

Chromosomal differentiation of *Solanum vespertilio* and *S. lidii* (Solanaceae), rare, endemic species of the Canary Islands (Spain)

CHIARINI¹ FRANCO, GABRIEL BERNARDELLO^{1,*}, GREGORY ANDERSON² and ARNOLDO SANTOS GUERRA³

¹Instituto Multidisciplinario de Biología Vegetal (CONICET-Universidad Nacional de Córdoba), Casilla de Correo 495, 5000 Córdoba, Argentina.

²Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, CT 06269-3043, U.S.A.

³Jardín de Aclimatación La Orotava, Puerto de La Cruz, Tenerife, Spain.

Abstract — A morphometric karyotype analysis was performed on the two *Solanum* subgenus *Leptostemonum* species of the Canary Islands (*S. lidii* and *S. vespertilio*) to understand patterns of chromosome differentiation, taxonomic relationships and evolutionary implications. The somatic chromosome number, $2n = 24$, was documented for both species, supporting the basic chromosome number of *Solanum* ($x = 12$). For *S. vespertilio*, our data confirm a previous report based on meiotic counts, while the chromosome number of *S. lidii* is reported for the first time. Chromosomes are very small: for *S. vespertilio* the average chromosome length was $1.5 \pm 0.3 \mu\text{m}$ and the haploid karyotype length $18.4 \pm 3.6 \mu\text{m}$, and for *S. lidii* $1.3 \pm 0.09 \mu\text{m}$ and $15.85 \pm 1.0 \mu\text{m}$, respectively. These sizes are among the smallest for *Solanum*. Both species have symmetrical karyotypes with the same formula: 8 m pairs + 4 sm pairs. However, in addition to the length differences between the species, the only chromosome pair with a satellite on the short arm is different: it is found on chromosome pair #2 in *S. lidii* and on a slightly shorter chromosome, pair # 4, in *S. vespertilio*. Satellites were visualized in almost 100% of the cells of both species. Our karyotype data thus imply that these island species are closely related, and likely evolved *in situ* on the islands, via sympatric or sequential speciation (*S. vespertilio* is the more likely most derived member of the pair). In addition, although both species show a number of derived reproductive traits, like heterandry, zygomorphy, and andromonoecy, they retain the presumptively more generalized symmetrical karyotypes.

Key words: Canary Islands, cytotaxonomy, karyotype evolution, Solanaceae, *Solanum*, subgenus *Leptostemonum*, speciation.

INTRODUCTION

Around 40% of the vascular plant species of the Canary Islands flora are endemic (SANTOS 2001). The Solanaceae is not common on islands in general, nor is it in the Canaries where it is represented by only four species (BRAMWELL and BRAMWELL 2001). However, all four species are endemic. One is in *Withania* (*W. aristata* (AITON) PERS.) and three are in *Solanum*, the latter constituting one of the largest genera of angiosperms, and elsewhere represented by several species of economic, pharmaceutical, or ornamental value (HEISER 1987; HUNZIKER 2001). The three *Sola-*

num species are *S. nava* WEBB. and BERTHEL. (previously in the genus *Normania*; BOHS and OLMSTEAD 2001), *S. lidii* SUNDING, and *S. vespertilio* AITON. The latter two are a closely related species pair placed in subgenus *Leptostemonum* (Dunal) Bitter (WHALEN 1984; BOHS et al., unpubl.). This subgenus is considered to be a monophyletic group, likely of ancient origin, conclusions most recently supported by chloroplast DNA restriction site, chloroplast *ndhF* and nuclear ITS DNA sequence analyses (OLMSTEAD and PALMER 1997; BOHS and OLMSTEAD 1999; 2001). These two Canarian species are particularly notable because of the presence of highly zygomorphic flowers with unequal anthers (i.e. heterandry) and andromonoecy (WHALEN 1984; ANDERSON et al. unpubl.), morphological features that have linked them with similar species from Mexico (WHALEN 1984). More recent work has indicated a geographically

* Corresponding author: phone (Fax) ++54 351 4331056; e-mail: gabyberna@arnet.com.ar

more logical linkage with African solanums (BOHS et al. unpubl.). This species pair is of interest as well in the context of the origin of the taxa. Both species are found on one of the islands (Gran Canaria – older, and closer to the African source for the species) – thus they are geographically sympatric in that context (BOHS et al., unpubl.). The somewhat more abundant species, *S. vespertilio*, is also found on the younger, and more distant (from Africa), Tenerife. Thus, the species may have had a sympatric origin on Gran Canaria, or *S. vespertilio* may have been derived from the African progenitors independently, and/or later, on Tenerife, and then colonized the nearby Gran Canaria.

Comparative karyotype studies have proved to be useful in determining systematic and evolutionary relationships in some *Solanum* sections (BERNARDELLO and ANDERSON 1990; BERNARDELLO et al. 1994; ACOSTA et al. 2005). This is in spite of the fact that they are generally composed of homomorphic chromosomes of small size, and are mostly diploid (STEBBINS 1971; MOSCONE 1992; ACOSTA et al. 2005).

In this contribution, a morphometric karyotype analysis has been performed on these two *Solanum* subgen. *Leptostemonum* species with the aim of reporting comparative karyotype data for the first time, as well as the chromosome number of *S. lidii* (the gametic chromosome number of *S. vespertilio* has been published by ALDRIDGE and ORTEGA in 1976). The data are employed to understand patterns of chromosome differentiation and taxonomic relationships.

MATERIAL AND METHODS

The provenance of the plant material studied is: *Solanum lidii*: Spain, Canary Islands, Gran Canaria, Temisas, Anderson and Santos Guerra 4801, 01/June/2004.

S. vespertilio: Spain, Canary Islands, Tenerife, Las Bodegas, Anderson and Santos Guerra 4601, 01/January/2004.

Vouchers are deposited in the herbarium of the Instituto Canario de Investigaciones Agrarias (ORT) and the George Safford Torrey Herbarium (CONN).

Primary roots obtained by germinating seeds were used to study the somatic chromosomes. Root tips were pretreated with paradichlorobenzene-saturated solution for 2 h at room temperature, and then fixed in 3:1 ethanol:acetic acid mixture for a minimum of 12 h. Meristem cells were

isolated, macerated, and squashed in a drop of 45% acetic acid after staining with alcoholic hydrochloric acid carmine (SNOW 1963) for two hours at 60°C. Slides were made permanent by removing the cover slip by freezing with liquid nitrogen. Thirty five cells of 20 individuals per species (i.e., a total of 700 cells) were examined under a Zeiss Axiophot microscope. Ten metaphase plates from 10 individuals of each species were photographed with a Leica DFC300 FX digital camera and the photographs were used to take measurements of the following features for each chromosome pair: s (short arm length), l (long arm length), and c (total chromosome length). The arm ratio ($r = l/s$) was calculated and utilized to classify the chromosomes as recognized by LEVAN et al. (1964) as: m – metacentric ($r = 1.00-1.69$) or sm – submetacentric ($r = 1.70-2.99$). BATTAGLIA's (1955) terminology for satellites was used. The satellite lengths were added to the lengths of the corresponding arms. In addition, haploid karyotype length based on the mean chromosome lengths for each species, average chromosome length, and average arm ratio were calculated. Idiograms were based on the mean values for each species. The chromosomes were arranged, as usual, into groups according to their increasing arm ratio, and then according to the decreasing length within each group. Karyotype asymmetry was estimated using the following parameters: A_1 = intrachromosomal 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 (ROMERO ZARCO 1986).

RESULTS AND DISCUSSION

The somatic chromosome number $2n = 24$ was found in all cells of both species (Fig. 1, 2). For *S. vespertilio*, our data confirm a previous report based on meiotic counts (ALDRIDGE and ORTEGA 1976), while the chromosome number of *S. lidii* is reported for the first time. As in most genera of subfamily Solanoideae SCHLTDL., the basic chromosome number of *Solanum* is $x = 12$, mainly found at the diploid level ($2n = 2x = 24$), although polyploid series are found in some groups (e.g., RANDELL and SYMON 1976; EDMONDS 1977; HAWKES 1990; OCHOA 1999). In addition, some species show atypical numbers like $x = 11, 15, \text{ or } 23$ (FEDOROV 1974).

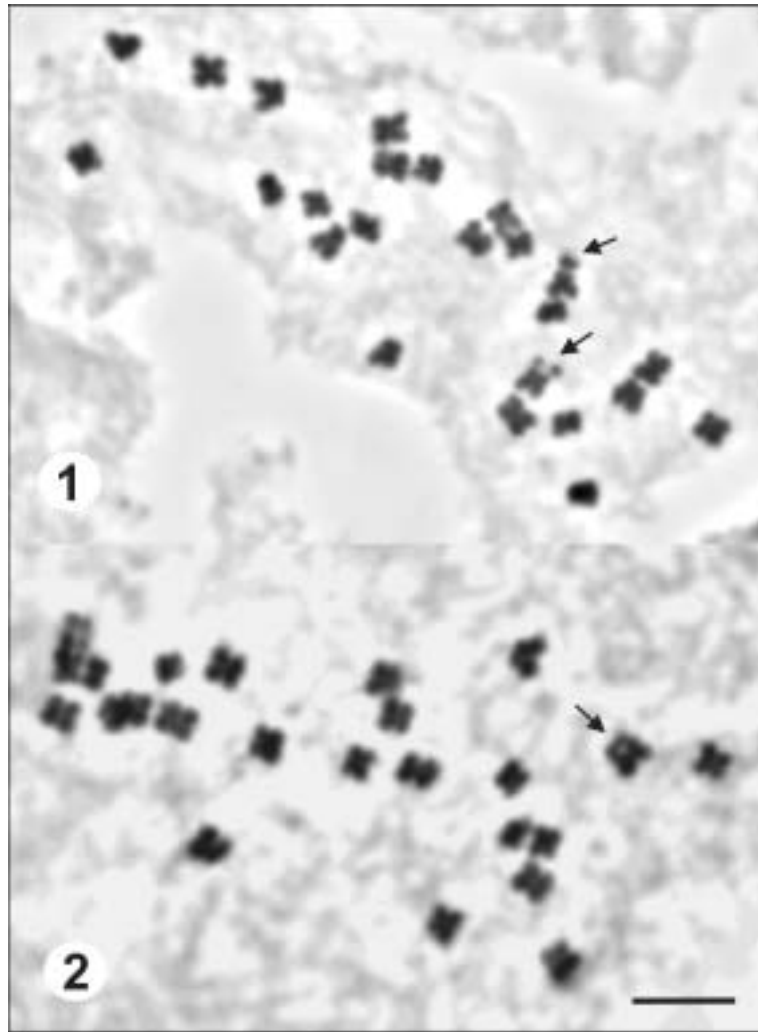


Fig. 1-2 — Photomicrographs of mitotic metaphases of *Solanum* subgenus *Leptostemonum* species from the Canary Islands. 1. *S. lidii*, 2. *S. vespertilio*. Bar represents 5 μm ; both photographs are at the same scale.

These *Solanum* chromosomes are very small (Table 1; Fig. 1-4). The average chromosome length was $1.5 \pm 0.3 \mu\text{m}$ for *S. vespertilio* and $1.3 \pm 0.09 \mu\text{m}$ for *S. lidii*. The shortest chromosome was found in a cell of *S. lidii* ($0.9 \mu\text{m}$), while the longest ($2.1 \mu\text{m}$) was found in a cell of *S. vespertilio*. The haploid karyotype size was $15.85 \mu\text{m} \pm 1.0$ for *S. lidii* and $18.4 \mu\text{m} \pm 3.6$ for *S. vespertilio*. As a whole, and in comparison with a number of taxa (e.g., *Allium*, TANG *et al.* 2005) *Solanum* chromosomes are small ($<4 \mu\text{m}$), except in sections *Cyphomandropsis* Bitter and *Pachyphylla* (DUNAL) DUNAL, where the chromosomes range from 4 to $10 \mu\text{m}$ (e.g., ROE 1967; PRINGLE and MURRAY 1991; MOSCONE 1992; BOHS 1994; 2001). Interestingly, the chromosomes of the species here studied are among the smallest in the entire genus (BERNARDELLO and ANDERSON 1990; BER-

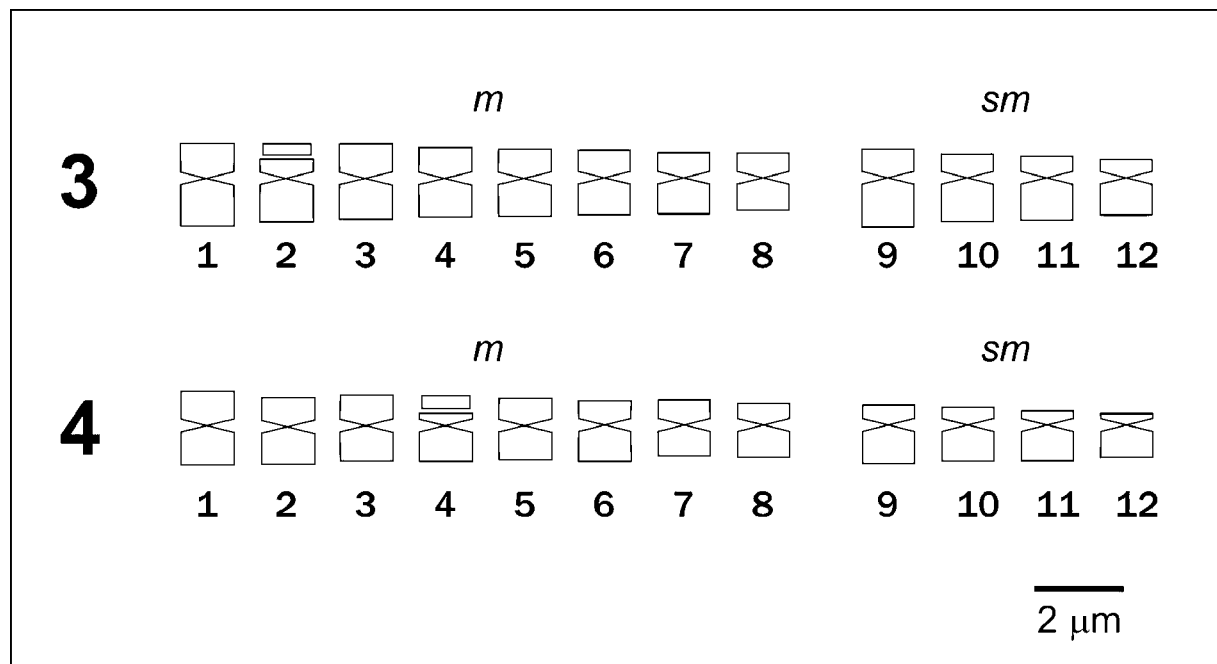
NARDELLO *et al.* 1994; BADR *et al.* 1997; ACOSTA *et al.* 2005). It is tempting to speculate that the unusual, and likely derived (BOHS *et al.*, unpubl.), mating systems evident in these species is paralleled by a reduction in overall karyotype size (following the general pattern that Stebbins touted for angiosperms – e.g., STEBBINS 1971).

Both species show the same karyotype formula: 8 m pairs + 4 sm pairs. Karyotypes are symmetrical, and both species are similar in asymmetry indices: $A_1 = 0.3$ for *S. vespertilio* and 0.31 for *S. lidii*, $A_2 = 0.14$ for *S. vespertilio* and 0.16 for *S. lidii*, indicating that there is little variation among the smallest and largest chromosomes in both species.

Although we find variation in karyotype composition for both chromosome size and morphology, the taxa studied display symmetrical karyo-

Table 1 — Measurements in μm (s = short arm, l = long arm, c = total chromosome length) and arm ratio (r) of somatic chromosomes of *Solanum lidii* and *S. vespertilio*. Satellited pairs are indicated with an asterisk.

Species	pair	Chromosome lengths: mean \pm SD			r
		s	l	c	
<i>S. lidii</i>	1	0.77 \pm 0.08	0.89 \pm 0.08	1.66 \pm 0.15	1.15
	2	0.62 \pm 0.06	0.87 \pm 0.07	1.50 \pm 0.10	1.41
	3	0.68 \pm 0.07	0.79 \pm 0.06	1.47 \pm 0.12	1.16
	4*	0.66 \pm 0.06	0.76 \pm 0.08	1.42 \pm 0.13	1.15
	5	0.61 \pm 0.07	0.76 \pm 0.11	1.37 \pm 0.17	1.26
	6	0.56 \pm 0.06	0.80 \pm 0.09	1.36 \pm 0.13	1.44
	7	0.58 \pm 0.07	0.68 \pm 0.07	1.26 \pm 0.13	1.17
	8	0.50 \pm 0.09	0.71 \pm 0.07	1.21 \pm 0.13	1.43
	9	0.46 \pm 0.09	0.85 \pm 0.08	1.32 \pm 0.15	1.93
	10	0.41 \pm 0.07	0.79 \pm 0.08	1.20 \pm 0.12	2.01
	11	0.33 \pm 0.06	0.79 \pm 0.09	1.12 \pm 0.13	2.49
	12	0.27 \pm 0.08	0.71 \pm 0.07	0.98 \pm 0.13	2.83
<i>S. vespertilio</i>	1	0.79 \pm 0.20	1.06 \pm 0.32	1.85 \pm 0.52	1.36
	2*	0.74 \pm 0.17	0.98 \pm 0.22	1.72 \pm 0.38	1.34
	3	0.77 \pm 0.10	0.92 \pm 0.28	1.69 \pm 0.37	1.22
	4	0.69 \pm 0.13	0.87 \pm 0.21	1.55 \pm 0.33	1.28
	5	0.66 \pm 0.18	0.85 \pm 0.25	1.51 \pm 0.42	1.31
	6	0.63 \pm 0.14	0.83 \pm 0.15	1.46 \pm 0.28	1.34
	7	0.57 \pm 0.11	0.80 \pm 0.11	1.37 \pm 0.22	1.41
	8	0.56 \pm 0.08	0.72 \pm 0.15	1.28 \pm 0.21	1.31
	9	0.66 \pm 0.12	1.09 \pm 0.13	1.75 \pm 0.24	1.68
	10	0.54 \pm 0.09	0.97 \pm 0.13	1.51 \pm 0.21	1.89
	11	0.49 \pm 0.11	0.94 \pm 0.13	1.43 \pm 0.22	1.91
	12	0.42 \pm 0.18	0.83 \pm 0.27	1.25 \pm 0.41	2.10

Fig. 3-4 — Idiograms of *Solanum* subgenus *Leptostemonum* species from the Canary Islands. 3. *S. vespertilio*, 4. *S. lidii*. Both diagrams are at the same scale.

types – the condition typical for *Solanum* (e.g., STEBBINS 1971; BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994; ACOSTA *et al.* 2005). *Solanum* karyotypes usually have a majority of *m* and *sm* chromosomes (e.g., PIJNACKER and FERWERDA 1984; WU and LI 1985; BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994; BADR *et al.* 1997), with metacentrics being more frequent, the karyotype condition documented for these species as well.

Usually, as documented here as well, the satellited pair in *Solanum* is comparatively larger in size and is among the six largest in the karyotype (cf. ACOSTA *et al.* 2005). However, in addition to the length differences discussed above, the position of the single chromosome pair with a microsatellite is different (Fig. 3, 4). Though satellites in both species are restricted to one *m* chromosome, the pair is different. In *S. lidii*, almost 100% of the cells had satellites present on both homologous chromosomes (pair #4). However, in *S. vespertilio* about 30% of the cells had a single satellited *m* chromosome pair (#2). The presence of one chromosome pair with satellites on short arms, as found here, is frequent in several diploid *Solanum* species (e.g., WU and LI 1985; TRIVEDI and SINHA 1986; OKOLI 1988; BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994; ACOSTA *et al.* 2005). The exceptions to this general condition are found in: *S. pseudolulo* HEISER with two satellited pairs, one of them on long arms (BERNARDELLO *et al.* 1994), *S. basendopogon* BITTER with one satellited pair on long arms (BERNARDELLO and ANDERSON 1990), and the *S. indicum* L. complex with a maximum of three satellited pairs (KRISHNAPPA and CHENNAVEERIAH 1975).

Karyotype features in *Solanum* generally allow individual species to be distinguished (e.g., BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994; ACOSTA *et al.* 2005). Thus, some morphological chromosome variation, although not great, has accompanied evolutionary divergence of the taxa, as is the case for many other plants and animals as well (e.g., GOODSPEED 1954; RIESEBERG 2001). Thus, in *Solanum* species diversification seems not to have been associated with large, obvious chromosome rearrangements – at least as seen with conventional staining – nor with polyploidy. Instead, cumulative small and cryptic structural changes have been proposed to be important, as suggested for in sections *Basaribrum* BITTER and *Lasiocarpa* (DUNAL) D'ARCY (BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994). A common karyotype pattern of rela-

tively homogeneous *m* and *sm* chromosomes appears widely distributed in *Solanum* (e.g., WU and LI 1985; OKOLI 1988; BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994; BADR *et al.* 1997; ACOSTA *et al.* 2005). Thus, karyotypic orthoselection has been proposed to occur in this genus, as in other Solanaceae (cf. BRANDHAM and DOHERTY 1998; STIEFKENS and BERNARDELLO 2002; MOSCONE *et al.* 2003; ACOSTA *et al.* 2005). This sort of selection results in rather similar karyotypic complements, independent of chromosome size, that range throughout a higher taxon – presumably because they are more stable.

In some plant groups, increased asymmetry is associated with advanced taxa (cf. STEBBINS 1971). This has also been proposed (ACOSTA *et al.* 2005) for *Solanum* subgen. *Leptostemonum* Sect. *Acanthophora* Dunal, which shows more asymmetrical karyotypes, and, interestingly, some derived morphological features. However, in general, *Solanum* sections are characterized by small differences in karyotype asymmetry among species (cf. BERNARDELLO and ANDERSON 1990; BERNARDELLO *et al.* 1994; ACOSTA *et al.* 2005). The two island *Solanum* species studied here show a number of derived morphological (reproductive) traits, like heterandry, zygomorphy, and andromonoecy – but they retain quite symmetrical karyotypes. There is, it would seem, little or no association between at least some elements of morphological/reproductive speciation, and karyotype asymmetry (at least based on what we can perceive with standard staining techniques). Perhaps, as sequencing becomes more prominent, we will be able to identify sequence variation. Or, it may be that significant reproductive morphological variation is simply not associated with significant sequence/karyotype reorganization or speciation. The question of sympatric, parallel, or sequential speciation is not addressed, in particular, by the chromosome data. The co-existence of both *S. lidii* and *S. vespertilio* on Gran Canaria might suggest sympatric speciation, with subsequent dispersal of *S. vespertilio* to Tenerife, but the data do not provide evidence for or against this hypothesis.

Acknowledgements — We thank the American Philosophical Society, the University of Connecticut, Jardín de Aclimatación de La Orotava (Tenerife), CONICET, Agencia Córdoba Ciencia, and SECYT (Universidad Nacional de Córdoba, Argentina) for support.

REFERENCES

- ACOSTA M.C., BERNARDELLO G., GUERRA M. and MOSCONE E.A., 2005 — *Karyotype analysis in several South American species of Solanum and Lycianthes rantonnei (Solanaceae)*. *Taxon*, 54: 713-723.
- ALDRIDGE A.E. and ORTEGA J., 1976 — *Estudios en la flora de Macaronesia: algunos números de cromosomas II*. *Botánica Macaronésica*, 2: 9-18.
- BADR A., KHALIFA S.F., ABOEL-ATTA A. I. and ABOUEL-ENAIN M.M., 1997 — *Chromosomal criteria and taxonomic relationships in the Solanaceae*. *Cytologia*, 62: 103-113.
- BATTAGLIA E., 1955 — *Chromosome morphology and terminology*. *Caryologia*, 8: 179-187.
- BERNARDELLO L.M. and ANDERSON G.J., 1990 — *Karyotypic studies in Solanum section Basarthurum (Solanaceae)*. *American Journal of Botany*, 77: 420-431.
- , HEISER C.B. and PIAZZANO M., 1994 — *Karyotypic studies in Solanum section Lasiocarpa (Solanaceae)*. *American Journal of Botany*, 81: 95-103.
- BOHS L., 1994 — *Cyphomandra (Solanaceae)*. *Flora Neotropica Monographs*, 63: 1-75.
- , 2001 — *Revision of Solanum Section Cyphomandropsis (Solanaceae)*. *Systematic Botany Monographs*, 61: 1-85.
- and OLMSTEAD R.G., 1999 — *Solanum phylogeny inferred from chloroplast DNA sequence data*. M. Nee, D.E. Symon, R.N. Lester and J.P. Jessop (Eds.), "Solanaceae IV: Advances in Biology and Utilization", p. 97-110. Royal Botanic Gardens, Kew.
- and —, 2001 — *A reassessment of Normanina and Triguera (Solanaceae)*. *Plant Systematics and Evolution*, 228: 33-48.
- BRANDHAM P.E. and DOHERTY M.J., 1998 — *Genome size variation in Aloaceae, an angiosperm family displaying karyotypic orthoselection*. *Annals of Botany*, 82 (Suppl. A): 67-73.
- BRAMWELL D. and BRAMWELL Z., 2001 — *Flores silvestres de las Islas Canarias*. 4° ed. Editorial Rueda, Madrid.
- EDMONDS J.M., 1977 — *Taxonomic studies on Solanum section Solanum (Maurella)*. *Botanical Journal of the Linnean Society*, 75: 141-178.
- FEDEROV A.(ed.), 1969 — *Chromosome numbers of flowering plants*. V. L. Komarov. Bot. Inst. Leningrad (Reprinted by O. Koeltz Sci. Publ., Koenigstein. 1974).
- GOODSPEED T.H., 1954 — *The Genus Nicotiana*. Chronica Botanica Co., Waltham.
- HAWKES J.G., 1990 — *The Potatoe: Evolution, Biodiversity and Genetic Resources*. Smithsonian Institution Press, Washington.
- HEISER C. B., 1987 — *The Fascinating World of the Nightshades*. Dover Publications, New York.
- HUNZIKER A.T., 2001 — *Genera Solanacearum. The genera of Solanaceae illustrated, arranged according to a new system*. A.R.G. Gantner Verlag K.-G, Ruggell.
- KRISHNAPPA D.G. and CHENNAVEERAIH M.S., 1975 — *Cytotaxonomy of Solanum indicum complex*. *Cytologia*, 40: 323-331.
- LEVAN A., FREDGA L. and SANDBERG A., 1964 — *Nomenclature for centromeric position on chromosomes*. *Hereditas*, 52: 201-220.
- MOSCONE E., 1992 — *Estudios sobre cromosomas meióticos en Solanaceae de Argentina*. *Darwiniana*, 31: 261-297.
- , BARANYI M., EBERT I., GREILHUBER J., EHRENDORFER F. and HUNZIKER A.T., 2003 — *Analysis of nuclear DNA content in Capsicum (Solanaceae) by flow cytometry and Feulgen densitometry*. *Annals of Botany*, 92: 21-29.
- OCHOA C.M., 1999 — *Las Papas de Sudamérica: Peru. Parte I*. Allen Press, Lawrence.
- OKOLI B.E., 1988 — *Cytotaxonomic study of five West African species of Solanum L. (Solanaceae)*. *Feddes Repertorium*, 99: 183-187.
- OLMSTEAD R.G. and PALMER J.D., 1997 — *Implications for the phylogeny, classification, and biogeography of Solanum from cpDNA restriction site variation*. *Systematic Botany*, 22: 19-29.
- PIJNACKER L.P. and FERWERDA M.A., 1984 — *Giemsa C-banding of potato chromosomes*. *Canadian Journal of Genetics and Cytology*, 26: 415-419.
- PRINGLE G.J. and MURRAY B.G., 1991 — *Karyotype diversity and nuclear DNA variation in Cyphomandra*. J.G. Hawkes, R.N. Lester, M. Nee and N. Estrada (Eds.), "Solanaceae III: Taxonomy, Chemistry, Evolution", p. 247-252. Royal Botanic Gardens, Kew.
- RANDELL B.R. and SYMON D.E., 1976 — *Chromosome numbers in Australian Solanum species*. *Australian Journal of Botany*, 24: 369-379.
- RIESEBERG L.H., 2001 — *Chromosomal rearrangements and speciation*. *Trends in Ecology and Evolution*, 16: 351-358.
- ROE K.E., 1967 — *Chromosome size in Solanum and Cyphomandra: taxonomic and phylogenetic implications*. *American Naturalist*, 101: 295-297.
- ROMERO ZARCO C., 1986 — *A new method for estimating karyotype asymmetry*. *Taxon*, 35: 526-530.
- SANTOS GUERRA A., 2001 — *Flora Vascular Nativa*. J.M. Fernandez-Palacios and J.L.M. Esquivel (Eds.), "Naturaleza de las Islas Canarias", p. 185-192. Turquesa Ed., Tenerife.
- SNOW R., 1963 — *Alcoholic hydrochloric acid-carmines as a stain for chromosomes in squash preparations*. *Stain Technology*, 38: 9-13.
- STEBBINS G.L., 1971 — *Chromosomal evolution in higher plants*. E. Arnold, London.
- STIEFKENS L. and BERNARDELLO G., 2002 — *Karyotypic studies in Lycium section Mesoscope (Solanaceae) from South America*. *Caryologia*, 55: 199-206.
- TANG H., LIHUA M., SHIQING A., and JIANQUAN L., 2005 — *Origin of the Qinghai-Tibetan Plateau endemic Milula (Liliaceae): further insights from karyological comparisons with Allium*. *Caryologia*, 58: 320-331.

- TRIVEDI R.N. and SINHA A.K., 1986 — *Karyomorphological studies in three populations of Solanum surattense, a weed*. Cytologia, 51: 157-161.
- WHALEN M.D., 1984 — *Conspectus of species groups in Solanum subgenus Leptostemonum*. Gentes Herbarum, 12: 179-282.

- WU S. and LI Z., 1985 — *Preliminary studies of chromosome morphology of several wild and cultivated eggplants*. Acta Botanica Sinica, 27: 361-369.

Received ???.?.2006; accepted ???.?.2006