Parallel Evolution of Multiple Sex-Chromosome Systems in the Phyllostomatid Bats, *Carollia* and *Choeroniscus*

A multiple sex-chromosome system consisting of XX females and XY_1Y_2 males has been described recently for several genera of bats of the family Phyllostomatidae[1-6]. Within this group of leaf-nosed bats, the sex chromosomes of 2 species of the genus *Carollia* and 1 species of the genus *Choeroniscus* have been described. These species are *Choeroniscus godmani* (Thomas) and *Carollia subrufa* (Hahn)[7] from localities in México, and *Carollia perspicillata* (Linnaeus) from México to Venezuela, Trinidad, and Brazil. Herein, we present chromosomal data for 2 additional species of *Carollia*, *C. brevicauda* (Wied, *in* Schinz, 1821) and *C. castanea* H. Allen, as well as for additional material of *Choeroniscus godmani* from Costa Rica and *Carollia perspicillata* from Costa Rica and Perú.

The Costa Rican specimens, a female *C. perspicillata*, a female *C. castanea*, and a female *C. godmani*, were collected at Pacuare, Río Pacuare, Prov. Cartago. The first is deposited in the collection of the Costa Rican Ministerio de Agricultura, Sección de Pesca y Vida Silvestre, and the latter two in the Museum of Zoology, Louisiana State University (LSUMZ 12773 and 12739, respectively), all as skins with skulls. Most of the Peruvian material was collected at Balta, Río Curanja, Depto. Loreto, elevation 300 m (lat. 10°08′ S, long. 71°13′ W), and is catalogued in either the Museum of Vertebrate Zoology, University of California, or the Museum of Zoology, Louisiana State University. Three species of *Carollia* are represented from this locality: 3 male and 2 female *C. perspicillata* (MVZ 136444, 136445, 136446, 136454, and LSUMZ 14151); 2 male and 2 female *C. brevicauda* (MVZ 136461, LSUMZ 14152, 14153, and 14154); and 3 male and 2 female *C. castanea* (MVZ 136462, 136463, 136464, 136440, and LSUMZ 14134). In addition, a female *C. perspicillata* from Yarinacocha, Depto. Loreto, Perú was examined (LSUMZ 14149).

Carollia perspicillata from both Costa Rica and Perú have chromosomal complements indistinguishable from those reported elsewhere. Males are $2n = 21$ with an XY_1Y_2 sex complement and females are $2n = 20$ with an XX complement. The autosomes consist of one very large pair of submetacentrics, 2 medium-sized pairs of subtelocentrics, and 6 pairs of small submetacentrics and subtelocentrics. The subtelocentric X is larger than any similar autosome and has a distinct secondary constriction in the long arm. The two Y-chromosomes are a medium-small acrocentric and a very small acrocentric (Figure 1). The karyotypes of *C. brevicauda* from Perú and of *C. castanea* from Costa Rica agree exactly with this description. However, the specimens of *C. castanea* from Perú (Figure 2) differ from other *Carollia* in 4 important features of the karyotype: 1. The diploid number is 22 for both sexes; 2. There is a single Y-chromosome in males (a small acrocentric); 3. There is a single pair of medium-small acrocentrics in the autosomal complement; and 4. The X-chromosome is a small submetacentric and is equal in size to the series of similar autosomal elements.

The karyotype of *Choeroniscus godmani* has been reported on from males collected in southern México. These had a diploid number of 19 with a presumed XY_1Y_2 sex complement. Females of this population are expected to have a diploid number of 18[1,2]. The autosomes of the Mexican specimens consisted of 1 very large pair of submetacentrics, 1 large pair of subtelocentrics, 3 pairs of medium-sized subtelocentrics, and 1 small pair each of metacentrics, submetacentrics, and subtelocentrics. The X was considered to be a medium-sized submetacentric, one Y a medium-sized subtelocentric, and the second Y a small acrocentric. The female from Costa Rica, however, possessed a diploid number of 20, not the expected 18 (Figure 3). Differences between this karyotype and that expected include an extra pair of medium-sized subtelocentrics, an extra pair of small metacentrics, and the lack of a medium-sized submetacentric pair corresponding to the element designated as the X-chromosome by previous investigators.

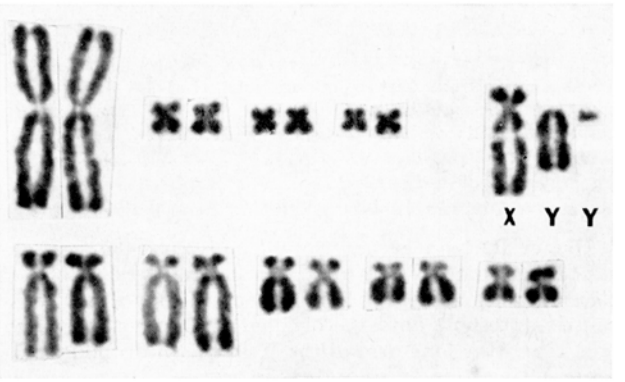

Fig. 1. Karyotype of a male *Carollia perspicillata* from Balta, Río Curanja, Depto. Loreto, Perú (MVZ 136445).

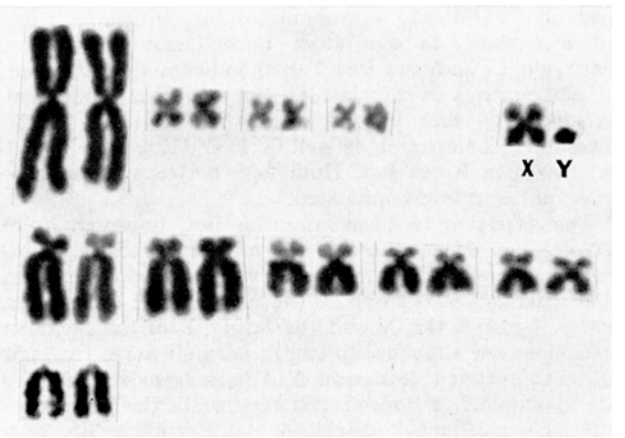

Fig. 2. Karyotype of a male *Carollia castanea* from Balta, Río Curanja, Depto. Loreto, Perú (MVZ 136440).

[1] R. J. Baker, SWest. Nat. *12*, 407 (1967).
[2] T. C. Hsu, R. J. Baker and T. Utakoji, Cytogenetics *7*, 27 (1968).
[3] P. Kiblisky, Experientia *25*, 1203 (1969).
[4] M. L. Beçak, R. F. Batistic, L. D. Vizotto and W. Beçak, Experientia *25*, 81 (1969).
[5] Y. Yonenaga, O. Frota-Pessoa and K. R. Lewis, Caryologia *22*, 63 (1969).
[6] R. J. Baker and T. C. Hsu, Cytogenetics *9*, 131 (1970).
[7] Specimens from Veracruz, México, allocated to *C. subrufa* by previous investigators[1,2] probably represent *C. brevicauda* [see R. H. Pine, Ph. D. dissertation, Texas A & M University Department of Wildlife Science (1968)].

Comparison of the relative sizes (expressed as a percentage of the haploid genome) of the X-chromosome and acrocentric autosome of Peruvian *C. castanea* with the X-chromosome of Costa Rican *C. castanea*

Carollia castanea Perú		*Carollia castanea* Costa Rica	
% X/haploid complement	6.17 ± 0.52	% orig. X/haploid complement	6.07 ± 0.37
% A/haploid complement	8.82 ± 0.61	% trans. A/haploid complement	8.56 ± 0.54
% X + A/haploid complement	14.99 ± 0.45	% neo-X/haploid complement	14.63 ± 0.62

The numbers are mean percentages calculated from the measurement of 10 mitotic metaphases, followed by the standard error of the mean. For the Costa Rican specimen, the original X is considered to be that portion of the X-chromosome including the centromere but proximal to the secondary constriction, and the translocated autosome to be that part of the neo-X distal to the constriction.

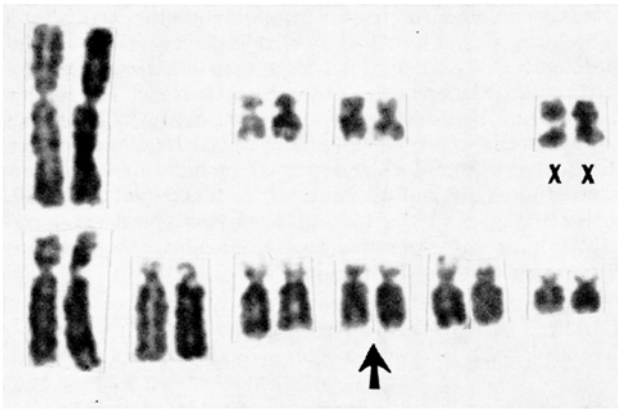

Fig. 3. Karyotype of a female *Choeroniscus godmani* from Pacuare, Río Pacuare, Prov. Cartago, Costa Rica (LSUMZ 12739). The presumed X-chromosome pair is labeled, and the arrow indicates the unique subtelocentric autosomal pair (see text for discussion)

HSU et al.[2] have argued convincingly that the multiple sex-chromosome system of *Carollia*, and presumably of *Choeroniscus*, arose by the tandem fusion of an acrocentric autosome onto the original X-chromosome, with one Y and the long arm of the X in the multiple system representing this translocated autosome. Their conclusions are strongly supported by the complete pairing of these elements in prophase I of meiosis. Our data suggest, therefore, that Peruvian *C. castanea* with a small metacentric X-chromosome and the unique pair of medium-small acrocentric autosomes represent the ancestral system for *Carollia*. Comparative measurements from 10 metaphase mitoses from both Costa Rican and Peruvian *C. castanea* (see Table) indicate that the pair of acrocentrics in the latter's karyotype is equivalent in length to that portion of the neo-X distal to the secondary constriction as well as to the large Y element of the Costa Rican bat. Homology between these chromosomes is strongly indicated.

The situation in *Choeroniscus* is not, however, quite so obvious. First, there is no medium-sized submetacentric element in the female karyotype from Costa Rica that directly corresponds to the suggested X of Mexican males. Second, the X and the larger Y of the Mexican specimens are subequal in length, an indication that not all of the original autosome had been translocated onto the original X, if indeed this represents the same evolutionary mechanism described above for *Carollia*. This problem can be resolved, however, in the following manner. The elements unique to the female $2n = 20$ karyotype are a small pair of metacentrics and a medium-sized pair of subtelocentrics. Assuming that the metacentric pair represents the original X and that the subtelocentric pair represents the autosomes to be translocated, the neo-X would necessarily have to be formed by the translocation of only a portion of the long arm of that element. Otherwise, a dicentric neo-X would result. This explanation would necessitate the loss of the short arm of one subtelocentric element during the translocation process, which would result in the formation of a medium-sized submetacentric neo-X only slightly longer than the new subtelocentric Y-chromosome.

We feel that the evolution of this sex-chromosome system has been parallel for *Carollia* and *Choeroniscus*. However, the development of the multiple sex-chromosome system must have occurred independently since the primitive XX/XY condition is found within living members of both genera. The presence of the multiple system in these genera cannot be used to substantiate a close phylogenetic relationship between them, although the assumption of such a relationship may be valid on other grounds[8].

Resumen. Se describen los cariotipos de *Carollia perspicillata*, *C. brevicauda*, y *C. castanea* de Costa Rica y del Perú, y de *Choeroniscus godmani* de Costa Rica. La sistema de multiple cromosomas sexuales de machos XY_1Y_2/hembras XX reportado por investigadores anteriores se encontraba en todos individuos con la excepcion de *C. castanea* del Perú y *Choeroniscus godmani* de Costa Rica. Estas poblaciones se consideran de haberse mantenido la sistema primitiva de cromosomas sexuales XX/XY.

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[8] Costa Rican specimens were collected and karyotyped by GARDNER during 1966 and 1967 while he held an appointment as a 'Fellow in Tropical Medicine' with the Louisiana State University International Center for Medical Research and Training funded under National Institutes of Health grant No. AI-00007. John S. McIlhenny, Eugene du Pont III, and the Louisiana State University Graduate Research Council supported the 1968 LSU Peruvian expedition, of which GARDNER was a member. We thank J. P. O'NEILL of the Museum of Zoology, Louisiana State University, for assistance in the field and R. H. PINE of the Division of Mammals, U.S. National Museum, for verifying the identification of most of the *Carollia* examined.