Cytogenet. Cell Genet. *35:* 131–135 (1983)

Numerous chromosomal polymorphisms in a natural population of rice rats (*Oryzomys*, Cricetidae)

B.F. Koop, R.J. Baker, and H.H. Genoways

The Museum, Texas Tech University, Lubbock, Tex.

Abstract. Based on G- and C-banded karyotypes of 10 specimens of rice rats, genus *Oryzomys* (a member of the *macconnelli-capito* complex but species identification is not possible at this time) from a single isolated population, we found at least nine different centric fusion/fission polymorphisms. No two individuals examined had the same karyotype. Polymorphic variation appears to be stable in the population and not the result of hybridization, human disturbance, or non-specific mutagenic agents. Among the 14 largest chromosomes, polymorphism is restricted to fusion/fission rearrangements. Among the smaller ones, there is polymorphism in the total number of euchromatic arms, which indicates that rearrangements other than fusion/fission exist within our sample. Data from these rice rats document the presence of a greater number of chromosomal polymorphisms within a single, natural population than have previously been reported in a higher vertebrate.

Chromosomal polymorphisms (variation within a single population) in natural populations are less common than genic polymorphisms. This is thought to be true because: (1) many chromosomal rearrangements result in reduced fertility in heterozygotes (White, 1973; Lande, 1979); (2) chromosomal rearrangements rarely result in a positive phenotypic effect (Lande, 1979; Patton et al., 1980), and (3) chromosomal mutations occur at a sufficiently low rate (10^{-3} or 10^{-4}, Lande, 1979) that few individuals contain a chromosomal mutation. Nonetheless, chromosomal polymorphisms have been described for a wide variety of mammalian species (Baker and Mascarello, 1969; Hsu, 1969; Ford and Hamerton, 1970; Ford and Evans, 1973; Baker, 1979; Fedyk, 1980; Patton et al., 1980; John, 1981; Maia and Hulak, 1981). However, as would be expected, most polymorphisms are the result of variation from a single rearrangement.

Here we describe the chromosomal characteristics of a sample of 10 specimens of *Oryzomys* (the exact species identification of this population is still under study; it is a member of the *macconnelli-capito* complex but may represent an undescribed taxon) from a single population which contains at least nine different centric fusion/fission polymorphisms. Variation is so extensive that no two individuals had the same karyotype.

The Tafelberg (Saramace District, 3° 54-56′N, 56° 10-11′W) in central Suriname from which these rice rats (*Oryzomys*) were collected is the easternmost sandstone table mountain outlier of the Guianan Highlands. These table mountains in northeastern South America are the erosional remnants of the pre-Cambrian Guianan Shield. The mountain's sides are vertical cliffs of 40 to 300 m except in the northwest corner. In this area, talus from erosion of the wall of the mountain makes access by foot possible, albeit difficult. The top of the mountain slopes from 550 m at the northwest rim to over 1,000 m at the southern extreme of the mountain. In the center of the mountain is a great basin which is filled with dense high tropical forest. The vegetation of the top of the moun-

The small mammal research project in Suriname was supported by a grant from the Alcoa Foundation, Pittsburgh, Penn. The expedition to the Tafelberg was supported by the M. Graham Netting Research Fund, Carnegie Museum of Natural History, which was established by a grant from the Cordelia S. May Charitable Trust.

Laboratory and some field work was supported by National Science Foundation grants DEB-76-20580 and DEB-80-04293.

Request reprints from: Dr. Robert J. Baker, The Museum, Texas Tech University, Box 4499, Lubbock, TX 79409 (USA).

tain is much more diverse than that of the lowland rainforest surrounding the base of the mountain (Maguire, 1945*a* and *b*; Maguire et al., 1953). The rice rats were taken in traps set along streams in the basin and along the banks of Geijskes Creek. These were some of the more moist areas sampled.

Materials and methods

Ten specimens (six females and four males) of *Oryzomys* were collected during October, 1981. Standard bone marrow chromosomal preparations were made in the field. The bone marrow-fixative suspension was frozen in liquid nitrogen, and slides for G- and C-banding were prepared later at Texas Tech University following the procedures described by Baker et al. (1982). G-bands were produced by trypsin digestion and Giemsa staining (Seabright, 1971, as modified by Baker et al., 1982). C-band procedures have been described by Stefos and Arrighi (1971). Skins and skulls of voucher specimens have been deposited in the Carnegie Museum of Natural History, Pittsburgh, Penn. TK numbers in table I and fig. 1 are field numbers used to reference tissues and voucher specimens. The numbering of chromosomes in figs. 1 and 2 refer to proposed homology to those of *Peromyscus* (Committee for Standardization of *Peromyscus*, 1977). Chromosomes are arranged in order of decreasing size.

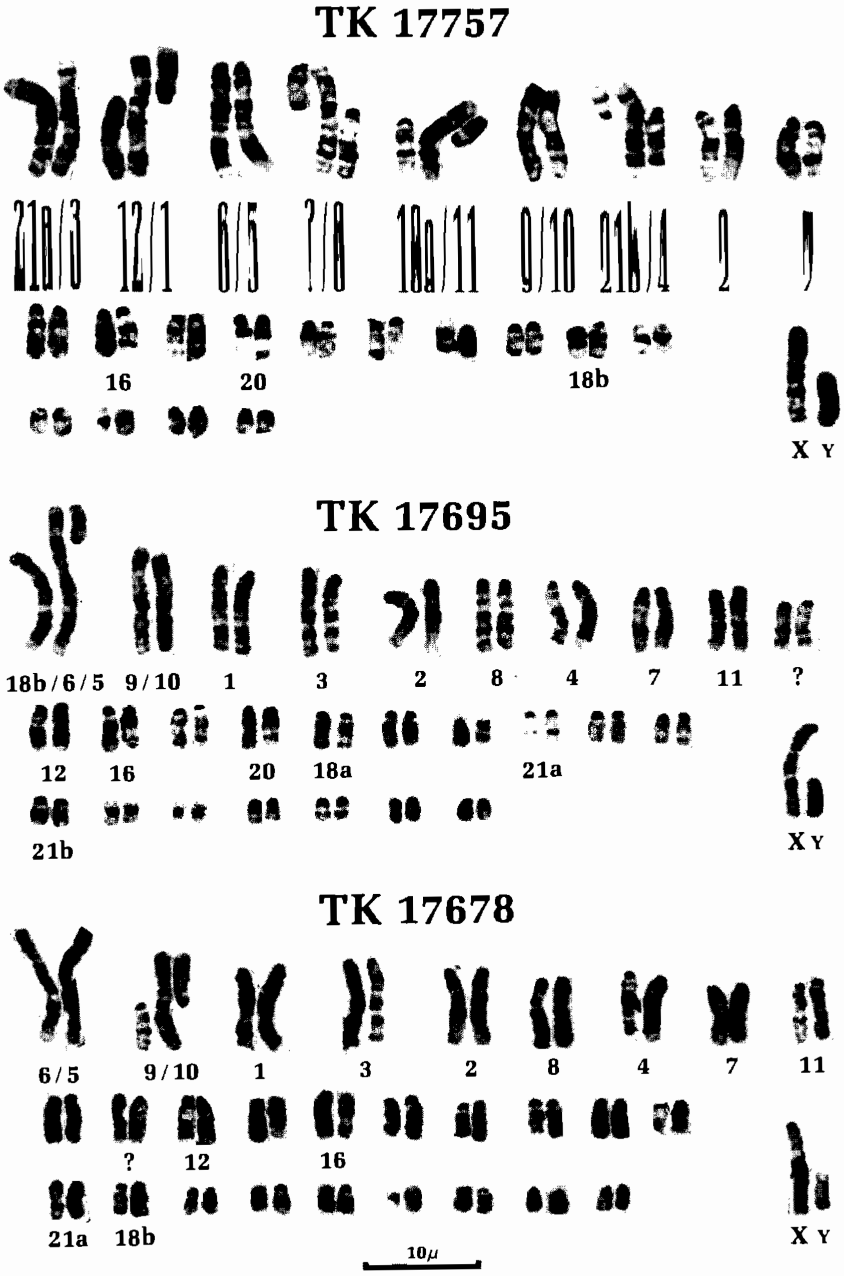

Fig. 1. G-banded karyotypes of three of the ten specimens examined from Tafelberg.

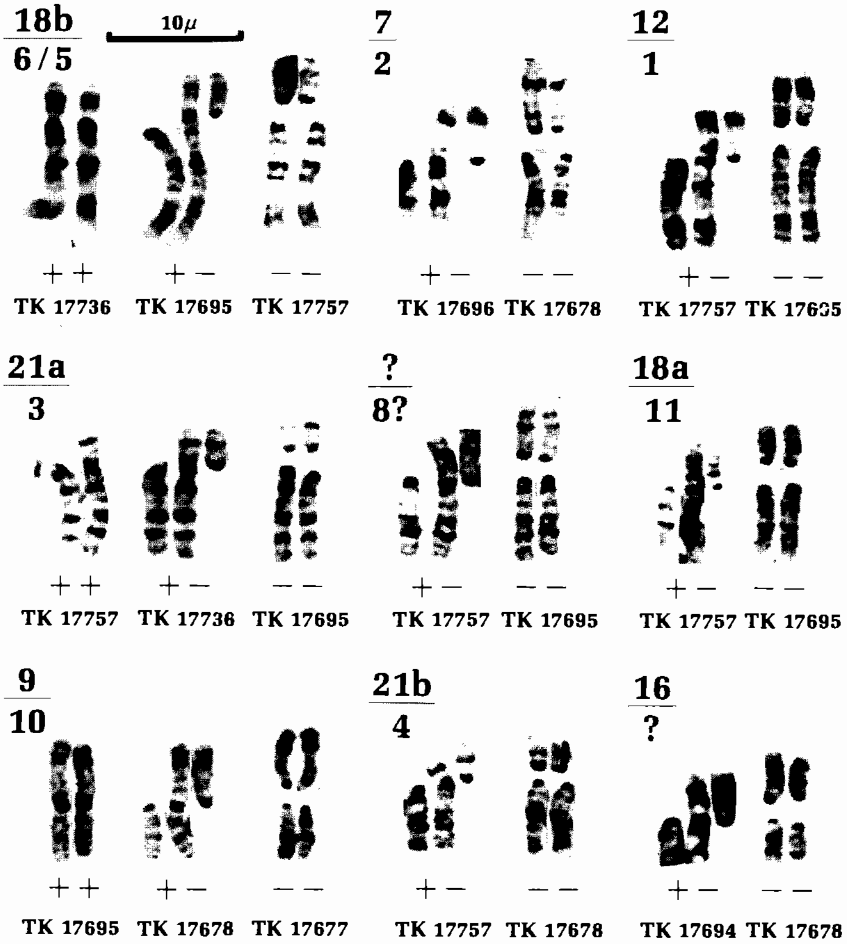

Fig. 2. G-banded chromosomes showing the nine polymorphic centric fusions/fissions observed in specimens of *Oryzomys* from Tafelberg. +: fusion morph; –: fission morph.

Results

Each individual in the sample had a unique karyotype. Examples of complete chromosomal complements for three individuals are shown in fig. 1. There has been an addition of euchromatin to the 11 and some euchromatin has been lost from the 6 compared to the homologous *Peromyscus* chromosomes. Homology of the different segments of 18 and 21, labeled a and b, could not distinguished. Two types of rearrangements are evident in the sample. The first type is centric fusion/fission events. Nine different fusion/fission polymorphisms have been identified (fig. 2) which involve the nine largest acrocentric chromosomes. The second type of rearrangement involves several of the smaller chromosomes which may be either acrocentric or biarmed. Because of limited G-band definition, we could not positively identify all of the smaller homologous elements within and between individuals. C-band positive material was restricted to centromeric regions, and these data suggest that the variation in these smaller elements which alters the fundamental number is not due to additions or deletions of heterochromatin. A summary of the karyotypes of the 10 individuals examined is given in table I.

Discussion

In light of the relatively low frequency of chromosomal polymorphisms in natural populations of vertebrates, it is somewhat unusual to find variation which occurs as a result of nine different chromosomal fusions/fissions plus numerous other rearrangements in the smaller elements in such a small sample (10 individuals) from a single locality. Several features of this data set are worthy of note.

Table I. Summary of the fusion/fission chromosomes shown in fig. 2 of the ten specimens of *Oryzomys*

Karyotype number	Museum number	Diploid number	Fundamental number	Polymorphism[1]								
				18b	7	12	21a	?	18a	9	21b	16
				6/5	2	1	3	8?	11	10	4	?
TK 17757	CM76937	52	66	− −	− −	+ −	+ +	+ +	+ −	+ +	+ −	− −
TK 17677	CM76935	54	59	− −	− −	− −	− −	− −	− −	− −	− −	− −
TK 17736	CM76926	54	64	+ +	+ −	+ −	+ −	+ −	− −	+ −	− −	− −
TK 17722	CM76930	54	65	− −	+ −	+ −	+ −	− −	+ −	+ −	− −	− −
TK 17723	CM76932	54	58	− −	− −	− −	− −	− −	− −	− −	− −	− −
TK 17695	CM76928	57	64	+ −	− −	− −	− −	− −	− −	+ +	− −	− −
TK 17696	CM76929	57	67	+ −	+ −	− −	− −	− −	+ −	+ −	− −	− −
TK 17737	CM76927	58	66	− −	+ −	− −	− −	− −	− −	+ −	− −	− −
TK 17694	CM76931	59	67	− −	− −	− −	− −	+ −	− −	− −	− −	+ −
TK 17678	CM76936	59	66	− −	− −	− −	− −	− −	− −	+ −	− −	− −

[1] +: fusion morph (Robertsonian translocation); −: fission morph

All rearrangements clearly identified by G-band patterns are centric fusion/fission events. Robertsonian variation can result in balanced gamete production in a heterozygote (John, 1981). Only 20% (two of 10) of our sample was homozygous for all of the larger chromosomal pairs. Three of the eight other individuals were heterozygous for a single fusion, two were heterozygous for two fusions, one was heterozygous for four fusions, and two were heterozygous for five fusions.

Other chromosomal variation existed within the sample as the fundamental number varied from 58 to 67. Robertsonian variation, as identified in fig. 2, does not result in a change in the fundamental number. The cause of the variation in fundamental number was the presence or absence of euchromatic arms on some of the smaller elements. Additionally, the two individuals that had none of the larger centric fusions, had a lower diploid number (54) than some of the individuals with several fusions, indicating the involvement of other unidentified chromosomal rearrangements (possibly additional fusions among the smaller elements).

Within the larger elements, karyotypic orthoselection as defined by White (1975) seems to be operating in that only centric fusion/fission events are observed. In many ways, the genus *Oryzomys* is the neotropical ecological equivalent of the Neartic genus *Peromyscus*. In 18 species of *Peromyscus* studied by G- and C-banding, no fusions have been identified. Of the 60 chromosomal rearrangements identified, 34 were heterochromatic additions and 26 were pericentric inversions (Robbins and Baker, 1981). Fusions, which are so obviously absent in the evolution of the *Peromyscus* genome, are the only identifiable mode of change in the larger elements in this species of *Oryzomys*. Gardner and Patton (1976) and Maia and Hulak (1981) also suggest that Robertsonian variation is a primary rearrangement in evolution of the *Oryzomys* genome. Comparison of the G-banding patterns of the *Oryzomys* karyotype to that proposed as a standard for *Peromyscus* (Committee for Standardization of Chromosomes of *Peromyscus*, 1977), reveals that chromosomal banding sequences of the 14 largest elements of *Peromyscus* are readily identifiable in *Oryzomys*. Although the G-banding pattern for most major euchromatic segments can be recognized in both genera, the factors regulating the favored rearrangements in karyotypic orthoselection has changed in the evolution of the two lineages.

The polymorphisms may be the result of hybridization between different chromosomal morphs as has been identified for some mammalian populations (Wahrman and Gourevitz, 1973; Baker, 1981). However, if this is true, then our sample did not permit identification of either parental type. The habitat of this population is undisturbed by man. Additionally, the habitat found on top of this mountain is located above vertical stone walls which form an unsuitable habitat for *Oryzomys*. Such an isolated mountain top is an unlikely locale for hybridization of two parental types, because one type must invade an area held by the second type over a very narrow access route.

One possible explanation of such extensive polymorphism is an environmental mutagen which could drastically increase the mutation rate. Examination of the standard karyotypes of 29 specimens of *Proechimys* (2n = 40; FN = 50) from the same trap lines failed to reveal a single case of chromosomal variation. Although this observation does not totally eliminate the possibility of a mutagen being important in producing this variation in *Oryzomys*, it does indicate that the mutagen is not acting on all species in this area.

As suggested by Gardner and Patton (1976) and Maia and Hulak (1981), understanding of the factors and patterns of chromosomal evolution in *Oryzomys* will be challenging and rewarding. The data set we describe above certainly suggest that this is accurate.

Acknowledgements

Our work in Suriname would not have been possible without the cooperation of Henry A. Reichart, Director, Foundation for Nature Preservation in Suriname. Permits to collect specimens were issued by Ferdinand L.J. Baal. We would like to thank the members of the Tafelberg Expedition, especially Henry A. Reichart, Ferdinand L.J. Baal, Stephen L. Williams, Jane A. Groen, Carleton J. Phillips, Keith Studhome, Leo Roberts, and Michael Arnold. We are particularly grateful to the late Vorster Ford of the Parimaribo Mining Company, who skillfully piloted the helicopter that transported our field crew to and from the top of Tafelberg.

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Received: 12 August 1982
Accepted: 2 November 1982