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# Caryological studies of the genus *Convolvulus* L.

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## ABSTRACT

LUQUE, T. & Z. DÍAZ LIFANTE (1994). Caryological studies of the genus *Convolvulus* L. *Candollea* 49: 233-243. In English, English and Spanish abstracts.

In Spain 15 taxa belonging to the genus *Convolvulus* L. have been found. The caryological characters of eight out of the 11 taxa represented in SW Spain have been studied. Data for *C. betonicifolius* Miller are reported for the first time. The chromosome number found for *C. lineatus* L. corresponds to a higher polyploidy level than that previously described. *C. althaeoides* L. and *C. siculus* L. from Iberian Peninsula have been studied for the first time.

## RESUMEN

LUQUE, T. & Z. DÍAZ LIFANTE (1994). Estudio cariológico del género *Convolvulus* L. *Candollea* 49: 233-243. En inglés, resúmenes en inglés y en español.

El género *Convolvulus* L. está representado en la Península por 15 taxones. Se han estudiado cariológicamente 8 de los 11 taxones existentes en el SW de España. Se aporta por primera vez información cariológica de *C. betonicifolius* Miller. El número cromosómico encontrado en *C. lineatus* L. corresponde a un nivel de ploidía superior a los anteriormente ya conocidos para la especie. *C. althaeoides* L. y *C. siculus* L. son estudiados por primera vez con material de la Península Ibérica.

**KEY-WORDS:** *Convolvulus* — Caryology — Chromosome numbers — Polyploidy — Spain — Cytogenetic.

## Introduction

The genus *Convolvulus* L. is mainly represented in temperate and subtropical regions, being more infrequent in the tropics, while it is very well represented in W Asia and the Mediterranean region. In this region, about 53 species are found, 15 of them in Spain (GREUTER & al., 1986). They can be grouped into three Sections (SA'AD, 1967), two of which are represented in the studied area: Sect. *Convolvulus* (*C. arvensis* L., *C. betonicifolius* Miller and *C. althaeoides* L. subsp. *althaeoides*) and Sect. *Inermes* Boiss. (*C. lanuginosus* Desr., *C. cantabrica* L., *C. lineatus* L., *C. boissieri* Steudel subsp. *boissieri*, *C. humilis* Jacq., *C. tricolor* L. subsp. *tricolor*, *C. meonanthus* Hoffmanns. & Link and *C. siculus* L. subsp. *siculus*).

Most caryological data regarding the genus are dispersed, since the most part of the literature deal with chromosome counts. It is well known that caryomorphological studies are difficult in plants with small chromosomes. Only occasionally, some complete works about the genus are found (see SA'AD, 1967; STACE, 1973; SAMPATHKUMAR & RANGASWAMI, 1981).

This paper is a contribution to the caryology of the genus *Convolvulus*. We have started by studying populations from the SW Spain area, where this genus has not been caryologically well studied. Caryological data are present in eight of the 11 taxa described in this area, being new those

of *C. betonicifolius*. For *C. lineatus* a new chromosome number has been found, which apparently corresponds to a new ploidy level. Finally, this seems to be the first caryological study of *C. althaeoides* and *C. siculus* subsp. *siculus* carried out with Iberian Peninsula material.

### Materials and method

The study has been made on somatic metaphases of root tips obtained from seeds of wild plants germinated in wet filter paper in Petri dishes. These root tips were pre-treated with 2 mM 8-hydroxyquinoline at room temperature for 3-3.5 hours, fixed in Farmer's Fluid (LÖVE & LÖVE, 1975) for 24 hours and preserved at 4°C in 70% ethanol until staining out.

The material was stained in alcohol-hydrochloric acid-carmin solution (SNOW, 1963) for 48-72 hours. It was heated to accelerate the staining. The material was then squashed; 45% acetic acid was used as montage solution.

The seeds were obtained of plants that have been conserved and deposited in the Herbarium of the Department of Plant Biology and Ecology, University of Seville (SEV). Voucher numbers are cited in the text.

The terminology of STEBBINS (1938, 1971) has been used for apparent size and caryotype asymmetry. For chromosome morphology we have followed LEVAN & al. (1965).

### Results

#### Sect. *Convolvulus*

##### *Convolvulus arvensis* L., Sp. Pl. 153 (1753).

*Material studied.* — SEVILLA. Between Algámitas and Villanueva de San Juan, 1988.07.11, Díaz Lifante (SEV 124617),  $2n = 48$ . Montellano, 1988.07.11, Díaz Lifante (SEV 126576),  $2n = 48$ . Sevilla, Heliópolis, 1988.07.30, Díaz Lifante (SEV 124615),  $2n = 48$ .

In every plant of the populations studied, the somatic number of  $2n = 48$  has been found. This number agrees with the one given by the following authors: STACE (1973), for material collected in Britain; LÖVE & KJELLQVIST (1974) for Spanish plants from Sierra de Cazorla (Jaén); VIJ & SINGH (1976) for Indian plants, and QUEIRÓS (1978) for plants collected in Portugal. The gametic number  $n = 24$  has been reported by VIJ & al. (1974) for Indian material.

For this taxon, other chromosome numbers, such as  $2n = 50$ ,  $n = 12$  and  $n = 16?$  have been reported. The somatic number  $2n = 50$  has been cited by HEISER & WHITAKER (1948) for plants of California (EE.UU.), by GÁRAJOVÁ (1959, sec. MÁJOVSKÝ & al., 1970b) for material collected in Czechoslovak, by SA'AD (1967) without indication of origin, by POGAN & WCISLO (1977) and by WCISLO (1980, sec. POGAN & al., 1980) for plants collected in Poland and by LÖVE & LÖVE (1982) for Italian material.

BIR & NEELAM (1980) have cited the gametic number  $n = 12$  for plants collected in India. On the other hand,  $n = 16$  also has been quoted for Indian plants (VIJ & SINGH, 1976).

The chromosomes of the plants collected in Seville (SEV 124617) have an apparent size that varies between 1.23 and 1.84  $\mu\text{m}$ , which can be considered as small (Fig. 2a). This is consistent with the 1-2  $\mu\text{m}$  described for this taxon by STACE (1973). Considering data, a type A asymmetry can be postulated.

It has not been possible to determine with accuracy the morphology of chromosomes due to their small size. However, mainly metacentrics and submetacentrics have been observed in the somatic metaphase, with a higher proportion of the former). Therefore, their asymmetry corresponds to type 1A.

To conclude about the basic number for this taxa, some comments are necessary to relate the chromosomal variability found in the literature.

LÖVE & KJELLQVIST (1974) have reported  $x = 6$  as the basic number for this taxon, corresponding consequently to an octoploid level. They also believe that  $x = 6$  could be the basic number for the genus, in such a way that those taxa with chromosome numbers  $2n = 20$  and  $30$  need to be reviewed.

On the other hand, HEISER & WHITAKER (1948) consider  $2n = 48$  as polyploid, without specifying the ploidy level. VIJ & SINGH (1976) suggest  $x = 8$  and two ploidy level: tetraploid ( $n = 16$ ) and hexaploid ( $n = 24$ ). As  $n = 16$  has only been observed in some cells, this hypothesis will not be taken into account for the moment.

The previous chromosome numbers, and those of other taxa of *Convolvulus* commented later, allow to consider  $x = 12$  as the basic number for *C. arvensis*, in which two ploidy levels, diploid ( $n = 12$ ) and tetraploid ( $n = 24$  and  $2n = 48$ ) have been found up to date. The somatic number  $2n = 50$  could be considered as a hypertetraploid with an aneuploid origin. This process happens quite often in *Convolvulus*, and even in the family Convolvulaceae (SAMPATHKUMAR & RAN-GASWAMI, 1981).

#### ***Convolvulus betonicifolius* Miller, Gard. Dict., ed. 8, n. 20 (1768).**

*Material studied.* — SEVILLA. Between Villanueva de San Juan and Algámitas, 1988.07.11, Díaz Lifante (SEV 124613),  $2n = 36$ .

According to references consulted, this could be the first caryological study of this taxon.

The apparent chromosome size varies between  $1.78$  and  $2.57 \mu\text{m}$ . They can be classified as small and medium small, being about 50% of each type.

The chromosomes of the karyotype can be grouped as follows (Fig. 1a, 1b): fourteen metacentrics (M), with the centromere in the median point (pairs 3, 7, 12, 13, 15, 16 and 17); twelve metacentrics (m), with the centromere in the median region (pairs 2, 4, 8, 9, 11 and 14), one pair metacentric-submetacentrics (m-sm), one chromosome with the centromere in the median region and the other with the centromere in the submedian region (pair 5) and eight submetacentrics (sm), with the centromere in the submedian region (pairs 1, 6, 10, 18). This karyotype has the idiogrammatic formula  $14M + 12 m + 2 m\text{-sm} + 8 sm$ , and an asymmetry of the type 2A. In the pair 1 it is possible to observe one secondary constriction in the long arm.

The discussion about the basic number and ploidy level corresponding to this taxon will be considered later.

#### ***Convolvulus althaeoides* L., Sp. Pl. 156 (1753) subsp. *althaeoides*.**

*Material studied.* — HUELVA. Almonte, 1988.07.05, Díaz Lifante (SEV 126447),  $2n = 40$ . SEVILLA. Utrera, Pantano Torre del Aguila, 1988.07.13, Díaz Lifante (SEV 124614),  $2n = 40$ .

The chromosome number found  $2n = 40$  agrees with the one indicated by COLOMBO & al. (1980) for plants collected in Palermo (Italy). However, it differs from the  $n = 10$  found by AMIN (1973) for plants from Egypt. This is a taxon with a basic number of  $x = 10$ . Consequently, both the populations here studied, so as the Italian populations, have to be tetraploids, while the Egyptian populations correspond to a diploid level. This seems to be the first caryological study carried out with Spanish material.

The apparent size of chromosome is less than  $2 \mu\text{m}$ . They are thus included in the group of small chromosomes.

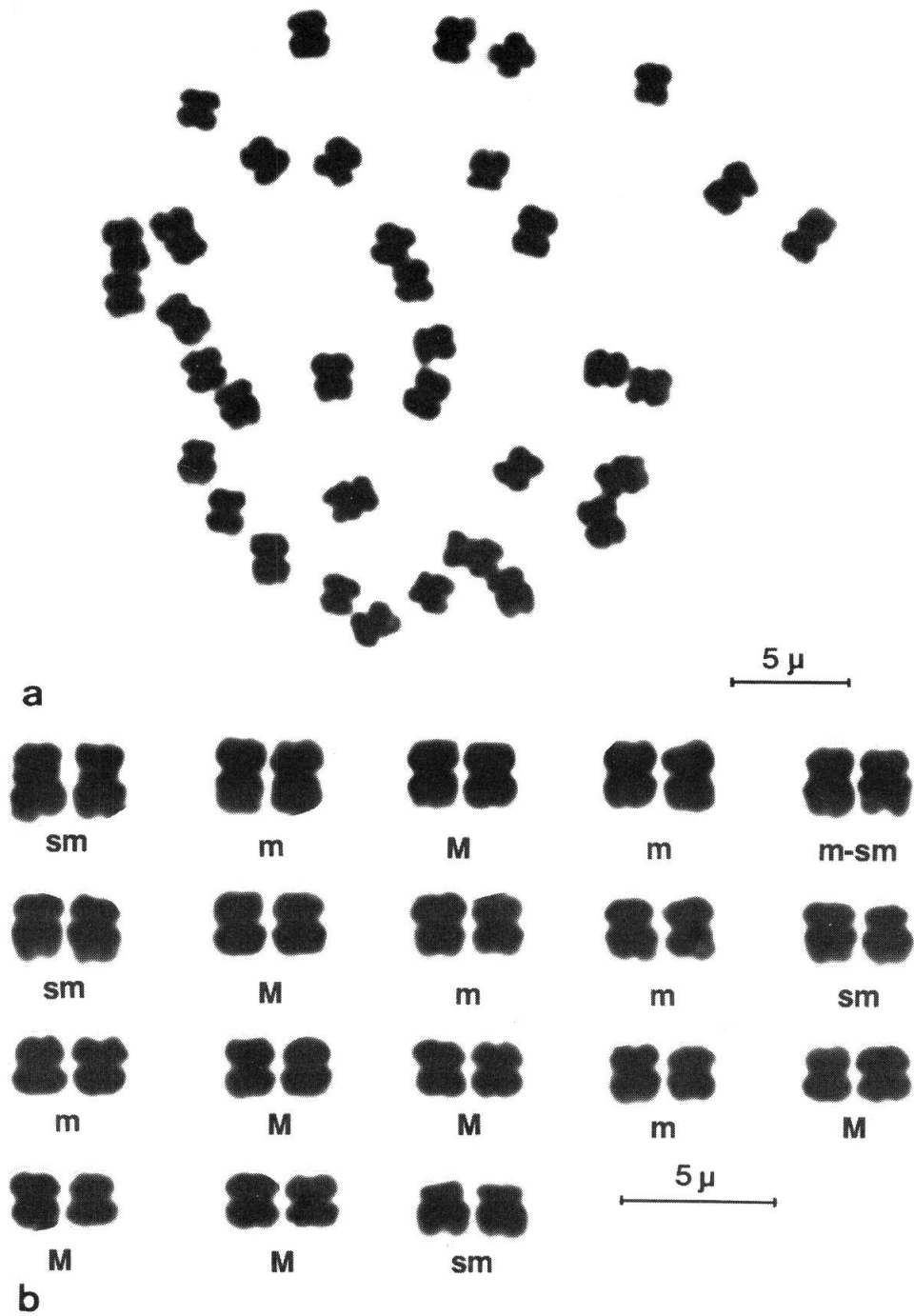


Fig. 1. — Caryotype and caryogram of *C. betonicifolius* Miller: a, somatic metaphase; b, caryogram.

Sect. **Inermes** Boiss.**Convolvulus cantabrica** L., Sp. Pl. 158 (1753).

*Material studied.* — CÓRDOBA. Rute, Sierra del Pollo, 1989.07.26, Díaz Lifante & Santa Bárbara (SEV 126526),  $2n = 30$ . Cerro del Majano, 1989.07.26, Díaz Lifante & Santa Bárbara (SEV 124648),  $2n = 30$ .

In the studied populations, the somatic number  $2n = 30$  has been found. This agrees with that indicated by SA'AD (1967), who does not state the origin of the material, by HINDÁKOVÁ (sec MÁJOVSKÝ & al., 1970a) for plants collected in Czechoslovakia, by VAN LOON & KIEFT (1980) for material of Yugoslavia, by NATARAJAN (1981, 1988) for french plants, and by VAN LOON (1982) for plants collected in Greece, and with the gametic number  $n = 15$  found by PASTOR (1984) for Spanish plants collected in Córdoba.

DOLCHER & PIGNATTI (1960), who studied seeds of Botanical Gardens, and COLOMBO & al. (1980), who studied plants collected in Italy, report a chromosome number  $2n = 22$ . NATARAJAN (1988), following the ideas of LÖVE & LÖVE (1961, 1974) indicate that this is a "hexaploid taxon with basic number  $x = 5$  and that the chromosome number  $2n = 22$  represent the diploid level with  $x = 11$ ".

Since this genus, as well as others of Convolvulaceae, present high basic numbers (it will be seen later on), it could be inferred that it is a diploid taxon with  $x = 15$ . Moreover, populations with lower ploidy levels have not been found.

The apparent chromosome sizes vary between 1.1 and 1.97  $\mu\text{m}$ . Thus all chromosomes of the karyotype belong to the group of small chromosomes (Fig. 2b). DOLCHER & PIGNATTI (1960) report sizes smaller than 3  $\mu\text{m}$ .

As shown in Figure 2b, most of the chromosomes are metacentrics (M or m) and only some of them are submetacentric (sm). Considering this, together with the relationship between the chromosome sizes, it is possible to maintain that the asymmetry corresponds to type 2A. In the same figure, two satellized chromosomes can be seen. This was also observed by NATARAJAN (1988).

**Convolvulus lineatus** L., Syst. Nat., ed. 10, 2: 923 (1759).

*Material studied.* — MURCIA. Jumilla. El Prado, 1992.12.10, Díaz Lifante (SEV 134714),  $2n = 60$ . SEVILLA. San Martín de la Jara. Laguna de Gosque, 1988.07.11, Díaz Lifante (SEV 125399),  $2n = 60$ .

The somatic number found  $2n = 60$  differs from the  $2n = 30$  reported by GUINOCHET & LEFRANC (1981) for Russian plants. It seems to be the first caryological study carried out with Spanish populations.

A very frequent basic number in this genus as well as in Convolvulaceae is  $x = 15$  (SAMPATHKUMAR & RANGASWAMI, 1981). If this number is considered as the basic in the genus, two ploidy levels are present in this species: diploid in the Russian populations and tetraploids in the Spanish ones. So,  $2n = 60$  is the highest chromosome number found for the genus *Convolvulus*.

The chromosome of studied somatic metaphases are small size, with an apparent size smaller than 2  $\mu\text{m}$  (0.96-1.68  $\mu\text{m}$ ) (Fig. 2c).

**Convolvulus tricolor** L., Sp. Pl. 158 (1753) subsp. **tricolor**.

*Material studied.* — CÁDIZ. Facinas, Embalse de Almodóvar, 1989.06.16, Díaz Lifante & Valdés (SEV 126525),  $2n = 20$ . Zahara de los Atunes, 1989.06.16, Díaz Lifante & Valdés (SEV 126574),  $2n = 20$ .

In the two populations studied, a chromosome number of  $2n = 20$  has been found. This agrees with QUEIRÓS (1978) for material collected in Portugal, as well as with the gametic number

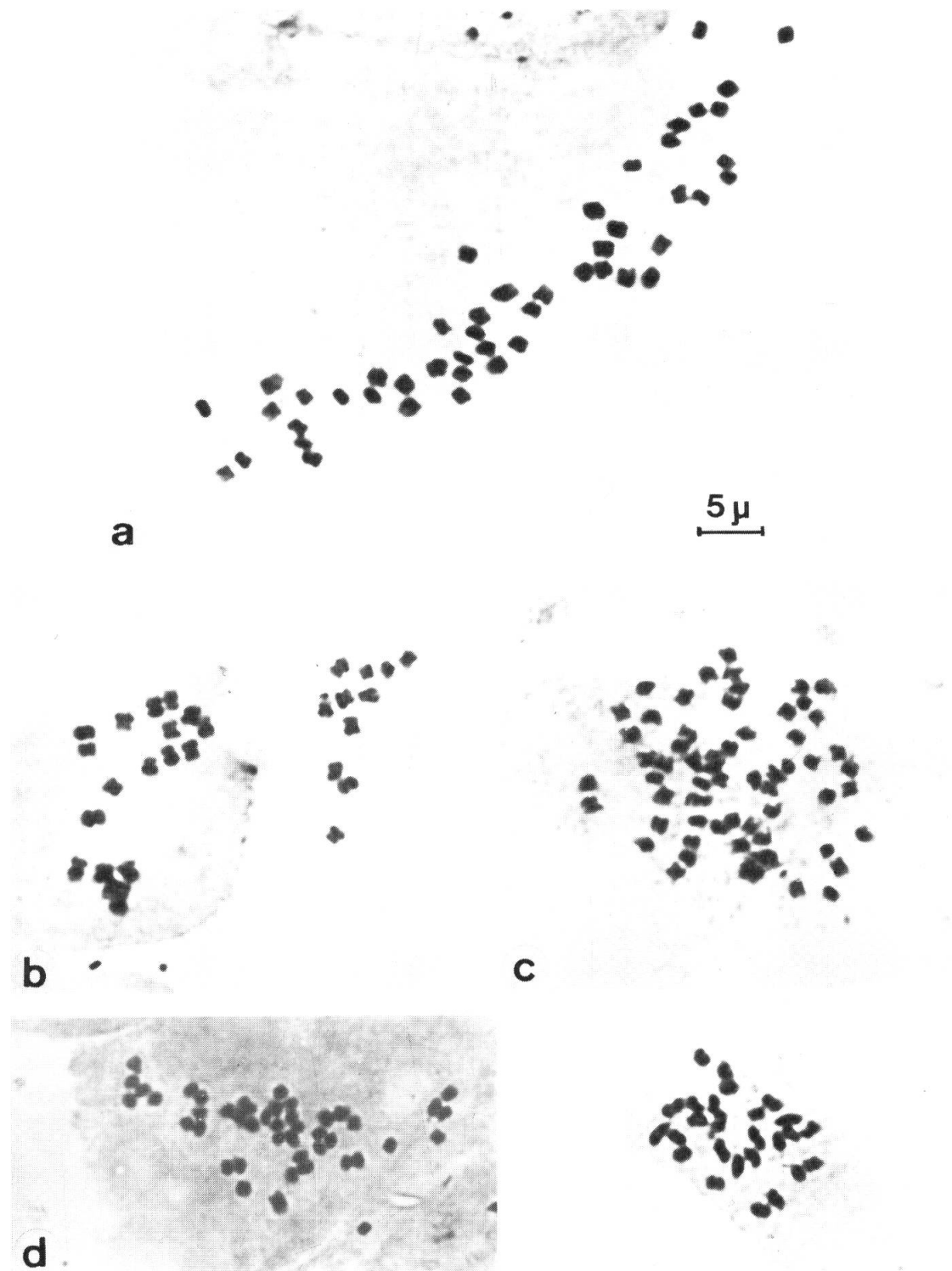


Fig. 2. — Caryotypes of sundry *Convolvulus*: a, *C. arvensis* L.; b, *C. cantabrica* L.; c, *C. lineatus* L.; d, *C. siculus* L. subsp. *siculus*; e, *C. meoanthus* Hoffmanns. & Link.

$n = 10$  reported by RUÍZ DE CLAVIJO & UBERA JIMÉNEZ (1982) for Spanish plants. It is thus a diploid taxon with a basic number of  $x = 10$ .

The apparent chromosome sizes found in this work is less than  $2 \mu\text{m}$ . Therefore, they are small. Likewise, it has been proved that the proportion between the size of the large and the small chromosomes is less than 2:1. This means that its chromosomic asymmetry is of the type A.

***Convolvulus meonanthus* Hoffmanns. & Link, Fl. Port. 1: 369 (1813-1820).**

*Material studied.* — CÁDIZ. Grazalema, Puerto Alhamillos, 1988.06.28, Díaz Lifante, Pérez & Santa Bárbara (SEV 124664),  $2n = 26$ .

The somatic number found  $2n = 26$  (Fig. 2e) agrees with that obtained by SA'AD (1967) for plants without indication of their origin, with that of QUEIRÓS (1979) for material collected in Portugal and with the gametic number  $n = 13$  indicated by RUÍZ DE CLAVIJO & GALÁN SOLDEVILLA (1984) for Spanish plants collected in Seville. However, LÖVE & KJELLQVIST (1974) found the chromosome number  $2n = 24$  for Spanish plants from Jaén.

This taxon has been and it is now considered by some authors subordinated to *C. tricolor*. It has been treated as subspecies or as variety depending on the author. According to caryological results it does not seem convenient to accept such a subordination, since though both taxa are diploid, they present different basic number,  $x = 13$  for *C. meonanthus* and  $x = 10$  for *C. tricolor*.

The apparent chromosome sizes vary between  $1.23$  and  $2.15 \mu\text{m}$  (Fig. 2e). Most of them are small. The caryotype asymmetry corresponds to type 2A, in relation to the size and morphology of the chromosomes.

***Convolvulus siculus* L., Sp. Pl. 156 (1753) subsp. *siculus*.**

*Material studied.* — SEVILLA. Morón. Finca Espartero, 1989.05.03, Díaz Lifante & Luque (SEV 124632),  $2n = 44$ . Peñón de Algámitas, 1989.05.03, Díaz Lifante & Luque (SEV 126530),  $2n = 44$ .

The chromosome number found  $2n = 44$  agrees with that indicated by DAHLGREN & al. (1971) for Spanish plants collected in the Balearic Islands, by COLOMBO & al. (1980) for material of Italy and by DÍAZ LIFANTE & al. (1992) for plants of Israel. Apparently it is the first caryological study carried out with material of the Iberian Peninsula.

SA'AD (1967) suggests a chromosome number of  $2n = 44$  for var. *siculus*, and  $2n = 22$  for var. *elongatus* (Willd.) Batt.

According to data it could be inferred that *C. siculus* has  $x = 11$  as basic number with two levels of ploidy: diploid ( $2n = 22$ ) and tetraploid ( $2n = 44$ ). The Spanish populations would belong to the latter.

The apparent sizes of the chromosomes are less than  $2 \mu\text{m}$  (Fig. 2d). Thus, they are small. In the somatic metaphases, a pair of satellitized chromosomes have been observed, being the satellite size quite big compared with the chromosome size.

### Discussion

The chromosomes of the taxa of *Convolvulus* studied are generally small ( $< 2 \mu\text{m}$ ). This size has been only exceeded by few chromosomes of some caryotypes (*C. betonicifolius* and *C. meonanthus*).

Though very few authors have carried out a study on *Convolvulus* caryology, their results agree to a large extent with the results here presented. STACE (1973) indicates a size varying between



<i>Taxa</i>	<i>habit</i>	<i>n</i>	<i>2n</i>	<i>x</i>	<i>Authors</i>
<b>Sect. Convolvulus</b>					
Subsect. <i>Convolvulus</i>					
<i>C. arvensis</i> L. ....	P		24, 48, 50	12 (2x, 4x)	see text
<i>C. betonicifolius</i> Miller .	P		36	9 (4x)	see text
<i>C. farinosus</i> L. ....	P		24	12 (2x)	SA'AD (1967)
<i>C. fatmensis</i> Kunze.....	P		20	10 (2x)	SA'AD (1967)
<i>C. althaeoides</i> L.....	P		20, 40	10 (2x, 4x)	see text
<i>C. scammonia</i> L.....	P		24	12 (2x)	HEITZ (1926, sec. SA'AD, 1967)
<b>Sect. Inermes Boiss.</b>					
Subsect. <i>Oleifolii</i> Peter					
<i>C. cantabrica</i> L. ....	P	15	30	15 (2x)	see text
<i>C. cneorum</i> L.....	P		30	15 (2x)	BRULLO & PAVONE (1978)
<i>C. lineatus</i> L.....	P		30, 60	15 (2x, 4x)	see text
Subsect. <i>Diffusi</i> Boiss.					
<i>C. humilis</i> Jacq. ....	A		22?	11 (2x)?	HEITZ (1926, sec. SA'AD, 1967)
			24	12 (2x)	COLOMBO & al. (1979)
<i>C. tricolor</i> L.....	A		20	10 (2x)	see text
<i>C. meonanthus</i> Hoffmanns. & Link.....	A		26	13 (2x)	see text
<i>C. siculus</i> L.....	A		22, 44	11 (2x, 4x)	see text
<i>C. sabatius</i> Viv. subsp. <i>mauritanicus</i> (Boiss.) Murb. ....	P		22	11 (2x)	SA'AD (1967); TORNADORE & al. (1974)
			40	10 (4x)	GALLAND (1988)
<i>C. microphyllus</i> Sieb. ...	P	12		12 (2x)	BIR & NEELAM (1980)
<i>C. pluricaulis</i> Chois ....	P	9, 18		9 (2x, 4x)	VIJ & al. (1974); VIJ & SINGH (1976)
(= <i>C. prostratus</i> Forskål)		10, 20		10 (2x, 4x)	SINGH (1951, sec. SA'AD, 1967)
<i>C. gharbensis</i> Batt. ....	A		22	11 (2x)	SA'AD (1967)

Table 1. — Chromosome numbers of *Convolvulus* taxa. (A: annual, P: perennial).

1-2  $\mu\text{m}$  for *C. arvensis*; SAMPATHKUMAR & RANGASWAMI (1981), studying Indian Convolvulaceae, have concluded that chromosome sizes are small to a large extent and most of them are between 1.6 and 3.8  $\mu\text{m}$ .

On the other hand, the studied karyotypes are quite symmetric. Most of the chromosomes are metacentrics (with asymmetry of type 2A and 1A). Apparently the degree of asymmetry has not increased, despite a high variety of chromosome numbers and ploidy levels, these processes very frequent in this genus.

In relation to basic numbers variability,  $x = 9, 10, 11, 12, 13$  and  $15$  have been found for the taxa studied. SA'AD (1967) reports for the genus all these numbers except  $x = 9$ . VIJ & SINGH (1976) report the number  $x = 8$  for *C. arvensis*, based on the findings of plants with  $n = 24$ , as well as plants with "some cells" with  $n = 16$ . The data do not seem to be good enough to establish  $x = 8$  as basic number. However, that number does not exist for any other taxon of the genus, not even for Convolvulaceae.

For the family, a gradual series of haploid numbers are suggested by SAMPATHKUMAR & RANGASWAMI (1981). These numbers are  $n = 7, 9, 10, 11, 12, 13, 14, 15, 16, 18, 20, 21, 22, 23, 24, 25, 28, 29, 30, 42$  and  $45$ , and specifically for the genus *Convolvulus*  $n = 9, 10, 11, 12, 14, 15, 18, 20, 22, 23, 24, 25$  and  $30$ . To these series, it should be added  $x = 13$  as basic number of *C. meonanthus*. This number has very small representation in *Convolvulus*, since it is the only taxon presenting it.

The chromosome and basic numbers, and the ploidy levels of the studied taxa are summarized in Table 1. Other taxa with known karyological characters have also been included.

From that Table, it can be deduced that the taxa included in the Subsect. *Oleifolii* of the Sect. *Inermes* can be clearly differentiated from the rest of the subsections, because of its constant  $x = 15$  and perennial habits in all taxa.

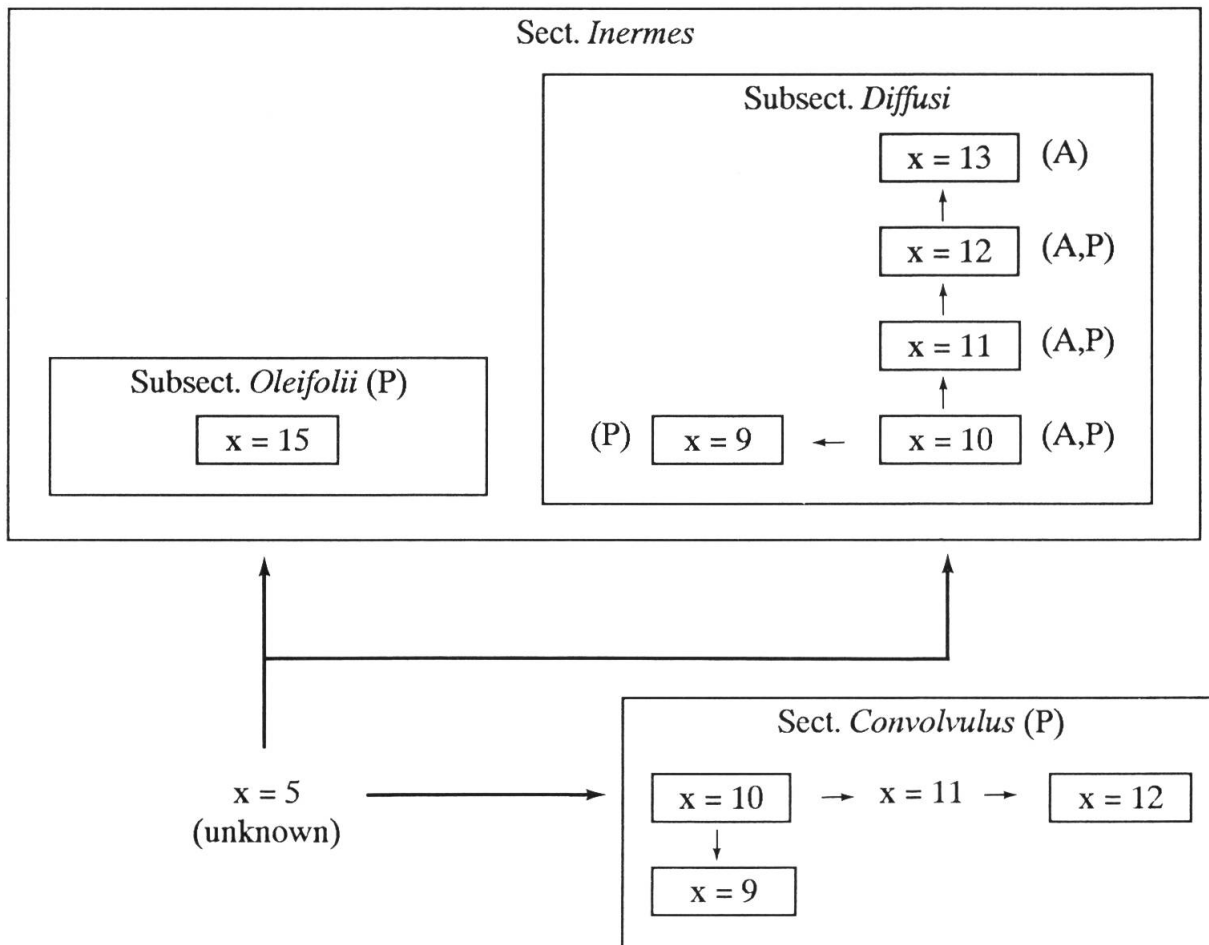


Fig. 3. — Possible evolutionary tendencies of *Convolvulus*. Boxes correspond to basic numbers found in this paper. Thick and thin arrows indicate processes of polyploidization and dysploidization, respectively (A: annual, P: perennial).

According to SA'AD (1967), this basic number is common to most genera of Convolvulaceae. Likewise, SAMPATHKUMAR (1970) and SAMPATHKUMAR & RANGASWAMI (1981) believe that it is the most frequent number. From the numbers reported by these authors, it has been calculated that 48.83% of the taxa of Convolvulaceae would have it.

These results suggest that  $x = 15$  correspond to the principal basic number, the rest ones derived from it by aneuploid process. According to several authors, aneuploidy has played a very important role in evolution and speciation of Convolvulaceae. This mechanism has made easier to understand the chromosome number diversity.

LÖVE & LÖVE (1961) and SAMPATHKUMAR & RANGASWAMI (1981) believe that  $x = 15$  could be a secondary basic number derived from  $x = 5$ , which would be the primary basic number. This primary basic number has already disappeared. In fact, the lower gametic number found for Convolvulaceae is  $n = 7$ . The origin of  $x = 15$  could have been then produced by fusion of a normal gamete ( $n = 5$ ) with an unreduced ( $n = 2x = 10$ ) one, followed by a polyploidization ( $2n = 30$ ).

Following with the Sect. *Inermes*, the Subject. *Diffusi* (Table 1) include both perennial and annual habit taxa. The first has  $x = 9, 10, 11$  and  $12$  as basic numbers; the second,  $x = 10, 11, 12$  and  $13$ . The most important chromosome numbers in herbaceous dicots are  $x = 6-10$ , taking into account their frequency of appearance. Numbers higher than these are not as common. This could mean that they have been generated later (STEBBINS, 1938, 1971; GRANT, 1982a, 1982b) from a lower basic number.

In view of the preceding comments, an hypothetic evolutive scheme on basic numbers can be drawn within the Subject. *Diffusi* (Fig. 3). According to it, the most primitive number that still

exists is  $x = 10$ . It could have originated by a polyploidy process from the ancestral  $x = 5$  (already disappeared). This number  $x = 10$  would be found in derived taxa with perennial and annual habits, two lines arising from it both by dysploidization. One of them could give rise to taxa with  $x = 9$  and perennial habits only. The other, increase to  $x = 13$ . This last number is only present in annual taxa.

Finally, in relation to Sect. *Convolvulus*, all the taxa are perennial and have the basic numbers  $x = 9, 10$  and  $12$ . According to the above stated hypothesis,  $x = 10$  could be considered as more primitive. The rest could have been originated from dysploidization.

In short, the chromosome number diversity found in *Convolvulus* could have been originated by polyploidization and dysploidization from an ancestral basic number  $x = 5$ , unknown up to date. Both processes seem to be very frequent within the group (Fig. 3).

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