

Genetic variation and origin of the most chromosomally polymorphic natural mammalian population

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Abstract. Examination of allozymic variation in a chromosomally highly polymorphic population of *Oryzomys* documented that the sample consisted of two species, one that was chromosomally monomorphic and the other containing nine centric fusion

polymorphisms. The existence of allozymic variation indicates that it is highly improbable that the polymorphic sample was the result of hybridization. These centric fusion polymorphisms appeared to cause little or no negative selection.

The rodent genus *Oryzomys* (rice rats) contains what appears to be the most chromosomally polymorphic natural population of mammals thus far reported (Koop et al., 1983). Koop et al. (1983) reported a sample of 10 individuals from a single locality that contained nine different centric fusion polymorphisms. The diploid number varied from 52 to 59, while the fundamental number (FN) ranged from 58 to 67. Koop et al. (1983) concluded that, in addition to the centric fusion polymorphisms, the population also contained some non-Robertsonian polymorphisms. The ecological situation associated with this population is unique (an isolated tabletop mountain in Surinam) and was interpreted by Koop et al. (1983) as involving circumstances that made a hybrid origin for these polymorphisms highly improbable.

Koop et al. (1983) concluded that they were dealing with chromosomal variation in a single species from the *O. macconnelli-capito* complex. The importance of the chromosomal variation in the Tafelberg samples of *Oryzomys* was clouded when subsequent analyses by H. H. Genoways (personal communication) of the cranial morphology and pelage characteristics suggested that the sample contained representatives of two different genetic entities. Three individuals (two of which, TK 17677 and 17723, were G- and C-banded by Koop et al., 1983), were identified as representatives of the species *O. capito*, whereas nine other individuals (eight of which were G- and C-banded by Koop et al., 1983) were identified as *O. yunganus*.

It thus becomes critical to determine how many species are involved in the chromosomal polymorphisms reported by Koop et al. (1983), because the biological implications are quite different if all chromosomal variation is found within a single species or, alternatively, the variation is either an artifact of lumping together two species or the result of hybridization between two species.

This study examines the allozymic variation in the Tafelberg sample of *Oryzomys* to estimate how many species were involved in that sample and to determine if the magnitude of genic variability in that sample was greater than that characteristic of typical populations of rodents.

Materials and methods

Liver, heart, and kidney from the Tafelberg specimens were frozen in the field in liquid nitrogen when they were karyotyped. These tissues were examined by standard starch-gel electrophoretic techniques (Selander et al., 1971). Other species of *O. capito* collected by field parties in Surinam were also studied as a reference sample. Numbers that identify each specimen are the original field numbers that were reported in Koop et al. (1983). As the goal was to determine the relationship between the 12 Tafelberg specimens, each was treated as a separate taxonomic unit in all analyses.

Presumed loci that were examined included: sorbitol dehydrogenase (SORD), lactate dehydrogenase (LDHA and LDHB), hexokinase I (HK1), isocitrate dehydrogenase (IDH1 and IDH2), peptidase C (PEPC), 6-phosphogluconate dehydrogenase (PGD), malate dehydrogenase (MDH1 and MDH2) malic enzyme (ME), nucleoside phosphorylase (NP), alcohol dehydrogenase (ADH), phosphoglucomutase (PGM), aconitase (ACO1 and ACO2), and glutamate dehydrogenase (GLUD).

Alleles for each locus were letter coded for entry into the computer and analyzed using BIOSYS-1, a computer program for analysis of allelic variation (Swofford and Selander, 1981). Analyses performed on the data generated similarity and distance measures for all pairwise comparisons. The 12 specimens from the Tafelberg sample were entered separately and subjected to analysis by the Fitch-Margoliash method to produce an unrooted tree showing Rogers' (1972) distance relationships among the specimens. A further analysis was performed using the same data and method as above, but with the addition of data from 18 Surinam *O. capito* individuals.

Results and discussion

Using skin and skull morphology, H.H. Genoways (personal communication) identified 3 of the 12 Tafelberg specimens as *O. capito* and referred the remaining 9 to as *O. yunganus* (Gardner, personal communication). Our Fitch-Margoliash tree using Rogers' (1972) distance divides the Tafelberg specimens into the exact groups of three and nine specimens (Fig. 1) defined by Geno-

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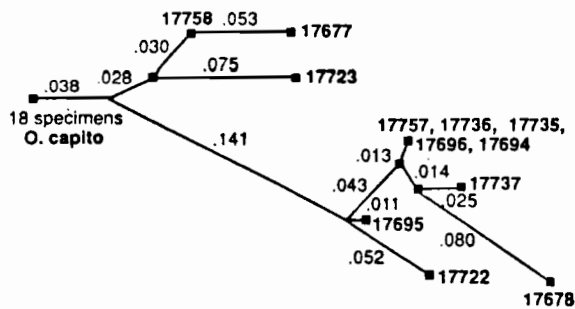


Fig. 1. Unrooted Fitch-Margoliash tree using Rogers' genetic distance of the 12 specimens of *Oryzomys* from Tafelberg, Surinam, and 18 individuals of *O. capito* from other localities in Surinam. Note the division of the 12 Tafelberg specimens into two groups, one of which is closely associated with the 18 specimens of *O. capito*. Bold numbers indicate specimen numbers, whereas other numbers indicate the Rogers' distance.

ways and Gardner. All other analyses, such as a UPGMA, gave similar results. Also, when the three specimens identified by Genoways as *O. capito* are compared genetically to 18 other specimens of *O. capito* from Surinam, these three Tafelberg specimens are more akin to *O. capito* than to the nine Tafelberg specimens assigned to *O. yunganus* (Fig. 1). We interpret these data as being compatible with the conclusion that the Tafelberg sample described chromosomally by Koop et al. (1983) was a composite of two species. How does this affect the conclusions of Koop et al. (1983)?

Koop et al. (1983) concluded that the Tafelberg sample represented the greatest amount of chromosomal polymorphism thus far identified in a single naturally occurring mammalian population. Additionally, they concluded that the polymorphism was probably not the result of hybridization between two species. The discovery that their sample actually contained individuals from two separate species calls for a reevaluation of their conclusions. Of the three individuals identified by electrophoresis in this study as *O. capito*, only two (TK 17677 and 17723) were included in the chromosomal analysis performed by Koop et al. (1983). These two

representatives of *O. capito* were the only individuals in the Tafelberg sample that contained no karyotypic centric fusion polymorphisms, both being homozygous for all of the larger acrocentric chromosomal pairs (Table I). Additionally, the two specimens of *O. capito* had FN values (number of arms of the autosomal complement) outside the range of the other eight specimens of *O. yunganus* (the FNs for *O. capito* were 58 and 59, whereas the FNs for *O. yunganus* ranged from 64 to 67). Therefore, removal of the two specimens of *O. capito* (i.e., TK 17677 and 17723) reduces the variation in FN, but all of the fusions identified by G-bands remain assigned to a single species (*O. yunganus*) and the polymorphism is still greater than that described of any other naturally occurring population of mammals.

Considering that the Tafelberg sample contained two species, are the data compatible with the possibility that the chromosomal polymorphism in *O. yunganus* (Table I) is the result of hybridization between *O. capito* and a third, yet to be identified, species? If *O. capito* is one of the parental types, what would be the chromosomal and genic characteristics of the other parental type?

Two points seem worthy of note. First, if the three individuals identified as *O. capito* are representative of one of the parental types, then the other parental types would need to be homozygous, or at least polymorphic, for all nine centric fusion polymorphisms found in the eight Tafelberg specimens of *O. yunganus*. Such a hypothetical parental type was not found in the Tafelberg sample, and none of the fusion banded chromosomes found in the Tafelberg *O. yunganus* specimens thus far examined by G-banding have been observed in any other *Oryzomys* individuals.

Concerning the second point, there are three loci documenting that Tafelberg *O. capito* probably are not a parental type involved in the production of the chromosomal polymorphism in *O. yunganus* from Tafelberg. At the PGD and GLUD loci, respectively, the Tafelberg *O. capito* specimens are fixed for one allele, whereas the nine chromosomally polymorphic *O. yunganus* specimens are fixed for an alternative allele. At the ADH locus, the three *O. capito* individuals are polymorphic for two alleles, whereas the chromosomally polymorphic *O. yunganus* specimens are fixed for a third allele.

Table I. Summary of the fusion chromosomes for 10 specimens of *Oryzomys* (modified from Koop et al., 1983) to show the partitioning of chromosomal polymorphism if the sample is divided into two species (*O. capito* and *O. yunganus*) as documented by genetic data

Karyotype No.	Diploid number	Fundamental number	Polymorphism ^a								Heterozygosity
			$\frac{18b}{6/5}$	$\frac{7}{2}$	$\frac{12}{1}$	$\frac{21a}{3}$	$\frac{?}{8?}$	$\frac{18a}{11}$	$\frac{9}{10}$	$\frac{21b}{4}$	
<i>O. capito</i>											
TK17677	54	59	--	--	--	--	--	--	--	--	0
TK17723	54	58	--	--	--	--	--	--	--	--	0
<i>O. yunganus</i>											
TK17757	52	66	--	--	+-	++	++	+-	++	+-	3
TK17736	54	64	++	+-	+-	+-	+-	--	+-	--	5
TK17722	54	65	--	+-	+-	+-	--	+-	+-	--	5
TK17695	57	64	+-	--	--	--	--	--	++	--	1
TK17696	57	67	+-	+-	--	--	--	+-	+-	--	4
TK17737	58	66	--	+-	--	--	--	--	+-	--	2
TK17694	59	67	--	--	--	--	+-	--	--	+-	2
TK17678	59	66	--	--	--	--	--	--	+-	--	1

^a + = Fusion morph (Robertsonian translocation); -- = fission morph.

The absence of *O. capito* alleles in the sample of chromosomally polymorphic *O. yunganus* specimens is clearly not compatible with the hypothesis that the chromosomal polymorphism resulted from recent hybridization between Tafelberg *O. capito* and some other, as yet unidentified, species. What this study does reveal, however, is that within a sample of nine individuals of *O. yunganus*, there are nine centric fusion polymorphisms, and none of these individuals was homozygous for all chromosomal fusions. What are the implications of this new evidence?

It is generally thought that, for most types of chromosomal rearrangements, heterozygous individuals experience some level of reduced fertility as a result of production of unbalanced gametes. For centric fusions in *Mus*, the level of reduced fertility ranged from 5% to 18% (Capanna et al., 1976). Individuals of *Mus* heterozygous for three centric fusions produced about 25% aneuploid gametes (White et al., 1978). Under most circumstances, such a level of negative selection on heterozygotes would cause chromosomal polymorphisms to be short lived in natural populations. If such a level of reduced fertility is characteristic of *O. yunganus*, then how could it maintain chromosomal polymorphism at the high level observed in the eight karyotyped specimens examined by Koop et al. (1983)? One possibility is the continued production of new polymorphisms by hybridization between taxa with different karyotypes. For the reasons outlined above, a recent hybrid origin of the chromosomally polymorphic *O. yunganus* is unlikely. If the *O. yunganus* polymorphism is not of recent hybrid origin, then an alternative explanation is that the chromosomally polymorphic individuals of *Oryzomys* are experiencing little or no

reduced fertility. The fact that all eight specimens karyotyped by Koop et al. (1983) were polymorphic for at least one centric fusion and that two were polymorphic for five suggests that these polymorphisms are under little or no negative selection. The possibility that these centric fusions might have a selective advantage, as was found in another rodent, *Geomys* (Baker et al., 1983), cannot be eliminated with these data.

There is a growing body of evidence that there are circumstances associated with some chromosomal mutations that produce little or no reduced fitness in the heterozygote. Baker et al. (1988) concluded that such a mechanism is probably molecular or cellular (rather than demographic) and is commonly associated with a rearrangement that becomes fixed in natural populations, especially as related to karyotypic orthoselection and karyotypic megaevolution (Baker and Bickham, 1980). Polymorphisms for nine centric fusions in a sample of eight individuals are compatible with the conclusions of Baker et al. (1988).

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