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Cytotaxonomy of *Sapindaceae* with special reference to the tribe *Paullinieae**

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INTRODUCTION

Sapindaceae is a tropical and subtropical family comprising approximately 136 genera and about 2000 species. Radlkofer (1931-1934) recognized 14 tribes, of which *Paullinieae* is the only tribe characterized by a climbing habit, with the remaining tribes being shrubs or trees.

The most comprehensive studies on the karyology of *Sapindaceae* were done in the last decade (Ferrucci, 1989; Hemmer and Morawetz, 1990; Nogueira *et al.*, 1995; Ferrucci and Solís Neffa, 1997; Solís Neffa and Ferrucci, 1997, 1998; Lombello and Forni-Martins, 1998), and chromosome numbers of 127 species have been reported and the complete karyotypes of 35 species are known, although only a few papers give information on interphase nucleus structure, chromosome condensing behavior, Giemsa C-banding, NOR-banding and nucleolus counts (Eichhorn and Franquet, 1936; Guervin, 1961; Hemmer and Morawetz, 1990; Nogueira *et al.*, 1995).

In the present study chromosome numbers are reported for 19 South American species of the tribe *Paullinieae* (Table I), with ten of them representing new records while previous reports are confirmed for other 9 species. These results are compared with a review of the karyology of the whole family, with special reference to the tribe *Paullinieae* in an attempt to improve the understanding of the evolution of the family.

The species studied, chromosome numbers, localities and collectors are listed in Table I. Voucher specimens have been deposited in the herbaria of the Instituto de Botánica del Nordeste (CTES), Argentina.

Cytological studies were carried out using root meristems of germinating seeds, except for *Cardiospermum anomalum*, where roots from adult plant were used. The roots were pre-treated for 3 h in 0.002 M 8-hydroxyquinoline at room temperature, fixed in ethanol and lactic acid (5:1) at 4°C and then stored in 70% ethanol. The roots were hydrolyzed in 1 N HCl at 60ºC for 8 min and stained with Feulgen's technique using Schiff reagent and squashed in a drop of 2% acetic orcein. Slides were made permanent using Bowen's method (1956) and mounted in Euparal.

BASIC CHROMOSOME NUMBERS

In the *Sapindaceae*, chromosome numbers for 42 genera belonging to 13 tribes and approximately 138 species have been reported, including the new counts presented in this paper, leaving only one tribe karyologically undefined.

Table II shows that there is a considerable variation in chromosome numbers within the family as a whole. *Paullinieae* showed an almost complete aneuploidy series, from x = 7 to x = 14, only x = 8 and x = 13 being absent. The discovery of 2n = 14 in *Cardiospermum integerrimum* Radlk. (Ferrucci, 1989) was the first record of x = 7 in New World *Sapindales*, while the count of 2n = 18 in *C. anomalum* (Table I) establishes a new basic chromosome number, x = 9, for the family. In *Sapindales*, the families *Bretschneideraceae* and *Akaniaceae* included in the past in *Sapindaceae* have x = 9.

The basic chromosome numbers x = 7, 9 and 10 are exclusive to New World species, while x = 13 is only known for two closely allied tribes of the Old World. Among the 42 genera cytologically explored, only 7 exhibit more than two basic numbers.

According to available data, x = 15, x = 16 and x = 14 occur with the greatest frequency, while other basic numbers are less frequent (Table II). In *Paullinieae*, the most advanced tribe of the family, the higher basic chromosome numbers x = 15 and x = 16 are absent. Considering that x = 7 would be the primitive base number for the family (Ferrucci, 1989), the other chromosome numbers would be derived by polyploidy and aneuploidy.

POLYPLOIDY

One-third to one-half of the angiosperms are estimated to be polyploid which has, thus, played an important role in the evolution of higher plants (Stebbins, 1971; Greilhuber and Ehrendorfer, 1988), but polyploid frequency in *Sapindaceae* is scarce, with only three genera from different tribes exhibiting polyploid species, all American species with distinct life forms, such as climbers, shrubs and trees. In this context *Urvillea* Kunth (*Paullinieae*) possesses two basic numbers, x = 11 and x = 12, while among the four species studied with x = 11 three ploidy levels are present, 2n = 2x = 22, 2n = 4x = 44 and 2n = 8x = 86. The widespread species *U. ulmacea* is a unique species with two known cytotypes 2n = 2x = 22 as well as 2n = 8x = 86 in which polyploidy has been followed by reductional aneuploidy (Nogueira *et al.*, 1995).

Table I - Chromosome numbers of some South American *Sapindaceae*, *Paullinieae*. *New species counts, ** participation of the author in material collection.

Taxon	2n	Figure	Locality and collectors
Cardiospermum anomalum Cambess.	18*	1A	Brasil, Minas Gerais, Hatschbach *et al.*, 64784
C. corindum L.	22	1B	Brasil, Bahia, Hatschbach *et al.*, 65042
C. grandiflorum Sw.	20	1C	Brasil, Bahia, Ferrucci *et al.*, 1021
Paullinia coriacea Casar.	24*	1D	Brasil, Rio de Janeiro, Somner *et al.*, 929
P. weinmanniaefolia Mart.	24	1E	Brasil, Rio de Janeiro, Ferrucci *et al.*, 938
Serjania acutidentata Radlk.	24*	1F	Brasil, Bahia, Correntina, Ferrucci *et al.*, 997
S. cissoides Radlk.	24	1G	Paraguay, Amambay, Schinini *et al.*, 33441
S. communis Cambess.	24	1H	Brasil, Rio de Janeiro, Ferrucci *et al.*, 955
S. confertiflora Radlk.	24		Brasil, Bahia, Jardim, 951
S. grammatophora Radlk.	24*	1I	Brasil, Bahia, Ferrucci *et al.*, 985
S. lethalis St. Hil.	24*	1J	Brasil, Mato Grosso do Sul, Pott *et al.*, 3261
S. obtusidentata Radlk.	24*		Brasil, Minas Gerais, Lombardi, 2037
S. pernambucensis Radlk.	24*	1K	Brasil, Bahia, Arbo *et al.*, 7205**
S. purpurascens Radlk.	24*	1L	Brasil, Minas Gerais, Carvalho *et al.*, 6580**
S. salzmanniana Schltdl.	24*		Brasil, Pernambuco, Ferrucci *et al.*, 1135
S. subimpunctata Radlk.	24		Brasil, Bahia, Ferrucci *et al.*, 1031
S. suborbicularis Radlk.	24*	1M	Brasil, Minas Gerais, Carvalho *et al.*, 6518**
Urvillea ulmacea Kunth	22		Brasil, Bahia, Ferrucci *et al.*, 971
	22	1N	Brasil, Mato Grosso do Sul, Pott *et al.*, 7781
U. chacoënsis Hunz.	22	1O	Argentina, Catamarca, S. Toledo *et al.*, 12792

Table II - Distribution of basic chromosome numbers of 42 studied genera in 13 tribes of *Sapindaceae*.

Tribes \ Basic numbers	x=7	x=9	x=10	x=11	x=12	x=13	x=14	x=15	x=16
Paullinieae	1	1	1	2	4		2		
Thouinieae							1	1	
Sapindeae							4	3	
Aphanieae						1	1		
Lepisantheae						1			2
Melicocceae									1
Schleichereae								1	1
Nephelieae								5	2
Cupanieae							1	1	4
Koelreuterieae								1	1
Cossignieae			1						
Dodonaeeae							1		
Harpullieae					1		1	3	2
Percentage	2.4	2.4	4.6	4.6	14	4.6	24	35	30

The largest and most cosmopolitan genus *Allophylus* L. (*Thouinieae*) shows two ploidy levels, with four species possessing 2n = 2x = 28 while *A. guaraniticus* (A.St.-Hil.) Radlk. has 2n = 4x = 56 (Ferrucci and Solís Neffa, 1997).

Melicoccus P. Browne (*Melicocceae*) with its two cytologically studied species has two ploidy levels, 2n = 2x = 32 as well as 2n = 6x = 96, which represents the highest chromosome number of the *Sapindaceae* (Ferrucci and Solís Neffa, 1997).

Although there is relatively little information on the cytology of the family as a whole, the rareness of polyploids is obvious, indicating that other mechanism of speciation plays the main role.

KARYOTYPES AND SYSTEMATICS IN *PAULLINIEAE*

The *Paullinieae* with 7 genera and about 430 species include a quarter of the species of the family, the tribe presenting an almost exclusively neotropical distribution. In Radlkofer's (1931-1934) system there are two subtribes, the *Thinouiinae* with only one genus, *Thinouia* Triana & Planch., and the *Paulliniinae* with *Lophostigma* Radlk., *Serjania* Mill., *Houssayanthus* Hunz., *Paullinia* L., *Cardiospermum* L. and *Urvillea*. Chromosome numbers have been determined in 58 species distributed amongst the 7 genera of *Paullinieae* and the karyotypes of 32 species have been described, and, from a cytological point of view, it is the best explored tribe.

The genus *Thinouia* is considered the most primitive genus in the tribe, and although it has only 9 species karyotype analysis and chromosome number (2n = 28) are only known for *T. mucronata* Radlk. (Ferrucci and Solís Neffa, 1997; Solís Neffa and Ferrucci, 1998), with karyotype characteristics confirming its basal position in the

tribe. When compared to other genera of *Paullinieae*, *T. mucronata* is characterized by small chromosomes with an average chromosome length of 1.47 μm as well as by a symmetric karyotype due to the predominance of m-type chromosomes, agreeing well with macromorphological evidence and pollen type. On the basis of cladistic analysis Acevedo-Rodríguez (1993) proposed to place *Thinouia* in the tribe *Cupanieae*, but current knowledge supports its position in *Paullinieae*.

Lophostigma comprises only two species, native to Ecuador, Peru and Bolivia. Karyological information is confined to the chromosome number, 2n = 28 of *L. plumosum* Radlk. (Ferrucci and Solís Neffa, 1997). Characters such as climbing habit, stipules and lightly zygomorphic flowers are essential for placing *Lophostigma* in the subtribe, and the calyx with five free sepals and the semiannular disc suggest a basal position in the *Paullininae*, the chromosome number supporting this hypothesis (Ferrucci and Anzótegui, 1993). Distinctive pollen, unique within *Sapindaceae* (Acevedo-Rodríguez, 1993; Ferrucci and Anzótegui, 1993), and the chromosome number are the characters that distinguish *Lophostigma* from *Serjania*, its most closely allied genus.

Serjania Mill. with about 231 species is the largest genus of *Paullinieae*. Chromosome studies include the chromosome counts of 35 species belonging to eleven of the twelve sections of the genus, all with 2n = 24 (Guervin, 1961; Fernández Casas and Fernández Piqueras, 1981; Ferrucci, 1981, 1985; Sarkar *et al*., 1982; Maglio *et al*., 1984; Hemmer and Morawetz, 1990; Acevedo-Rodríguez, 1993; Nogueira *et al*., 1995; Ferrucci and Solís Neffa, 1997; Solís Neffa and Ferrucci, 1997 and this paper), while new counts for *S. acutidentata* (Figure 1F), *S. grammatophora* (Figure 1I), *S. lethalis* (Figure 1J), *S. obtusidentata*, *S. pernambucensis* (Figure 1K), *S. purpurascens* (Figure 1L), *S. salzmanniana* and *S. suborbicularis* (Figure 1M), all with 2n = 24, confirm the consistency of this chromosome number.

The karyotypes of 21 species of *Serjania* have been studied, in five of which two populations were analyzed (Hemmer and Morawetz, 1990; Nogueira *et al*., 1995; Solís Neffa and Ferrucci, 1997; Lombello and Forni-Martins, 1998), with the karyotypes showing a moderate degree of asymmetry and gradual differences in chromosome size. Although the predominance of m-type and sm-type chromosomes has been noted, st-type and t-type chromosomes are also generally present. Satellite nucleic acid is difficult to detect, although some species have 1 to 3 chromosome pairs with microsatellite nucleic acid attached to the short and long arms of m-type and t-type chromosomes, while *S. hebecarpa* Benth. is the only species in which macrosatellite nucleic acid has been detected associated with one chromosome pair. The size of *Serjania* chromosomes varies from 0.97 μm in *S. gracilis* Radlk. to 4.7 μm in *S. meridionalis* Cambess. In the species analyzed there was significant interspecific and intraspecific variation in chromosome length and karyotype formulae.

Within the tribe, *Serjania* shows morphological affinities to both *Lophostigma* and *Houssayanthus*, but differs from *Lophostigma* in the characters mentioned above and from *Houssayanthus* only by fruit morphology.

Houssayanthus with only 3 species is distributed from Venezuela to northeastern Argentina, with chromosome numbers being known for 2 species, *H. incanus* (Radlk.) Ferrucci and *H. monogynus* (Schltdl.) Ferrucci, both with 2n = 24 (Ferrucci, 1981). The karyotype of *H. incanus* has been studied and is characterized by a moderate degree of asymmetry due to its high number of sm-type chromosomes; one pair of st-type chromosomes bears a microsatellite in the short arm (Solís Neffa and Ferrucci, 1998). The mean chromosome length as well as the degree of asymmetry is similar to the *Serjania* species studied, which agrees with the close relationship between *Houssayanthus* and *Serjania* in which only fruit characteristics differentiate between genera.

Paullinia with about 150 species is mostly neotropical, with chromosome counts having been reported for seven species, including a new count for *P. coriacea,* the cytologically characterized species belonging to four of the 13 sections of the genus, all with 2n= 24 (Mangenot and Mangenot, 1958; Semple, 1974; Ferrucci, 1981; Guerra, 1986; Ferrucci and Solís Neffa, 1997 and this paper). The karyotypes of three species have been studied in detail, the analysis showing a moderate degree of asymmetry, with *P. racemosa* Wawra having the smallest degree of asymmetry with a predominance of m-type chromosomes, while *P. meliaefolia* Juss. has the highest degree of asymmetry due to its high number of sm- and st-type chromosomes, and bears a microsatellite on its pair of t-type chromosomes (Solís Neffa and Ferrucci, 1998). In the tribe, *Paullinia* is recognized by its capsular fruit, arillated seeds and pollen type.

Cardiospermum is a genus of herbs, vines or suffrutescent herbs and has 14 species native to the Americas, three of them being also present in the paleotropics. Chromosome counts are now known for six species representing the three sections of the genus, *C. integerrimum* Radlk., 2n = 14 (Ferrucci, 1989); *C. grandiflorum*, 2n = 20 (Ferrucci, 1981, 1989) and 2n = 22 (Dalgaard, 1986; Paiva and Leitão, 1989); *C. halicacabum* L., 2n = 22 (Sugiura, 1931); *C. halicacabum* L. var. *microcarpum* (Kunth) Blume, 2n = 22 (Ferrucci, 1981), *C. corindum* L., 2n = 22 (Diers, 1961); *C. pterocarpum* Radlk., 2n = 22 (Ferrucci, 1989) and *C. anomalum*, 2n = 18 (this paper).

The genus presents four basic numbers, x = 7, x = 10 and x = 11 belong to the species of the *Ceratadenia* section, x = 11 to species of the *Cardiospermum* section and x = 9 to species of the *Carphospermum* section. The presence of different basic chromosome numbers supports the macromorphological characters that identify the sections. The karyotype of 4 species has been studied in detail (Ferrucci, 1989; Hemmer and Morawetz, 1990), with *C. halicacabum* showing small chromosomes ranging from 0.6

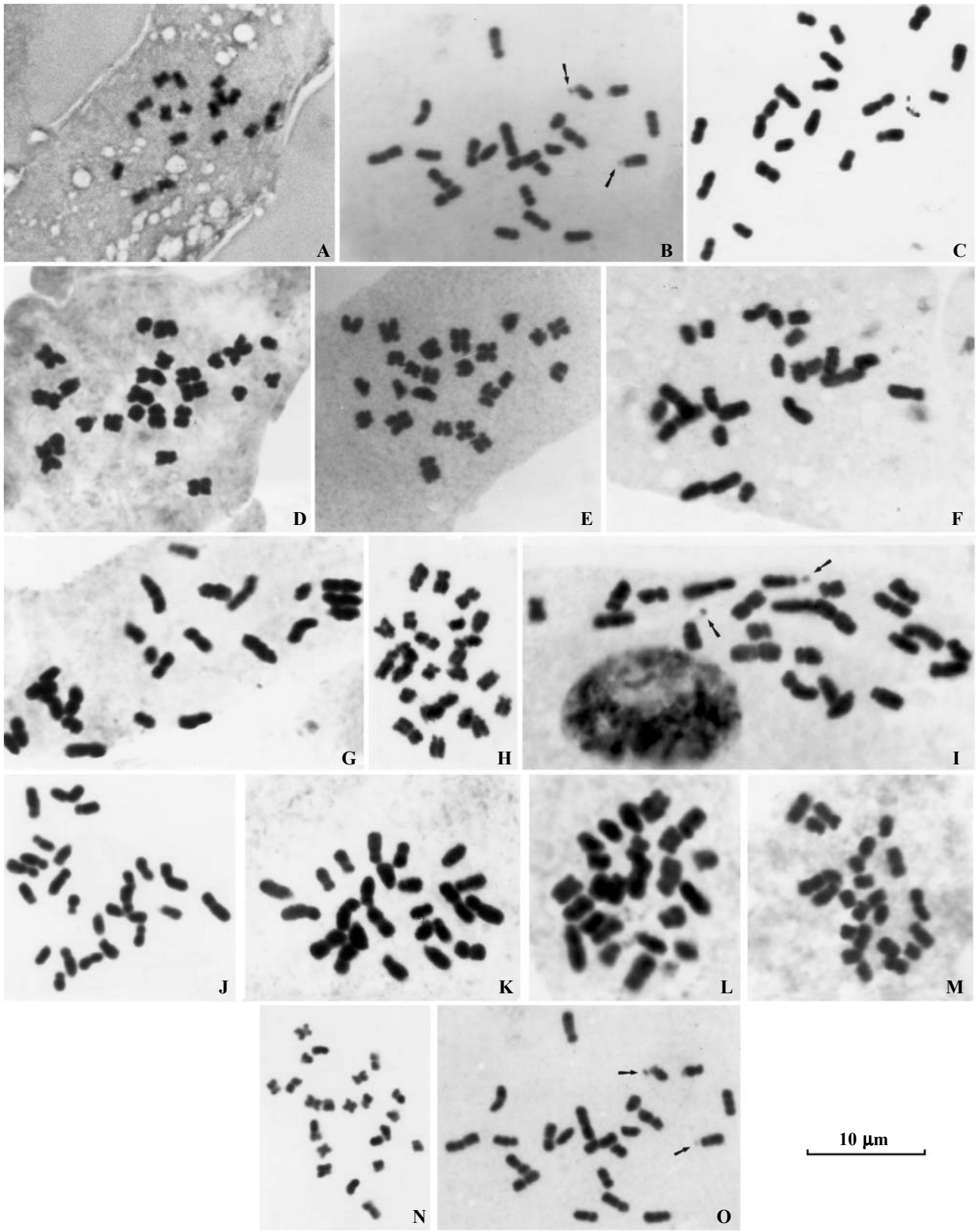

Figure 1 - Somatic chromosomes of *Sapindaceae, Paullinieae*. **A**: *Cardiospermum anomalum*, 2n = 18. **B**: *C. corindum*, 2n = 22. **C**: *C. grandiflorum*, 2n= 20. **D**: *Paullinia coriacea*, 2n= 24. **E**: *P. weinmanniaefolia*, 2n = 24. **F**: *Serjania acutidentata*, 2n = 24. **G**: *S. cissoides*, 2n = 24. **H**: *S. communis*, 2n = 24. **I**: *S. grammatophora*, 2n = 24. **J**: *S. lethalis*, 2n = 24. **K**: *S. pernambucensis*, 2n = 24. **L**: *S. purpurascens*, 2n = 24. **M**: *S. suborbicularis*, 2n = 24. **N**: *Urvillea ulmacea*, 2n = 22. **O**: *U. chacoënsis*, 2n = 22. Arrows indicate microsatellites.

to 1.5 µm, while in *C. integerrimum* the chromosome length ranges from 2.57 to 4.36 µm. The analysis of asymmetry level showed that *C. pterocarpum* has a symmetric karyotype, mainly composed of m-type and several sm-type chromosomes, while *C. integerrimum* has the most asymmetric karyotype with one submetacentric, one subtelocentric and one telocentric pair. In two species microsatellite nucleic acid was observed. In the *Paullinieae*, *Cardiospermum* is differenciated from *Urvillea* by flower and fruit characters.

Urvillea has 17 species distributed from the southern United States to central Argentina. Only 5 species have been cytologically studied, *U. uniloba* Radlk., 2n = 44, *U. chacoënsis*, 2n = 22 (Ferrucci, 1981), *U. ulmacea*, 2n = 22, 86 (Ferrucci, 1991; Nogueira *et al*., 1995), *U. peruviana* Ferrucci, 2n = 22 (Ferrucci, 1997a) and *U. laevis* Radlk., 2n = 24 (Ferrucci, 1997b; Lombello and Forni-Martins, 1998). *Urvillea* possesses two basic chromosome numbers, x = 11 in diploids and polyploid species of the section *Urvillea*, and x = 12 in *U. laevis* which belongs to the *Stenelytron* section, the other section of the genus. The two basic chromosome numbers provide additional evidence for the distinctness of the two sections of *Urvillea*. The karyotypes of *U. ulmacea*, 2n = 86, and *U. laevis* have been analyzed (Nogueira *et al.*, 1995; Ferrucci, 1997b; Lombello and Forni-Martins, 1998). In the *U. ulmacea* analysis showed small chromosomes, ranging from 0.64 to 2.4 µm, while in *U. laevis* the chromosome size ranged from 2.5 to 6.57 µm, both species having symmetric karyotypes with a predominance of m-type chromosomes. In *U. laevis* one pair of sm-type chromosomes bears a microsatellite in the short arm.

CONCLUSIONS

The genera of the tribe *Paullinieae* appear to exhibit rather different chromosome patterns. *Thinouia* and *Lophostigma* share the chromosome number 2n = 28, as well as the small size of the chromosomes, data which are in accordance with the basal position of both genera in the tribe.

The morphologically similar assemblages of *Serjania*, *Houssayanthus* and *Paullinia* appear to have a constant chromosome number of 2n = 24. Cytologic data available of *Serjania* suggest that karyotypic evolution involved structural rearrangements.

Cardiospermum is cytologically characterized by a heterogeneity of chromosome numbers, 2n = 14, 18, 20 and 22; these data indicate the important role of aneuploidy in karyotypic evolution. *Urvillea*, a close relative of *Cardiospermum*, has chromosome numbers of 2n = 22, 24, 44 and 86, and appears to have polyploidy and aneuploidy related to evolutionary changes.

Paullinieae shows variation in chromosome numbers taxonomically useful at the generic level, and also, in certain genera (such as *Cardiospermum* and *Urvillea*), at the infrageneric level.

The primitive basic number for *Sapindaceae* is x = 7, from which the widespread x = 14 has been derived, while x = 9, 10, 11, 12, 13, 15 and 16 have been derived via polyploidy and aneuploidy.

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