

# Karyotype Studies in South American Species of *Solanum* subgen. *Leptostemonum* (Solanaceae)

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**Abstract:** Mitotic chromosome numbers and karyotypes of 13 South American species (12 native and one naturalized) from four sections of *Solanum* subgen. *Leptostemonum* were studied. Chromosome numbers of *S. acerifolium*, *S. aenictum*, *S. conditum*, *S. consimile*, *S. incarceratum*, and *S. platense* are reported for the first time. The number  $2n = 24$  was found in most species, while  $2n = 22$  was found in *S. mammosum* and *S. platense*. The latter is the second *Solanum* with this unusual number. Satellites are always present and were visible in more than 50% of the cells studied. Karyotypes are symmetrical: *m* and *sm* chromosomes are common, whereas *st* chromosomes are rare. The karyotypes of *S. aenictum*, *S. mammosum*, and *S. paniculatum* are comparatively asymmetrical. Species can be distinguished by a combination of chromosome number, karyotype formulae, karyotype length, the position of satellites in a particular chromosome pair, and asymmetry indices. The phenogram obtained does not reflect the sectional arrangements or the systematic affinities of the species studied. In sect. *Acanthophora*, increased asymmetry is associated with derived characters (strong andromonoecy, winged seeds, mammiform fruits). Diversification in the subgenus is suggested to be related to visible chromosome rearrangements and cumulative, cryptic structural changes may have also played a relevant evolutionary role.

**Key words:** Karyotype, *Leptostemonum*, Solanaceae, *Solanum*, somatic chromosome number, South America.

## Introduction

Solanaceae, a family of considerable economic importance, is cosmopolitan and has its centre of diversification in South America (D'Arcy, 1991; Hunziker, 2001). It includes 92 genera and around 2300 species, *Solanum* L. being the largest genus with ca. 1400 species. Thus, it is one of the largest genera of the flowering plants.

Although *Solanum* is traditionally subdivided into seven subgenera (D'Arcy, 1972, 1991; Hunziker, 2001), recent phylogenies suggest that only some of these infrageneric groups are supported, such as subgen. *Leptostemonum* (Dunal) Bitter (Olmstead and Palmer, 1992, 1997; Olmstead et al., 1999; Bohs and Olmstead, 2001; Bohs, 2004, 2005; Levin et al., 2005). This is the largest subgenus, with 350–450 species spread over tropical and subtropical regions of the world and with centres of diversification in South America, Australia, and Africa (Whalen, 1984). In his synopsis of *Solanum* in the New World, Nee (1999) estimates 185 species of which notable representatives are the edible species *S. quitoense* Lam. (naranjilla or lulo), and *S. sessiliflorum* Dunal (cocona or cubiu). Other species, such as *S. viarum* Dunal (tropical soda apple), *S. elaeagnifolium* Cav. (silverleaf nightshade), *S. sisymbriifolium* Lam. (sticky nightshade or wild tomato), *S. carolinense* L. (horse nettle), and *S. rostratum* Dunal (buffalo burr) should be mentioned as weeds.

The subgen. *Leptostemonum* is easy to recognize morphologically because of its key features: the presence of prickles (giving this group the common name of “spiny solanums”), stellate hairs in most vegetative organs, and attenuate anthers (Seithe, 1979; Whalen, 1984; Nee, 1999). However, these species show variability in their habit (annual herbs, climbers, shrubs, small trees), their floral traits (enantiostyly, heterostyly), their sexual system (hermaphroditic, andromonoecious, functionally dioecious), and their dispersal syndrome (anemochory, hydrochory, zoochory).

Members of this subgenus have been studied from different points of view, such as morphological (e.g., Seithe, 1979; Nee, 1986; Dottori and Cosa, 2003), reproductive (e.g., Bowers, 1975; Whalen and Costich, 1986; Anderson and Symon, 1989; Miller and Diggle, 2003), phytochemical (e.g., Cipollini et al., 2002), systematic (e.g., Whalen, 1984; Nee, 1991, 1999; Matesevach, 2002; Auler Mentz and de Oliveira, 2004), and cladistic (Bohs, 2004; Levin et al., 2005). However, cytogenetic information is meager, a circumstance that also applies to other *Solanum* subgenera as a whole. There are many chromosome numbers reported (e.g., Bolkhovskikh et al., 1969; Maheswar Hassan and Krishnan, 1984; Kumaraswamy and Krishnan, 1987; Carvalheira et al., 1991), but scarce karyotypic analyses taking into account the number of species involved; the few exceptions are representatives of sect. *Lasiocarpa*, sect. *Melongena*, and sect. *Acanthophora* (Rai, 1959; Okoli, 1988; Bernardello

**Table 1** Provenance, collectors, and accessions numbers of the *Solanum* sect. *Leptostemonum* species studied. F. Chiarini has identified voucher specimens

Section	Species	Sources	Figs.
<i>Acanthophora</i> Dunal	<i>S. acerifolium</i> Sendt.	Venezuela, Aragua state, Benítez and Rojas 6496 (MY); Mérida state, Benítez and Rojas 6477 (MY)	<b>1C, 3E</b>
	<i>S. aenictum</i> Morton	Argentina, Corrientes prov., Barboza et al. 1020, 1049 (CORD)	<b>2A, 3A</b>
	<i>S. incarceratum</i> Ruiz et Pav.	Brasil, São Paulo state, Marcondes et al. (CORD 1028)	<b>2F, 3F</b>
	<i>S. mammosum</i> L.	Venezuela, Carabobo state, Granada 72 (MY)	<b>2D, 3D</b>
	<i>S. platense</i> Dieckmann	Argentina, Misiones prov., Barboza et al. 441 (CORD)	<b>2E, 3C</b>
	<i>S. viarum</i> Dunal	Argentina, Corrientes prov., Chiarini 538 (CORD)	<b>1D, 3B</b>
<i>Torva</i> Nees	<i>S. consimile</i> Morton	Bolivia, Tarija dpt., Barboza et al. 307 (CORD)	<b>1B, 4A</b>
	<i>S. guaraniticum</i> St. Hil.	Argentina, Misiones prov., Barboza et al. 922 (CORD)	<b>1G, 4D</b>
	<i>S. paniculatum</i> L.	Brasil, São Paulo state, Marcondes et al. (CORD 1029)	<b>1A, 4C</b>
	<i>S. tabacifolium</i> Dunal	Brasil, São Paulo state, Marcondes et al. (CORD 1030)	<b>1E, 4B</b>
<i>Crinitum</i> (Whalen) Child	<i>S. lycocarpum</i> St. Hil.	Brasil, São Paulo state, Marcondes et al. (CORD 1031)	<b>1F, 4F</b>
<i>Melongena</i> (Mill.) Dunal	<i>S. conditum</i> Morton	Argentina, Salta prov., Barboza 782 (CORD)	<b>2C, 4E</b>
	<i>S. marginatum</i> L. f.	Spain, Canary Islands, Santa Cruz de Tenerife, cultivated, Oberti s.n. (CORD 1040)	<b>2B, 4G</b>

**Table 2** Somatic number (2n), haploid karyotype formulae, ordering number of the satellited pair (SAT), mean chromosome length (in  $\mu\text{m}$ )  $\pm$  SD (C), mean arm ratio  $\pm$  SD (R), mean total haploid chromosome length (in  $\mu\text{m}$ )  $\pm$  SD (tl), mean intrachromosomal ( $A_1$ ) and interchromosomal ( $A_2$ ) asymmetry indices of the *Solanum* subgen. *Leptostemonum* taxa studied. Asterisks indicate species where chromosome number is reported for the first time

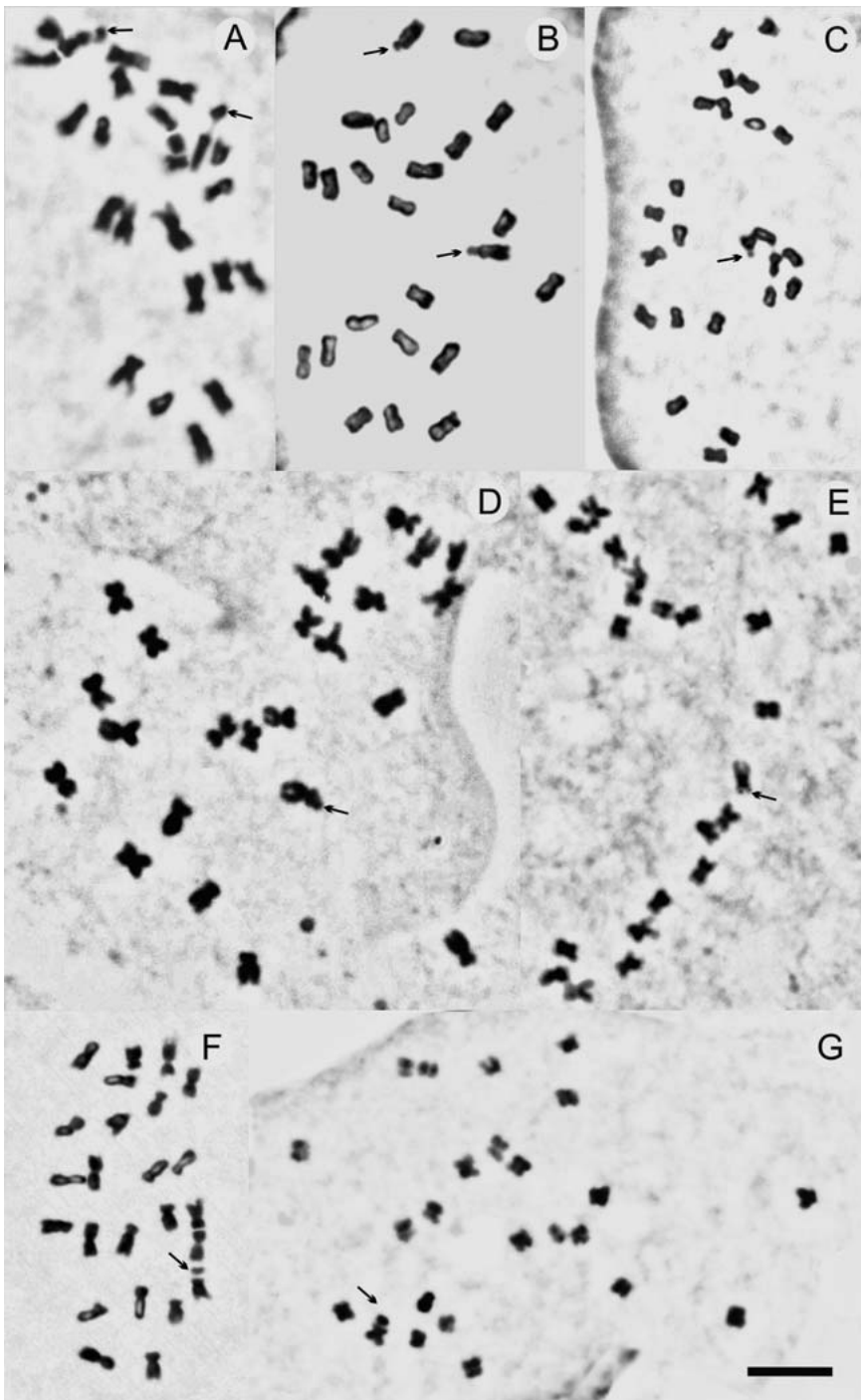
Species	2n	Haploid karyotype formulae	SAT	C	R	tl	$A_1$	$A_2$	Stebbins' category
<i>S. acerifolium</i> *	24	7 m + 5 sm	11	1.94 $\pm$ 0.17	1.72 $\pm$ 0.13	23.33 $\pm$ 2.03	0.36	0.14	2A
<i>S. aenictum</i> *	24	4 m + 6 sm + 2 st	6	2.81 $\pm$ 0.11	2.19 $\pm$ 0.21	33.71 $\pm$ 1.66	0.46	0.18	3A
<i>S. conditum</i> *	24	8 m + 4 sm	1	1.42 $\pm$ 0.24	1.57 $\pm$ 0.17	17.03 $\pm$ 2.93	0.37	0.15	2A
<i>S. consimile</i> *	24	10 m + 2 sm	1	1.33 $\pm$ 0.14	1.38 $\pm$ 0.25	27.73 $\pm$ 2.72	0.26	0.22	2A
<i>S. guaraniticum</i>	24	9 m + 3 sm	1	1.51 $\pm$ 0.26	1.47 $\pm$ 0.43	18.17 $\pm$ 2.02	0.27	0.14	2A
<i>S. incarceratum</i> *	24	9 m + 3 sm	3	2.05 $\pm$ 0.21	1.49 $\pm$ 0.08	24.61 $\pm$ 2.51	0.29	0.24	2A
<i>S. lycocarpum</i>	24	8 m + 4 sm	5	2.01 $\pm$ 0.21	1.64 $\pm$ 0.06	24.09 $\pm$ 4.70	0.33	0.14	2A
<i>S. mammosum</i>	22	6 m + 3 sm + 2 st	4	2.55 $\pm$ 0.23	2.07 $\pm$ 0.27	28.04 $\pm$ 2.46	0.39	0.24	2A
<i>S. marginatum</i>	24	11 m* + 1 sm	1	2.27 $\pm$ 0.16	1.33 $\pm$ 0.05	27.19 $\pm$ 1.88	0.22	0.15	1A
<i>S. paniculatum</i>	24	8 m + 4 sm	1	2.06 $\pm$ 0.15	1.60 $\pm$ 0.11	26.44 $\pm$ 2.12	0.40	0.23	1B
<i>S. platense</i> *	22	7 m + 4 sm	5	2.93 $\pm$ 0.62	1.64 $\pm$ 0.57	19.44 $\pm$ 2.09	0.33	0.21	2A
<i>S. tabacifolium</i>	24	10 m + 2 sm	3	1.79 $\pm$ 0.15	1.45 $\pm$ 0.07	21.47 $\pm$ 1.80	0.27	0.17	2A
<i>S. viarum</i>	24	8 m + 4 sm	2	1.57 $\pm$ 0.06	1.57 $\pm$ 0.06	29.20 $\pm$ 5.64	0.33	0.16	2A

et al., 1994; Acosta et al., 2005). This is unfortunate because karyotypic features can be as systematically informative as morphological features (e.g., Stebbins, 1971; Kenton et al., 1986; Bernardello and Anderson, 1990). Thus, the aim of this work is to survey the karyotypes of South American species of *Solanum* sect. *Leptostemonum*, belonging to four sections, in order to elucidate their taxonomic relationships and to assess the karyotype to obtain possible insights into the evolutionary processes in this group. Twelve of the species studied are native, whereas *S. marginatum* L. f. is native to Africa and grows naturalized in disturbed areas of the Andes from Colombia to Chile.

## Materials and Methods

The species studied and collections used are listed in Table 1. Species are arranged in sections according to the system proposed by Nee (1999).

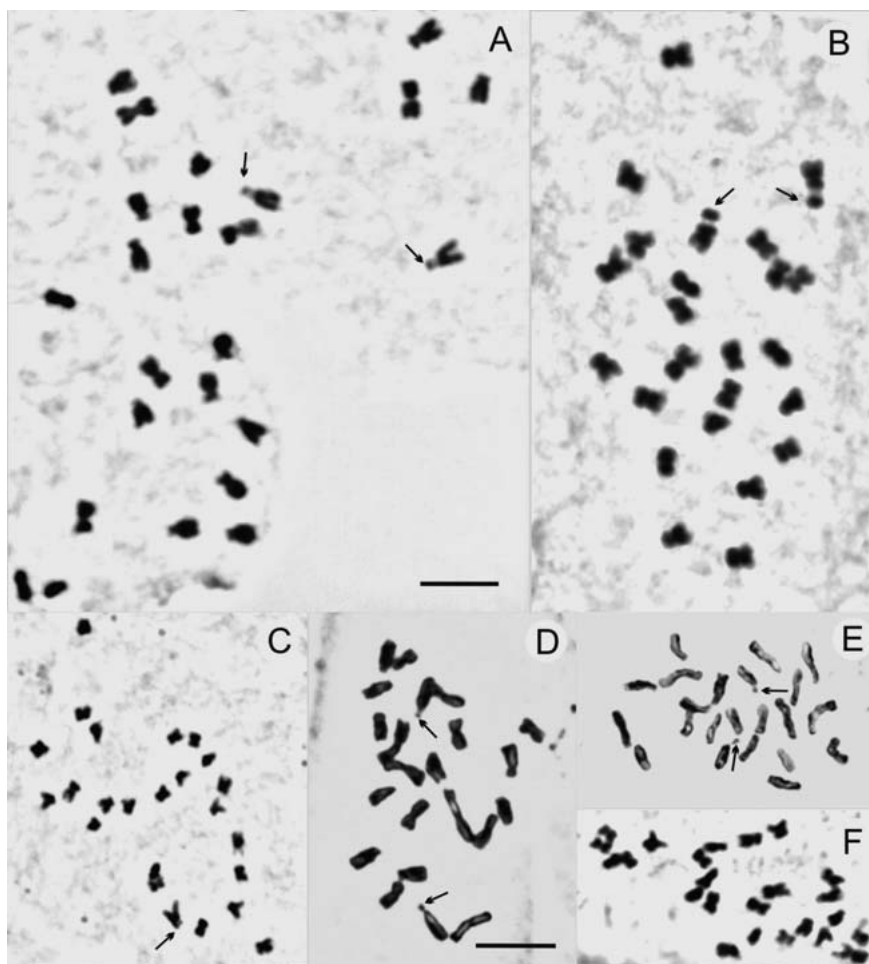
Primary roots obtained from germinating seeds were used to study somatic chromosomes. Root tips were pretreated with a paradichlorobenzene-saturated water solution for 2 h at room temperature, fixed in a 3:1 ethanol:acetic acid mixture for a minimum of 12 h, and stained with the Feulgen technique. Permanent mounts were made following Bowen's method (1956). At least ten metaphases of each species were photographed with phase contrast in a Zeiss Axiophot microscope. Photo-



**Fig. 1** Photomicrographs of mitotic metaphases of *Solanum* subgen. *Leptostemonum* species. (A) *S. paniculatum*; (B) *S. consimile*; (C) *S. acerifolium* (Benitez and Rojas 6477); (D) *S. viarum*; (E) *S. tabacifolium*; (F) *S. lycocarpum*; (G) *S. guaraniticum*. Arrows point to satellites. Bar represents 5  $\mu$ m; all pictures at the same scale.

graphs were used to take the following measurements for each chromosome pair: *s* (short arm), *l* (long arm), and *c* (total chromosome length). The arm ratio ( $r=l/s$ ) was then calculated and used to classify the chromosomes as recognized by Levan et al. (1964). Satellites were designated according to Battaglia (1955). Satellite lengths were added to the lengths of the corresponding arms. In addition, total haploid chromosome length of the karyotype (*tl*), based on the mean chromosome lengths for each species, average chromosome length (*C*), and average arm ratio (*R*) were calculated. Karyotype asymmetry

was estimated using Romero Zarco's (1986) indices ( $A_1$  = intra-chromosomal asymmetry index, which indicates the length difference among the chromosome arms, and  $A_2$  = interchromosomal asymmetry index, which indicates the size variation among the chromosomes), and Stebbins' (1971) karyotype asymmetry categories. Idiograms were based on the mean values for each species. The chromosomes were arranged first into groups according to their increasing arm ratio (from *m* to *st*) and then according to the decreasing length within each group.



**Fig. 2** Photomicrographs of mitotic metaphases of *Solanum* subgen. *Leptostemonum* species. (A) *S. aenictum*; (B) *S. marginatum*; (C) *S. conditum*; (D) *S. mammosum*; (E) *S. platense*; (F) *S. incarceratum*. Arrows point to satellites. Bars represent 5  $\mu\text{m}$ ; B–F at the same scale.

To test for a correlation among the abovementioned values, lineal regression tests were conducted using the software INFOSTAT (version 1.1, Infostat Group 2002). Scatter diagrams involving asymmetry indices were plotted. In order to compare the data obtained, a cluster analysis was performed using six variables per genome:  $tl$ ,  $R$ ,  $C$ ,  $A_1$ ,  $A_2$ , and the somatic chromosome number; these variables were employed because they do not assume homologies among the genomes. The program SYSTAT (version 7.0, SPSS Inc., 1997) was used to standardize a data matrix, to calculate the average Euclidean distance, and to generate a UPGMA (unweighted pair-group method using arithmetical averages) dendrogram.

## Results

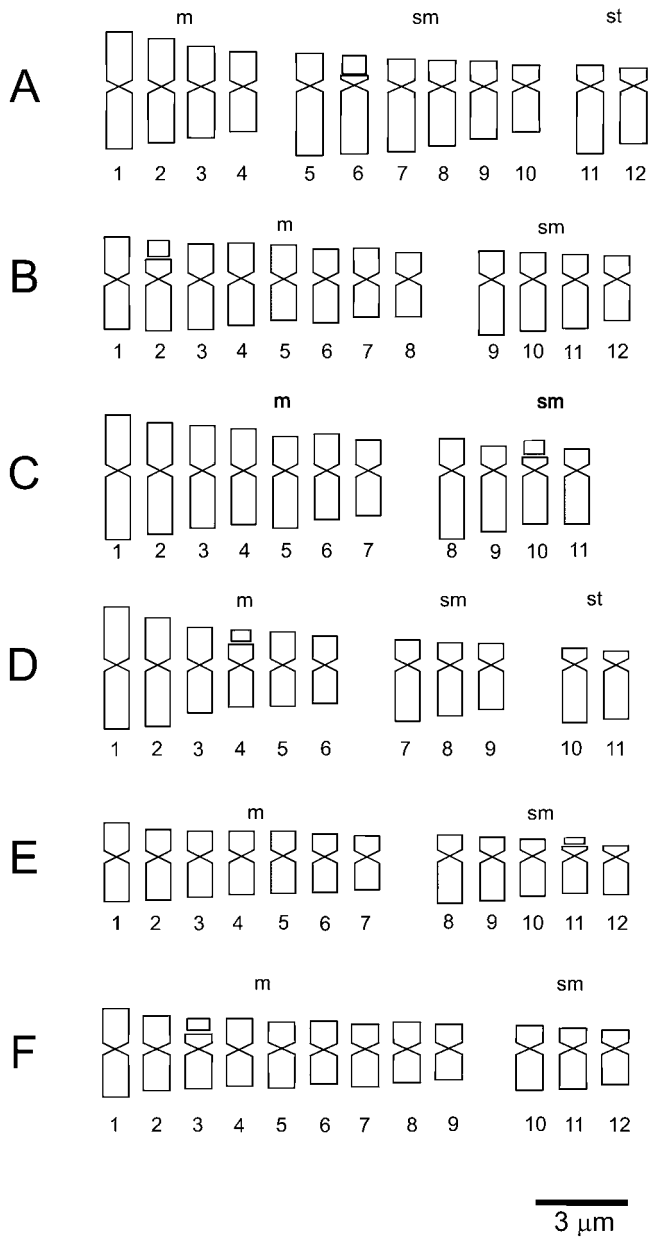
Only two of the taxa examined (*S. mammosum*, *S. platense*) have the somatic chromosome number  $2n=22$ , whereas the remaining species were  $2n=24$  (Table 2). The chromosome numbers of six species, indicated with an asterisk in Table 1, are reported for the first time.

Figs. 1 and 2 illustrate the range of chromosomes encountered. Precise idiograms calculated from means are given in Figs. 3 and 4. As a whole, the chromosomes are small (Table 2). The average chromosome length varies from 1.33 to 2.93  $\mu\text{m}$ . The

shortest measured chromosome was pair no. 12 in one cell of *S. conditum* (0.75  $\mu\text{m}$ ) and the longest was pair no. 1 in a cell of *S. mammosum* (4.25  $\mu\text{m}$ ).

Satellites are present on all entities (Table 2, Figs. 1, 2). According to their shape and position, they are always terminal and microsatellites, with the exception of *S. marginatum* that has macrosatellites (Fig. 2B). Their frequency of appearance varies according to the taxa: in most of them, satellites are found in more than the 50% of the cells, except in *S. conditum* where they are visible in only 31%. Usually, satellites are observed in both members of the respective chromosome pair, although sometimes they appear in only one homologue.

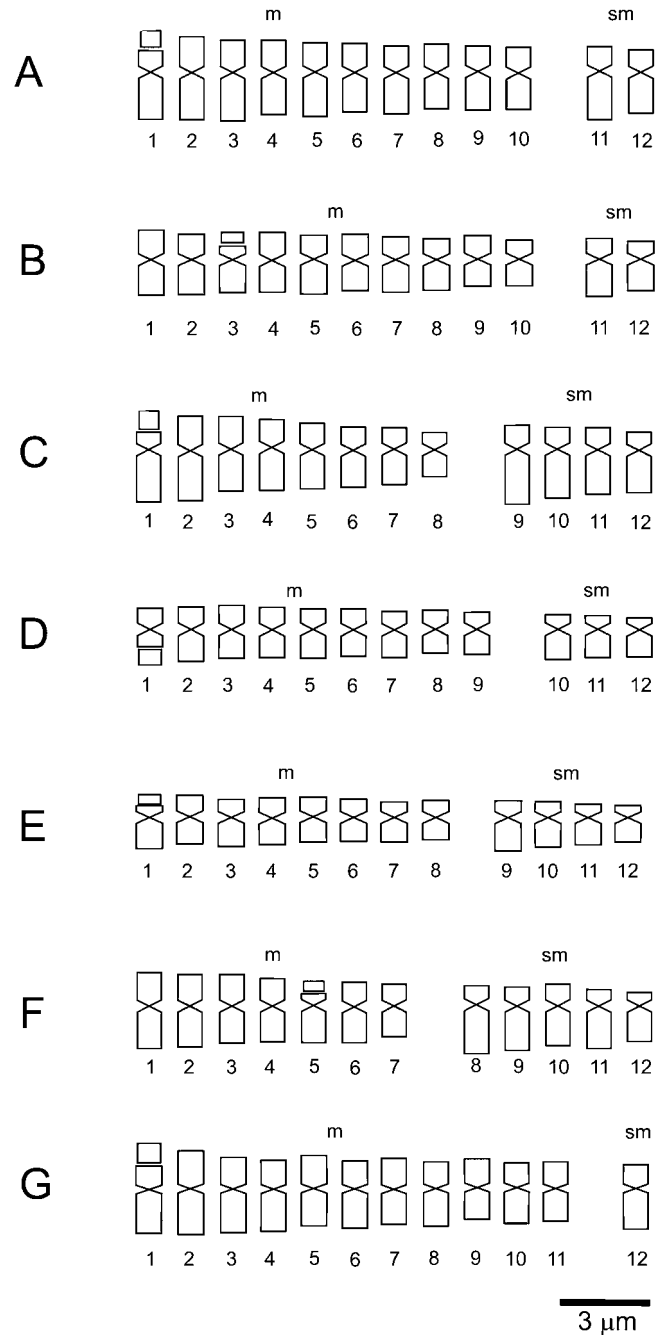
Overall, karyotypes are quite symmetrical: most species fall into 2A category in Stebbins' classification (1971), and Romero Zarco's (1986) asymmetry indices ranges are:  $A_1 = 0.22-0.46$  and  $A_2 = 0.14-0.24$  (Table 2). In all species,  $m$  chromosomes are the most common (66% of all the chromosomes);  $sm$  chromosomes follow in frequency (31%), whereas  $st$  chromosomes are rare (3%). The karyotypes of *S. marginatum*, *S. consimile*, and *S. guaraniticum* are the most symmetrical and those of *S. aenictum*, *S. mammosum*, and *S. paniculatum* are comparatively asymmetrical.



**Fig. 3** Idiograms for *Solanum* subgen. *Leptostemonum* sect. *Acanthophora* species, based on mean values. (A) *S. aenictum*; (B) *S. viarum*; (C) *S. platense*; (D) *S. mammosum*; (E) *S. acerifolium*; (F) *S. incarceratum*. All at the same scale.

As a result of the regression tests, no association between karyotype length and asymmetry or other associations with biological meaning could be drawn (data not shown). Scatter diagrams show little or no clustering among the species according to their sections (Fig. 5).

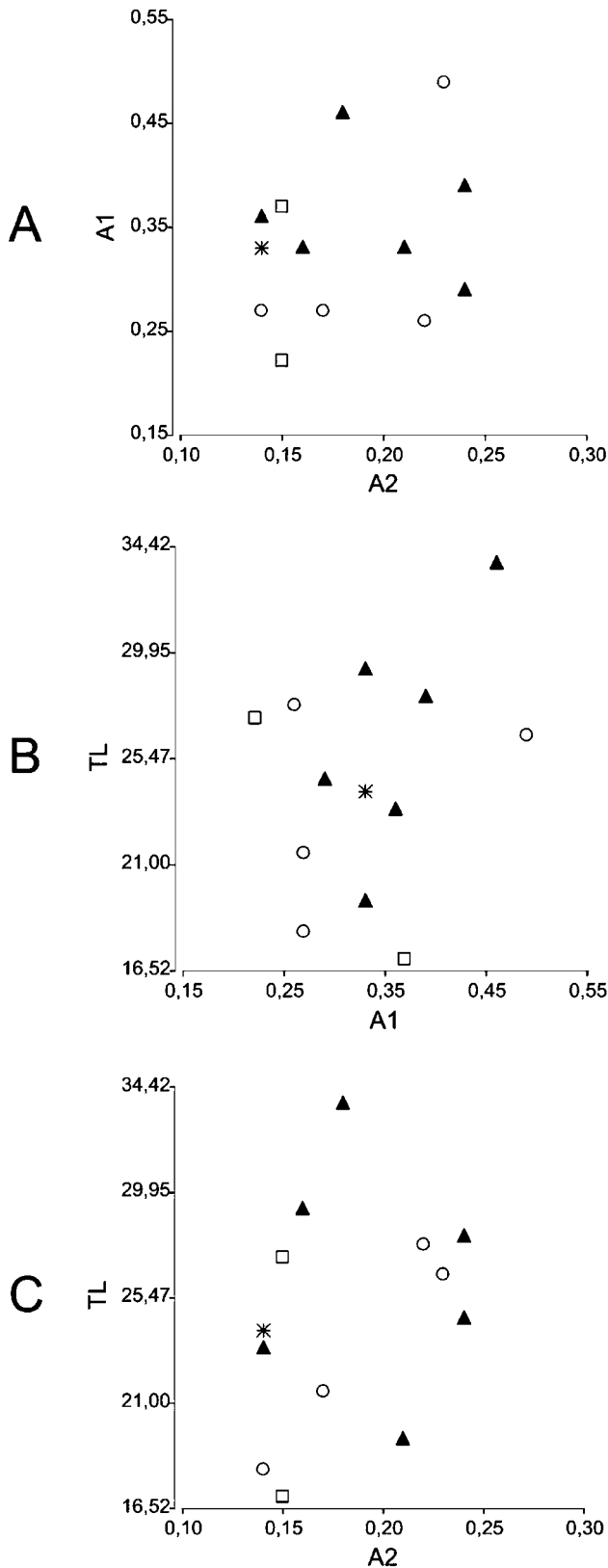
Species can be distinguished by a combination of chromosome number, karyotype formulae, and the position of satellites in a particular chromosome pair (Table 2). Karyotype length and asymmetry indices are also useful to discriminate some taxa (Table 2).



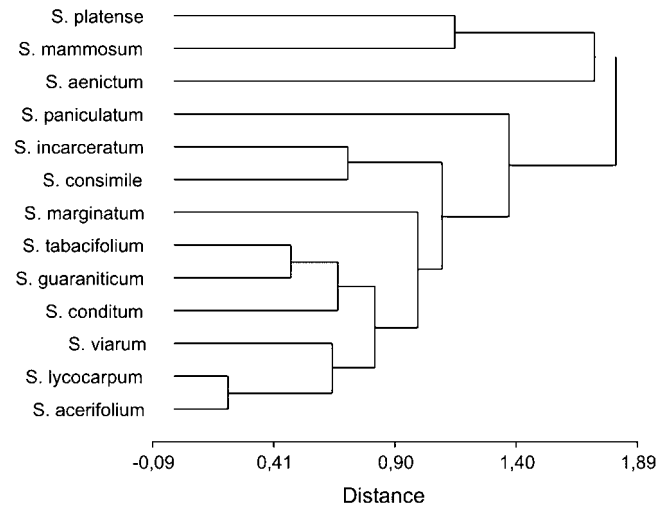
**Fig. 4** Idiograms for *Solanum* subgen. *Leptostemonum* sect. *Torva*, *Crinitum*, and *Melongena* species, based on mean values. (A) *S. consimile*; (B) *S. tabacifolium*; (C) *S. paniculatum*; (D) *S. guaraniticum*; (E) *S. conditum*; (F) *S. lycocarpum*; (G) *S. marginatum*. All at the same scale.

The dendrogram obtained, based on some karyotype features (Fig. 6), does not reflect the sectional arrangements. Three species out of the six studied of sect. *Acanthophora* are first isolated in a cluster: *S. aenictum*, as the most different because of its longer chromosomes and asymmetrical karyotype, and *S. mammosum* and *S. platense* together supported by the same chromosome number ( $2n = 22$ ). The remaining species, regardless of their section, form a cluster in which *S. paniculatum*, *S. incarceratum*, and *S. consimile* are first separated according





**Fig. 5** Scatter diagrams based on mean values for each species. (A) Asymmetry index A<sub>1</sub> plotted against asymmetry index A<sub>2</sub>. (B) Total genome length, TL, plotted against A<sub>2</sub>. (C) TL plotted against A<sub>1</sub>. Black triangles represent species of section *Acanthophora*; white circles, species of section *Torva*; an asterisk, *Solanum lycocarpum*; a white square, species of section *Melongena*.



**Fig. 6** UPGMA phenogram derived from average Euclidean distance among species of *Solanum* sect. *Leptostemonum*.

to comparatively high A<sub>2</sub> values, and then the rest of the species that share shorter chromosomes.

**Discussion**

Seven counts (species without an asterisk in Table 2) confirm previous data obtained from plants from different geographical areas (cf. Jørgensen, 1928; Randell and Symon, 1976; Coleman, 1982; Maglio et al., 1984; Maheswar Hassan and Krishnan, 1984; Kumaraswamy and Krishnan, 1987; Carvalheira et al., 1991; Forni-Martins et al., 1995).

The majority of the species here examined show 2n = 24, with x = 12. This basic number is frequent in the family, where about 50% of the species studied up to now have it (cf. Bolkhovskikh et al., 1969; Hunziker, 2001). At the same time, it is predominant in both subfam. Solanoideae and genus *Solanum* as well (cf. Moscone, 1992; Olmstead et al., 1999; Hunziker, 2001; Acosta et al., 2005). The number 2n = 22 (x = 11) was previously known only for *S. mammosum* of sect. *Acanthophora*. We here report a second *Solanum* species of the same section (*S. platense*) with this unusual number. In other Solanoideae genera, x = 11 was exclusively found in *Quincula lobata* (Menzel, 1950), whereas it is more common in the basal subfamily Cestroideae (cf. Olmstead et al., 1999; Hunziker, 2001). Thus, in *Solanum* subgen. *Leptostemonum* x = 12 is the rule. Nevertheless, rare dysploid changes originating x = 11 have occurred, as well as euploid series based on x = 12 (Randell and Symon, 1976; Moscone, 1992).

The two species studied with x = 11 show comparatively larger chromosomes with noticeable differences in size among the pairs of the complement. The origin of this number reduction may have been produced either by successive unequal translocations increasing the differences in relative size among chromosomes (Stebbins, 1971) or by a Robertsonian fusion (John and Freeman, 1975).

Except for *Solanum* sect. *Cyphomadropsis*, with large chromosomes ranging from 3 to 14  $\mu\text{m}$ , the remaining *Solanum* sections have chromosomes two to five times smaller (Roe, 1967; Pringle and Murray, 1991; Bohs, 1994), as found in the species here studied.

In most of karyotypes, the shortest chromosomes of the complement are *sm* or *st*, i.e., as chromosome size decreases the centromere becomes more terminal, as also reported for other *Solanum* species (Pringle and Murray, 1991).

The presence of one satellited chromosome pair is usual in most diploid *Solanum* species (e.g., Krishnappa and Chennaveeraiah, 1975; Trivedi and Sinha, 1986; Okoli, 1988; Bernardello et al., 1994; Acosta et al., 2005). The same situation is observed in sect. *Leptostemonum*, except for *S. pseudolulo* Heiser with two satellited pairs (Bernardello et al., 1994) and the species of the *S. indicum* complex, with a maximum of three pairs with satellites (Krishnappa and Chennaveeraiah, 1975). Concerning the type of chromosome, satellites in *Solanum* are commonly placed in *m* chromosomes (Acosta et al., 2005), whereas in subgenus *Leptostemonum* they may be either in *m*, *sm*, or *st* chromosomes (Patil, 1968; Bernardello et al., 1994; Acosta et al., 2005; our results). Most species studied karyologically in this subgenus present satellites in short arms (e.g., Krishnappa and Chennaveeraiah, 1975; Trivedi and Sinha, 1986; Okoli, 1988; Bernardello et al., 1994; Acosta et al., 2005); so far, only *S. pseudolulo* (Bernardello et al., 1994) and *S. guaraniticum* (our results) have satellites attached to long arms. In the karyotypes here detailed, the satellited pair is among the largest five chromosomes of the complement. A similar phenomenon occurs in other *Leptostemonum* species, where the satellited pair is comparatively large (e.g., Krishnappa and Chennaveeraiah, 1975; Trivedi and Sinha, 1986; Okoli, 1988; Acosta et al., 2005).

A perusal of the available literature shows that there is a common karyotype pattern in the genus *Solanum* with chromosomes of approximately the same length, with median or submedian centromeres (Mitra, 1967; Krishnappa and Chennaveeraiah, 1975; Trivedi and Sinha, 1986; Okoli, 1988; Bernardello et al., 1994; Acosta et al., 2005). Following this trend, the karyotypes here analyzed have a majority of *m* and *sm* chromosomes, with the former being widespread. At the same time, *t* chromosomes are atypical: only two species of sect. *Basarthurum* (Bernardello and Anderson, 1990) and *S. surattense* (Trivedi and Sinha, 1986) are reported so far to have one pair of this kind.

Within subgen. *Leptostemonum*, species of sect. *Acanthophora* show the most asymmetrical karyotypes, a fact also detected by Acosta et al. (2005). Stebbins (1971) noted that, in certain plant groups, increased asymmetry is associated with derived characters. Accordingly, some of the species here studied display derived morphological features (Whalen, 1984; Nee, 1991), such as strong andromonoecy (*S. aenicium*, *S. platense*, *S. mammosum*), flattened, winged seeds (*S. platense*), or mamiform fruits (*S. mammosum*).

Our data suggest that diversification in the subgenus has been associated with visible chromosome rearrangements (e.g., duplications, pericentric inversions, and translocations). In this sense, it has been proposed that cumulative and cryptic struc-

tural changes have played a relevant evolutionary role in sect. *Lasiocarpa* (Bernardello et al., 1994). As a result, most individual species can be chromosomically distinguished, as shown in the phenogram obtained (Fig. 6). For instance, some phenotypically closely related species, e.g., *S. aenicium* and *S. palinacanthum* (Matesevach, 2002), *S. paniculatum* and *S. guaraniticum* (Auler Mentz and de Oliveira, 2004), proved to be karyotypically different. Thus, an extensive karyotype analysis in *Solanum* subgen. *Leptostemonum* is needed in order to improve our knowledge of its evolutionary trends.

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