

The inflorescence architecture of *Solanum acaule* and related taxa of *Solanum* section *Petota* (Solanaceae)

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SUMMARY

In this morphological study a special and yet unrecorded inflorescence type is described in the polyploid series *Acaulia* (*Solanum* sect. *Petota*) and compared to those of other tuber-bearing *Solanum* species. This inflorescence can be characterized as a monochasium with a strongly reduced peduncle and one or two 'extra' flowers in the axil of the subtending leaf. Species showing this inflorescence architecture have a rosette-habit, which is correlated with the high altitudes in the Andes where they occur naturally. 'Extra' flowers and other inflorescence architectural traits such as the dimensions of pedicels, peduncles and corollas are discussed in relation to the taxonomy of *Solanum* sect. *Petota* species, their habitat and breeding behaviour.

Key-words: inflorescence, morphology, potato, Solanaceae, *Solanum*, taxonomy.

INTRODUCTION

Inflorescences and branching patterns within Solanaceae have been described by Danert (1967) and Child (1979). The general branching pattern within this family is acrotonic, i.e. the shoots terminate with a flower or inflorescence and a secondary sprout emerges from the axils of the top leaf or lower leaves of the primary shoot. After this new continuing sprout has produced a number of foliar organs, it ends again in an inflorescence. This reiterative process continues throughout the growing period. Each section of foliose leaves and flowers together is termed anthoclade (Weberling 1989). The morphological interpretation of structures in Solanaceae is troublesome because many parts of the plant can be metatopically displaced due to processes of recaulescence and/or concaulescence (Danert 1957; Troll 1957; Weberling 1989). For example, the partial inflorescence grows concaulescent with the terminal flower that ends the anthoclade (Danert 1957). These shifts make the interpretation of structures difficult, as can be illustrated by the remarks of Correll (1962) on *Solanum* inflorescences. He (incorrectly) named the inflorescences pseudo-terminal (p. 29) and stated that technically they are always lateral. Actually, the inflorescences are terminal (Hayward 1938; Danert 1957) and 'pushed' aside laterally by the shoot growing from the axil of a lower leaf.

The three- to plurifoliate anthoclades of *Solanum* section *Petota* Dumort., comprising all tuber-bearing potato species, end in a thyrsoid inflorescence. The mono- to pleiochasia inflorescences (Child 1979; Child & Lester 1991) are composed of scorpioid, ebracteate, partial inflorescences (Hawkes & Hjerting 1989; Weberling 1989). The

general inflorescence stalk or peduncle is mostly dichasial branched, but species such as *S. acaule* and species of series *Megistacroloba* normally have an unforked peduncle (Hawkes & Hjerting 1969, 1989).

Studying the morphology of *S. acaule* and related species (Kardolus 1998), it became obvious that the inflorescence architecture of taxa of the polyploid series *Acaulia* (which includes two species, namely *S. acaule* and *S. albicans*) does not conform to this general architecture. Often 'extra' flowers are found at the base of the inflorescence in these species. This observation contradicts the conclusion (Danert 1957) that inflorescences of *S. acaule* have the same morphology as those of *S. tuberosum* L., namely a dichasium. The main objective of our study is to compare the inflorescence structure of species of series *Acaulia* with that of related species of series *Demissa*, *Megistacroloba* and *Tuberosa*, and determine the taxonomic value of this trait.

Besides the general architecture of inflorescences, other inflorescence traits have been used in potato taxonomy. For example, the lengths of the unforked and forked parts of the peduncle can differ among species in section *Petota*. In most species the unforked part is much longer than the branches. However, in *S. acaule* and *S. megistacrolobum* ssp. *megistacrolobum* the peduncle is very short (Hawkes & Hjerting 1989). The compact habit of these taxa seems to be associated with their extreme environment. Their distribution is in the high-mountain areas of the Andes at elevations up to 4400 m, where both species have occasionally been found at the same locality (Hawkes & Hjerting 1989: p. 192; Ochoa 1990). However, *S. acaule* and *S. megistacrolobum* have different pollination mechanisms. *Solanum acaule* and *S. albicans* are self-fertile and inbreeding (Hawkes & Hjerting 1969). Sometimes their pollination is even cleistogamous (Ugent 1981). The polyploid species *S. demissum* from Mexico, that has been demonstrated to be closely related to *S. acaule* and *S. albicans* (Kardolus *et al.* 1998), shows the same breeding pattern. The diploid species of series *Megistacroloba* and *Tuberosa* are outbreeders and need pollinating insects. In this study, we investigate inflorescences to determine a possible correlation between the morphometric proportions of the inflorescences of *S. acaule* and related species and their habitat and breeding behaviour.

MATERIALS AND METHODS

Morphological observations

In total 44 genebank accessions of 17 (sub)species belonging to four different taxonomic series in section *Petota* were examined from 1993 until 1996 (Appendix 1). The accessions were received as seeds from the potato genebank collections at Braunschweig, Germany, presently relocated in Wageningen at the Centre for Genetic Resources, The Netherlands (BGRC numbers), and at Sturgeon Bay, USA (PI numbers). At least five seedlings of each accession were grown in pots in a standard greenhouse. Plants were studied twice a week during their flowering period to follow the development of inflorescences. Variation in inflorescence structure, within and between species, was described. Simple drawings were made of the different inflorescence types. Photographs of all inflorescence types were taken in the greenhouse and detailed botanical drawings were made of the most important types. The inflorescences were also observed for other properties, such as the presence of leaves in the inflorescence. Morphological comparisons with plants collected in the wild were made by studying herbarium material of *S. acaule* and *S. albicans* (Appendix 2).

Morphometric data

Data were measured in the trial field in Sturgeon Bay in 1993. Plant material of this experiment has been described in detail by Kardolus (1998). The identification of the accessions belonging to series *Acaulia* is displayed in Table 5 of the same paper. Three plants per accession of the following taxa were studied: *S. acaule* ssp. *acaule* (25 accessions) / ssp. *punae* (nine accessions) / ssp. *aemulans* (13 accessions), *S. albicans* (nine accessions), *S. brevicaule* (two accessions), *S. demissum* (two accessions) and *S. megistacrolobum* ssp. *megistacrolobum* (two accessions) / ssp. *toralapanum* (one accession). Five characters of one inflorescence per plant were analysed, as follows: (1) the length of the peduncle from the subtending leaf (or when there is no subtending leaf, from the stem) to the first fork or pedicel; (2) the total number of flowers per inflorescence; (3) the length of the pedicel, that is the length of the ultimate flower stalk up to the base of the calyx; (4) the diameter of the corolla; (5) the exertion of the style from the anther column. Data from these five characters were analysed statistically using the JMP® software package, version 3.1.4 (SAS Institute Inc., Cary, NC, USA). Tukey–Kramer honestly-significant-difference-test (Tukey 1953; Kramer 1956) was applied to check for significant differences among the character means of all pairs of the eight taxa listed above.

RESULTS

Morphological observations

The architecture of the inflorescences of the taxa examined was variable. Nevertheless, a morphological pattern could be distinguished. We assigned the inflorescences to three general ‘types’, namely: (1) the monochasium, (2) the monochasium with an ‘extra’ flower at the base of the monochasium and (3) a dichasial branched inflorescence. The architecture of the inflorescence is not a constant species-specific diagnostic trait. Often more types of inflorescences were present within a species (Table 1) and even in one

Table 1. Percentage of inflorescence types observed

Species	Total number of inflorescences observed	Type 1	Type 2	Type 2A	Type 3	Type 3A
<i>Solanum acaule</i>						
ssp. <i>acaule</i>	117	9%	44%	29%	12%	6%
ssp. <i>aemulans</i>	36	19%	45%	—	33%	3%
ssp. <i>punae</i>	28	14%	61%	—	25%	—
<i>S. albicans</i>	32	3%	25%	3%	50%	19%
<i>S. boliviense</i>	104	76%	19%	—	5%	—
<i>S. megistacrolobum</i>						
ssp. <i>megistacrolobum</i>	51	67%	25%	2%	6%	—
ssp. <i>toralapanum</i>	47	68%	13%	6%	13%	—
<i>S. raphanifolium</i>	37	73%	—	—	24%	3%
<i>S. sanctae-rosae</i>	49	98%	—	—	2%	—
<i>S. demissum</i>	56	38%	29%	6%	18%	9%
<i>S. brevicaule</i>	56	9%	—	—	91%	—
<i>S. bukasovii</i>	38	8%	—	—	76%	16%

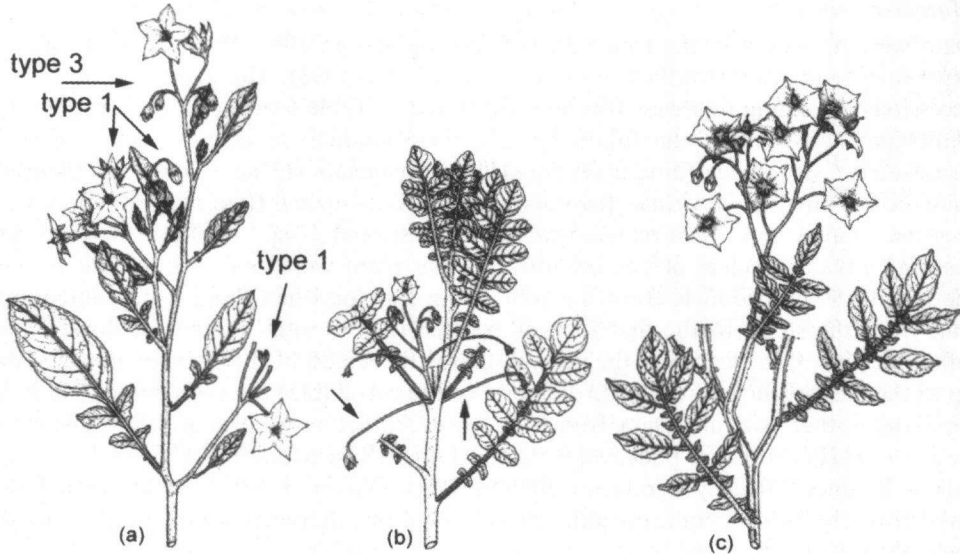


Fig. 1. Botanical drawings ($\times 0.3$). (a) *S. megistacrolobum* (BGRC 17642) with the lower three inflorescences as type 1, and an upper inflorescence with a forked peduncle (type 3). (b) A type 2A inflorescence in *S. acaule* ssp. *acaule* (BGRC 16835): a monochasium with two 'extra' flowers in the axil of the leaf. Arrows point to the 'extra' flowers. (c) *S. brevicaulis* (BGRC 28038): inflorescence with a forked peduncle bearing two monochasia (type 3).

plant (Fig. 1a). The frequency of occurrence of the observed inflorescence types differed among species. Furthermore, the second type of inflorescence occurred only in a part of the studied taxa (Table 1).

Monochasiums, i.e. inflorescences with an unforked peduncle, were observed in all taxa. We named this 'Type 1' (Figs 1a, 2a–c, e). Type 1 was most frequent in series *Megistacroloba* and *S. demissum* (Table 1). In series *Acaulia* type 1-inflorescences were characterized by a relatively short peduncle (see Morphometric data).

In series *Acaulia* a second type was often observed (Fig. 2d–e). We named this type of inflorescence 'Type 2'. It differs in an exceptional way from the 'normal' monochasium. The peduncle is absent or strongly reduced in length and one 'extra' flower is placed in the axil of the leaf blade. This flower is placed separately from the monochasium. The 'extra' flowers were the first developed flowers in the inflorescences and often also the largest flowers in an inflorescence. The pedicels of the 'extra' flowers curved downwards soon after anthesis (Figs 1b, 2h). About half the studied inflorescences of *S. acaule* were type 2, and a quarter of the *S. albicans* inflorescences. Also inflorescences with two 'extra', single flowers were observed and called 'Type 2A' (Figs 1b, 2g–h). These were mainly recorded in *S. acaule* ssp. *acaule* (Table 1).

In *S. demissum*, *S. megistacrolobum* and *S. boliviense* type 2-inflorescences were also present (Table 1), but regularly with a short peduncle. In most of their inflorescences the structural position of the 'extra' flower differed from that in series *Acaulia*: the 'extra' flower was not positioned separately in the axil of the subtending leaf, but placed at the base of the monochasium and definitely forming part of it (Fig. 2f). However, in some *S. megistacrolobum* inflorescences the 'extra' flower was positioned in the axil

of a leaf as in series *Acaulia*. Type 2-inflorescences were never observed in series *Tuberosa*. Also *S. sanctae-rosae* and *S. raphanifolium* (series *Megistacroloba*) did not exhibit type 2-inflorescences.

Inflorescences with a forked peduncle bearing two monochasia, named 'Type 3', were present in all taxa (Table 1; Figs 1a,c, 2i-j). One might speak of a real dichasium when a terminal flower is present within the inflorescence ('Type 3A'). In *S. brevicaulis* and *S. bukasovii* more than 90% of the inflorescences were type 3 or 3A (Table 1).

Usually one leaf grows concaulescent with the inflorescence (Fig. 2b). This leaf resembles the leaves in the vegetative part of the anthoclade, but is often smaller. Also inflorescences without this leaf on the peduncle were observed. On most peduncles of type 3-inflorescences only one leaf was present (Fig. 1a, upper inflorescence, and 1c). Leaves within the inflorescences were not often observed. In *S. megistacrolobum* and *S. demissum* we did occasionally find small leaves (Fig. 2f). They were randomly distributed within the inflorescence, but never above the articulation of the pedicel. Regularly placed bracts were not observed in the material of this study.

The plants grown in the greenhouse were much longer and more elongated than the herbarium specimens of material collected in South America. This facilitated the observations on the structure of inflorescences, especially of the plants belonging to series *Acaulia* and *S. megistacrolobum* (see Fig. 1). In herbarium material of *S. acaule* and *S. albicans* (Appendix 2) it was possible to observe 'extra' flowers in certain specimens (*S. acaule* specimens Hawkes, Hjerting, Cribb & Huamán 4243, Ochoa & Salas 11824, 11830 and 11895, Venturi 6993).

Morphometric data

In the trial field at Sturgeon Bay (USA) the plants showed a more compact habit such as found under natural conditions. The reduced length of inflorescences in series *Acaulia* (*S. acaule* and *S. albicans*) and *S. demissum* and *S. megistacrolobum* ssp. *megistacrolobum* was expressed in the relative shortness of their peduncle (see Fig. 3a). The plants of these taxa had peduncles with an average length of less than 1 cm. *S. brevicaulis* and *S. megistacrolobum* ssp. *toralapanum* had a significantly longer peduncle compared to these four species (Tukey-Kramer HSD-test, $\alpha = 0.05$).

S. brevicaulis had the highest number of flowers (mean = 11) per inflorescence compared to all other taxa (Fig. 3b). This high number of flowers in *S. brevicaulis* is obviously correlated with the high percentage of forked peduncles bearing two monochasia (Table 1). Monochasia, also those with 'extra' flower(s) (Type 2/2A), generally consist of few flowers. For example, the inflorescences of *S. acaule* (all three subspecies), which are mostly of type 2/2A and type 1 (Table 1), had only three to four flowers (Fig. 3b).

All the taxa, except *S. megistacrolobum* ssp. *megistacrolobum*, had a pedicel length between 15 and 30 mm (Fig. 3c). No correlation could be found between peduncle length and pedicel length of the observed taxa. *S. megistacrolobum* ssp. *megistacrolobum* has conspicuously long pedicels with an average length of 40 mm. These pedicels position the flowers beyond the leaves of this compact plant. The studied accession of *S. megistacrolobum* ssp. *toralapanum* displayed relatively long peduncles with medium-length pedicels. In series *Acaulia* the flowers are hidden in the foliage, which is most obvious in the herbarium specimens of plants collected in South America.

The flowers of the inbreeding species *S. acaule* and *S. albicans* were relatively small (Fig. 3d). The average corolla diameter of these taxa ranged between 13.5 and 17.5 mm.

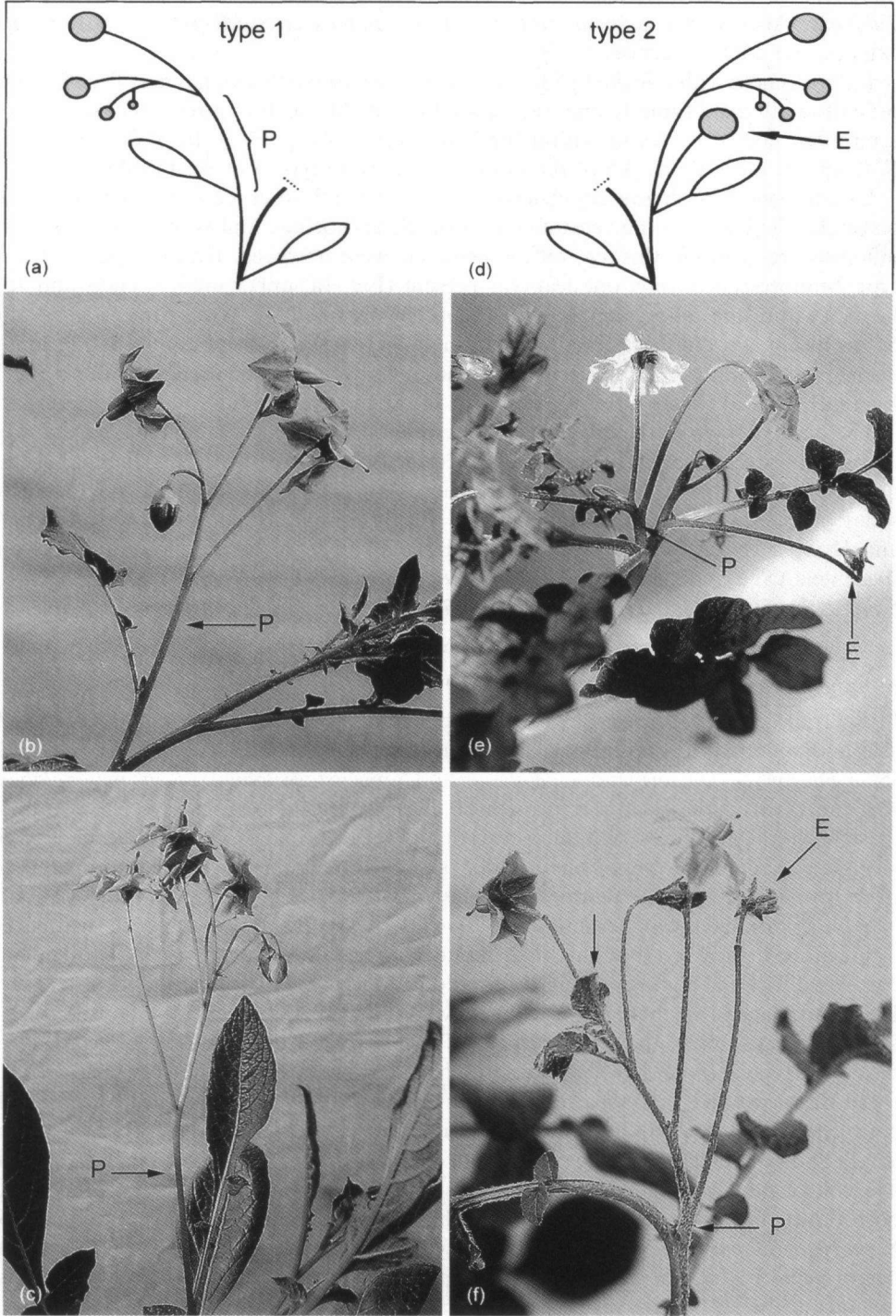


Fig. 2.

The outbreeders *S. brevicaule* and *S. megistacrolobum* had statistically significant (HSD-test, $\alpha=0.05$) larger corollas (22–23 mm). The corolla dimensions of *S. demissum* were of intermediate size.

The styles of all three inbreeding species (*S. acaule*, *S. albicans* and *S. demissum*) were generally not much exerted from the anther column. The average style exertion

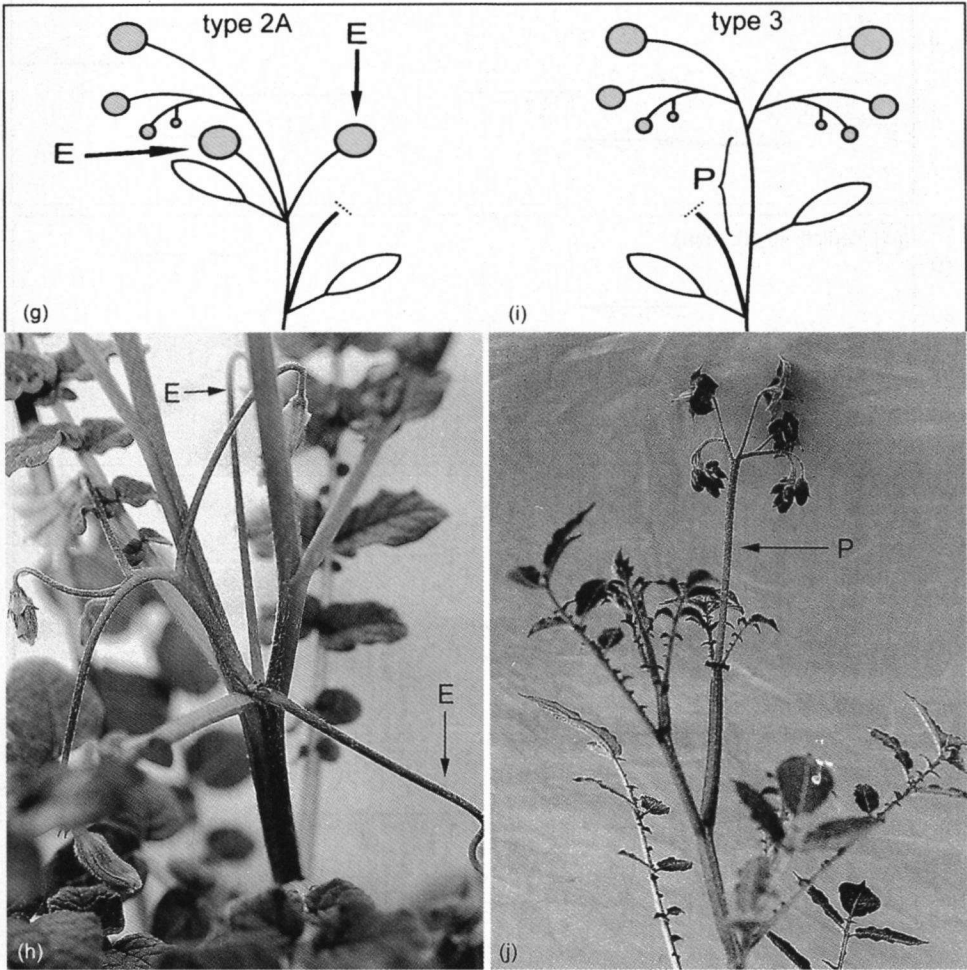


Fig. 2. Overview of the inflorescence types as described in this study. P=peduncle; E='extra' flower. (a) Schematic drawing of type 1, the monochasium. (b) A photograph of *S. sanctae-rosae* (BGRC 24674) showing a type 1-inflorescence. (c) Type 1-inflorescence in *S. megistacrolobum* ssp. *toralapamum* (BGRC 27115). (d) Type 2, a monochasium with an 'extra' flower in the axil of the subtending leaf. (e) Type 1 (left) and type 2 (right) inflorescences in *S. acaule* (BGRC 16835). (f) Type 2-inflorescence with a short peduncle in *S. demissum* (BGRC 9990). Note the randomly placed leaves in the inflorescence (arrow). (g,h) Schematic drawing and photograph (*S. acaule*, BGRC 16835) of a type 2A-inflorescence, a monochasium with two 'extra' flowers. (i) Type 3: the forked peduncle with two monochasia. This is the most common type of inflorescence in *Solanum* sect. *Petota*. (j) *S. brevicaule* (BGRC 28038) showing this type of inflorescence.

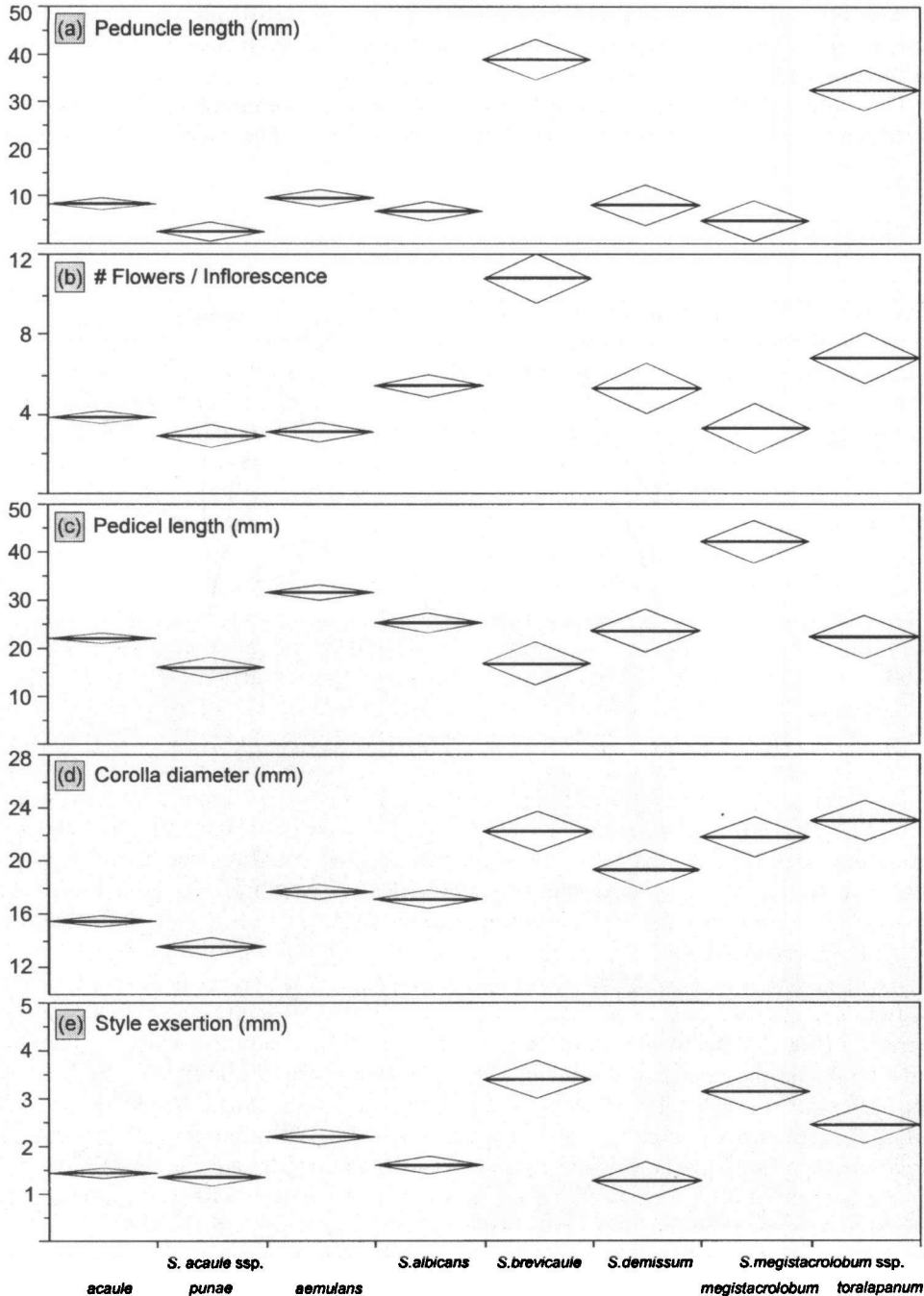


Fig. 3. Morphometric data on eight taxa, measured in a field plot at Sturgeon Bay. Displayed are the means (horizontal lines) and 95% confidence interval (diamond) of: (a) the peduncle length from the subtending leaf to the first fork or pedicel, (b) total number of flowers per inflorescence, (c) pedicel length, (d) corolla diameter and (e) style exertion.

ranged in this group of five taxa from 1.4 mm (*S. acaule* ssp. *punae*) to 2.2 mm (*S. acaule* ssp. *aemulans*). The exertion in the two outbreeding species was larger: in *S. megistacrolobum* ssp. *toralapanum* the average exertion was 2.5 mm and in *S. brevicaule* even 3.4 mm, which is significantly different from all inbreeding taxa.

DISCUSSION

Inflorescence architecture

The 'Type 2' inflorescence has never been mentioned explicitly in taxonomic studies of *Solanum*. We studied plants grown in a greenhouse. Their habit was quite elongated. To ascertain that this unnatural environment did not cause aberrations in the inflorescence architecture, such as the formation of 'extra' flowers, a comparison was made with herbarium material. In herbarium specimens of *S. acaule* we also observed 'extra' flowers. Apparently, the architecture of the plants did not change fundamentally by the growth under greenhouse conditions. Until now, the structure of this type of inflorescence has apparently been overlooked due to the compact habit of species having inflorescences with 'extra' flowers.

In the taxonomic diagnoses of tuber-bearing *Solanum* species, inflorescence structural characters such as the 'extra' flower(s) in type 2-inflorescences of *S. acaule*, *S. albicans*, *S. megistacrolobum*, *S. boliviense* and *S. demissum* should be used with care. The inflorescence architecture is often quite variable, even within individual plants. However, most other *Solanum* sect. *Petota* species do not exhibit these 'extra' flowers in the inflorescence. During this and earlier studies (Van den Berg *et al.* 1996, 1998) we have never observed 'extra' flowers in series *Tuberosa*.

Regarding the interpretation of the 'extra' flower(s) in type 2-inflorescences of series *Acaulia*, *S. megistacrolobum*, *S. boliviense* and *S. demissum*, two different structural situations have been described in the results. In the first situation, the 'extra' flower is placed directly in the axil of the subtending leaf and is not associated with the accompanying monochasium. This configuration was observed in most inflorescences of series *Acaulia* plants and infrequently in *S. megistacrolobum*. On the other hand, in *S. megistacrolobum*, *S. boliviense* and *S. demissum* the 'extra' flower is generally placed at the very base of, and in the same plane as, the monochasium and is undoubtedly part of it (Fig. 2f). Below the 'extra' flower usually a (short) peduncle can be recognized. This could be the result of the incomplete concaulescence of the monochasium with the terminal flower, or the descent of the terminal flower. Accordingly, the type 2-inflorescences of these three taxa are then transformed type 1-monochasia. The terminal flower is separately placed from the monochasium and appears as an 'extra' flower.

The first situation, in which the 'extra' flower is not connected to the monochasium, needs some further discussion. Only Danert (1957) has described the inflorescence of *S. acaule* in more detail. In his view the inflorescence of *S. acaule* is a normal dichasium, as in *S. tuberosum*. He showed a figure of an inflorescence of *S. acaule* in flower bud stage. In this figure one flower bud is unmistakably larger than the other buds. He stated that this was the terminal flower of the dichasium. In our view this bud is the 'extra' flower as described above. A hypothesis to explain the occurrence of the 'extra' flower could be that, as described above, this flower is indeed the terminal flower of the anthoclade, and that the accompanying monochasium did not grow concaulescent

with this flower. However, this explanation does not take into account that 30% of the subspecies *acaule* inflorescences have two 'extra' flowers (Table 1: type 2A; Fig. 2g–h).

Other considerations could be put forward on the presence of 'extra' flowers. In his treatment on the structure of inflorescences, Weberling (1989) described the formation of accessory buds in inflorescences. The 'extra' flowers could have been developed from these buds. Weberling (1989) has given an example of *Ipomopsis rubra* (L.) Wherry (Polemoniaceae). In this species accessory buds grow out to flowering accessory shoots after anthesis of the primary flowers. In *S. acaule* the 'extra' flowers are the first flowers and develop before the rest of the flowers of the monochasium, so the explanation on 'extra' flowers as accessory buds may be questioned. Finally, it could be proposed that one of the two 'extra' flowers is the terminal flower of a single-flowered partial inflorescence. The other 'extra' flower could then again be assigned as the terminal flower of the monochasium, as described above. It may be concluded that no satisfying hypothesis on the explanation of 'extra' flowers can be given, but the presence of these flowers in series *Acaulia* is of importance for potato taxonomy.

The highest leaf in the main axis has been considered by Danert (1967) as the bract of the first partial inflorescence. Danert designated this subtending leaf on the peduncle as a diagnostic character for sect. *Petota*. The diagnostic value of this trait may be questioned because we regularly observed inflorescences without such a leaf in section *Petota*. Danert (1967) also remarked that in compound inflorescences with two, three or more forks an equal number of leaves on the peduncle could be observed. Danert previously (1957) asserted that the upper partial inflorescence in a dichasium is placed without a subtending leaf (*tragblattlos*) and that the leaf on the peduncle belongs to the terminal flower of the inflorescence. Usually we also observed only one leaf on the peduncle.

We frequently found small normal to bract-like leaves in the inflorescences of various taxa, e.g. in *S. demissum* (Fig. 2f). The placement of these leaves is random and hence it is questionable to define these leaves as bracts subtending the individual flowers. However, the term 'ebracteate' of the inflorescences of *Solanum* sect. *Petota* described by Hawkes & Hjerting (1989) is too strict. Danert (1957) has displayed a scheme of a potato inflorescence with bracts at the base of every pedicel. In recent studies on tuber-bearing *Solanum* species of various taxonomic series (Kardolus 1998; Spooner & Van den Berg 1992; Spooner *et al.* 1995; Van den Berg *et al.* 1996, 1998; Van den Berg & Groendijk-Wilders 1998) these bracts were never observed.

The inflorescence architecture in relation to habitat and breeding behaviour

The wild potato species are most abundantly distributed in the high mountains of South and Central America (Correll 1962). Taxa such as the species belonging to series *Acaulia* have a rosette habit and inflorescences with short peduncles (Fig. 2e, 3a). Therefore they can prosper at elevations up to 4400 m (Bamberg *et al.* 1996).

The breeding behaviour of the polyploid species in series *Acaulia* and *S. demissum* differs from the diploid and obligate outcrossing wild potato species. *S. acaule*, *S. albicans* and *S. demissum* are self-pollinators and the flowers can be cleistogamically pollinated (Hawkes & Hjerting 1969; Ugent 1981). This mechanism is facilitated by the short, hardly exerted style (Fig. 3e). Inbreeding potato species do not have to attract insects. Consequently they can suffice with less pronounced inflorescences with relatively few and small flowers (Fig. 3b, d). *S. megistacrolobum*, however, is a diploid outbreeder

and needs to exhibit its flowers to pollinators. Notwithstanding the compact habit of *S. megistacrolobum*, the flowers are well presented because of the length of the pedicels (Fig. 3c) and relatively large corollas (Fig. 3d). In series *Acaulia* the flowers are positioned among the foliage. Moreover, the peduncles and pedicels bend downwards with maturing fruits (Hawkes & Hjerting 1969, 1989; Ochoa 1990), especially the pedicels of the 'extra' flowers. Due to this geotrophic tendency the fruits of these high-Andes species are embedded in the soil and in this way ensure seed production in areas of early frost.

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APPENDIX 1

List of plant material studied

Taxonomic series	Species	Genebank number
<i>Acaulia</i> Juz.	<i>Solanum acaule</i> Bitter ssp. <i>acaule</i>	BGRC 16835, 17090, 17111, 17128, 17141, 17181, 24579, 27206, 27244, 27361, 27362, 47624, 47627
	<i>S. acaule</i> ssp. <i>aemulans</i> (Bitter et Wittm.) Hawkes et Hjert.	BGRC 17180, 17182
	<i>S. acaule</i> ssp. <i>punae</i> (Juz.) Hawkes et Hjert.	BGRC 7958; PI 24657
	<i>S. albicans</i> (Ochoa) Ochoa	BGRC 18287; PI 365376, 498203, 561642
	<i>S. boliviense</i> Dunal	BGRC 27248
<i>Megistacroloba</i> Cárdenas et Hawkes	<i>S. megistacrolobum</i> Bitter ssp. <i>megistacrolobum</i>	BGRC 8113, 8117, 17642, 27262
	<i>S. megistacrolobum</i> ssp. <i>toralapanum</i> (Cárdenas et Hawkes) Giannattasio et Spooner	BGRC 28020
	<i>S. raphanifolium</i> Cárdenas et Hawkes	BGRC 7207, 8185
	<i>S. sanctae-rosae</i> Hawkes	BGRC 15454, 17568
<i>Demissa</i> Bukasov	<i>S. demissum</i> Lindl.	BGRC 9990, 10022, 10030
<i>Tuberosa</i> (Rydb.) Hawkes	<i>S. brevicaule</i> Bitter	BGRC 18291, 28038
	<i>S. bukasovii</i> Rybin	BGRC 7993, 15424; PI 210044

APPENDIX 2

List of flowering herbarium specimens of *Solanum acaule* and *S. albicans* (marked with an asterisk) studied

Herbarium	Specimen
CIP	HHCH 4236, 4243, 4271, 4324, 4416; Ochoa 2065* (holotype), 2495*, 11961, 11989, 12083*, 13238*, 16023*, 16173*; Ochoa & Salas 11823, 11824, 11826, 11830, 11831, 11833, 11895, 14947, 14949–14953, 15468, 15476, 15519, 15569, 15570, 16024*, 16028*; SOA 53, 54; SCLp 5070*
G	Hieronimus & Niederlein 474
K	Balls 5987, 6026, 6201; Cabrera-Schwabe 11; Correll P298, B636; HHR 3813; Iltis & Ugent 1435; Sandeman 3933; Saunders 819, 1384; Sharpe 120; Stafford 431; Vargas 2005
LIL	Budin 7439; Castillon 468, 3195; Krapovickas 8745; Lillo 1231, 2957, 4212, 5521, 7403, 11476, 18154; O'Donnell 4596; Olea 221, 253; Schreiter 352, 353, 4841, 6203, 6965, 7097, 7103; Shepard 231; Sleumer 228, 1838, 2689, 2750, 3252, 3462, 3589, 4113; Sparre 5989, 6102
S	Correll B601; Fiebrig 3429 (lectotype ssp. <i>acaule</i>); Hammarlund 128; Kurtz 11396; Regnell 979
US	Balls 6404; Cabrera 8264; Cárdenas 606; Cook & Gilbert 180, 181, 182a; Ochoa & Salas 11895; Shepard 231; Venturi 6672, 6993, 9526