

A SURVEY OF CYTOGENETIC DATA ON BRAZILIAN BATS

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ABSTRACT

Cytogenetic data obtained from Brazilian specimens of 33 species of the order Chiroptera, belonging to the families Noctilionidae, Phyllostomidae, Vespertilionidae and Molossidae are summarized. These species represent about 25% of the known Brazilian bat fauna. Considering that karyotypic studies could provide interesting information for clarifying systematic aspects and phylogenetic relationships this progress report is presented in order to emphasize the need for further studies on this subject.

INTRODUCTION

Bats are mammals with special morphological and physiological features that enable them to perform true flight. The nocturnal orientation of most bats is provided by a phenomenon known as echolocation which has permitted many species to exploit a variety of sheltered roosts that offer such advantages as microclimate stability and small risk of predation. Bats can also exploit environmental resources more efficiently due to diversified feeding habits. Because of these characteristics, bats constitute a successful taxon distributed throughout most of the tropical and warm temperate regions of all continents. Among mammals, they are exceeded in number of species only by rodents (Nowak and Paradiso, 1983).

The order Chiroptera is divided into the suborder Megachiroptera, comprising the single family Pteropodidae, and the suborder Microchiroptera, which includes 16

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families. There are approximately 900 currently recognized species distributed in 175 genera (Honacki *et al.*, 1982; Koopman, 1984). Nine families of the suborder Microchiroptera have been recorded in Brazil: Emballonuridae, Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Furipteridae, Thyropteridae, Vespertilionidae and Molossidae.

Most bats have insectivorous or frugivorous feeding habits and carry out important functions in nature by destroying harmful insects and pollinating many plant species. Nevertheless, they can be natural reservoirs of infectious agents such as the rabies viruses, as well as *Toxoplasma gondii* and *Trypanosoma cruzi*. High organic content of soils enriched with bat droppings favor the growth of pathogenic fungi such as *Histoplasma capsulatum* in their shelters (Constantine, 1970). In addition, bat guano deposits on the roofs of buildings have been identified as strong allergens inducing rhinitis and asthma in humans (El-Ansary *et al.*, 1987).

The special biological features of these animals, together with their role in ecological, economical and human health and welfare aspects, have stimulated extensive morphologic, physiological, behavioral and systematic research. However, there are still several unanswered taxonomic questions and unresolved phylogenetic relationships to be ascertained.

The systematics of the New World bats are based primarily on classical morphological characteristics such as shoulder articulation, dentition, and other cranial features. More recently, karyotype data have shown considerable promise as a valuable tool for systematic studies. The order Chiroptera is an interesting group with chromosome evolution ranging from considerably conservative to quite divergent.

Of the nearly 280 species of bats from the New World, about 134 are found in Brazil. Information on the number of species in each family or subfamily occurring in Brazil and on the number of species for which cytogenetic data are available is presented in Table I. Karyotypic information for most of these species has been obtained from specimens collected outside Brazil, mainly in Mexico, Central America and northern South America.

In this report, we review data on Brazilian bats and illustrate standard and banded karyotypes as yet unpublished but presented at scientific meetings or studied in Masters and Doctoral theses in an attempt to provide a general view of the present status of cytogenetic research on Brazilian bats. All karyotypes illustrated in this paper were obtained from specimens from northwestern São Paulo state.

CYTOGENETIC DATA

Available karyotypic data on Brazilian bats are summarized in Table II. Basic karyotypes are described for 34 species, though G-banded karyotypes are reported for 17 species, C-banded karyotypes for 19, Ag-NOR-stained karyotypes for 20 species and R banded karyotypes for only 1 species.

Table I - Number of currently recognized species of the suborder Microchiroptera occurring in the New World and in Brazil.

Taxon	New World species		Species occurring in Brazil		
	Total ^a	Cytogenetically studied	Total	Cytogenetically studied	
				Non-Brazilian specimens ^b	Brazilian specimens ^c
Emballonuridae	18	11	15	10	
Noctilionidae	2	2	2	2	2*
Mormoopidae	8	8	4	4	
Phyllostomidae	139	108	75	62	20
Phyllostominae	33	26	25	22	5
Glossophaginae	32	20	13	7	2
Brachyphyllinae	5	5	0		
Carollinae	7	6	5	5	2
Stenodermatinae	59	48	29	25	8
Desmodontinae	3	3	3	3	3
Natalidae	4	2	1	1	
Furipteridae	2	1	1	1	
Thyropteridae	2	2	2	2	
Vespertilionidae	72	45	17	13	6*
Molossidae	31	16	17	13	5
Total	278	195	134	108	33

^aBased primarily on Honacki *et al.* (1982).^bReferences in Varella-Garcia and Taddei (1989).^cReferences in Table II.

*Including data from the present paper.

Emballonuridae

This family, with 12 genera and about 47 species (Koopman, 1984) has a broad pantropical distribution. In the New World, these bats occur from Mexico to southern Brazil and a total of 18 species has already been reported from South America, 15 of which occur in Brazil (Table I). Despite this, no karyotypic data have been published for Brazilian members of this family.

Table II - Karyotypic data for species of bats for which Brazilian specimens were analyzed with genera and species arranged in alphabetical order by family or subfamily.

Taxon	Reference ^a	Technique	2n ^b	FN ^c	Sex ^d		Collection Site ^e
					M	F	
Noctilionidae							
<i>Noctilio albiventris</i>	22	St*, Ag-NOR*	34	62	1	1	NW São Paulo
<i>Noctilio leporinus</i>	1	St*	34	58	1		NW Sao Paulo
	5	St*	34	60	1	1	C São Paulo
	6	St*	34	54	2	4	E Pernambuco
Phyllostomidae							
Phyllostominae							
<i>Chrotopterus auritus</i>	4	St*	28	52	1		NW São Paulo
	5	St*	28	52	1	1	S São Paulo
<i>Micronycteris minuta</i>	5	St*	28	52		1	E Bahia
<i>Phyllostomus discolor</i>	4	St*	32	60		1	NW São Paulo
	5	St*	32	60	3	2	E Bahia
	6	St*, G*, C*	32	60	6	8	E Pernambuco
	12	Ag-NOR	32	60	2	2	Pernambuco
	11, 17, 20	St*, Ag-NOR*	32	60	1	1	W Minas Gerais
<i>Phyllostomus elongatus</i>	6	St*	32	58	1	1	E Pernambuco
<i>Phyllostomus hastatus</i>	4	St*	32	58	3	2	NW São Paulo
	5	St*	32	58	6	2	E Bahia, SW Rio de Janeiro

Continued

Table II - Continued

Taxon	Reference ^a	Technique	2n ^b	FN ^c	Sex ^d		Collection Site ^e
					M	F	
Glossophaginae							
<i>Anoura caudifer</i>	6	St*	32	58		1	E Pernambuco
	12	Ag-NOR	32	58	2	2	Pernambuco
	11, 17, 20	St*, G*, C*, Ag-NOR*	32	58	4	3	W São Paulo
<i>Glossophaga soricina</i>	1	St	30			1	NW São Paulo
	5	St*	30	54-56	6	4	C São Paulo
	11, 17, 20	St*, G*, C*, Ag-NOR*	30	54	1	6	NW and NE São Paulo
	5	St*	32	60	8	5	C São Paulo
	12	Ag-NOR	32	60	2	1	Pernambuco
	11, 17, 20	St*, G*, C*, Ag-NOR*	32	60	4	3	NW São Paulo
Carollinae							
<i>Carollia perspicillata</i>	4	St*	20/21	36	2	2	NE and SE São Paulo
	5	St*	20/21	36	7	4	E Bahia, SW Rio de Janeiro, C São Paulo
	6	St*, G*, C*	20/21	36	9	18	E Pernambuco
	17	St*, G*, Ag-NOR*	20/21	36	4	3	NW São Paulo
<i>Rhinophylla pumilio</i>	5	St*	26	48	1		E Bahia
Stenodermatinae							
<i>Artibeus cinereus</i>	6	St*	30	56	1		E Pernambuco

Continued

Table II - Continued

Taxon	Reference ^a	Technique	2n ^b	FN ^c	Sex ^d		Collection Site ^e
					M	F	
<i>Artibeus jamaicensis</i>	9	Ag-NOR	30		3	1	Pernambuco
	15, 19	C	30	56	2	6	Pernambuco
	5	St*	30/31	56		1	E Bahia
	15, 19	C	30/31	56	5	1	Pernambuco
<i>Artibeus lituratus</i>	2, 3	St	30/31	56	2	2	NW São Paulo
	4	St*	30/31	56	1	1	NW São Paulo
	5	St*	30/31	56	3	3	E Bahia, SW Rio de Janeiro, C São Paulo
	6	St*	30/31	56	6	9	E Pernambuco
	7	C, R*, Ag-NOR	30/31	56	2	1	SE São Paulo
	19	C	30/31	56			Pernambuco
<i>Artibeus planirostris</i>	10, 17, 18, 20	St*, G*, C*, Ag-NOR*	30/31	56	5	2	NW and C São Paulo
	10, 17, 18, 20	St*, G*, C*, Ag-NOR*	30/31	56	3	4	NW and C São Paulo
<i>Chiroderma doriae</i>	10, 13, 17, 20	St*, G*, C*, Ag-NOR*	26	48		4	W Minas Gerais, SE São Paulo
<i>Chiroderma villosum</i>	10, 17, 18, 20	St*, C*, Ag-NOR*	26	48	1	1	W Minas Gerais, SE São Paulo
<i>Sturnira lilium</i>	5	St*	30	56	1		E Bahia
	6	St*, G*	~ 30	56	6	5	E Pernambuco
	12	Ag-NOR	30	56	2	2	Pernambuco
<i>Vampyrops lineatus</i>	17, 18, 20	St*, G*, C*, Ag-NOR*	30	56	5	2	NW and C São Paulo
	5	St*	30	56	4	3	SW Rio de Janeiro, SE São Paulo
	6	St*	30	56	1	1	E Pernambuco

Continued

Table II - Continued

Taxon	Reference ^a	Technique	2n ^b	FN ^c	Sex ^d		Collection Site ^e
					M	F	
<i>Desmodontinae</i>							
<i>Desmodius rotundus</i>	8	C	30	56	3	3	SE São Paulo
	12	Ag-NOR	30	56	1	3	Pernambuco
	17, 18, 20	St*, G*, C*, Ag-NOR*	30	56	4	3	W Minas Gerais, NW São Paulo
	4	St*	28	52	3	3	NW São Paulo
	5	St*	28	52	3	4	E Bahia, SW Rio de Janeiro, SE and S São Paulo
	6	St*, G*	28	52	1	5	E Pernambuco
	12	Ag-NOR	28	52	4	2	Pernambuco
	15	G, C, Ag-NOR	28	52			Pernambuco
	14, 17, 20	St*, G*, C*, Ag-NOR*	28	52	5	2	NE, NW São Paulo
<i>Diaemus youngi</i>	14, 17, 20	St*, G*, C*, Ag-NOR*	32	60	1		NE São Paulo
<i>Diphylla ecaudata</i>	6	St*, G*	32	60	2	3	E Pernambuco
<i>Vespertilionidae</i>							
<i>Eptesicus brasiliensis</i>	6	St*	50	48	2		E Pernambuco
	16	G, C, Ag-NOR	50	48	2	7	S Rio Grande do Sul
<i>Eptesicus furiatilis</i>	22	St, Ag-NOR	50	48	1	1	NW São Paulo
<i>Histiotus velatus</i>	5	St*	50	48	5	6	SW Rio de Janeiro, SE São Paulo

Continued

Table II - Continued

Taxon	Reference ^a	Technique	2n ^b	FN ^c	Sex ^d		Collection Site ^e
					M	F	
<i>Lastiurus borealis</i>	22	G*, C*, Ag-NOR	28	46	1		NW São Paulo
<i>Lastiurus ega</i>	5	St*	28	50	4	1	SW Rio de Janeiro, C São Paulo
<i>Myotis nigricans</i>	5	St*	44	50	2		SW Rio de Janeiro
	22	St*	44	50	1		NW São Paulo
Molossidae							
<i>Eumops auripendulus</i>	5	St*	42	62	1	4	SW Rio de Janeiro
<i>Eumops glaucinus</i>	21	St, G*, C*, Ag-NOR*	40	64	1	1	NW São Paulo
<i>Eumops perotis</i>	5	St*	48	54	1	2	SW Rio de Janeiro
<i>Eumops sp.</i>	5	St*	48	56		4	C São Paulo
<i>Molossus ater</i>	5	St*	48	60	5	5	SW Rio de Janeiro, SE São Paulo
	6	St*	48	60	2	1	E Pernambuco
<i>Molossus molossus</i>	6	St*	48	56	5	4	E Pernambuco
	16	G, C, Ag-NOR	48	56	2	7	S Rio Grande do Sul

^a References: 1. Yonenaga, 1968; 2. Beçak *et al.*, 1968; 3. Beçak *et al.*, 1969; 4. Yonenaga *et al.*, 1969; 5. Toledo, 1973; 6. Lopes, 1978; 7. Kasahara and Dutrillaux, 1983; 8. Seixas *et al.*, 1983; 9. Souza and Correia, 1984; 10. Morielle *et al.*, 1985a; 11. Morielle *et al.*, 1985b; 12. Souza, 1985; 13. Varella-Garcia and Taddei, 1985; 14. Morielle *et al.*, 1986; 15. Araujo and Souza, 1987; 16. Christoff *et al.*, 1987; 17. Morielle, 1987; 18. Morielle *et al.*, 1987; 19. Souza and Araujo, 1987; 20. Morielle and Varella-Garcia, 1988; 21. Morielle *et al.*, 1988; 22. This paper.

^b 2n, Diploid number.

^c FN: number of arms of the autosomal complement.

^d M, male; F, female.

^e E, eastern; W, western; S, southern; C, central; NE, northeastern; NW, northwestern; SE, southeastern; SW, southwestern.

*Karyotype illustrated.

Noctilionidae

This is a small family with one genus and two species, restricted to, but widely distributed throughout, the Neotropical Region, being found both in South and Central America and throughout most of the West Indies (Taddei *et al.*, 1986).

Standard karyotypes were obtained for specimens of *Noctilio leporinus* from São Paulo (Yonenaga *et al.*, 1969; Toledo, 1973) and Pernambuco (Lopes, 1978) and for *N. albiventris* from São Paulo (this paper), all of them with $2n = 34$.

Although the fundamental number ranges from 54 to 62 among specimens from different geographical regions (Table II), this diversity may be attributed more to different morphological chromosome classification than to actual differences. In general, chromosomes were quite contracted and it was not easy to decide between acrocentric and subtelocentric forms. *N. albiventris* from Honduras (Patton e Baker, 1978) and *N. leporinus* collected outside South America (Baker *et al.*, 1982) have also been reported to have $FN = 62$.

A large constriction near the centromere on the long arm of the smallest medium-sized submetacentric chromosome has been reported by Yonenaga *et al.* (1969) and by Lopes (1978) for *N. leporinus* and can be observed in Figure 1A for *N. albiventris*, where it includes the single nucleolus organizer region detected in the karyotype (Figure 1B).

No G- or C-banding data have been published for any species of Brazilian noctilionids but the two species are known to have indistinguishable G-banded karyotypes (Baker and Bickham, 1980) which seem to be more closely related to that of *Pteronotus*, a Mormoopidae genus, than to any karyotype thus far described for any species of Phyllostomidae (Patton and Baker, 1978; Sites *et al.*, 1981). *P. parnellii* and *P. davyi* have NORs on the centromeric regions of three acrocentric chromosomes (Sites *et al.*, 1981). A composite karyotype constructed for *P. parnellii* and *N. albiventris* has demonstrated that the banded NOR-bearing chromosome in *Noctilio* is probably a fusion of the two small NOR-bearing chromosomes of *Pteronotus* and homologous to the 30 and 28 autosomal arms of *Macrotus* (Patton and Baker, 1978).

Mormoopidae

The family Mormoopidae is endemic to the New World and ranges from southern Texas through Mexico and Central America to South America and southern Brazil. It is also represented in the Greater and Lesser Antilles, Trinidad and the Dutch West Indies (Smith, 1972). It comprises two genera and eight species.

Four species of this family have been detected in Brazil: *Pteronotus davyi*, *P. gymnonotus*, *P. parnellii* and *P. personatus* but no Brazilian specimen has been cytogenetically studied. Sites *et al.* (1981) have provided data from G-banded karyo-

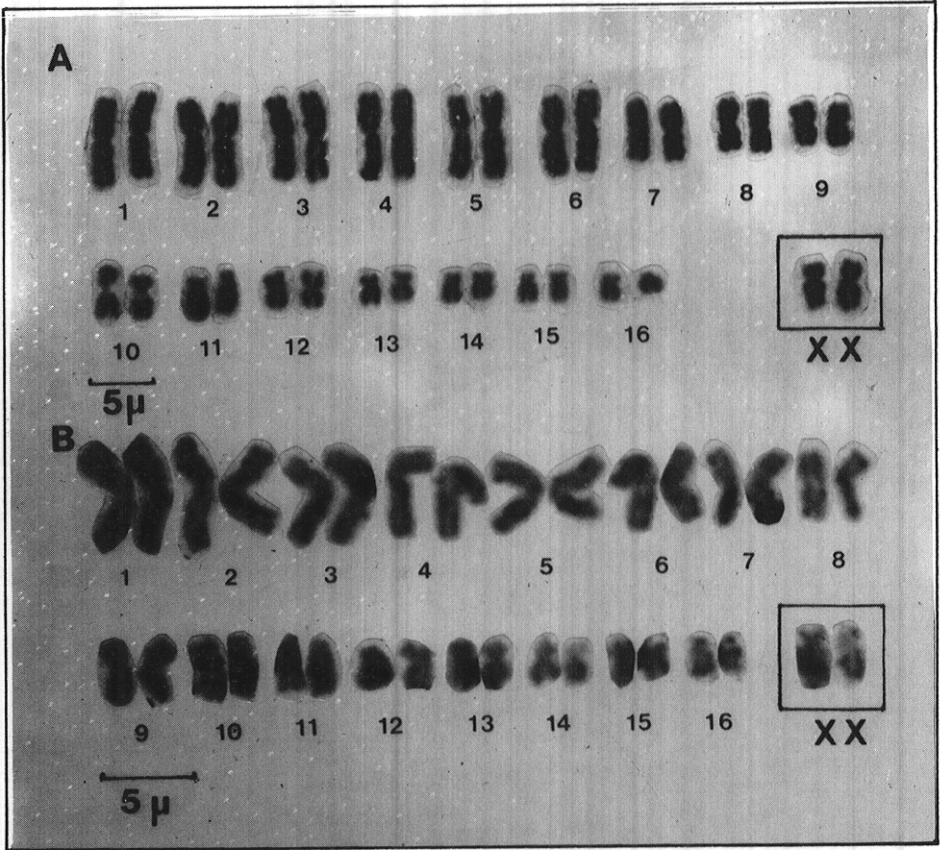


Figure 1 - Standard (A) and Ag-NOR-stained (B) karyotypes of a female *Noctilio albiventris* specimen.

types for all the eight currently recognized species of this family using specimens from Mexico, Jamaica, Nicaragua and Venezuela, and have proposed the karyotype of *Pteronotus*, which shows no difference among the six species, to be the primitive one for the family. As noted above, the G-banded karyotypes of the family Noctilionidae are similar quite to those of *Pteronotus* and all chromosomes of *P. parnellii* were also identified in the karyotype of *Macrotus waterhousii*, the probable ancestor of the family Phyllostomidae, further supporting the conclusions of Sites *et al.* (1981).

Phyllostomidae

Phyllostomidae is the family with the largest number of genera and species among Neotropical Chiroptera (Table I). It comprises six subfamilies: Phyllostominae,

Glossophaginae, Brachyphyllinae, Carollinae, Stenodermatinae and Desmodontinae, with a wide geographical distribution ranging from the southern US to Argentina (Koopman, 1970). These New World leaf-nosed bats vary in feeding habits and morphological features from species to species but available data are still insufficient for a full understanding of the systematics and genetics of members of this family.

Phyllostominae

There are 25 species of Phyllostominae occurring in Brazil; chromosomal data have been described for 22 of them, though Brazilian specimens were used for only 5 of these species (Table I).

Patton and Baker (1978) proposed three primary clades for this subfamily: the *Macrotus* group, the *Micronycteris* group and the *Tonatia-Mimon-Phyllostomus* group. The *Macrotus* clade and the *Noctilio-Pteronotus* clade show intensive homology and the karyotype of *Macrotus waterhousii* is the most likely candidate for the primitive condition of the Phyllostomidae (Patton and Baker, 1978). *Macrotus* is restricted to North and Central America, the Greater Antilles and the Bahamas (Jones and Carter, 1976). For the second clade, chromosome information is available from one specimen of *Micronycteris minuta* from Bahia ($2n = 28$; FN = 52; Toledo, 1973), whose karyotype is similar to that of a specimen from Trinidad ($2n = 28$; FN = 50; Patton and Baker, 1978). Twelve of the thirteen chromosome pairs of the Brazilian specimen are morphologically identical to those of the Trinidad specimen. Only a small pair was assumed to be biarmed by Toledo (1973), and acrocentric by Patton and Baker (1978). This difference may represent a rearrangement or may reflect analytical differences due to strongly contracted chromosomes.

Chrotopterus auritus ($2n = 28$; FN = 52) has a standard karyotype closer to that of the *Micronycteris* clade. The Brazilian specimens analyzed, collected from northwestern and southern São Paulo state, have a conspicuous constriction close to the centromere on the long arm of the largest chromosome.

The other three analyzed Brazilian species belong to the *Phyllostomus* genus. *P. discolor* and *P. hastatus* specimens from several sites separated by great distances (Table II) showed no differences in G- and C-banding patterns or in the location of the NORs (Lopes, 1978; Morielle, 1987; Morielle and Varella-Garcia, 1988). *P. hastatus* differs from *P. discolor* only by an apparent inversion in the smallest autosome pair, which converts the biarmed element of *discolor* to an acrocentric in *hastatus* (Figure 2). This pair is the NOR-bearing chromosome in both species (Morielle and Varella-Garcia, 1988) and seems to correspond to autosomal arms 28 and 30 of *Macrotus waterhousii* (Patton and Baker, 1978). G-banded and C-banded karyotypes of *P. hastatus* are presented in Figure 3.

The standard karyotype of *P. elongatus* from eastern Pernambuco (Lopes,

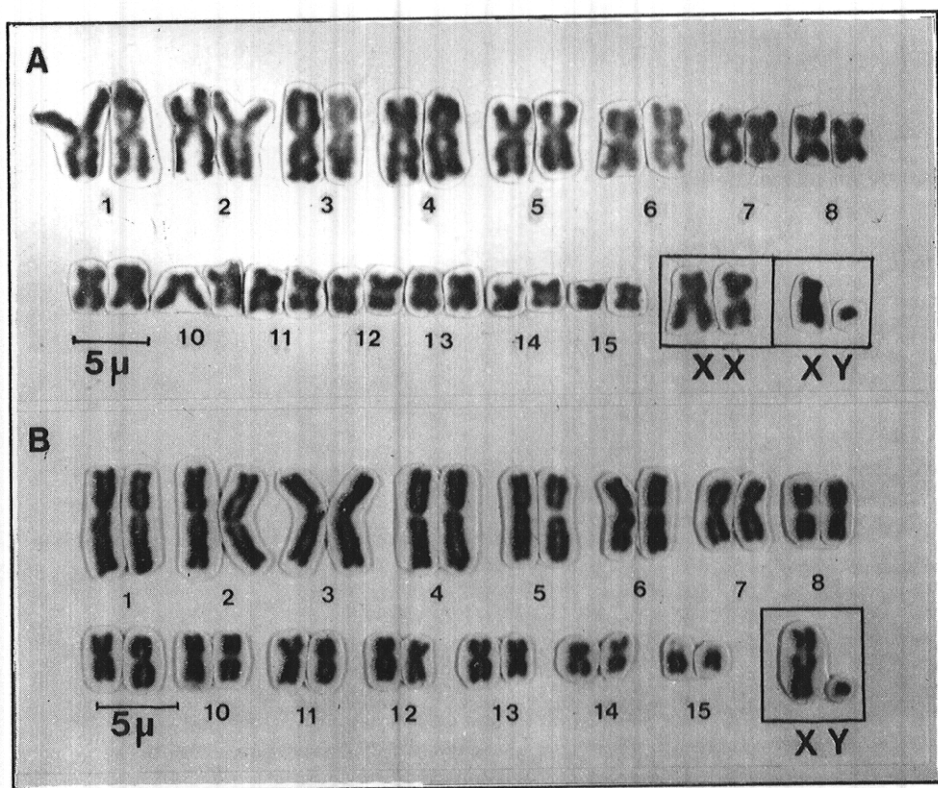


Figure 2 - Standard karyotypes of *Phyllostomus discolor* (A) and *Phyllostomus hastatus* (B). Inset: sex chromosomes of male and female specimens.

1978) is similar to that of a specimen from Colombia (Baker, 1979) and to that of the Brazilian *P. hastatus*.

The genus *Phyllostomus* appears to have a conservative rate of chromosomal evolution, as observed in other taxa such as *Macrotus*, whereas other phyllostomine genera, such as *Tonatia*, have karyotypes in which none of the arms proposed as primitive for the family could be identified (Patton and Baker, 1978). The recognizable homology among *Noctilio*, *Pteronotus*, *Macrotus* and *Phyllostomus* is an example of extensive morphological evolution accompanied by little chromosomal evolution. Alternatively, species with karyotypes strongly different from all the others thus far examined, such as *Tonatia bidens* and *Micronycteris megalotis*, are examples of extensive chromosomal evolution accompanied by little morphological evolution.

Glossophaginae

The Glossophaginae subfamily comprises about 32 species sharing

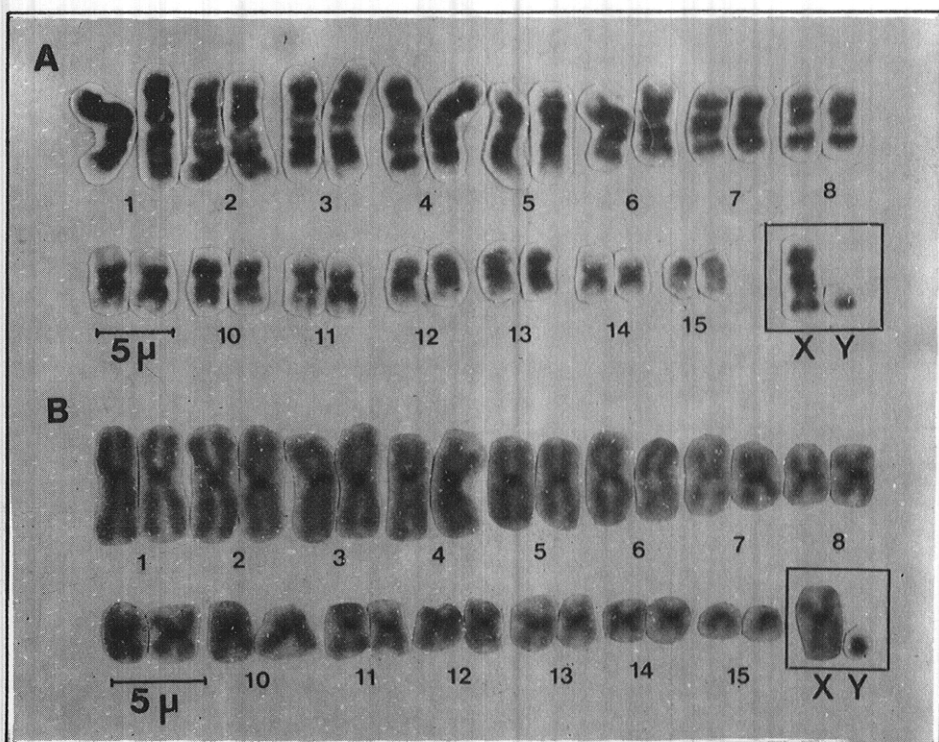


Figure 3 - G-banded (A) and C-banded (B) karyotypes of a male *Phyllostomus hastatus* specimen.

morphological adaptations to a nectarivorous feeding habit. Although previous data had suggested a polyphyletic origin for this subfamily, Haiduk and Baker (1982) have provided information compatible with the hypothesis that the Glossophaginae are monophyletic. About 13 species can be found in Brazil, 7 of which have been cytogenetically analyzed, though only 2 (*Glossophaga soricina* and *Anoura caudifer*) using Brazilian specimens (Table I).

Two distinct groups are recognized in this family on the basis of chromosomal data: a conservative one, including *Glossophaga*, and a rapidly evolving derived group, including *Anoura*. *Glossophaga soricina* has a karyotype in which all the primitive *Macrotus* chromosomal arms could be recognized, although some of these arms were found in unique combinations (Baker and Bass, 1979). On the other hand, except for the largest autosome, the rest of the *Anoura caudifer* karyotype has undergone sufficient rearrangements to prevent the identification of the banding sequences of *Macrotus* or *Glossophaga*.

All Brazilian specimens of *Anoura caudifer* were collected in São Paulo (Yonenaga, 1968; Toledo, 1973; Morielle, 1987) and their G- and C-banded karyotypes

are shown in Figure 4. The G-banding pattern is similar to that described by Haiduk and Baker (1982) for Suriname and Venezuela specimens and the C-bands revealed only centromeric heterochromatin. The NORs are located on the short arm of the smallest autosome, an acrocentric (Morielle and Varella-Garcia, 1988), for which Yonenaga (1968) reported the presence of satellites. The Brazilian specimens of *Glossophaga soricina* were obtained in São Paulo (Toledo, 1973; Morielle, 1987) and Pernambuco (Souza, 1985). G- and C-banded karyotypes of this species are presented in Figure 5. The G-banding pattern is similar to that described by Baker and Bass (1979) for a specimen from Jamaica and the C-bands reveal heterochromatin in centromeric regions and on the distal segment of the long arm of the smallest autosome (Figure 5). In 7 specimens from northwestern São Paulo the NORs are located in the conspicuous constriction on the long arm of the smallest autosome (Morielle and Varella-Garcia, 1988) but in 3 specimens from Pernambuco they were located on a medium-sized metacentric or submetacentric chromosome (Souza, 1985).

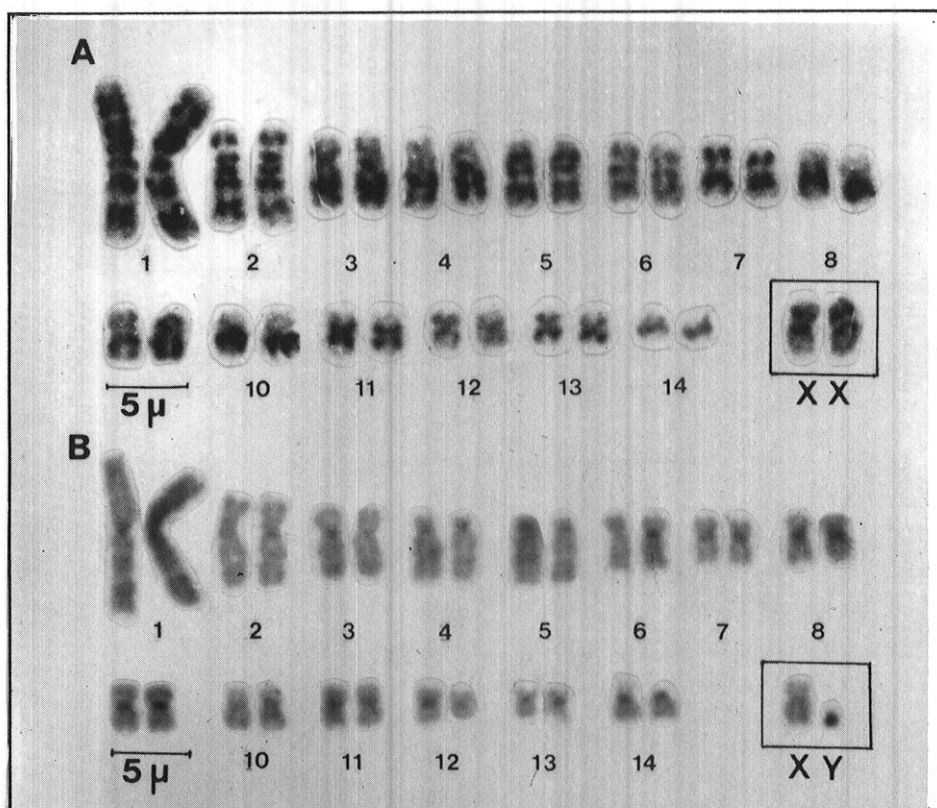


Figure 4 - G-banded (A) and C-banded (B) karyotypes of *Anoura caudifer*.

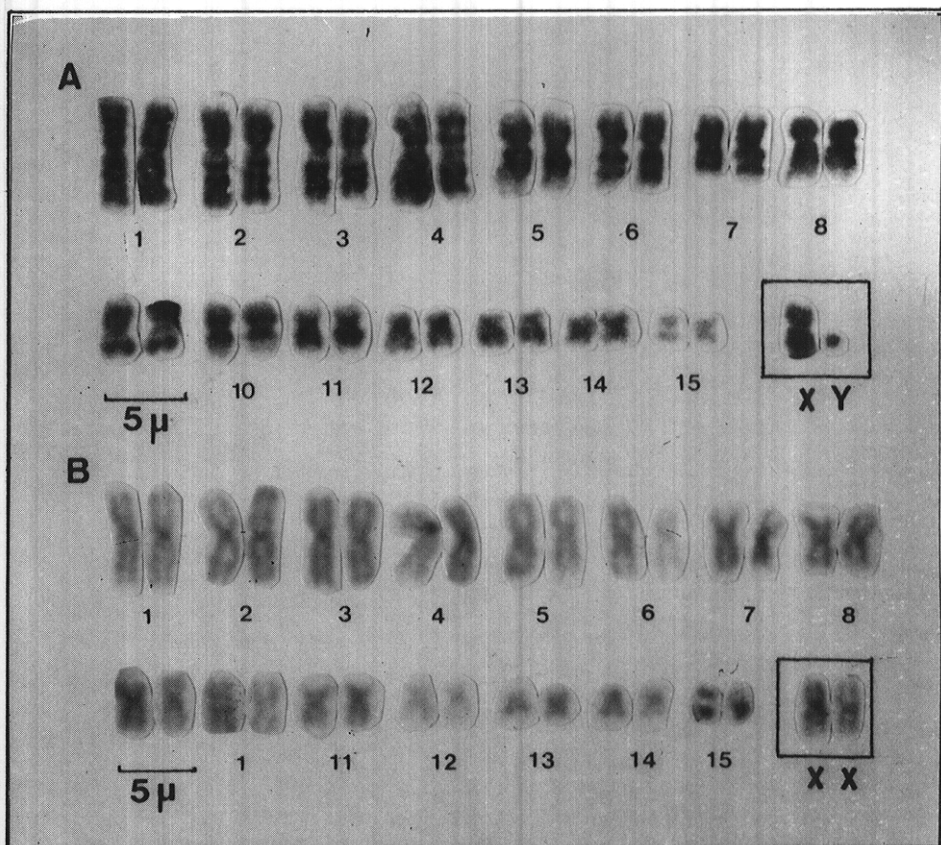


Figure 5 - G-banded (A) and C-banded (B) karyotypes of *Glossophaga soricina*.

The smallest autosome of *Glossophaga* is homologous to chromosomal arm 29 of *Macrotus*, which corresponds to the short arm of chromosome 12 of *Phyllostomus hastatus*, in which no NORs were detected. Thus it may be concluded that the DNAr location changed in the evolution of the *G. soricina* and *P. hastatus* karyotypes.

Carollinae

The subfamily Carollinae consists of only two genera, *Carollia* and *Rhinophylla*, both with representatives in Brazil (Table I). However, Brazilian specimens of only two species have been cytogenetically analyzed: *C. perspicillata* (Yonenaga *et al.*, 1969; Toledo, 1973; Morielle, 1987) and *R. pumilio* (Toledo, 1973).

The G- and C-banded karyotypes of *Carollia perspicillata* are shown in Figure 6

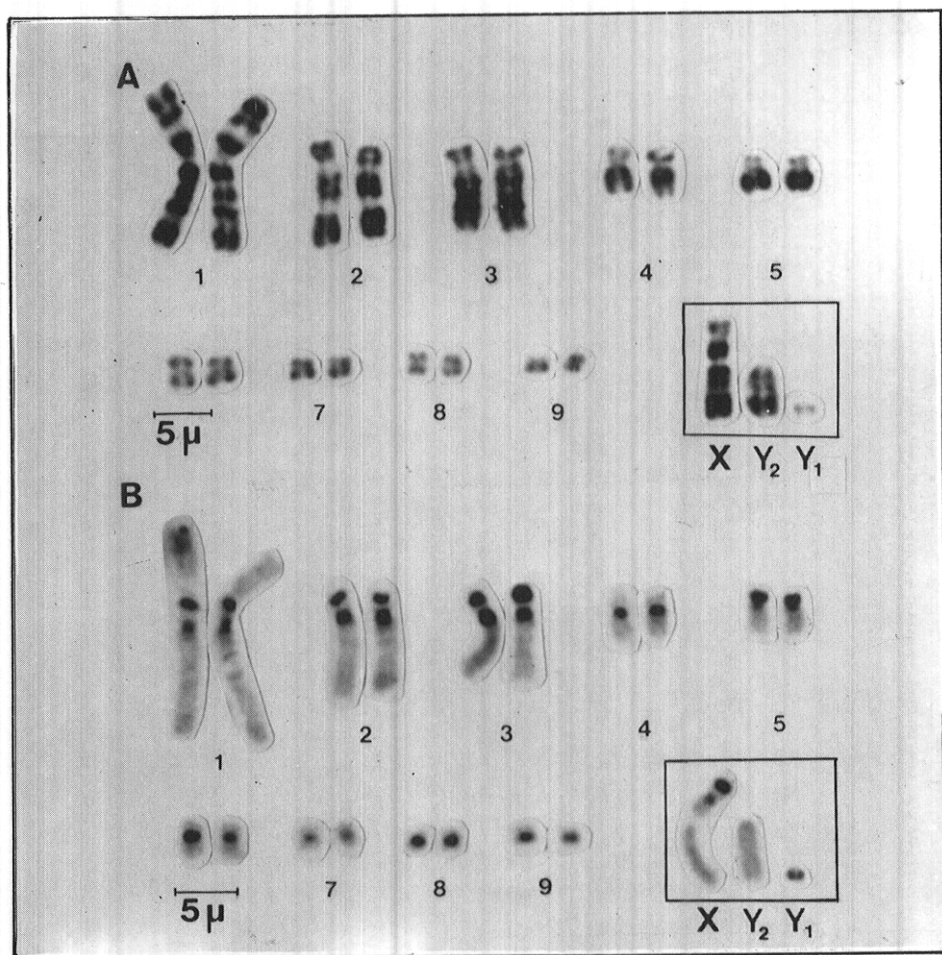


Figure 6 - G-banded (A) and C-banded (B) karyotypes of a male *Carollia perspicillata* specimen.

and are similar to those reported by Pathak *et al.* (1973). This species has a sex chromosome-autosome translocation, the same as detected in *C. brevicauda*, *C. subrufa* and in specimens of *C. castanea* from Central America and Colombia but not from Peru (Baker and Bleier, 1971; Patton and Gardner, 1971). *C. perspicillata* has large heterochromatin blocks in the centromeres, in the intermediate region of the largest autosome and in the short arm telomere of three autosome pairs and of the X chromosome, differing from the other phyllostomid bats in which C-banding material is usually restricted to the centromeric regions.

In situ DNA/RNA hybridization studies have shown that the nucleolus organizer region appears to be located at the junction of the X/autosome translocation

in *C. perspicillata* (Hsu *et al.*, 1975) and the same result was obtained for Brazilian specimens using the Ag-NOR staining technique (Morielle and Varella-Garcia, 1988).

R. pumilio from Bahia ($2n = 26$; $FN = 48$; Toledo, 1973) differs significantly from specimens from Bolivia and Colombia ($2n = 36$; $FN = 62$; Baker and Bleir, 1971; Baker, 1979) and from Suriname ($2n = 34$; $FN = 64$; Honeycutt *et al.*, 1980). A centric fusion of two acrocentric pairs and a pericentric inversion or short arm addition of heterochromatin could explain the differences between the cytotypes from Bolivia-Colombia and from Surinam. However, the striking difference between the Brazilian cytotype and the two others will probably be understood only by analyses of banded karyotypes.

Stenodermatinae

This is the largest Phyllostomidae subfamily, with about 59 species. The karyotypes of all 25 species occurring in Brazil have been published (Table I). Though the data were based on Brazilian specimens in only 8 species from 4 genera (*Artibeus*, *Chiroderma*, *Sturnira* and *Vampyrops*) (Table II).

The studied species of the genus *Artibeus* were: *A. cinereus* from Pernambuco, *A. jamaicensis* from Bahia, *A. lituratus* from Pernambuco, Bahia, Rio de Janeiro and São Paulo, and *A. planirostris* from São Paulo. The diploid number is $2n = 31$ for all males and $2n = 30$ for the females of the three latter species. This difference is due to a translocation between a medium-sized acrocentric X chromosome and a small autosome, well demonstrated by Kasahara and Dutrillaux (1983) and Tucker (1986). Nevertheless, specimens of *A. cinereus* from Trinidad (Baker and Hsu, 1970; Tucker, 1986) have the same translocation of an autosome to a sex chromosome, but male and female specimens from Pernambuco have $2n = 30$, probably representing a neo-XY type, with both X- and Y-autosome translocations, as reported for some other species of *Artibeus* (*A. toltecus* and *A. watsoni*) by Tucker (1986).

G- and C-banded karyotypes of *A. lituratus* and *A. planirostris* are shown in Figures 7 and 8. C-banding revealed the presence of heterochromatin in the centromeric regions, in the interstitial regions of several autosome arms, and in the short arm telomere of the four subtelocentric autosomes and of the X chromosome. The minute Y_1 , the true Y chromosome, is entirely heterochromatic in both species. The acrocentric Y_2 , the free autosome, with no role in sex determination, has heterochromatin in the centromere and telomere and shows a C-banding pattern similar to that of the short arm of the X chromosome in each species. *A. jamaicensis* has the same karyotype pattern, and *A. cinereus* has the same autosome complement pattern (Souza and Araujo, 1987).

Two species of the genus *Chiroderma* were analyzed: *C. doriae* and *C. villosum* from São Paulo and Minas Gerais (Table II). The standard G- and C banded karyotypes

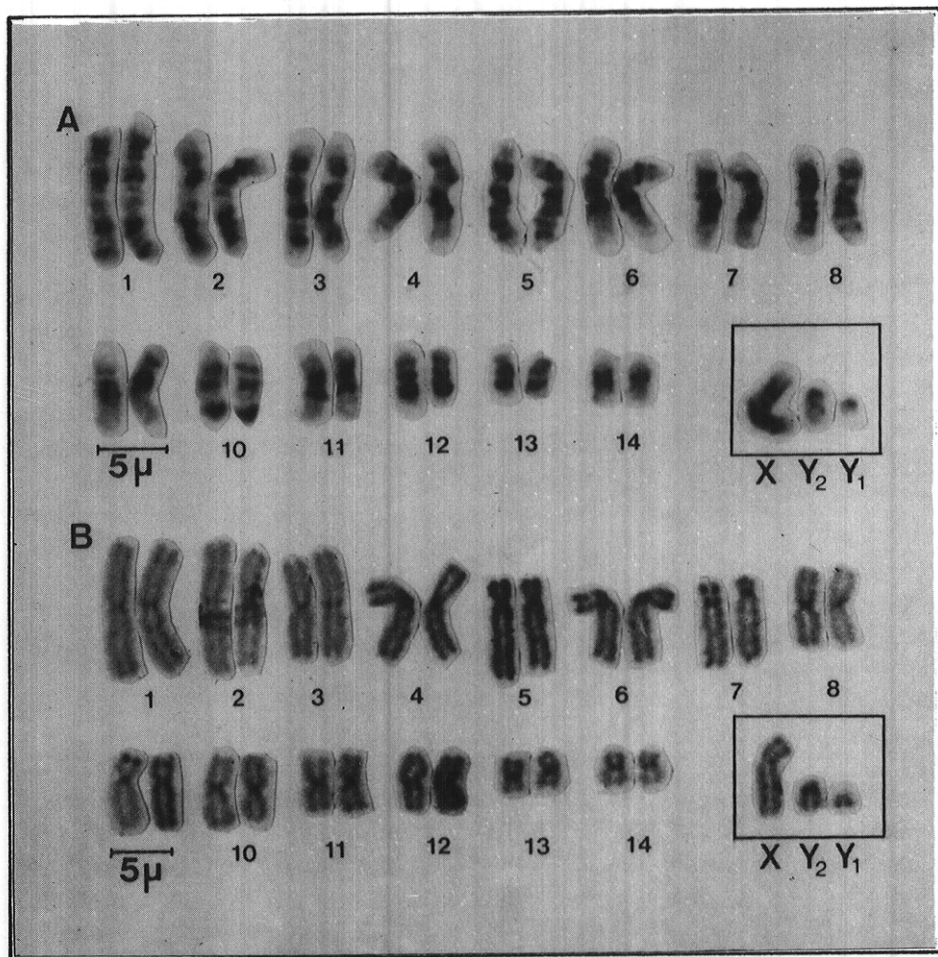


Figure 7 - G-banded (A) and C-banded (B) karyotypes of a male *Artibeus lituratus* specimen.

of a *C. doriae* female are shown in Figure 9 and the standard and C banded karyotypes of a *C. villosum* male are shown in Figure 10. C-band analysis revealed only the presence of centromeric heterochromatin. The NORs are located in the short arm telomere of the subtelocentric chromosomes (# 6, 7 and 9) in *C. doriae*, but only in chromosome 6 in *C. villosum* (Morielle and Varella-Garcia, 1988).

Sturnira lilium and *Vampyrops lineatus* have karyotypes very similar to that of *Artibeus* except for the sex chromosomes. The nucleolus organizer regions are located in the short arm telomere of the smallest subtelocentric autosome (# 7) both in *S. lilium* and *V. lineatus* (Morielle and Varella-Garcia, 1988). The G- and C-banded karyotypes are presented in Figure 11 for *S. lilium* and in Figure 12 for *V. lineatus*.

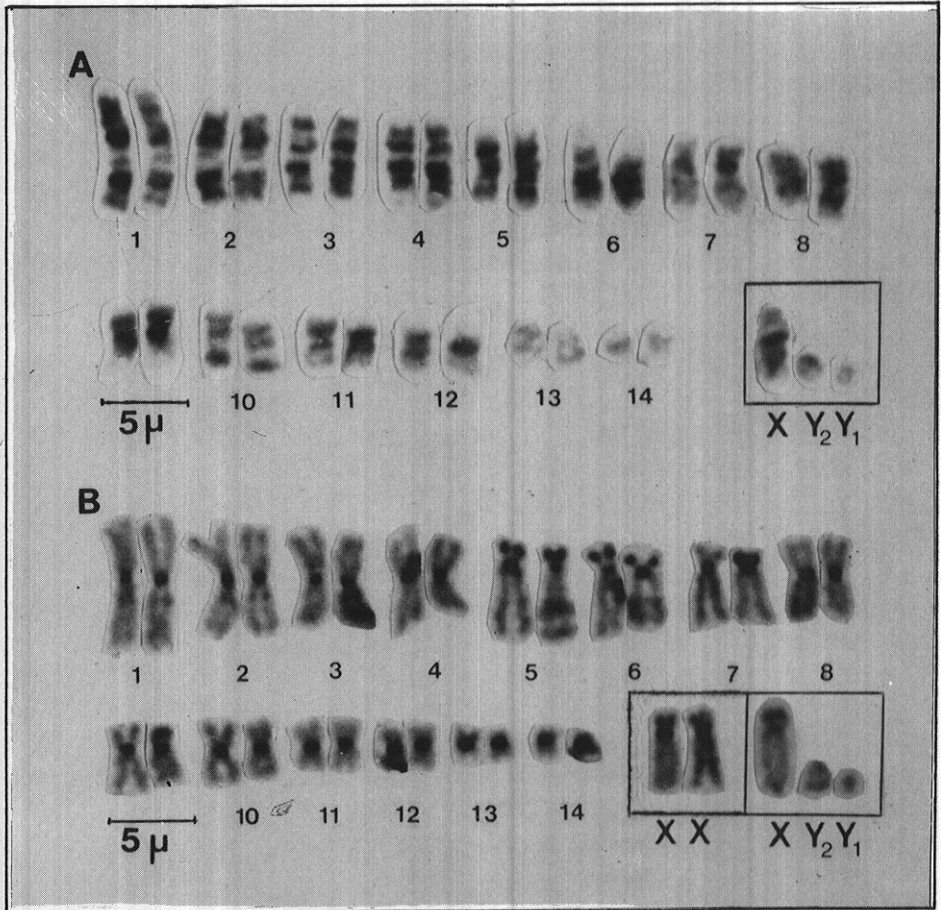


Figure 8 - G-banded (A) and C-banded (B) karyotypes of *Artibeus planirostris*. Inset: sex chromosomes of male and female specimens.

Centromeric, interstitial and telomeric heterochromatin is present in the autosome. The X chromosomes have a C-banding pattern similar to that of *A. lituratus* and *A. planirostris*, with heterochromatin in the centromere and short arm telomere. One arm of the Y is entirely heterochromatic and comparable to the Y₁ of *Artibeus* and the other arm shows the same C-banding pattern as the short arm of the X in each species, which is comparable to the Y₂ of the *Artibeus*. These findings support the conclusion that these species of *Sturnira* and *Vampyrops* have autosomes translocated to both the X and the Y chromosomes (neo-XY types) as previously pointed out by Tucker (1986) for *S. lilium* from Costa Rica, *Sturnira* sp. from Peru and Trinidad and for *V. vittatus* from Peru.

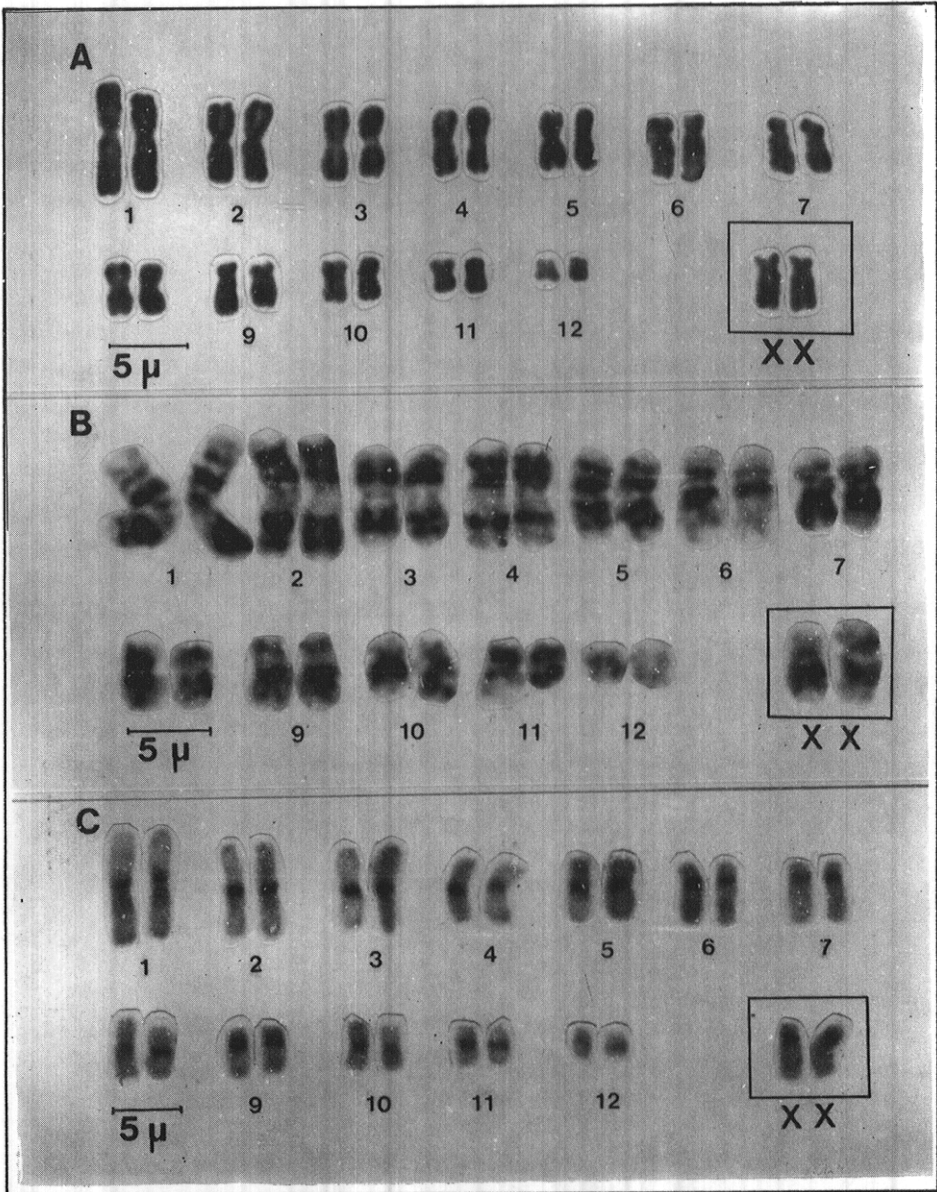


Figure 9 - Standard (A), G-banded (B) and C-banded (C) karyotypes of female *Chiroderma doriae* specimen.

An intermediate replicating band on the long arm of the X chromosomes in stenodermatines was detected by Tucker (1986), and was proposed as evidence of a

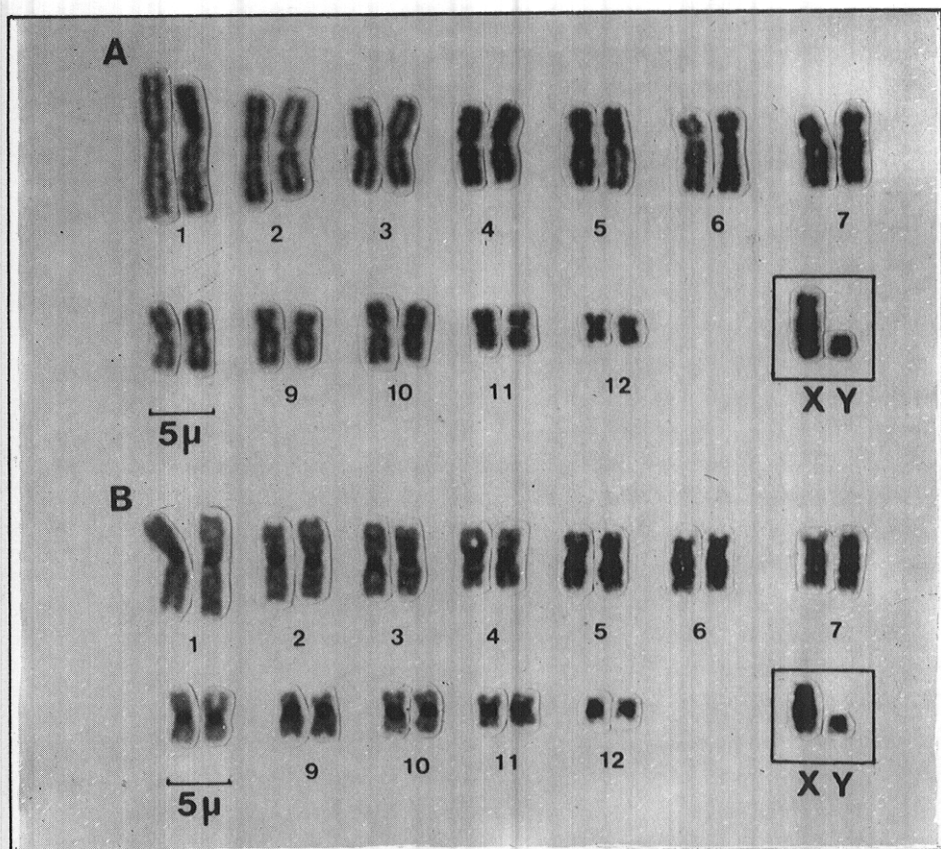


Figure 10 - Standard (A) and C-banded (B) karyotypes of a male *Chiroderma villosum* specimen.

hypothetical translocation of an autosomal element to the X chromosome as an ancestral rearrangement occurring in the sex chromosomal evolution in Phyllostomidae. The intermediate C-band observed in this chromosome region in the specimens of *Artibeus*, *Sturnira* and *Vampyrops* described here reinforces the hypothesis proposed by Tucker (1986) to explain the evolution of sex chromosome heteromorphism.

The cytogenetic data for specimens of *S. lilium* from Pernambuco (Lopes, 1978; Souza, 1985), Bahia (Toledo, 1973) and São Paulo (Morielle, 1987) are similar. In contrast, chromosomal variation was found in *V. lineatus* at a single location (Seixas *et al.*, 1983). In addition to the common cytotype, we found a specimen from southeastern São Paulo that showed addition of heterochromatin to the short arm of the largest subtelocentric autosome, which clearly became submetacentric, and large heterochromatin blocks on both arms of a small metacentric autosome (Figure 12C). These data indicate the occurrence of intraspecific variation in *V. lineatus*.

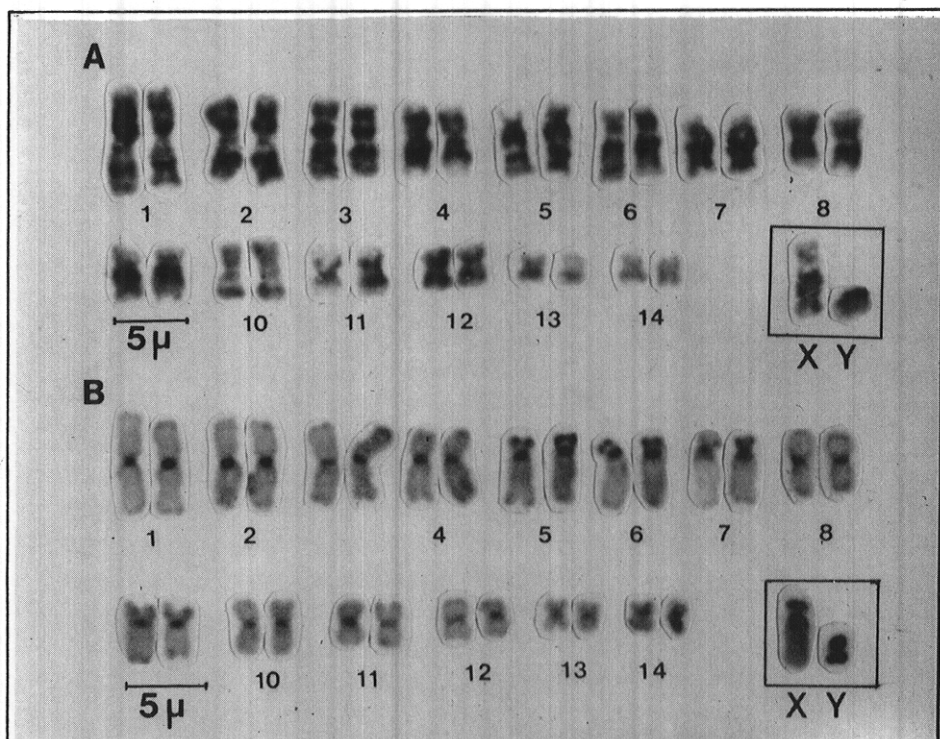


Figure 11 - G-banded (A) and C-banded (B) karyotypes of a male *Sturnira lilium* specimen.

Cytogenetic data on Brazilian stenodermatine bats permit their classification in two groups: the *Artibeus*, *Sturnira* and *Vampyrops* clade and the *Chiroderma* clade. Species of the first group have $2n = 30$ or $30/31$, show similarity in chromosome morphology and extensive homology in G-banding patterns, except for chromosome 7, which differs by a paracentric inversion between *Artibeus* and *Sturnira-Vampyrops*. There is also an increase in the amount of constitutive heterochromatin revealed by C-banding procedures and a decrease in the number of active NORs per genome from *Artibeus* to *Sturnira-Vampyrops*. Species in the second group have $2n = 26$ and G- and C-banding patterns are shared by *C. doriae* and *C. villosum* but a decrease in the number of active NORs occurred from *C. doriae* to *C. villosum*.

Extensive homology can be identified in banded karyotypes of the species of these two groups despite the difference in diploid numbers. Chromosomes 1-4, 6-11, 13 and X have similar patterns and a pericentric inversion in the subtelocentric chromosome of the first group may have originated the metacentric chromosome 5 of *Chiroderma*. Other events such as chromosomal fusion, addition of heterochromatin, duplication or loss of genetic material cannot be ruled out.

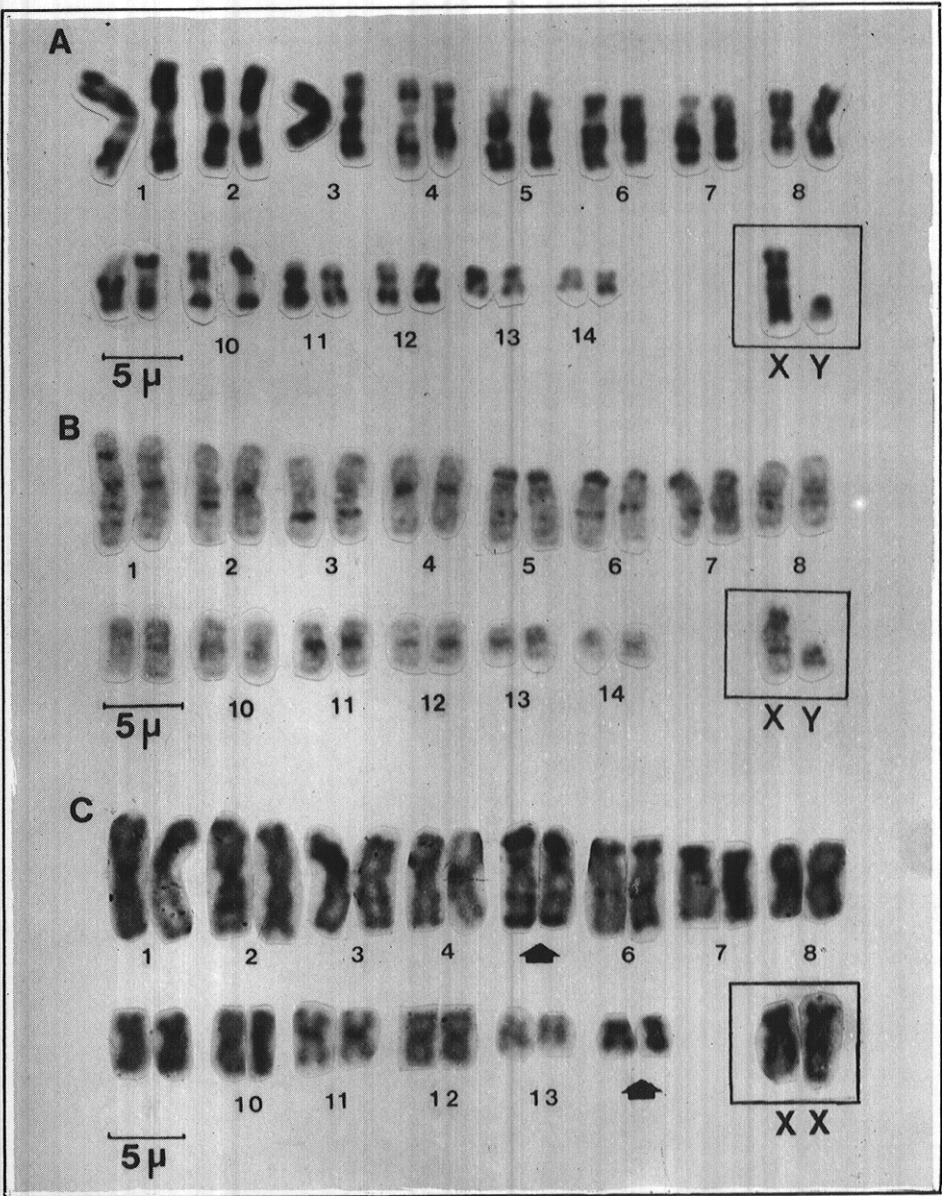


Figure 12 - Karyotype of *Vampyrops lineatus* after G-banding (A) and C-banding (B,C). Arrows indicate large heterochromatin blocks in chromosomes 5 and 14.

Several chromosome arms of *Macrotus waterhousii* can be easily recognized in the karyotypes of these stenodermines, clearly showing preserved chromosomal characteristics in their evolutionary process.

The same is not true regarding other interesting stenodermatine genera, such as *Uroderma* and *Vampyressa* (Baker *et al.*, 1979; Baker and Bickham, 1980), which have several chromosomal races (Baker, 1979) though Brazilian representatives have not yet been studied.

Desmodontinae

The three genera of vampire bats, *Desmodus*, *Diaemus* and *Diphylla*, have undergone extreme structural modifications associated with their blood feeding habits, which have been the basis for assigning them to a distinct family. However, Forman *et al.* (1968) have provided immunologic, biochemical and cytogenetic data supporting their classification as a subfamily of the Phyllostomidae.

Hematophagous bats only occur in the neotropical region from Mexico to Argentina. "Vampires" are a cause of great concern in Latin American countries, especially in Brazil. Vampire-borne rabies has been declared the primary livestock disease problem and has become a formidable obstacle to the expansion of the agricultural economy. Furthermore, in some parts of the state of São Paulo, such as the southeastern region, humans are also commonly attacked by vampires so that special programs of population control of these bats are needed (Taddei, 1983).

The three species of desmodontine bats have been cytogenetically studied in Brazil: *Desmodus rotundus* from São Paulo and Pernambuco, *Diaemus youngi* from São Paulo and *Diphylla ecaudata* from Pernambuco (Table II). G- and C-banded karyotypes of *Desmodus* and standard and G-banded karyotypes of *Diaemus* are shown in Figures 13 and 14. Almost all chromosomes are shared by both species, but inversions can be detected, such as that in chromosome 6. Constitutive heterochromatin was found in the centromere of all chromosomes and in intermediate regions of both arms of some autosomes in *Desmodus*. In *Diaemus* there are also heterochromatin bands in the telomere of the seven smallest autosomes. Both species have slightly heterochromatic Y chromosomes.

The NOR was found on chromosome 8 of *Desmodus* and on chromosome 15 of *Diaemus* (Morielle and Varella-Garcia, 1988). Based on G-banding patterns it may be assumed that the DNAr from *Diaemus* was inserted into its chromosome 7, making it similar to the NOR-bearing chromosome 8 of *Desmodus*.

Diphylla ecaudata from Pernambuco (Lopes, 1978) shows extensive chromosomal homology with *Diaemus* and *Desmodus*, pointing out the monophyletic origin of these species. Nevertheless, fairly good banded chromosome preparations are still needed to permit accurate identification of chromosome homology within this subfamily. On the basis of behavioral (Sazima and Uieda, 1980), morphological (Smith, 1976), and molecular data (Honeycutt *et al.*, 1981) to date it seems likely that a divergence of *Desmodus* and *Diaemus* occurred after the divergence of the *Diphylla* lineage.

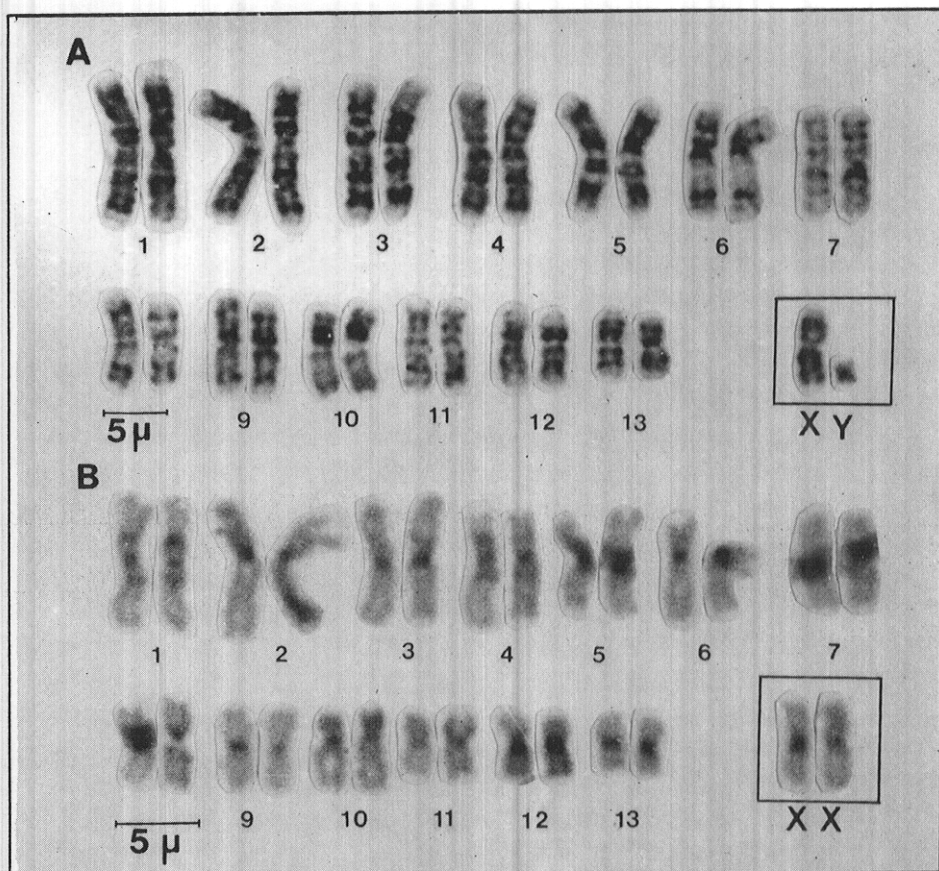


Figure 13 - G-banded (A) and C-banded (B) karyotypes of *Desmodus rotundus*.

Natalidae, Furipteridae and Thyropteridae

Four species of these families occur in Brazil, *Natalus stramineus*, *Furipterus horrens*, *Thyroptera discifera* and *Thyroptera tricolor*, but no chromosome data have been published for Brazilian members of any of them.

Vespertilionidae

This cosmopolitan family has the largest range of any family of bats, occurring in all continents and many oceanic islands (Koopman, 1970), but only 17 species can be found in Brazil (Table I). Chromosomal data have been described for thirteen of them, but only for 6 species were the analyzed specimens collected in Brazil (Table II).

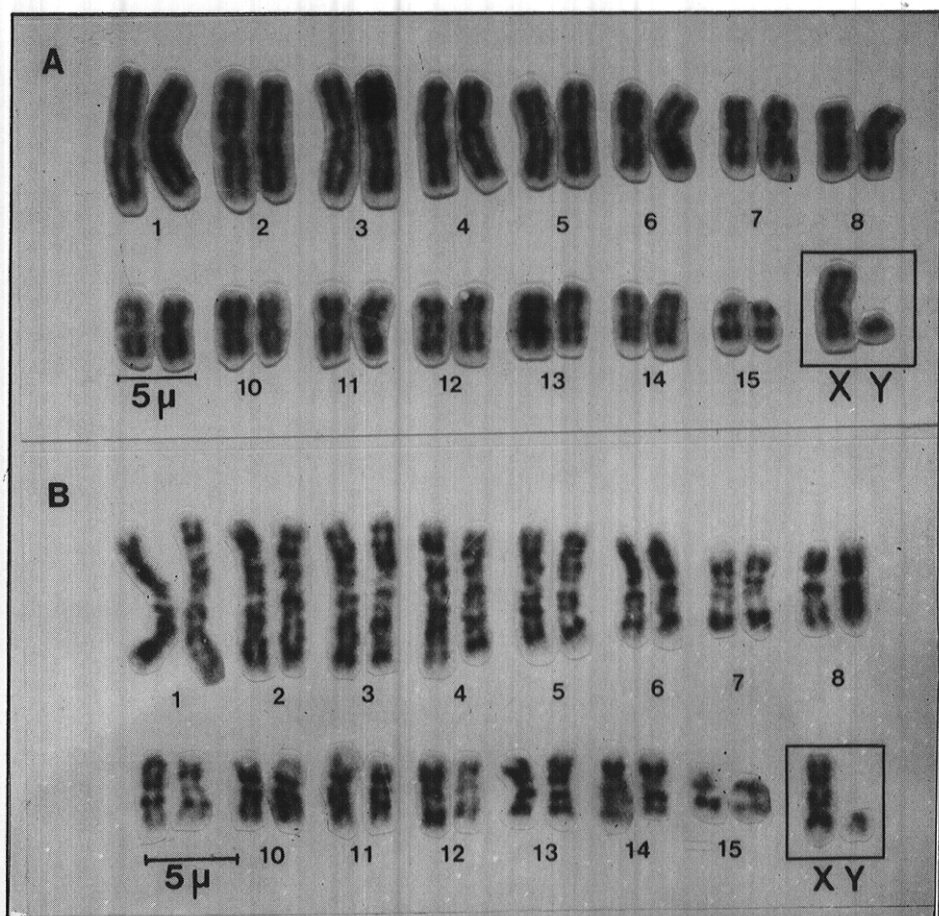


Figure 14 - Standard (A) and G-banded karyotypes of a male *Diaemus youngi* specimen.

Generally this family reveals conservative karyotypes, at least at the genus level. Species belonging to one genus or a group of related genera usually have the same diploid and fundamental numbers or the same fundamental numbers and not very different diploid numbers. The genus *Myotis*, for instance, has the largest number of species within mammals and is strongly conserved in chromosome features (Bickham *et al.*, 1986). On the other hand, to this family belongs a complex, the *Rhogeessa tumida-parvula*, which is unique in terms of intraspecific variation. Within this complex there are seven cytotypes which evolved diploid numbers of 30, 32, 34, 42, 44 and 52 (Bickman and Baker, 1977; Honeycutt *et al.*, 1980; Baker *et al.*, 1985).

A Brazilian representative of only one species of the genus *Myotis* has been studied, *M. nigricans*. Although banding data are not available for this species, karyo-

types of specimens from Rio de Janeiro and São Paulo show no recognizable differences from those described for the Mexico and Trinidad specimens (Bickham, 1979).

Two other genera for which Brazilian specimens were analyzed, *Eptesicus* and *Lasiurus*, also show a high level of conservatism. *E. brasiliensis* (Lopes, 1978) and *E. furinalis* (this paper) have $2n = 50$ and $FN = 48$, with only acrocentric autosomes. Lopes (1978) reported the presence of a constriction on one medium-sized autosome close to the centromere in *E. brasiliensis*, and we detected an NOR in a similar location in *E. furinalis*, by Ag-NOR staining procedures. *L. borealis* (this paper) has $2n = 28$ and $FN = 46$. G- and C-banded karyotypes are shown in Figure 15. The NOR was assigned to the smallest autosome. Specimens of *L. ega* were described with $2n = 28$ and $FN = 50$ (Toledo, 1973), differing from specimens from other locations (Baker *et al.*, 1982). This difference, however, could be due to a change in the classification of the small chromosomes and to the erroneous identification of the X chromosome, which may be a submetacentric and not a subtelocentric/acrocentric, as proposed by Toledo (1973).

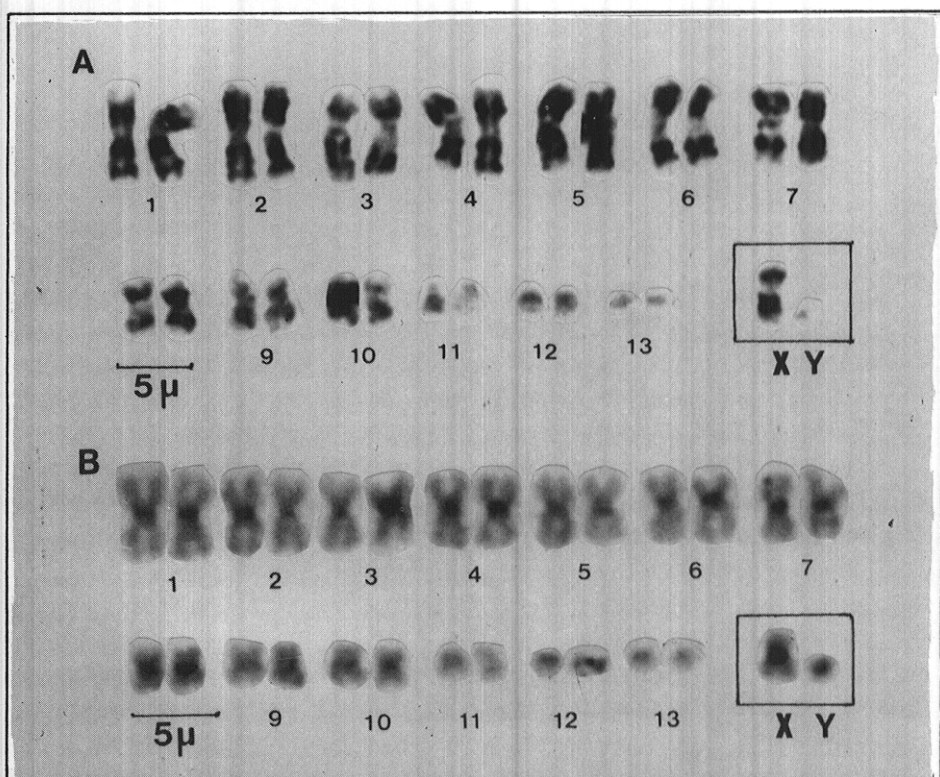


Figure 15 - G-banded (A) and C-banded (B) karyotypes of a male *Lasiurus borealis* specimen.

The other cytogenetically analyzed Brazilian vespertilionid species is *Histiotus velatus* (Toledo, 1973) whose karyotype has not been published for specimens from another country. Its chromosome complement is similar to that of *Eptesicus* and consists of 24 acrocentric autosomes; the X chromosome is submetacentric and the Y is a minute chromosome.

Molossidae

This family comprises 12 genera and approximately 80 species widely distributed in the tropical and warm temperature regions of the world. Seventeen of them occur in Brazil and cytogenetic data are available for 16 (Table I). However, chromosome information on Brazilian specimens is available only for 6 species from two genera, *Eumops* and *Molossus* (Table II).

Specimens of *E. auripendulus* from Rio de Janeiro have $2n = 42$ and $FN = 62$ (Toledo, 1973) and specimens from Trinidad have $2n = 42$ and $FN = 60$ (Warner *et al.*, 1974). The Y chromosome is described as a small acrocentric in the former, and as a medium-sized subtelocentric in the latter. Toledo (1973) also reported the presence of conspicuous satellites on the short arms of a pair of subtelocentric chromosomes.

E. glaucinus from São Paulo has $2n = 40$ and $FN = 64$. This type is very similar to that found in Colombia, but differs from specimens from Mexico, Costa Rica and Honduras, which have $2n = 38$ and $FN = 64$ (Warner *et al.*, 1974). Brazilian specimens have NORs on the short arms of three medium-sized submetacentric pairs (Morielle *et al.*, 1988).

E. perotis has been described to have $2n = 48$, $FN = 54$ in specimens from Rio de Janeiro (Toledo, 1973) and $2n = 48$, $FN = 56$ in specimens from Mexico (Warner *et al.*, 1974), but the karyotypes showed overcontracted chromosomes in both cases, so that this difference may be only an artifact. Warner *et al.* (1974) reported that one of the largest acrocentric pairs of has visible secondary constrictions.

Specimens of *Eumops* sp. (*E. hansae*?) from São Paulo (Toledo, 1973) have shown $2n = 48$, $FN = 56$, with a karyotype resembling that described by Warner *et al.*, (1974) for *E. perotis*.

Brazilian *Molossus ater* have been reported to have $2n = 48$, $FN = 60$ in specimens from São Paulo (Toledo, 1973) and $2n = 48$, $FN = 56$ in specimens from Pernambuco (Lopes, 1978). Warner *et al.* (1974) have described specimens from Costa Rica with $2n = 48$, $FN = 58$. However, all karyotypes are very similar and differences may be due to variable classification criteria.

The karyotype of *M. molossus* from Pernambuco (Lopes, 1978) and Rio Grande do Sul (Christoff and Freitas, 1987) shows $2n = 48$, $FN = 56$ and is very similar to that described by Baker and Lopez (1970).

Molossidae represents a significant component of the rich South American

bat fauna but the phylogenetic relationship proposed for its members should be regarded as tentative. G-banding data have been published only for *Tadarida brasiliensis* (Baker *et al.*, 1982) and *E. glaucinus* (Morielle *et al.*, 1988) and more data are needed in order to understand the karyotype evolution within this family and to interpret the relationships with other Chiroptera families.

CONCLUDING REMARKS

The karyotype evolution of bats shows wide variation among taxa. Some of them, such as species of *Pteronotus*, *Artibeus*, *Myotis* and *Eptesicus* are strongly conservative and few or no chromosomal rearrangements have been detected among them. Other groups such as *Rhogeessa* and *Uroderma* have a few or even many karyotype rearrangements but all of them showing one or few kinds of rearrangements, mainly centric fusions and inversions. In contrast, some species such as *Tonatia bidens*, *Micronycteris minuta*, *M. megalotis* and *Vampyressa pusilla* have shown a radical reorganization of their genome, a phenomenon named karyotypic megaevolution (Baker and Bickham, 1980), which remains unexplained by current theories of chromosomal evolution. Their karyotypes are so different that banding homologies with closely related species cannot be determined. Thus, cytogenetic studies on bats are an interesting subject for research.

Unfortunately few karyotypic studies have been performed on Brazilian bats and the data thus far available are not representative of any family as a whole. In addition, most information was obtained from standard karyotypes and it has been well demonstrated that over four times as many rearrangements are identified by banded data as are detectable in standard preparations (Baker and Bickham, 1980; Haiduk *et al.*, 1981).

Therefore, a primary need is to obtain fairly good banded chromosome preparations by establishing tissue cultures from which mitotic cells could be harvested. Although results can be obtained by simply processing the specimens immediately or within 24 hours of capture, frequently the mitotic index is not as high as necessary and overcontracted chromosomes are common in bone marrow preparations. Fibroblast cultures, however, provide excellent material not only to obtain high-resolution banded chromosomes but also for treatment of living cells with 5-bromo-deoxyuridine (5-BrdU) and other drugs which represent valuable tools to obtain more detailed banding patterns as well as information about other chromosome phenomena such as replication patterns and fragile sites.

All of these cytogenetic techniques promise to provide a precise measure of homology and consequently an accurate estimate of chromosomal changes. However, in spite of the outstanding contribution of cytogenetic data to the establishment of phylogenetic relationships among the families of the New World bats, they can be

completely understood only by the use of multiple and differentially resolving character sets.

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RESUMO

São apresentados dados de estudos citogenéticos desenvolvidos em exemplares brasileiros de 33 espécies da ordem Chiroptera, pertencentes às famílias Noctilionidae, Phyllostomidae, Vespertilionidae e Molossidae, que correspondem a cerca de 25% das espécies de morcegos já registradas no Brasil. Destaca-se a necessidade de incrementar os estudos sobre o assunto, tendo em vista que as informações cariotípicas podem fornecer interessantes subsídios para o esclarecimento de aspectos sistemáticos e de relações filogenéticas.

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