* (no tubers were available of the third species, *S. soestii*) produce extremely small tubers. They sprout only with difficulty, giving short light sprouts (up to 1 cm). The colour of the base of the sprouts is green, with only weak anthocyanin intensity in the distal part of the sprouts. The pubescence consists of long, spreading glandular hairs. The number of root tips around the leaves is two. The type of leaf is invariably simple. The sprouts of both species are similar, and in a recent treatment (Ochoa 1990) *S. capsicibaccatum* is considered a variety of *S. circaeifolium*.



**Fig. 3.** Examples of light sprouts of wild tuberiferous *Solanum* species. (a) Tuber and light sprout of *S. chacoense* (PI 320286). (b) *S. megistacrolobum* (BGRC 17456). (c) Detail of glandular pubescence of *S. berthaultii* (BGRC 10063). (d) *S. acaule* (PI 365306). (e) *S. brachistotrichum* (BGRC 7986). (f) *S. gourlayi* (BGRC 16953). Bars represent 5 mm.

## COMMERSONIANA

A number of species, formerly accommodated in series *Commersoniana*, are treated by Hawkes (1990) in series *Yungasensia*. The light sprouts of the remaining investigated species, *S. commersonii*, are characterized by the presence of a large number of dark coloured lenticels and the early production of many lateral shoots. The pubescence consists of rather short spreading glandular hairs. There are two root tips at the leaves, which are simple.



## CUNEOALATA

The only investigated species of this series, *S. infundibuliforme*, mostly produces short (c. 2 cm) light sprouts, sparsely pubescent with non-glandular, spreading hairs, two root tips, and pinnate leaves.

## DEMISSA

The species of this series produce short light sprouts (up to 2.5 cm), except for *S. verrucosum* which may reach 7 cm. *S. demissum* and *S. brachycarpum* remain green, resembling the light sprouts of *S. acaule* in some degree. The other species show distinct anthocyanin coloration. All species have simple leaves, also at the tips. The number of root tips varies between two and five, in *S. guerreroense* sometimes up to seven.

## LONGIPEDICELLATA

The pubescence of the light sprouts of the species in this series is usually strong, consisting of long, spreading, non-glandular hairs. The number of root tips is two or three. The sprouts grow to a length of 5–15 cm, except those of *S. hjertingii* and *S. polytrichon* which remain short (7–10 mm). The leaf type is pinnate on the entire sprout in *S. papita* and *S. stoloniferum*. In *S. fendleri*, *S. hjertingii* and *S. polytrichon* the leaves are pinnate at the tip, but simple along the length of the sprout. The colour of the base is rather variable.

## MEGISTACROLOBA

The majority of the species of this series produce light sprouts rather reluctantly. They grow very slowly and only reach lengths of c. 2 cm (Fig. 3b). The exception is *S. boliviense*, a species that was placed in series *Tuberosa* by Correll (1962) but is generally accepted as fitting well in series *Megistacroloba*. The growth curve of this species is very different from that of the rest of the *Megistacroloba* species like *S. megistacrolobum*, *S. toralapanum*, *S. sanctae-rosae*, and *S. raphanifolium*. These species have similar light sprouts with a simple leaf type, both along the sprout and at the tip. The number of root tips is mostly two, sometimes three in *S. megistacrolobum*. Their pubescence is rather variable. *S. raphanifolium* has been hypothesized to be a hybrid between *S. megistacrolobum* and *S. canasense* (series *Tuberosa*) by Ugent (1970a). Spooner *et al.* (1991) tested this hypothesis using cpDNA and nrDNA data. They found no evidence for recent hybrid origin and suggest that *S. raphanifolium* may not be related to other members of series *Megistacroloba*. On the basis of its light sprout morphology *S. raphanifolium* seems to fit rather well in this series, and no influence of a *Tuberosa* species as a putative parent could be established.

## PINNATISECTA

Several species in this series are characterized by pubescent root tips, a feature not found in other species, with the exception of *S. hypacathrum* (series *Piurana*). Especially in *S. pinnatisectum* (Fig. 2) the pubescence of the root tips is very striking, consisting of short glandular hairs. In *S. jamesii* and *S. tarnii* fewer hairs are present on the root tips. These species also share with *S. pinnatisectum* the pinnate leaf type in all leaves on the

sprout. The leaves are simple in *S. brachistotrichum* (Fig. 3e) and *S. × michoacanum*. The latter species has been hypothesized to be a hybrid between *S. bulbocastanum* and *S. pinnatisectum* (Correll 1962). The growth curve of its light sprout is similar to that of *S. pinnatisectum* (Fig. 1), but it differs from that species in the glabrous root tips, simple leaves, and absence of glandular hairs. The two accessions of *S. cardiophyllum* were rather variable in pubescence and leaf type, but one of them produced light sprouts which were remarkably similar to those of *S. bulbocastanum*. Spooner & Sytsma (1992) indicate an unexpectedly close relationship between these species on the basis of cpDNA.

## PIURANA

Only three species were examined: *S. blanco-galdosii*, *S. hypacrarthrum*, and *S. piurae*. They produce short light sprouts (up to 27 mm in *S. piurae*) with variable pubescence, consisting of glandular hairs (*S. hypacrarthrum*), non-glandular hairs (*S. piurae*), or both (*S. blanco-galdosii*). Remarkable is the presence of (glandular) hairs on the root tips of *S. hypacrarthrum*, which feature has so far only been encountered in species of series *Pinnatisecta*. Leaf type is simple, except in *S. piurae*. *S. blanco-galdosii* was placed by its author, C. Ochoa, in series *Cuneoalata*. Hawkes (1990) assigned it to *Piurana*.

## POLYADENIA

The pubescence of the light sprouts of the species in this series (*S. polyadenium* and *S. lesteri*) is very dense, consisting of very long, spreading, glandular and non-glandular hairs. Glandular hairs predominate in *S. polyadenium*, non-glandular hairs in *S. lesteri*. The colour of the base is green in *S. polyadenium*, with only low anthocyanin intensity in the rest of the sprout, and purple in *S. lesteri*. The number of root tips is one or two in *S. polyadenium*, three in *S. lesteri*. The morphology of the light sprouts thus leads to the same conclusion as the general morphology of the plants: these are distinct, but closely related species.

## TUBEROSA

This large group of species displays a wide range of variability in light sprout morphology. In the present study only a limited number of species is investigated. These include a number of 'cultivated species' like *S. phureja*, *S. stenotomum* and *S. tuberosum* ssp. *andigena*, with the closely related *S. sparsipilum* and *S. × sucrense*, and several members of a complex group of species which are considered to be closely related (Correll 1962; Ugent 1970b): *S. brevicaule*, *S. bukasovii*, *S. canasense*, *S. leptophyes*, *S. gourlayi*, *S. spgazzinii*, and others. They have been called the 'brevicaule-complex' (Ugent 1970b) or the 'leptophyes-group' (Grun 1990). Two species probably not closely related to this group, *S. berthaultii* and *S. microdontum*, have also been investigated. *S. verrucosum*, placed by Hawkes (1990) in series *Tuberosa*, but thought to be an ancestral form of all *Demissa* species, is treated under that series.

Light sprouts of *S. tuberosum* ssp. *andigena* and related species (*S. phureja*, *S. stenotomum*) are rather variable, even though only one accession was available of each of these species. The intensity of anthocyanin can be extreme, giving a black-purple hue in *S. tuberosum* ssp. *andigena* or, in *S. phureja* and *S. stenotomum*, displaying the red- rather than blue-purple colour characteristic of many cultivated potatoes. The pubescence of all

these species is only moderately dense and non-glandular. Number of root tips varies from two to four. In some specimens of *S. phureja* the root tips show anthocyanin coloration. Leaf type along the sprout is simple except in *S. tuberosum* ssp. *andigena* and *S. × sucrense*. It is difficult to distinguish the species, and especially *S. sparsipilum* and *S. × sucrense* are very similar. Correll (1962) considered *S. × sucrense* as synonymous to a variety of *S. sparsipilum*, Ugent (1970b) designated *S. sparsipilum* as a weedy species derived from cultivated material, and Hawkes (1990) recognized *S. × sucrense* as a hybrid between *S. oplocense* and *S. tuberosum* ssp. *andigena*.

The species of the 'brevicaule-' or 'leptophyes-group' have light sprouts with a strong non-glandular pubescence and pinnate leaves (Fig. 3f). They show a bewildering variability in most other characters. Number of root tips, for instance, varies from zero to six, and the length reached by the sprouts ranges from very short (5 mm) to elongations nearly as long as that of *S. bulbocastanum* (up to 347 mm in *S. spagazzinii*). A number of accessions of *S. gourlayi* produced long lateral shoots. Furthermore, the variability encountered in many characters is also present within single accessions. It is impossible to recognize these species on their light sprout morphology. Further study may show the need to revise the present taxonomy of this group. Interestingly, this group of species is hypothesized to play an important role in the origin of the cultivated potato (Grun 1990). It is well known that there is extensive variation in light sprout morphology in the cultivated species, and the variation found during the present study in the presumed progenitors of these cultivated species may be indicative of the influence of the first phases of the domestication process.

*S. berthaultii* possesses characteristic light sprouts with a very strong pubescence consisting of long, glandular hairs (Fig. 3c). Glandular hairs are very uncommon in the light sprouts of the investigated species of series *Tuberosa*, the only other example being *S. microdontum*. In type and intensity of the pubescence, colour of the base, type of leaves, and number of root tips (two), the light sprouts of *S. berthaultii* are very similar to those of *S. tarijense*. Although recent treatments place the latter species in series *Commersoniana* (Ochoa 1990) or series *Yungasensia* (Hawkes 1990), Spooner & van den Berg (1992) argue for combining *S. berthaultii* and *S. tarijense*, based on a morphological comparison of all the gene bank accessions available at Sturgeon Bay. This is now supported by light sprout morphology.

*S. microdontum* differs from the species of the 'brevicaule-group' in its glandular pubescence, and from *S. berthaultii* in its simple leaves.

## YUNGASENSIA

Three species of this series, formerly accommodated in series *Commersoniana* were investigated. The light sprouts of *S. tarijense* are characterized by the strong to very strong pubescence of glandular hairs, and resemble those of *S. berthaultii* (series *Tuberosa*). *S. huancabambense* has been placed in series *Tuberosa* (Ochoa 1962), series *Piurana* (Hawkes 1963), and series *Yungasensia* (Hawkes 1990). Its light sprouts differ from those of the *Piurana* species investigated here, but light sprout morphology of that series and, especially, of series *Tuberosa* is very variable, making it difficult to use this aspect to assign the species to one or the other. Characteristics of the light sprouts of *S. huancabambense* comprise the green colour of the base with only a very weak anthocyanin intensity, the number of root tips which can reach up to five, and the pinnate leaves. The accessions of *S. chacoense* (Fig. 3a) produced light sprouts which were rather variable in pubescence and anthocyanin intensity. In part they developed many lateral shoots reminiscent of *S.*

*commersonii*. The number of root tips is three and the leaf type is simple along the sprout and pinnate at the tip.

## DISCUSSION

The taxonomy of the wild relatives of the potato (*Solanum* sect. *Petota*) has been studied extensively by various authors, resulting in several treatments (Correll 1962; Ochoa 1962; Hawkes 1963, 1990). These treatments group the species in series. The most recent comprehensive treatment (Hawkes 1990) recognizes 232 species grouped in 21 series, which in their turn are grouped in two superseries, *Stellata* and *Rotata*, based on the shape of the corolla. The circumscription of species, series, and superseries is largely based on morphological characters. Many tuberiferous *Solanum* species display phenotypic plasticity and may vary extensively in the characters used by taxonomists to delimit them. There is a need for reliable, taxon specific, constant characters. To a certain extent, it is possible to find additional characters in the light sprouts of the tuber-bearing species.

Evaluating the current system of series, *Megistacroloba* and *Pinnatisecta* are supported by light sprout morphology. Also series *Acaulia* is distinct. On the other hand, the isolated position of series *Cuneolata* is less evident. The light sprouts of *S. infundibuliforme* are rather similar to those of many species of series *Tuberosa*. Series like *Piurana*, *Yungasensia*, and especially *Tuberosa* are very variable, reflecting the widely different species grouped together in these heterogeneous assemblages. On the species level, the relationship between species indicated by their classification in series is questioned in a number of cases (e.g. *S. bulbocastanum* and *S. clarum* in series *Bulbocastana*, *S. boliviense* in series *Megistacroloba*, *S. cardiophyllum* in series *Pinnatisecta*). These results in some instances agree with recent data obtained with DNA techniques (Spooner & Sytsma 1992). Within series *Pinnatisecta* the species *S. pinnatisectum*, *S. jamesii*, and *S. tarnii* seem to be more closely related to each other than to the other investigated species in the series, while *S. ×michoacanum* may very well be of hybrid origin from *S. bulbocastanum* and *S. pinnatisectum*. The similarities between light sprouts of *S. circaeifolium* and *S. capsicibaccatum*, and between those of *S. berthaultii* and *S. tarijense* support the close relationship between these pairs of taxa. In the latter case this conflicts with the classification of these species in different series belonging to different superseries. There is no greater overall similarity in light sprouts of the series of superseries *Stellata* as compared with the series of superseries *Rotata*.

The morphology of light sprouts can be used to evaluate the circumscription of species (groups) and to test hypotheses of the hybrid origin of taxa. The variability of this feature is rather high in certain groups, however, especially in those with affinities to the cultivated potato, and this makes it difficult to draw unequivocal conclusions.

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