

Further studies on the sex-chromosome systems of the American leaf-nosed bats (Chiroptera, Phyllostomatidae)¹

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Abstract. Two additional genera, *Ametrida* and *Enchisthenes*, and another species of *Artibeus* were found to have an XX/XY₁Y₂ sex-chromosome system, bringing the total number of species possessing this system in the family Phyllostomatidae to nine. Another species (*Mesophylla macconnelli*) of this family has somatic chromosomes suggesting an XX/XO sex-chromosome system; however, the Y may be present in the genome but is probably translocated to an autosome. The incidence of either the XX/XY₁Y₂ or XX/XO? system is rare in mammals, and the presence of both types in one group of closely related forms is without precedent. Involvement of an autosome with sex chromosomes is suggested as a common factor for the two systems.

Introduction

The sex-chromosome systems of bats of the family Phyllostomatidae were discussed by Hsu *et al.* (1968) and BAKER (1967). A total of 24 species of this family have been reported; 18 have the classic XX/XY system, but 6 have an XX/XY₁Y₂ system. These investigators hypothesized that the XX/XY₁Y₂ system had occurred more than once within the family. New data presented here are the results of studies conducted on the island of Trinidad, West Indies, during the summer of 1967.

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Materials and methods

The techniques used in this study were those described by PATTON (1967) for bone marrow and by HSU *et al.* (1968) for tissue culture, except that the bone-marrow slides prepared in Trinidad were not stained until they were returned to the United States. This modification proved to be unfortunate since there was considerable deterioration in quality before the slides were mounted in a permanent manner.

Sex chromosomes were determined by comparing somatic karyotypes of males and females of the same species. Unfortunately, preparations for testes yielded no useful information; therefore, the results of somatic studies are presented for their own merit. Voucher specimens are prepared as museum specimens and are deposited in the collection of mammals, Department of Biology, Texas Tech University. Accurate locality data are available, but for the purpose of this report the locality of Trinidad appears sufficient.

Results

The species of the family Phyllostomatidae from Trinidad that were studied cytologically are given in the table. Of the total 22 species analyzed for sex chromosomes, 15 demonstrated the classical XX/XY sex chromosome system, 6 had the XX/XY₁Y₂ system and 1 appeared to be of the XX/XO type. A brief description for the chromosomes of the species having an atypical sex-chromosome system follows:

Carollia perspicillata SAUSSURE. 2N = 20 (♀), 21 (♂). The chromosomes of the specimens examined were similar to those described by HSU *et al.* (1968).

Artibeus jamaicensis LEACH. 2N = 30 (♀), 31 (♂). All *Artibeus* species studied had indistinguishable karyotypes except for the Y chromosomes. The longer Y chromosome (Y₁) of males of *A. jamaicensis* from Trinidad had a second arm, whereas the Y₁ of the specimens collected in Mexico (HSU *et al.*, 1968) was an acrocentric.

Artibeus lituratus LICHTENSTEIN. The specimens of this species from Mexico had two small Y chromosomes of approximately the same size (HSU *et al.*, 1968). The Trinidad specimens had one Y about twice as large as the other, and both appeared to be acrocentric.

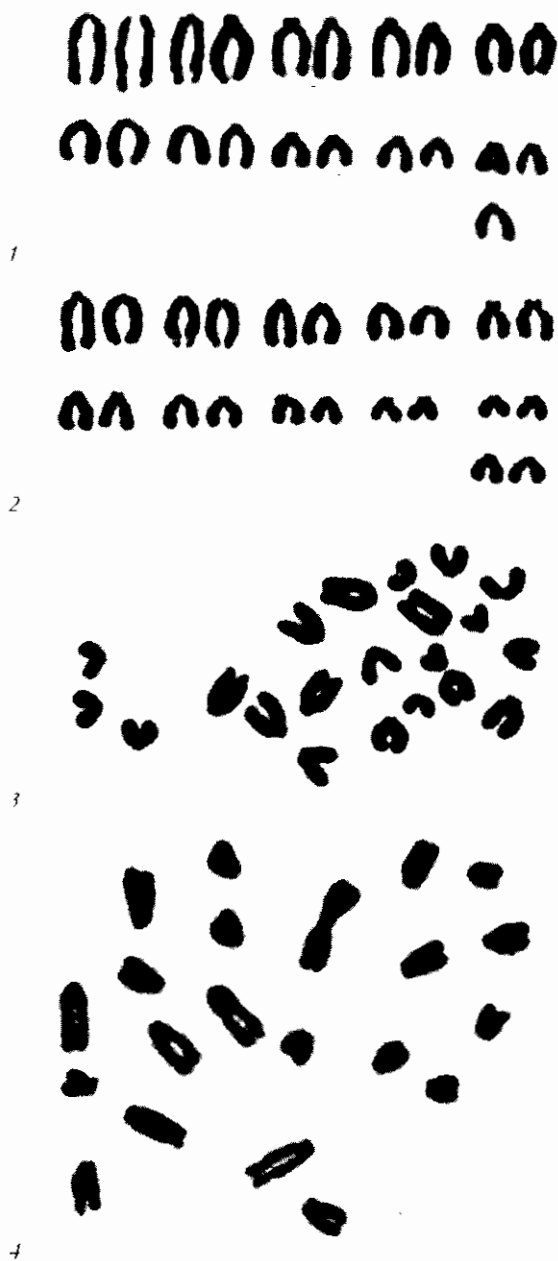
Artibeus cinereus (GERVAIS). General size of Y chromosomes was like those of *Artibeus jamaicensis*, but both Y elements were biarmed.

Enchisthenes bartii (THOMAS). 2N = 30 (♀), 31 (♂). The autosomes of the specimens examined were like those from Mexican specimens described by BAKER (1967). The X was a subtelocentric similar to

Chromosomal values of Phyllostomatid bats from Trinidad, W.I.

Subfamily and species	2n	X ¹	Y ¹	♂	♀
CHILONYCTERINAE					
<i>Mormoops megalophylla</i> (PETERS)	38	—	—	0	1
PHYLLOSTOMATINAE					
<i>Micronycteris nicefori</i> SANBORN	28	M	A	3	2
<i>Lonchorhina aurita</i> TOMES	32	M	A	0	2
<i>Tonatia bidens</i> (SPIX)	16	M	A	2	1
<i>T. minuta</i> GOODWIN	30	SM	A	2	1
<i>Mimon crenulatum</i> (SAINT-HILAIRE)	32	—	—	0	2
<i>Phyllostomus discolor</i> WAGNER	32	SM	A	1	1
<i>P. hastatus</i> PALLAS	32	SM	A	1	1
<i>Phylloderma stenops</i> (PETERS)	32	—	—	0	1
<i>Vampyrus spectrum</i> LINNAEUS	32	—	—	0	1
GLOSSOPHAGINAE					
<i>Glossophaga soricina</i> (PALLAS)	32	M	A	2	2
<i>Anoura geoffroyi</i> GRAY	30	SM	A	2	1
CAROLLINAE					
<i>Carollia perspicillata</i> SAUSSURE	20-21	ST	A-A	2	2
STERNODERMINAE					
<i>Sturnira lilium</i> (GEOFFROY)	30	ST	SM	2	2
<i>S. tildae</i> DE LA TORRE	30	ST	SM	1	2
<i>Uroderma bilobatum</i> PETERS	42	ST	SM	2	1
<i>Vampyrus helleri</i> PETERS	30	ST	SM	2	2
<i>Vampyrodes caraccioloii</i> (THOMAS)	30	ST	SM	2	2
<i>Chiroderma villosum</i> PETERS	26	ST	SM	2	2
<i>C. trinitatum</i> GOODWIN	26	ST	SM	1	2
<i>Mesophylla macconnelli</i> (THOMAS)	21-22	A	?	7	9
<i>Mesophylla macconnelli</i>	21	?	—	0	1
<i>Artibeus jamaicensis</i> LEACH	30-31	ST	A-A	2	1
<i>A. lituratus</i> LICHTENSTEIN	30-31	ST	ST-A	1	1
<i>A. cinereus</i> (GERVAIS)	30-31	ST	SM-M	2	2
<i>Echistobates bartii</i> (THOMAS)	30-31	ST	SM-A	1	1
<i>Centurio senex</i> GRAY	28	ST	SM	1	0
<i>Ametrida centurio</i> GRAY	30-31	ST	SM-M	3	2

¹ M = metacentric (arm ratio of less than 1:1.1), SM = submetacentric (arm ratio between 1:1.1 and 1:1.9), ST = subtolocentric (arm ratio 1:2 or greater), and A = acrocentric (second arm not visible).



the X described by Hsu *et al.* (1968) for *Artibeus*. The two Y chromosomes were small and like those described for *Artibeus jamaicensis* (Hsu *et al.*, 1968), but the larger Y was biarmed.

Ametrida centurio (GRAY). $2N = 30$ (♀), 31 (♂). The autosomes and the X chromosome of the specimens studied were like those of *Artibeus*, but the size of the two Y chromosomes was slightly larger than those described for *Artibeus jamaicensis*, and both Y's were nearly metacentric.

Mesophylla macconnelli (THOMAS). $2N = 22$ (♀), 21 (♂). With the exception of one chromosome in one animal, all chromosomes were either acrocentric or nearly acrocentric (Figs. 1 to 4). Nine of the 10 females examined had a somatic chromosome number of 22, but a pregnant female possessed only 21 chromosomes, and her complement contained a large metacentric element. The highest number of chromosomes observed in a diploid metaphase from males was 21. More than 500 spreads from males were scored, with approximately 90% having 21 chromosomes, 5% having 20, 2% having 19 and 3% having 18 or less.

Discussion

It is not a great surprise to find two additional genera and another species of *Artibeus* having XX/XY₁Y₂ sex chromosomes, especially since these genera are in the subfamily Stenoderminae, which contains four species known to have this sex-chromosome system (Hsu *et al.*, 1968). It was not expected, however, that another species, *Mesophylla macconnelli*, in the same subfamily would have a sex-chromosome system suggestive of XX/XO with only acrocentric chromosomes present (Figs. 1, 2 and 3). All species of bats reported to have an XX/XY₁Y₂ sex-chromosome system have very few acrocentric autosomes.

Fig. 1. Representative karyotype of a male *Mesophylla macconnelli*. Note only 21 chromosomes; probable X chromosome is at bottom.

Fig. 2. Representative karyotype of a female *Mesophylla macconnelli*. Probable X chromosomes are at bottom.

Fig. 3. Representative spread of a male *Mesophylla macconnelli*.

Fig. 4. Representative spread of a female *Mesophylla macconnelli* with only 21 somatic chromosomes. Note large biarmed chromosome.

In mammals, true XO individuals are always females (FORD *et al.*, 1959; FRACCARO *et al.*, 1959; WELSHONS and RUSSELL, 1959; KINDRED, 1961; CATTANACH, 1962). In the Indian mongoose, *Herpestes auro-punctatus*, FREDGA (1964) reported a diploid number of 36 for females and 35 for males. Meiotic studies of males, however, discovered a trivalent in which the X chromosome was found to associate with an autosome pair, suggesting that the Y of the mongoose is present but has been translocated to an autosome. Probably the Y is so small that after its translocation to an autosome it is not detected as an extra segment in karyotyping of somatic chromosomes. Thus the XO constitution of the male Indian mongoose does not indicate a complete loss of male-determining genetic material. The somatic chromosomes of the marsh mongoose, *Atilax paludinosus*, are 36 in females and 35 in males (WURSTER and BENIRSCHKE, 1968), suggesting a sex-determining system like that of *H. auro-punctatus*.

In the African pygmy mice numerous types of chromosomal changes have been found. In a sample from Southern Rhodesia, MATTHEY (1965) found 35 chromosomes in the male and 36 in the female. All the autosomes as well as the X chromosomes are acrocentric, but the large Y chromosome is metacentric. During meiosis the Y chromosome associates with two other chromosomes, thus forming a trivalent. MATTHEY concluded that the short arm of the Y pairs with the original X chromosome (X_1), while the long arm pairs with the homolog of the autosomal segment. Since the autosome is now involved in the sex-determination system also, it is termed X_2 by MATTHEY. Therefore, the sex chromosomes of the female mice of the Rhodesian population is X_1X_2/X_1X_2 , and of the male, X_1X_2/X_2Y .

In our *Mesophylla*, the seemingly XO condition for the males may well be similar to that of the mongoose, *viz.*, the Y is present but translocated to an autosome. It is highly improbable that the chromosome constitution is a transient anomaly, as in one female which had a 'fusion' between two autosomes (Fig. 4), because all seven males showed an identical karyotype. It is regrettable that testicular material from five males revealed not a single spermatocyte beyond pachynema stage, so that the pairing behavior could not be analyzed. Before specimens can be captured and their meiosis analyzed, we can only propose that essential material for the Y chromosome is present in the males but is hidden.

Of great interest to cytologists, irrespective of the whereabouts of the Y in *Mesophylla*, is that in one subfamily of the leaf-nosed bats,

Sternoderminae, both anomalous sex-determination systems, XY_1Y_2 males and 'XO' males, are found. Since the XY_1Y_2 system is of rare occurrence in mammals (two in Marsupialia, two in Insectivora, one in Rodentia) and the seeming 'XO' system has been reported only twice (FREDGA, 1964; WURSTER and BENIRSCHKE, 1968), the abundance of these cases in Stenoderminae is unique. In either case, an autosomal pair becomes sex-linked. In order to avoid the production of sperms with an anomalous chromosome constitution, a mechanism must exist for regulating proper segregation during the first meiotic division. Otherwise, the species must pay a high price (gametic lethality) for the translocations, whether it be the XY_1Y_2 or 'XO' system. Furthermore, the genes located in the autosome involved in the translocation may become inactivated during development because they are now part of the sex chromosome.

The last specimen (Fig. 4) provides another example to support the idea that the Robertsonian process is probably accomplished by a fusion of two acrocentrics into a metacentric rather than the reverse, *viz.*, a fission of a metacentric into two acrocentrics.

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