

J. Mamm., 69(1):131-134, 1988

COMPLEX CHROMOSOMAL POLYMORPHISM IN *GERBILLUS NIGERIAE*  
(RODENTIA, GERBILLIDAE)

Gautin

VITALY T. VOLOBOUEV, EVANI VIEGAS-PÉQUIGNOT, FRANCIS PETTER,  
JEAN-CLAUDE GAUTIN, BRUNO SICARD, AND BERNARD DUTRILLAUX

Structure et Mutagenèse Chromosomique, UA 620 C.N.R.S.—Institut Curie,  
26, rue d'Ulm, 75231 Paris Cédex 05 (VTV, EVP, BD)

Mammifères et Oiseaux, Museum National d'Histoire Naturelle de Paris,  
55, rue de Buffon, 75005 Paris (FP)

ORSTOM, B.P. 182, Ouagadougou, Burkina-Faso (JCG, BS)

Present address of VTV: Génétique écologique E.P.H.E., Université Montpellier-2,  
Place Eugène Bataillon, 34060 Montpellier (France)

Among the many mammalian species studied karyologically the species of the genus *Gerbillus* are distinctive. The evolution of sex chromosomes has been found to involve X-autosome and Y-autosome translocations (Viegas-Péquignot et al., 1982a; Wahrman et al., 1983). Numerous rearrangements of autosomes make it difficult to compare karyotypes of related species. The complexity of analysis is increased by the presence of long segments of heterochromatin in many autosomes. One part of this heterochromatin is stained by R-banding technique, whereas the second part remains unstained. Moreover, the first part is capable of fixing Z-DNA antibodies (Viegas-Péquignot et al., 1982b, 1984). We found *Gerbillus nigeriae* to have a complex polymorphism, with large variations in heterochromatin and multiple Robertsonian translocations. During our study it became obvious that observed chromosomal modifications did not occur at random: chromosomes with the longest euchromatic parts had the largest heterochromatic segments and they were involved more frequently in translocations than others.

The karyotypes of 11 specimens were studied on fibroblast cultures obtained from a biopsy taken from the tail. Two males were trapped from near Niamey, Niger, and five females and four males were from Oursi, in northern Burkina-Faso. The mitotic chromosomes were studied with R- (RHG and RBG) and C- (CBG) banding techniques (Dutrillaux and Lejeune, 1971; Sumner, 1972). For certain individuals additional studies (BrdU incorporation, immunofluorescence, NOR-staining) were performed.

Each of the 11 animals studied had a unique karyotype. However, considering only euchromatic arms, the fundamental number is constant (74) in all specimens. The variation in chromosome number from 68 to 72 is caused by the number of pairs involved in Robertsonian fusions.

To simplify chromosomal analysis, we reconstructed the ancestral karyotype of the species. For this purpose, we considered as ancestral each chromosome observed in an acrocentric state at least once. The acrocentric state was chosen as a primitive character because of the observation that two pairs of acrocentrics (namely 4 and 5) are to be found in two different metacentric combinations (namely 4 and 1, 4 and 8; 5 and 3, 5 and 10; Table 1). This led us to the karyotype shown in Fig. 1 (heterochromatic arms have not been taken into account).

TABLE 1.—Different combinations for six Robertsonian translocations found in 11 animals studied. H = homozygote for translocation, h = heterozygote, a = homozygote for acrocentrics.

Animal	t(3q5q)	t(2q9q)	t(1q4q)	t(6q7q)	t(4q8q)	t(5q10q)	2N
1	h	a	a	H	a	a	71
2	a	h	H	H	a	a	69
3	H	a	a	H	h	a	69
4	H	H	a	H	a	a	68
5	h	a	H	H	a	a	69
6	H	a	a	H	a	a	70
7	H	a	a	h	a	a	71
8	H	a	h	h	a	a	69
9	H	h	h	H	a	a	68
10	a	a	a	a	h	h	72
11	h	a	H	H	a	a	69

Fonds Documentaire ORSTOM



010020053

Fonds Documentaire ORSTOM

Cote: B-X20053 Ex: unique

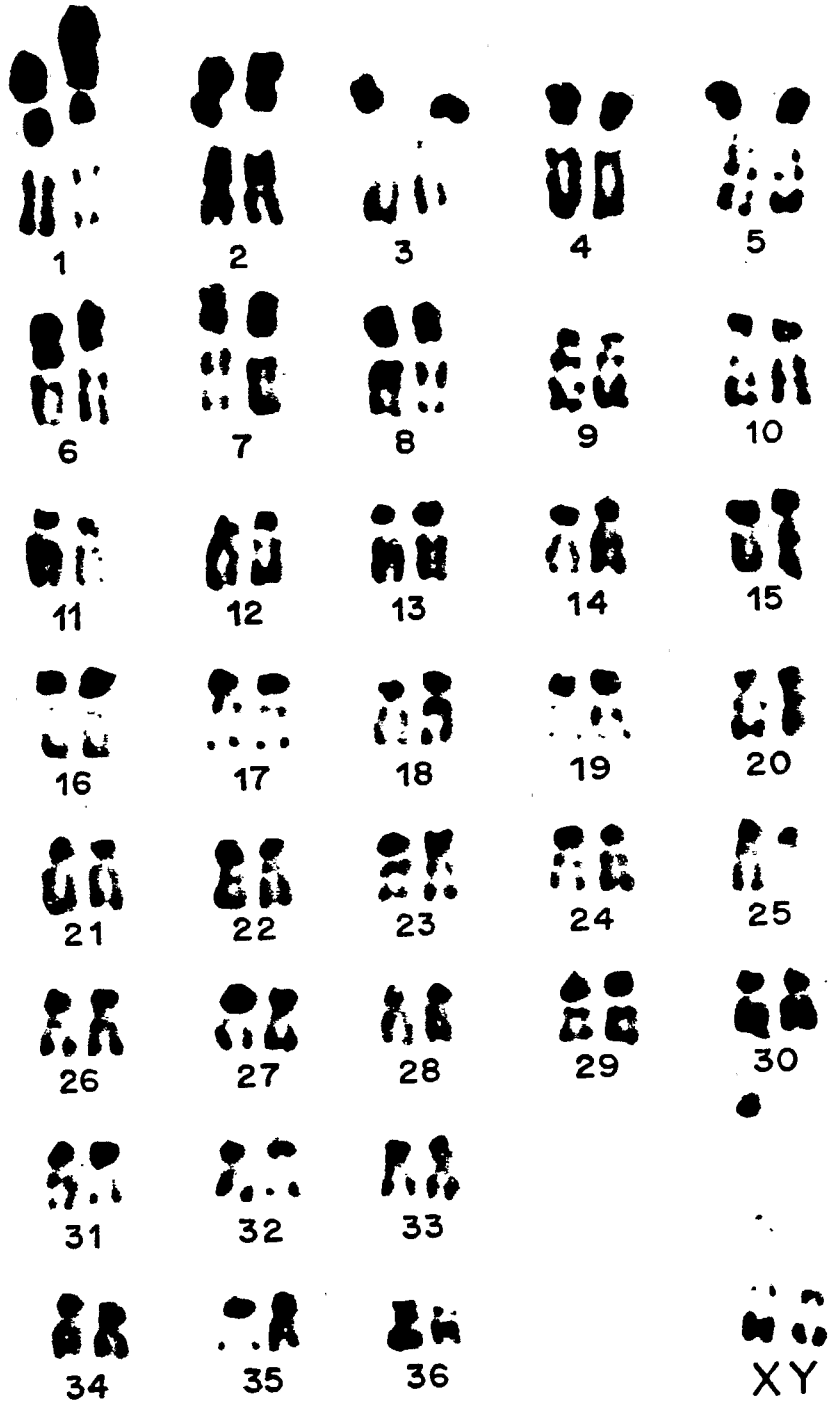


FIG. 1.—Hypothetical ancestral male karyotype of *Gerbillus nigeriae*. The karyotype was reconstructed from a specimen with the translocation t(3q5q) in homozygous state and translocation t(6q7q) in heterozygous state. Like all specimens of the species there were X-autosome and Y-autosome translocations.

tra  
acr  
het  
lon  
sta  
pa  
1-  
tio  
he  
of  
an  
Re  
chi  
chi  
inc  
(B)  
the  
sh  
no  
(D)  
pat  
et  
inv  
10  
var  
inv  
de  
of  
1  
by  
uni  
ha

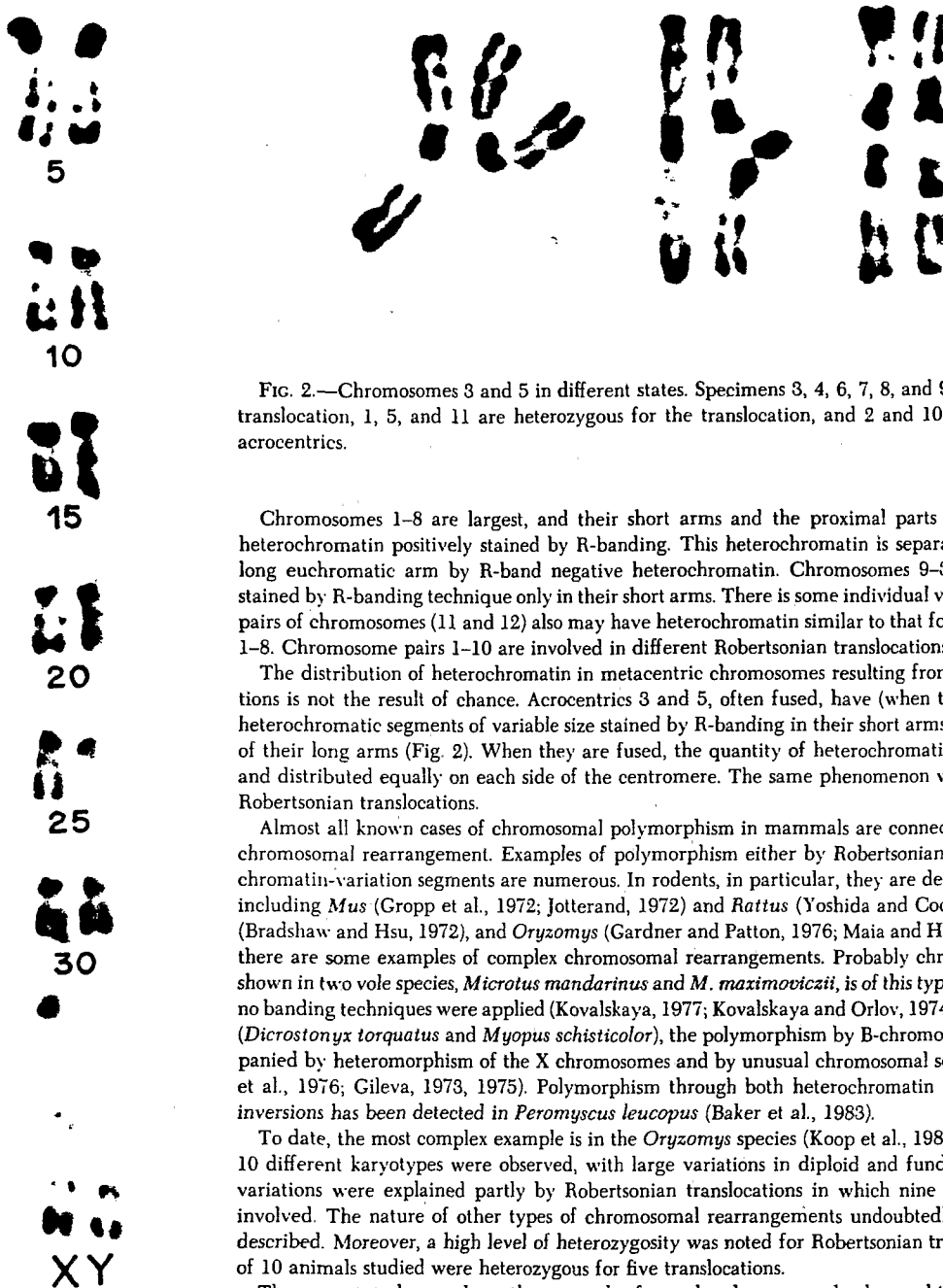


FIG. 2.—Chromosomes 3 and 5 in different states. Specimens 3, 4, 6, 7, 8, and 9 are homozygous for the translocation, 1, 5, and 11 are heterozygous for the translocation, and 2 and 10 are homozygous for the acrocentrics.

Chromosomes 1–8 are largest, and their short arms and the proximal parts of their long arms have heterochromatin positively stained by R-banding. This heterochromatin is separated from the rest of the long euchromatic arm by R-band negative heterochromatin. Chromosomes 9–36 have heterochromatin stained by R-banding technique only in their short arms. There is some individual variation. In some animals, pairs of chromosomes (11 and 12) also may have heterochromatin similar to that found in chromosome pairs 1–8. Chromosome pairs 1–10 are involved in different Robertsonian translocations (Table 1).

The distribution of heterochromatin in metacentric chromosomes resulting from Robertsonian translocations is not the result of chance. Acrocentrics 3 and 5, often fused, have (when they are not translocated) heterochromatic segments of variable size stained by R-banding in their short arms and at the proximal part of their long arms (Fig. 2). When they are fused, the quantity of heterochromatin is consistently reduced, and distributed equally on each side of the centromere. The same phenomenon was observed for all other Robertsonian translocations.

Almost all known cases of chromosomal polymorphism in mammals are connected with a single type of chromosomal rearrangement. Examples of polymorphism either by Robertsonian translocations or heterochromatin-variation segments are numerous. In rodents, in particular, they are described for many murids, including *Mus* (Gropp et al., 1972; Jotterand, 1972) and *Rattus* (Yoshida and Codama, 1983), *Peromyscus* (Bradshaw and Hsu, 1972), and *Oryzomys* (Gardner and Patton, 1976; Maia and Hulak, 1981). Nevertheless, there are some examples of complex chromosomal rearrangements. Probably chromosomal polymorphism shown in two vole species, *Microtus mandarinus* and *M. maximoviczii*, is of this type, although unfortunately no banding techniques were applied (Kovalskaya, 1977; Kovalskaya and Orlov, 1974). In Palearctic lemmings (*Dicrostonyx torquatus* and *Myopus schisticolor*), the polymorphism by B-chromosomes variation is accompanied by heteromorphism of the X chromosomes and by unusual chromosomal sex determination (Fredga et al., 1976; Gileva, 1973, 1975). Polymorphism through both heterochromatin variation and pericentric inversions has been detected in *Peromyscus leucopus* (Baker et al., 1983).

To date, the most complex example is in the *Oryzomys* species (Koop et al., 1983). In 10 animals studied, 10 different karyotypes were observed, with large variations in diploid and fundamental numbers. These variations were explained partly by Robertsonian translocations in which nine pairs of autosomes were involved. The nature of other types of chromosomal rearrangements undoubtedly present have not been described. Moreover, a high level of heterozygosity was noted for Robertsonian translocations, because two of 10 animals studied were heterozygous for five translocations.

The present study reveals another example of complex chromosomal polymorphism caused simultaneously by Robertsonian translocations and high variation in heterochromatin. Each of 11 animals studied had a unique karyotype. Because of a large variation of heterochromatin blocks, even the homologous chromosomes have different sizes in different individuals.

There is an apparent relationship between the presence of the heterochromatin and the origin of Rob-

e karyotype was reconstructed  
location t(6q7q) in heterozygous  
me translocations.

ertsonian translocations. Chromosomes with the largest euchromatic segments were those with heterochromatin at the proximal part of their long arms. These chromosomes also were those involved in Robertsonian translocations. This already has been noted in connection with Robertsonian evolution in lemurs and may be explained as a result of selection pressure (Dutrillaux, 1979). The meiotic malsegregations of translocations will be less favorable if they involve two small chromosomes because trisomy-monosomy for these chromosomes is compatible with survival of an abnormal progeny. Another factor, that does not exclude the first one, may favor occurrence of transmission of Robertsonian translocations: free acrocentrics, homologous to the arms of metacentrics, are carriers of long heterochromatic segments that may influence meiotic segregation (study of the synaptonemal complex is now in progress) or induction of other Robertsonian translocations.

The study of *G. nigeriae* from some new African localities is now in progress, and some problems of a general character connected with this unusual type of chromosomal variation will be discussed in greater detail later.

We are indebted to Miss Martine Lombard and Miss Michelle Prod'homme for technical assistance.

#### LITERATURE CITED

- BAKER, R. J., L. W. ROBBINS, F. B. STANGLE, JR., AND E. C. BIRNEY. 1983. Chromosomal evidence for a major subdivision in *Peromyscus leucopus*. *J. Mamm.*, 64:356-359.
- BRADSHAW, W. N., AND T. C. HSU. 1972. Chromosomes of *Peromyscus* (Rodentia, Cricetidae). III. Polymorphism in *Peromyscus maniculatus*. *Cytogenetics*, 11:435-451.
- DUTRILLAUX, B. 1979. Chromosomal evolution in primates: tentative phylogeny from *Microcebus murinus* (prosimian) to man. *Human Genet.*, 48: 251-314.
- DUTRILLAUX, B., AND J. LEJEUNE. 1971. Sur une nouvelle technique d'analyse du caryotype humain. *C. R. Acad. Sci. (Paris)*, 272:2638-2640.
- FREDGA, K., A. GROPP, H. WINKING, AND F. FRANK. 1976. Fertile XX- and XY-type females in the wood lemming *Myopus schisticolor*. *Nature*, 261: 225-227.
- GARDNER, A. L., AND J. L. PATTON. 1976. Karyotypic variation in oryzomyine rodents (Cricetidae) with comment on chromosomal evolution in the neotropical cricetine complex. *Occas. Papers Mus. Zool., Louisiana State Univ.*, 49:1-48.
- GILEVA, E. A. 1973. B-chromosomes, unusual inheritance of sex chromosomes and sex ratio in the lemming *Dicrostonyx torquatus torquatus* Pallas, 1779. *Doklady Akad. Nauk SSSR*, 213:952-955.
- . 1975. Karyotype of *Dicrostonyx torquatus chinopaes* Allen and the unusual chromosome mechanism of sex determination in palearctic lemmings. *Doklady Akad. Nauk SSSR*, 224:697-700.
- GROPP, A., H. WINKING, L. ZEACH, AND H. MILLER. 1972. Robertsonian chromosomal variation and identification of metacentric chromosomes in feral mice. *Chromosoma*, 39:265-288.
- JOTTERAND, M. 1972. Le polymorphisme chromosomique de *Mus (Leggades)* africains. *Cytogénétique, zoogéographie, évolution. Rev. Suisse Zool.*, 79:287-359.
- KOOP, B. F., R. J. BAKER, AND H. H. GENOWAYS. 1983. Numerous chromosomal polymorphisms in a natural population of rice rats (*Oryzomys, Cricetidae*). *Cytogenet. Cell Genet.*, 35:131-135.
- KOVALSKAYA, U. M. 1977. Chromosomnyi polymorphism u polevki Maksimovitcha *Microtus maximoviczii* Schrenk, 1858 (Rodentia, Cricetidae). *Bull. Moskovskouo obshchestva ispitately prirody (Moscow)*, Biol. Ser., 82:38-48.
- KOVALSKAYA, U. M., AND V. N. ORLOV. 1974. Neobychnye polovye chromosomy i vnutripopulatsionnyi polymorphism u kitskoi polevki. *Tsitologia (Leningrad)*, 16:497-503.
- MAIA, V., AND A. HULAK. 1981. Robertsonian polymorphism in chromosomes of *Oryzomys subflavus* (Rodentia, Cricetidae). *Cytogenet. Cell Genet.*, 31: 33-39.
- SUMNER, A. T. 1972. A simple technique for demonstrating centromeric heterochromatin. *Exp. Cell Res.*, 75:304-306.
- VIEGAS-PÉQUIGNOT, E., T. BENAZZOU, B. DUTRILLAUX, AND F. PETTER. 1982a. Complex evolution of sex chromosomes in Gerbillidae (Rodentia). *Cytogenet. Cell Genet.*, 34:158-167.
- VIEGAS-PÉQUIGNOT, E., C. DERBIN, F. LEMEUNIER, AND E. TAILLANDER. 1982b. Identification of left-handed DNA by indirect immunomethods in metaphasic chromosomes of the mammal *Gerbillus nigeriae* (Gerbillidae, Rodentia). *Ann. Genet.*, 25:218-222.
- VIEGAS-PÉQUIGNOT, E., T. BENAZZOU, M. PROD'HOMME, AND B. DUTRILLAUX. 1984. Characterization of very complex heterochromatin in two species of *Gerbillus* (Rodentia). *Chromosoma*, 89: 42-47.
- WAHRMAN, J., C. RICHLER, E. NEUFELD, AND A. FRIEMAN. 1983. The origin of multiple sex chromosomes in *Gerbillus gerbillus*. *Cytogenet. Cell Genet.*, 35:161-180.
- YOSHIDA, M. C., AND Y. CODAMA. 1983. The C-band pattern of chromosomes in 17 strains of mice. *Cytogenet. Cell Genet.*, 35:51-56.

Submitted 27 December 1985. Accepted 26 November 1986.