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Mitotic karyotype stability and meiotic irregularities in the families Loranthaceae Juss. and Viscaceae Miq.

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Abstract — Chromosome number, interphase nuclear structure, prophase chromosome condensation patterns, and meiotic behaviour were analysed in 14 Brazilian species within the families Loranthaceae and Viscaceae. All the species showed reticulate interphase nuclei and an uniform pattern of prophase chromosome condensation. The eleven species of Loranthaceae studied had 2n=16, whereas the three species of Viscaceae (*Phoradendron*) had 2n=28. The mitotic chromosome of only two species of *Phoradendron* revealed a significant karyotype asymmetry, while the remaining karyotypes were more symmetrical, and similar to each other. By contrast, the meiotic behaviour of ten species analysed exhibited several meiotic irregularities, characteristics of structural heterozygosis. In one sample of *Struthanthus syringifolius,* the majority of the meiocytes showed a ring tetravalent. The stability in mitotic karyotype associated with the meiotic irregularities observed in several genera of these families suggest that in spite of the structural changes orthoselection has preserved a diploid basal karyotype with large and symmetrical chromosomes. It is hypothesized that this karyotype was established before the diversification of these families and its large DNA amount has hindered the occurrence of polyploidy in these families.

Key words: Karyotype evolution, meiotic irregularities, *Phoradendron, Phthirusa, Psittacanthus, Struthanthus*.

INTRODUCTION

The families Loranthaceae and Viscaceae include hemi-parasitic plants with a reduced ovary and undifferentiated ovules. They have a pantropical distribution, but also occur in temperate regions in both hemispheres (Barlow 1964a). Loranthaceae is the most diversified family, with approximately 65 genera and 900 species, while Viscaceae contains seven genera and ca. 400 species (Barlow 1983).

The two families were traditionally recognised as sub-families (Loranthoideae and Viscoideae) of Loranthaceae, and were included within the Order Santalales. Their separation into two distinct families was based on differences in their floral structure and embryology (Barlow 1964b). Chromosomal and molecular evidences further supported this division. Loranthaceae has a primary basic number of x=12, which is reduced to x=8 and x=9 in some taxa, while Viscaceae has a primary basic number of x=14, with dysploid reductions to x=13, 12, 11, or 10 (Barlow and Wiens 1971; Wiens and Barlow 1971). The analysis of 18S rDNA sequences indicated a close relationship of Loranthaceae to Olocaceae (the most primitive family in this order), while Viscaceae appeared closer to Santalaceae (Nickrent 1996). These relationships had been suggested earlier, based on the position of the ovaries (Calder 1983).

Most of the karyological research in these families were restricted to meiotic analyses, mainly the chromosome number and their role in cytogeography. There are chromosomal registers for 22 % of the species and 91 % of the genera in the Loranthaceae, and for 30 % of the species belonging to six of the seven genera of Viscaceae.

Most contributions to the cytology of Loranthaceae and Viscaceae were done by Barlow and Wiens (Barlow 1963; 1964a; Wiens 1964; 1968; 1975; Barlow and Wiens 1971; Wiens and Barlow 1971), who studied a large number of Australian, North American, and African species. The use of non-conventional karyological techniques is restricted to the studies of Martin (1983) and Barlow and Martin (1984), who examined the DNA content of 56 Australian species, and the C-

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band pattern of some of them. In general, these families have karyotypes with large chromosomes, and chromosome numbers varying between n=8 and n=18 in Loranthaceae (BARLOW and WIENS 1971), and n=10 and n=28 in Viscaceae (WIENS 1975). Chromosome numbers are well conserved within each genus. The principal mechanism of chromosome evolution in these families seem to be dysploidy, whereas polyploidy is rather uncommon (WIENS and BARLOW 1971; WIENS 1975; BARLOW and MARTIN 1984).

According to RIZZINI (1956), 126 species of Loranthaceae and 128 species of Viscaceae were reported in Brazil, although only 19 of them have chromosomal registers. This work presents a karyological analysis of 14 Brazilian species within the families Loranthaceae and Viscaceae, including meiotic analysis from 10 of them.

MATERIALS AND METHODS

Table 1 lists the species analysed (identified according to RIZZINI 1956), their herbarium numbers, as well as their collection sites. Voucher specimens were deposited in the herbarium at the Federal University of Pernambuco (UFP).

Since these plants do not have roots, mitotic analysis were performed on floral buds or in young embryos and endosperms. They were pretreated with 2 mM 8-hydroxyquinoline for 20 to 24 hrs at 6 ºC, or fixed directly in Carnoy 3:1 (ethanol: acetic acid) for 20 hrs at room temperature, and stored at -20 ºC. Meristematic tissues from floral buds (mainly ovary walls and young anthers) and seeds (endosperm and embryo) were analysed. For meiotic analysis, the anthers were fixed directly in Carnoy 3:1 and stored in the freezer.

Slide preparation was performed by washing the plant material twice in distilled water (5 min) and then hydrolysing it in 5N HCl at room temperature (10 or 20 min for meiosis and mitosis, respectively). Meristematic tissue was isolated with the aid of a stereomicroscope, squashed in a drop of 45% acetic acid, and the coverslip was removed by freezing in liquid nitrogen. The slides were air-dried, stained in 2% acetic carmine or 1% acetic hematoxylin (GUERRA 1999), and mounted in Entellan (Merck). In some cases, when the contrast between chromosomes and cy-

Table 1 — List of the species analysed, their respective herbarium numbers, collection localities, observed chromosome numbers and corresponding illustration.

Taxon	Collection locality* (voucher number)	Chromosome number			Figure
		n	2n	3n	
Loranthaceae					
Phthirusa pyrifolia var. *grandifolia* Eichl.	Recife/PE (30.042, 31.090, 31.091, 31.092, 31.094)		16	24	1d
P. pyrifolia var. *parvifolia* Eichl.	Garanhuns/PE (30.027)	8			
	Bonito/PE (31.093)		16	24	1e
Psittacanthus bicalyculatus Mart.	Ituaçu/BA (30.020-1, 30.020-2, 30.020-3)	8			1h
P. dichrous Mart.	Mamanguape/PB (30.016)	8			3d
	Pedras de Fogo/PE (29.909)		16		
	Recife/PE (30.021)	8			
	Bonito/PE (30.078)		16		1g
	Mataraca/PB (30.051)	8			
	Feira de Santana (31.095)		16		
P. robustus Mart.	Rio de Contas/BA (30.033)		16		1f
Struthanthus concinnus Mart.	Rio de Contas/BA (29.908)		16		
	Recife/PE (31.086)	8			2f
S. cf. *flexicaulis* Mart.	Rio de Contas/BA (29.906)	8	16		2g
S. marginatus (Desr.) Bl.	Rio de Janeiro/RJ (31.239)	8			2e
S. polyrhizus Mart.	Gravatá/PE (30.142)	8	16		2d
S. sincorensis Ule.	Bonito/PE (31.097)	8	16		2a
S. syringifolius Mart.	João Pessoa/PB (30.012, 30.057, 30.059, 31.088)	8	16		2c
S. vulgaris Mart.	Botafogo/RJ (31.235)		16		2b
Viscaceae					
Phoradendron cf. *emarginatum* Mart.	João Pessoa/PB (30.055)		28		1b
P. perrottetii (DC.) Eichl.	Rio de Contas/BA (29.905)		28		1a
	João Pessoa/PB (30.113)	14			
P. cf. *racemosa* (Aubl.) Kr. et Urb.	Itapororoca/PB (30.018)		c. 28		1c

* Abbreviation of Brazilian states: BA=Bahia, PB=Paraíba, PE=Pernambuco, RJ=Rio de Janeiro.

toplasm was good, cell were analysed without staining.

Photomicrographs of the best cells were made with a Leica DMRB photomicroscope, using Kodak Imagelink HQ ASA 25 film. Negatives were copied onto Kodak Kodabromide F3 paper, or digitised using a HP Scanjet 7450 scanner. Images were mounted using an Adobe Photoshop 5.5 software package. The five best cells from four species were used to construct idiograms.

RESULTS

Twenty-eight populations of Loranthaceae and four populations of Viscaceae were analysed. Table 1 presents the chromosome numbers obtained from each sample, with indication of a representative illustration for each species.

All plants examined from both families showed reticulate interphase nuclei (Fig. 1d), uniform prophase chromosome condensation pattern (Fig. 1f), and symmetrical karyotypes formed by large, metacentric or sub-metacentric chromosomes. Exception to the karyotype symmetry was only found in *Phoradendron* species, which were slightly asymmetrics. The chromosome number was constant within each family (Figs. 1 and 2). The species of Loranthaceae had 2n=16, while Viscaceae had 2n=28 or ca. 28 (Table 1). In two varieties of *Phthirusa pyrifolia* (var. *grandifolia* and var. *parvifolia*) the chromosome number of the endosperm was also determined (2n=3x=24). One or two satellite chromosomes were observed in cells of *P. pyrifolia* var. *grandifolia* (Fig. 1d), *Psittacanthus robustus* (Fig. 1f), *Struthanthus* cf. *flexicaulis, S. concinnus,* and *S. syringifolius.*

Meiotic behaviour was examined in 10 species. They generally showed chiasmata in the interstitial region of one or both chromosomal arms (Figs. 1h, 2c-g, 3a). A low frequency (< 10 %) of meiotic irregularities was observed in most of the species, including precocious segregation of one or more bivalents during metaphase I and II (Figs 3b and 3c) and, mainly, anaphase bridges with fragment (Fig. 3e). The latter, observed in *Psittacanthus bicalyculatus, P. dichrous, Struthanthus* cf. *flexicaulis, S. syringifolius,* and *Phoradendron perrottetii*, is probably related to the occurrence of irregular tetrads (Fig. 3d) and micronuclei. Five species exhibited higher frequency (15-30 %) of meiotic irregularities, including anaphase I bridges in *Phoradendron perrottetii,* laggard chromosomes in anaphase I in *Struthanthus polyrhizus,* and micronuclei in *Psittacanthus dichrous, S. polyrhizus,* and *P. perrottetii.* Additionally, one population of *S. syringifolius* showed one tetravalent in 83 % of the cells analysed (Fig. 3a).

Most mitotic divisions did not exhibit the chromosomal spreading necessary for karyological analysis, although several anti-mitotic treatments were tested, including α-bromonaphthalene, paradiclorobenzene, colchicine, and cold-treatment. However, a single sample of *Psittacanthus dichrous* responded well to pre-treatment with 8-hydroxyquinoline, producing a larger number of well condensed and spread metaphase cells (Figs. 1g). Figure 4 shows the idiograms of two species of *Psittacanthus*, one of *Struthanthus,* and one of *Phthirusa,* based on chromosome measurements in three to six cells per species. The relatively smaller size of the chromosomes of *Psittacanthus dichrous* is most likely due to the fact that their chromosomes were pre-treated. In mitotic metaphases of *P.* cf. *racemosa* and *P. emarginatum*, three to four smaller chromosome pairs were recognised (Figs. 1b and 1c), suggesting a small karyotype asymmetry in this genus.

DISCUSSION

Most species here analyzed are reported for the first time, except *Phthirusa pyrifolia, Struthanthus marginatus,* and *S.* cf. *flexicaulis,* investigated previously by Barlow and Wiens (1971). The chromosome numbers n=8 and n=14, found in all these species, confirms the chromosome number stability suggested by Barlow and Martin (1984) for Neotropical representatives of Viscaceae and Loranthaceae. These species also presented the same prophase chromosome condensation pattern and nuclear structure, as well as similar chromosome size and morphology. The conservation of interphase and prophase features is most likely the result of the stability in other cytological parameters, like chromosome size and nuclear DNA amount (Martin 1983; Guerra 1987). The large chromosomes, common to all representatives of both families and rare among dicotyledon genera, constitute an additional indication of the close phylogenetic relationship between these two families.

Among the Loranthaceae, the *Struthanthus* species here investigated, as well as all other registers from Argentina (Covas 1949), Mexico (Wiens 1964) and Costa Rica (Barlow and Wiens 1971), displayed n=8. In *Psittacanthus,* the three species examined in the present work had

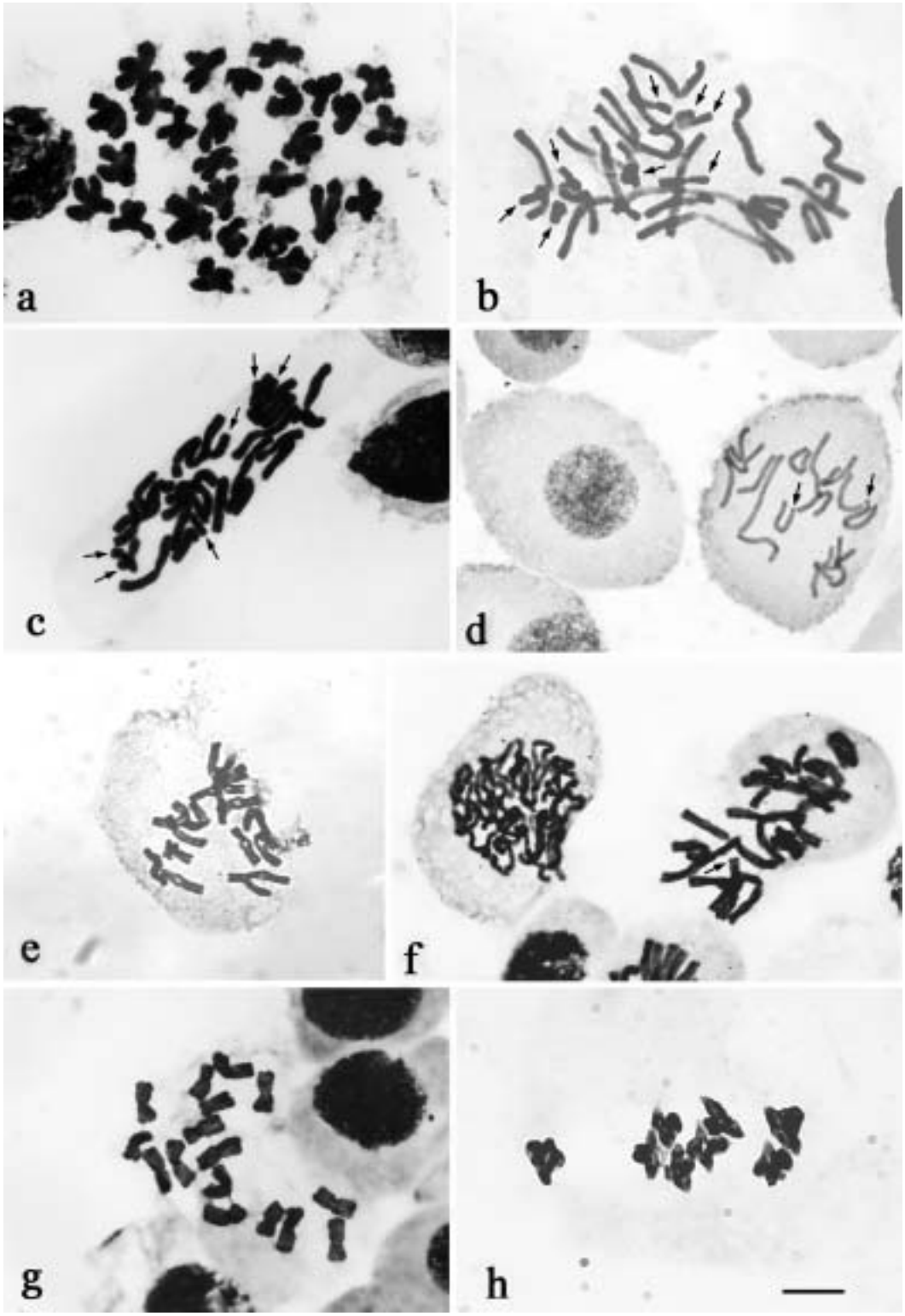

Fig. 1 — Cytological characteristics of species of *Phoradendron* (Viscaceae), *Phthirusa*, and *Psittacanthus* (Loranthaceae). a) Metaphase II of *Phoradendron perrottetii* showing two superimposed chromosome complements totalizing 28 chromosomes, b) *P.* cf. *emarginatum* (2n = 28), c) *P.* cf. *racemosa* (2n=c.28), d) Interphase and metaphase of *Phthirusa pyrifolia* var. *grandifolia* (2 n= 16), e) *P. pyrifolia* var. *parvifolia* (2n = 16), f) Prophase and metaphase of *Psittacanthus robustus* (2n = 16), g) *P. dichrous* (2n = 16), and h) Meiotic metaphase I in *P. bicalyculatus* (n = 8). Arrows indicate smaller chromosomes, in b and c, and satellites, in d and f. Bar in h corresponds to 10 μm.

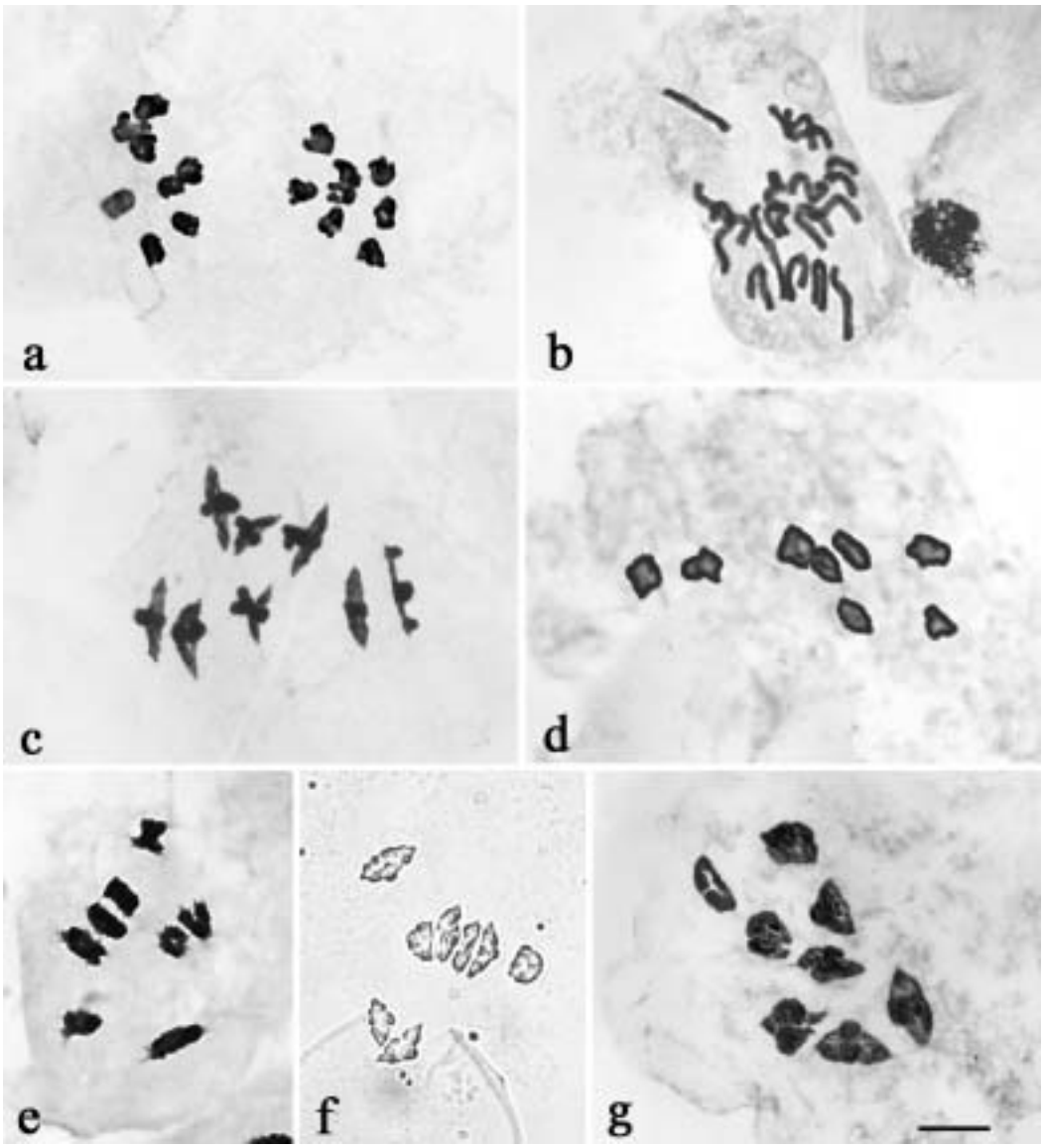

Fig. 2 — Chromosomal complements of *Struthanthus* species (Loranthaceae). a) *S. sincorensis* (n=8), b) *S. vulgaris* (2n=16), c) *S. syringifolius* (n=8), d) *S. polyrhizus* (n=8), e) *S. marginatus* (n=8), f) *S. concinnus* (n=8), g) *S.* cf. *flexicaulis* (n=8). a, anaphase I; b, mitotic metaphase; c, d, f, g, metaphase I; e, diakinesis. Bar in g corresponds to 10 μm.

n=8, with small differences in chromosome morphology revealed only by their ideograms. Eight other species have n=8, two have n=10 (Covas and Schnack 1946; King 1961; Wiens 1964; Barlow and Wiens 1971), and *P. calyculatus* (DC.) D. Don. has n=8 and n=10 (King 1961; Wiens 1964; Barlow and Wiens 1971).

A similar chromosome number stability was found in (Viscaceae). The three species here investigated and other 36 species of *Phoradendron* displayed n=14, one had n=27, and another had n=28 (Wiens 1964; Wiens and Barlow 1971). We observed a marked reduction in the size of some chromosomes in two of the three species analysed, suggesting the existence of structural changes within these karyotypes. Wiens (1964) and Barlow and Martin (1984) noted the occurrence of B chromosomes in this genus, which is also indicative of karyotypic rearrangements (Puertas 2002). A rare and extreme case of structural changes is observed in several species of *Viscum,* where heterozygosity for large chromosomal interchanges are associated with a complex sex-determining chromosome system and dysploid chromosome numbers (Wiens and Barlow 1979; Aparicio 1993).

These data suggest that in spite of the apparent mitotic karyotype stability, structural changes

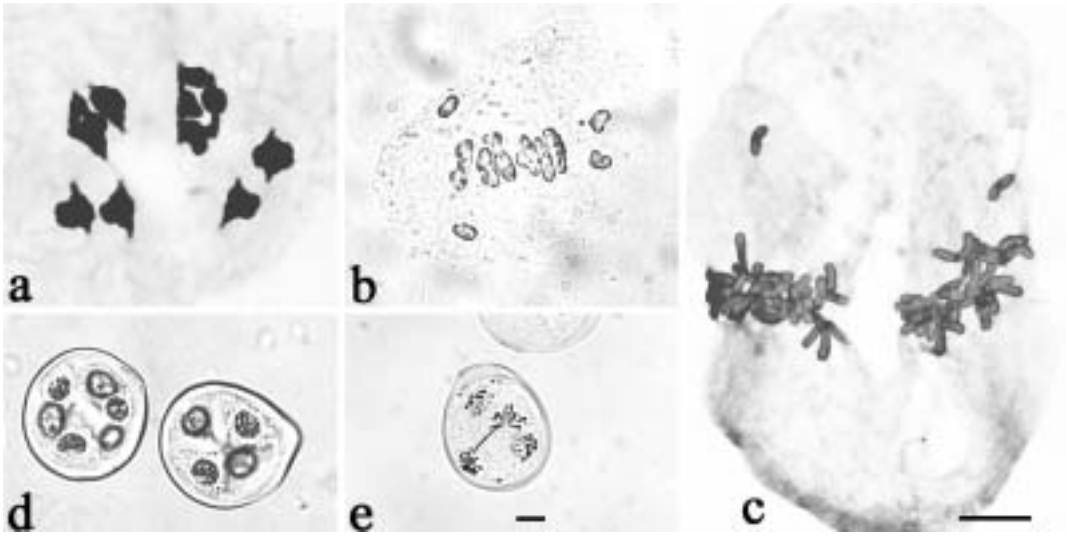

Fig. 3 — Meiotic alterations in species of *Struthanthus, Psittacanthus,* and *Phoradendron*. a) Tetravalent in *S. syringifolius,* b) Precocious separation of two chromosomal pairs in metaphase I of *S. concinnus*, c) Precocious chromosomal separation in metaphase II of *Psittacanthus bicalyculatus,* d) Irregular tetrad of *P. dichrous,* and e) Anaphase II bridge in *P. bicalyculatus*. Bars correspond to 10 μm. The bar in c is valid for a, b, c and in e is only valid for e, d.

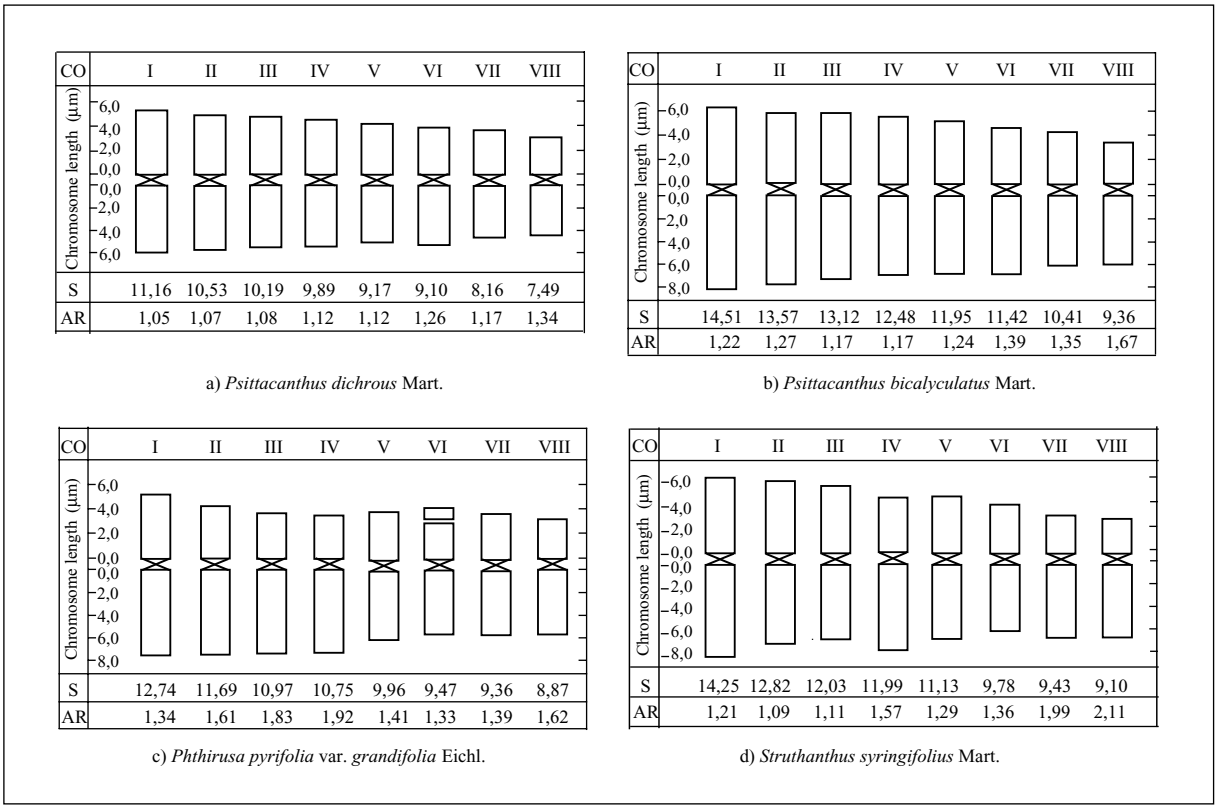

Fig. 4 — Idiograms of four species of Loranthaceae. a) *Psittacanthus dichrous*, b) *Psittacanthus bicalyculatus*, c) *Phthirusa pyrifolia* var. *grandifolia,* d) *Struthanthus syringifolius*. CO = chromosome ordering; S = chromosome size; AR = arm ratio.

are playing an important role in the karyological evolution of these genera. Accordingly, a number of species within these families show high frequencies of meiotic alterations, including the formation of non-reduced spores. In the present work, the most frequent alterations observed were anaphase bridges and precocious separation of bivalents in metaphase I. A tetravalent ring observed in *Struthanthus syringifolius* indicates that heterozygosity for chromosomal interchange is also occurring. Similar alterations were reported by HUNZIKER and PEREZ-MOREAU (1961), BIR *et al.* (1980, 1984), and SOMAN and RAMACHANDRAN (1987). The latter authors observed a 42 % rate of meiotic irregularity and pollen sterility in *Helicanthes elastica.* Therefore, an intense structural polymorphism is operating under the mitotic karyotypic orthoselection in both families.

The low degree of polyploidy in these families (3 % in Loranthaceae and 9 % in Viscaceae), almost restricted to the level of tetraploidy, stands in contrast to the 70 % value accepted to angiosperms in general (LEITCH and BENNETT 1997). BIR *et al.* (1980, 1984) and BARLOW (1983) have suggested that the unique characteristics of both the habit and the reproductive system of these plants served as barriers to the establishment of polyploid forms. However, even in parasitic plants, polyploidy seems to be rather common, such as in *Cassytha* (OKADA and TANAKA 1975; GOLDBLATT 1981) and *Cuscuta* (PAZY and PLITMANN 1995). A recent investigation of the association between chromosomal characters and parasitic habit did not find any correlation (PAZY and PLITMANN 2002).

An alternative explanation for the low levels of polyploidy observed is that the large chromosomes displayed by Loranthaceae and Viscaceae species restrict the success of higher polyploids. The average DNA content recorded for Loranthaceae is among the largest of angiosperms (MARTIN 1983, LEITCH *et al.* 1998). BRANDHAM *et al.* (1995) observed that in some genera of cultivated monocotyledons with large chromosomes, the quantity of DNA seems to be a limiting factor for the perpetuation of polyploid forms. In these monocots, "optimal" levels of DNA amount, around 4C=100 pg, would be restricted to diploids or tetraploids. DNA values in this range were encountered in the majority of the Loranthaceae examined by MARTIN (1983) and may also represent a constraint factor to polyploidization. Other plant families with large chromosomes, stable karyotypes and with few or without polyploids are commonly found among old established gymnosperms (KOSHOO 1962). In monocotyledons, on the other hand, polyploidy is rarer among genera with large chromosomes, but karyotype instability, with intrageneric variability in chromosome number or morphology, is very frequent (see GREILHUBER 1995).

The basal karyotype of Viscaceae and Loranthaceae, with large, meta- or submetacentric chromosomes, seems to have preceded the families and genera diversification (WIENS 1964). Further increase in the DNA amount, by polyploidy or repetitive sequences, was avoided independently in all genera, probably by physiological restrictions (see BRANDHAM *et al.* 1995; GREILHUBER 1995). However, why structural changes that do not change the karyotype morphology, like paracentric inversion (detected as meiotic anaphase bridges in several species), are more easily tolerated than other alterations is still unknown.

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