

G- AND C-BANDING CHROMOSOMAL STUDIES OF BATS OF THE FAMILY EMBALLONURIDAE

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ABSTRACT.—Extent and nature of chromosomal change among nine species representing six genera (*Saccopteryx*, *Rhynchonycteris*, *Diclidurus*, *Balantiopteryx*, *Cormura*, and *Taphozous*) were examined using data from G- and C-banded chromosomes. Heterochromatin was restricted to centromeric regions in most taxa; extensive additions of C-positive material occurred in *Balantiopteryx* and *Cormura*. Comparisons of G-bands of euchromatic arms revealed considerable variation in G-band pattern and imply extensive chromosomal evolution among emballonurid species. Outgroup comparisons of G-band karyotypes proposed as primitive for several families of bats failed to reveal conserved G-band patterns, thus limiting the usefulness of differentially stained chromosomal data for resolving phylogenetic relationships of the Emballonuridae. The karyotype of *Cormura brevirostris* includes an extraordinarily large X chromosome that is mostly euchromatic. Evolution of the X chromosome and the nature of the sex-determining system in *Cormura* are unclear, but the species appears to possess a unique sex chromosome mechanism.

The bat family Emballonuridae contains 13 genera and about 50 species and has a broad, pantropical distribution (Corbet and Hill, 1980; Hill and Smith, 1983). From both a systematic and cytogenetic standpoint these bats represent one of the least understood chiropteran families. With the exception of a G-band figure presented in Baker et al. (1982) for *Saccopteryx canescens*, published chromosomal data are limited to nondifferentially-stained karyotypes for 13 species representing 9 genera (Baker et al., 1982, and references therein; Harada et al., 1982; Ray-Chaudhuri et al., 1971).

Data from other studies suggest that most species from a given bat family have retained sufficiently conserved G-band patterns that the path of evolutionary change can be postulated and systematic relationships can be proposed (Baker and Bass, 1979; Baker and Bickham, 1980; Baker et al., 1979; Bickham, 1979a; Haiduk et al., 1981). If this is true for emballonurids, then such data could be extremely valuable in elucidating the evolutionary relationships of this poorly understood group.

We have examined the G- and C-band chromosomes of nine species representing six genera from the two currently recognized subfamilies, in order to document the nature of chromosomal change, to determine if chromosomal G-band homology can be detected between emballonurids and other bat families that have been studied, and to evaluate phylogenetic relationships among the taxa examined.

MATERIALS AND METHODS

Specimens were collected from natural populations. In vivo bone marrow (Baker et al., 1982; Lee and Elder, 1980) and in vitro tissue culture methods (from ear and lung biopsies. Baker and Bass, 1979) were used to prepare chromosomes for G- and C-banding. In all cases, G- and C-banding procedures followed the protocol described in Baker and Qumsiyeh (in press). To determine G-band homology within and among taxa, a minimum of five cells were photographed and compared on a side by side basis for all specimens examined. Voucher specimens are deposited in the mammal collections of The Museum, Texas Tech University, and Carnegie Museum of Natural History.

Specimens examined.—TK numbers listed below are used as field numbers for tissues and specimens karyotyped. **Rhynchonycteris naso.**—Venezuela: Guarico, 45 km S Calabozo, TK 15109 S; Suriname: Nickerie, Sipaliwini Airstrip, TK 10143 S. **Saccopteryx bilineata.**—Suriname; Marowijne, Perica, TK 17612-17613 2 SS. **Saccopteryx canescens.**—Venezuela: Guarico, 45 km S Calabozo, TK 15120 S. **Saccopteryx leptura.**—Venezuela: Guarico, 45 km S Calabozo, TK 15023 S. Suriname: Marowijne, Perica, TK 17621 S. **Cormura brevirostris.**—Suriname: Marowijne, Perica, TK 17632 9. **Balantiopteryx plicata.**—Mexico: Jalisco, 2.8 mi N Campo Acosta, TK 27592-27593, TK 27610-27611 4 SS. **Taphozous melanopogon.**—Thailand:

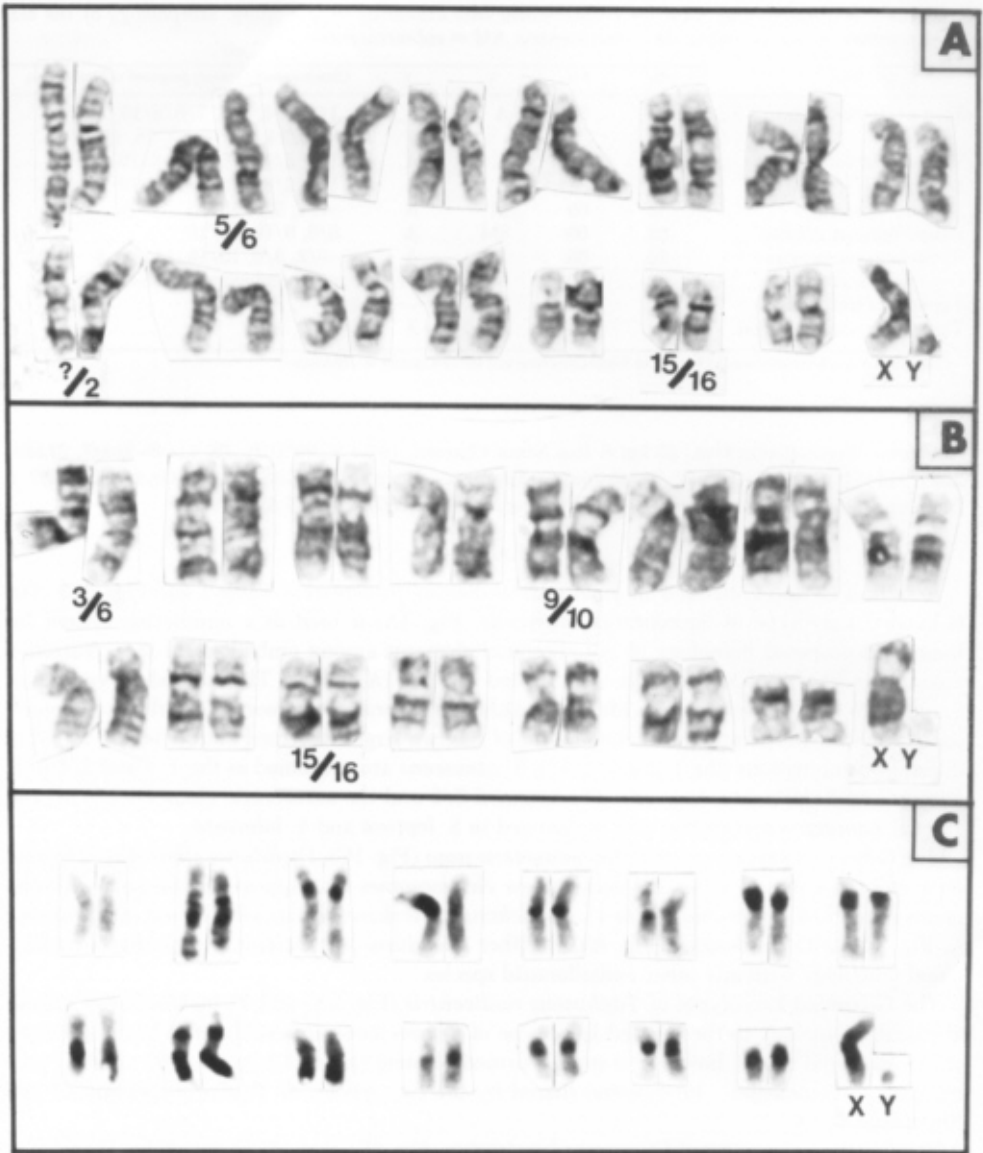


FIG. 1.—Banded karyotypes of *Saccopteryx* and *Rhynchonycteris*. A, G-banded karyotype of a male *Saccopteryx canescens* (TK 15120) used as a reference for comparisons of G-bands among taxa. B, G- and C-banded karyotypes of a male *Saccopteryx leptura* (TK 17621) from Suriname. C, G-banded karyotype of male *Rhynchonycteris naso* (TK 15109) from Venezuela. Chromosome A is found in this species and in *Taphozous*; see Fig. 3.

TABLE 1.—*Chromosomal data for emballonurid bats examined in this study. Morphology of the sex chromosomes: A = acrocentric, M = metacentric, SM = submetacentric.*

Taxon	2n	FN	X	Y	Chromosomal elements proposed as homologous
<i>Saccopteryx canescens</i>	24	38	A	A	1/2,3/4,5/6,7/8,9/10,11/12, 13/14, 15/16, 17, 18, 19
<i>Saccopteryx bilineata</i>	26	36	A	A	1/3, 2/4,5/6, 17, 18, 19
<i>Saccopteryx leptura</i>	28	38	A	A	1/3, 2/4, 5/6, 17, 18, 19
<i>Diclidurus albus</i>	32	60	M	A	—/2, 5/6, 15/16
<i>Balantiopteryx plicata</i>	32	60	SM	A	3/6, 9/10, 15/16
<i>Rhynchonycteris naso</i>	22	36	A	A	—/2, 3/6, 15/16, 18, 19, A
<i>Cormura brevirostris</i>	22	40	M	M	no homologous elements
<i>Taphozous nudiventris</i>	42	64	SM	—	3/—, A
<i>Taphozous melanopogon</i>	42	64	SM	A	3/—, A

Chromosome A is a biarmed element found in *Rhynchonycteris* and the two species of *Taphozous*.

Chumphon Prov., Pathin Dist, 25 km E Ban Nimit Charoen, 10°54'N, 99°31'E, TK 21446-21447, 21449-21451, 21454-21455 4 SS, 3 9S. **Taphozous nudiventris**—Egypt, Giza Governorate, Giza, TK 16597 \$. **Diclidurus albus**—Mexico: Jalisco, 8 km SW Chamela, TK 27600-27603 3 33, 1 9.

RESULTS

Results of G- and C-banded chromosomal studies are presented in Table 1 and Figs. 1-3. The G-banded karyotype of *Saccopteryx canescens* (Fig. 1A) is used as a numbering system for indicating proposed homology of chromosomal elements among emballonurid taxa. Variation among two species of *Saccopteryx* is illustrated in Figs. 1A and 1B. The banded karyotypes of *S. bilineata* and *S. leptura* were identical. Although several chromosomes clearly have homologous euchromatic arms, chromosomal arms of the two largest biarmed autosomes are found in different combinations (the 1/2 and 3/4 in *S. canescens* are combined as the 1/3 and 2/4 in *S. leptura* and *S. bilineata*; Fig. 1B). The biarmed 5/6 and the acrocentric elements 17, 18, and 19 of *S. canescens* are present and unchanged in *S. leptura* and *S. bilineata*.

The G-banded karyotypes of *Rhynchonycteris naso* (Fig. 1C), *Diclidurus albus* (Fig. 2A), and *Balantiopteryx plicata* (Fig. 2B) contain few chromosomes that appear homologous with elements found in *S. canescens* (Table 1). *Rhynchonycteris* shares a biarmed element (chromosome A, Fig. 1C) with *Taphozous* (Fig. 3A). Neither *Diclidurus* nor *Balantiopteryx* share chromosomal homology with any other emballonurid species.

The G-banded karyotypes of *Taphozous nudiventris* (Fig. 3A) and *T. melanopogon* appear identical. Homology to the banded karyotype of *S. canescens* appears limited to the presence of chromosomal arm 3; however, a small biarmed element (labeled A in Figs. 1C and 3A) may represent a homologous chromosome shared by the two species of *Taphozous* examined and *Rhynchonycteris*.

The G-banded karyotype of *Cormura brevirostris* (Fig. 3B) contains no detectable homologies with any of the emballonurids examined in this study. In this species, the X is probably the largest known for a species of mammal (Baker and Jordan, 1970), and a block of heterochromatin is found at the centromere (Fig. 3C). In the single individual we examined, there appears to be a polymorphism involving a euchromatic segment of the smallest autosome (Fig. 3B, C).

C-positive material was restricted to centromeric regions in all emballonurids examined in this study, except in *Rhynchonycteris naso* which has an interstitial C-band on the largest acrocentric autosome (not figured), and in *Balantiopteryx plicata* and *Cormura brevirostris* which have incorporated large amounts of heterochromatin in their autosomal complements (Figs. 2C and 3C, respectively).

DISCUSSION

Table 1 and Figs. 1-3 illustrate that the emballonurids we examined have undergone a considerable amount of chromosomal evolution. Among the three species of *Saccopteryx* (ca-

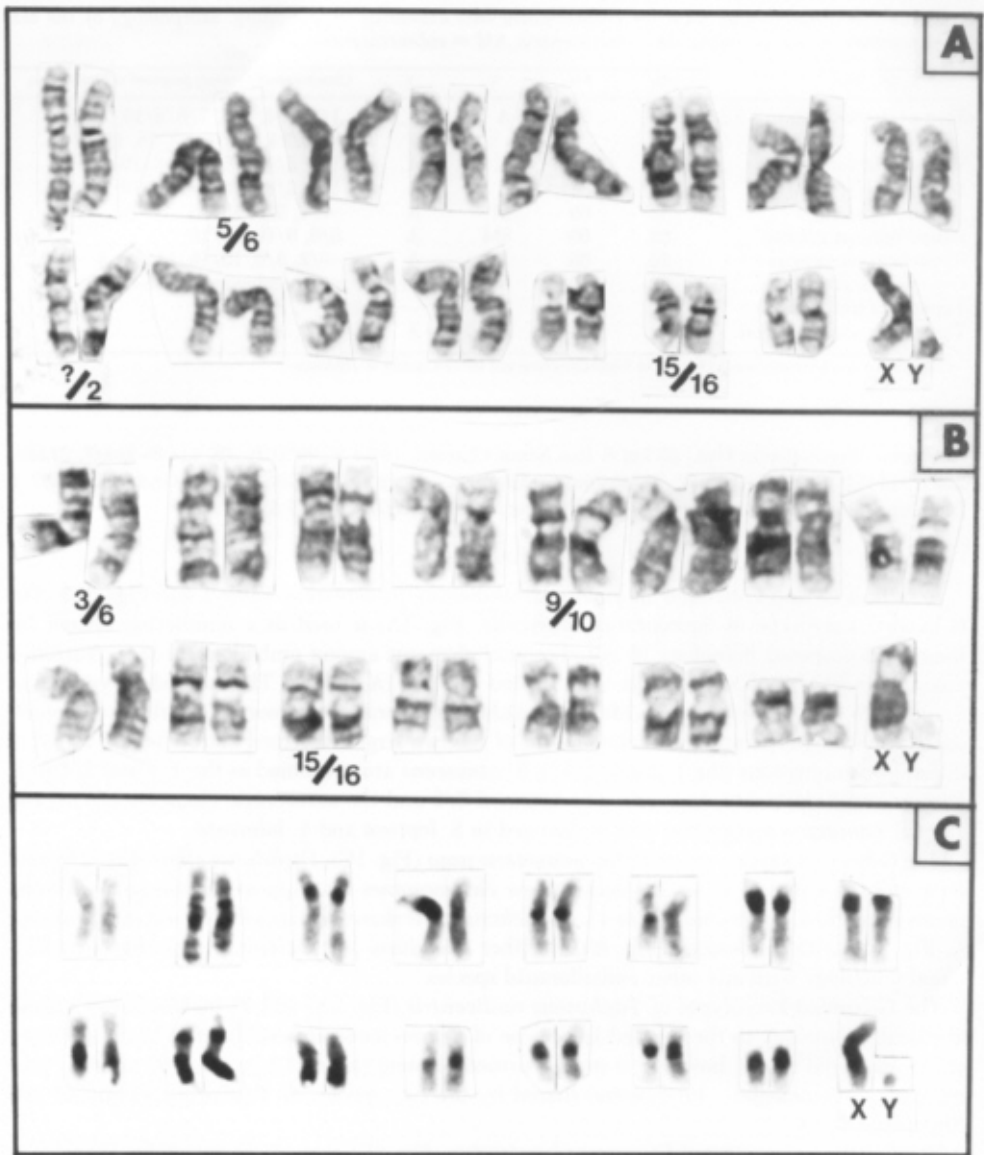


FIG. 2.—Banded karyotypes of *Diclidurus* and *Balantiopteryx*. A, G-banded karyotype of *Diclidurus albus* (TK 27603) from Mexico. B and C, G- and C-banded karyotypes of male *Balantiopteryx plicata* (TK 27610) from Mexico.

nescens, *leptura*, *bilineata*), two of the three largest biarmed chromosomes have undergone fission/fusion rearrangements resulting in monobrachial homology of chromosome arms 1-4. Although G-band homology could not be resolved for the remaining five pairs of biarmed autosomes, it is apparent that the karyotypic evolution leading to diploid numbers of 24, 26, and 28 for these taxa did not occur as a result of only a few rearrangements as the most parsimonious explanation of the nondifferentially-stained chromosomal data would suggest.

Few homologous euchromatic elements are shared among genera within the family. This is in marked contrast to the conservative nature of chromosomal change in the Vespertilionidae

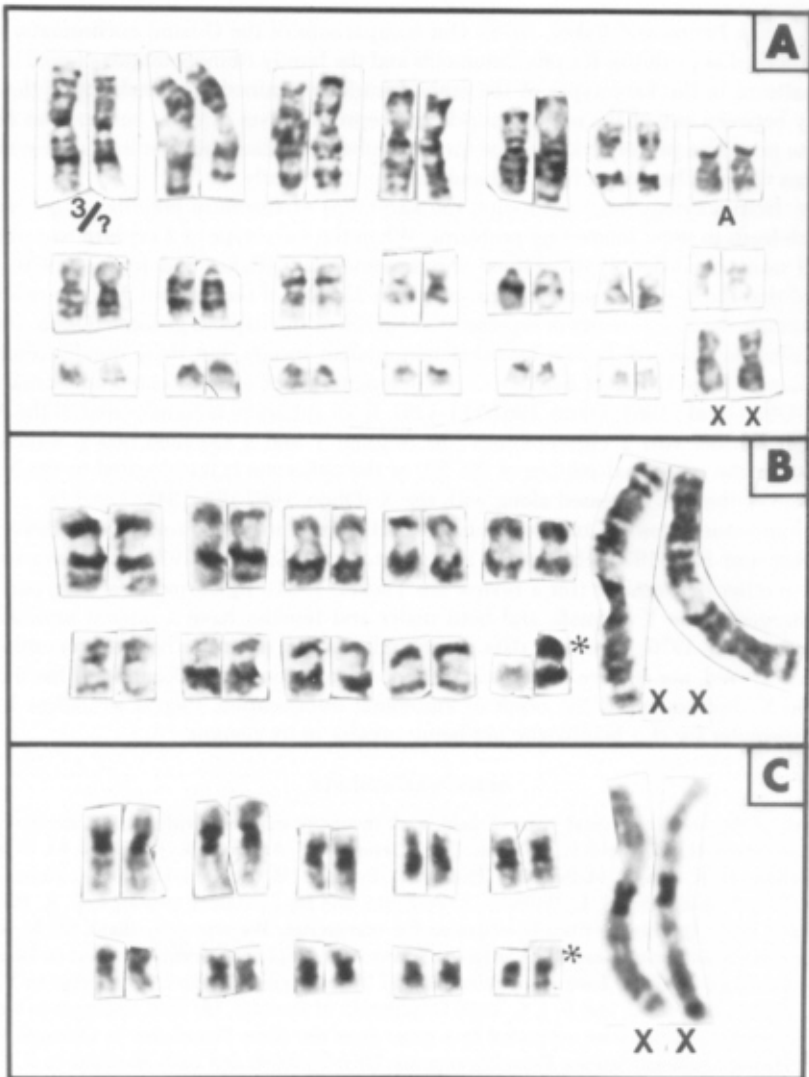


Fig 3—Banded karyotypes of *Taphozous* and *Cormura*. A, G-banded karyotype of female *Taphozous nudiventris* (TK 16597) from Egypt. B and C, G- and C-banded karyotypes of female *Cormura brevirostris* (TK 17632) from Suriname. Asterisk indicates an apparent polymorphism involving the smallest chromosomal pair.

(Baker and Bickham, 1980; Bickham, 1979a, 1979fo), Mormoopidae and Noctilionidae (Patton and Baker, 1978; Sites et al., 1981), and for several genera of Phyllostomidae (Baker and Bass, 1979; Baker et al., 1979). One explanation for such extensive chromosomal divergence is that the lineages representing the extant genera are very ancient (Bickham and Baker, 1979). The family Emballonuridae has been generally thought to represent a very old family of Chiroptera (Hill, 1974; Miller, 1907; Smith, 1972). Indeed, one of the earliest known bat fossils is assigned to the family (*Vespertiliavus* Schlosser from the Eocene of Europe, Barghoorn, 1977; Hill and Smith, 1983; for a review of fossil Chiroptera see Smith, 1976).

Homologous G-band patterns have been proposed for the ancestor of the Megachiroptera and the Microchiroptera (Qumsiyeh and Baker, 1985) and for the phyllostomoid bats (Baker and

Bickham, 1980; Patton and Baker, 1978). Our comparisons of the G-band euchromatic linkage groups proposed as primitive for phyllostomoids and the family Rhinopomatidae failed to reveal similar patterns in the karyotypes of the emballonurids examined. The inability to determine homology between any of the emballonurids and representatives of other bat families does not allow us to propose a primitive karyotype for the Emballonuridae, and thus limits the systematic conclusions that can be drawn from G-band data for this family.

Finally, from a cytogenetic standpoint, the karyotype of *Cormura brevirostris* is unusual, a fact which leads to some interesting problems. When the karyotype of *Cormura* was originally described using nondifferentially-stained chromosomal data (Baker and Jordan, 1970), it was concluded that the X chromosome comprised about 25-30% of the haploid genome, whereas in most mammals the X chromosome represents about 5% of the haploid genome (Ohno, 1967:89). Large X chromosomes are known for other mammalian species, but these usually result from the insertion of large blocks of inactive C-positive material, or a translocated autosomal region to the X (Ohno et al., 1964; Ohno, 1967:114-115). If an autosome is translocated to the X, then the male has either two Y chromosomes (the original Y and a so-called neo-Y, which is the homologue to the autosomal portion of the X), or the autosome is translocated to the X and Y and the size of the Y is increased along with the X (Ohno, 1967:132-134).

Sex chromosome-autosome translocations are well known in phyllostomid bats (Baker, 1973, 1979; Baker and Hsu, 1970; Hsu et al., 1968; Patton and Gardner, 1971), but have not been reported in other bat families (for a review see Tucker, 1984). In *Cormura*, a large part of the X is euchromatic, the Y is small, and both males and females have a diploid number of 22 (Baker and Jordan, 1970). Available data do not indicate that extensive heterochromatization of the X has occurred, nor is there the typical evidence of autosomal translocation. If the increased size of the X chromosome is the result of autosomal translocation, then it is unclear how the male compensates for this homologue not being present in its genome.

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