Botanical Journal of the Linnean Society, 2002, **138**, 451–459. With 15 figures

Chromosome studies in Andean taxa of *Alstroemeria* (Alstroemeriaceae)

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Received May 2001; accepted for publication August 2001

Meiotic or mitotic chromosomes of seven *Alstroemeria* taxa, native in Argentina and Chile and with Andean distribution were studied: *A. andina* ssp. *venustula, A. hookeri* ssp. *cummingiana*, *A. hookeri* ssp. *recumbens*, *A. pallida*, *A. patagonica*, *A. pseudospathulata* and *A. pygmaea*. All were diploid with $2n = 16$. Karyotypes of *A. andina* ssp. *venustula* and *A. pygmaea* were analysed, revealing similarity to previously analysed species. Thus, to all existing arguments for not retaining *Schickendantzia* as a separate genus, we can add another one which merges *A. pygmaea* with other *Alstroemeria* species, and does not support its taxonomic uniqueness. In general, the meiotic behaviour was normal, with regular formation of eight bivalents except in *A. hookeri* ssp. *cummingiana*, in one plant of which meiotic irregularities at various stages were observed. At the tetrad stage a large percentage of the cells presented micronuclei. The presence of 0–2 supernumerary chromosomes in *A. hookeri* ssp. *recumbens* is recorded. The karyotype asymmetry presented by most *Alstroemeria* species is discussed. © 2002 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2002, **138**, 451–459.

ADDITIONAL KEY WORDS: *Alstroemeria andina* – *A. hookeri* – *A. pallida* – *A. patagonica* – *A. pseudospathulata* – *A. pygmaea* – karyotype – meiosis – *Schickendantzia*.

INTRODUCTION

Alstroemeria L. is an exclusively South American genus comprising about 50 species that occur from Venezuela to Argentina, from sea level to 4500 m altitude. However, the number of species will be considerably increased when the revision of the Brazilian species by Marta Camargo (University of Saõ Paulo) is finished. Because of their showy flowers, these herbaceous plants have been successfully introduced into cultivation and are used as vase flowers. Many other wild taxa, that are scarcely known so far, are also of potential use in breeding programmes.

Within the framework of biosystematic research in the family Alstroemeriaceae (Sanso & Xifreda, 1995; Sanso, 1996; Aagesen & Sanso, 1998; Sanso & Xifreda, 1998, 2001), chromosome studies in *Alstroemeria* were carried out. In the present contribution, seven native taxa from the Andes were investigated: *Alstroemeria andina* Phil. ssp. *venustula* (Phil.) Ehr. Bayer, *A. hookeri* Lodd. ssp. *cummingiana* (Herb.) Ehr. Bayer, *A. hookeri* Lodd. ssp. *recumbens* (Herb.) Ehr. Bayer, *A. pallida* Graham, *A. patagonica* Phil., *A. pseudospathulata* Ehr. Bayer and *A. pygmaea* Herb.

Alstroemeria pygmaea is a small herb growing at 3500–4400 m in the Andean mountains, in Perú, Bolivia and north-west Argentina (Sanso & Xifreda 1999). The taxonomic position of this taxon has long been under debate. Many authors have treated *A. pygmaea* as a distinct genus, *Schickendantzia* Pax (Dahlgren *et al.*, 1985; Kosenko, 1994; Stevenson & Loconte, 1995; Bayer, 1998). Its chromosomes and karyotype have not been investigated previously.

Alstroemeria andina ssp. *venustula* is also a small herb, 5–16 cm tall, occurring at 2800–3700 m in Argentina and Chile (Sanso, 1996).

Alstroemeria patagonica and *A. pseudospathulata*, two other *trans*-Andean species of Argentina and Chile, inhabit the Patagonian meseta in Argentina: *A. patagonica* from Neuquén to Santa Cruz and Tierra

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del Fuego and *A. pseudospathulata* in Calmuco Valley, Mendoza, and on the Limay River, bordering the area between the Neuquén and the Río Negro provinces (Sanso, 1996).

A. hookeri ssp. *cummingiana*, *A. hookeri* ssp. *recumbens* (both at less than 500 m) and *A. pallida* (1500–2800 m) are native in central Chile, between 32° and 34°S (Bayer 1987).

MATERIAL AND METHODS

Plant material

Flower buds of Argentine origin were collected from wild populations between 1995 and 1997 and those of Chilean source were obtained from plants cultivated at Copenhagen Botanical Garden (Denmark) in 1999. The origin of the accessions studied is shown in Table 1. Voucher specimens are deposited in the Herbarium of Instituto Darwinion (SI).

The Argentine *Alstroemeria* species were identified according to Sanso (1996) and those of Chile following Bayer (1987).

Meiotic studies

For meiotic studies, flower buds were fixed in either ethanol–chloroform–glacial acetic acid (6:3:1), or in acetic acid–ethanol (1:3) for at least 24 h, and then transferred into 70% ethanol and stored at 4–5 °C until required. Immature anthers were squashed directly in propionic acid haematoxylin (2%) using ferric citrate as a mordant (Sáez, 1960). Meiosis was studied using a minimum of 25 pollen mother cells per plant.

Pollen stainability was studied with Alexander's differential staining (Alexander, 1969).

Karyotype analysis

Karyotypes of *A. pygmaea* were obtained from mitosis of ovules and those of *A. andina* ssp. *venustula* from mitosis of anthers, both without pretreatment. Immature flower buds were fixed in ethanol–chloroform–glacial acetic acid (6:3:1), placed in 70% alcohol, and stored at 4–5 °C until required. Immature ovules were stained and squashed using propionic acid haematoxylin (2%).

The determination of karyotype parameters was carried out from enlarged photomicrographs of selected cells. Measurements were made on five cells, but the karyotype of *A. pygmaea* was described from ten mid-metaphases. As only one cell was considered for *A. andina* ssp. *venustula* karyotype data, standard errors in that case are not given. The mean chromosome length (CL) and centromeric index (CI) were calculated for each chromosome pair. The nomenclature and abbreviations used for the description of the chromosome morphology is that proposed by Levan *et al.* (1964). Chromosome pairs were aligned and numbered in order of their decreasing length. For each cell, values of CL were added to give the total chromosome length (TCL). The chromosome length percentage of TCL for each chromosome type (RL) was then calculated.

Intrachromosome asymmetry index, A_1, and interchromosome asymmetry index, A_2, two numerical parameters for the estimation of karyotype asymmetry, were calculated according to Romero Zarco (1986).

RESULTS

Chromosome numbers

All *Alstroemeria* plants studied were diploid with $2n = 2x = 16$ chromosomes (Table 1), but some meiotic cells of *A. hookeri* ssp. *cummingiana* presented as many as two B chromosomes, either as univalents or forming a bivalent.

Karyotype analyses

The karyotype of *Alstroemeria andina* ssp. *venustula* is given in Figure 1A. Its formula is 3 m pairs, 1 sm pair and 4 t (1 t-st) with microsatellites observed on pairs n°3 and n°6 (Table 2). Chromosome lengths are from 5.55 µm to 22.78 µm. Pair n°1 constitutes about 29% of the total length of the chromosome complement and pairs n°1 and 2 are about 45% of it (Table 2). The sampled individual was apparently heterozygous for pair n°3, in relation to its length.

The karyotype of *Alstroemeria pygmaea* does not differ much from the above (Fig. 1B). It consists of two pairs of chromosomes with their centromeres in the median region (m), one with centromeres in the submedian region (sm), one with centromeres in the submedian-subterminal region (sm-st) and four with centromeres in the terminal region (t) (Table 2). Three of the t-chromosome pairs bear microsatellites on the short arm, pairs n°3, 5 and 6.

Chromosome pairs of *A. pygmaea* are very long, ranging from 8.50 ± 0.50 µm to 28.67 ± 1.15 µm in length (Table 2). The large size of chromosome pair n°1 is a striking peculiarity in all *Alstroemeria* species. Comparing it to the shortest pair, it was about 3.4 times longer than pair n°8. It was about one-and-a-half times the length of chromosome pair n°2, being about 9 µm longer. Values of chromosome asymmetry indexes were calculated: $A_1 = 0.59$ and $A_2 = 0.47$ (Table 3). The total chromosome length of *A. andina* ssp. *venustula* is smaller (157.2 µm) than in *A. pygmaea* (224 µm) but the interchromosome asymmetry is higher ($A_2 = 0.54$) than that of *A. pygmaea* (Table 3).

Table 1. Taxa, origins, chromosome numbers and type of studied chromosomes

Taxon	Place of collection and voucher	2*n*	Chromosomes
Alstroemeria andina Phil. ssp. *venustula* (Phil.) Ehr. Bayer	Argentina. Prov. San Juan. Dpto. Calingasta. Puesto de Gendarmería, Las Juntas. 29-I-1997. *Fortunato & Kiesling* 5630 (SI)	16	Mitotic
A. hookeri Lodd. ssp. *cummingiana* (Herb.) Ehr. Bayer	Cult. Copenhagen Botanical Garden P1995-5011 (SI). Origin: Chile. IV Región of Coquimbo. Prov. Choapa. Pan Am N 250 km	16	Meiotic
A. hookeri Lodd. ssp. *recumbens* (Herb.) Ehr. Bayer	Cult. Copenhagen Botanical Garden P1995-5010 (SI). Origin: Chile. V Región of Valparaíso. Prov. Aconcagua. Longotoma, 225 msm	16	Meiotic
A. pallida Graham	Cult. Copenhagen Botanical Garden P1995-5035 (SI). Origin: Chile. Región Metropolitana of Santiago. Santiago. Lagunillas, 2000–2700 msm	16	Meiotic
A. patagonica Phil.	Argentina. Prov. Neuquén. Dpto. Zapala. Parque Nac. Laguna Blanca. 16-XII-1997. *Xifreda & Sanso* 2035 (SI)	16	Meiotic
A. pseudospathulata Ehr. Bayer	Argentina. Prov. Neuquén. Dpto. Chos- Malal. 14 km from Chos-Malal road to Andacollo. 12-XII-1997. *Xifreda & Sanso* 2004 (SI)	16	Meiotic
A. pygmaea Herb.	Argentina. Prov. Tucumán. Dpto. Trancas. Hualinchay. Near Rodeo Largo. *c.* 3500 msm. 15-XII-1995. *Sanso & Pereyra* 8 (SI)	16	Mitotic

Table 2. Centromere position, chromosome length (CL) and chromosome length percentage relative to TCL for each chromosome type (RL) of *Alstroemeria andina* ssp. *venustula* (*A.a.v)* and *Alstroemeria pygmaea* (*A.p)* haploid genomes. Average values (CL) and standard error (S.E., only for *A. pygmaea*) are presented

		CL (μm)		RL (%)	
Chromosome pair	Centromere position	*A.a.v.*	*A.p.*	*A.a.v*	*A.p.*
1	m	22.78	28.67 ± 1.15	28.98	26.00
2	m (*A.a.v*), sm (*A.p*)	12.50	19.33 ± 0.58	15.90	17.26
3	t – with microsatellite	9.17	14.17 ± 0.29	11.67	12.65
4	t	8.61	11.83 ± 0.29	10.95	10.56
5	t (st) (*A.a.v*), t – with microsatellite (*A.p*)	8.05	10.33 ± 1.26	10.24	9.22
6	t – with microsatellite	6.39	9.83 ± 0.29	8.13	8.78
7	m	5.55	9.33 ± 0.58	7.06	8.33
8	sm (*A.a.v*), sm-st (*A.p*)	5.55	8.50 ± 0.50	7.06	7.59

MEIOSIS

Both *Alstroemeria pseudospathulata* (Figs 2–5) and *A. patagonica* (Figs 6,7) showed normal male meiotic behaviour, with eight bivalents of different morphologies at diakinesis and metaphase I, two of them easily discernable because of their notably larger size. These pairs usually form close bivalents, the largest one with three or more chiasmata. Bivalents present proximal, interstitial and terminal chiasmata.

The presence of supernumerary chromosomes is remarkable in *A. hookeri* ssp. *recumbens* (Figs 8,9), in which one or two B chromosomes could be detected in most of the cells of the accession studied. When two B chromosomes were observed, they could be seen as univalents (Fig. 9) or forming a bivalent. They are

Figure 1. Karyograms. A. *Alstroemeria andina* ssp. *venustula* (*Fortunato & Kiesling* 5630), from anther without pretreatment. B. *Alstroemeria pygmaea* Herb. (*Sanso & Pereyra* 8), from ovule without pretreatment. One of the first chromasome pairs was lost (from the cell analysed, but this absence is not typical of the whole plant).

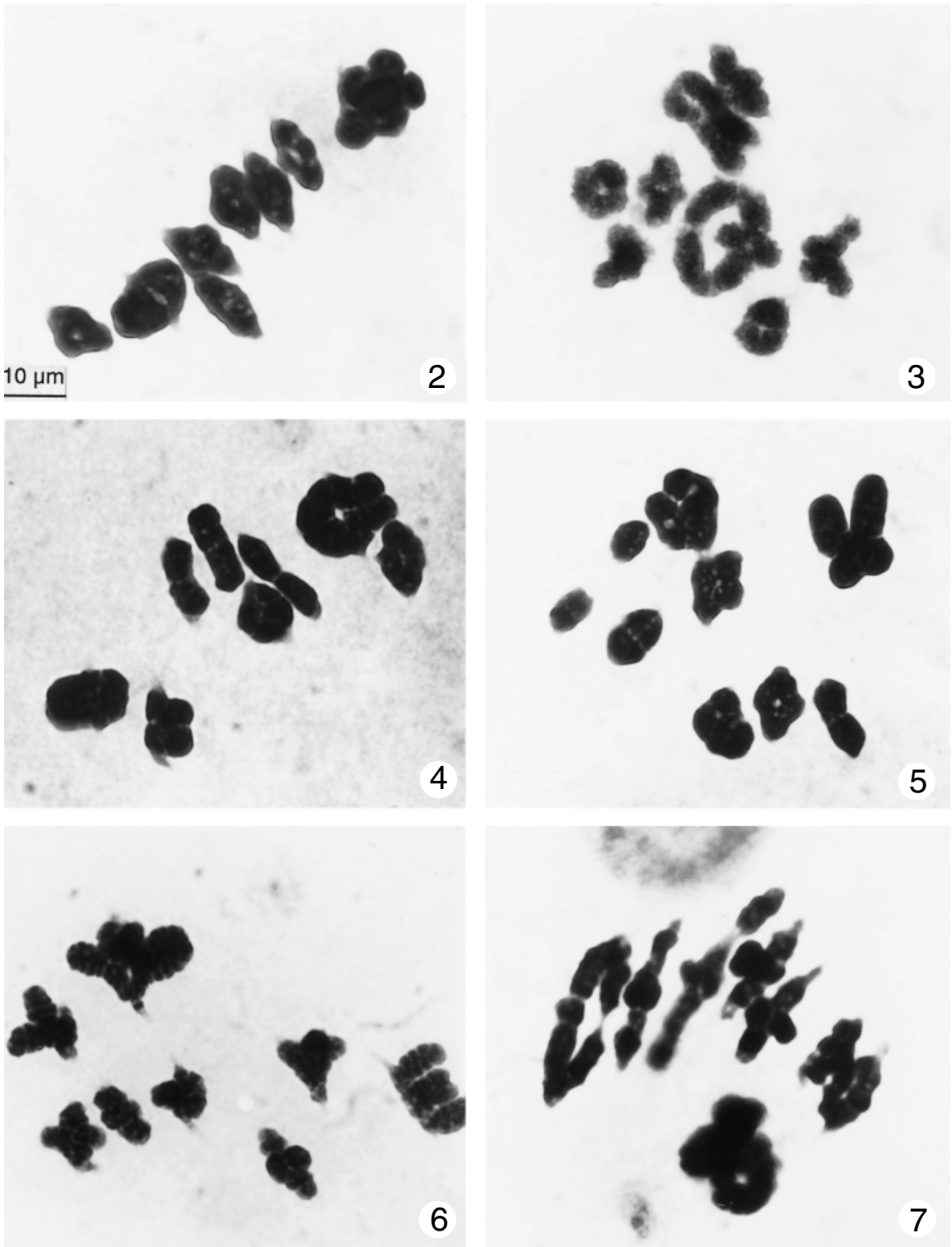
Table 3. Karyotype characteristics of *Alstroemeria andina* ssp. *venustula* and *A. pygmaea*. TCL: total chromosome length (2*n*); CL: average chromosome length; A_1: intrachromosome asymmetry index; A_2: interchromosome asymmetry index. Averages are indicated and SE only for *A. pygmaea*

Taxon	*A. andina* ssp. *venustula*	*A. pygmaea*
2*n*	16	16
Karyotype formulae	3 m + 1 sm + 3 t + 1 t (st)	2 m + 1 sm + 1 sm-st + 4 t
Number of satellites observed	4	6
TCL (µm)	157.2	224 ± 2.00
CL (µm)	9.82	14 ± 0.25
A_1 Asymmetry Index	0.56	0.59 ± 0.02
A_2 Asymmetry Index	0.54	0.47 ± 0.02
Length longest pair/ Length shortest pair	4.10	3.45 ± 0.32
Length pair n°1- Length pair n°2 (µm)	10.28	9.33 ± 1.53

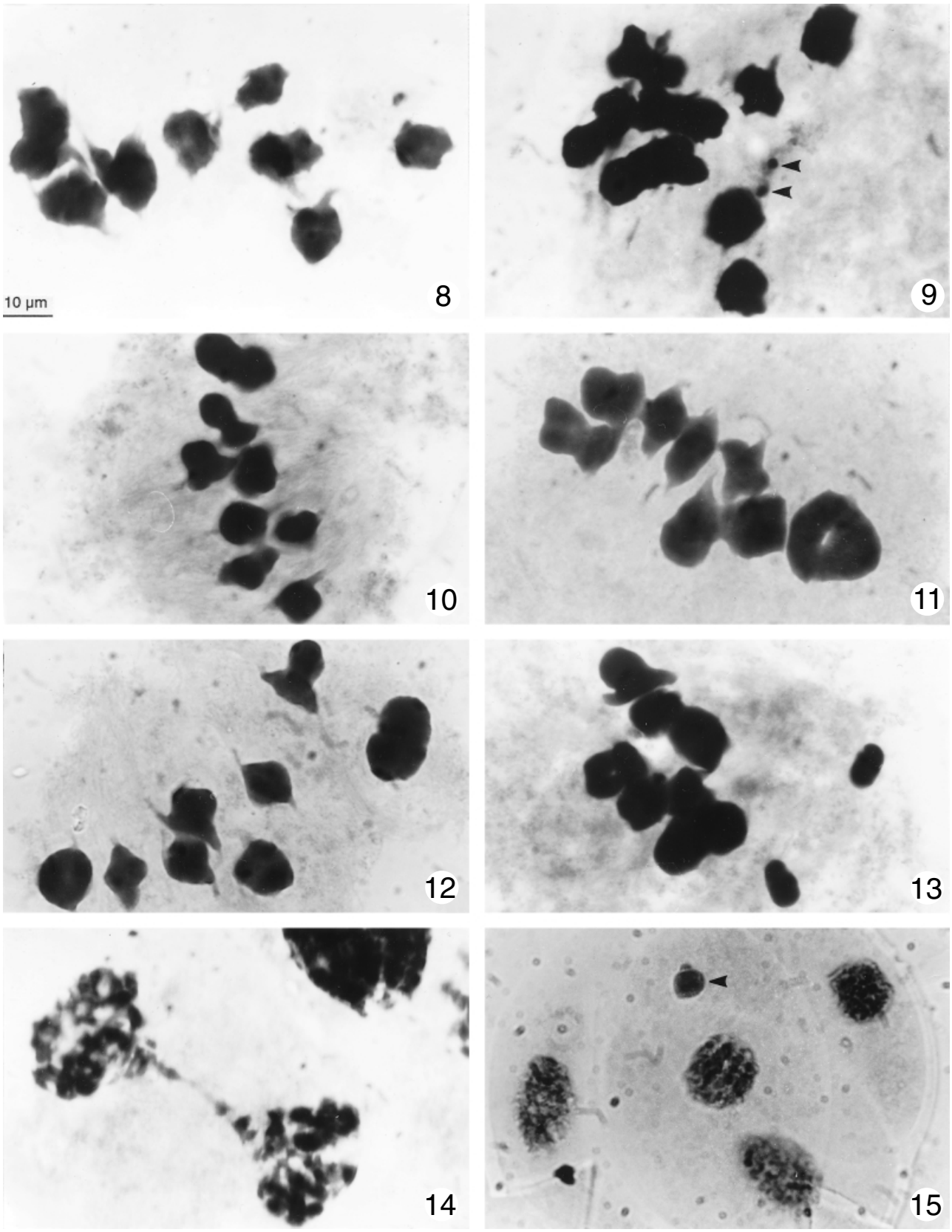
smaller (1.5–2.5 µm) than the A-chromosomes and at metaphase I they tended to be non-congressed.

The meiotic behaviour of *A. pallida* was fairly normal (Figs 10–13), but in a few cells 7 II + 2 I were observed (Fig. 13).

Meiotic irregularities at various stages were observed in *A. hookeri* ssp. *cummingiana* (Figs 14,15). Occasionally, at metaphase I, one or more bivalents were observed to be non-congressed. At telophase I, presence of bridges (Fig. 14), fragments and lagging



Figures 2–7. Meiotic chromosomes. Figs 2–5. *Alstroemeria pseudospathulata* (*Xifreda & Sanso* 2004). Figs 6,7. *Alstroemeria patagonica* (*Xifreda & Sanso* 2035). In all cases 8 II are seen, except in Fig. 5, which shows 7 II + 2 I. Figs 2,7. Metaphase I; the rest, diakinesis. Scale bar = 10 µm. All figures to same scale.



Figures 8–15. Meiotic chromosomes. Figs 8,9. *Alstroemeria hookeri* ssp. *recumbens* (P1995-5010). Fig. 8. 8 II, without B chromosomes. Fig. 9. 8 II + 2 B chromosomes (arrowheads). Figs 10–13. *Alstroemeria pallida* (P1995-5035). Figs 10–12. 8 II. Fig. 13. 7 II + 2 I. Figs 14,15. *Alstroemeria hookeri* ssp.*cummingiana* (P1995-5011). Fig. 14. Telophase I, bridge. Fig. 15. Tetrad with a micronucleus (arrowhead). Scale bar = 10 μm in Fig. 8. All figures to same scale.

Table 4. Numbers and percentage of tetrads with and without micronuclei in *Alstroemeria hookeri* ssp. *cummingiana*

Micronuclei number	0	1	2	3	4	Total
Tetrads number	696	69	16	1	1	783
	–	79.31%	18.39%	1.15%	1.15%	
Percentage	88.89%		11.11%			100%

chromosomes were relatively common. At the tetrad stage, a considerable percentage (11%) presented micronuclei (1–4, Table 4; Fig. 15); also some dyads showed micronuclei.

Pollen stainability

The frequency of pollen grain stainability in the species that could be analysed was high, ranging from 87% (*A. hookeri* ssp. *recumbens*) to 94% (*A. pseudospathulata*), with intermediate values in *A. pallida* and *A. patagonica* (92%). Pollen stainability in *Alstroemeria hookeri* ssp. *cummingiana* was expected to be low because of the irregularities observed at male meiosis. Unfortunately, it could not be evaluated.

DISCUSSION

Chromosome data for all the taxa considered are given here for the first time. There is a previous record for *A. hookeri* (Tsuchiya & Hang 1989), but the authors did not indicate the provenance of the material studied or mention the existence of a voucher for it.

Alstroemeria may be considered chromosomally stable with a constancy of the chromosome number ($2n = 16$) and an asymmetrical complement. *Alstroemeria pygmaea* and *A. andina* ssp. *venustula* karyotypes are also asymmetrical, with large chromosomes as in the species studied previously: *A. angustifolia* ssp. *angustifolia*, *A. aurea, A. brasiliensis*, *A. chilensis*, *A. haemantha*, *A. isabellana, A. magnifica* ssp. *magnifica*, *A. pelegrina*, *A. philippii* and *A. psittacina* (Tsuchiya & Hang, 1989; Stephens *et al.*, 1993; Buitendijk & Ramanna, 1996, Sanso & Hunziker, 1998). The only exception to the uniform basic karyotype structure is *A. ligtu* ssp. *ligtu*, which has a relatively symmetrical complement and an exceptional, large, metacentric chromosome 6 (Buitendijk & Ramanna, 1996).

Heterozygosity for some chromosome pairs in relation to the length, as in *A. andina* ssp. *venustula*, pair n°3, and/or satellite presence has been reported previously (Buitendijk & Ramanna, 1996; Sanso & Hunziker, 1998). Another kind of difference between homologous chromosomes of *Alstroemeria* is in the amount of heterochromatin (e.g. size and number of C-bands, Buitendijk & Ramanna, 1996)

It is clear that although chromosome sizes in *Alstroemeria* vary from species to species, they are karyotypically very similar in terms of relative size relationships between the chromosomes. The values obtained for species reported here were not significantly different from the values obtained for the species studied previously (Buitendijk & Ramanna, 1996; Sanso & Hunziker, 1998), with the exception of *A. ligtu* ssp. *ligtu* which differs from the other *Alstroemeria* species (Buitendijk & Ramanna, 1996). The proportion of the total complement occupied by the largest chromosome pair and the two largest ones varies between 21.4% and 36%, respectively, in *A. aurea* ((Buitendijk & Ramanna, 1996) to 28.98% and 45% in *A. andina* ssp. *venustula* (this paper), with the exception of *A. ligtu* ssp. *ligtu* (Buitendijk & Ramanna, 1996).

Between species, there is a considerable variation in nuclear DNA content, the amount of C-banded heterochromatin (Buitendijk & Ramanna, 1996; Buitendijk *et al.*, 1997) and the presence or lack of satellites on several pairs of chromosomes. Two species differed by about a factor of two in the total chromosome length; *A. magnifica* = 116 μm (Buitendijk & Ramanna, 1996) and *A. pygmaea* = 224 μm (this paper), although this difference is perhaps overestimated because their chromosomes, obtained from anthers and ovules, did not receive pretreatment. However, in *Alstroemeria*, bimodal karyotypes occur despite these differences in the total chromosome

length. It seems that in this group DNA has been added to the complements without altering the karyotype morphology too much.

Alstroemeria has special interest because of its large chromosomes and its asymmetric karyotypes. Bimodality is widespread and may represent a specialized kind of nuclear architecture that is selected for at the level of the genome, independently of genetic status (Kenton *et al*., 1990). The existence of taxa with similar bimodal karyotypes could be explained by karyotype orthoselection or karyotype conservation (White, 1973). In the first case, structural chromosome mutations occur in a characteristic way, while in the second case there is a lack of structural mutation preserving the existing chromosome morphology. In *Alstroemeria*, the species maintain their karyotypes' asymmetry indexes A_1 and A_2, suggesting that some orthoselection mechanism is in process.

From a morphological-anatomical point of view, *A. pygmaea* falls clearly within the variation range of *Alstroemeria* (Sanso, 1996; Sanso & Xifreda, 1999). The karyotype of *Alstroemeria pygmaea* shares a further interesting similarity to those studied previously. Thus, to all existing arguments for not retaining *Schickendantzia* as a separate genus, we can add another one which obviously merges *A. pygmaea* with other *Alstroemeria* species, and does not further support its taxonomic uniqueness.

Supernumerary or B chromosomes are known to occur in a great number of plant and animal taxa. In *Alstroemeria* they have been reported previously only in *A. angustifolia* ssp. *angustifolia*, by Buitendijk & Ramanna (1996), who observed three at mitosis. B chromosomes have been found to have adaptative effects, conferring a superior fitness in some taxa (Jones & Rees, 1982; Holmes & Bougourd, 1989, 1991). The occurrence of B chromosomes may have played such a role in the colonization of different environments by some members of *A. hookeri*. Whether they are eventually lost or whether they persist over many generations is unknown. It would be interesting to carry out an extensive survey along the distribution areas of *A. hookeri* ssp. *cummingiana*, *A. hookeri* ssp. *hookeri*, *A. hookeri* ssp. *maculata* and *A. hookeri* ssp. *recumbens* in order to estimate the frequency of B chromosomes in the different natural populations of this species.

ACKNOWLEDGEMENTS

I am very grateful to Lone Aagesen for providing material cultivated at Copenhagen Botanical Garden (Denmark), Roberto Kiesling for material of *Alstroemeria andina* from San Juan (Argentina) and Arturo Wulff for his help in many ways. I am also especially grateful to Juan H. Hunziker for supervising the project and helpful suggestions on this manuscript. The financial support of the Consejo Nacional de Investigaciones Científicas y Tecnológicas de Argentina (CONICET: Project PEI 0339/98) and the Universidad de Buenos Aires (UBA: Project TW 057) to Juan H. Hunziker are gratefully acknowledged.

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