Botanical Journal of the Linnean Society, 2008, **158**, 613–620. With 15 figures

South African fireweed *Senecio madagascariensis* (Asteraceae) in Argentina: relevance of chromosome studies to its systematics

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Received 21 August 2007; accepted for publication 10 April 2008

The systematic identity of *Senecio madagascariensis* is ratified against the opinion that it is conspecific with *Senecio inaequidens*. Both species are native to South Africa and have been merged in the '*Senecio inaequidens* complex', a group of entities difficult to distinguish from each other. *Senecio madagascariensis* is widespread in South America and Australia, where it is an invasive weed. Mitotic and meiotic studies were conducted on Argentinian material; chromosome counts solved the chromosome number controversy, validating $2n = 20$. The karyotype was symmetrical, composed of ten pairs of metacentric chromosomes varying from 1.62 to 2.38 µm in length. The most frequent number of satellited chromosomes was three, but their position was difficult to assign. Meiosis was regular, with a configuration of ten predominantly open bivalents. Univalents and quadrivalents were rarely observed. High frequencies of secondary associations of bivalents, chromosome asynchrony and bivalent grouping were documented, reinforcing the hypothesis that $x = 5$ is the basic chromosome number. Pollen stainability ranged from 94 to 99%. The relevance of chromosomal studies in the circumscription of *S. madagascariensis* is discussed. Hybridization and polyploidy, as principal evolutionary forces in this genus, explain the systematic difficulties. *Botanical Journal of the Linnean Society*, 2008, **158**, 613–620.

ADDITIONAL KEYWORDS: basic chromosome number – hybridization – karyotype – meiotic analysis – polyploidy – secondary association of bivalents – *Senecio inaequidens*.

INTRODUCTION

Senecio madagascariensis Poir. is an African native plant, described from Madagascar by Poiret (1817). The species is an alien weed, in the sense of Pyšek *et al.* (2004), in Australia (Sindel, 1996), East Asia (Kinoshita *et al.*, 1999) and South America. This opportunistic perennial herb has a short lifespan and develops three seed morphs differing in dormancy and germination rate, ensuring constant seedling emergence (Verona *et al.*, 1982; Sindel, 1996).

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The first Argentinian specimen of *S. madagascariensis* was collected in 1940 by Cabrera, who named it as a new species, *S. incognitus* (Cabrera, 1941). Later, it was again determined erroneously, as *S. burchellii* DC. (Cabrera, 1963). Finally, the name *S. madagascariensis* was adopted by Cabrera & Zardini (1978) following the revision of Asteraceae of Natal Province, South Africa, by Hilliard (1977).

More recently, *S. madagascariensis* has been considered to be part of the '*Senecio inaequidens* complex' and conspecific with the *S. inaequidens* (Lafuma *et al.*, 2003). Although *S. madagascariensis* and *S. inaequidens* are morphologically very similar, Radford

Table 1. Vouchers, the herbaria at which they were deposited and the provenance of the Argentinian material of *Senecio madagascariensis* studied

Voucher	Herbarium	Provenance
AFW 930	SI	Tucumán, Departamento Tafí, San Javier
AFW 970	BAFC	Buenos Aires, Partido de Avellaneda, Sarandí
CCX & MGL 3215, 3216, 3217	SI	Córdoba, Departamento Punilla, Sierra Chica
CCX & MGL 3221, 3222, 3223, 3224	SI	Buenos Aires, Partido de San Pedro, Ciudad
CCX & MGL 3225, 3226	SI	Buenos Aires, La Plata
CCX & MGL 3227, 3228, 3229	SI	Distrito Federal
MGL 48, 49, 50*, 51, 52, 53, 54*	SI	Buenos Aires, Partido de Balcarce, Sierra El Volcán
MGL, CCX & MNS 179	BAFC	Salta, Departamento Capital, Ciudad

AFW, Arturo F. Wulff; CCX, Cecilia C. Xifreda; MGL, Mariana G. López; MNS, Micaela N. Seo.
*Only pollen stainability.

et al. (2000) differentiated them, basing their conclusions on the micromorphology of the cypsela surface. Another distinctive feature is the chromosome number. Although this is $2n = 40$ for *S. inaequidens* (Chichiricco, Frizzi & Tammaro in Goldblatt, 1984; Harland in Radford, Liu & Michael, 1995), two chromosome numbers have been published for *S. madagascariensis*, namely $n = 10$ (Turner & Lewis, 1965, as *S. pellucidus* DC.; Verona *et al.*, 1982; Radford *et al.*, 1995) and $n = 20$ (Hunziker *et al.*, 1989), $2n = 20$ and $2n = 40$, respectively.

In order to clarify the identity and status of the species, we undertook a study of the chromosome number and ploidy level in *S. madagascariensis*, with special emphasis on Argentinian representatives. Our data are discussed in comparison with the concepts of Lafuma *et al.* (2003), and our different point of view is considered with regard to the model of evolution of the genus.

MATERIAL AND METHODS

Plant material

The studied material and its provenance are summarized in Table 1. Vouchers were deposited at the herbaria SI or BAFC. Additional geographical distribution data of Argentinian material (Fig. 1) were obtained from the literature and from specimen labels in the herbaria SI, BA, BAA, BAB, BAF, LP, LIL, MCNS and CORD.

Chromosome studies

Young capitula were collected from 22 plants from eight different localities (Table 1). The inflorescences were fixed *in situ* in ethanol–chloroform–glacial acetic acid (6 : 3 : 1) for at least 24 h, transferred into 70% ethanol (v/v) and stored at 4–5 °C until use. Immature anthers were squashed in a drop of 2% propionic acid–haematoxylin solution, using ferric citrate as a mordant (Núñez, 1968). Photographs of meiosis were taken using a Leica DMLB photomicroscope and a Leitz camera. Open (IIo) and closed (IIc) bivalents per cell were recorded, and the mean and standard deviation of the frequencies were calculated.

For mitotic studies, seeds were germinated in humidity chambers and incubated under constant light at room temperature until the appearance of the root tips. The cell cycle was synchronized by the incubation of germinated seeds at 4 °C for 24 h. Afterwards, root tips were treated as follows: 2 h 30 min at room temperature, incubation for 2 h at 37 °C, transfer to 2 mM 8-hydroxyquinoline solution for 2 h at room temperature, followed by 1 h at 4 °C. Root tips were finally fixed in an ethanol–glacial acetic acid (3 : 1) solution for at least 24 h and stored at 4–5 °C until required. Prior to slide preparation, root tips were hydrolysed for 40 min in 5 M HCl at room temperature, rinsed once in distilled water and stained with 2% propionic acid–haematoxylin solution. Slide preparations were photographed as described above. The karyotype was determined from 18 cells at metaphase belonging to nine different individuals from Balcarce. For each metaphase, the absolute lengths of the short (s) and long (l) chromosome arms, whole chromosome length (c) and haploid karyotype length (HKL) were measured. Relative values of c, s and l were calculated to minimize the error caused by variation in the amount of chromosome contraction, considering HKL as 100%. The measurements were made from photographs, using a Zeiss stereoscopic microscope and an eyepiece micrometer. The centromere position in each chromosome was obtained using the arm ratio index ($r = l/s$), according to Levan, Fredga & Sandberg (1964).

Pollen stainability

In order to estimate pollen grain fertility, anthers from fixed material were dissected and stained using

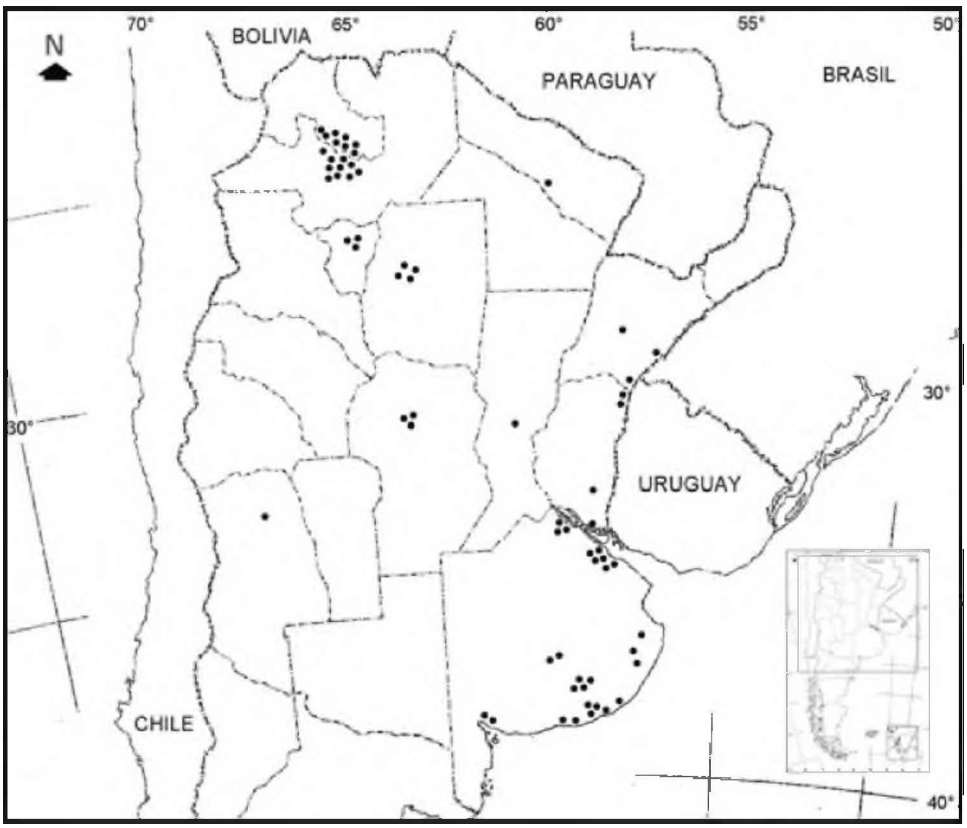


Figure 1. Geographical distribution of *Senecio madagascariensis* in Argentina. Circles represent data obtained from collection sites, herbarium labels, literature and field observations.

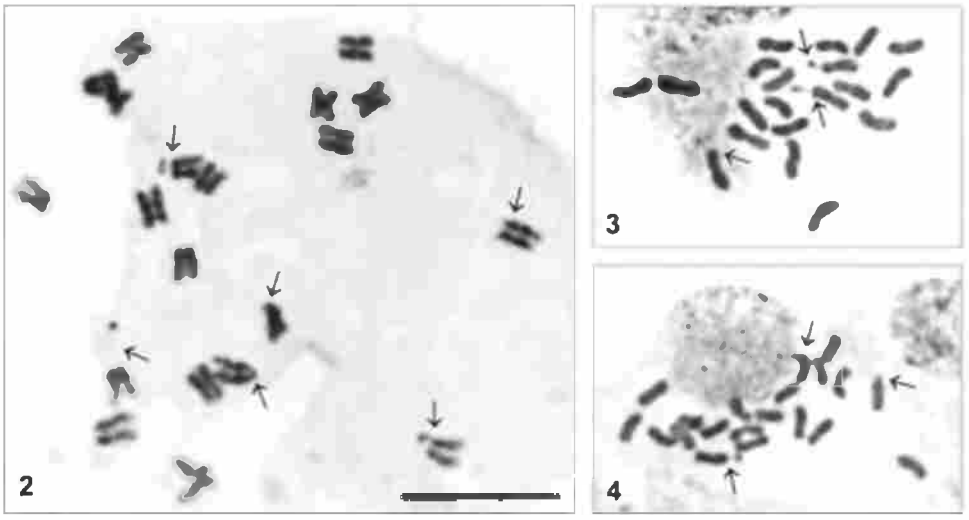
Alexander's differential method (Alexander, 1969). The individuals examined were: CCX & MGL 3215, 3216, 3217, 3222, 3223, 3224, 3225, 3227, 3228, 3229; MGL 48, 49, 50, 52, 53, 54; AFW 930 (Table 1).

RESULTS

The Argentinian *S. madagascariensis* specimens studied here had a sporophytic chromosome number of $2n = 20$ (Figs 2–4) with a symmetrical karyotype composed of ten pairs of metacentric chromosomes. Detailed chromosome measurements are shown in Table 2 and the idiogram is illustrated in Figure 5. Metaphase cells exhibited one to six satellited chromosomes (Fig. 2), with three being the most frequent number (Figs 3, 4). Because of the morphological and dimensional similarities of the chromosomes, only one pair of satellites could be unambiguously located on the first chromosome pair (Fig. 5).

Meiotic analysis of 200 cells is shown in Table 3. Diakinesis or metaphase I revealed the uniform gametic number $n = 10$ (Figs 6–14). The main meiotic configuration was ten bivalents (II) (Fig. 6), although two univalents (I) or one quadrivalent (IV) per cell were sometimes observed (Fig. 7). Open bivalents appeared to be more frequent than closed bivalents (Table 3; Fig. 8).

Although the meiotic behaviour was regular (Figs 6–14), the bivalents showed a peculiar distribution, exhibiting secondary association. All the bivalents were associated in pairs in 8.59% of the cells studied (Table 4), whereas eight bivalents were associated in 25% of meiocytes (Table 4, Figs 9, 12). Six was the most frequent number of associated bivalents observed (Table 4, Fig. 7), with the remaining four not or doubtfully associated. Only 10 of 128 cells displayed no associations, whereas four cells showed indeterminate association. Some of the latter cells exhibited unusual behaviour. In one, two groups of five bivalents were observed, each at different dissociation states (Fig. 10). In another, two distinctive groups of five bivalents each were found (Fig. 11). In addition, fused prometaphase IIs and large pollen grains (Fig. 15) were also observed, although at low frequency. A high degree of pollen grain stainability was observed in all individuals studied, ranging from 94 to 99%.



Figures 2–4. Mitotic metaphases of Argentinian *Senecio madagascariensis*, all with $2n = 20$. Arrows indicate secondary constrictions. Scale bar, 10 μm.

Table 2. Chromosome measurements of the specimens of *Senecio madagascariensis* studied

	Chromosome length (*c*)		Short arm length (*s*)		Long arm length (*l*)		
Chromosome pair number	Absolute (μm) $\bar{x} \pm$ SD	Relative (% HKL*)	Absolute (μm) $\bar{x} \pm$ SD	Relative (% HKL)	Absolute (μm) $\bar{x} \pm$ SD	Relative (% HKL)	Arm ratio $r = l/s$ $\bar{x} \pm$ SD
1	2.38 ± 0.38	12.06	1.06 ± 0.21	5.38	1.32 ± 0.21	6.69	1.27 ± 0.20
2	2.23 ± 0.32	11.28	0.98 ± 0.12	4.95	1.25 ± 0.24	6.33	1.28 ± 0.21
3	2.12 ± 0.28	10.77	0.93 ± 0.14	4.73	1.19 ± 0.16	6.04	1.29 ± 0.17
4	2.06 ± 0.28	10.42	0.90 ± 0.13	4.55	1.16 ± 0.18	5.86	1.30 ± 0.18
5	2.00 ± 0.28	10.13	0.87 ± 0.16	4.38	1.14 ± 0.16	5.75	1.34 ± 0.23
6	1.94 ± 0.26	9.82	0.83 ± 0.12	4.22	1.11 ± 0.20	5.60	1.34 ± 0.26
7	1.87 ± 0.26	9.49	0.79 ± 0.14	4.00	1.08 ± 0.15	5.49	1.39 ± 0.18
8	1.80 ± 0.26	9.14	0.80 ± 0.11	4.06	1.00 ± 0.17	5.07	1.25 ± 0.15
9	1.72 ± 0.25	8.70	0.75 ± 0.12	3.79	0.97 ± 0.18	4.93	1.32 ± 0.25
10	1.62 ± 0.26	8.19	0.67 ± 0.11	3.40	0.94 ± 0.18	4.78	1.42 ± 0.24

HKL, haploid karyotype length; SD, standard deviation; $\bar{x}$, mean value.
*HKL value is 19.74 ± 2.78 μm.

DISCUSSION

The karyotype of *S. madagascariensis* ($2n = 20$) is presented here for the first time. It displays a high level of inter- and intrachromosomal symmetry. All chromosomes are metacentric, a feature held in common with other species of this genus (Dematteis & Fernández, 1998; López *et al.*, 2002a). Because the chromosomes were similar and small in size, the identification of pairs was difficult. Our results suggest the existence of at least six satellited chromosomes, but only one pair could be identified with confidence. The difficulties in assigning the correct positions of the secondary constrictions have already been documented by Stace (2000).

The present cytological study of Argentinian representatives of *S. madagascariensis* confirms the previous reports ($2n = 20$) for Africa (Turner & Lewis, 1965), Australia (Radford *et al.*, 1995) and Argentina (Verona *et al.*, 1982). Unfortunately, the latter authors did not refer their counts to any voucher specimen, preventing us from comparing our results with theirs.

By contrast, Hunziker *et al.* (1989) published the only known record of $2n = 40$ in material from Balcarce (Sa. de Volcán). Our results showed $2n = 20$ for many individuals from the same geographical region. We re-examined herbarium material and original chromosome drawings of the $2n = 40$ specimen in Hunziker *et al.* (1989) and his field diary, and found that the plant with $2n = 40$ is a different

Table 3. Meiotic analysis of the Argentinian *Senecio madagascariensis* individuals

Meiotic configuration ($N = 200$ cells)	Meiotic figures per cell $\bar{x} \pm$ SD			
	I	IIo	IIc	IV
20 II	0.02 ± 0.21	9.30 ± 0.91	0.67 ± 0.90	0.01 ± 0.01

I, univalents; IIc, closed bivalents; IIo, open bivalents; IV, quadrivalents; SD, standard deviation; $\bar{x}$, mean value.

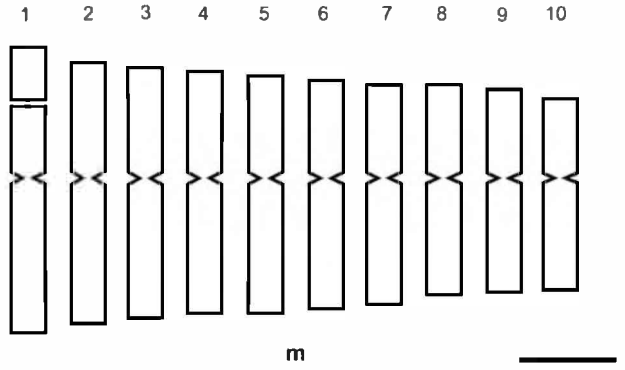


Figure 5. Idiogram of *Senecio madagascariensis* showing the basic karyotype composed of $n = 10$ metacentric chromosomes. Scale bar, 1 μm.

native *Senecio* species [*Senecio brasiliensis* (Spreng.) Less.], establishing the chromosomal uniformity of *S. madagascariensis*.

Our meiotic analysis in Argentinian specimens of *S. madagascariensis* revealed a high frequency of secondary associations of bivalents, i.e. their occurrence together, in pairs or groups, at metaphase I, as described in wheat (Riley, 1960). This phenomenon has been interpreted as evidence of residual homology or homoeology between chromosomes (Poggio, Naranjo & Jones, 1986; Naranjo, Molina & Poggio, 1990; Argimón, Wulff & Xifreda, 1999), and suggests the possible existence of an ancient polyploid condition. Moreover, the quadrivalent observation in Argentinian *S. madagascariensis*, although rare, reinforces the palaeo-tetraploid condition of this species. The rare appearance of multivalents in the meiosis of suspected polyploids is referred to as 'diploidized' meiotic behaviour (Riley & Chapman, 1958; López, Wulff & Xifreda, 2002b), because the predominant occurrence of bivalents resembles the meiosis of diploids. This behaviour could be attributed to *Ph*-like genes, which suppress multivalent formation and avoid this source of sterility in polyploids (Moore, 1998; Sybenga, 1999), or to the low chiasma frequency (revealed by the high frequency of IIo). The diploidized meiotic behaviour explains the regularity of the meiotic process in this species and, consequently, the high level of pollen fertility (López *et al.*, 2005).

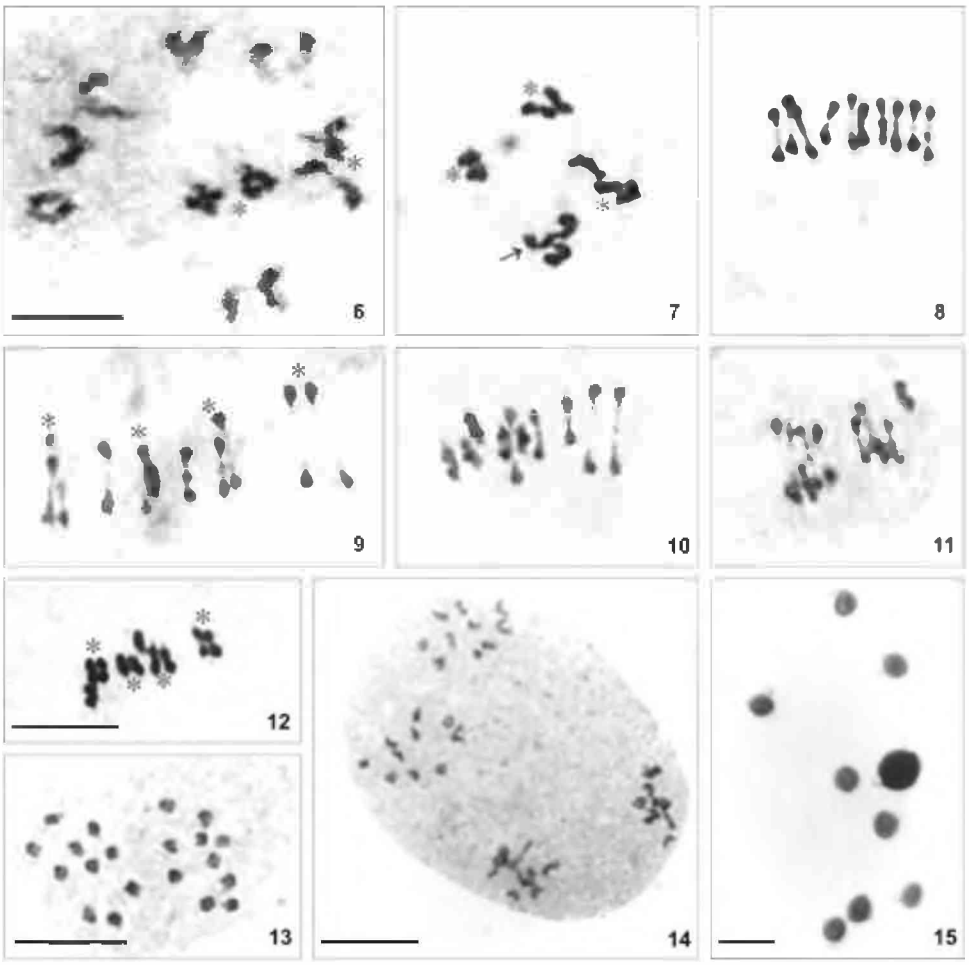
Table 4. Secondary association of bivalents observed in Argentinian *Senecio madagascariensis* individuals

Number of bivalents associated per cell	Cells with the corresponding associated bivalents	
	Diakinesis Number (%)	Metaphase I Number (%)
0	7 (5.47)	7 (5.47)
2	2 (1.56)	8 (6.25)
4	1 (0.78)	18 (14.07)
6	–	42 (32.81)
8	1 (0.78)	31 (24.22)
10	–	11 (8.59)

The percentage values (of all 128 cells observed) are given in parentheses (see text).

This 'polyploidy camouflage' raises some difficulties in basic chromosome number determination, and our detailed analysis of meiotic chromosomes in *S. madagascariensis* highlights this matter. By contrast with the previous view establishing a basic number of $x = 10$ in *Senecio* (Ornduff *et al.*, 1963), the evidence revealed above strongly supports our previous hypothesis of $x = 5$ as the basic chromosome number (López *et al.*, 2005). This is also strengthened by the existence of *Senecio* species with $2n = 10$ (Lawrence, 1980). In addition, chromosome asynchrony and bivalent groupings of five are evidence of the co-existence of two genomes in the same nucleus (Poggio, Rosato & Naranjo, 1997). Otherwise, the existence of fused prometaphase II is common in polyploids as a source of large pollen grains (i.e. non-reduced gamete formation).

The clarification of the chromosome number of *S. madagascariensis* contributes to the taxonomic controversy over this species and the related *S. inaequidens*. The two species differ from each other by leaf morphology, cypsela anatomy and micromorphology (M. G. López *et al.*, unpubl. data), but, despite these differences, Lafuma *et al.* (2003) considered them to be conspecific, being cytotypes of *S. inaequidens*, based on research performed in South Africa. Three points sustain their conclusion: (1) the



Figures 6–15. Meiotic chromosomes of *Senecio madagascariensis*. Fig. 6. Diakinesis (CCX & MGL 3225). Fig. 7. Prometaphase I. Arrow indicates one quadrivalent (CCX & MGL 3224). Figs 8–12. Metaphase I. Fig. 8. Two groups of five bivalents, each in a different plane (CCX & MGL 3225). Fig. 9. CCX & MGL 3225. Fig. 10. Five early separating bivalents (CCX & MGL 3225). Fig. 11. Two well-separated groups of five bivalents each (CCX & MGL 3221). Fig. 12. MGL 48. Fig. 13. Prometaphase II (CCX & MGL 3215). Fig. 14. Anaphase II (MGL 48). Fig. 15. Pollen grains showing size differences (CCX & MGL 3229). Asterisks indicate secondary association of bivalents in Figs 6, 7, 9, 12. Scale bars, 10 μm; the scale bar in Fig. 6 also applies to Figs 7–11.

morphological similarities between the two species; (2) ploidy level; and (3) molecular differences.

Morphological similarities

The species are similar, but there are some differences that separate them, i.e. leaf and cypsela morphology (Sindel, 1996; Radford *et al.*, 2000). They have different distributions. Both occur in South Africa, but *S. inaequidens* is a weed restricted to Europe (Ernst, 1998), whereas *S. madagascariensis* has dispersed to America and Australia (see 'Introduction'). They are part of a polyploid complex that also includes *S. harveianus* MacOwan, *S. burchellii* DC. and *S. pellucidus* DC. In South Africa, species recognition is difficult, mostly because of hybridization amongst the members of the complex. This evolutionary force, widespread in *Senecio* (Hodálová, 1999; López, 2001; López *et al.*, 2005), results in a morphological continuum, confusing the separation of the taxa (Soltis & Soltis, 1999). Following this idea, the entities mentioned by Lafuma *et al.* (2003) as 'undefined' could be hybrids between members of the complex or introgressed forms. Thus, species identification must be conducted carefully in South Africa.

Ploidy level

Two ploidy levels were recognized for *S. inaequidens* in South Africa (Lafuma *et al.*, 2003). As this result was not obtained by chromosome observations, but from DNA content analysis, and was performed on a

complex of hybrids (see above), it must be interpreted with caution (Stace, 2000; Suda *et al.*, 2006). Only a chromosomal study could confirm the two numbers proposed. Although this result suggests the existence of two cytotypes within *S. inaequidens*, it is not evidence of conspecificity with *S. madagascariensis*.

Molecular differences

More molecular differences were found within *S. madagascariensis* from different locations (South Africa, Madagascar and Australia) than the variation observed between *S. madagascariensis* and *S. inaequidens* from South Africa (Scott, Congdon & Playford, 1998). These findings were interpreted by Lafuma *et al.* (2003) as evidence of conspecificity between the two species. Conversely, we believe that these similarities could again be consequences of hybridization within the *S. inaequidens* complex, which maintains a mixed gene pool in South Africa, blurring the differences between species.

The situation in South Africa will be solved only through an extensive research programme including cytological studies. Special attention should be given to species identification, ploidy level and chromosome number assignment in the species complex.

Finally, the sum of the morphological, chromosomal and geographical distribution differences provides sufficient evidence to maintain *S. madagascariensis* and *S. inaequidens* as separate species. There is abundant evidence to suggest that polyploidy and hybridization have been important processes in the evolution of the genus *Senecio*. These processes, with their reticulate as opposed to divergent evolution, could explain the systematic difficulties encountered in the group.

ACKNOWLEDGEMENTS

The authors thank the curators of LP and Dr Fernando Zuloaga (SI) for loans and information assistance. They are also grateful to Dr Peter Brandham for a critical review of the manuscript. M.G.L. is gratful to the International Association for Plant Taxonomy (IAPT) for the research grant given. C.C.X. is grateful to Comisión de Investigaciones Científicas – Provincia de Buenos Aires (CIC-PBA) for the research funds provided. This work was also supported by PICT 03-14119 (Agencia Nacional de Promoción Científica y Técnica) and PIP 5927, Comisión de Investigaciones Científicas y Tecnológicas (CONICET).

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