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CHROMOSOMAL PHYLOGENY AND EVOLUTION IN THE GENUS *MASTOMYS* (MAMMALIA, RODENTIA)

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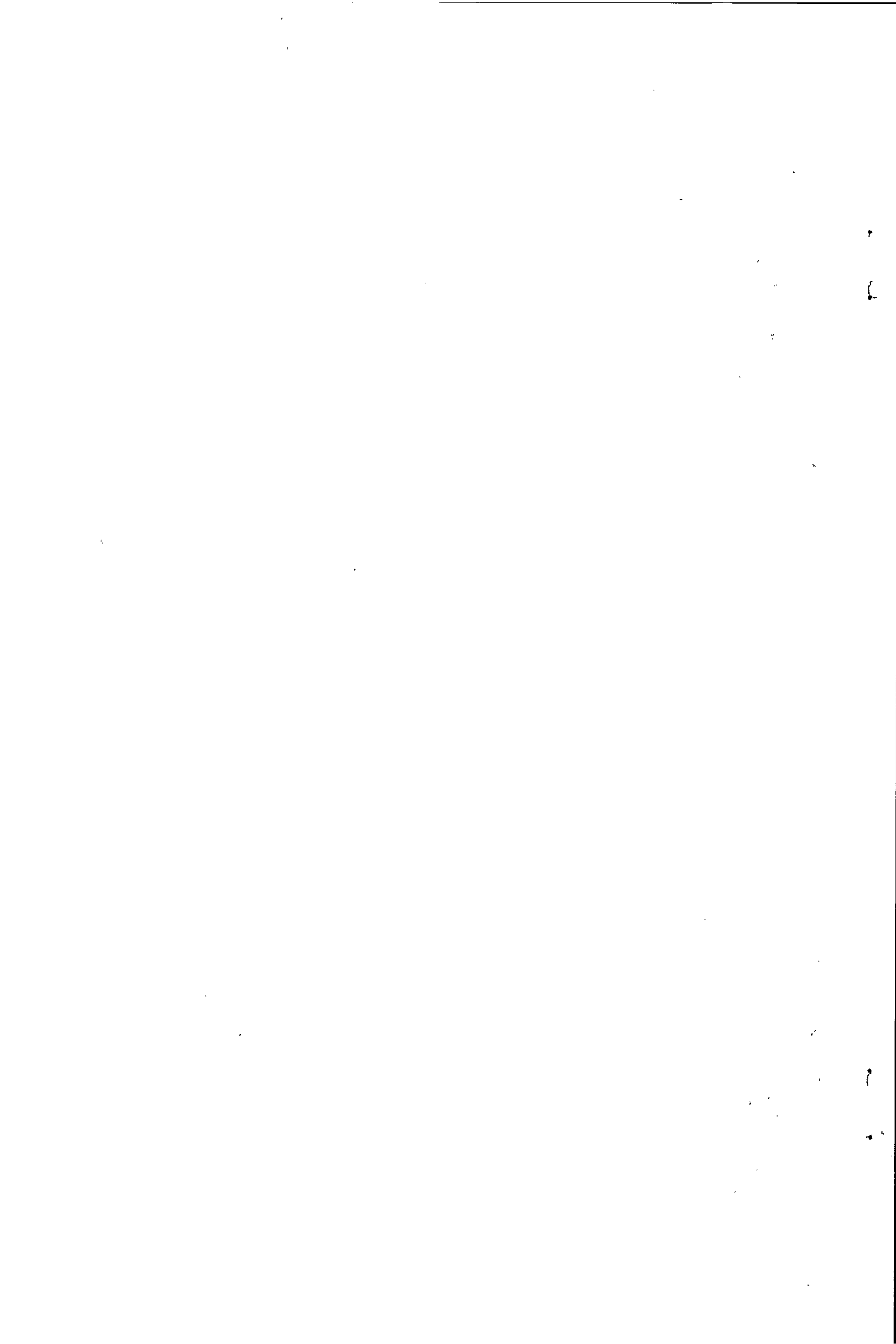
The chromosomal phylogeny of the African genus *Mastomys* was undertaken to clarify their taxonomic position and to estimate the relevance of chromosomal evolution in the diversification of this genus. Four species of *Mastomys* (*M. erythroleucus, M. huberti, M. natalensis,* and *M. coucha*) were compared to closely related African rats, *Myomys daltoni* and *Praomys tullbergi,* and to three species of European murids. The phylogenetic trees generated could be grouped into two topologies in which *Mastomys* was either monophyletic or paraphyletic. A cladistic and phenetic analysis of available allozymic data clearly showed, however, that *Mastomys* species form a closely related group and agreed with a monophyletic origin for this genus. Chromosomal evolution in *Mastomys* is characterized by seven different types of rearrangements, the most frequent being pericentric inversions. The latter also are involved in intraspecific, chromosomal polymorphisms suggesting that pericentric inversions are a recurrent event in the evolution of this genus. However, pericentric inversions modify the fundamental number, but not the diploid number, which is a criterion often used to identify the different species of *Mastomys.* These observations suggest the following pattern of chromosomal change in this genus. Rearrangements modifying the diploid number occurred at the same time as major speciation events resulting in different diploid numbers for each species whereas subsequent divergence of karyotypes proceeded mainly by accumulation of pericentric inversions.

Key words: chromosomes, evolution, phylogeny, *Mastomys,* African multimammate rats

The study of chromosomal evolution has shown that the amount and type of chromosomal modifications vary greatly among taxa (Koop et al., 1984). In some instances, karyotypic change has taken place so rapidly that it may be accompanied by little morphological or genic differentiation (Baverstock and Adams, 1987; Meester, 1988). In these cases, chromosomal analysis remains the most reliable method for correct assignment of species. Multimammate rats of the genus *Mastomys* are no exception because various morphologically similar species have been described throughout sub-Saharan Africa. This slight morphological divergence is also evidenced in East African fossil lineages dating back 3.6×10^6 years ago, which show slow rates of morphological change (Denys and Jaeger, 1986). The taxonomic relationships of species of multimammate rats have been solved in part through the use of chromosomal techniques that have identified reproductively isolated species by their diploid numbers: *Mastomys erythroleucus* (2n = 38—Hubert et al., 1983; Matthey, 1965; Petter, 1977), *Mastomys coucha* (2n = 36—Green et al., 1980; Matthey, 1966*a*) and *Mastomys natalensis* (2n = 32—Green et al., 1980; Hallett, 1979). More recently, an



additional species with 32 chromosomes was identified in Senegal, *Mastomys huberti,* characterized by a different fundamental number (Duplantier et al., 1990*a*; Viegas-Pequignot et al., 1983).

Considerable debate has involved the taxonomic definition and diagnosis of species in this genus. The low level of morphological differentiation among these rodents and representatives of other African genera such as *Praomys, Hylomyscus, Myomys,* and *Myomyscus* has led certain authors to group *Mastomys* and the latter taxa within the genera *Epimys* (Thomas, 1915), *Rattus* (Ellerman, 1941), or *Praomys* (Davis, 1962; Honacki et al., 1982; Misonne, 1969, 1971; Nowak and Paradiso, 1983). Recently, Qumsiyeh et al. (1990) questioned the validity of the genus *Mastomys* on the basis of a chromosomal phylogenetic study of *Praomys* and *Mastomys.* Conversely, an increasing number of researchers recognize *Mastomys* as a distinct genus (Ansell and Dowsett, 1988; Duplantier, 1988; Happold, 1988; Meester et al., 1986; Misonne, 1969, 1971; Nowak, 1991; Petter, 1957; Robbins and Van Der Straeten, 1989; Rosevear, 1969; Van Der Straeten, 1979; Wilson and Reeder, 1993).

The purpose of the present study was to determine the taxonomic relationships among species of *Mastomys* and related genera and the evolutionary consequences of chromosomal variation within this genus. A previous report presented the standard karyotypes of three species of *Mastomys* (*M. erythroleucus, M. huberti,* and *M. natalensis*) and described the intraspecific chromosomal polymorphism observed in Senegal (Duplantier et al., 1990*a*). The present study extends this karyological analysis to G-, C-, and NOR (nuclear organizer region)-banding of these and additional specimens as well as of individuals from a breeding colony of *M. coucha.* Phylogenetic relationships were investigated using *Praomys tullbergi* and *Myomys daltoni* as the related species and European murids as the outgroup.

Materials and Methods

Metaphase spreads were prepared from bone-marrow cells of yeast-stimulated (Lee and Elder, 1980) individuals (Appendix I) using the air-drying technique (Evans et al., 1963) and stored at −20°C in fixative. G-banding was performed on slides aged overnight at 45°C following the method of Seabright (1971). C-banding and NOR-staining were performed on G-banded slides following Sumner (1972) and Howell and Black (1980), respectively. Several G- and C-banded and NOR-stained metaphase spreads were photographed for each individual and karyotypes were mounted by pairing photographs of chromosomes according to their banding patterns.

Presumptive chromosomal homology of G-banding patterns was identified for 15 pairs of autosomes and for the X chromosome by visually comparing band sequences within species, among species and among genera. The chromosomes of *Mastomys huberti* were used as the reference in the phylogenetic analysis. Each chromosome was regarded as a character within which the chromosomal forms observed represented different states. Polarity of chromosomal change was established by comparison with the karyotypes of the European genera used as outgroups. Heterochromatic alterations except those involving the X chromosome also were included in the phylogenetic analysis. In species showing chromosomal polymorphisms, only the most common chromosomal state was chosen as representative of the species, because most of the polymorphisms involved unique derived states.

Phylogenetic analyses were conducted using the computer program PHYLIP (Felsenstein, 1982, 1985). Chromosomal character states were ordered when possible. Different assumptions of karyotypic evolution were tested by using four parsimony methods: Dollo; Camin-Sokal; Dollop; mixed Camin-Sokal and Wagner. The programs used were Dolpenny (for Dollo and Dollop), Penny (for Camin-Sokal) and Mix (for mixed Camin-Sokal and Wagner). The cladistic allozymic analysis was based on data from Iskandar and Bonhomme (1984), who studied 10 loci by sequential electrophoresis. Each allele was considered as a character with two states (presence or absence) yielding a total of 25 character states. Character-state changes were coded as unordered. Phylogenetic trees were generated using Dollo's parsimony criterion favoring re-

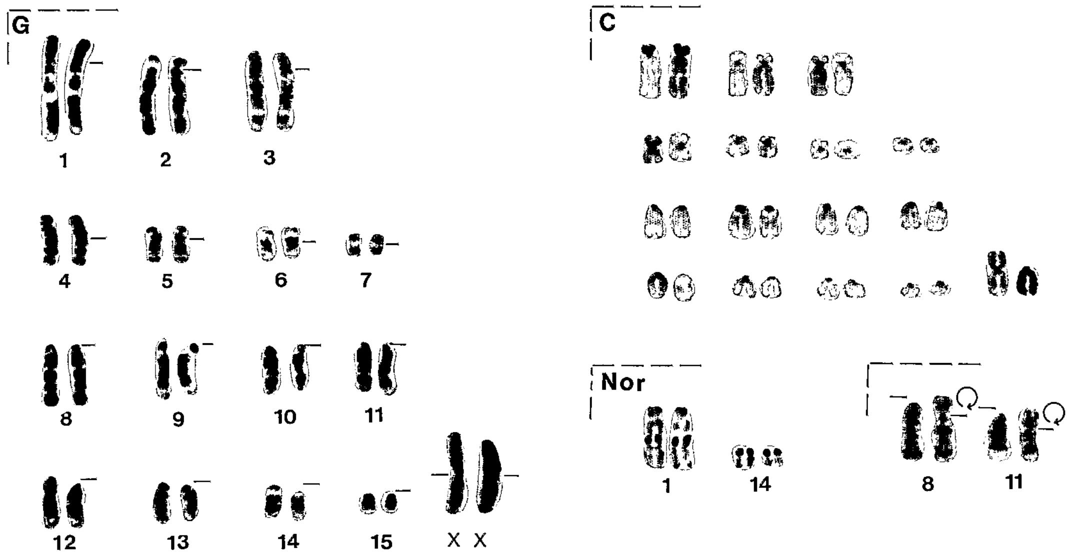


FIG. 1.—Karyotype of *Mastomys huberti*: 2n = 32; autosomal FN = 44. G-banding, C-banding, NOR (nuclear organizer region)-bearing chromosomes, and chromosomes involved in pericentric inversions. Dashes indicate position of centromere.

versals to ancestral states over multiple events. Outgroup species were the same as in the chromosomal analysis. The phenetic trees (unweighted pair-group method using arithmetic average) were produced from allelic frequencies at 12 loci (data from Duplantier et al., 1990*b*, and Iskandar and Bonhomme, 1984) with the computer program BIOSYS-1 (Swofford and Selander, 1981).

RESULTS

Intraspecific chromosomal variability.—Thirty-one *M. huberti* that were examined displayed a diploid number of 32 (Duplantier et al., 1990*a*). The autosomal fundamental number, however, varied from 44 to 46. G-banded karyotypes (Fig. 1) indicated that the variability resulted from pericentric inversions involving chromosome pairs 8 and 11, in which the acrocentric forms were the most widespread. C-banding (Fig. 1) revealed that all chromosome pairs carried pericentromeric heterochromatin and that the short arm of chromosome 1 was entirely heterochromatic. Silver-stained NORs were located interstitially in chromosome pair 1 and proximally in chromosome pair 14 (Fig. 1).

Twenty-six *M. natalensis* yielded a diploid number of 32. Chromosomal polymorphism involved variation in autosomal fundamental number from 54 to 52 due to a pericentric inversion on chromosome 14 with the metacentric form being the most widespread. A block of pericentromeric heterochromatin was present in the metacentric form but absent in the acrocentric one (Fig. 2). C-banding of karyotypes revealed pericentromeric heterochromatin on all chromosomes. The short arms of three submetacentric chromosomes (pairs 1, 2, and 6) were entirely heterochromatic (Fig. 2). Variant forms (deletion or addition of heterochromatin) were found for two of these chromosome pairs (1 and 6). Two chromosome pairs exhibited NORs that were either proximal (pair 13) or interstitial (pair 3).

Karyotypes of 46 *M. erythroleucus* showed a diploid number of 38 chromosomes except for four rats that were mosaics (Duplantier et al., 1990*a*). Chromo-

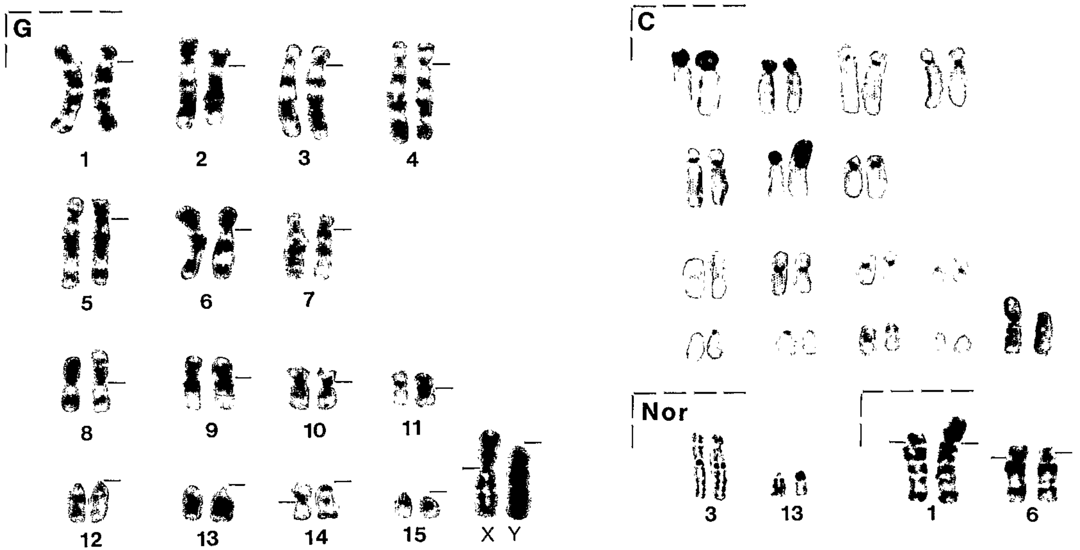


FIG. 2.—Karyotype of *Mastomys natalensis*: 2n = 32; autosomal FN = 53. G-banding, C-banding, NOR (nuclear organizer region)-bearing chromosomes, and chromosomes 1 and 6 showing variation in heterochromatin content of the short arms. The pericentric inversion on chromosome 14 is shown both on the G- and the C-banded karyotype. Dashes indicate position of centromere.

somal polymorphism in autosomal fundamental number was due to pericentric inversions in chromosome pairs 2 and 9 (Fig. 3), resulting in autosomal fundamental numbers ranging from 51 to 54. C-banding revealed pericentromeric heterochromatin on all autosomes. NORs were present on six pairs of chromosomes (Fig. 3) and were

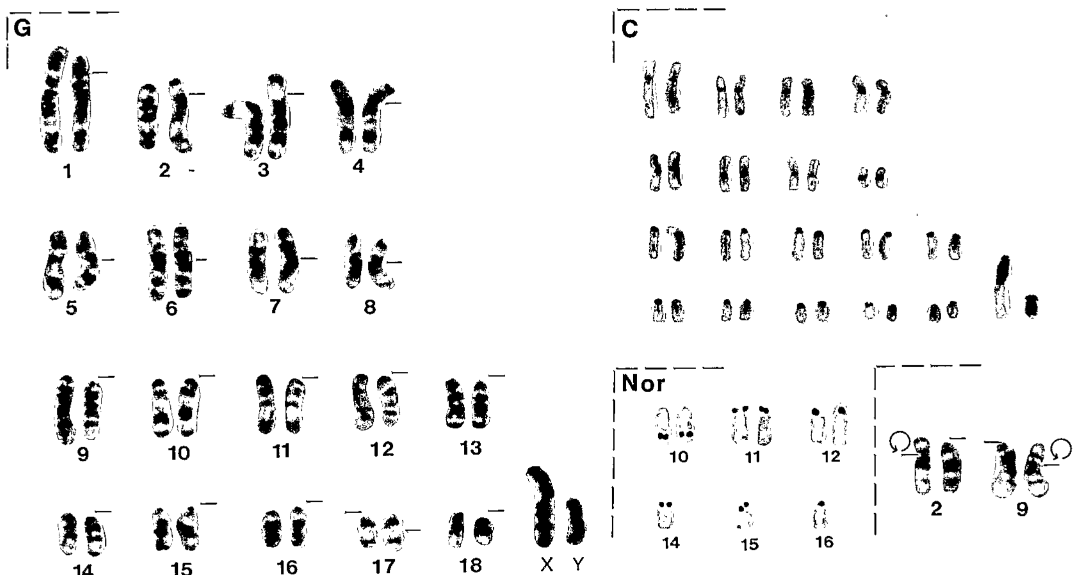


FIG. 3.—Karyotype of *Mastomys erythroleucus*: 2n = 38; autosomal FN = 52. G-banding, C-banding, NOR (nuclear organizer region)-bearing chromosomes, and chromosomes involved in pericentric inversions. Dashes indicate position of centromere.

pericentromeric for five of them (chromosomes 11, 12, 14, 15, and 16) and peritelomeric on chromosome pair 10.

Chromosomal rearrangements.—Homologous chromosomes or chromosomal arms for 16 chromosomes could be recognized (Fig. 4). Homology with chromosomes or chromosomal segments of the outgroup species was established for 13 of these, so that ancestral states for these chromosomes could be identified (Table 1). A problem arose in determining the polarity for chromosome 1 in *M. erythroleucus,* which lacks the tandem fusion. The ancestral morphotype present in this species was considered a derived character produced by fission on the basis of the distribution of NORs (Fig. 4). Thirty-three events were determined representing 34 rearrangements due to the multiple event occurring on chromosome 2 (Table 2). A total of seven different types of rearrangements was observed, of which pericentric inversions were by far the most frequent (16 of 34; Table 2).

Phylogenetic trees.—As with other types of data, problems in establishing chromosomal phylogenies may arise due to homoplasy of chromosomal rearrangements caused by higher rates of chromosomal mutation at certain breakpoints (pericentric inversions; Baker et al., 1987), higher fixation rates resulting from their lower meiotic disadvantage or simply limitation in G-band resolution (Robertsonian fusions or fissions; Qumsiyeh, 1989; Qumsiyeh et al., 1987). For these reasons, four methods based on different assumptions of chromosomal change were used in the cladistic analysis: reversals are more probable than recurrence of derived states; multiple events are more probable than reversals to the ancestral state; retention of polymorphisms is allowed; multiple events are favored for all characters except those for which the ancestral state is not known (characters 7, 9, and 15; Table 2) in which case a forward change or a reversion are equally probable (mixed method).

Using these four parsimony methods, eight trees were produced representing four topologies (Fig. 5), one of which was common to all methods (type I). In two of the remaining trees, the position of *M. erythroleucus* relative to that of *M. coucha* is switched around (types II and III), while the last one (type IV) clustered *M. erythroleucus* with the *Myomys-Praomys* complex. The number of steps involved in generating the trees varies from 37 to 40 according to the method (Fig. 5). This indicates that at least four and at the most seven homoplastic events (reversal-multiple events) or polymorphisms need to be postulated, which yield a level of homoplasy between 13 and 21%. The homoplastic events common to all trees involve two tandem fusions (chromosomes 1 and 8) and two pericentric inversions (chromosomes 9 and 11). The additional events specific to some of the tree topologies concern two pericentric inversions (chromosomes 3 and 4) and the multiple event on chromosome 2 (fusion and paracentric inversion).

Discussion

Chromosomal phylogeny of Mastomys.—In an attempt to solve the taxonomic status of species of *Mastomys,* chromosomal phylogenies were generated using a cladistic approach. Different assumptions of homoplasy yielded from one to three equally parsimonious trees. When reversals are favored, a unique tree is produced (Fig. 5a) involving the lowest number of steps and only one reversal for each of the four characters. Conversely, when retention of polymorphism is assumed, the three trees produced all postulate that two tandem fusions remain polymorphic through one or two ancestral nodes (Figs. 5b, 5c, and 5d). This is highly unlikely in view of what is known of the meiotic disadvantage they incur when in the heterozygous state (White, 1973). This also is true for the multiple event on chromosome 2 (fusion and paracentric inversion), which appears polymorphic in tree d. The method that favors multiple events indicates that the same tandem

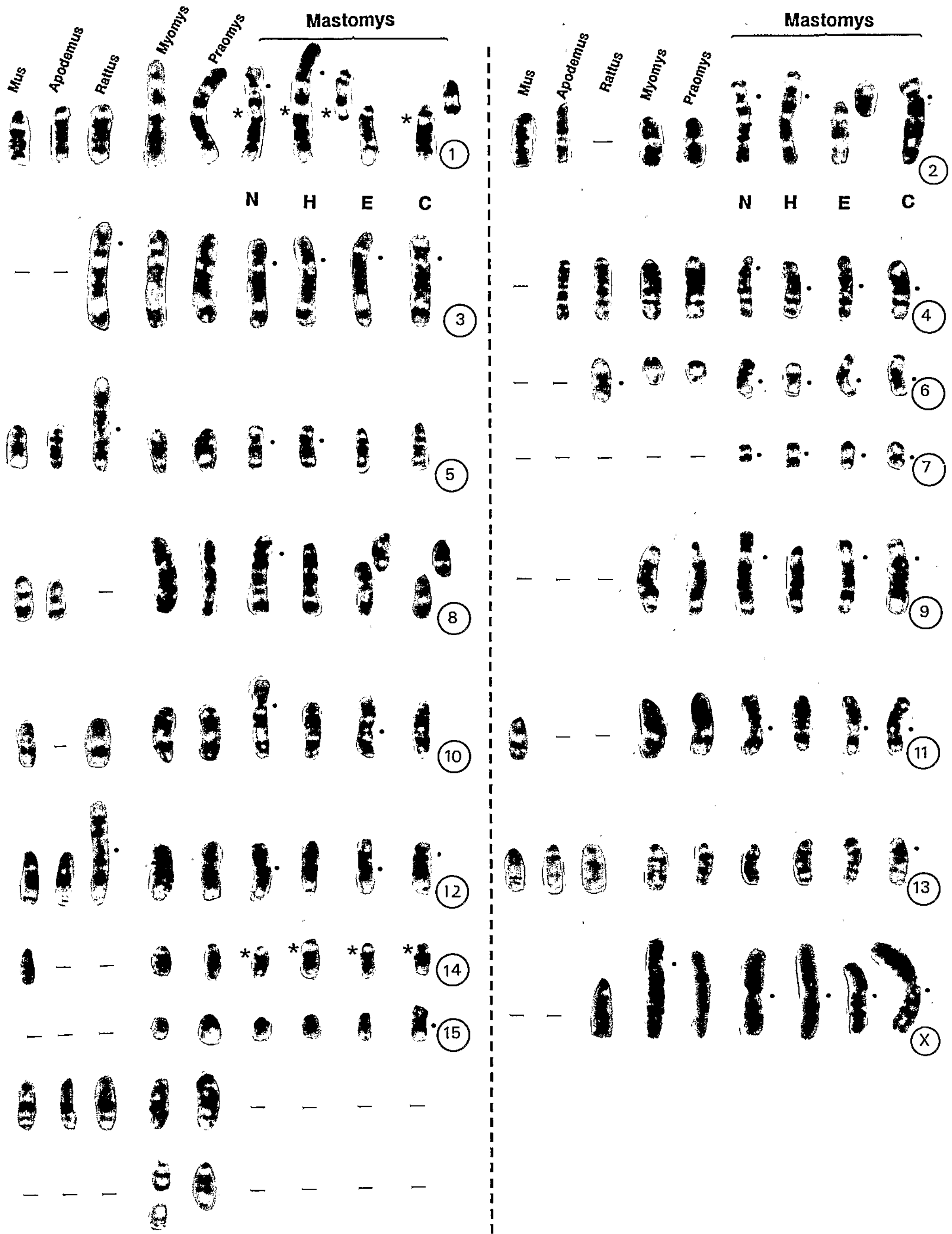


FIG. 4.—Homology of G-banded chromosomes in the species studied: Mus = *Mus musculus domesticus*; Apodemus = *Apodemus sylvaticus*; Rattus = *Rattus rattus*; Myomys = *Myomys daltoni*; Praomys = *Praomys tullbergi*; N = *Mastomys natalensis*; H = *Mastomys huberti*; E = *Mastomys erythroleucus*; and C = *Mastomys coucha*. The 15 autosomal pairs and the X chromosome of *M. huberti* are used as the reference chromosomes. Dots indicate the position of the centromere in other than acrocentric forms; stars refer to the location of nuclear organizer regions when present on homologous chromosomes in several species.

TABLE 1.—*Homology of the 15 chromosomes of* Mastomys huberti *used as the reference to the chromosome or chromosome arms in the other species. The X chromosome is not included. Chromosome numbers refer to those presented in Figs. 1–3 for* M. huberti, Mastomys natalensis *and* Mastomys erythroleucus *to that in Lee and Martin (1980) for* Mastomys coucha, *in Viegas-Pequignot et al. (1983) for* Myomys daltoni *(chromosomes were identified by reversing their R-banding), to the official nomenclature (Committee on Standardized Genetic Nomenclature for Mice, 1972) for* Mus musculus domesticus *and to Baverstock et al. (1983) for* Rattus rattus.

Mastomys huberti	*Mastomys natalensis*	*Mastomys erythroleucus*	*Mastomys coucha*	*Myomys daltoni*	*Praomys tullbergi*	*Mus musculus domesticus*	*Rattus rattus*	*Apodemus sylvaticus*
1	3	9 and 10	7 and 12	1	1	2	3	6
2	4	2 and 14	1	10	8	3		4
3	5	1	2	2	2		1	
4	7	6	14	6	6		4	2
5	10	13	10	12	10	15	7 (5.7)	9
6	11	8	16	16	15		15	
7	14	17	17					
8	1	11 and 15	9 and 11	3	3	14		19
9	2	3	3	5	4			
10	6	5	8	8	5	9	8	7
11	8	4	13	7	7	13		
12	9	7	4	4	9	4	5 (5.7)	3
13	12	12	5	11	13	11	10	10
14	13	16	6	13	14	18		
15	15	18	15	15	16			
				9	11	12	6	5
				14 and 17				
					12			

fusions have to be derived three times (Fig. 5e), which is considered as less probable than having been derived twice as shown in tree f. The mixed method reduces the number of steps by one compared to the former trees, but implies that either the two tandem fusions are derived three times or that the multiple event on chromosome 2 occurs twice, both of these assumptions being highly unlikely. On the basis of these considerations, the six trees that imply fewer probable homoplastic events are not taken into account in favor of the two remaining ones (Figs. 5a and 5f). These two trees provide different phylogenetic arrangements of species of *Mastomys*. The first one (Fig. 5a) clusters all *Mastomys* in one group separate from the *Myomys-Praomys* suggesting that the former genus is monophyletic. In the second one (Fig. 5f), the branching order includes *Mastomys erythroleucus* in the *Myomys-Praomys* branch indicating that *Mastomys* is a paraphyletic group. In both cases, however, *Mastomys huberti* and *Mastomys natalensis* are always the most closely related species and are further related to *Mastomys coucha.*

The information provided by the chromosomal phylogenies presented here does not provide a clear solution to the taxonomic status of *Mastomys*. To choose between the two topologies solely on the basis of strict parsimony (37 versus 40 steps) does not seem a valid argument in regard to recent work (Baker et al., 1987; Qumsiyeh et al., 1987). A more interesting approach, which has been suggested by several authors (Baverstock and Adams, 1987; Qumsiyeh, 1989; Qumsiyeh et al., 1987), is to confront the chromosomal phylogenies with independent datasets to obtain a more reli-

TABLE 2.—*Polarity of chromosomal rearrangements using the 15 pairs of autosomes and the X chromosome of* Mastomys huberti *as the reference chromosomes.*

Chromosome	Character-state changes[a]	Type of chromosomal rearrangement
1	0+?:1	Tandem fusion
	1:2	Heterochromatic addition
	1:3	Pericentric inversion
	1:4	Fission
2	0:1	Euchromatic deletion
	0:2	Paracentric inversion
	2:3	Centric fusion + paracentric inversion
3	0:1	Pericentric inversion
	0:2	Pericentric inversion
4	0:2	Pericentric inversion
	2:1	Pericentric inversion
5	0:1	Pericentric inversion
6	0:1	Fission
7	1:-:2	Pericentric inversion
8	0+?:1	Tandem fusion
	1:2	Heterochromatic addition
	1:3	Fission
9	1:-:2	Pericentric inversion
	1:3	Heterochromatic addition
10	0+?:1	Tandem fusion
	1:2	Heterochromatic addition
	1:3	Pericentric inversion
11	0+?:1	Tandem fusion
	1:2	Pericentric inversion
12	0:1	Pericentric inversion
	0:2	Pericentric inversion
	0:3	Pericentric inversion
13	0:1	Pericentric inversion
14	0:1	Pericentric inversion
15	1:-:2	Centric fusion or centric fission
X	0:1	Heterochromatic addition
	1:2	Pericentric inversion
	1:3	Pericentric inversion

[a] Numbers 1–4 refer to chromosomal states; the form to the right of the colon derives from the form to the left of the colon. When states are separated by ":-:," there is no polarity. When present, 0 represents the ancestral state.

able estimate of the evolutionary relationships among species.

Two allozymic studies are available for these African rats that investigate the relationship of *Mastomys erythroleucus* to both the *Myomys-Praomys* group and the other *Mastomys*. The first of these studies dealt with the analysis of 10 loci by sequential electrophoresis in which three species of *Praomys* were compared to *Myomys daltoni* and *Mastomys erythroleucus* (data from Iskandar and Bonhomme, 1984). These data were used to undertake a cladistic analysis. Two equally parsimonious tree topologies (26 steps) were generated by this method differing only by the relative positions of *Myomys daltoni* and *Praomys lukolelae,* which could be switched around. However, both cladograms (only one presented here, Fig. 6a) showed that *Mastomys erythroleucus* does not form a cluster with species of *Myomys* or *Praomys.* The second analysis was performed by Duplantier et al. (1990*b*) who investigated the extent of genic divergence at 20 loci among species of *Mastomys* in Senegal. They showed that *M. erythroleucus, M. huberti,* and *M. natalensis* were similar to each other, there being no fixed allelic differences among species. Both sets of allozymic data were reanalyzed using the 12 loci common to both studies. The two phenograms (Fig. 6b) clearly showed that *M. huberti* and *M. natalensis* are more closely related to *M. erythroleucus* than the latter is to *Praomys* and *Myomys.* Further support for the close relatedness of the four species of *Mastomys* is provided by DNA-DNA-hybridization data on the same set of species including *M. coucha* (Chevret et al., in press). These results favor *Mastomys* as a monophyletic group. This is not compatible with the topology of the phylogenetic tree in which *Mastomys* appears as a paraphyletic group (Fig. 5f).

The most plausible chromosomal phylogeny, thus, appears to be the one proposed by Fig. 5a, which suggests that four reversals have occurred. The ancestral node of these African murids is characterized by four tandem fusions and the addition of heterochromatin on the X chromosome, which are derived characters specific to this group (Fig. 7a). Pericentric inversions, the most frequent events, are almost entirely limited to the *Mastomys* branch of the tree throughout which they are evenly distributed. Pericentric inversions also are the most common

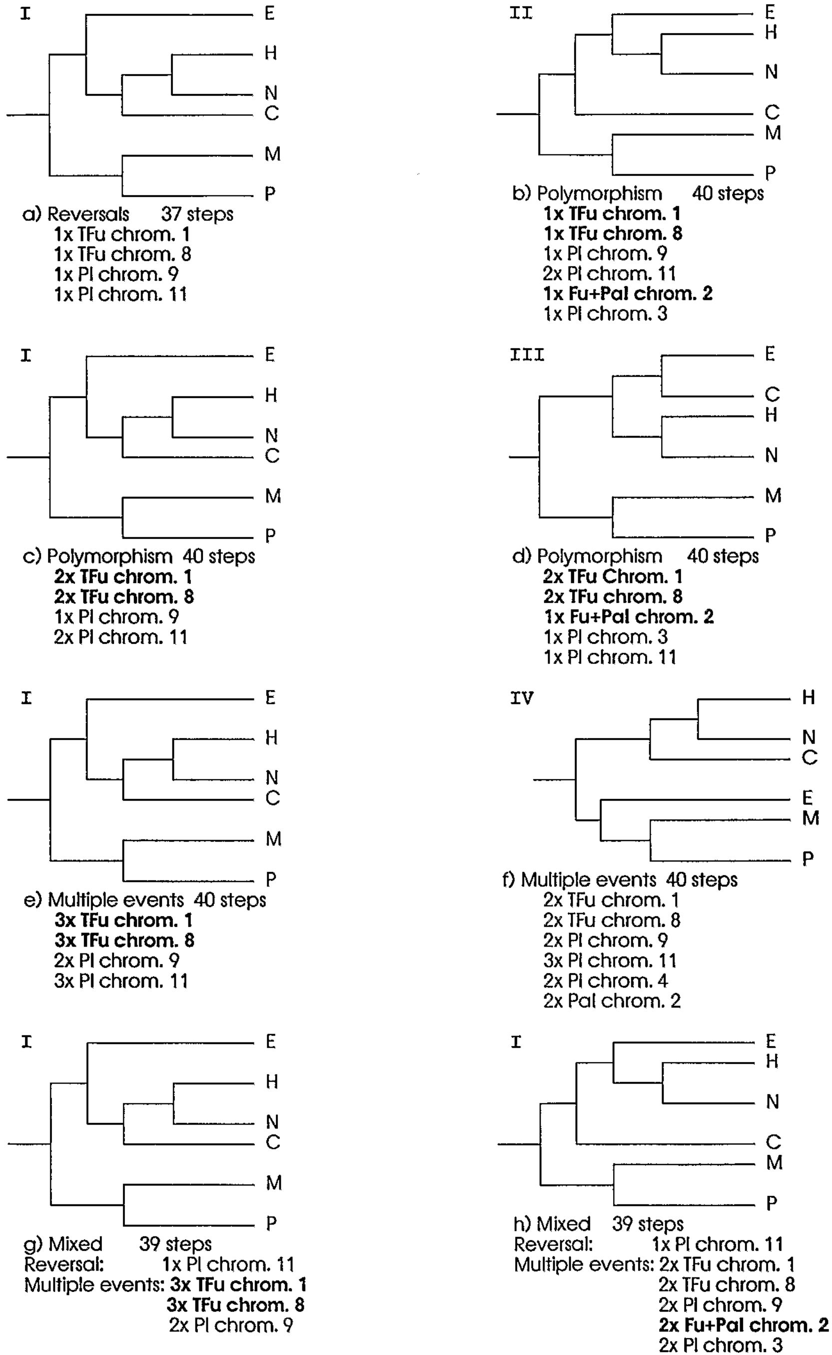


FIG. 5.—Phylogenetic trees produced by four different programs in the PHYLIP package (see text for explanation). The homoplastic events inferred by each program are shown below the trees, which are rooted by the outgroups. I to IV indicate the different tree topologies. TFU = tandem fusion; PI = pericentric inversion; Pal = paracentric inversion; FU = centric fusion. E = *Mastomys erythroleucus*; H = *Mastomys huberti*; N = *Mastomys natalensis*; C = *Mastomys coucha*; M = *Myomys daltoni*; P = *Praomys tullbergi.*

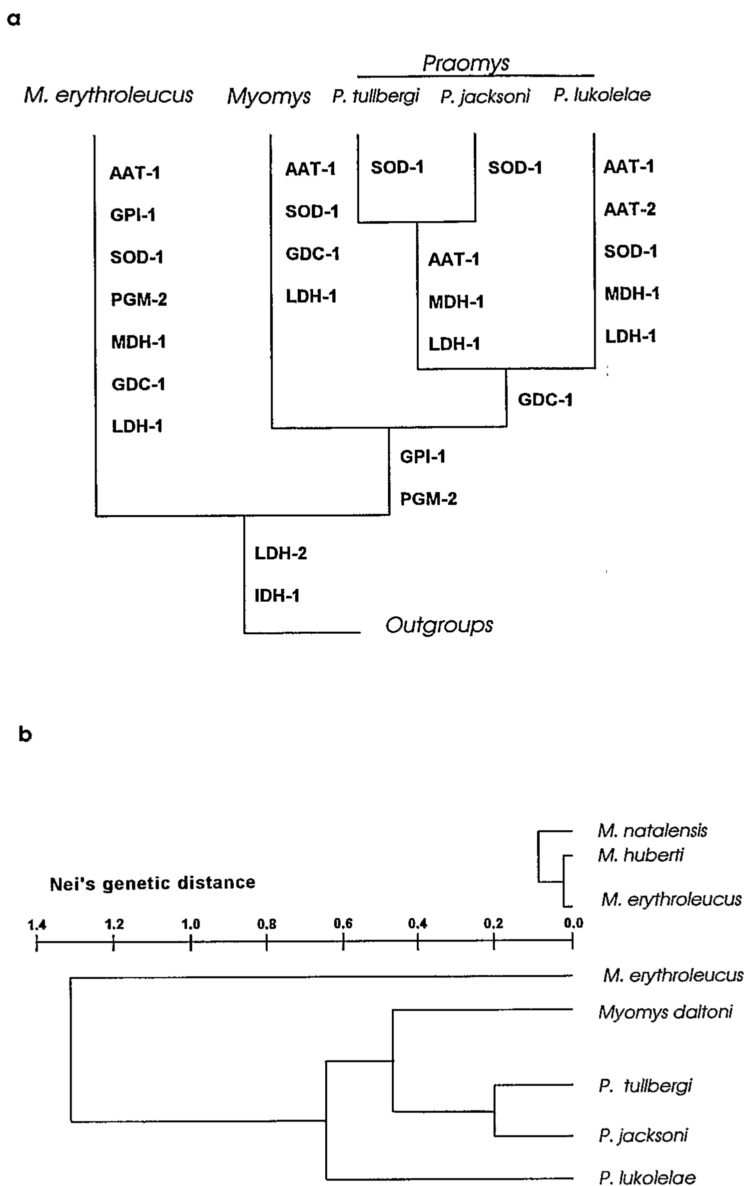


FIG. 6.—Genic relationships between African rats. a) Cladistic analysis using the computer program PHYLIP based on 10 loci analyzed by sequential electrophoresis (from Iskandar and Bonhomme, 1984); the tree is rooted by the same outgroup species as in the chromosomal analysis, *Mus musculus domesticus, Apodemus sylvaticus,* and *Rattus rattus.* Gain of alleles is indicated along the branches by the loci at which they occur. AAT = aminoaspartate transaminase; GPI = glucose phosphate isomerase; SOD = superoxide dismutase; PGM = phosphoglucomutase; MDH = NAD-malate dehydrogenase; GDC = glycerophosphate dehydrogenase; LDH = lactate dehydrogenase; IDH = isocitrate dehydrogenase. Myomys = *M. daltoni.* b) Phenograms from the unweighted pair-group method using arithmetic average and the computer program BIOSYS-1. Both trees are generated from distance data for the same set of 12 loci (Duplantier et al., 1990*b*; Iskandar and Bonhomme, 1984: nine sequentially and three conventionally analyzed loci): AAT-1; AAT-2; GDC-1; IDH-1; IDH-2; LDH-1; LDH-2; MDH-1; MDH-2; PGD-1; PGM-2; SOD-1.

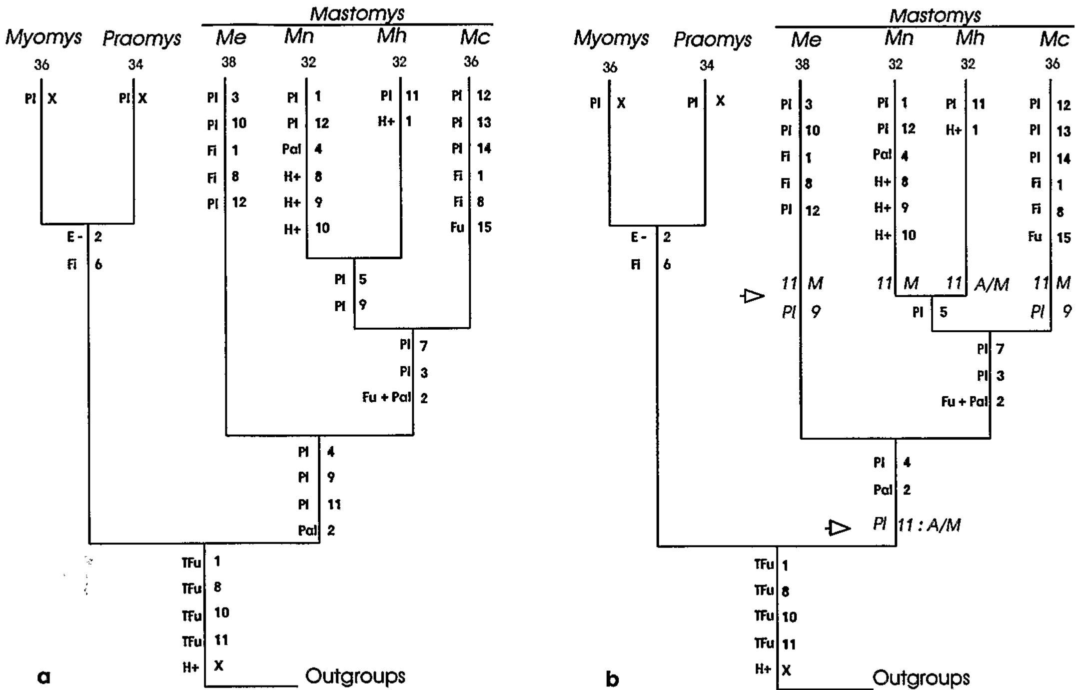


FIG. 7.—Chromosomal phylogenies of the African murids. The different events as well as the chromosomes they affect are indicated. a) Same tree as in Fig. 5a; b) tree modified by assuming independently derived pericentric inversions for chromosome 9 and retention of polymorphism for chromosome 11. PI = pericentric inversion; E− = euchromatin deletion; TFu = tandem fusion; H^+ = heterochromatin addition; Pal = paracentric inversion; Fu = centric fusion; Fi = centric fission; M = metacentric; A = acrocentric. Me = *Mastomys erythroleucus*; Mn = *Mastomys natalensis*; Mh = *Mastomys huberti*; Mc = *Mastomys coucha.*

chromosomal rearrangement separating species, although they never occur alone.

The phylogenetic relationships described by this method postulate that homoplasy has involved only reversals. Using information on chromosomal polymorphism in populations from Senegal, it is possible to propose alternate types of homoplasy (Fig. 7b). The metacentric form of chromosome 9, which appeared by pericentric inversion in the node leading to *Mastomys,* is shared by *M. erythroleucus* and *M. coucha.* However, the homologous chromosome in *M. coucha* carries NORs whereas that in *M. erythroleucus* does not. This suggests that the same morphotype of chromosome 9 in *M. erythroleucus* and *M. coucha* may in fact result from two independent pericentric inversions. Similarly, chromosome 11 exists in a metacentric and an acrocentric form produced by pericentric inversion. The fact that this chromosome is polymorphic in *M. huberti* from Senegal indicates that the initial metacentric form may have been maintained as a polymorphism with fixation of the metacentric form in *M. erythroleucus, M. coucha,* and *M. natalensis* and persistence of the polymorphism in *M. huberti.* These modifications of the nature of the homoplasy do not alter the branching order nor the number of steps necessary to construct the phylogeny but integrate data on the chromosomal patterns of the extant species.

Chromosomal rearrangements and evolutionary consequences.—Although species

of *Mastomys* are classically distinguished by their diploid number, most of the intraspecific polymorphism observed in Senegal involves pericentric inversions. On a more widespread scale, numerous reports of variation in fundamental number throughout Africa have been published by different authors (Capanna et al., 1982; Duplantier et al., 1990*a*; Hallett, 1979; Lee and Martin, 1980; Lyons et al., 1980; Matthey, 1966*a*, 1966*b*, 1970; Orlov and Bulatova, 1991), and this is particularly true for *M. erythroleucus* (Hubert et al., 1983; Kràl, 1971; Matthey, 1965, 1967; Orlov et al., 1989; Tranier, 1974; Viegas-Pequignot et al., 1987). In most cases, unfortunately, these studies are based on standard staining procedures, so no accurate knowledge of all the rearrangements involved are available. Pericentric inversions appear as a recurrent event in the chromosomal evolution of *Mastomys*. However, pericentric inversions will change the fundamental number, but not the diploid number, and so may not account for the apparent differentiation in chromosome number among species. These data then suggest the following pattern of chromosomal change in this genus: first, events modifying the diploid number (fusions-fissions) have occurred at the same time as the major speciation events resulting in a different diploid number for each species; second, within each diploid form, chromosomal diversification has proceeded for the most part by changes in fundamental number, mainly due to pericentric inversions. This propensity to accumulate pericentric inversions has resulted in local (*M. erythroleucus*) or widespread (*M. natalensis*) polymorphisms. If this were the case, we would expect species with the same diploid number to be more closely related to each other than to species differing by diploid number. Analysis of the chromosomal phylogeny shows that this may be the case, because *M. huberti* and *M. natalensis,* which share the same diploid number, also are those that are the most closely related. Additional data on morphology and life history also argue for the relatedness of these two species (Duplantier, 1988), although the mean genetic distances do not. However, the latter need to be confirmed because only one geographically marginal sample of *M. natalensis* was studied (Duplantier et al., 1990*b*).

Although fusion-fission rearrangements could be mapped to cladogenic events and pericentric inversions to diversification of karyotypes, confirmation of the evolutionary implication of these rearrangements relies on information of their selective meiotic effect (King, 1987; Patton and Sherwood, 1983; Sites and Moritz, 1987), which is not available at the present for *Mastomys.* To verify the hypothesis concerning the mode of chromosomal evolution in *Mastomys,* additional samples from other regions in Africa need to be analyzed karyotypically to determine the nature of the chromosomal differentiation and genically to assess their taxonomic status.

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LITERATURE CITED

ANSELL, W. S. H., AND R. J. DOWSETT. 1988. Mammals of Malawi. Tendrine Press, Cornwall, United Kingdom, 224 pp.

BAKER, R. J., M. B. QUMSIYEH, AND C. S. HOOD. 1987. Role of chromosomal banding patterns in understanding mammalian evolution. Current Mammalogy, 1:67–96.

BAVERSTOCK, P. R., AND M. ADAMS. 1987. Comparative rates of molecular, chromosomal, and morphological evolution in some Australian vertebrates. Pp. 175–188, *in* Rates of evolution (K. S. W. Campbell and M. F. Day, eds.). Allen and Unwin, London, United Kingdom, 314 pp.

BAVERSTOCK, P. R., M. GELDER, AND A. JAHNKE. 1983. Chromosome evolution in Australian *Rattus*. G-banding and hybrid meiosis. Genetica, 60:93–103.

CAPANNA, E., M. V. CIVITELLI, AND A. CERASO. 1982. Karyotypes of Somalian rodent populations. 3. *Mastomys huberti* (Wroughton, 1908) (Mammalia Rodentia). Monitore Zoologico Italiano, 16:141–152.

CHEVRET, P., L. GRANJON, J.-M. DUPLANTIER, C. DENYS, AND F. M. CATZEFLIS. In press. Molecular phylogeny of the *Praomys* complex (Rodentia, Murinae): a study based on DNA/DNA hybridization experiments. Zoological Journal of the Linnean Society.

COMMITTEE ON STANDARDIZED GENETIC NOMENCLATURE FOR MICE. 1972. Standard karyotype of the mouse, *Mus musculus*. Journal of Heredity, 63:69–72.

DAVIS, D. H. S. 1962. Distribution patterns of southern African Muridae with notes on some of their fossil antecedents. Annals of the Cape Province Museum, 2:56–76.

DENYS, C., AND J.-J. JAEGER. 1986. A biostratigraphic problem: the case of the East-African Plio-Pleistocene rodent faunas. Modern Geology, 10:215–233.

DUPLANTIER, J.-M. 1988. Biologie évolutive de populations du genre *Mastomys* (rongeur, muridé) au Sénégal. Ph.D. dissert., Université Montpellier II, Montpellier, France, 215 pp.

DUPLANTIER, J.-M., J. BRITTON-DAVIDIAN, AND L. GRANJON. 1990*a*. Chromosomal characterization of three species of the genus *Mastomys* in Senegal. Zeitschrift für zoologische Systematik und Evolutionsforschung, 28:289–298.

DUPLANTIER, J.-M., L. GRANJON, E. MATHIEU, AND F. BONHOMME. 1990*b*. Structures génétiques comparées de trois espèces de rongeurs africains du genre *Mastomys* au Sénégal. Genetica, 81:179–192.

ELLERMAN, J. R. 1941. The families and genera of living rodents. Muridae. Trustees of the British Museum (Natural History), London, United Kingdom, 2:1–690.

EVANS, E. P., G. BRECKON, AND C. E. FORD. 1963. An air-drying method for meiotic preparations from mammalian testes. Cytogenetics, 3:289–294.

FELSENSTEIN, J. 1982. Numerical methods for inferring evolutionary trees. The Quarterly Review of Biology, 57:379–404.

———. 1985. Phylogenies and the comparative method. The American Naturalist, 125:1–15.

GREEN, C. A., H. KEOGH, D. H. GORDON, M. PINTO, AND E. K. HARTWIG. 1980. The distribution, identification, and naming of the *Mastomys natalensis* species complex in southern Africa (Rodentia: Muridae). Journal of Zoology (London), 192:17–23.

HALLETT, J. M. 1979. Chromosome polymorphism in *Praomys* (*Mastomys*) *natalensis* in southern Africa: diploid studies. South African Journal of Science, 75:413–415.

HAPPOLD, D. C. D. 1988. Mammals of Nigeria. Oxford Science Publication, Clarendon Press, Oxford, United Kingdom, 402 pp.

HONACKI, J. H., K. E. KINMAN, AND J. W. KOEPPL (EDS.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc., and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.

HOWELL, W. M., AND D. A. BLACK. 1980. Controlled silver-staining of nucleolus organizer regions with a protective colloidal developer: a 1-step method. Experientia, 36:1014–1015.

HUBERT, B., A. MEYLAN, F. PETTER, A. POULET, AND M. TRANIER. 1983. Different species in genus *Mastomys* from western, central and southern Africa (Rodentia, Muridae). Annales du Musée Royal de l'Afrique Centrale (Sciences Zoologiques), 237: 143–148.

ISKANDAR, D., AND F. BONHOMME. 1984. Variabilité électrophorétique totale à 11 loci structuraux chez les rongeurs (Muridae, Rodentia). Canadian Journal of Genetics and Cytology, 26:622–627.

KING, M. 1987. Chromosomal rearrangements, speciation and the theoretical approach. Heredity, 59: 1–6.

KOOP, B. F., R. J. BAKER, M. W. HAIDUK, AND M. D. ENGSTROM. 1984. Cladistical analysis of primitive G-band sequences for the karyotype of the ancestor of the Cricetidae complex of rodents. Genetica, 64: 199–208.

KRÀL, B. 1971. Non-Robertsonian variability of karyotype in rats of the subgenus *Mastomys*. Zoologické Listy, 20:39–49.

LEE, M. R., AND F. F. B. ELDER. 1980. Yeast stimulation of bone marrow mitosis for cytogenetic investigations. Cytogenetics and Cell Genetics, 26:36–40.

LEE, M. R., AND L. K. MARTIN. 1980. *Mastomys* (=*Praomys*) *natalensis* is not a *Rattus* (Mammalia: Rodentia): karyological evidence. Cytogenetics and Cell Genetics, 28:95–103.

LYONS, N. F., D. H. GORDON, AND C. R. GREEN. 1980. G-banding chromosome analysis of species A of the *Mastomys natalensis* complex (Smith, 1834) (Rodentia, Muridae). Genetica, 54:209–212.

MATTHEY, R. 1965. Etudes de cytogénétique sur des muridés africains appartenant aux genres *Arvicanthis, Praomys, Acomys* et *Mastomys* (Rodentia). Mammalia, 29:228–249.

———. 1966*a*. Cytogénétique et taxonomie des rats appartenant au sous-genre *Mastomys* Thomas (Rodentia, Muridae). Mammalia, 30:105–119.

———. 1966*b*. Une inversion péricentrique à l'origine d'un polymorphisme chromosomique non-Robertsonien dans une population de *Mastomys* (Rodentia-Murinae). Chromosoma, 18:188–200.

———. 1967. Note sur la cytogénétique de quelques muridés africains. Mammalia, 31:281–287.

———. 1970. Caryotypes de muridés et dendromuridés originaires de République Centrafricaine. Mammalia, 34:459–466.

MEESTER, J. A. 1988. Chromosomal speciation in southern African small mammals. South African Journal of Science, 84:721–724.

MEESTER, J. A., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. Transvaal Museum Monographies, Pretoria, 5:1–359.

MISONNE, X. 1969. African and Indo-Australian Muridae, evolutionary trends. Annales du Musée Royal de l'Afrique Centrale (Sciences Zoologiques), 172: 1–219.

———. 1971. Part 6, Order Rodentia. Pp. 1–39, *in* The mammals of Africa. An identification manual,

Parts 1–15 (J. A. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D.C., 93 pp.

NOWAK, R. M. 1991. Walker's mammals of the world. Fifth ed. The Johns Hopkins University Press, Baltimore, Maryland, 1:1–642, 2:643–1629.

NOWAK, R. M., AND J. L. PARADISO. 1983. Walker's mammals of the world. Fourth ed. The John Hopkins University Press, Baltimore, Maryland, 1:1–568, 2: 569–1362.

ORLOV, V. N., AND N. S. BULATOVA. 1991. Intrageneric variations in structural heterochromatin of African rats (Rodentia: Muridae). Doklady Akademii Nauk SSSR, 288:996–998 (English translation).

ORLOV, V. N., N. S. BULATOVA, AND A. N. MILISHNIKOV. 1989. Karyotypes of some mammalian species (Insectivora, Rodentia) in Ethiopia. Pp. 93–109, *in* Collective scientific papers: ecological faunistic researches in south-western Ethiopia. Soviet M & B Committee, Moscow, Russia, 325 pp.

PATTON, J. L., AND S. W. SHERWOOD. 1983. Chromosome evolution and speciation in rodents. Annual Review of Ecology and Systematics, 14:139–158.

PETTER, F. 1957. Remarques sur la systématique des *Rattus* africains et description d'une forme nouvelle de l'Aïr. Mammalia, 11:125–132.

———. 1977. Les rats à mammelles multiples d'Afrique occidentale et centrale: *Mastomys erythroleucus* (Temminck 1853) et *Mastomys huberti* (Wroughton 1908). Mammalia, 41:441–444.

QUMSIYEH, M. B. 1989. Chromosomal fissions and phylogenetic hypothesis: cytogenetic and allozymic variation among species of Meriones (Rodentia: Gerbillidae). Occasional Papers, The Museum, Texas Tech University, 132:1–16.

QUMSIYEH, M. B., M. J. HAMILTON, AND D. A. SCHLITTER. 1987. Problems in using Robertsonian rearrangements in determining monophyly: examples from the genera *Tatera* and *Gerbillurus*. Cytogenetics and Cell Genetics, 44:198–208.

QUMSIYEH, M. B., ET AL. 1990. Chromosomal and protein evolution in morphogically similar species of *Praomys sensu lato* (Rodentia, Muridae). Journal of Heredity, 81:58–65.

ROBBINS, C. B., AND E. VAN DER STRAETEN. 1989. Comments on the systematics of *Mastomys* Thomas 1915 with the description of a new West African species. Senckenbergiana Biologica, 69:1–14.

ROSEVEAR, D. R. 1969. The rodents of West-Africa. British Museum, London, United Kingdom, 604 pp.

SEABRIGHT, M. 1971. A rapid banding technique for human chromosomes. Lancet, II:971.

SITES, J. W., AND C. MORITZ. 1987. Chromosomal evolution and speciation revisited. Systematic Zoology, 36:153–174.

SUMNER, A. T. 1972. A simple technique for demonstrating centromeric heterochromatin. Experimental Cell Research, 75:304–306.

SWOFFORD, D. L., AND R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. Journal of Heredity, 72:281–283.

THOMAS, O. 1915. List of mammals (exclusive of Ungulata) collected on the upper Congo by Dr. Christy for the Congo Museum, Tervuren. Annals and Magazine of Natural History, 16:465–481.

TRANIER, M. 1974. Parenté des *Mastomys* du Maroc et du Sénégal (rongeurs, muridés). Mammalia, 38: 558–560.

VAN DER STRAETEN, E. 1979. Biometrical relationship between *Praomys-Myomys-Mastomys* and *Myomyscus* (*Praomys* complex) (Mammalia, Muridae). African Small Mammal Newsletter, 3:27–30.

VIEGAS-PEQUIGNOT, E., B. DUTRILLAUX, M. PROD'HOMME, AND F. PETTER. 1983. Chromosomal phylogeny of Muridae: a study of 10 genera. Cytogenetics and Cell Genetics, 35:269–278.

VIEGAS-PEQUIGNOT, E., M. RICOUL, F. PETTER, AND B. DUTRILLAUX. 1987. Cytogenetic study of three forms of *Mastomys* (Rodentia, Muridae). Revista Brasileira de Genetica, 10:221–228.

WHITE, M. J. D. 1973. Animal cytology and evolution. Cambridge University Press, London, United Kingdom, 961 pp.

WILSON, D. E., AND D. M. REEDER. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution Press, Washington, D.C., 1206 pp.

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APPENDIX I

Specimens examined.—One-hundred three wild rats belonging to the three previously described species from Senegal, *M. erythroleucus, M. huberti* (sensu Petter, 1977), and *M. natalensis,* were karyotyped as well as a male and a female of *M. coucha* from a laboratory colony established from wild-caught material originally from South Africa. The species of *Mastomys* from Senegal with 2n = 32 (FN = 54) will be considered here as synonymous to the South African species *M. natalensis* owing to their similarity in G-banding. For outgroup comparisons, preparations of chromosomes were made from wild specimens of *Myomys daltoni* from Nema Nding, Senegal, *Praomys tullbergi* from Diattacounda, Senegal, *Mus musculus domesticus* from Cascina Bonola, Italy, *Rattus rattus* from Kabrousse, Senegal, and *Apodemus sylvaticus* from Carnon, France. The specimens of *Mastomys* for which skulls are deposited at the Muséum National d'Histoire Naturelle (Paris, France) are indicated in parenthesis: *M. huberti*—Dagana, 4 males (4); Diattacounda, 3 males (1); Gouk Island, 2 females (1); Ile aux Boeufs, 1 male (1), 1 female (1); Mbaouane, 1 male (1), 1 female (1); Casamance National Park, 4 males (4); Poutak Island, 2 males (2); Richard-Toll, 3 males (1), 3 females (2); Ibel, 1 male (1); Fa-

diga, 2 males (1), 3 females (3). *M. natalensis*—Bombou-Mandingue, 1 male (1), 1 female; Bransan, 1 male; Bafoundou, 1 male; Kedougou, 1 female (1); Ibel, 1 male; Fadiga, 9 males (7), 11 females (9). *M. erythroleucus*—Bombou-Peuhl, 1 male (1); Diattacounda, 1 male (1); Diboli, 3 females (1); Fadiga, 12 males (9), 9 females (9); Kabrousse, 1 male (1), 2 females (2); Kedougou, 2 males (2), 1 female (1); Madeleine Island, 3 males (2), 3 females (1); Missira, 1 male (1), 1 female (1); Niaga, 2 males (1), 1 female; Niakhar, 1 female (1); Palmarin, 1 female (1); Salemata, 1 male (1). Two fluid-preserved specimens of *M. coucha* (1 male, 1 female) are deposited at the Institut des Sciences de l'Evolution (Montpellier, France). The geographical position of the localities in Senegal are provided in Duplantier et al. (1990*a*).