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KARYOTYPES OF FIVE *RHODOPHIALA* SPECIES (AMARYLLIDACEAE)*

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Summary: *Rhodophiala bifida* (Herb.) Cabrera (2n = 16 and 18), *R. elwessi* (C. H. Wright) Traub (2n = 18, 36 and 72), *R. araucana* (Phil.) Traub (2n = 54), *R. andicola* (Poepp.) Traub (2n = 16), and *R. rhodolirion* (Baker)Traub (2n = 16) are the species the karyotypes of which are analyzed in this paper. The chromosome number of *R. bifida* is confirmed and those of the other four species are reported here for the first time. The findings for *R. elwessi* (2n = 36 and 72) and *R. araucana* (2n = 54) are the first cases of polyploidy recorded for the genus. There exist in *Rhodophiala* two basic chromosome numbers, i.e., x = 8 and 9 and the basic karyotype of their respective species remain constant. For x = 8: 1 m (small) + 1 m (large) + 5 m (medium-large) + 1 st (large); for x = 9: 1 m (small) + 1 sm (small) + 7 sm or st (medium-large). Interspecific variations in the position of the Nuclear Organizer Region (NOR) was detected. In two other genera of this family, *Amaryllis* and *Hippeastrum*, the latter of which is akin to *Rhodophiala*, the basic chromosome number is x = 11 which is considered to be the ancestral one. We propose that x = 8 in *R. bifida* is derived from x = 9 by means of a reciprocal exchange between one m small and one sm or st medium, diminishing to one the number of m-sm small. A similar mechanism could explain the reduction from x = 11 to x = 9. *Rodophiala andicola* and *R. rhodolirium* have a similar karyotype composed of 5 m (2 small + 3 mediums) + 1 sm (small) + 2 st (small) which is quite apart from those found in the remainder species of the genus. This fact is also supported by an analysis of the asymmetry index characteristic of the group. Moreover, significant differences in the exomorphology of the latter species with respect to the others give additional evidence to rehabilitate the genus *Rhodolirion* where both species were originally included.

Key words: Amaryllidaceae, *Rhodophiala*, *Rhodolirion,* karyotype, karyotype orthoselection.

Resumen: Cariotipos de cinco especies de *Rhodophiala* (Amaryllidaceae). En el presente trabajo se analizan los cariotipos de *R. bifida* (Herb.) Cabrera (2n = 16 y 18), *R. elwessi* (C. H. Wright) Traub (2n = 18, 36 y 72), *R. araucana* (Phil.) Traub (2n = 54), *R. andicola* (Poepp.) Traub (2n = 16), y *R. rhodolirion* (Baker) Traub (2n = 16). Se confirma 2n = 16 para *R. bifida*, siendo nuevos el resto de los recuentos cromosómicos. Los números hallados en *R. elwesii* (2n = 36 y 72) y en *R. araucana* (2n = 54) serían los primeros casos de poliploidía descriptos en el género. En *Rhodophiala* existen dos números cromosómicos básicos x = 8 y x = 9, siendo constantes sus cariotipos. Los mismos son 1 m (chico) + 1 m (grande) + 5 sm (medianos-grandes) + 1 st (grande) para un x = 8 y 1 m (chico) + 1 sm (chico) + 7 sm ó st (grande) para el x = 9. Existe variación interespecífica en la posición del organizador nucleolar (NOR). El número básico ancestral de la familia sería x = 11. En géneros con x = 11 afines a *Rhodophiala*, como *Hippeastrum,* se encontró que poseen 4 m pequeños. En *R. bifida* el número básico x = 8 habría derivado de x = 9 por translocación recíproca entre un m chico y un sm ó st mediano, reduciendo a uno la cantidad de m-sm chicos. Este mecanismo podría ser generalizado para explicar la reducción de x = 11 a x = 9. *Rhodophiala andicola* y *R. rhololirion* son cromosómicamente semejantes entre si y sus cariotipos básicos compuestos por 5 m (dos chicos y tres medianos) + 1 sm (chico) + 2 st (chicos) se apartan mucho de los encontrados en el resto de las especies del género. Este hecho se ve apoyado por el análisis de los índices de asimetría cariotípica del grupo. Esto, sumado a las diferencias importantes en la exomorfología de estas dos especies, en relación con las restantes del género, daría bases para rehabilitar al género *Rhodolirion* donde las dos especies citadas estaban originalmente incluidas.

Palabras clave: Amaryllidaceae, *Rhodophiala*, *Rhodolirion,* cariotipos, ortoselección cariotípica.

INTRODUCTION

In Amaryllidaceae, karyotype analysis has been a useful tool to solving taxonomical problems. It is generally agreed that the ancestral basic number of the family is x = 11, which is found in genera such as *Amaryllis* and *Hippeastrum* (Naranjo, 1969; Naranjo & Andrada, 1975; Naranjo & Poggio, 1988; Poggio & Naranjo, 1990). The genus *Rhodophiala* Presl. is composed of more than 40 species from South American tropical and sub-tropical regions (Uruguay, Argentina, Bolivia, and Chile). Previous studies have reported the chromosome number of only four *Rhodophiala* species. Two basic chromosome numbers are known in this genus: x = 9 and 8 (Flory, 1968;

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Naranjo, 1969).

This paper presents the karyotypes of several populations of R. *bifida* (Herb.) Cabrera, which is common in Buenos Aires and Entre Ríos Provinces, and the karyotypes of the Patagonian species *R. elwessi* (C. H. Wright) Traub, *R. araucana* (Phil.) Traub, R. *andicola* (Poepp.) Traub, and *R. rhodolirion* (Baker) Traub. These studies were intended as a contribution to understand the origin of the two basic chromosome numbers of the genus and their relationships.

Material and Methods

The source of the material studied, all from Argentina, is indicated below. Abbreviations: AB = Arturo Burkart, ATH = Armando T. Hunziker, AW = Arturo Wulf, CAN = Carlos A. Naranjo, OB = Osvaldo Boelke, ZR & AM = Zulma Rúgolo & A. Martínez, GB & EM = Gabriel Bernardello & Eduardo Moscone, K = Kew number (Royal Botanic Gardens, Kew, UK). Voucher specimens are deposited at Kew Hebarium (K), "Instituto de Botánica Darwinion" Herbarium (SI), or "Museo Botánico de Córdoba" Herbarium (CORD).

Rhodophiala bifida.- (CAN 141), *Prov. Buenos Aires, Part. Tandil*, Tandil (2n = 16); (CAN 2372, AB29649), *Prov. Entre Ríos, Dpto. Victoria*, Siete Colinas (2n = 18); (K417-76-03984), *Prov. Buenos Aires* (2n = 18).

R. elwesii.- (CAN 736), *Prov. La Pampa, Dpto. Utracán*, Chacharramendi (2n = 18); (OB 15785), *Prov. Mendoza, Dpto. San Rafael*, San Rafael, El nevado (2n = 18); (CAN 527), *Prov. Neuquén, Dpto. Los Lagos*, Villa La Angostura (2n = 36); (CAN 563), *Prov. Neuquén, Dpto. Huiliches*, Lago Huechulauquen (2n = 72).

R. aff. *elwesii.*- (AW 365), *Prov. Neuquén, Dpto. Huiliches*, Laguna Epulauquen (2n = 18), det. ATH; (AW 360), *Prov. Neuquén, Dpto. Huiliches*, Laguna Epulauquen (2n = 18+1B or 2B) det. ATH.

R. araucana.- (ZR & AM, BAA 12241), *Prov. Neuquén, Dpto. Norquín*, Copahue, det. ATH (2n = 54).

R. andicola.- (GB & EM 621), *Prov. Neuquén, Dpto. Lácar*, between Lacar lake and Lolog lake, det. ATH (2n = 16).

R. rhodolirion.- (AW349), *Prov. Mendoza, Dpto. Malargüe*, Valle de Las Leñas, det. ATH (2n = 16).

Cytological analysis was performed on root tips of 3-10 mm from bulbs that were pretreated for 2.5 h in a 0.002 M solution of 8 hydroxyquinoline at 20±2°C, fixed in 3:1 (absolute ethanol:acetic acid) and stained in Feulgen solution after 50 minutes of hydrolysis in 5 N HCl at 20° C. Slides were made permanent by freezing with liquid CO_2, removing the coverslip, dehydrating in absolute alcohol and mounting in Euparal. The nomenclature used for the description of chromosome morphology is that proposed by Levan *et al.* (1964). The practical method proposed by Naranjo *et al.* (1986) was used to classify each chromosomes. The total chromosome volume (TCV) was estimated using the formula $TCV = (P \times r^2 \times TCL) \times 2$ (r = average radius of the chromatid; TCL = total chromosome length). To estimate the karyotype asymmetry, two numerical parameters were used according to Romero Zarco (1986): A_1 = intrachromosomal asymmetry index = $1 - [S_1^n (\text{short arm}/\text{long arm})] / n$) and A_2 = interchromosomal index = standard division (S)/ mean length (x). Both indexes are independent of chromosome number and size. The determination of the karyotype parameters was carried out using a Mini-Mop (Kontron) Image Analyser and working with photomicrographs. Mean descriptive values for the karyotypes were calculated with the information obtained from a minimum of five scattered metaphase plates measured in each accession.

Results

In Table 1, the karyotype characteristics of different cytotypes we found in five species of *Rhodophiala* are described.

In *Rhodophiala bifida* we found populations with 2n = 16 and 2n = 18 (Table 1; Fig. 1). The basic karyotype of cytotype 2n = 16 is composed of 1 m (small) + 1 m + 5 sm + 1 st and the chromosome length ranged from 3.9 to 8.6 µm. The cytotype 2n = 18 had 1 m (small) + 1 sm (small) + 6 sm + 1 st and the chromosome length ranged from 4.0 to 8.9 µm. In both cases the nucleolar organizer region (NOR) was located on the short arm of the pair st. In one population with

Table 1. Karyotype characteristics of *Rhodophiala* species. **TCL** = total chromosome length; **TCV** = total chromosome volume; A_1 and A_2 see methods. **NOR** = Nuclear Organiser Region.

Species and voucher number	2n	Ploidy	Basic karyotype formula		Position of the NOR	TCL (µm)	TCV (µm³)	Asymmetry indexes	
			small (≤ 5µm)	medium-Large (> 5µm)				A_1	A_2
R. bifida									
CAN 141	16	2x	1 m	+ 1m + 5 sm + 1 st	st, on short arm	92.86	30.25	0.61	0.22
CAN 2372	18	2x	1 m + 1sm	+ 6 sm + 1 st	st, on short arm	119.28	30.51	0.55	0.17
R. elwesii									
A 1067	18	2x	1 m + 1 sm	+ 2 sm + 5 st	medium sm, on long arm	92.67	32.00	0.61	0.31
CAN 527	36	4x	1 m + 1 sm	+ 2 sm + 5 st	sm, on long arm	267.89	58.05	0.65	0.30
CAN 563	72	8x	1 m + 1 sm	+ 2 sm + 5 st	sm, on long arm	480.00	104.02	0.66	0.26
R.* aff. *elwesii									
AW 365	18	2x	1 m + 1 sm	+ 2 sm + 5 st	st, on long arm	102.78	36.00	0.68	0.22
R. araucana									
BAA 12241	54	6x	1 m + 1 sm	+ 3 sm +1 sm-st + 3 st	medium sm, on long arm	313.85	93.67	0.59	0.24
R. andicola									
GB & EM 621	16	2x	2 m + 1 sm + 2 st	+ 3m	st, on short arm	78.05	23.63	0.23	0.33
R. rhodolirion									
AW 349	16	2x	2m + 1 sm + 2 st	+ 3m	st, on short arm	90.73	24.50	0.36	0.47

2n = 18 from Buenos Aires Province we found one individual with two heteromorphic pairs of chromosomes (Fig. 1 E, F, pairs 2 and 3).

Rhodophiala elwessi is a complex that includes diploid (2n = 18), tetraploid (2n = 36) and octoploid (2n = 72) cytotypes (Table 1; Figs. 2 and 3). The basic karyotype of this species is composed of 1 m (small) +1 sm (small) + 2 sm (mediums) + 5 st (mediums) the chromosome length ranging from 2.2 to 6.5 µm (Fig. 2). The NOR is located on the long arm of one medium sm, with a punctiform satellite. This satellite cannot be seen sometimes, and in these cases only the terminal secondary constriction (NOR) remains visible. The tetraploid (2n = 36) and octoploid (2n = 72) cytotypes of this species possess the same basic karyotype described for the diploids (Fig. 3): 1 m (small) + 1 sm (small) + 2 sm (mediums) + 5 st (mediums), and the chromosome length ranges from 2.8 to 10.2 µm.

Rhodophiala aff. *elwesii* (2n = 18) possess differences with *R. elwesii* in respect of the size of the flowers, but they are similar in other exomorphological features and in their karyotype formula: 1 m (small)+ 1 sm (small), 2 sm (mediums) + 5 st (mediums), and the chromosome length ranges from 2.7 to 8.1 µm. In these taxa the NOR is located on the long arm, but in one of the st medium chromosome pairs instead of a medium sm one. In the same population, individuals with 1 and 2 B chromosomes were found. These Bs are m and smaller (1.5 to 1.8µm) than the A-chromosomes (Fig. 2 C-F).

In *Rhodophiala araucana* we found an hexaploid cytotype with 2n = 54 and the karyotype is composed of 1m + 1 sm (both small) + 3 sm + 1 sm-st + 3 st, and the chromosome length ranged from 3.1 to 9.2 µm (Table 1, Fig. 4A and B). The NOR is terminal on the long arm of a sm medium chromosome pair (shown with arrow in Fig. 4A). Some individuals possess 1 or 2 B chromosomes. This accessory chromosome presents a different morphology (st small) from the Bs found in *R.* aff. *elwessi* (m small).

In *Rhodophiala andicola* and *R. rhodolirion,* both species present diploid individuals with 2n = 16 (x = 8) and similar karyotype formula composed of 2 m + 1 sm + 2 st (all small) + 3 m (long) (Fig. 5), and the chromosome length ranged from 3.2 to 8.5 µm. The NOR is located on the short arm of the smaller st pair, and possesses a terminal microsatellite.

In interphase nuclei, the maximum numbers of nucleoli observed were 2 in the diploid (2n = 16 and 2n = 18), 4 in the tetraploid (2n = 32), 6 in the hexaploid (2n = 54) and 8 in the octoploid (2n = 72) species. This data indicates that each basic genome posses one functional NOR in all the studied species.

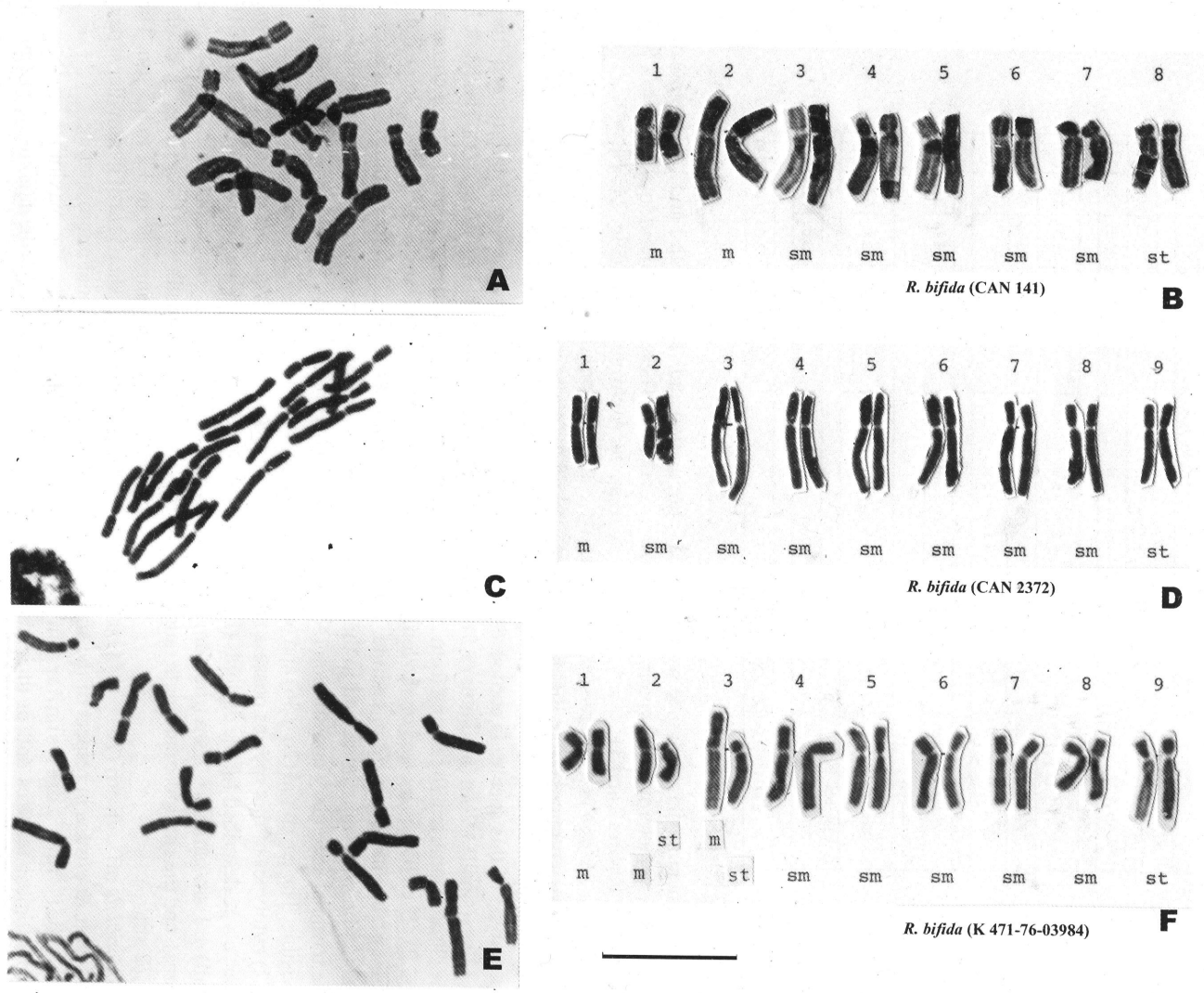

Fig. 1, A, C and **E**; Mitotic metaphases, and **B, D** and **F**: respective karyograms of three different samples of *Rhodophiala bifida*. The scale represents 10 μm.

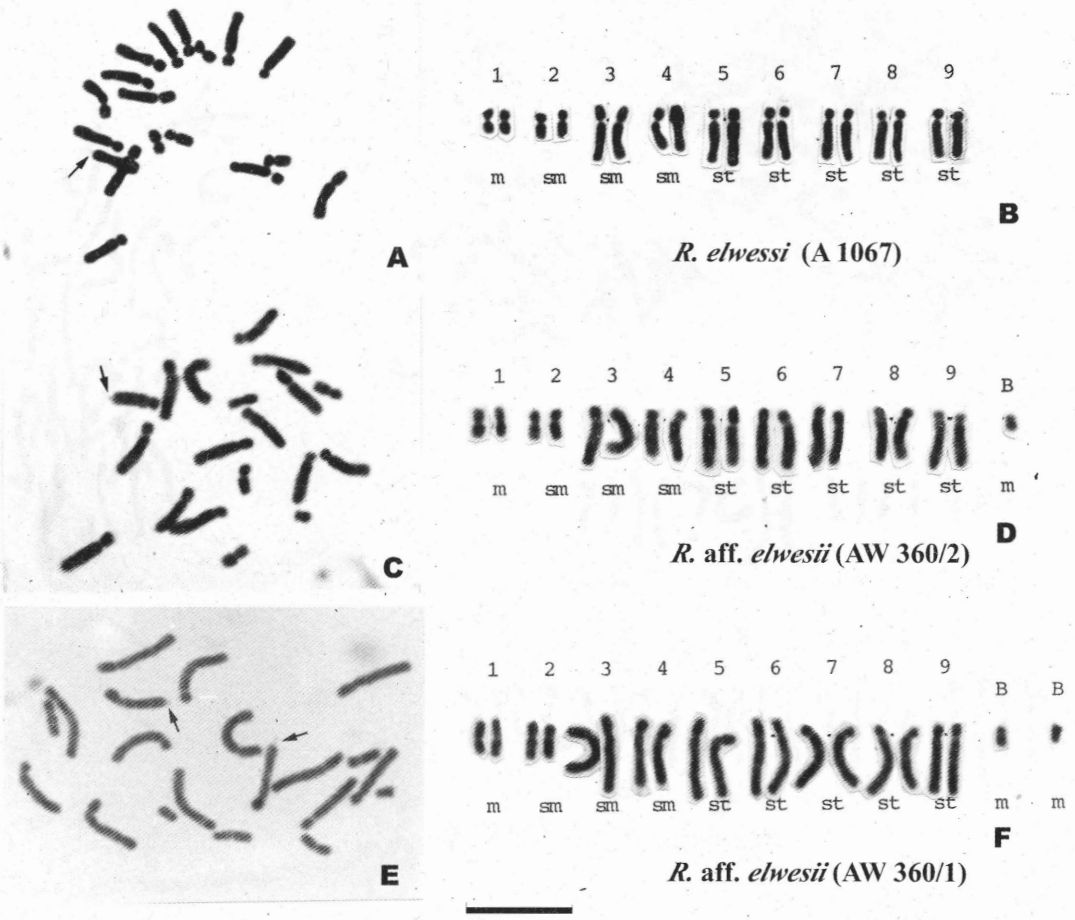

Fig. 2. A, C and **E:** Mitotic metaphases, and **B, D** and **F:** respective karyograms of diploid populations of *Rhodophiala elwesii* and two diploid samples of *R.* aff. *elwesii*. Arrows show NOR regions. The scale represents 10 μm.

Discussion

Bimodal and constant karyotypes occur in many plants and animals, and represent a very specialized karyotypic form, as we found in tribe Zephyrantheae of Amaryllidaceae, e.g., *Rhodophiala*, *Zephyranthes* and especially in *Hippeastrum* (Naranjo, 1969, 1974; Naranjo & Andrada, 1975; Greizerstein & Naranjo, 1987; Poggio & Naranjo, 1990; this paper). In plants, they frequently characterize groups of genera and/or species (Brandham, 1983; Kenton *et al.,* 1990; Naranjo *et al.,* 1998).

The existence of groups 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 mutations preserving the existing chromosome morphology. Chromosome mutations were detected in *Hippeastrum*: in *H. argentinum*, Naranjo & Andrada (1975) found an individual with a heterozigotic asymmetric pericentric invertion, and similar observations were done by Baldwin & Speese (1947) in *H. solandriflorum*. In the present paper, one individual with two heteromorphic pairs of chromosomes in *R. bifida* was described (Fig. 1 E, F, pairs 2 and 3). These cases show that chromosome rearrangements occur with some frequency in the group. Nevertheless, in *Hippeastrum* and *Rhodophiala* the species main-

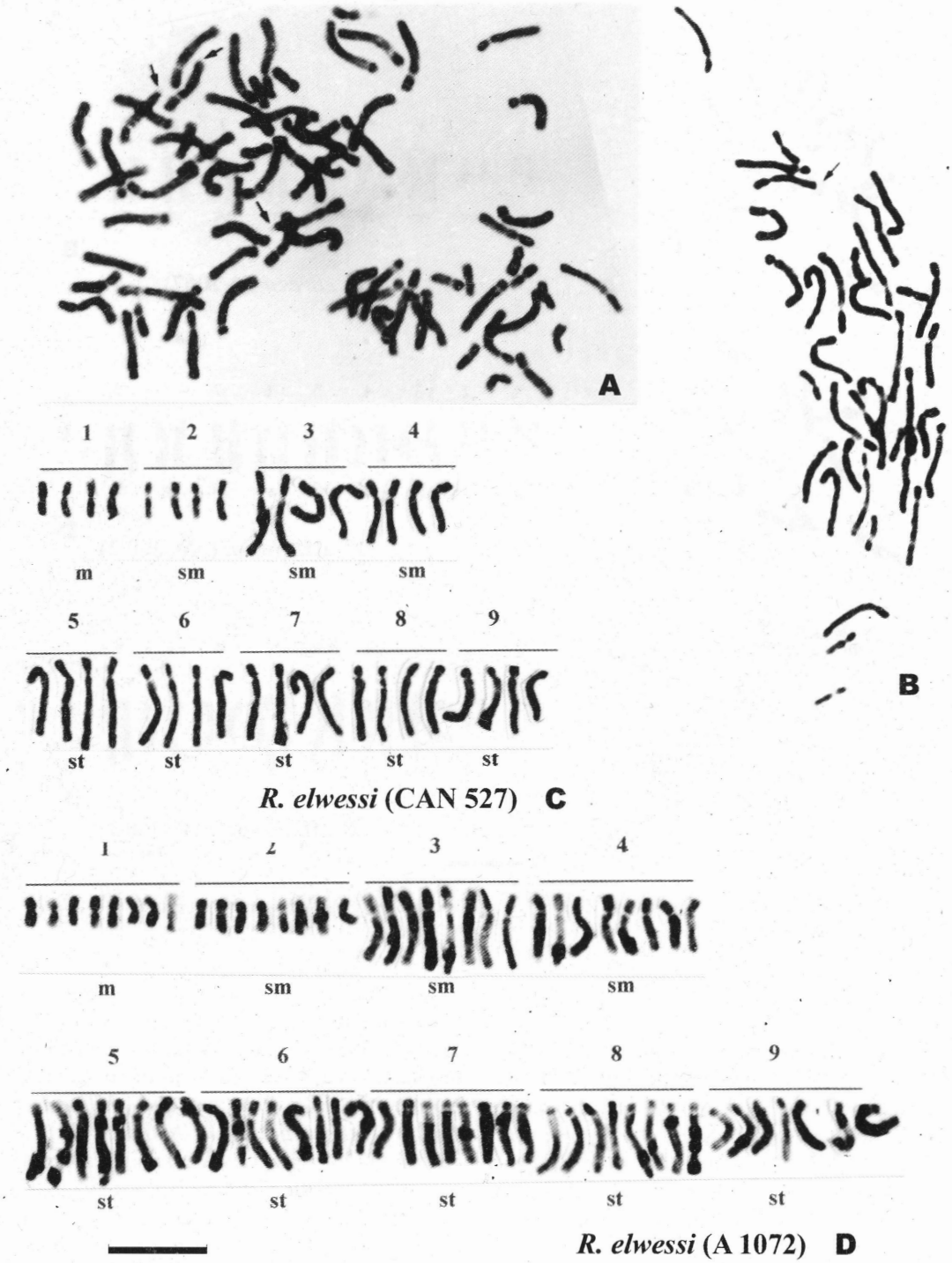

Fig. 3. A and **B**: Mitotic metaphase and **C** and **D**: respective karyograms of tetraploid (2n = 36, **B**) and octoploid (2n = 72, **A**) samples of *Rhodophiala elwesii*. Arrows show NOR regions. The scale represents 10 μm.

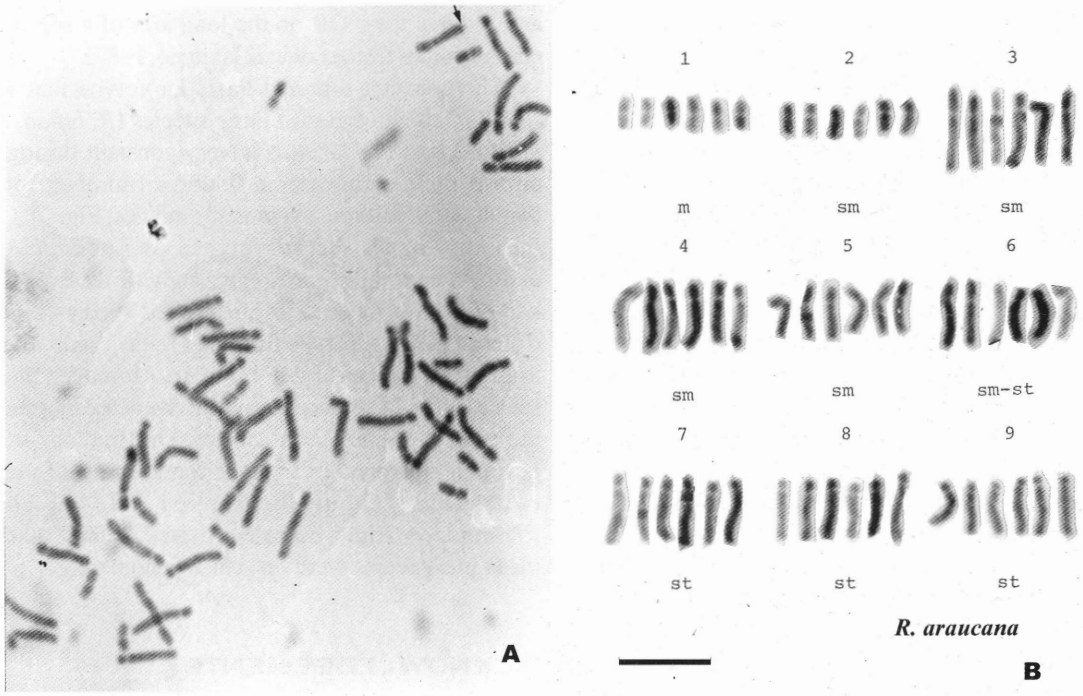

Fig. 4. A: Mitotic metaphase and **B:** respective karyogram of the tetraploid *Rhodophiala araucana* (2n = 54). Arrows show NOR regions. The scale represents 10 μm.

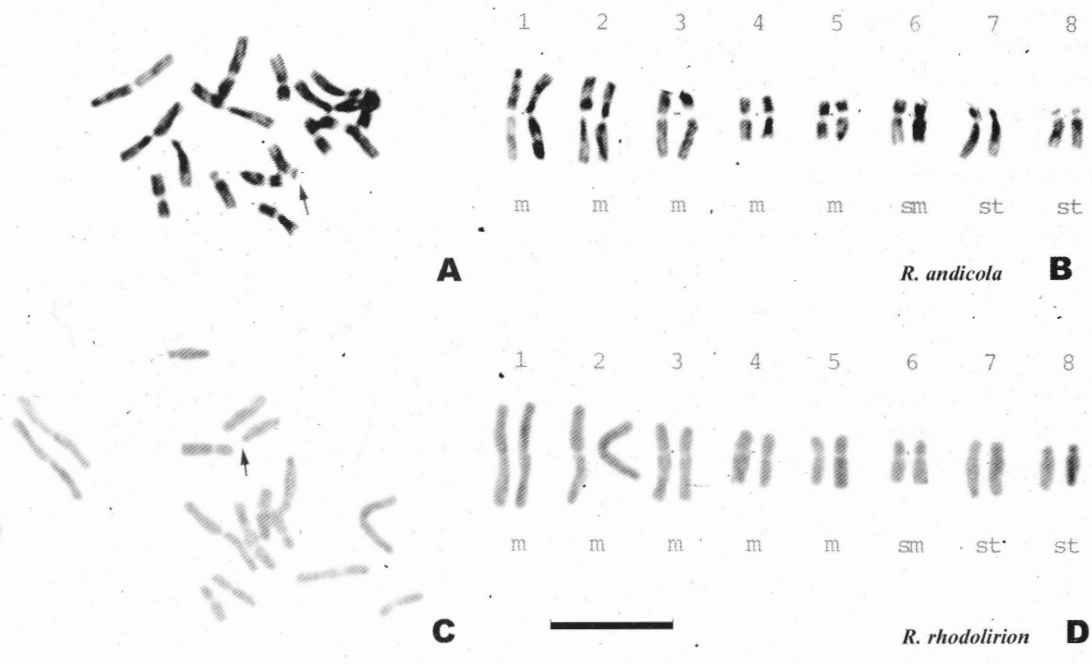

Fig. 5. A and **B**: Mitotic metaphases and **C** and **D**: respective karyograms of *Rhodophiala andicola* (2n = 16) and *Rhodophiala rhodolirion* (2n = 16). Arrows show NOR regions. The scale represents 10 μm.

tain their karyotype formula and asymmetry indexes A_1 and A_2, suggesting that some orthoselection mechanism is in process.

In *Rhodophiala*, previous studies have reported the chromosome number of only four species: of *R. bifida,* 2n = 16 with a karyotype similar to that described in the present work (Naranjo, 1969), and *R. igneum*, 2n = 16, *R. spathacea* (Herb.) Traub, *2n* = 16, and *R. ananuca*, 2n = 18 (Flory, 1968). While poliploidy is a common phenomenon in other genera of Amaryllidaceae, such as *Hippeastrum* and *Zephyranthes* (Naranjo, 1969; Naranjo & Andrada, 1975; Greizerstein & Naranjo, 1987; Naranjo & Poggio, 1988), in *Rhodophiala* only diploid species were found (2n = 16 and 2n = 18). *Rhodophiala elwesii* and *R. araucana* would be the first polyploids species described in the genus. The polyploid species had basic kayotypes with less total chromosomes length and volume.

To explain the existence of two basic chromosome numbers in *R. bifida* (x = 8 and 9), we propose that 2n = 16 cytotypes have been derived from 2n = 18 cytotypes. Since x = 11 is the more frequent basic number in the Amaryllidaceae and it is considered the ancestral basic number for the family; it is possible that x = 9 and 8 are basic numbers derived by a reduction process from x = 11. The diminution of one small m chromosome pair in 2n = 16 individuals of *R. bifida* could be explained if the genetic materials of this chromosome were translocated to another one of the complement in 2n = 18 individuals. The existence of a heterozygous individual for a translocations between a small m and a large sm chromosome (Fig. 1E, F), gives support to the reduction hypothesis through reciprocal translocation. Several genera with x = 11 such as *Hippeastrum*, possess 4 small m. The mechanism postulated to explain the reduction in *Rhodophiala* could explain the reduction of x = 11 to x = 9. Another related genus in the family is *Zephyranthes.* All diploid species of this genus (2n = 12 and 14) have a common chromosome characteristic consisting of the absence of small m or sm chromosomes (Greizerstein & Naranjo, 1987). Nevertheless, this chromosome type is present in the putative more primitive basic karyotype of the family with x = 11, 9, and 8, such as *Hippeastrum* and *Rhodophiala* species (Naranjo, 1969; Naranjo & Andrada, 1975; Poggio & Naranjo, 1990). In *Zephyranthes* the diminution of the basic chromosome number is correlated with a diminution in the number of small m chromosomes. *Zephyranthes* species with x = 7 and 6 lost this type of chromosomes (Greizerstein & Naranjo, 1987). Moreover, all species of *Zephyranthes* (x = 6 and 7) have the NOR on the long arm of a sm or st chromosome (Greizerstein & Naranjo, 1987).

The constant bimodal basic karyotype that we found in all cytotypes of three species (*R. bifida*, *R. elwesii* and *R. araucana*) is very constant throughout all their chromosome features (number, total length, total volume, asymmetry indices; Fig. 6). On the other hand, the karyotypes of *Rhodophiala andicola* and *R. rhodolirion* strongly differ from the karyotypes of those three mentioned species. They differ in their karyotype formula (Table 1) and in the asymmetry indices (Table 1, Fig. 6). Moreover, these species differ in exomorphological characteristics from the typical *Rhodophiala* species. Our findings suggest that a revision of the taxonomic status of these two species should be carried out, and that *Rhodolirion* could be rehabilitated, genus where these two species were originally included.

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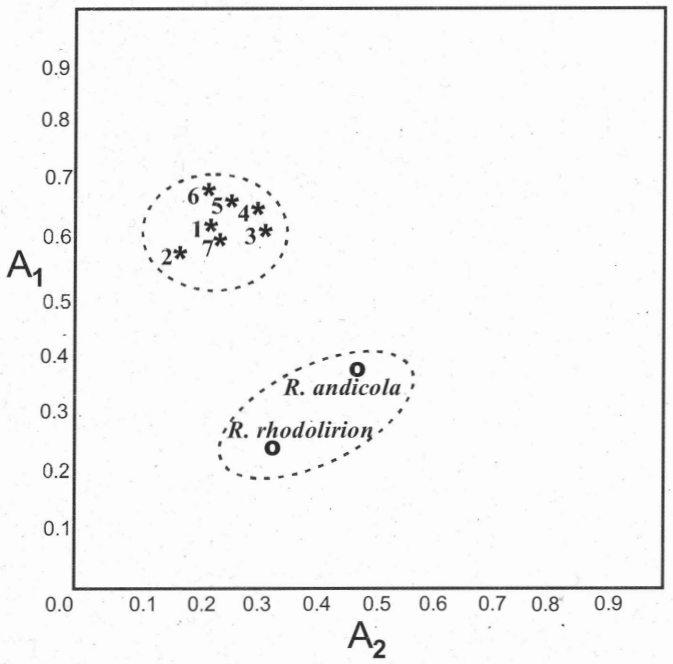

Fig. 6. Scatter diagram showing karyotype asymmetry indicated by the ratio between arm length (A_1) plotted against that due to variation between chromosome length (A_2). The A_1 and A_2 values are consigned in Table 1. **1:** *R. bifida* CAN 141 (2n = 16); **2**: *R. bifida* CAN 2372 (2n = 18); **3**: *R. elwessi* A 1067 (2n = 18); 18): **4** = *R. elwessi* CAN 527 (2n = 36); **5**: *R. elwessi* CAN 563 (2n = 72); **6:** *R.* aff. *elwessi* CAN 360/1 (2n = 18+1B); **7:** *R. araucana* (2n = 54).

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