

KARYOLOGICAL STUDIES IN IBERIAN *SONCHUS* (*ASTERACEAE: LACTUCEAE*): *S. OLERACEUS*, *S. MICROCEPHALUS* AND *S. ASPER* AND A GENERAL DISCUSSION

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Abstract: Chromosome numbers and karyotypes of *Sonchus oleraceus* ($n=16$, $2n=32$), *S. asper* ($n=9$, $2n=18$ for subsp. *asper* and subsp. *glaucescens*, and *S. microcephalus* ($n=15$, $2n=30$) are studied; for the first time their idiograms are given. Karyotypes mainly comprise small chromosomes with a degree of asymmetry 2B in *S. oleraceus* and *S. microcephalus* and 2A or 2A–2B in *S. asper*. No karyological differences can be pointed out between *S. asper* subspecies. Data presented support the amphiploid character of *S. oleraceus*, and the origin of *S. microcephalus* through a dysploid process involving the former taxon. In Iberian representatives of the genus, diagrams of karyotype asymmetry indices show a cluster grouping for species, with the detached exceptions of *S. maritimus* and *S. crassifolius*, which spontaneously hybridize in central Spain.

A review of available karyological data shows that in the evolution of the genus *Sonchus* s.l. and relatives, the basic chromosome number $x=9$ has generally been maintained. Dysploidy is restricted to the series *S. bourgeaui* ($n=8$) – *S. tenerrimus* ($n=7$) and *S. oleraceus* ($n=16$) – *S. microcephalus* ($n=15$), evolutionarily related and included in the present subgenus *Sonchus*. Polyploidy has been detected in a total of nine taxa of *Sonchus* and in the genera *Embergeria*, *Kirkianella*, and *Dendroseris*, being more common in peripheral regions of the distribution area of the group. Five diversification centers are proposed for the whole group, of which the Western Mediterranean area, including the Iberian Peninsula, is related to diversification of the present subgenus *Sonchus*.

Keywords: Basic number, Chromosome morphology, Dysploidy, Karyotype evolution, Mediterranean region, Polyploidy

INTRODUCTION

The genus *Sonchus* L. shows a scattered, almost cosmopolitan distribution, being absent from Central and South America exclusively. It is commonly considered related to *Aetheorhiza* CASS., *Reichardia* ROTH and *Launaea* CASS. (STEBBINS 1953, SELL 1975), and probably raising from *Launaea* (STEBBINS 1953, BOULOS 1974b). These four genera have recently been incorporated in the subtribe *Sonchinae* K. BREMER (BREMER 1994) with some other small genera, although molecular phylogenetic analysis recommends some modifications in the subtribe (KIM et al. 1996b, 1999b).

The attainment of laterally compressed cypselas, a process also detected in the *Lactuca* group (MORENO-SOCÍAS et al. 1994), has been considered the main morphological character involved in the differentiation and definition of the genus *Sonchus*. BOULOS (1972), in a comprehensively systematic work, divided *Sonchus* L. *sensu lato* in four genera: the

monospecific *Babcockia* BOULOS and *Taeckholmia* BOULOS that comprises seven species (both genera being endemic to the Canary Islands), *Embergeria* BOULOS, comprising two species from New Zealand and Australia (BOULOS 1974b), and *Sonchus* L. that represents the highest diversity of the group. He also distributed the species of the last genus into three subgenera: *Origosonchus* BOULOS, proposed as the most primitive, that comprises 14 perennial or suffruticose species from sub-Saharan Africa and Madagascar (BOULOS 1974b), *Dendrosonchus* SCH.BIP. ex BOULOS, a set of 19 suffruticose Macaronesian endemics (BOULOS 1974a), and the subgenus *Sonchus*. This one comprises 27 mainly herbaceous taxa: 23 species and 4 subspecies (BOULOS 1973, MEJÍAS & VALDÉS 1988, MEJÍAS 1990) among which the widely distributed weeds *S. oleraceus* L., *S. asper* L. and *S. arvensis* L. are included. ALDRIDGE (1979) agreed to Boulos' systematic proposal for *Sonchus* but, according to anatomical data, she considered the subgenus *Dendrosonchus* as the most primitive one. On the contrary, phylogenetic molecular analyses of the tribe *Sonchinae* (KIM et al. 1996b, 1999b) has clearly shown that neither monophyly of the genus *Sonchus* and the three subgenera nor phylogenetic relationships within the group as proposed by Boulos are supported by those data.

The West Mediterranean Region shows the highest diversity of the subgenus *Sonchus* with 14 representatives. In the area, the Iberian Peninsula concentrates a set of ten taxa: *S. oleraceus* L., *S. microcephalus* MEJÍAS, *S. tenerrimus* L., *S. asper* L. subsp. *asper*, *S. asper* subsp. *glaucescens* (JORD.) BALL, *S. maritimus* L., *S. aquatilis* POURR., *S. crassifolius* POURR. and *S. pustulatus* WILLK. plus the hybrid *S. ×novocastellanus* CIRUJANO; some of these are endemic in the Iberian Peninsula (*S. crassifolius* and *S. ×novocastellanus*) or the West Mediterranean area (*S. pustulatus* and *S. aquatilis*).

The karyological reports in *Sonchus* are diverse because of the wide distribution of the genus but they consist mainly of chromosome counts, concisely compiled by ROUX & BOULOS (1972) until that date. Neither chromosome morphology studies nor idiograms were included in that paper. Nevertheless, MEJÍAS (1988) compared the karyotypes of *S. tenerrimus* and *S. pustulatus*, and MEJÍAS & VALDÉS (1988) studied the idiograms in the Iberian representatives of *S. sect. Maritimi* (KIRP.) BOULOS. A taxonomic approach was mainly used in those papers, showing the interest of karyology in *Sonchus* taxonomy. Here we report cytological observations on the remaining representatives of the genus in the Iberian Peninsula (*S. oleraceus*, *S. microcephalus*, *S. asper* subsp. *asper* and *S. asper* subsp. *glaucescens*), and discuss the karyotype evolution of the genus, emphasizing the interest of the Iberian Peninsula in relation to its general diversification in the world.

MATERIAL AND METHODS

For meiotic studies, flower buds of an average of four plants from each population were fixed in the field in Carnoy's fixative – ethanol : chloroform : acetic acid (6 : 3 : 1) (LÖVE & LÖVE 1975). They were kept in this for at least 24 h and preserved in 70% ethanol at $4\text{ }^{\circ}\text{C} \pm 2\text{ }^{\circ}\text{C}$. Material was stained in cold alcoholic hydrochloric acid-carmine solution (SNOW 1963) for 48 to 72 h and squashed and mounted in 45% acetic acid.

Mitotic studies were done with root tips of plants obtained from seeds collected in the field, or with seedlings obtained by germinating seeds from either self-fecundated cypsela or wild

seeds. For chromosome numbers, an average of three plants per population was studied in *Sonchus oleraceus* and six plants for the remaining taxa. The root tips were treated with 0.002 M 8-hydroxyquinoline for about 3.5 h at room temperature (TJIO & LEVAN 1950), fixed in Farmer's fixative – ethanol : acetic acid (3 : 1) (LÖVE & LÖVE 1975) and stored at $4\text{ }^{\circ}\text{C} \pm 2\text{ }^{\circ}\text{C}$ in 70% ethanol. At first, material was stained in cold alcoholic-hydrochloric carmine solution but staining with acetic orceine gave better results, so it was used afterwards. For this procedure, material was macerated in the orceine solution for about 4 h and gently heated during 3 minutes. Finally 45% acetic acid was added to stop stain reaction and for squashing.

Whenever possible, chromosome morphology and idiograms were analyzed in three or four mitotic metaphase plates per population, preferably from different plants. The terminology of LEVAN et al. (1964) modified by KÜPFER (1974) has been used for describing the morphology of chromosomes and the pairs established. These authors classified the chromosomes in six categories or classes, depending on the rate $r = \text{long arm length/short arm length}$: metacentric (M; $r = 1$), metacentric (m; $1 < r < 1.7$), submetacentric (sm; $1.7 \leq r < 3.0$), subtelocentric (st; $3.0 \leq r < 7.0$), telocentric (t; $7.0 \leq r < 39$), and telocentric (T; $39 \leq r \leq \infty$). The terminology of STEBBINS (1938, 1971) has been used for the apparent size of chromosomes and general karyotype asymmetry. Coefficients A_1 of intrachromosomal asymmetry ($A_1 = 1 - \sum(b_i/B_i)/n$; where b_i is the average length for short arms in every homologous chromosome pair and B_i is the average length for long arms in every homologous chromosome pair) and A_2 of interchromosomal asymmetry ($A_2 = s/\bar{x}$, with s being the standard deviation and \bar{x} the mean of chromosome length) proposed by ROMERO (1986) have also been used for a more accurate estimation of karyotype asymmetry. If two chromosomes, assumed homologues, had to be included in different categories, an intermediate category for the pair was considered (e.g., m-sm for pairs comprising a metacentric chromosome and a submetacentric chromosome).

Voucher specimens are conserved in the Herbarium of the Department of Botany, Faculty of Biology, University of Seville (SEV; see Appendix).

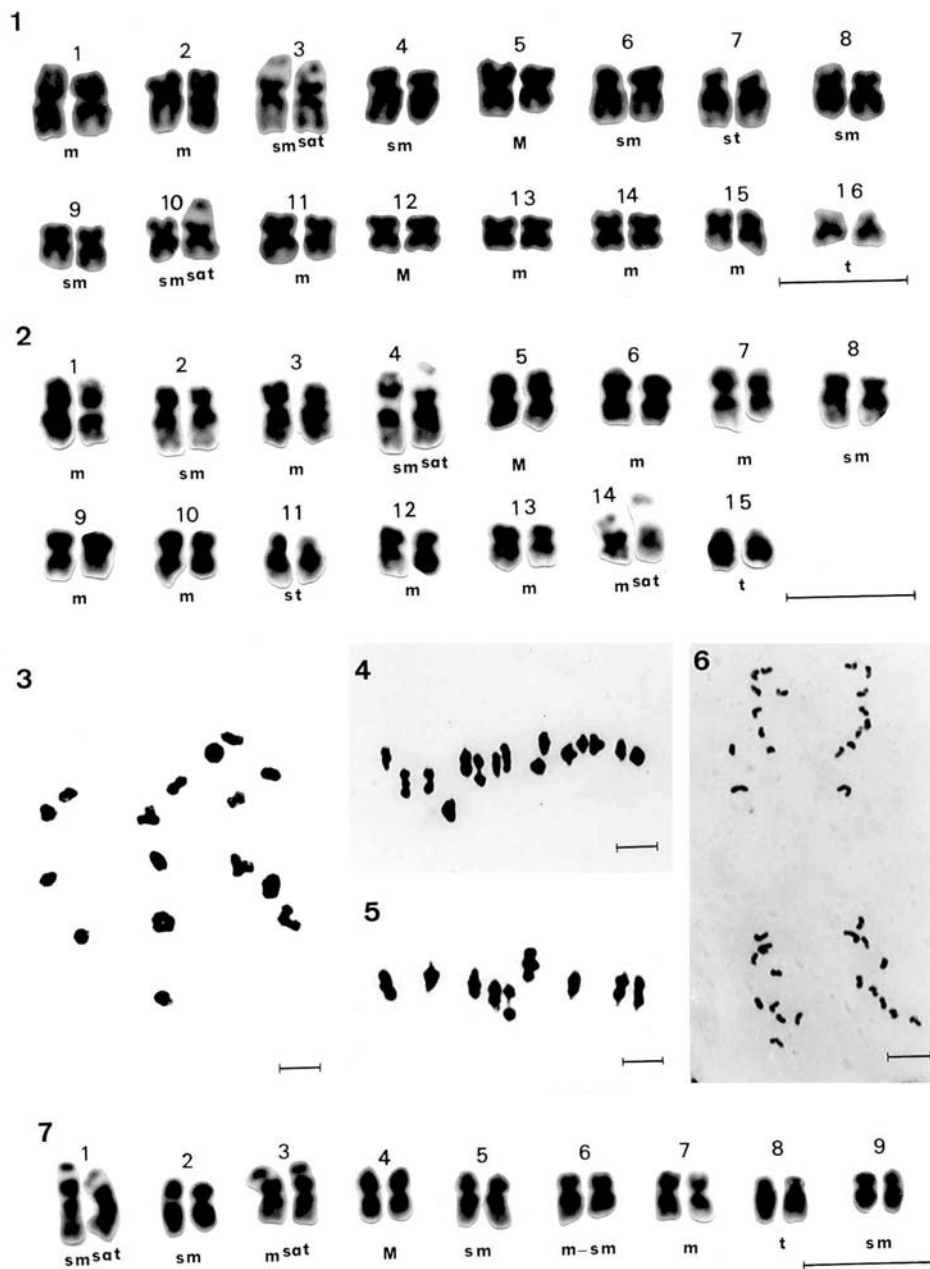
RESULTS

Chromosome numbers

The chromosome numbers of the taxa studied are $n=16$, $2n=32$ for *S. oleraceus*, $n=15$, $2n=30$ for *S. microcephalus* and $n=9$, $2n=18$ for both subspecies of *S. asper* (Figs. 1–7; see Appendix). Meiotic behaviour of chromosomes has always been observed to be regular in diakinesis and metaphase I (Figs. 3–5) for the four taxa, and also in anaphase I for *S. asper* subsp. *glaucescens* and anaphase II for *S. micorcephalus* and *S. asper* subsp. *asper* (Fig. 6).

Chromosome morphology and idiograms

In the observations presented here (Table 1; Figs. 1, 2 and 7), the chromosome morphology was found to vary between the metacentric (M and m) and telocentric (t) classes. The categories of metacentric chromosomes (M and m) are the most common in *Sonchus oleraceus* (50%–56% of all chromosomes) and *S. microcephalus* (67%). In *S. asper* subsp.



Figs. 1–7. 1 – Karyogram of *S. oleraceus* (SEV 126485), 2n=32. 2 – Karyogram of *S. microcephalus* (SEV 126504), 2n=30. 3 – Diakinesis of *S. oleraceus* (SEV 126457), n=16. 4 – Metaphase I of *S. microcephalus* (SEV 126491), n=15. 5 – Metaphase I of *S. asper* subsp. *glaucescens* (SEV 126466), n=9. 6 – Anaphase II of *S. asper* subsp. *asper* (SEV 126472), n=9. 7 – Karyogram of *S. asper* subsp. *asper* (SEV 126488), 2n=18. Scale bar = 5 mm.

glaucescens, the metacentric (M and m) categories are both present at 44%; meanwhile the submetacentric (sm) class is the most common in *S. asper* subsp. *asper* (56%). A pair of telocentric chromosomes (t) was observed in all taxa, and usually two subtelocentric chromosomes (st) were also found in *S. oleraceus* and *S. microcephalus*. Within one taxon, there is some degree of interpopulation variation in arm ratio, which is reflected in the different number of pairs included in M, m and sm categories (Table 1). Two satellite pairs of chromosomes were observed in each of the species presented here, except *S. asper* subsp. *glaucescens*, bearing one satellite pair exclusively (Table 1).

Size of the chromosomes

The apparent chromosome length detected varies from about 0.73–2.69 μm , corresponding to small and medium small categories (STEBBINS 1938). Only small chromosomes were observed in *S. asper*, except a single pair of medium small chromosomes in the karyotype of *S. asper* subsp. *asper* from Calasparra and in the karyotype of *S. asper* subsp. *glaucescens* from El Burgo-Álora. In *S. oleraceus* several karyotypes have been found to comprise small chromosomes exclusively (e.g., the plants from Sancti Petri, Bruguera, Sierra Nevada and Baños de Río Tobía-Mahave), but some medium small chromosomes (2 to 10 chromosomes of 32) are present in the karyotype studied. Likewise, karyotypes of *S. microcephalus* are commonly composed of small chromosomes (e.g., the plants from Sancti Petri and Calahonda) but in the karyotype of plants from El Gandul 14 medium small chromosomes have been detected.

Karyotype asymmetry

Generally, the karyotype asymmetry in *S. oleraceus* and *S. microcephalus* corresponds to the 2B category. In *S. asper*, it has been found to be 2A in the plants of *S. asper* subsp. *asper* and 2A–2B in *S. asper* subsp. *glaucescens* (Table 1).

The A_1 index of intrachromosomal variability is 0.35 or 0.37 in the three populations of *S. oleraceus* studied (Table 1). A very similar value, $A_1 = 0.35$, is shown in the plants of *S. microcephalus* from El Gandul. In *S. asper*, the index ranges from 0.40 to 0.43.

The interchromosomal variability index shows considerable variation in *S. oleraceus*, ranging from $A_2 = 0.21$ in the plants from Cullera – Favareta and $A_2 = 0.34$ in the plants from Sevilla (Table 1). The single karyotype of *S. microcephalus* studied shows $A_2 = 0.26$. In the karyotypes of *S. asper*, the A_2 index ranges from 0.17 to 0.23, differences not having been detected between subspecies.

Asymmetry indices for the remaining Iberian taxa, estimated from karyotypes presented in previous papers (MEJÍAS 1988, MEJÍAS & VALDÉS 1988), are also given in Table 1.

DISCUSSION

Sonchus oleraceus, *S. microcephalus*, and *S. asper*

The chromosome numbers presented here for these three species agree with most previous counts (Table 2). Nevertheless, MARCHAL (1920, sec. STEBBINS et al. 1953) indicated $2n=16$ for plants of *S. oleraceus*, and FERNANDES & QUEIRÓS (1971) reported the number $2n=32$ for

Table 1. Chromosome number, idiograms, karyotype asymmetry (A , A_1 and A_2 coefficients) and chromosome apparent lengths for the Iberian taxa of *Sonchus*, according to observations here presented and data from MEJÍAS (1988) and MEJÍAS & VALDÉS (1988).

Taxon and locality	Idiograms	A	A_1	A_2	Mean chromosome length range (μm)
Sect. <i>Sonchus</i> L.					
<i>S. oleraceus</i> L., n=16, 2n=32					
Bruguera	16m + 2m ^{sat} + 8sm + 2sm ^{sat} + 2st + 2t	2B	0.37	0.25	0.77–2.07
Sevilla	4M + 12m + 8sm + 4sm ^{sat} + 2st + 2t	2B	0.37	0.32	0.90–2.52
Cullera – Favareta	2M + 14m + 2m ^{sat} + 8sm + 2sm ^{sat} + 2sm-st + 2t	2A-2B	0.35	0.21	1.31–2.60
<i>S. microcephalus</i> MEJÍAS, n=15, 2n=30					
El Gandul	2M + 16m + 2m ^{sat} + 4sm + 2sm ^{sat} + 2st + 2t	2B	0.35	0.22	1.22–2.56
<i>S. tenerrimus</i> L., n=7, 2n=14 (from MEJÍAS 1988)					
Cabo de Gata	8m + 2m ^{sat} + 2sm + 2sm ^{sat}	2A	0.31	0.21	1.81–3.11
El Gandul	6m + 2m ^{sat} + 2m-sm + 2sm + 2sm ^{sat}	1A-2A	0.33	0.22	1.91–3.00
Olvera	8m + 2m ^{sat} + 2sm + 2sm ^{sat}	2A	0.29	0.20	2.12–3.50
Sect. <i>Asperi</i> BOULOS					
<i>S. asper</i> (L.) HILL subsp. <i>asper</i> , n=9, 2n=18					
Monasterio de Hermo	2M + 2m + 2m ^{sat} + 8sm + 2sm ^{sat} + 2t	2A	0.42	0.17	0.80–1.32
Cortelazor	2M + 2m + 2m ^{sat} + 8sm + 2sm ^{sat} + 2t	2A	0.43	0.19	0.92–1.65
Calasparra	2M + 2m + 2m ^{sat} + 2m-sm + 6sm + 2sm ^{sat} + 2t	2A	0.40	0.17	1.27–2.21
<i>S. asper</i> subsp. <i>glaucescens</i> (JORD.) BALL, n=9, 2n=18					
El Burgo – Alora	2M + 6m + 6sm + 2sm ^{sat} + 2t	2A-2B	0.41	0.23	1.06–2.16
Venta del Obispo	8m + 6sm + 2sm ^{sat} + 2t	2A-2B	0.43	0.18	0.93–1.86
Sect. <i>Maritimi</i> (KIRP.) BOULOS (from MEJÍAS & VALDÉS 1988)					
<i>S. maritimus</i> L., n=9, 2n=18					
Elche	6m + 2m-sm + 6sm + 2st ^{sat} + 2t	2A	0.47	0.17	1.72–2.57
Palma de Mallorca	6m + 2m-sm + 6sm + 2st ^{sat} + 2t	2A	0.46	0.14	1.92–3.21
Alcázar de San Juan	10m + 4sm + 2sm ^{sat} + 2t	2A	0.38	0.16	2.14–3.64
Aranjuez	10m + 4sm + 2sm ^{sat} + 2t	2A	0.34	0.10	2.34–3.13
<i>S. aquatilis</i> POURR., n=9, 2n=18					
San Aniol	12m + 2m ^{sat} + 2m-sm + 2sm ^{sat}	1A	0.25	0.12	1.61–2.68
Riofrío	12m + 2m ^{sat} + 2m-sm + 2sm ^{sat}	1A	0.22	0.12	2.36–3.64
<i>S. crassifolius</i> POURR., n=9, 2n=18					
Albacete-Balazote	12m + 2m-sm + 2sm + 2sm-st ^{sat}	2A	0.36	0.10	2.57–3.64
Alcázar de San Juan	10m + 2m-sm + 4sm + 2st ^{sat}	2A	0.34	0.14	2.05–3.08
<i>S. ×novocastellanus</i> CIRUJANO, n=9, 2n=18					
Alcázar de San Juan	8m + 7sm + 2sm-st ^{sat} + 1t	2A	0.43	0.16	1.72–3.43
Sect. <i>Pustulati</i> BOULOS (from MEJÍAS 1988)					
<i>S. pustulatus</i> WILLK., n=9, 2n=18					
Almería	10m + 2m ^{sat} + 4sm + 4sm ^{sat}	2A	0.32	0.14	1.95–2.97

S. asper subsp. *glaucescens*, but such divergences may be considered erroneous because they have not been confirmed subsequently. Of considerable interest is the record of *S. microcephalus* in Israel, from where its chromosome number has been published (DÍAZ LIFANTE et al. 1992: 232). This taxon was described in southern Spain (MEJÍAS 1990) but its actual range may be considerably wider, though probably restricted to the Mediterranean Basin. This is a rather unknown and poorly cited species, very similar to *S. tenerrimus* in fruit and leaf morphology, but showing self-compatible capitula (MEJÍAS 1992). In voucher specimens, fruits often become deformed and very flat, so that they may be confused with some *S. oleraceus* morphological forms that show similar pinnatifidous leaves. The two taxa commonly co-exist in low-altitude areas of southern Spain, but the regular presence of bivalents and the behavior of chromosomes during meiosis indicate the absence of hybridization, and an effective reproductive isolation, which has probably been provided by the autogamous character of both taxa.

As far as we know, the present studies are the first indication of chromosome morphology for these taxa. It can be deduced from Table 1 and Figs. 1, 2, and 7 that karyotypes consist mainly of small chromosomes with similar chromosome morphology and asymmetry indices, although the asymmetry type is mainly 2B in *S. oleraceus* and *S. microcephalus*, and 2A or 2A–2B in *S. asper*. Karyotypes of both subspecies in *S. asper* are very similar, the presence of satellites being the most notable difference. We have detected two satellite pairs in *S. asper* subsp. *asper* and a single pair in *S. asper* subsp. *glaucescens* (Table 1), but BOULOS (1973) indicated the opposite situation. Perhaps the number of satellite chromosomes is variable among populations.

STEBBINS et al. (1953: 419) proposed an amphidiploid origin for *S. oleraceus* ($n=16$, $2n=32$) through natural crossing of *S. tenerrimus* ($n=7$, $2n=14$) and *S. asper* ($n=9$, $2n=18$). Certainly, the morphological characters of *S. oleraceus* are intermediate between the two putative parents. This hypothesis is supported by meiotic observations of regular bivalent pairing and the high fertility observed in *S. oleraceus* (MEJÍAS 1992), although it has been reported that some autopolyploids show diploidization mechanisms (LEVIN 2002). HSIEH et al. (1972) indicated meiotic multivalent formation and partial sterility of North American plants, supporting an autotetraploid origin of this taxon. However, taxonomic identity of the studied material remains unclear, since several chromosome numbers were indicated and the authors suspected the influence of hybridization with *S. arvensis* in the samples of *S. oleraceus*. Phylogenetic molecular analysis indicates that *S. asper* and *S. oleraceus* are close taxa (KIM et al. 1996b), but unfortunately *S. tenerrimus* was not included in the analysis; its inclusion would have been helpful in elucidating the origin of *S. oleraceus*. In any case, RIESEBERG (1997) considered that the use of molecular markers can generate ambiguous results for identifying hybrid taxa. The $2n=30$ chromosome number in *S. microcephalus* seems to have originated from *S. oleraceus* through a dysploid process. The taxon shows very similar fruits and leaves to those of *S. tenerrimus*; in consequence, it can be proposed that the loss or silencing of some genetic information from *S. asper* is involved in the origin of *S. microcephalus*, reinforcing the hypothesis of an amphidiploid origin for *S. oleraceus*.

A detailed karyological review of Iberian *Sonchus*

The genus *Sonchus* is represented in the Iberian Peninsula by a set of nine taxa and a natural hybrid, all of them included in the subgenus *Sonchus*. In Table 1, it can be seen that the somatic chromosome number diversity includes $2n=14$, 18, 30, and 32, with the basic numbers $x=7$, 9, 15 and 16. The number $x=8$, exclusive to the genus for the Macaronesian and Moroccan endemic *S. bourgeauii* SCH.BIP., is the one not represented. The numbers $2n=36$ ($4x$) and $2n=54$ ($6x$) are also lacking in the area.

Karyotypes in Iberian *Sonchus* species comprise medium-small and small chromosomes, never exceeding $3.6\ \mu\text{m}$, which makes the study of chromosome morphology difficult. The smallest chromosomes are found in *S. oleraceus*, *S. microcephalus*, and *S. asper*, i.e. annual or short-life-cycle invasive plants. It seems that this pattern is quite common (BABCOCK & JENKINS 1943, STEBBINS 1950, DÍAZ LIFANTE 1996). The ecological and evolutionary significance of the relationship between life cycle and chromosome size probably lies in the effect of DNA amount on the duration of the cell cycle and determinate developmental processes (STEBBINS 1966, BENNETT 1972, THOMPSON 1990).

The most common asymmetry type is 2A, but *S. oleraceus* and *S. microcephalus* show 2B asymmetry, and *S. aquatilis* shows 1A. The A_1 and A_2 indexes range from 0.22 to 0.47 and 0.10 to 0.32 respectively (Table 1). The scatter diagram of A_1 and A_2 (Fig. 8) shows some differences in karyotype asymmetry between populations for a single taxa. This can be partially explained by an unavoidable variation in the premitotic treatment and staining technique; nevertheless, there is a general tendency for cluster formation among taxa, a reflection of clear differences in karyotype organization, with the remarkable exception of *S. maritimus* and *S. crassifolius*. The former is mainly distributed throughout the Mediterranean region, whereas *S. crassifolius* is endemic to the central Iberian Peninsula. They have been reported to hybridize and to give origin to *S. \times novocastellanus* in the humid salt areas of central Spain where they coexist (CIRUJANO 1983, MEJÍAS 1987). The hybrid shows karyograms that clearly denote its origin (MEJÍAS & VALDÉS 1988). Notably, plants of *S. maritimus* from central Spain (Table 1: Aranjuez, Alcázar de San Juan) show indices quite similar to those of *S. crassifolius* (possibly due to introgressive hybridization) and clearly distinct from plants of other areas (Table 1: Elche, Palma de Mallorca). *S. aquatilis* is the single taxon clearly detached in Fig. 8 – in particular, from the remaining representatives of section *Maritimi* (KIRP.) BOULOS. This supports the distinction of *S. aquatilis* and *S. maritimus* at species level (MEJÍAS & VALDÉS 1988), taxa often considered as subspecies. In contrast, no distance separates *S. asper* subsp. *asper* and *S. asper* subsp. *glaucescens*. Quite notable is the difference between the A_2 indices of the three karyotypes of *S. oleraceus* analyzed. No clear general evolutionary trends in karyotype asymmetry have been found among sections. It is, however, remarkable that taxa behaving as weeds, mainly *S. oleraceus* (and its relative *S. microcephalus*), but also *S. asper* and *S. tenerrimus* in the Mediterranean region, show higher intrachromosomal asymmetry.

Chromosome number evolution in *Sonchus*

Table 2 gives the chromosome numbers and geographical distribution of 23 species, 4 subspecies, and 3 natural hybrids recognized in *Sonchus* subgenus *Sonchus*, according to

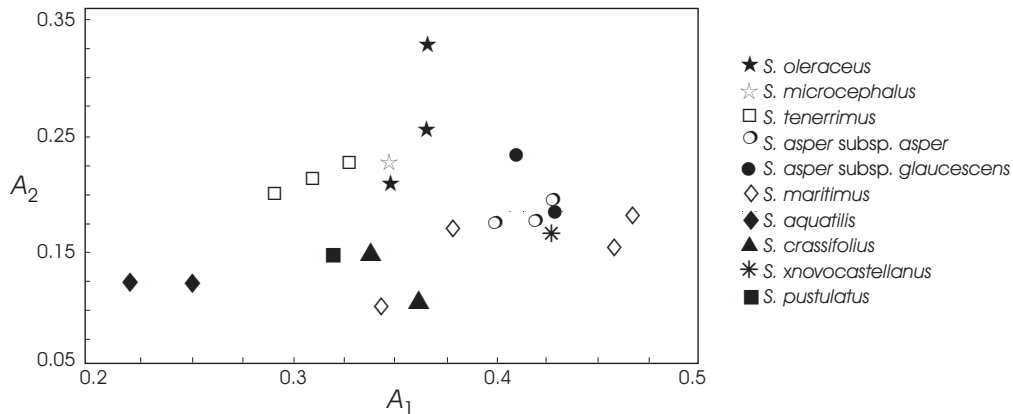


Fig. 8. Scatter diagram showing distribution of A_1 and A_2 indices in the Iberian taxa of *Sonchus*.

BOULOS (1973, 1976), MEJÍAS & VALDÉS (1988), and MEJÍAS (1990). Chromosome numbers have been reported for 19 non-hybrid taxa, and $2n=14$, 16, 18, 30, 32, 36, and 54 have been indicated. The number $n=9$, $2n=18$ is the most common, found in 10 taxa. Taxa showing $2n=36$ (three taxa) and $2n=54$ (two taxa) seem to be polyploids with basic number $x=9$. Two related dysploids with $n=8$, $2n=16$ (*S. bourgeauii*) and $n=7$, $2n=14$ (*S. tenerrimus*), and the polyploids *S. oleraceus* ($n=16$, $2n=32$) and *S. microcephalus* ($n=15$, $2n=30$) with basic number different from $x=9$, complete the karyological diversity of the group. For the remaining taxonomic groups of *Sonchus* s.l., the number $2n=18$ has been reported for three representatives of the subgenus *Origosonchus* (ROUX & BOULOS 1972: 308), 16 representatives of the subgenus *Dendrosonchus* (ROUX & BOULOS 1972: 308, ARDÉVOL GONZÁLEZ et al. 1993: 17–18), three species of the genus *Taeckholmia* (BOULOS 1967), and the single species of the genus *Babcockia* (BOULOS 1965: 66, ARDÉVOL GONZÁLEZ et al. 1993: 13). In addition, the genus *Embergeria* comprises two polyploid species with $2n=36$ (ROUX & BOULOS 1972: 308–309).

According to the hypotheses of BOULOS (1974b) and ALDRIDGE (1979) about the evolution of the genus *Sonchus* s.l., the primitive representatives of the group, subgenus *Origosonchus* or subg. *Dendrosonchus*, show $n=9$, $2n=18$. The same numbers have been detected in *Sonchus pustulatus* and some other representatives of subgenus *Sonchus* section *Pustulati* BOULOS (unpubl. data), a group of frutescent species claimed to retain primitive characters (BOULOS 1973). However, phylogenetic molecular analysis of the subtribe *Sonchinae* (KIM et al. 1996a, b, 1999b) has clearly shown that both the genus *Sonchus* and the subgenus *Sonchus* are polyphyletic. In any case, relationships inferred from that analysis also support the consideration of $n=9$ as the ancestral chromosome number for the groups including *Sonchus* representatives. This number prevails as the most common, and the basic one for most polyploids in the subtribe (see BEUZENBERG & HAIR 1984, SPOONER et al. 1987, ARDÉVOL GONZÁLEZ et al. 1993, MEJÍAS 1993, SANG et al. 1994), so it must also be considered the base number for the *Sonchinae*.

Table 2. Chromosome numbers and geographical distribution of *Sonchus* subgenus *Sonchus*. Distribution areas have been taken from BOULOS 1973. Authors: 1 – BARBER 1941: 376. 2 – BIR & SIDHU 1974: 376. 3 – BJORKQUIST et al. 1969: 277. 4 – BRAND et al. 1979: 397. 5 – CARDONA 1974: 216. 6 – CASTROVIEJO 1982: 259. 7 – CHATERJEE & SHARMA 1969: 581. 8 – CHING-I-PENG & CHIENG-CHANG HSU 1977: 564. 9 – COOPER & MAHONY 1935: 846. 10 – DAHLGREN et al. 1971: 251. 11 – DELAY 1968: 20. 12 – DÍAZ LIFANTE et al. 1992: 232. 13 – EDMONDS et al. 1974: 160. 14 – FERNANDES & FRANCA 1975: 87. 15 – FERNANDES & QUEIRÓS 1971: 81–82. 16 – FERNÁNDEZ CASAS & FERNÁNDEZ PIQUERAS 1977: 201. 17 – FERNÁNDEZ CASAS & MACHÍN SANTAMARÍA 1977: 206. 18 – FERNÁNDEZ CASAS et al. 1979: 402. 19 – GADELLA & KLIPHUIS 1967: 12. 20 – GADELLA & KLIPHUIS 1973: 307. 21 – GALLEGO 1985: 312. 22 – GILL 1978: 230. 23 – HEISER & WHITAKER 1948: 185. 24 – HENIN in BOULOS 1959. 25 – HENIN in BOULOS 1960: 408. 26 – HENIN in ROUX & BOULOS 1972: 307. 27 – HSIEH et al. 1972: 792. 28 – KIRSCHNER et al. 1982: 574. 29 – KLIPHUIS & WIEFFERING 1979: 400. 30 – KUZMANOV & GEORGIEVA 1976: 500. 31 – KUZMANOV & KOZUHAROV 1970: 266. 32 – LABADIE 1976: 639. 33 – LARSEN 1960: 32. 34 – LOON 1980: 720. 35 – LÖVE & KJELLQUIST 1974: 194. 36 – LÖVE & LÖVE 1956: 212. 37 – LUQUE 1983: 129. 38 – MARCHANT 1970: 102. 39 – MEHRA et al. 1965: 45. 40 – MEJÍAS 1988: 349. 41 – MEJÍAS 1990: 169. 42 – MEJÍAS & VALDÉS 1988: 63. 43 – MESQUITA 1953: 133. 44 – MITRA & DATTA 1967: 461. 45 – MULLIGAN 1957: 781. 46 – NORDENSTAM 1972: 394. 47 – PACKER 1964: 483. 48 – PAJARÓN SOTOMAYOR 1982: 250. 49 – PAVONE et al. 1981: 279. 50 – PÓLYA 1949: 134. 51 – QUEIRÓS 1973: 311. 52 – RATTER & MILNE 1973: 434. 53 – ROUX & BOULOS 1970: 102. 54 – ROUX & BOULOS 1972: 307–308. 55 – RUÍZ DE CALVIJO 1990: 429. 56 – RUTLAND 1941: 211. 57 – SCHAACK et al. 1974: 623. 58 – SILVESTRE 1984: 300. 59 – STEBBINS 1953: 427. 60 – STEBBINS et al. 1953: 426–427. 61 – STRID & FRANZÉN 1981: 842. 62 – TALAVERA et al. 1984: 276. 63 – TOMB et al. 1978: 719. 64 – TURNER et al. 1961: 222. 65 – VALDÉS BERMEJO & CASTROVIEJO 1977: 332. 66 – WALTER & KUTA 1971: 103–109. 67 – WULF 1937: 267.

Taxa	Geographical distribution	n	2n	Authors
Sect. <i>Sonchus</i>				
<i>S. oleraceus</i> L.	Cosmopolite	16	32	8, 9, 10, 13, 14, 17, 21, 23, 27, 29, 31, 33, 34, 39, 43, 45, 46, 48, 50, 54, 56, 60, 62, 64, 66
<i>S. microcephalus</i> MEJÍAS	Southern Iberian Peninsula, Israel	15	30	12, 43
<i>S. tenerrimus</i> L.	Mediterranean Region, Macaronesia, Middle East; introduced in other Mediterranean areas	7	14	3, 5, 6, 21, 40, 46, 49, 54, 55, 60
<i>S. bourgeauii</i> SCH.BIP.	Canary Islands, Morocco	8		25
Sect. <i>Asperi</i> BOULOS				
<i>S. asper</i> (L.) HILL subsp. <i>asper</i>	Cosmopolitan	9	18	4, 7, 18, 22, 23, 28, 30, 32, 36, 39, 45, 50, 56, 61, 62, 66
<i>S. asper</i> subsp. <i>glaucescens</i> JORD. (BALL)	Mediterranean Region	9	18	15, 26, 35, 62
<i>S. littoralis</i> (KIRK) ALLAN	New Zealand			
<i>S. mauritanicus</i> BOISS. et REUT.	Algeria, Tunisia			
<i>S. macrocarpus</i> BOULOS et C. JEFFREY	Egypt		36	24
<i>S. gigas</i> BOULOS ex HUMBERT	Subsaharan Africa		36	38, 52
<i>S. hydrophilus</i> BOULOS	New Guinea, Australia, New Zealand			

Taxa	Geographical distribution	n	2n	Authors
Sect. <i>Maritimi</i> (KIRP.) BOULOS				
<i>S. maritimus</i> L.	Mediterranean Region, Middle East, Southern Africa	9	18	11, 15, 32, 42, 51, 54, 58
<i>S. aquatilis</i> POURR.	Western Mediterranean Region	9	18	17, 35, 37, 42, 65
<i>S. palustris</i> L. subsp. <i>palustris</i>	Non-Mediterranean Europe		18	25, 59, 67
<i>S. palustris</i> subsp. <i>sosnowskyi</i> (SCHCIAN) BOULOS	Caucasus			
<i>S. crassifolius</i> POURR.	Iberian Peninsula	9	18	16, 42
Sect. <i>Arvenses</i> (KIRP.) BOULOS				
<i>S. arvensis</i> L. subsp. <i>arvensis</i>	Non-Mediterranean Europe, North America		54	13, 19, 20, 45
<i>S. arvensis</i> subsp. <i>uliginosus</i> (M. BIEB.) BÉG.	Non-Mediterranean Europe, North America	18	36	2, 46, 48, 58
<i>S. brachyotus</i> DC.	Eastern and Central Asia		18	53
<i>S. wightianus</i> DC. subsp. <i>wightianus</i>	Eastern and Southern Asia	9		44
<i>S. wightianus</i> subsp. <i>wallichianus</i> (DC.) BOULOS	<i>Eastern and Southern Asia</i>			
<i>S. malaianus</i> MIQ.	Indonesia		54	60
Sect. <i>Pustulati</i> BOULOS				
<i>S. pustulatus</i> WILLK.	Iberian Peninsula, Morocco, Algeria	9	18	40, 42, 60, 62
<i>S. fragilis</i> BALL	Morocco			
<i>S. briquetianus</i> GAND.	Morocco			
<i>S. masguindalii</i> PAU et FONT QUER	Morocco			
Sect. <i>Tuberiferi</i> BOULOS				
<i>S. tuberiferi</i> SVENT.	Tenerife (Canary Islands)		18	54
Natural hybrids				
<i>S. × novocastellanus</i> CIRUJANO (<i>S. crassifolius</i> × <i>S. maritimus</i>)	Iberian Peninsula	9	18	42
<i>S. arvensis</i> subsp. <i>arvensis</i> ×	Canada		45	45
<i>S. arvensis</i> subsp. <i>uliginosus</i>				
<i>S. asper</i> × <i>S. oleraceus</i>	North America?		25	1

In the evolutionary process of the *Sonchus* groups and the subtribe *Sonchinae* as a whole, the ancestral base number has generally been maintained. Dysploidy is rare, being restricted to the series *S. bourgeaii*-*S. tenerrimus* and *S. oleraceus*-*S. microcephalus* within the present genus *Sonchus* (subgenus *Sonchus*), and also exemplified in *Reichardia* (GALLEGO 1980, ARDÉVOL GONZÁLEZ et al. 1993) and *Launaea* (MEJÍAS 1993) within the subtribe. The latter two genera have been considered to be basal groups of the subtribe and not part of their main radiation according to the phylogenetic tree obtained by the use of ITS of nuclear ribosomal DNA (KIM et al. 1996a,b). However, their significance in the *Sonchinae* seems to be

underestimated in that analysis, since 2 out of 54 species of the genus *Launaea* (KILIAN 1997) were tested. By contrast, evolution and adaptative radiation within the considered main group of *Sonchinae*, including part of the subgenus *Sonchus* (section *Tuberiferi* BOULOS, section *Maritimi* (KIRP.) BOULOS and section *Arvenses* (KIRP.) BOULOS), the whole subgenera *Origosonchus* and *Dendrosonchus*, and the genera *Sventenia* FONT QUER, *Babcockia*, *Taeckholmia*, *Lactucosonchus* SVENT., *Kirkianella* ALLAN, *Embergeria*, and the nested genus *Dendroseris*, have taken place without dysploid processes.

Polyploidy is represented in a scattered way within the subtribe. Polyploid representatives in the genus *Sonchus* are restricted to the present subgenus *Sonchus*. Of them, *S. oleraceus* shows a probable amphidiploid origin, probably risen in the Mediterranean Region, where natural distributions of the two putative parents overlap. In turn, it gave origin to *S. microcephalus* through a dysploid process. According to HSIEH et al. (1972), *S. arvensis* can also be considered an amphidiploid on the basis of regular bivalent associations during meiosis, but no hypothesis about the concrete origin has been formulated. The section *Arvenses* is clearly related to the section *Maritimi* morphologically and phylogenetically (KIM et al. 1996b); perhaps this latter section is involved in the origin of *S. arvensis*. There is no evidence for the origin of the remaining polyploids, but according to the observations of BOULOS (1973), *S. macrocarpus* BOULOS et C. JEFFREY and *S. gigas* BOULOS ex HUMBERT are close relatives of *S. asper*, so an autotetraploid origin could be considered.

Biogeographical relationships within the group of the present genus *Sonchus* and its relatives are quite complex, as shown by the evidence of several main diversification centers: (i) for *Sonchus* subgenus *Origosonchus*, sub-Saharan East Africa must be proposed (BOULOS 1974b); (ii) the woody Macaronesian alliance, which includes the subgenus *Dendrosonchus* and genera *Babcockia*, *Sventenia*, *Taeckholmia*, *Lactucosonchus*, and *Prenanthes pendula* SCH.BIP., probably radiated during late Tertiary from Gran Canaria or Tenerife in the Canary Islands (KIM et al. 1996a, 1999a); (iii) the West Mediterranean Region (including areas of western Morocco with Mediterranean-type climate) seems to be the main center of diversification of the groups included in the polyphyletic subgenus *Sonchus*. In the area, 14 out of the 27 taxa that make up the whole subgenus are represented, corresponding to four sections: *Sonchus* sect. *Sonchus*, *S.* sect. *Asperi* BOULOS, *S.* sect. *Maritimi* (KIRP.) BOULOS, and *S.* sect. *Pustulati* BOULOS (see Table 2). Of the remaining two sections, the polyploid *S.* sect. *Arvenses* (KIRP.) BOULOS is clearly derived, and the *S.* sect. *Tuberiferi* BOULOS is a narrow endemic related to the woody Macaronesian alliance; (iv) Australia and/or New Zealand are probably the center of origin of the polyploid genera *Embergeria* and *Kirkianella* (BOULOS 1974b); (v) finally, the genus *Dendroseris* represents a recent rapid adaptative radiation in the Juan Fernández Islands of the south-eastern Pacific, involving polyploidy (SANG et al. 1994). It is noteworthy that dysploidy is exclusively related to West Mediterranean radiation of *Sonchus* subgenus *Sonchus*, and that polyploidy is more common among taxa spreading beyond the first three diversification areas.

It is not possible to formulate any founded hypothesis about the ancestral representatives of the group; it seems evident that the woody Macaronesian *Sonchus* alliance represents a secondary derivation from a single introduction of continental herbaceous perennial ancestors (KIM et al. 1996a, 1999a); but the polyploid genera *Embergeria*, *Dendroseris*, and

Kirkianella are also probably derived. Thus, primitive representatives should be related to *Sonchus* subgenera *Origosonchus* and/or *Sonchus*. The analysis of phylogenetic relations of the two groups with the supposed basal genera *Reichardia* and *Launaea* could help to clarify the matter.

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APPENDIX

Origin of the material studied (voucher specimens) and chromosomic numbers

Sonchus oleraceus L.: CÁDIZ: Sancti Petri, 36°17'N 6°15'W (29.I.1985 MEJÍAS SEV 126486) – n=16, 2n=32. Idem (24.IV.1985 MEJÍAS SEV 126479) – n=16. CORUÑA: Cementerio de Noya, 43°02'N 9°01'E (8.VIII.1987 BARRERA & MEJÍAS SEV 126474) – n=16. GERONA: Bruguera, 41°52'N 2°54'E (8.VIII.1985 (MEJÍAS, POLO & ROMERO SEV 126459) – 2n=32. GRANADA: Sierra Nevada, Barranco de las Víboras, 37°08'N 3°27'W (25.VII.1984 MEJÍAS SEV 126482) – 2n=32. HUELVA: Mazagón, Punta del Loro, 37°05'N 6°44'W (13.I.1985 MEJÍAS SEV 126465) – 2n=32. HUESCA: Lanavé, 42°25'N 0°24'W (13.VIII.1985 MEJÍAS, POLO & ROMERO SEV 126457) – n=16. LUGO: Rubín, 42°50'N 7°22'W (26.V.1985 LUQUE, POLO & VALDÉS SEV 126484) – 2n=32. MADRID: Aranjuez, Mar de Ontígola 40°00'N 3°35'W (16.V.1985 MEJÍAS & POLO SEV 126481) – 2n=32. MÁLAGA: Entre El Burgo y Alora, 36°52'N 4°45'W (28.V.1985 GARCÍA & MEJÍAS SEV 126464) – n=16. MURCIA: Calasparra, 38°16'N 1°40'W (5.VI.1985 GARCÍA & MEJÍAS SEV 126469) – 2n=32. LA RIOJA: Entre Baños de Río Tobía y Mahave, río Najerilla, 42°23'N 2°45'W (19.IX.1985 GARCÍA & MEJÍAS SEV 126449) – 2n=32. SEVILLA: Cruce de las Cabezas, 36°58'N 5°53'W (28.VI.1984 MEJÍAS SEV 126480) – 2n=32. Sevilla, 37°46'N 5°55'W (IV.1985 MEJÍAS SEV 126485) – 2n=32. VALENCIA: Entre Cullera y Favareta, 39°08'N 0°16'W (1.VI.1985 GARCÍA & MEJÍAS SEV 126470) – 2n=32.

Sonchus microcephalus MEJÍAS: CÁDIZ: Sancti Petri, 36°17'N 6°15'W (24.IV.1985 MEJÍAS SEV 126494, SEV 126495) – n=15. Idem (VI.1985 MEJÍAS SEV 126491, SEV 126492). Idem (18.IV.1985 MEJÍAS SEV 126496, SEV 126497, SEV 126498, SEV 126499) – 2n=30. Idem (1.IV.1987 MEJÍAS & MONTERO SEV 126508, SEV 126509) – 2n=30. GRANADA: Calahonda, 36°43'N 3°25'W (14.III.1985 MEJÍAS & POLO SEV 126500, SEV 126501) – n=15. Idem (21.IV.1987 LÓPEZ & MEJÍAS SEV 126502, SEV 126503) – 2n=30. SEVILLA: El Gandul, 37°20'N 5°47'W (26.IV.1985 LÓPEZ & MEJÍAS SEV 126504, SEV 126505) – 2n=30. Villanueva del Ariscal, 37°23'N 6°08'W (4.IV.1985 MEJÍAS & VALDÉS SEV 126506) – n=15.

Sonchus asper (L.) HILL subsp. *asper*: ASTURIAS: Subida a Monasterio de Hermo, 42°57'N 6°32'W (14.VIII.1987 BARRERA & MEJÍAS SEV 126475) – 2n=18. CÁDIZ: Sacti Petri, 36°17'N 6°15'W (24.IV.1985 MEJÍAS SEV 126472) – n=9. Villaluenga del Rosario, 36°40'N 5°22'W (28.VI.1984 MEJÍAS SEV 126478) – 2n=18. HUELVA: Cortelazor, 37°55'N 6°38'W (12.VII.1984 MEJÍAS SEV 126477) – 2n=18. Hinojos, 37°19'N 6°22'W (3.II.1988 ARROYO & MEJÍAS SEV 126476) – 2n=18. HUESCA: Lanavé, 42°25'N 0°24'W (13.VII.1985 MEJÍAS, POLO & ROMERO SEV 126453) – n=9. MÁLAGA: Montecorto, 36°49'N 5°17'W (29.VI.1984 MEJÍAS SEV 126487) – 2n=18. MURCIA: Calasparra, 38°16'N 1°40'W (5.VI.1985 GARCÍA & MEJÍAS SEV 126488) – 2n=18. LA RIOJA: Entre Baños de Río Tobía y Mahave, río Najerilla, 42°23'N 2°45'W (19.IX.1985 GARCÍA & MEJÍAS SEV 126447) – 2n=18.

Sonchus asper subsp. *glaucescens* (JORD.) BALL: ALBACETE: Bienservida, 38°31'N 2°37'W (18.VII.1985 ARROYO & MEJÍAS SEV 126463) – 2n=18. ÁVILA: Venta del Obispo, 40°23'N 5°01'W (17.IX.1985 GARCÍA & MEJÍAS SEV 126451) – 2n=18. MÁLAGA: Entre El Burgo y Álora, 36°52'N 4°45'W (28.V.1985 GARCÍA & MEJÍAS SEV 126466) – n=9, 2n=18.

