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Chromosome numbers and meiotic studies in species of *Senecio* (Asteraceae) from Argentina

MARIANA G. LÓPEZ[1,2,3]*, ARTURO F. WULFF[3,4], LIDIA POGGIO[2,3,4] and CECILIA C. XIFREDA[1,5]

[1]*CIC-PBA and* [2]*CIGEN, Instituto Fitotécnico de Santa Catalina, Garibaldi 3310 (B1836AML) Lavallol, Argentina*
[3]*Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes y Costanera Norte (C1428EHA), Buenos Aires, Argentina*
[4]*CONICET and* [5]*LEBA, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n (1900), La Plata, Argentina*

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Meiotic chromosome counts, chromosomal behaviour and meiotic configurations of ten taxa of *Senecio* from Argentina were examined. Most counts are original: *S. crepidifolius* DC., *S. francisci* Phil. and *S. octolepis* Griseb. var. *saltensis* (Hicken) Cabrera & Zardini have $2n = 40$, and *S. chrysolepis* Phil., $2n = 80 + 8B$. We confirmed previous reports for *S. deferens* Griseb. ($2n = 40 + 4B$), *S. filaginoides* DC. var. *filaginoides* ($2n = 40$), *S. hieronymi* Griseb. ($2n = 40 + 7B$), *S. pampeanus* Cabrera ($2n = 40$) and *S. rudbeckiifolius* Meyen & Walp. ($2n = 40 + 7B$). In *S. bracteolatus* Hook. & Arn. var. *bracteolatus*, we found a new number ($2n = 40$) that differs from the one cited previously. In four species, numerical polymorphisms for B-chromosomes were observed. Several of the analysed species presented secondary bivalent association. This phenomenon, together with other evidence, supports $x = 5$ as the basic chromosome number. The number of chiasmata and their positions were also surveyed, with the finding that open bivalents were the most frequent meiotic figures and terminal chiasmata the preferential position. These features are related to recombination rate, and the success and persistence of these polyploids. We discuss some systematic and evolutionary aspects in the light of cytogenetic data and conclude that polyploidy is the major force modelling the chromosome evolution within this genus. © 2005 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2005, **148**, 465–474.

ADDITIONAL KEYWORDS: basic chromosome number – bivalent structure – polyploidy – recombination – secondary association – secondary cycle of polyploidy.

INTRODUCTION

Senecio L. (Asteraceae, Senecioneae) is a cosmopolitan genus with over 3000 species growing in a wide range of environments. Argentina possesses a great diversity, with approximately 270 species belonging to four sections (Cabrera & Iharlegui, 1999) and with an important amount of endemism (Zuloaga, Morrone & Rodríguez, 1999). The native taxa are grouped in three of the sections proposed by Cabrera, Freire & Ariza Espinar, 1999), *Senecio* section *Senecio* being the most extensive one with 14 series. It is a very interesting group because most species are toxic due to the presence of alkaloids (Burkart, 1974). Others are used in popular medicine (Cabrera, 1978) and a few are cultivated as ornamentals.

The lack of defined taxonomic boundaries among taxa is one of the major conflicts in this genus (Vincent & Getliffe, 1992). However, since many groups are currently working at different levels in the genus, much progress in taxonomic knowledge is expected soon (Nordenstam, 2003).

At the cytogenetic level, the genus is highly diverse, with haploid numbers varying from $n = 5$ to *c*. 92, with a modal number of $n = 20$. Polyploidy could be

*Corresponding author. E-mail: magalo@bg.fcen.uba.ar

regarded as one of its most distinctive features, being strongly related to its success, persistence and diversification (Lawrence, 1980). We previously proposed the existence of a polyploid complex in *Senecio* that could explain some of the difficulties in the species' identification (López, Wulff & Xifreda, 2002). In this sense, chromosome studies would help to enlarge the understanding of the evolutionary patterns of this group.

With the aim of increasing knowledge of the genus in Argentina, we carried out a meiotic analysis of ten native taxa belonging to four different series of *Senecio* section *Senecio*. This paper is a continuation of a previous contribution about Andean species (López *et al*., 2002). The extant chromosome counts for the Argentine taxa (see Bolkhovskikh *et al*., 1974; Cabrera *et al*., 1999; and the *Index to Plant Chromosome Numbers* for review), including our last publication (loc. cit.), have reached 55 records, which represent only 20% of the species growing in Argentina. Five new records and a discussion about the speciation models and evolution within this group are included here.

MATERIAL AND METHODS

The species with their series, subseries and the studied populations are summarized in Table 1. Voucher specimens are deposited at the SI Herbarium, Instituto de Botánica Darwinion, San Isidro, Argentina.

Meiotic studies were performed on young capitula collected from wild populations and fixed *in situ* in ethanol-chloroform-glacial acetic acid (6 : 3 : 1) for at least 24 h, then transferred into 70% ethanol and stored at 4–5 °C. Immature anthers were squashed in a drop of propionic acid haematoxylin (2%) using ferric citrate as a mordant (Núñez, 1968). The analyses were carried out using a minimum of 20 PMCs (pollen mother cells) in different meiotic stages. Photographs were taken using a Leica DMLB Photomicroscope and a Leitz Camera. Pollen stainability was studied with Alexander's differential staining method (Alexander, 1969).

Mean and standard deviation were calculated for each meiotic figure (open and closed bivalents). The number of excess chiasmata was calculated as: total number of chiasmata per cell minus the gametic chromosome number (Koella, 1993).

RESULTS AND DISCUSSION

Chromosome numbers ($2n$), meiotic configurations, number of open and closed bivalents, number of excess chiasmata per cell and meiotic behaviour of the ten *Senecio* species studied here are summarized in Table 2. Two different chromosome numbers were found: $2n = 40$ for *S. bracteolatus* var. *bracteolatus*, *S. crepidifolius*, *S. deferens*, *S. filaginoides* var. *filaginoides*, *S. francisci*, *S. hieronymi*, *S. octolepis* var. *saltensis*, *S. pampeanus* and *S. rudbeckiifolius*, and one

Table 1. Series, subseries, species, provenance and vouchers of the *Senecio* material studied

Series	Subseries	Species	Provenance and voucher
Corymbosi	Brasilienses	*S. pampeanus* Cabrera	San Luis. Dpto. Ayacucho. *López & Rodríguez 55, 56* (SI)
		S. rudbeckiifolius Meyen & Walp.	Salta. Dpto. Chicoana. *Sanso & Xifreda 168* (SI)
			Tucumán. Dpto. Tafí. *Wulff 916, 917, 918, 940, 942, 952* (SI)
	Simplices	*S. octolepis* Griseb. var. *saltensis* (Hicken) Cabrera & Zardini	Salta. Dpto. Chicoana. *Sanso & Xifreda 169* (SI) Tucumán. Dpto. Tafí. *Wulff 915* (SI)
		S. hieronymi Griseb.	Tucumán. Dpto. Tafí. *Wulff 926, 927* (SI)
			Salta. Dpto. Chicoana. *Sanso & Xifreda 178* (SI)
	Viscosi	*S. crepidifolius* DC.	Salta. Dpto. Santa Victoria. *Sanso & Xifreda 222* (SI)
Otopteri		*S. deferens* Griseb.	Tucumán. Dpto. Tafí. *Wulff 931, 932* (SI)
Suffruticosi	Candidi	*S. chrysolepis* Phil.	Tucumán. Dpto. Tafí. *Wulff 945, 946, 949* (SI)
Xerosenecio	Filaginoidei	*S. filaginoides* DC. var. *filaginoides*	Tucumán. Dpto. Tafí. *Wulff 944* (SI)
	Microcephali	*S. bracteolatus* Hook. & Arn. var. *bracteolatus*	Neuquén. Dpto. Huiliches. *Sanso 89* (SI)
		S. francisci Phil.	Neuquén. Dpto. Aluminé. Sanso 106 (SI)

Table 2. Chromosome numbers and meiotic configurations, number of open (IIo) and closed (IIc) bivalents (mean ± SD), number of excess chiasmata (Chexc., mean ± SD) and observations on meiotic behaviour of the ten *Senecio* taxa studied. The numbers in parentheses in the first column indicate number of individuals and cells taken into account for the measurements

Species	2*n*	Meiotic configurations	IIo	IIc	Chexc	Meiotic observations	Figure
**S. bracteolatus* var. *bracteolatus* (1, 15)	40	20 II (80%) 18 II +1 IV (20%)	16.20 ± 2.27	3.40 ± 2.32	3.67 ± 2.32	2–4 II associated.	1
**S. chrysolepis* (2, 19)	80 + 0–8B	38II +1 IV (36.8%) 36 II +2 IV (36.8%) 32 II +4 IV (10.5%) 40 II (5.3%) 34 II +3 IV (5.3%) 30 II +5 IV (5.3%)	26.42 ± 4.27	9.68 ± 3.93	12.26 ± 4.34	Chromosomes out of plate, laggard chromosomes, micronuclei, 2–8 II associated	2–6
**S. crepidifolius* (1, 17)	40	20 II (88.2%) 19 II +2 I (5.9%) 18 II +4 I (5.9%)	13.88 ± 2.34	5.94 ± 2.54	5.76 ± 2.82	2–3 II associated.	7–8
S. deferens (2, 51)	40 + 0–4B	20 II (82.3%) 18 II +2 I (9.8%) 19 II +2 I (5.9%) 16 II +2 IV (2%)	11.43 ± 2.59	8.23 ± 2.33	8.35 ± 2.51		9–10
S. filaginoides var. *filaginoides* (1, 25)	40	20 II (96%) 18 II +1 IV (4%)	8.32 ± 1.99	11.60 ± 2.02	11.68 ± 1.99	2 II associated.	11
**S. francisci* (1, 17)	40	20 II (94.1%) 18 II +1 IV (5.9%)	16.94 ± 2.90	2.94 ± 2.77	3.00 ± 2.83	2–3 II associated.	12
S. hieronymi (3, 61)	40 + 0–7B	20 II (96.7%) 18 II +1 IV (3.3%)	12.25 ± 2.58	7.69 ± 2.53	7.75 ± 2.58	2 II associated.	13–14
**S. octolepis* var. *saltensis* (2, 51)	40	20 II (94.1%) 16 II +2 IV (3.9%) 18 II +1 IV (2%)	15.21 ± 3.14	4.59 ± 3.15	4.70 ± 3.11	2–4 II associated, fused metaphases	15–16
S. pampeanus (2, 10)	40 + 0–1B	20 II (90%) 18 II +1 IV (10%)	12.50 ± 2.95	7.30 ± 2.83	7.40 ± 2.87	Micronuclei.	17–18
S. rudbeckiifolius (6, 79)	40 + 0–7B	20 II (84.8%) 18 II +1 IV (10.1%) 16 II +2 IV (3.8%) 15 II +1 IV +1 VI (1.3%)	11.61 ± 2.37	7.97 ± 2.11	8.29 ± 2.24	2–4 II associated.	19–20

*New records.

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record of $2n = 80$ for *S. chrysolepis*. Five of the reported chromosome numbers represent new records. Numerical polymorphisms for B-chromosomes were observed in four of the entities (Table 2).

The degree of pollen grain stainability was high in all the studied species, ranging from 85.7% in *S. chrysolepis* to 99.1% in *S. octolepis* var. *saltensis*.

S. BRACTEOLATUS HOOK. & ARN. VAR. *BRACTEOLATUS*

A new chromosome number of $2n = 40$ (Table 2, Fig. 1) is reported, although evidence for $n = c.\ 40 + 1B$ was found by Wulff (1984) but without mentioning the variety of *S. bracteolatus.* An examination of the corresponding voucher (AFW 307-SI) proved that it might be *S. bracteolatus* var. *valderramae* (Phil.) Cabrera.

The meiotic configurations observed in diakinesis and metaphase I were: 20 II (Fig. 1) or 18 II + 1 IV with open bivalents observed more frequently than closed ones (Table 2). Secondary associations of bivalents in groups of two to four were found (Fig. 1).

Senecio series *Xerosenecio* subseries *Microcephali* presents another previous record of chromosome numbers for *S. subumbellatus* Phil. with $n = 20$ (Hunziker *et al*., 1989). The same number was obtained in this work for the two species belonging to this subseries (see Table 1). However, there is evidence of another ploidy level as was mentioned above (Wulff, 1984).

S. CHRYSOLEPIS PHIL.

This species presented the highest chromosome number. Several meiotic configurations were found in diakinesis and metaphase I. Only one cell showed 40 II. Others presented one to five quadrivalents, 38 II + 1 IV and 36 II + 2 IV being the most frequent configurations (Table 2). The presence of a maximum of 5 IV suggests a basic number of five, involving at least two similar genomes. Secondary associations of two to eight bivalents or quadrivalents were observed (Table 2).

Open bivalents were the predominant meiotic figures (Table 2). The meiotic behaviour was irregular, with a low frequency of chromosomes out of plate at metaphase I (Fig. 3) and laggard chromosomes and micronuclei at telophase I (Fig. 4), telophase II (Fig. 5) and immature pollen grains (Fig. 6). This species exhibited a polymorphism for B-chromosomes, which varied from zero to eight (Fig. 3).

Senecio series *Suffruticosi* subseries *Candidi*, in which this species is included, shows different chromosome numbers such as $n = 40$ for *S. volckmanni* Phil. (Hunziker *et al*., 1989), $n = 20$ for *S. laseguei* Hombr. & Jacquinot and $n = 60$ for *S. humifusus* (Hook f.) Cabrera (Moore, 1981).

S. CREPIDIFOLIUS DC.

This species showed a regular meiosis with noticeable secondary associations of two or three bivalents (Table 2, Fig. 7). Although the meiotic configuration was predominantly 20 II (Fig. 8) with a majority of open bivalents, cells with 19 II + 2 I and 18 II + 4 I were also found (Table 2).

The only chromosome numbers reported for species belonging to *Senecio* series *Corymbosi* subseries *Viscosi* are $2n = 40$. One record is presented here and another was reported by Hunziker *et al*. (1989) in *S. saltensis* Hook. & Arn.

S. DEFERENS GRISEB.

The chromosome number previously published by Turner *et al*. (1979) is confirmed. Furthermore, we report here the occurrence of up to four B-chromosomes (Fig. 9). Otherwise, the meiotic study did not show irregularities (Table 2). The proximity of some bivalents at diakinesis also suggests the presence of secondary associations (Fig. 10).

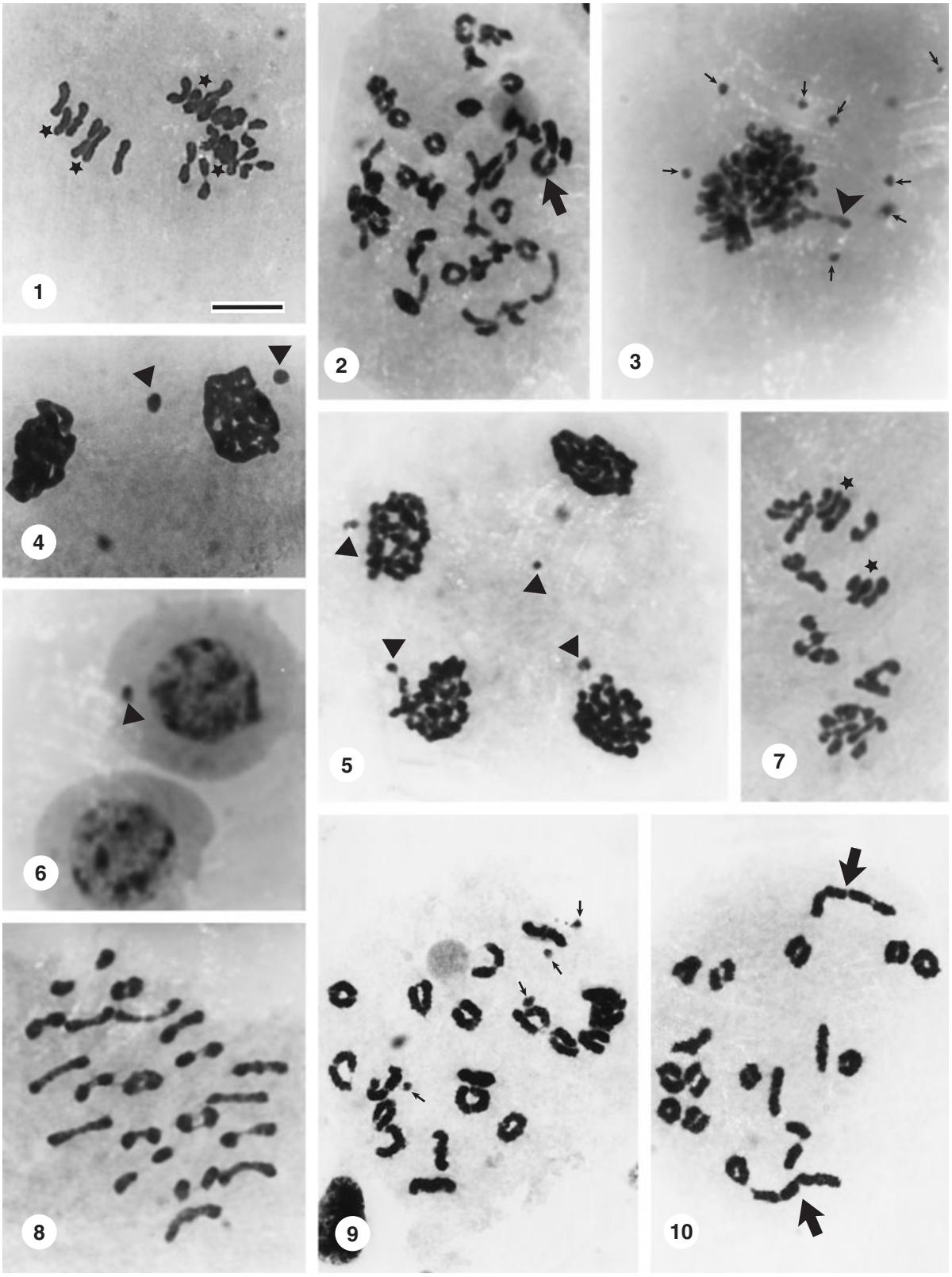
The most frequent meiotic configuration was 20 bivalents, but we also observed a few cells with 19 II + 2 I, 18 II + 1 IV and 16 II + 2 IV (Fig. 10). Most bivalents were open (Table 2).

This species belongs to *Senecio* series *Otopteri*, which also displays two other chromosome numbers: $n = 20$ for *S. deferens* and *S. lorentzii* Griseb. (Wulff, Hunziker & Escobar, 1996), and $n = c.\ 52$ reported for *S. otites* Kunze ex DC. (Hunziker *et al*., 1990).

S. FILAGINOIDES DC. VAR. *FILAGINOIDES*

Our result is the first report for this variety. Covas & Schnack (1947) published a previous count of $n = 20$

Figures 1–10. Meiotic analysis. Scale bar = 10 μm. Fig. 1. *Senecio bracteolatus*. Metaphase I, 20 II and secondary association of bivalents (stars). Figs 2–6. *S. chrysolepis*. Fig. 2. (*AFW 949*). Diakinesis, 38 II + 1 IV (bold arrow). Fig. 3. (*AFW 945*). Metaphase with eight B-chromosomes (thin arrows) and out of plate chromosomes (arrow head). Figs 4–6. (*AFW 945*). Micronuclei (triangles). Fig. 4. Telophase I. Fig. 5. Telophase II. Fig. 6. Immature pollen grains. Figs 7, 8. *S. crepidifolius*. Fig. 7. Prometaphase I with secondary association of bivalents (stars). Fig. 8. Metaphase I, 20 II. Figs 9, 10. *S. deferens*. Fig. 9. (*AFW 931*). Diakinesis, 20 II + 4 B-chromosomes (thin arrows). Fig. 10. (*AFW 932*). Diakinesis, 16 II + 2 IV (bold arrows).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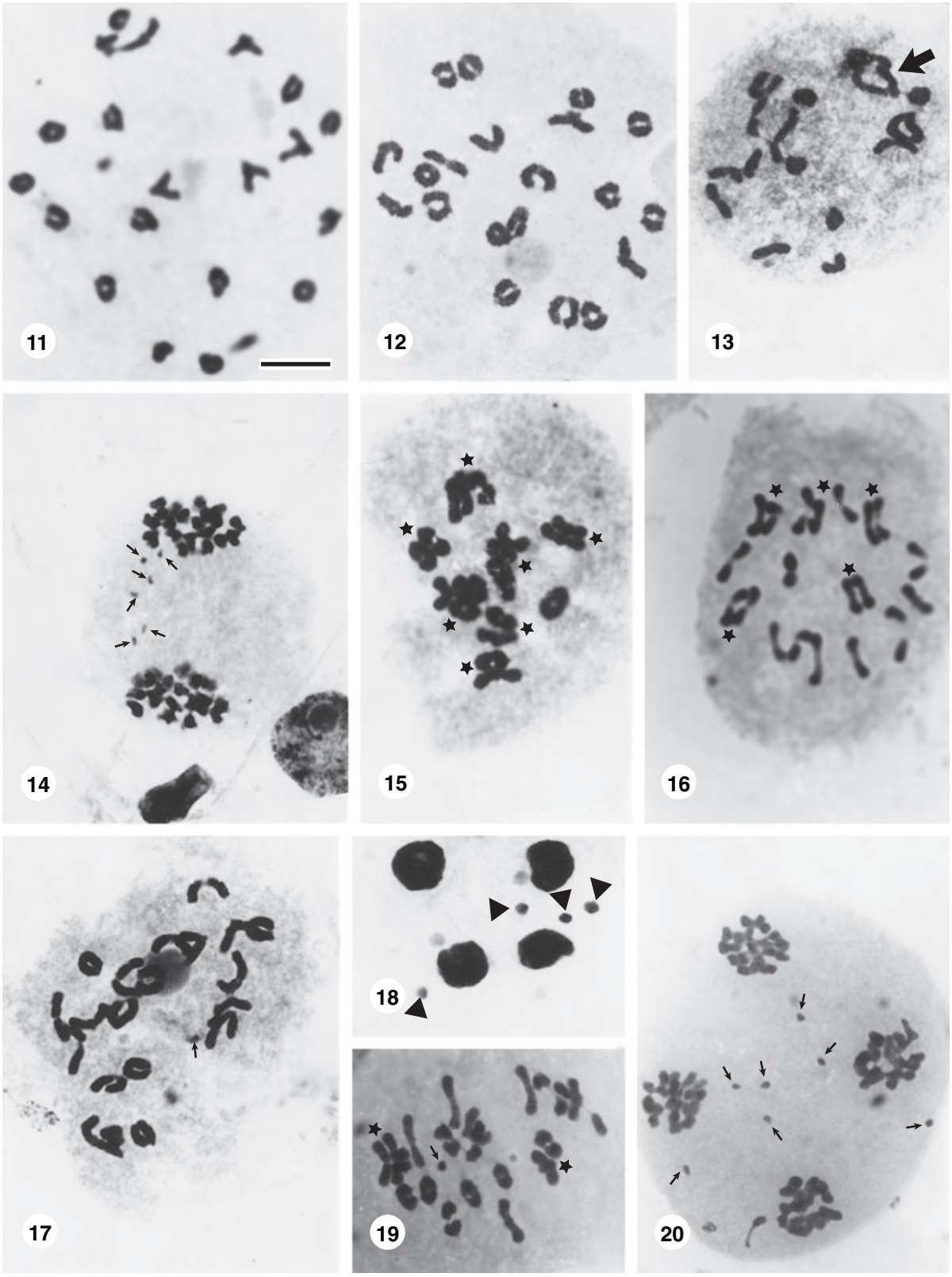
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for *S. filaginoides* without mentioning the variety name.

The most common meiotic configuration was 20 II (Fig. 11), but 18 II + 1 IV appeared with low frequency. This taxon had the largest occurrence of closed bivalents (Table 2). The meiotic behaviour was regular with secondary associations of two bivalents (Table 2).

Senecio series *Xerosenecio* subseries *Filaginoidei* exhibits two different chromosome numbers: $2n = 40$, also observed in *S. vira-vira* Hieron. (Bernardello, 1986), and $n = 40$ for *S. patagonicus* Hook. & Arn. (Moore, 1981).

S. FRANCISCI PHIL.

This species showed secondary associations of two to three bivalents (Table 2). The main meiotic configuration was 20 II (Fig. 12), with a low percentage of cells with 18 II + 1 IV. It exhibited the highest number of open bivalents among the studied species (Table 2).

S. HIERONYMI GRISEB.

Afzelius (1959) found $2n = 40$ and up to four B-chromosomes in this species. We confirmed the somatic chromosome number but also observed zero to seven Bs (Fig. 14, Table 2).

The most frequent meiotic configuration was 20 II, the majority of them being open. However, one cell with 18 II + 1 IV appeared (Fig. 13, Table 2). Secondary associations of two bivalents were noted (Table 2).

S. OCTOLEPIS GRISEB. VAR. *SALTENSIS* (HICKEN) CABRERA & ZARDINI

The observed meiotic configurations were 20 II (Figs 15, 16), 18 II + 1 IV and 16 II + 2 IV, with most bivalents open (Table 2). The meiotic analysis of this taxon revealed noticeable secondary associations of two to four bivalents at metaphase I (Figs 15, 16) and a low percentage of two joined metaphase I (Table 2), an occurrence that could be a possible source of non-reduced gametes.

The same chromosome number was found in all species included in *Senecio* series *Corymbosi* subseries *Simplices* studied until now: *S. clivicola* Wedd. (Afzelius, 1924) and *S. grisebachii* Baker (Waisman, Rozenblum & Hunziker, 1984), *S. hieronymi* and *S. octolepis* var. *saltensis* (this paper).

S. PAMPEANUS CABRERA

Previous records for this species (Hunziker, Xifreda & Wulff, 1985; Bernardello, 1986) are confirmed here. Otherwise, the presence of one B-chromosome in the examined individuals is reported for the first time (Fig. 17). The meiotic analysis revealed mainly 20 II (Fig. 17), with a predominance of open bivalents and an exceptional occurrence of 18 II + 1 IV (Table 2). Micronuclei were also observed at telophase II (Table 2, Fig. 18).

Two different ploidy levels were recorded for *Senecio* series *Corymbosi* subseries *Brasilienses*. The two species studied here (see Table 1) showed $2n = 40$, as in *S. brasiliensis* (Spreng.) Less. (Waisman *et al*., 1984), *S. gilliesianus* Hieron. (Covas & Schnack, 1946 Hunziker *et al*., 1985), *S. glaber* Less. var. *pratensis* (Phil.) Cabrera (Hunziker *et al*., 1990), *S. sectilis* Griseb. and *S. ragonesei* Cabrera (López *et al*., 2002). However, *S. uspallatensis* Hook. & Arn. (Schnack & Covas, 1947; Hunziker *et al*., 1989) and *S. subulatus* var. *subulatus* D. Don. (López *et al*., 2002) have $2n = 80$.

S. RUDBECKIIFOLIUS MEYEN & WALP.

This species was recorded previously under the name *S. flagellisectus* Griseb. (Wulff *et al*., 1996). We confirm the chromosome number $2n = 40$, with a polymorphism for B-chromosomes ranging from zero to seven (Figs 19, 20). The meiotic configurations observed were: 20 II (Fig. 19), 18 II + 1 IV, 16 II + 2 IV and 15 II + 1 IV + 1 VI. This species exhibited the greatest number of multivalents. However, the highest frequency of multivalents was observed in only one individual (*Sanso 168*). Secondary associations of two to four bivalents were observed (Table 2, Fig. 19). The most common meiotic figure was 20 open bivalents (Table 2).

EXCESS CHIASMATA

Values of excess chiasmata (Table 2) can be used as a measurement of the exchange recombination rate,

Figures 11–20. Meiotic analysis. Scale bar = 10 μm. Fig. 11. *Senecio filaginoides* var. *filaginoides*. Diakinesis, 20 II. Fig. 12. *S. francisci*. Diakinesis 20 II. Figs 13, 14. *S. hieronymi*. Fig. 13. (*AFW 926*). Diakinesis, 18 II + 1 IV (bold arrow). Fig. 14. (*AFW 927*). Telophase I with six B-chromosomes (thin arrows). Figs 15, 16. *S. octolepis* var. *saltensis*. Metaphase I, 20 II with secondary association of bivalents (stars). Fig. 15. (*Sanso 169*). Fig. 16. (*AFW 915*). Figs 17, 18. *S. pampeanus* (*MGL 55*). Fig. 17. Diakinesis, 20 II + 1 B-chromosome (thin arrows). Fig. 18. Telophase II with micronuclei (triangles). Figs 19, 20. *S. rudbeckiifolius*. Fig. 19. (*AFW 940*) Metaphase I, 20 II + 1 B-chromosome (thin arrow) with secondary association of bivalents (stars). Fig. 20. (*AFW 918*) Telophase II with seven B-chromosomes (thin arrows).

since the overall level of recombination between all genes enlarges with an increase in exchange frequency (Sybenga, 1992). In the case of the analysed species, the highest value of excess chiasmata was in *S. chrysolepis*, followed very closely by *S. filaginoides* var. *filaginoides*. In the former, the high value observed is clearly related to the large number of multivalents, which are in turn associated with the high chromosome number. In the latter, the observed value of excess chiasmata is a reflection of the high frequency of closed bivalents. The highest value of excess chiasmata in *S. filaginoides* could be related to the ecological behaviour of this species. The individuals of this taxon are well separated in the field and do not constitute dense populations (Ing. Agr. Dalmasso, pers. comm.). This feature may restrict the possibilities of outcrossing, with the resulting inbreeding compensated by enhancing intrarecombination (i.e. via greater numbers of excess chiasmata).

The variability in the numbers of excess chiasmata can be seen in Figure 21. Species with $2n = 40$ present values considerably lower than in *S. filaginoides* var. *filaginoides*.

As well as the number, the position of the chiasmata is extremely important in determining the degree of recombination. It is significant that the majority of the studied cells exhibited terminal chiasmata (see Figures 1, 2, 7–13, 15–17, 19), producing a low rate of recombination. Nevertheless, whole-chromosome recombination still occurs as a result of the alternative bivalent orientations at metaphase I. This is increased with higher chromosome numbers.

B-CHROMOSOMES

B-chromosomes are frequently observed in *Senecio* species, as in the entire Asteraceae family (Jones & Puertas, 1995). In the species studied, B-chromosomes do not pair during meiosis, so they remain as univalents and are observed to lag at the early post-metaphase stages (Figs 3, 14, 20), leading to their loss as micronuclei. These observations could indicate that B-chromosomes do not exhibit meiotic drive, so the mechanism for their maintenance, spreading and retention is still unknown.

Several authors have suggested that B-chromosomes favour homologous against homeologous pairing (Sybenga, 1992), and this has been observed in other *Senecio* species (López *et al*., 2002). However, in the species studied here, individuals with B-chromosomes presented quadrivalents (e.g. *S. deferens* AFW 931), while others without Bs showed only bivalents (e.g. *S. rudbeckiifolius* AFW 942). This could suggest that the influence of Bs on pairing differs among species or perhaps depends on the genotype.

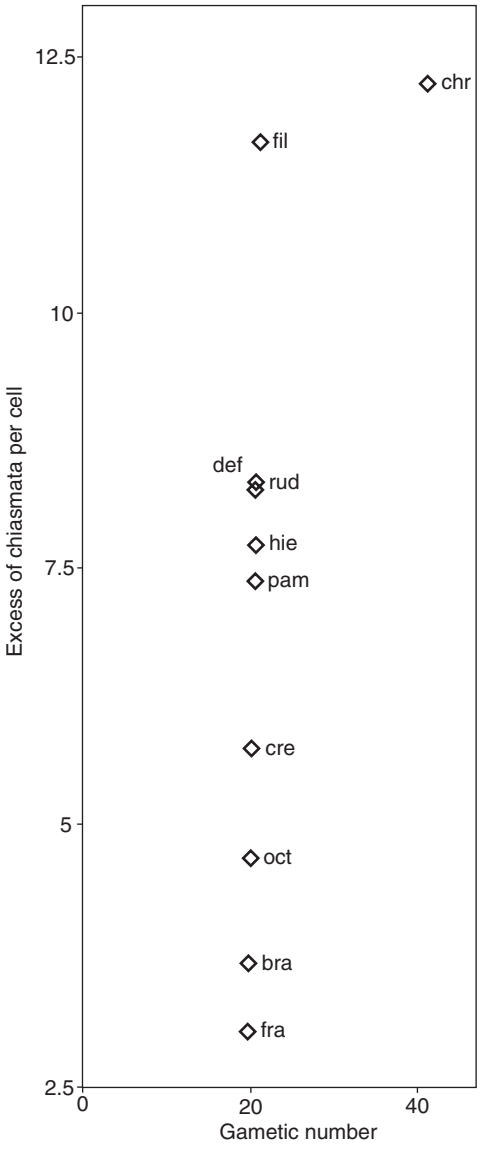

Figure 21. Association between gametic chromosome number and number of excess chiasmata for the studied species. The abbreviated species names refer to the list in Table 1.

CONCLUSIONS

A great diversity of chromosome numbers occurs in *Senecio* around the world (Lawrence, 1980). The most common records observed in the Argentine species are $n = 20$ and 40, the same numbers reported in this work.

The basic number of *Senecio* is under discussion, with $x = 5$ and $x = 10$ being the controversial values. Turner & Lewis (1965) accepted $x = 5$. These authors sustained, as major evidence, the lack of species with $n = 6$, 7, 8 and 9, the existence of species with $n = 5$

and a basic number of $x = 5$ for *Emilia*, a closely related genus. Conversely, for Ornduff *et al.* (1963), the frequency of numbers in multiples of ten instead of five was taken to support $x = 10$. In a previous work, we sustained $x = 10$ (López *et al*., 2002), but new evidence considered together with old data strongly supports five as the basic number. Thus, the species with $2n = 10$ are found in Africa, the most probable place of origin of the genus (Ornduff *et al*., 1963; Lawrence, 1980), the finding of four and eight bivalents showing secondary associations in species with $2n = 40$ and 80, respectively, and the observation of groups of two bivalents and chromosome asynchrony in one African species with $2n = 20$ (López *et al*., 2003). These surveys have been tools powerful enough to take similar decisions in other genera (Poggio, Naranjo & Jones, 1986; Molina & Naranjo, 1987; Argimón, Wulff & Xifreda, 1999). In concordance with $x = 5$, the species studied in this work are octoploids ($2n = 8x = 40$) and 16-ploids ($2n = 16x = 80$), respectively.

Despite the opinions mentioned above, we believe that the secondary cycle of polyploidy proposed by Stebbins (1971) is the best explanation for the basic number dilemma of *Senecio*, the differences of chromosome number in different continents and the lack of species with $n = 15, 25$, etc. (numbers in multiple of 5). As Stebbins pointed out, this process begins when part of a polyploid complex initiates a new series of polyploid numbers. This commonly occurs in a different continent where new polyploids are arising. However, the number that is multiplied is not the original basic number, five in the case of *Senecio*, but some multiple of it (i.e. ten).

In view of the present scenario, we suggest that different polyploids have colonized Australia, North America and South America, masking the original basic number by an easily accepted derivative of $x = 10$. Ancient diploids ($2n = 10$) still exist among native African species such as *S. abyssinicus* Sch. Bip., *S. discifolius* Oliver and *S. hockii* De Wild & Muschl. (Turner & Lewis, 1965), and polyploids with $n = 35$ (*S. orarius* J. M. Black) are rare but they do exist (Lawrence, 1985). Nevertheless, we must consider that the total available knowledge of chromosome numbers in *Senecio* is still insufficient to confirm this hypothesis.

Another consequence of the secondary cycle of polyploidy is that some species from the original complex could be recognized as distinct genera, explaining the taxonomic difficulties and lack of generic boundaries found in *Senecio* (for revision see Cabrera, 1949; Jeffrey *et al*., 1977; Nordenstam, 1978; Vincent & Getliffe, 1992).

Meiotic studies of the Argentine species show a diploidized behaviour with a low frequency of multivalents and closed bivalents. This feature, combined with the low frequency of excess chiasmata, could contribute to meiotic stabilization (Moore, 1998) and avoid sterility in these highly polyploid species. Although it seems to reduce their recombination rates (Soltis & Soltis, 1999), it might explain their success because it avoids the loss of adaptive genetic combinations that have arisen mostly as a consequence of genomic rearrangement, hybridization and heterozygosity (Stebbins, 1980; Thompson & Lumaret, 1992; Soltis & Soltis, 1993; Comes & Abbott, 1999; López *et al*., 2002).

Polyploids can also display secondary modifications (Stebbins, 1971). They may combine to give rise to a complex of polyploid species, which promotes morphological and ecological continua causing difficulties in taxonomic treatments.

The cytogenetic data support the idea that polyploidy is the principal specio-genic process modelling the evolution of *Senecio* and could explain the major systematic difficulties observed in the genus. Moreover, it is obvious that the systematics of this genus require considerable revision. This is now in progress (López, 2001; Nordenstam, 2003).

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