DARWINIANA 45(2): 163-174. 2007 ISSN 0011-6793

PLACENTATION PATTERNS AND SEED NUMBER IN FRUITS OF SOUTH AMERICAN *SOLANUM* SUBGEN. LEPTOSTEMONUM (SOLANACEAE) SPECIES

Franco E. Chiarini & Gloria E. Barboza

Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC), casilla de correo 495, 5000 Córdoba, Argentina; chiarini@imbiv.unc.edu.ar (author for correspondence).

Abstract. Chiarini, F. E. & G. E. Barboza. 2007. Placentation patterns and seed number in fruits of South American *Solanum* subgen. Leptostemonum (Solanaceae) species. *Darwiniana* 45(2): 163-174.

Thirty-seven South American species representing seven sections of *Solanum* subgen. Leptostemonum were analyzed. Andromonoecious as well as hermaphrodite species were considered. The length and width of their fruits was measured, and the number of seeds per fruit was counted. Medial cross sections of fresh, ripe fruits were observed with a stereoscopic microscope and illustrated. Six placentation patterns and three types of seeds were described. A relationship among seed number, fruit size, fruit color and sexual system was detected by means of statistical analysis. These results suggest that andromonoecy affects fruit size and placentation patterns, in order to contain a higher number of seeds per fruit.

Keywords. Andromonoecy, Leptostemonum, placentation, seed number, *Solanum*, South America.

Resumen. Chiarini, F. E. & G. E. Barboza. 2007. Patrones de placentación y número de semillas en frutos de especies sudamericanas de *Solanum* subgen. Leptostemonum (Solanaceae). *Darwiniana* 45(2): 163-174.

Se analizaron 37 especies sudamericanas pertenecientes a siete secciones de *Solanum* subgen. Leptostemonum. Fueron consideradas tanto especies andromonoicas como hermafroditas. Se midió el ancho y el largo de sus frutos y se contó el número de semillas por fruto. Se estudiaron bajo lupa y se ilustraron cortes por la zona media de frutos frescos maduros. Se describieron seis patrones de placentación y tres tipos de semillas. Mediante análisis estadístico, se detectó una relación entre el número de semillas, el tamaño del fruto, el color del fruto y el sistema sexual. Estos resultados sugieren que la andromonoecia afecta al tamaño del fruto y su patrón de placentación, para contener un mayor número de semillas.

Palabras clave. Andromonoecia, Leptostemonum, número de semillas, placentación, *Solanum*, Sudamérica.

INTRODUCTION

Solanum L. is one of the largest genera among Angiosperms, including about 1100-1400 species (Nee, 1999; Hunziker, 2001; Bohs, 2005) that grow in all kinds of habitats. The largest subgenus within *Solanum* is Leptostemonum (Dunal) Bitter, with ca. 450 species (Nee, 1999). This subgenus, with nine sections in South America, includes edible species of economic importance (*S. melongena* L., “Eggplant”; *S. sessiliflorum* Dunal, “Cocona” or “Cubiu”; *S. quitoense* Lam., “Naranjilla” or “Lulo”), and also weeds (*S. viarum* Dunal, “Tropical soda apple”; *S. elaeagnifolium* Cav., “Silverleaf nightshade”; *S. sisymbriifolium* Lam., “Sticky nightshade” or “Wild tomato”; *S. rostratum* Dunal, “Buffalo bur”, “Bull thistle” or “Texas thistle”).

Several species of *Solanum* subgen. Leptostemonum have been studied due to their andromonoecy or functional dioecy (Wakhloo, 1975a, b; Anderson, 1979; Dulberger et al., 1981; Coleman & Coleman, 1982; Solomon, 1987; Anderson & Symon, 1989; Diggle, 1991, 1993). The andromonoecy has been linked with fruit type, and a corre-

Original recibido el 10 de agosto de 2007; aceptado el 2 de noviembre de 2007

lation between fruit size and the degree of andromonoecy has been proposed for some species (Whalen & Costich, 1986). Recently, in a study that embraced five species of *Solanum* sect. Acanthophora and eight of sect. Lasiocarpa, Miller & Diggle (2007) demonstrated that fruit size is positively correlated with the proportion of staminate flowers produced within inflorescences. These authors concluded that andromonoecy is a mechanism to regulate allocation to female function (i.e., fruit production) independently of allocation to male function.

Despite these suggestive previous works, detailed studies on fruit structure of subgenus Leptostemonum are rare. Only some scattered species have been studied (Miller, 1969; Dave et al., 1979; Dottori & Cosa, 1999, 2003), but a comprehensive analysis of the subgenus as a natural group is lacking. With regard to the placentation patterns, only general surveys for Solanaceae (Nee, 1986), and for the genus *Solanum* (Symon, 1987) are available. This is unfortunate, since the contributions of morphology and anatomy to systematics are widely known, so a study considering any fruit structure would be valuable for *Solanum* subgen. Leptostemonum. The present work attempts to provide morpho-anatomical information in order for it to be used systematically, and as a contribution to understand the relationship between function and structure in South American species of *Solanum* subgen. Leptostemonum. Our proposal is that placentation and seed number are influenced by the sexual system.

MATERIALS AND METHODS

We analyzed as many species as possible, trying to study at least one species of each section. Thirty seven wild species representing seven sections of *Solanum* subgenus Leptostemonum were sampled (see appendix 1).

Several phylogenetic approaches have being carried out by different authors (Bohs, 2005; Levin et al., 2005, 2006) in which informal infrageneric grouping (clades) have been defined within *Solanum*, and probably will be given a formal status (Nee et al., 2006). Meanwhile, we have arranged the species according to the last conventional taxonomic treatment (Nee, 1999) (Table 1).

Samples of at least 10 fruits per species (of different individuals, when possible) were taken. The length and width of each fruit were measured with a Vernier calliper, and the number of seeds was counted. Averages of these measurements are detailed in Table 1. Medial cross sections of fresh, ripe fruits were observed in stereoscopic microscope preparations. Placentation patterns are based on these observations and are presented as sketches. Data about the sexual system of the species studied were taken from the literature, and from our own observations in the field (Table 1).

Kruskal-Wallis tests were performed in order to detect: a) differences in fruit size and seed number according to epidermis colours, b) differences in fruit size among andromonoecious and hermaphrodite species, and c) differences in seed number among andromonoecious and hermaphrodite species. A linear regression was also conducted to find out whether there is a relationship between fruit size and seeds number. Infostat (2001) was used for the statistical analysis.

RESULTS

The mean size, color, placentation pattern of the fruits, and type and mean number of seeds for each species are summarized in Table 1. Most of the taxa have spherical fruits (i.e. width = length = diameter), with some exceptions like *S. hieronymi*, which has depressed spherical fruits, *S. tenuispinum* or *S. aridum*, with ovoid fruits, and *S. mammosum* with its anomalous, 3-5 basally lobed fruit.

There are only two species with a hairy pericarp in mature fruits. In *S. lycocarpum* the hairs are stalked-stellate, while in *S. robustum* they are simple, non-glandular and 1-3-celled. At the early stages, *S. quitoense* and *S. asperolanatum* have a pubescent pericarp that turns glabrous at maturity. The remaining species analyzed are always glabrous.

Mature fruits are of a single color. They can be red, orange or orange-red (e.g. *S. capsicoides*, *S. sisymbriifolium*), yellow (most of the species), black or brownish (*S. mortonii*), dark green (*S. bolivianum*), greenish yellow (*S. platense*) or greenish grey (*S. comptum*, *S. euacanthum*). In hairy-fruited species, the color is given by the hairs. The fruit of *S. lycocarpum* is greyish due to its hairs, but the epicarp underneath them is green-

Table 1. Macroscopic and anatomical fruit features of the 37 species of *Solanum* subgen. Leptostemonum studied. Diameter is given when fruit is spherical, and length and width are given when fruit has another shape. Abbreviations: **A,** andromonoecious species; **H,** hermaphrodite species; **NS,** mean number of seeds per fruit.

Species	Sexual System	Placentation Pattern	NS	Seed Type	Fruit Color	Fruit shape and size (long. x lat., cm)
Sect. Acanthophora						
S. aculeatissimum	A	3	117.0	bulky	yellow	1.84
S. aenictum	A	4	180.2	bulky	yellow	2.75
S. atropurpureum	H	3	99.2	winged	red	1.45
S. capsicoides	A	4	298.5	winged	red	3.14
S. incarceratum	H	3	50.0	winged	greenish yellow	1.35
S. mammosum	A	3	300.0	bulky	yellow	7 x 4
S. palinacanthum	A	3	250.0	bulky	yellow	3.9
S. platense	A	3	80.0	winged	greenish yellow	2
S. tenuispinum	H	3	81.3	winged	yellow	1.37 x1.22
S. viarum	A	4	369.4	bulky	yellow	2.23
Sect. Crinitum						
S. lycocarpum	A	5	600.0	bulky	hairs greyish, epidermis greenish	10.00
S. urticans	A	5	431.0	bulky	yellow	4.067
Sect. Erythrotrichum						
S. robustum	A	5	326.0	bulky	hairs greyish, epidermis yellow	1.8
Sect. Herposolanum						
S. alternatopinnatum	A	1	150.0	bulky	yellow	4.2
Sect. Lasiocarpa						
S. quitoense	A	5	1444	bulky	yellow	4
Sect. Melongena						
S. aridum	H	1	63.7	bulky	yellow	1.567 x 1.1
S. comptum	A	1	112.4	rimmed	greenish grey	1.07
S. elaeagnifolium	A	1	58.8	bulky	yellow	1.01
S. euacanthum	H	3	57.0	bulky	greenish grey	0.88
S. hieronymi	A	2	249.0	bulky	yellow	1.86 x2.38
S. homalospermum	A	3	-	bulky	greenish grey	1.4
S. juvenale	H	1	91.9	bulky	yellow	1.64 x1.43

Table 1. (Continued)

S. marginatum	A	2	576.4	bulky	yellow	3.02
S. mortonii	A	1	182.5	Bulky (some flattened)	brown black	1.5
S. multispinum	A	3	325.0	bulky	yellow	3.2
S. sisymbriifolium	A	5	150.0	bulky	red	1.56
Sect. Torva						
S. albidum	H	5	221.6	bulky	dark green-black	1.268
S. asperolanatum	H	5	27.7	bulky	orange	1.252
S. bolivianum	H	3-carpellar	180.0	bulky	dark green	1.3
S. bonariense	H	5	80.6	bulky	orange-red	1.05
S. consimile	H	6	27.4	bulky	red	0.73
S. guaraniticum	H	5	40.8	bulky	orange	0.97
S. paniculatum	H	5	48.0	bulky	red	1.5
S. aff. *paniculatum*	H	5	73.6	bulky	orange-red	0.8
S. scuticum	H	2	350.0	bulky	yellow	1.3
S. toldense	H	5	40.0	bulky	brown black	1.23
S. variabile	H	6	80.0	bulky	red-orange	0.9

ish. The same occurs with *S. robustum*, which has a yellow epidermis.

In general, fruits are small to medium-sized, varying from 0.7 cm (*S. consimile*) to 4.2 cm (e.g. S. alternatopinnatum, *S. aenictum*) in diameter, with the exception of the large fruits of *S. lycocarpum*, which reach ca. 10 cm diameter. The Kruskal-Wallis test put in evidence significant differences (significance level 0.05, Table 2) in width among four colour types, namely, 1) yellow, 2) red, orange or orange-red, 3) brown, dark green or black, 4) greenish yellow or greenish grey. At the same time, andromonoecious species showed significantly larger fruits than the hermaphrodite ones (Table 2).

The number of seeds per fruit ranges from 27 (*S. consimile*) to ca. 370 (*S. viarum*), exceptionally many more in *S. lycocarpum* (up to 600) or in *S. quitoense* (ca. 1400) (Table 1). A significant correlation was found between fruit width and number of seeds (R2 = 0.32, p = 0.0003): the wider the fruit, the higher the number of seeds that it contains (Fig. 1). The Kruskal-Wallis test indicates that there are differences in seeds number among the four color types (significance level 0.05, Table 2), the higher mean (315.51) corresponding to yellow fruits. In addition, andromonoecious species have more seeds per fruit than hermaphrodite ones (Table 2).

Placentation patterns are presented as sketches in Figs. 2 and 3. All fruits show an axile placentation, the placentas growing from a bicarpellar gynoecium. In all species, a septum between the two carpels is present in the young fruit, but this septum may dissapear at some later stage as the fruit ripens. Exceptionally, all fruits of the only specimen of *S. bolivianum* analyzed are 3-carpellar (Fig. 2 S). Some fruits with three carpels were also found in *S. quitoense* and *S. marginatum*. There are several placentation patterns, and proliferation of the placentas into the locules may occur. Basically, six placentation patterns can be described: 1) bilocular fruit with normal placenta (*S. aridum*, *S. juvenale*, Fig. 2 R); 2) bilocular fruit

Table 2. Results of the Kruskal-Wallis tests.

Variable	Fruit color	N	Mean	SD	median	H	p
Fruit width (cm)	yellow	17	2.56	1.17	2.28	8.72	0.0332
	red, orange, orange-red	10	1.34	0.70	1.15		
	black, brown, dark green	4	1.33	0.12	1.28		
	greenish grey, greenish yellow	5	3.06	3.90	1.35		
Seed number	yellow	17	315.51	324.75	250.00	10.47	0.0150
	red, orange, orange-red	10	92.58	18.33	76.80		
	black, brown, dark green	4	156.03	79.66	181.25		
	greenish grey, greenish yellow	5	179.88	236.11	80.00		
Variable	Sexual system	N	Mean	SD	Median	H	p
Seed number	Andromonoecious	19	326.23	310.80	250.00	14.95	0.0001
	Hermaphrodite	17	94.87	83.33	73.60		
Fruit width (cm)	Andromonoecious	19	3.04	1.99	2.75	19.12	0.0001
	Hermaphrodite	17	1.16	0.24	1.23		

with placentas divided into branches (*S. scuticum*, *S. hieronymi*, Fig. 2 H, L); 3) unilocular fruit, due to a septum degeneration, with a single placenta (*S. tenuispinum*, *S. platense*, Figs. 2 N, 3 B); 4) unilocular fruit, due to a septum degeneration, with the placentas divided into two erect lobes (e.g., *S. viarum*, *S. aenictum*, Fig. 2 M, 2 C); 5) tetralocular fruit, due to the presence of a false septum (*S. bonariense*, *S. guaraniticum*, *S. lycocarpum*, *S. quitoense*, Figs. 2 B, O, G, 3 F), in which each false locule has a placental branch; 6) fruits with more than 4 false irregular locules, due to false septa, in which the placentas are scarcely differentiated from the pericarp and packed with the seeds (*S. variabile*, *S. consimile*, Fig. 2 J, F). The formation of the 4 locules follows the descriptions of Goebel (1905) and Murray (1945).

Seeds belong to three types: I. Winged, i.e., a strongly flattened seed, with the seed coat forming a prominent wing, 0.8-2 mm wide (e.g. *S. platense*, *S. capsicoides*, *S. atropurpureum*). II. Rimmed, i.e., a moderately flattened seed, with the seed coat thickened in the margin (e.g. *S. homalospermum*, *S. comptum*). III. Bulky, i.e., a slightly flattened or non-flattened lenticular seed, with the seed coat margin not thickened at all (e.g. *S. palinacanthum*, *S. multispinum*).

DISCUSSION

Symon (1987), in his general survey of placentation in the genus *Solanum*, considered only eight South American species of subgen. Leptostemonum. We performed a wider study on South American species, defining precisely the different placentation patterns. In agreement with the data obtained by Nee (1986) and Symon (1987) in accessions of other parts of the world, our results show that, within *Solanum* subgen. Leptostemonum, there are diverse placentation patterns apart from the type usually described in Solanaceae (type 1).

The anomalous increase in carpel number found in some individuals has already been

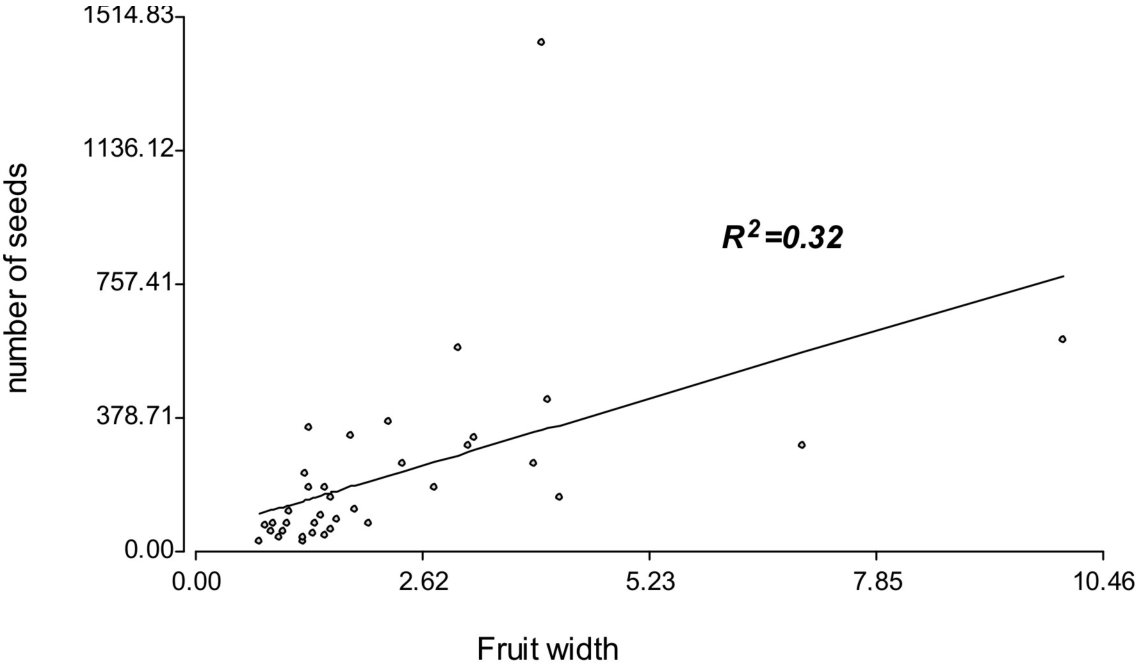

Fig. 1. The relationship between fruit size and number of seeds per fruit in 36 species of *Solanum* subgen. Leptostemonum. Data points are mean values for both variables for each species.

noticed in other *Solanum* species, both in wild and in domesticated ones (Nee, 1986; Symon, 1987), perhaps as a response to pressure for higher seed production. However, the basic condition seems to be axile placentation with a simple septum (type 1), from which the other specialized patterns would have arisen, through different modifications and degrees of complexity of the placentas. On the one hand, unilocular fruits are produced through a separation of the placentas into two erect lobes, with a degeneration of both the septum and the link between the two lobes (type 4). This pattern occurs in other species of sect. Acanthophora and Melongena, as Symon (1987) has already pointed out. In other species with unilocular fruits, the placenta does not divide into two erect lobes, but forms a single spindle-shaped structure (type 3, e.g. *S. incarceratum*, *S. platense*, and *S. tenuispinum*). On the other hand, in bilocular fruits the placentas divide into two branches once. In *S. scuticum* there is a modification in this sense, this species being the one with the highest number of seeds per fruit in section Torva (Fig. 2 H). Nee (1986) had already noted that the division of the placentas allows an increased production of seeds around the periphery of the branches. Another specialized pattern (type 5) comes from bilocular fruits in which a complete division occurs in the placentas, which forms false septa and results in a 4-locular fruit. All patterns described up to now would be different ways of containing a high number of seeds per fruit. It should be noticed that species with the highest number of seeds are 4-locular or have placentas divided into branches (*S. scuticum*, *S. lycocarpum*, *S. quitoense*).

As Nee (1986) mentioned, placentation patterns should be used with caution when establishing relationships, since they seem to respond quickly to selection constraints on the dispersal syndromes. Nevertheless, the placentation patterns here described may be useful to characterize each species and, in some regards, entire sections of the subgenus. For instance, in sect. Torva placentation patterns 5 or 6 prevail, the seeds being bulky and smooth in all cases. In sect. Acanthophora, placentation patterns 3 or 4 are present, and winged seeds were only found in some species of this section. Section Melongena is more variable since placentation patterns 1, 2, 3 and 5 were observed, and seeds can be bulky or rimmed, smooth or foveolate.

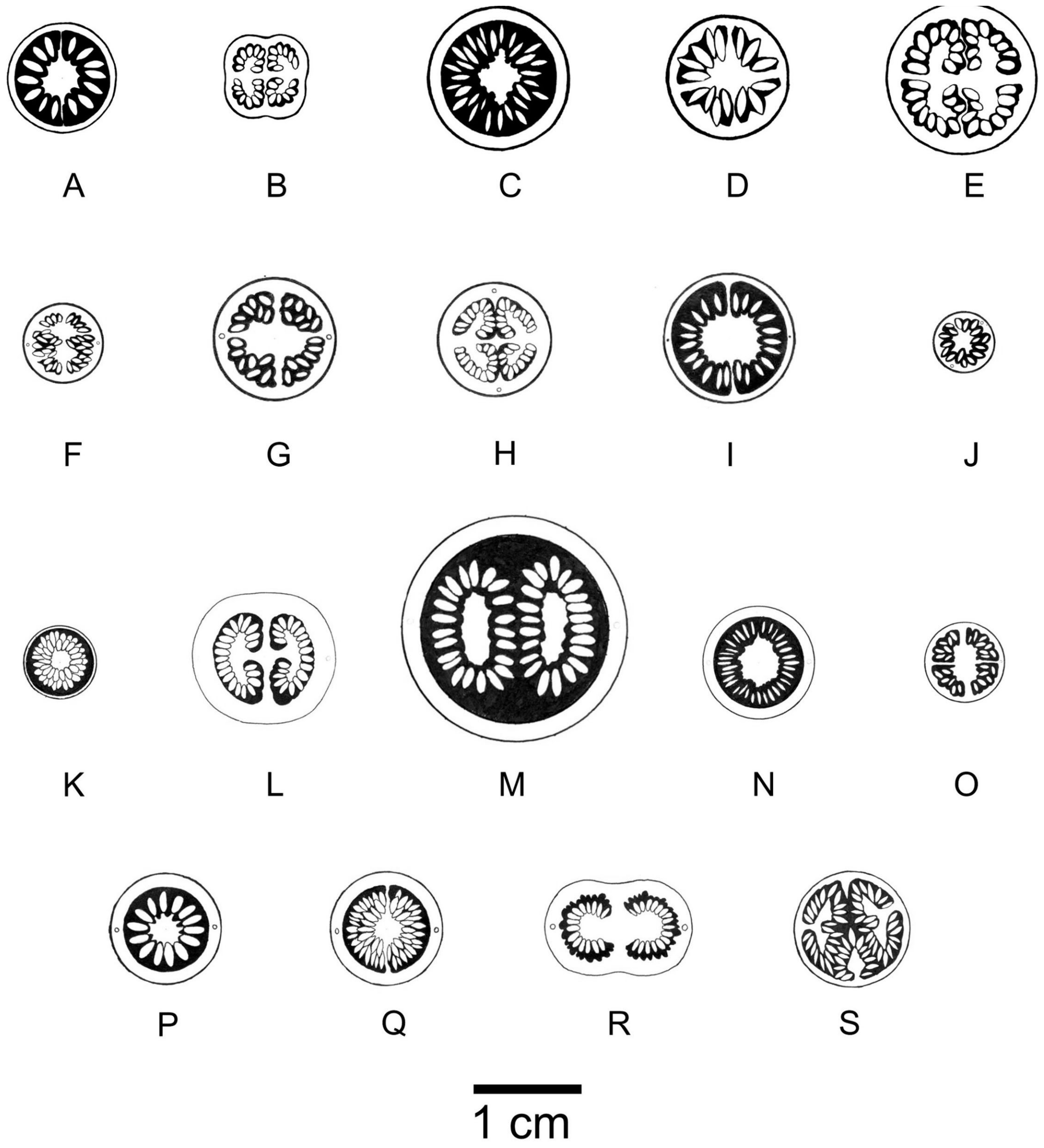

Fig. 2. Placentation patterns in mature fruits of *Solanum* subgen. Leptostemonum. The pericarp, septa, placentas and seeds are indicated in white, and the locules, in black. **A,** *S. elaeagnifolium*. **B,** *S. bonariense.* **C,** *S. atropurpureum.* **D,** *S. toldense*. **E,** *S. sisymbriifolium*. **F,** *S. variabile*. **G,** *S. paniculatum*. **H,** *S. scuticum*. **I,** *S. mortonii.* **J,** *S. consimile*. **K,** *S. euacanthum*. **L,** *S. hieronymi*. **M,** *S. viarum*. **N,** *S. tenuispinum*. **O,** *S. guaraniticum*. **P,** *S. incarceratum*. **Q,** *S. comptum*. **R,** *S. juvenale*. **S,** *S. bolivianum*. The bar represents 1 cm; all pictures are on the same scale.

Andromonoecious species tend to concentrate a high number of ovules in a few hermaphrodite flowers (Symon, 1979; Bertin, 1982; Whalen & Costich, 1986; Miller & Diggle, 2007); in consequence, they produce large fruits. In fact, our data on fruit size and its relationship with the sexual system are consistent with the conclusions of Miller & Diggle (2007), who demonstrated a correlation between fruit mass and strength of andromonoecy in species of *Solanum* sections Acanthophora and Lasiocarpa. Thus, andromonoecy would be an important factor influencing fruit features in

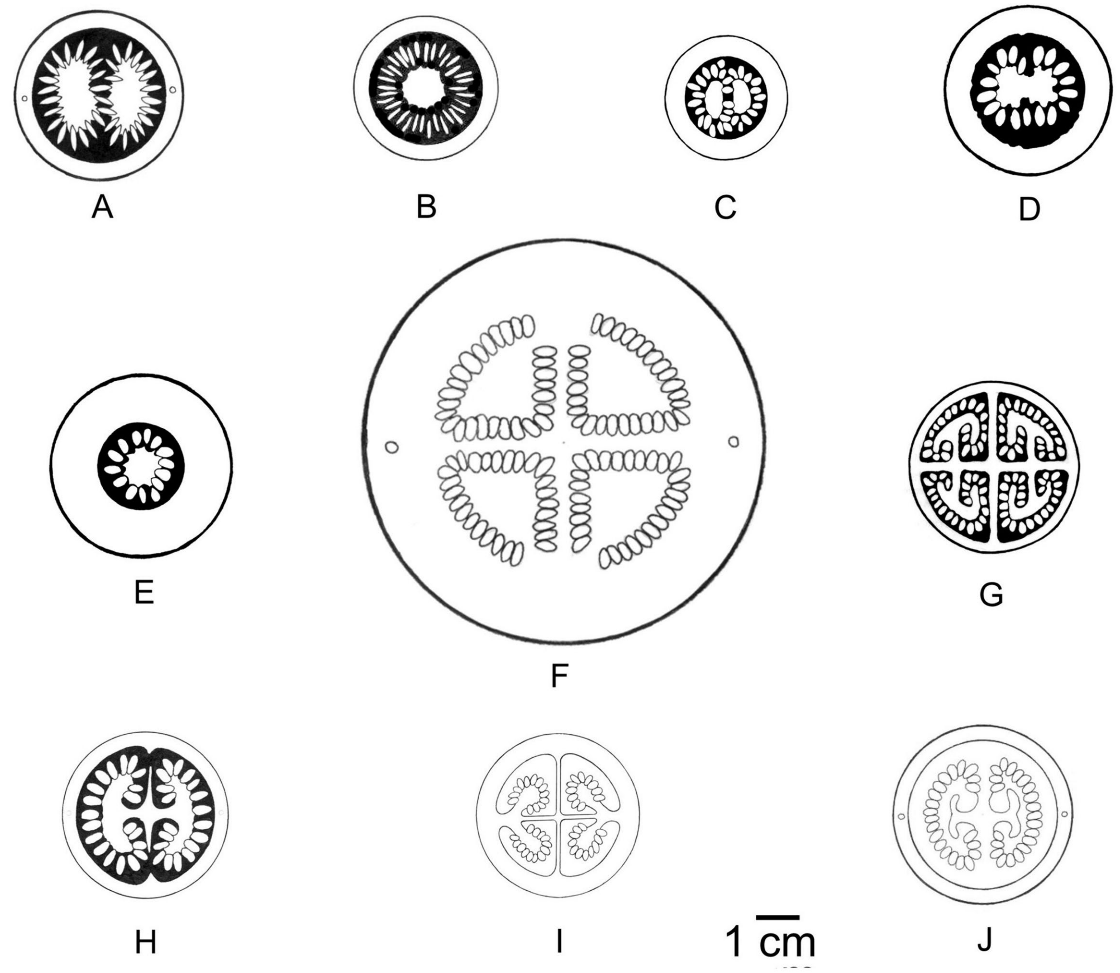

Fig. 3. Placentation patterns in mature fruits of *Solanum* subgen. Leptostemonum. The pericarp, septa, placentas and seeds are indicated in white, and the locules, in black. **A,** *S. capsicoides*. **B,** *S. platense*. **C,** *S. aenictum*. **D,** *S. palinacanthum*. **E,** *S. mammosum*. **F,** *S. lycocarpum*. **G,** *S. quitoense*. **H,** *S. multispinum*. **I,** *S. urticans*. **J,** *S. alternatopinnatum*. The bar represents 1 cm; all pictures are on the same scale.

Solanum subgen. *Leptostemonum*. This sexual system is a convergent phenomenon, a homoplasic character that varies secondarily (Whalen, 1984) and appears and disappears within the *Solanum* clades or natural groups independently (Whalen and Costich, 1986; Levin et al., 2006). The big, many-seeded fruits would be a collateral effect of the andromonoecy strategy, but this sexual system does not affect other fruit traits, such as color or type of seeds. There are andromonoecious species with yellow or red fruits, and with winged or bulky seeds. Placentation would also be influenced by the sexual system: in several andromonoecious species, placentas divide and turn over, and septa disappear, in order to contain a higher number of seeds.

The type of seeds does not seem to be related to any other fruit characteristic (fruit size, fruit color, number of seeds). As Nee (1991) has already reported, different kinds of seeds can be found in species of the same section, probably in response to environmental pressures. On their part, Levin et al. (2005) showed that, within sect. Acanthophora, species that share the same type of seed do not form a natural group.

It is interesting to at least speculate about the means of dispersal of the species here studied, since number and type of seeds, color and especially, size, are important factors in determining the dispersal agents (Van der Pijl, 1982). On one hand, species with big, fleshy fruits (i.e. *S. alternatopinnatum*, *S. robustum*, *S. lycocarpum*, *S. quitoense*) would be adapted to be dispersed by large vertebrates, such as mammals or parrots. In fact, the comsumption of the fruits of *S. lycocarpum* by the maned wolf *Chrysocyon brachyurus* (Canidae) is one of the few well documented cases of dispersion by large vertebrates in *Solanum* (Silva & Talamoni, 2003; Almeida Jácomo et al., 2004). On the other hand, big, indehiscent, spongy fruits with bulky seeds (i.e. *S. mammosum*, *S. palinacanthum*, *S. viarum*) are said to be dispersed by drain water after a rainstorm, the spongy tissue being an adaptation to flotation (Nee, 1979, 1991; Bryson & Byrd, 1994; Levin et al., 2005). In addition, Nee (1991) proposed a “shaker” mechanism as the dispersal syndrome for *S. capsicoides* and *S. platense*, species with apparently dehiscent, spongy fruits, and with winged seeds. Cipollini & Levey, (1997) and Cipollini et al. (2002) remark that large animals, like mammals, could actually feed on big spongy fruits, since they have a body size enough to tolerate the poisonous glycoalkaloids of these fruits.

In general, brightly colored, few-seeded, juicy fruits that are less than 15 mm in diam., with a thin pericarp and bulky seeds, would be presumably ornithochorous (Van der Pijl, 1982). This would be the case of the majority of species of sect. Torva. In fact, consumption by bats and diurnal birds has been documented for *S. granulosoleprosum* Dunal (Cáceres & Moura, 2003), a species of subgen. Brevantherum that has similar habit, inflorescence structure, and external fruit appearance.

In the same way, the soft, juicy, red and showy fruits of *S. sisymbriifolium* would be probably consumed by birds and another vertebrates (Von Reis Altschul, 1975). Although *Solanum atropurpureum* has also red fruits, in this case such color is combined with a slightly juicy mesocarp and winged seeds. Thus, Nee (1979, 1991) proposed epizoochory by birds as a dispersal mechanism for this species and for *S. acerifolium* Sendtn., a similar species, since their seeds do not resist the passage through the digestive system of birds.

The indehiscent, small to medium sized, yellow fruits of *S. juvenale*, *S. hieronymi* and *S. comptum* would be also eaten either by birds or by terrestrial vertebrates. In addition, the fruits of *S. juvenale* would be attractive to consumers, since they have a pleasant odour (Parodi, 1930; our observations).

Finally, some species (*S. euacanthum*, *S. homalospermum*, *S. mortonii*) develop the non-capsular dehiscent fruit type (Knapp, 2002; Chiarini & Barboza, in press). The pericap of these fruits cracks irregularly, and their color is dull and unattractive to predators or dispersers.

In recent molecular studies, some species, like *S. capsicoides* and *S. viarum*, appear closely related (Levin et al., 2005), but differ notably regarding fruit traits. We tend to think that similarities and differences in fruit features, as placentation patterns, can be due to either ecological or physiological conditions, but are especially due to reproductive conditions, like andromonoecy. Thus, the sexual system would have played a very important role in the subgenus Leptostemonum evolutionary lineages, since it affects not only the reproductive biology of its species (reproductive success, fitness, sexual allocation, etc.), but also the morphology and anatomy (Chiarini & Barboza, sine data.).

Finally, the comparison of our data on placentation and seeds number to the available molecular phylogenies (Bohs, 2005; Levin et al., 2005, 2006) suggests that, in some species, a significant morphological variation is not associated with significant changes in DNA sequences.

ACKNOWLEDGEMENTS

The authors thank SECYT (Universidad Nacional de Cordoba, Argentina), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina), Agencia Córdoba Ciencia S.E., and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES, Brazil) for financial support, and the anomymous reviewers for the valuable comments on our manuscript.

BIBLIOGRAPHY

Almeida Jácomo, A. T.; L. Silveira & J. A. Felizola Diniz-Filho. 2004. Niche separation between the maned wolf (*Chrysocyon brachyurus*), the crab-eating fox (*Dusicyon thous*) and the hoary fox (*Dusicyon vetulus*) in central Brazil. *J. Zool. (London)* 262: 99-106.

Anderson, G. J. 1979. Dioecious *Solanum* species of hermaphroditic origin is an example of a broad convergence. *Nature* 282: 836-838.

Anderson, G. J. & D. E. Symon. 1989. Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43: 204-219.

Bertin, R. I. 1982. The evolution and maintenance of andromonoecy. *Evol. Theory* 6: 25-32.

Bohs, L. 2005. Major clades in *Solanum* based on ndhF sequence data, en V. Hollowell, R. Keating, W. Lewis & T. Croat (eds.), A festschrift for William D'Arcy. *Monogr. Syst. Bot. Missouri Bot. Gard.*104: 27-50.

Bryson, C. T. & J. D. Byrd. 1994. *Solanum viarum* (Solanaceae), new to Mississippi. *Sida* 16: 382-385.

Cáceres, N. C. & M. O. Moura. 2003. Fruit removal of a wild tomato, *Solanum granulosoleprosum* Dunal (Solanaceae), by birds, bats, and non-flying mammals in an urban Brazilian environment. *Revista Brasileira de Zoologia* 20: 519-522.

Chiarini, F. & G. Barboza. 2007. Anatomical study of different fruit types in Argentine species of *Solanum* subgen. Leptostemonum (Solanaceae). *Anales Jard. Bot. Madrid* 64 (2); forthcoming.

Chiarini, F. & G. Barboza. Sine data. Fruit anatomy on species of *Solanum* sect. Acanthophora (Solanaceae); forthcoming.

Cipollini, M. L. & D. J. Levey. 1997. Why are some fruits toxic? Glycoalkaloids in *Solanum* and fruit choice by vertebrates. *Ecology* 78: 782-798.

Cipollini, M. L.; L. Bohs, K. Mink, E. Paulk & K. Böhning-Gaese. 2002. Secondary metabolites of ripe fleshy fruits. Ecology and phylogeny in genus *Solanum*, en D. J. Levey, W. R. Silva & M. Galetti (eds.), *Seed dispersal and frugivory. Ecology, evolution and conservation*, pp. 111-128. Wallingford, Oxforshire: CAB International Publishing.

Coleman, J. R. & M. A. Coleman. 1982. Reproductive biology of an andromonoecious *Solanum* (*S. palinacanthum* Dunal). *Biotropica* 14: 69-75.

Dave, Y. S., N. D. Patel & K. S. Rao. 1979. The study of origin of pericarp layers in *Solanum melongena*. *Phyton (Austria)* 19: 233-241.

Diggle, P. K. 1991. Labile sex expresión in andromonoecious *Solanum hirtum*: floral development and sex determination. *Amer. J. Bot.* 78: 377-393.

Diggle, P. K. 1993. Developmental plasticity, genetic variation, and the evolution of andromonoecy in *Solanum hirtum* (Solanaceae). *Amer. J. Bot.* 80: 967-973.

Dottori, N. & M. T. Cosa. 1999. Anatomía y ontogenia de fruto y semilla en *Solanum hieronymi* (Solanaceae). *Kurtziana* 27: 293-302.

Dottori, N. & M. T. Cosa. 2003. Desarrollo del fruto y semilla en *Solanum euacanthum* (Solanaceae). *Kurtziana* 30: 17-25.

Dulberger, R., A. Levy & D. Palevitch. 1981. Andromonoecy in *Solanum marginatum*. *Bot. Gaz.* 142: 259-266.

Goebel, K. 1905. *Organography of plants*. Oxford: Oxford University Press.

Hunziker, A. T. 2001. Genera Solanacearum. The genera of Solanaceae illustrated, arranged according to a new system. Ruggell: A.R.G. Gantner Verlag.

InfoStat. 2001. Versión 1.0. Estadística y Biometría, Facultad de Ciencias Agropecuarias, Universidad Nacional de Córdoba.

Knapp, S. 2002. Tobacco to tomatoes, a phylogenetic perspective on fruit diversity in the Solanaceae. *J. Exp. Bot.* 53: 2001-2022.

Levin, R. A., K. Watson & L. Bohs. 2005. A four-gene study of evolutionary relationships in *Solanum* section Acanthophora. *Amer. J. Bot.* 92: 603-612.

Levin, R. A., N. R. Myers & L. Bohs. 2006. Phylogenetics relationships among the "Spiny Solanums" (*Solanum* subgenus Leptostemonum, Solanaceae). *Amer. J. Bot.* 93: 157-169.

Miller, R. H. 1969. A morphological study of *Solanum mammosum* and its mammiform fruit. *Bot. Gaz.* 130: 230-237.

Miller, J. S. & P. K. Diggle. 2007. Correlated evolution of fruit size and sexual expression in andromonoecious *Solanum* sections Acanthophora and Lasiocarpa (Solanaceae). *Amer. J. Bot.* 94: 1706-1715.

Murray, M. A. 1945. Carpellary and placental structure in the Solanaceae. *Bot. Gaz.* 107: 243-260.

Nee, M. 1979. Patterns in biogeography in *Solanum*, section Acanthophora, en J. G. Hawkes, R. N. Lester & A. J. Skelding (eds.), *The biology and taxonomy of the Solanaceae,* Linnean Society Symposium Series 7, pp. 569-580. London: The Linnean Society of London.

Nee, M. 1986. Placentation patterns in the Solanaceae, en W.G. D'Arcy (ed.), *Solanaceae: biology and systematics,* pp. 169-175. New York: Columbia University Press.

Nee, M. 1991. Synopsis of *Solanum* Section Acanthophora: A group of interest for glycoalkaloids, en J. G. Hawkes, R. Lester, M. Nee & N. Estrada (eds.), *Solanaceae III: Taxonomy, Chemistry, Evolution*, pp. 257-266. Kew: Royal Botanic Gardens.

Nee, M. 1999. Synopsis of *Solanum* in the New World, en M. Nee, D. E. Symon, R. N. Lester & J. P. Jessop (eds.), Solanaceae IV. *Advances in Biology and Utilization*, pp. 285-333. Kew: Royal Botanic Gardens.

Nee, M.; L. Bohs & S. Knapp. 2006. New species of *Solanum* and *Capsicum* (Solanaceae) from Bolivia, with clarification of nomenclature in some Bolivian *Solanum*. *Brittonia* 58: 322-356.

Parodi, L. R. 1930. Ensayo fitogeográfico sobre el partido de Pergamino. *Revista Fac. Agron. Veterin.* 7: 65-271.

Silva, J. A. & S. A. Talamoni. 2003. Diet adjustments of maned wolves, *Chrysocyon brachyurus* (Illiger) (Mammalia, Canidae), subjected to supplemental feeding in a private natural reserve, Southeastern Brazil. *Revista Brasileira de Zoologia* 20: 339-345.

Solomon, B. P. 1987. The role of male flowers in *Solanum carolinense*: pollen donors or pollinator attractors? *Evol. Trends Pl.* 1: 89-93.

Symon, D. E. 1979. Sex forms in *Solanum* (Solanaceae) and the role of pollen collecting insects in *Solanum*, section Acanthophora, en J. G. Hawkes, R. N. Lester & A. J. Skelding (eds.), *The biology and taxonomy of the Solanaceae,* pp. 385-395. London: The Linnean Society of London.

Symon, D. E. 1987. Placentation patterns and seed numbers in *Solanum* (Solanaceae) fruits. *J. Adelaide Bot. Gard.* 10: 179-199.

Van der Pijl, L. 1982. *Principles of Dispersal in Higher Plants,* 3rd ed. Berlin, Heidelberg, New York: Springer.

Von Reis Altschul, S. 1975. Drugs and Foods from little-known plants. Notes in Harvard University Herbaria. Cambridge, Massachusetts and London: Harvard University Press.

Wakhloo, J. L. 1975a. Studies on growth, flowering, and production of female sterile flowers as affected by different levels of foliar potassium in *Solanum sisymbriifolium* Lam. III. Interaction between foliar potassium and applied daminozide, chlormequat chloride, and chlorflurecol-methyl. *J. Exp. Bot.* 26(92): 441-450.

Wakhloo, J. L. 1975b. Studies on growth, flowering, and production of female sterile flowers as affected by different levels of foliar potassium in *Solanum sisymbriifolium* Lam. II. Interaction between foliar potassium and applied gibberelic acid and 6-furfurylaminopurine. *J. Exp. Bot.* 26(92): 433-440.

Whalen, M. D. 1984. Conspectus of species groups in *Solanum* subgenus Leptostemonum. *Gentes Herb.* 12(4): 179-282.

Whalen, M. & D. E. Costich. 1986. Andromonoecy in Solanum, en W. G. D'Arcy, (ed.), *Solanaceae: Biology and Systematics*, pp. 284-302. New York: Columbia University Press.

APPENDIX 1

Specimen examined

Solanum aculeatissimum Jacq. BRAZIL. Santa Catarina. Munic. Monte Castelo, 28º38'12"S, 50º15'06"W, 23-II-06, *Barboza et al. 1617* (CORD).

Solanum aenictum C. V. Morton. ARGENTINA. Corrientes. Depto. Santo Tomé, 7-I-2002, *Chiarini 536* (CORD).

Solanum albidum Dunal. BOLIVIA. La Paz. Prov. Nor Yungas, 16º 13' 34" S, 67º 47' 12"W, 25-IV-2006, *Barboza et al. 1833* (CORD); Prov. Sud Yungas, near Circuata, 27-IV-2006, *Barboza et al. 1853* (CORD).

Solanum alternatopinnatum Steud. ARGENTINA. Misiones. Depto. Iguazú, 29-V-1987, *Subils & Moscone 4156* (CORD).

Solanum aridum Morong. ARGENTINA. Córdoba. Depto. Capital, 1-XII-1998, *Chiarini 16* (CORD); Salta. Depto. Capital, 19-I-2002, *Barboza 331* (CORD).

Solanum asperolanatum Ruiz & Pav. BOLIVIA. Santa Cruz. Prov. M. Caballero, from Comarapa to Laguna Verde, 30-IV-2006, *Barboza et al. 1902* (CORD).

Solanum atropurpureum Schrank. ARGENTINA. Corrientes. Depto. Santo Tomé, 7-I-2002, *Chiarini 531* (CORD); Depto. Goya, Arroyo Guazú, 29º 50'26"S, 59º 24'24"W, 3-XII-2002, *Barboza et al. 355* (CORD).

Solanum bolivianum Rusby. BOLIVIA. La Paz. Prov. Inquisivi, from Quime to Inquisivi, 16º 57' 01" S, 67º 11' 27"W, 28-IV-2006, *Barboza et al. 1856* (CORD).

Solanum bonariense L. ARGENTINA. Entre Ríos. Depto. Gualeguaychú, 33º39'28"S, 58º43'24"W, 28-VII-2005, *Chiarini 640* (CORD).

Solanum capsicoides All. ARGENTINA. Corrientes. Depto. Ituzaingó, Isla Apipé Grande, 4-XII-2002, *Barboza et al. 394* (CORD); BRAZIL. Santa Catarina. Munic. Trombudo Central, 24-XI-2003, *Mentz et al. 274* (CORD, ICN); Munic. Garuva, 24-II-2006, *Barboza et al. 1623* (CORD); São Paulo. Munic. Salesópolis, from Salesópolis to Paraibuna, SP 077, km 108.5, 25-II-2006, *Barboza et al. 1641* (CORD); Rio de Janeiro. Munic. Rio de Janeiro, Floresta de Tijuca, 15-VII-2003, *Barboza et al. s.n.* (GUA 48406).

Solanum comptum C. V. Morton. ARGENTINA. Corrientes. Depto. Capital, near the airport, 13-V-2004, *Barboza et al. 999* (CORD); Depto. Capital, Perichón, 29º 24' 34" S, 58º 45' 09" W, 13-V-2004, *Barboza et al. 1001* (CORD); Depto. San Cosme, 27º 18' 42" S, 58º 29' 22" W, 13-V-2004, *Barboza et al. 1005* (CORD).

Solanum consimile C. V. Morton. BOLIVIA. Tarija. Prov. Arce, near Aguas Blancas, 30-IX-2001, *Barboza et al. 279*; Prov. Arce, La Mamora, 22º14' 59"S, 64º34' 55"W, 5-X-2001, *Barboza et al. 307* (CORD).

Solanum elaeagnifolium Cav. ARGENTINA. Córdoba. Depto. Sobremonte, S. Francisco del Chañar, 9-XII-2001, *Chiarini 565* (CORD).

Solanum euacanthum Phil. ARGENTINA. Córdoba. Depto. Sobremonte, 29º 46'06"S, 64º 34' 03" W, 28-II-2002, *Chiarini et al. 560, 563* (CORD); Neuquén. Depto. Collón Curá, 20-II-2005, *Barboza et al. 1181* (CORD).

Solanum guaraniticum A. St.-Hil. ARGENTINA. Corrientes. Depto. Santo Tomé, 7-I-2002, *Chiarini 532* (CORD); Misiones. Depto. Capital, 27º23'29"S, 55º53'35"W, 7-XII-2002, *Barboza et al. 404* (CORD); Depto. Gral. San Martín, 26º59'08"S, 54º41'36"W, 28-III-2004, *Barboza et al. 922* (CORD).

Solanum hieronymi Kuntze. ARGENTINA. La Rioja. Depto. Chilecito, Puesto Las Trancas, 19-II-2003, *Barboza et al. 569* (CORD); Córdoba. Depto. San Javier, Yacanto, 9-I-1996, *Cosa 266* (CORD); Depto. Rio II, Colazo, 23-VI-1983, *Hunziker et al. 3674* (CORD); San Luis. Depto. Chacabuco, Concarán, 17-II-1989, *Hunziker et al. 25332* (CORD).

Solanum homalospermum Chiarini. ARGENTINA. Córdoba. Depto. Sobremonte, 29°46'34" S, 63°59'59" W, 29-XI-2001, *Chiarini 505* (CORD).

Solanum incarceratum Ruiz & Pav. BRAZIL. São Paulo. Munic. Itú, estrada Itú-Jundiaí, 25º 15'36"S, 47º 15'34"W, 29-VI-03, *Marcondes et al. s.n.* (CORD 1028).

Solanum juvenale Thell. ARGENTINA. Córdoba. Depto. Capital, 8-XII-2001, *Chiarini 504* (CORD); La Pampa. Depto. Toay, 36º 38' 51" S, 64º 22' 42" W, 19-II-2005, *Barboza et al. 1173* (CORD).

Solanum lycocarpum A. St.-Hil. BRAZIL. São Paulo. Munic. Campinas, Fazenda Irazema, 22º48'31"S, 46º55'28"W, 28-VI-2003, *Marcondes et al. s.n.* (CORD 1031); from Queluz to Areias, Route SP 068, 22º 33' 42" S, 44º 45' 48" W, 26-II-2006, *Barboza et al. 1645* (CORD).

Solanum mammosum L. ECUADOR. Napo. XII-1995, *Hunziker s.n.* (CORD 1024).

Solanum marginatum L. f. CHILE. V Región. Laguna Verde, 33º 06' 32" S, 71º 39' 09" O, 8-II-2007, *Chiapella et al. 1654* (CORD); SPAIN, Canary Islands, 15-VI-2005, *Oberti s.n.* (CORD 1040).

Solanum mortonii Hunz. ARGENTINA. Catamarca. Depto. Capayán, 28º 41' 55' S, 66º 02' 53" W, 23-II-2003; *Barboza et al. 633* (CORD); 28º 42' 23' S, 66º 01' 29" W, 23-II-2003, *Barboza et al. 639* (CORD); 28º 34' 56' S, 65º 56' 07" W, 23-II-2003, *Barboza et al. 644* (CORD).

Solanum multispinum N. E. Brown. ARGENTINA. Formosa. Depto. Pilcomayo, Laguna Blanca, 25º 07'50"S, 58º 15' 57"W, 14-XII-2002, *Barboza et al. 511* (CORD); Route 86, 25º 05'49"S, 51º 18'59"W, 14-XII-2002, *Barboza et al. 520* (CORD).

Solanum palinacanthum Dunal. ARGENTINA. Córdoba. Depto. Capital, 1-VI-2001, *Chiarini 465* (CORD); Tucumán. Depto. Famaillá, 1-IV-1977, *Hunziker et al. 23081* (CORD); PARAGUAY. Caaguazú. 25º 22'43"S, 56 00'42" W, 12-XII-2002, *Barboza et al. 495* (CORD).

Solanum paniculatum L. BRAZIL. São Paulo. Munic. Campinas, Faz. São Martinho, Síncroton, 2-VII-2003, *Marcondes et al. s.n.* (CORD 1029); PARAGUAY. Caazapá. 26º 11'08"S, 56º 22'14"W, 13-XII-2002, *Barboza et al. 500* (CORD).

Solanum aff. *paniculatum* L. ARGENTINA. Entre Ríos. Depto. Uruguay, Concepción del Uruguay, 28-VII-2005, *Chiarini & Marini 636* (CORD).

Solanum platense Dieckmann. ARGENTINA. Misiones. Depto. San Ignacio, arroyo Macaco, 7-XII-2002, *Barboza et al. 441* (CORD).

Solanum quitoense Lam. COLOMBIA. Cundinamarca. Bogotá, I-2005, *Oberti s.n.* (CORD 1079)

Solanum robustum Wendl. ARGENTINA. Misiones. Depto. Iguazú, Wanda, 11-XII-2002, *Barboza et al. 483* (CORD); Corrientes. Depto. Capital, Perichón, 29º 24'34"S, 58º 45'09"W, 5-XII-2002, *Barboza et al. 379*, 382 (CORD).

Solanum scuticum M. Nee. BRAZIL. São Paulo. Munic. Campinas, Souzas, 28-VI-2003, *Marcondes et al. s.n.* (CORD 1030); Munic. Salto, near Salto, 29-VI-2003, *Barboza et al. s.n.* (CORD 1065) ; Rio de Janeiro. Distrito Federal, 17-VII-2003, *Barboza et al. 801* (CORD).

Solanum sisymbriifolium Lam. ARGENTINA. Córdoba. Depto. Capital, XII-1998, *Chiarini 27* (CORD); Salta. Depto. Rosario de Lerma, Corralito, 29-XII-1987, *Novara 7363* (CORD).

Solanum tenuispinum Rusby. ARGENTINA. Salta. Depto. Santa Victoria, Baritú, 2-X-2001, *Barboza et al. 292* (CORD); Depto. Rosario de Lerma, 24º 58' 15"S, 65º 35' 37"W, 6-III-2002, *Negritto et al. 293* (CORD); Catamarca. Depto. Andalgalá, Río Chacras, 27º 23' 01' S, 65º 59' 29" W, 23-II-2003, *Barboza et al. 629* (CORD).

Solanum toldense Matesevach & Barboza. ARGENTINA. Salta. Depto. Santa Victoria, 22º 21' 53" S, 64º 43' 20" W, *Barboza et al. 281* (MCNS, CORD); Depto. Santa Victoria, 29-XI-2004, *Barboza et al. 1086* (CORD).

Solanum urticans Dunal. BOLIVIA. Santa Cruz. Prov. Ichilo, 4 km SW of Buenavista, along the river Surutú, alt. 360 m, 1-V-2006, *Barboza et al. 1915* (CORD).

Solanum variabile Mart. BRAZIL. Rio Grande do Sul. Munic. S. Francisco de Paula, 29º19'31"S, 50º07'22"W, 23-XI-2003, *Mentz et al. 266* (CORD, ICN)

Solanum viarum Dunal. ARGENTINA. Corrientes. Depto. Santo Tomé, 6-I-2002, *Chiarini 533, 537 and 538* (CORD); Depto. Ituzaingó, 14-V-2004, *Barboza et al. 1006* (CORD); Misiones. Depto. Gral. Manuel Belgrano, 25º 42' 24" S, 54º 5' 48" W, 30-XI-2003 *Barboza et al. 819* (CORD).