PATTERNS OF CHROMOSOMAL VARIATION IN SOUTHERN AFRICAN RODENTS

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Mechanisms of chromosomal change, distribution patterns, extent of genotypic, phenotypic and ecological divergence, and nature and degree of reproductive isolation were reviewed in 10 chromosomally variable southern African rodent species and species complexes. Genetically similar peripatric or parapatric chromosome races freely interbreed (striped mice, *Rhabdomys pumilio*; vlei rats, *Otomys irroratus*), while genotypically or phenotypically divergent, sympatric sibling species (multimammate mice, *Mastomys natalensis–M. coucha*; tree rats, *Thallomys paedulcus–T. nigricauda*; red veld rats, *Aethomys chrysophilus–A. ineptus*) appear reproductively isolated, suggesting a correlation between genetic distance and onset of reproductive isolation. The allopatric gerbil species pair, *Tatera brantsii–T. afra,* shows little or no prezygotic reproductive isolation despite well-developed male-biased postzygotic isolation (i.e., Haldane effect) that may be associated with a rearrangement on the Y chromosome. Within the actively speciating vlei rat, *Otomys irroratus,* complex, despite widespread laboratory interbreeding between chromosome races, postzygotic isolation (virtual hybrid sterility) was demonstrated due to fixation of a tandem fusion rearrangement in the high-altitude (>1,400 m) A1 race. Both post- and prezygotic isolation have developed in the absence of significant measurable genotypic divergence at either the gene or the DNA level. Acquisition of reproductive isolation and incipient speciation in the vlei rat complex appears to be mediated by both chromosomal (postzygotic) and non-chromosomal (prezygotic) processes.

Key words: allozymes, chromosomal speciation, Cricetomyinae, Gerbillinae, Muridae, Murinae, Otomyinae, reproductive isolation, Rodentia, southern Africa

Many rodent species show a tendency for extensive chromosomal variability within species and species complexes, making them excellent models for understanding chromosomal evolution. Chromosomal evolution in rodents has been reviewed previously (King 1993; Patton and Sherwood 1983). The role of chromosomal change in speciation remains elusive and disputed, with various authors arguing for (Capanna 1982; King 1993; Meester 1988; White 1978) and against (Carson 1982; Coyne 1994; Paterson 1985; Patton and Sherwood 1983; Vrba 1985) a causal role for chromosomal change in speciation.

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In discussing chromosomal speciation in southern African small mammals, Meester (1988) proposed that multidisciplinary studies of chromosomally differentiated but phenotypically similar sibling species (chromospecies) should provide insight into the role of chromosomal change during early stages of speciation. This argument can be extended to include an even earlier stage of (potential) speciation represented by chromosomally polytypic species.

King (1993) postulated 2 requirements for establishing a relationship between chromosome change and speciation: evidence that derived chromosomal changes resulted in effective postzygotic reproduc-

tive isolation (i.e., a totally impermeable barrier to gene flow) and evidence that chromosomal change predated any other form of genetic differentiation. King (1993) assumed that data on genetic distance were sufficient to indicate order of speciation of linear series of chromosomally differentiated races and relative antiquity of successive radiations. Based on low genetic distances in numerous case studies involving chromosomally differentiated actively speciating complexes, King (1993) argued that chromosomally mediated speciation was prevalent in nature. Coyne (1994) criticized King's (1993) assumption that electrophoretically detectable genetic distance was a sufficient measure of genetic differentiation in the genes responsible for reproductive isolation, being more an indication of age of a speciation event; thus, data employing other measures of genetic relationship (e.g., PCR–RAPDs, microsatellites, DNA sequencing, and restriction fragment length polymorphism) were required wherever possible, as were direct measurements of degree of pre- and postzygotic reproductive isolation.

Recent studies, mostly subsequent to King's (1993) synthesis, have contributed new multidimensional data on evolution of chromosomally variable rodent species and species complexes in southern Africa (Chimimba 1997; Contrafatto 1996; Contrafatto et al. 1992a, 1992c, 1997; Dempster 1996; Dempster and Perrin 1991, 1994; Dempster et al. 1991, 1992, 1993, in litt.; Dippenaar et al. 1993; Filippucci et al. 1997; Gordon 1986, 1991; Honeycutt et al. 1987, 1991; Meester et al. 1992; Nevo et al. 1986; Njobe 1997; Qumsiyeh 1986; Qumsiyeh and Schlitter 1991; Schlitter et al. 1984; Taylor et al. 1992, 1993, 1995).

I reviewed and characterized 10 chromosomally polytypic species or species complexes with respect to the following: mechanism(s) of chromosomal change, recognized taxonomic status of described chromosome races, distribution patterns of described chromosome races (peripatric, par-

apatric, sympatric, or allopatric), evidence for reproductive isolation between chromosome races (pre- and postzygotic), evidence for genotypic divergence, evidence for phenotypic divergence, and evidence for ecological divergence.

Data were loosely categorized, according to the recognized taxonomic status, interrace genetic distances, and distributional relationships of described chromosomal races, for comparison with patterns of chromosomal change obtained elsewhere in the world. Sufficient data were available to test the role of chromosomal change in speciation in only 2 complexes reviewed: the actively speciating vlei rat, *Otomys irroratus,* complex and the allopatric gerbil species pair, *Tatera afra–T. brantsii.*

PATTERNS OF CHROMOSOMAL VARIATION

Individual species and species complexes are discussed here with reference to 6 loosely recognized categories, defined on the basis of taxonomic status of chromosomal races, distributional relationships, and genetic or phenotypic divergence between races: peripatric chromosomal variation, parapatric races (genotypically similar), parapatric species or subspecies (genotypically or phenotypically divergent), allopatric sister species (genotypically or phenotypically divergent), sympatric sibling species (genotypically or phenotypically divergent), and unexplained patterns of chromosomal variation.

Peripatric chromosomal variation (pattern 1).—Where chromosomal rearrangements appear in populations peripheral to the main species' range, this may be regarded as peripatric. Where peripatric populations expand their distributional range, their distributions may in time be regarded to be parapatric to the main species' range. Peripatric occurrence of chromosomal changes has been shown, for example, in the house mouse, *Mus domesticus* (Capanna 1982), and in the Negev Desert population of the Israeli mole rat superspecies, *Spalax ehrenbergi* (Nevo 1985, 1991), and is predicted to occur under a peripatric model of chromosomal speciation (Capanna and Redi 1994; Mayr 1982; Nevo 1985, 1991).

Such a pattern may be present in the striped mouse (*Rhabdomys pumilio*), a ubiquitous, di-

urnal species having a broad habitat range and a panmictic population genetic structure (Mahida et al. 1999). In southern Africa, the species has a widespread karyotype of 2n = 48; however, N. Mahida (in litt.) documented the occurrence of a 2n = 46 form at Potchefstroom (Gauteng Province, South Africa) and Inyanga (Zimbabwe). This chromosomal change has resulted from a single Robertsonian fusion event that appears to have become fixed at Potchefstroom and Inyanga (a series from Zimbabwe and a single Potchefstroom animal contained the same fusion rearrangement). Potchefstroom is situated near the periphery of the species' range in South Africa, while Inyanga represents the geographically isolated (by the dry Limpopo Valley) peripheral population in Zimbabwe.

Allozyme analysis (Mahida et al. 1999) shows that this chromosomal change is not reflected in any significant genotypic divergence, suggesting that chromosomal change has occurred relatively recently. Preliminary breeding trials between the 2n = 46 (from Zimbabwe) and 2n = 48 (from Midmar Dam in KwaZulu–Natal) chromosome forms indicate little or no loss of fertility in F1 hybrids (N. Mahida and G. Campbell, in litt.), as would be expected from a single centric fusion (Redi and Capanna 1988).

Genotypically similar parapatric races (pattern 2).—*Otomys irroratus* displays extreme chromosomal variability and has been studied intensively over the past 10 years (Contrafatto 1996; Contrafatto et al. 1992a, 1992c; Meester 1988; Meester et al. 1992; Pillay et al. 1992, 1995a, 1995b; Robinson and Elder 1987; Taylor et al. 1992, 1993). This species is a member of the murid subfamily Otomyinae (laminate-toothed rats), of which there are 8 species in southern Africa. Although karyotypic monomorphism has been demonstrated in *O. unisulcatus* (Van Dyk 1990), *O. sloggetti* (Contrafatto et al. 1992b), and *O. angoniensis* (Contrafatto et al. 1992a), *O. irroratus* displays extreme intra- and interpopulational karyotypic variability, resulting in the description of 5 discrete, parapatric races that correspond closely with recognized climatic zones (Contrafatto, 1996; Taylor et al. 1994; Fig. 1). This species occurs sympatrically over parts of its range, with its closest sister species, *O. karoensis* (= *O. saundersiae*—Taylor et al. 1993) and with 2 additional sibling species, *O. laminatus* and *O. angoniensis.*

Based on karyotype, *O. irroratus* can be split into 5 parapatrically distributed chromosome races termed A, A1, A2, B, and C (Fig. 1). Chromosome races A, A1, and A2 contain only acrocentric autosomes (disregarding small, biarmed B chromosomes of which 0 to 4 members are variably present in any one chromosome race), while chromosome races B and C contain 6–8 and 4 pairs of large biarmed autosomes, respectively. Based on the standard karyotype proposed by Robinson and Elder (1987), the short arms of all but 1 of the biarmed autosomes consist entirely of heterochromatin (in pair 6, the biarmed condition is caused by a pericentric inversion). The A1 chromosome race is distinguished from others in possessing a tandem fusion involving autosomes 7 and 12. The A2 race contains 2 unique pairs of autosomes (Fig. 1). Chromosomal variations within each race include presence or absence of B chromosomes, occasional Robertsonian fusions, and pericentric inversions (Contrafatto et al. 1992a, 1992c).

Five important points have emerged from recent research on chromosomal evolution in *O. irroratus.* First, parapatric chromosome races are correlated with climatic zones and therefore may be ecologically distinct; in particular, the A1 race is restricted to the higher-altitude (>1,400 m) Drakensberg Range (Taylor et al. 1994; Fig. 1). Second, no natural hybrids have yet been collected despite intensive trapping in a predicted zone of contact (P. J. Taylor, in litt.). Third, based on allozymes (Taylor et al. 1992; Fig. 2) and immunoblotting (Contrafatto et al. 1997), chromosome races do not seem to have diverged genotypically from each other, except for a measure of phylogenetic structuring consistent with the oldest separation between certain populations from Eastern Cape of the proposed ancestral B race and other races. This separation is confirmed by more sensitive methods, such as mtDNA restriction polymorphism analysis (Rimmer 1994) and (PCR–RAPDs) polymerase chain reaction of randomly amplified DNA (H. Dace and J. Lamb, in litt.).

Particular populations show extremely high numbers of unique mtDNA haplotypes (30 *O. irroratus* specimens formed 19 different clones—Lamb et al. 1996; Raubenheimer 1993) and high genetic diversity measured by PCR–RAPDs (intrapopulational divergence at 1 population was 0.15–4.35%—H. Dace and J. Lamb, in litt.). Fourth, inter- and intrachromosome race breeding experiments by Pillay et al. (1992,
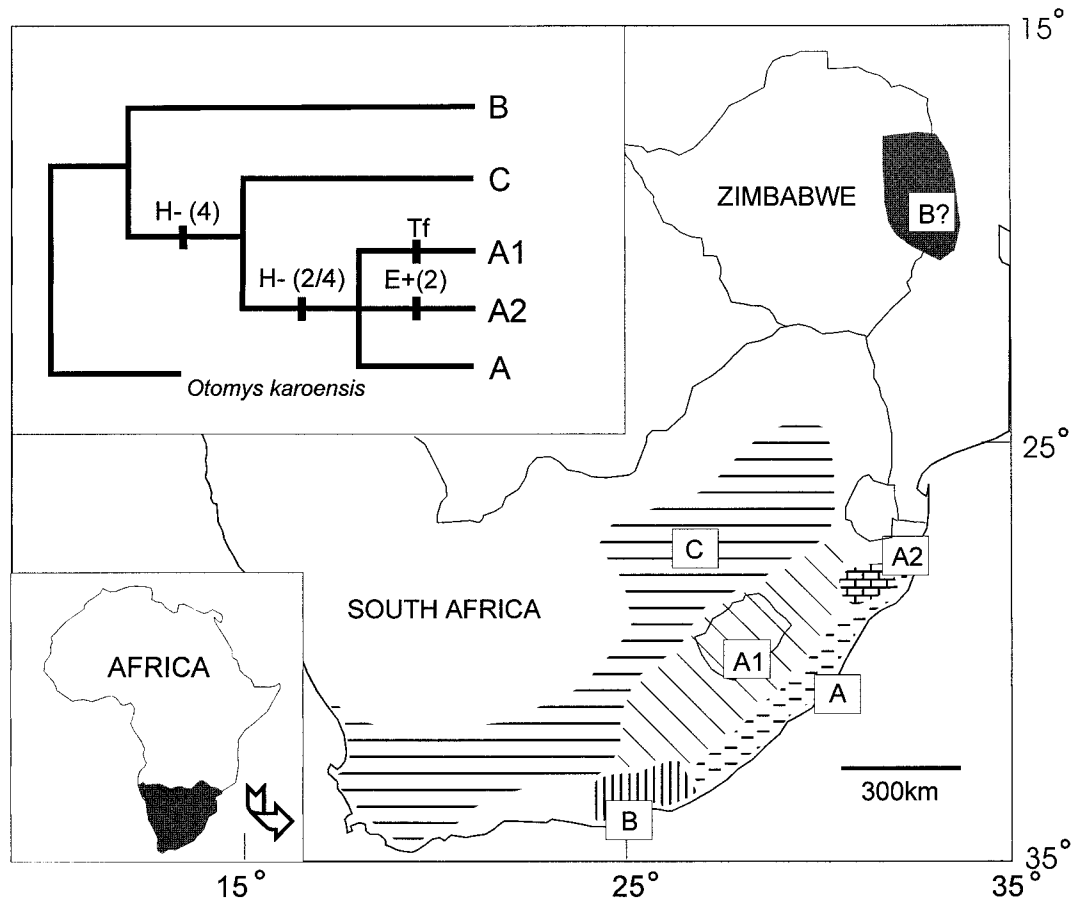
Fig. 1.—Distribution of chromosome races of *Otomys irroratus* in southern Africa; inset shows cladogram illustrating relationships between chromosomal races. Chromosomal changes are indicated as follows: H^- = loss of heterochromatic short arms (number of pairs indicated); $E^+(2)$ = euchromatic addition of 2 pairs of unexplained chromosomes; Tf = tandem fusion (modified from Contrafatto 1996; Contrafatto et al. 1992a; Taylor et al. 1993). Choice of outgroup for the cladogram was based on recent chromosomal data for *O. karoensis*, which showed it to be sister taxon to *O. irroratus* complex, with a karyotype highly similar to race B (A. Kumirai, pers. comm.). Unbanded karyotypes of individuals from Zimbabwe match the B race in diploid number and FN, but homology in G-banding pattern remains to be tested (A. Kumirai, pers. comm.).

1995a), involving the A1, A2, and B chromosome races, have demonstrated varying degrees (from low to high) of reduced fertility and viability of interrace hybrids relative to intrarace pairings. In particular, severely reduced fertility and viability of hybrids resulted from crosses where 1 partner carried the tandem fusion arrangement (i.e., A1 race). For example, only 4 litters were obtained from 96 backcross mating attempts (4% success) from hybrids involving the tandem fusion rearrangement (A1–A2 or

A1–B). In contrast, 100% of intrachromosome race matings were successful.

Fifth, Pillay (1990, 1993) and Pillay et al. (1995b) presented evidence for partial prezygotic isolation between chromosome races. For example, interrace pairings involving a population of the B race (Committee's Drift, Eastern Cape Province) and other populations of the A1 and A2 races led to increased levels of aggression and delayed mating compared with intrarace pairings (mating in *O. irroratus* occurs at the
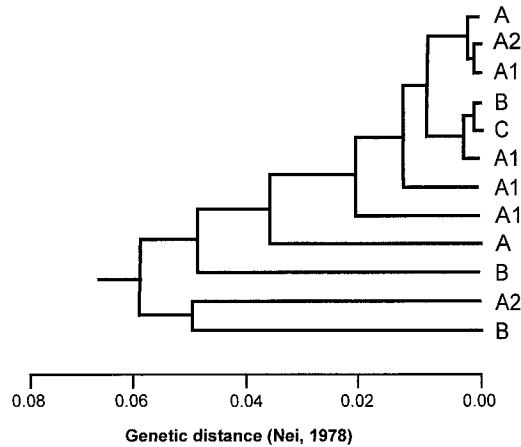
FIG. 2.—Phenogram depicting Nei's (1978) genetic distances between populations of *Otomys irroratus* depicting chromosome races A1, A2, B, and C (modified from Taylor et al. 1992).

point where percentage of agonistic encounters declines below that of amicable encounters—Pillay 1990).

In a separate experiment, Pillay et al. (1995b) analyzed mate recognition between partners from the A1 and A2 races (Kamberg and Karkloof, respectively, in the KwaZulu–Natal midlands) and found that in these genetically similar and geographically close (50 km) populations, females (but not males) displayed significant preference for homotype mates over heterotypes (that was true for tests involving live animals and odors associated with bedding material). Karkloof females (representing the ancestral unfused condition) differentiated better than Kamberg females.

Otomys irroratus appears to represent an actively speciating species complex in which both chromosomal polytypy and varying degrees of pre- and postzygotic reproductive isolation have evolved in a very short space of time (because genetic distances between chromosome races are still remarkably low). Contrafatto (1996) provided a synthesis of recent multidisciplinary research into this remarkable species complex, and the systematics of this complex is under review by A. Kumirai, Natural History Museum of Zimbabwe.

Genotypically divergent parapatric species and subspecies (pattern 3).—Two species complexes can be placed in this category, African mole rats of the genus *Cryptomys* and gerbils of the southern African genus, *Gerbillurus.* Taxonomy of *Cryptomys* has had a turbulent history, with some 49 species described by Ellerman et al. (1953) and only 7 by Honeycutt et al. (1991). Until recently (De Graaff 1975), *C. hottentotus* was recognized as a widespread polytypic species including, in southern Africa, *C. h. damarensis* from Namibia, Botswana, Zambia, and western Zimbabwe; *C. h. hottentotus* from the western and northern parts of South Africa and southern Zimbabwe; *C. h. natalensis* from eastern and northern parts of South Africa and parts of Mozambique; and *C. h. darlingi* from Zimbabwe and Mozambique. More recent assessments (Honeycutt et al. 1991; Woods, 1993) treat *C. damarensis* as specifically distinct from *C. hottentotus.*

Nevo et al. (1986) showed *C. damarensis* to be karyotypically distinct from *natalensis* and *hottentotus,* having 74 or 78 chromosomes as opposed to 54 in the other 2 (probably due to Robertsonian changes). *C. h. natalensis* differed from *C. h. hottentotus* in having 2 extra arms due to a pericentric inversion in chromosome pair 15. More recently, Aguilar (1993) described populations from Zimbabwe (*C. h. darlingi*) having 54 chromosomes but only 80 arms, which is best explained (in the absence of G-banding data) by numerous pericentric inversions.

Work by Honeycutt et al. (1987, 1991), Filippucci et al. (1994, 1997), Janecek et al. (1992), Nevo et al. (1987), and Faulkes et al. (1997) has demonstrated distinct allozymes and mtDNA- and DNA-sequence differences between all chromosomally defined taxa. Even the chromosomally similar subspecies *C. h. hottentotus* and *C. h. natalensis* may be better considered as good species, being separated by a Nei's (1972) genetic distance of 0.57 (with 6 fixed allelic differences—Nevo et al. 1987) and a percentage nucleotide divergence estimate of 15.7% (Honeycutt et al. 1987). Allozyme analysis (Filippucci et al. 1994, 1997) indicated a wide genetic separation of *damarensis* from both *natalensis* and *hottentotus* and separation of 2 unidentified Zambian populations from each other, from *C. damarensis* and from the giant mole rat, *C. mechowi.* The 2 unidentified Zambian populations possessed distinct diploid numbers (58 and 68), suggesting that they may represent undescribed species. Sequencing data from the mitochondrial 12S rRNA and cytochrome *b* genes support the

above groupings and further group *C. darlingi* with the *C. damarensis–C. mechowi* clade, distinct from the *C. hottentotus* clade (Faulkes et al. 1997). It is highly likely that future taxonomic treatments will recognize several distinct species within the *C. damarensis–C. hottentotus* species complex.

No natural hybrid zones have been detected yet between chromosomally defined *Cryptomys* taxa despite their ubiquitous occurrence in many classical cases of chromosomal evolution, such as *Spalax* (Nevo and Bar-El 1976), *Mus* (Capanna 1982), *Peromyscus leucopus* (Stangl 1986), *Thomomys* (Patton 1972, 1993; Patton and Yang 1977; Thaeler 1974), *Petrogale* (Sharman et al. 1990), and *Geomys* (Baker et al. 1989; Patton 1993; Qumsiyeh et al. 1988; Sudman et al. 1987). However, this may reflect inadequate sampling.

The genus *Gerbillurus* represents a comparatively recent southern African radiation of gerbils comprising 4 species (Musser and Carleton 1993). Three species of *Gerbillurus* occur more or less parapatrically in Namibia, *G. vallinus, G. setzeri*,, and *G. tytonis.* A 4th, probably ancestral, species, *G. paeba,* occupies a much broader geographic range in southern Africa, sympatric with all other 3 species (De Graaff 1981). Based on its broader distribution and ecological niche and its more generalized behavior, *G. paeba* can be considered to be ancestral to the other species (Dempster et al. 1991, 1992).

While *G. paeba* and *G. setzeri* superficially share a diploid number of 36 (separated by numerous structural rearrangements), *G. vallinus* and *G. tytonis* superficially share a diploid number of 60 (also separated by numerous rearrangements). Variation in fundamental number occurs within and between species (Qumsiyeh 1986; Qumsiyeh et al. 1991). Banding studies revealed both intra- and interspecies karyotypic differences, several chromosomal synapomorphies (primarily Robertsonian fissions) linking *G. vallinus* and *G. setzeri*, and an unresolved trichotomy involving *G. paeba, G. tytonis,* and the *G. vallinus–G.setzeri* sister-species pair.

Genotypic divergence and prezygotic reproductive isolation (acoustic and behavioral repertoires) appear to be well developed between species (Dempster and Perrin 1991; Dempster et al. 1991). On the other hand, allopatric subspecies of *G. paeba, G. p. paeba,* and *G. p. exilis* appear to be chromosomally similar and have not diverged in their acoustic signaling systems (Dempster and Perrin 1991; Qumsiyeh et al. 1991).

Genotypically or phenotypically divergent allopatric sister species (pattern 4).—Of the 3 related southern African gerbil species of the genus *Tatera, T. leucogaster* and *T. brantsii* are broadly sympatric over much of southern Africa excluding the Western Cape, while *T. afra* is endemic to the Western Cape and thus allopatric to both *T. leucogaster* and *T. brantsii.* Based on evidence from chromosomes and allozymes*, T. afra* and *T. brantsii* appear to be sister species (Dempster et al. 1993; Qumsiyeh 1986). They share the same diploid number of 44, which is differentiated from *T. leucogaster* (2n = 40) on the basis of 2 centric fusions and a difference in the Y chromosome. Although *T. brantsii* and *T. afra* appear to have identical karyotypes, Qumsiyeh (1986) found inconsistent differences in the G-banding homology of the Y chromosome and autosome pair 8.

Dempster and co-workers (Dempster 1996; Dempster and Perrin 1994; Dempster et al. 1993, in litt.) have investigated pre- and postzygotic isolating mechanisms in gerbils, including the 3 species of *Tatera* mentioned here. Based on analyses of courtship behavioral repertoires, they found that premating isolation tends to be incomplete and that the allopatric sister-species pair (*T. afra–T. brantsii*) share very similar behaviors and ultrasound acoustic signals compared with more marked differences between the sympatric pair (*T. leucogaster–T. brantsii*).

Laboratory breeding studies and analyses of spermatozoa and testis morphology of hybrids between *T. afra* and *T. brantsii* (Dempster 1996; E. R. Dempster et al., in litt.) indicated that female hybrids were fertile, while male hybrids were sterile. For example, preweaning mortality was higher than expected (50%) and also was male biased (sex ratio of survivors was 2 females : 1 male, significantly different from parity). No F_2 hybrids resulted from attempts to breed male hybrids with purebred females. Spermatazoa abnormalities were noted in hybrids, and testicular development in hybrids varied from no spermatazoa produced to normal. Male sterility could well be due to the subtle Y chromosome differences noted by Qumsiyeh (1986) and represents an example of Haldane's (1922) rule. Engstrom (1997) documented similar male (but not female) sterility between chromosome

races of collared lemmings (*Dicrostonyx*) separated by Robertsonian fusions involving the sex chromosomes but not between races defined by fusions involving only autosomes.

Genotypically divergent sympatric sibling species (pattern 5).—Three sibling species pairs are discussed here. Additional cases of sympatry were discussed previously, involving species ancestral to the parapatric or allopatric complexes or species pairs *Gerbillurus paeba* (sympatric to the parapatric complex, *G. vallinus–G.setzeri–G.tytonis*) and *Tatera leucogaster* (sympatric to *T. brantsii*).

The multimammate mouse (*Mastomys natalensis* sensu lato) was the 1st case of chromosomal polytypy to be investigated fully in southern Africa. The work of Green, Gordon, and others (e.g., Gordon 1984; Green et al. 1980) revealed the existence of 2 sibling chromosomal species having diploid numbers of 2n = 32 (*M. natalensis* sensu stricto) and 2n = 36 (*M. coucha*), within what was long regarded to be a single species. Despite their phenotypic similarity, these 2 species are not sister species. Based on cladistic analysis of chromosomal characters in 4 species of *Mastomys, M. natalensis* is related most closely to *M. huberti* from West Africa; *M. natalensis* and *M. coucha* are separated from each other by peri- and paracentric inversions, heterochromatic changes, and Robertsonian fusions and fissions (Britton-Davidian et al. 1995). Fixed genetic differences were found to occur between these 2 species at the hemoglobin locus (Robbins et al. 1983).

Based on distribution of karyotyped specimens, the 2n = 32 species (*M. natalensis*) was thought to occur in the eastern, wetter regions having >700 mm rainfall annually, while the 2n = 36 species (*M. coucha*) was thought to inhabit drier western areas having <600 mm, with sympatry in regions such as Zimbabwe having between 600 and 700 mm (Green et al. 1980). However, using discriminant functions analysis, Dippenaar et al. (1993) demonstrated distinct craniometric differences between *M. natalensis* and *M. coucha.* This approach permitted the craniometric diagnosis of existing museum collections (Njobe 1997). Results of this study refuted earlier indications of parapatry with limited sympatry between species (Green et al. 1980), showing instead a pattern of widespread sympatry. However, *M. coucha* appears to predominate in the drier west, while *M. natalensis* pre-

dominates in the more mesic eastern areas, and distributions of the 2 species appear to be significantly correlated with rainfall, implying some measure of ecological divergence between them (Njobe 1997).

Gordon (1984) has shown that the 2 southern African species have significantly distinct courtship behaviors (e.g., tail sniffing more common in *M. coucha* and lying more common in *M. natalensis*), ultrasound vocalizations (*M. natalensis* being more warbly and *M. coucha* more gravelly), and odors. The species mate positively assortatively in mixed species mate trials; only two hybrid litters were produced in 38 trials as opposed to 21 purebred litters (Gordon 1984).

Mastomys are opportunistic rodents with high reproductive potential and high vagility, being the first to invade disturbed areas (Ferreira and van Aarde 1996). Gordon (1984) has shown that although hybrids are formed (sired only by *M. coucha* and not by *M. natalensis*), no backcrosses are produced, demonstrating complete postzygotic isolation.

In summary, the well-studied multimammate mouse complex in southern Africa appears to conform to a situation where irreversible speciation has occurred, accompanied by pre- and postzygotic reproductive isolation, overt chromosomal change, and subtle but distinct phenotypic, genotypic, and ecological divergence. While chromosomally differentiated speciating complexes are typically distributed parapatrically (King 1993), a similar case of sympatry to that of the southern African multimammate mice was reported for 2 chromosomal forms of the agile kangaroo rat (*Dipodomys agilis*) in California (Sullivan and Best 1997). Discriminant analysis was used to demonstrate distinct morphometric differences between the forms (now considered species) and to identify a broad zone of sympatry not evident from previous karyotypic and biochemical studies.

The tree rat (*Thallomys paedulcus* sensu lato) demonstrates extreme variability in karyotype, with diploid numbers of 43 to 50 having been recorded, including some 11 unique variants (Gordon 1987). Gordon (1987) grouped these variants into 2 major groups that are now recognized as good species, *T. paedulcus* having 43–46 chromosomes and *T. nigricauda* having 47–50 chromosomes. Each species possesses intraspecific polymorphisms involving Robertsonian centric fusions, tandem fusions, and pericen-

tric inversions, while differences between species are due to the presence of an unexplained supernumerary pair in *T. nigricauda* (either 1 or both members may be present) and differences in banding morphology of the X chromosome. Based on the distribution of karyotyped specimens, Gordon (1987) proposed that distributions were parapatric, *T. nigricauda* being restricted to the Southwest Arid biome and *T. paedulcus* being restricted to the Savanna biome.

Taylor et al. (1995) demonstrated distinct craniometric differences between cytogenetically known samples of the 2 chromosome races of *Thallomys* using discriminant analysis. This approach was used for the a posteriori classification of a large museum collection, enabling a much more detailed study of species' distributions (Taylor et al. 1995). This study demonstrated almost complete sympatry between the 2 species, refuting earlier indications of parapatry (Gordon 1987; Fig. 3). Work remains to be done on this species, particularly with regard to assessing evolutionary and taxonomic implications of chromosomal variation and measuring genotypic divergence between recognized chromosomal species.

Gordon and Rautenbach (1980) and Visser and Robinson (1986) demonstrated the existence of 2 chromosome races (2n = 44 and 2n = 50), separated by 3 independent centric fusion events, within what was previously regarded to be a single species, the red veld rat (*Aethomys chrysophilus* senso lato). Chromosomal differences were also noted in both sex chromosomes and 2 unmatched chromosome pairs (Visser and Robinson 1986). Distinct allozymic and sperm morphological differences also characterize the 2 forms (Gordon and Rautenbach 1980). Recently, Chimimba (1997) used discriminant analysis to demonstrate craniometric differences between the 2 chromosome races and proposed the name *A. ineptus* to accommodate the 2n = 44 chromosome race while retaining *A. chrysophilus* (sensu stricto) to accommodate the 2n = 50 chromosome race. Craniometric diagnosis of existing museum collections demonstrated complete sympatry between the 2 species, with *A. ineptus* predominating in southern parts of the southern African range and *A. chrysophilus* predominating in the north (Chimimba 1997).

Unexplained patterns of chromosomal variation (pattern 6).—Chromosomal variation has been documented in several species of southern African rodents for which no further information is available, for example, pygmy mice (*Mus minutoides*), woodland mice (*Grammomys dolichurus*), and dormice (*Graphiurus murinus*—Dippenaar et al. 1983). These species are not discussed further, but cytogenetic analyses are urgently required.

In the little-known water rat (*Dasymys incomtus*), a specialized, relatively large (>100 g) species that is confined to wetland habitats, Gordon (1991) documented 2 karyotypes at 2 populations in South Africa: 2n = 46 at Klipfontein Farm in Northern Province and 2n = 38 at Richards Bay on the east coast of KwaZulu–Natal. The difference in karyotype can be attributed to 3 independent Robertsonian centric fusions. Geographic distributions and evolutionary implications of these chromosome races are not yet understood but are currently under review by S. Mullin (University of the Witwatersrand, Johannesburg, South Africa).

An unusual case of chromosomal variation that cannot be explained easily in terms of the categories listed previously involves the pouched mouse (*Saccostomus campestris*). Gordon (1986) demonstrated profound variation in diploid number (2n) in the pouched mouse from southern Africa, from 28 to 50, including 16 different 2n complements. While numerous centric fusions appear to explain differences in diploid number, heterochromatic additions (or deletions) and pericentric inversions explain differences in FN (Gordon 1986). Gordon (1986) recognized 2 groups and argued for species status based on the presence of fixed differences or large frequency differences at 3 allozyme loci. He argued that the species were essentially parapatric, with the 2n = 28–30 group occupying the Southwest Arid biome and the 2n = 46 group occupying the Savanna biome (forms having 2n = 42–50 could not easily be related to the above forms). However, given the fact that similar assumptions proposed for *Mastomys, Thallomys,* and *Aethomys,* on the basis of a limited number of karyotyped individuals, were later refuted on morphometric grounds (see pattern 5), the accurate distribution of the various chromosome races awaits further research. The pattern of karyotypes has been interpreted alternatively as a west–east cline of increasing diploid number (S. Ferreira and T. J. Robinson, pers. comm.).
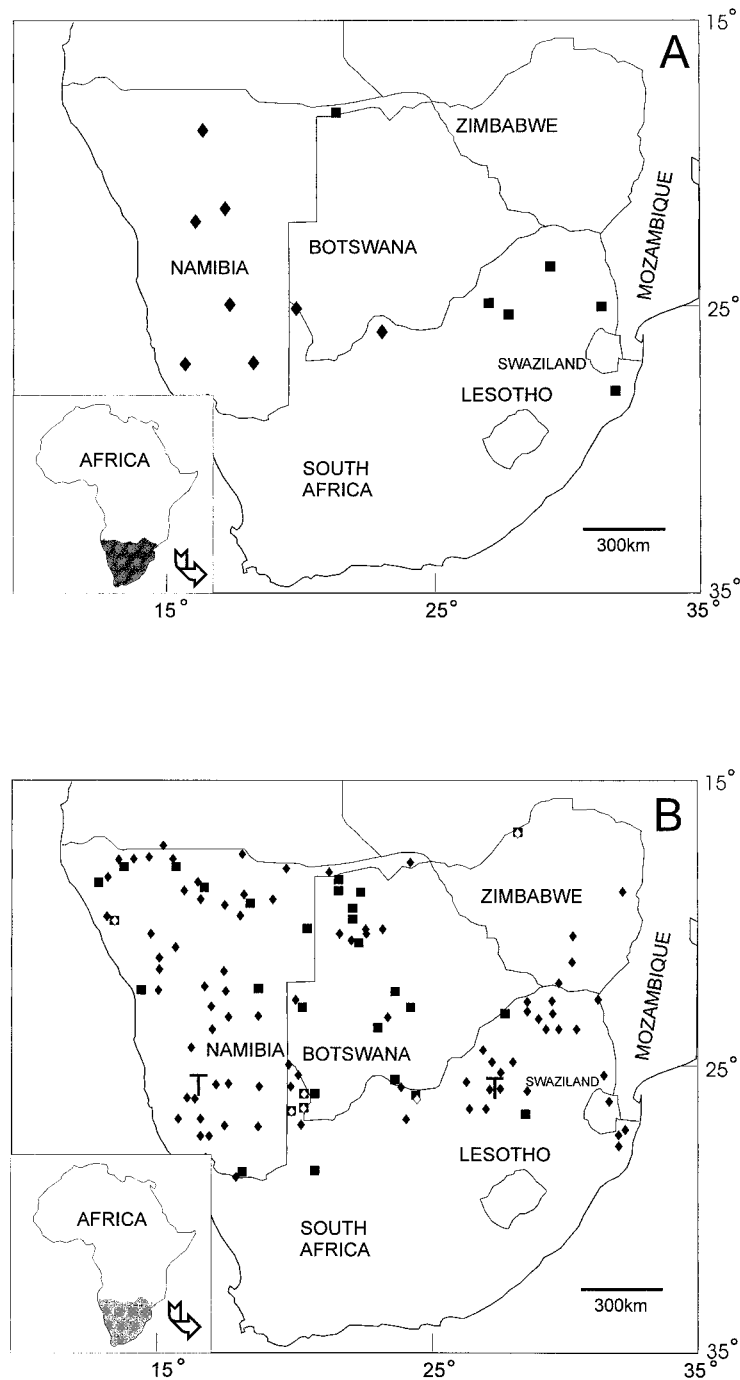
FIG. 3.—Distribution of tree rats, *Thallomys paedulcus* (closed squares) and *Thallomys nigricauda* (closed diamonds) in southern Africa, based on A) cytogenetic and B) morphometric criteria. "T" indicates positions of type localities of *T. paedulcus* in South Africa and *T. nigricauda* in Namibia (modified from Taylor et al. 1995).

COMPARISON WITH PATTERNS OF CHROMOSOMAL VARIATION WORLDWIDE

Actively speciating chromosomal complexes of rodents and other species frequently occur in parapatry (or less commonly in allopatry), often in chains or linear series of colonizing races, thus prompting the stasipatric model of chromosomal speciation advocated by White (1978). This pattern of parapatric races is repeated worldwide, for example, in Venezuelan spiny mice of the *Proechimys guairae* complex (Reig et al. 1980), deer mice (*Peromyscus*—Robbins and Baker 1981), pocket gophers (e.g., *Thomomys taploides*—Thaeler 1974), and geckos (*Sceloporus grammicus* complex—Sites et al. 1987) in North and Central America; common shrews (*Sorex araneus* complex—Hausser et al. 1994) and house mice (*Mus domesticus*—Winking et al. 1988) in Europe; the *Rattus rattus* complex in Asia (Yoshida 1980); mole rats of the *Spalax ehrenbergi* complex in Israel (Nevo 1991); and geckos (*Gehyra variegata–punctata* species complex—King 1979), rock wallabies (*Petrogale assimilis* complex—Eldridge et al. 1988), and flightless morabine grasshoppers (Key 1981) in Australia.

Three possible cases reviewed here conform to the common parapatric pattern outlined previously: the vlei rat, *Otomys irroratus* complex; the mole rat, *Cryptomys* complex; and 3 of the 4 southern African *Gerbillurus* species (*G. vallinus–G. setzeri–G. tytonis*). With additional research, parapatric patterns may apply in the case of the striped mouse, *Rhabdomys pumilio,* in southern Africa, where known karyotypic variants currently appear to be peripatrically located.

King (1993) recognized different classes of chromosomally speciating complexes, depending on genetic distances between races within colonizing series (A–B–C–D). In the present study, the *Otomys irroratus* complex conforms somewhat to King's (1993:172) class 3 complexes, that is, "A linear array of forms ranging from species to chromosome races, with some genic differences at the A end and no genic differences between C and D at the D end."

Cryptomys and *Gerbillurus* most closely represent King's (1993) class 2, presenting a continuum within a series of races, between genetically well-differentiated species at one end (A end of King, e.g., between recognized parapatric species of *Cryptomys* and *Gerbillurus*) and relatively more genetically similar subspecies at the other end (D end of King, e.g., recognized subspecies of *Cryptomys hottentotus* and *Gerbillurus paeba*).

A prevalent pattern among southern African rodents appears to be the sympatric occurrence of chromosomally distinguishable sibling species pairs: *Mastomys natalensis–M. coucha, Thallomys paedulcus–T. nigricauda, Aethomys chrysophilus–A. ineptus,* or the sympatric arrangement of ancestral species relative to parapatric or allopatric species complexes: *Gerbillurus paeba* (sister species to the parapatric complex, *vallinus–setzeri–tytonis*) and *Tatera leucogaster* (sister species to the allopatric *afra–brantsii* species pair). In these sympatric cases, species appear to have diverged genotypically, ecologically, and phenotypically and to have achieved a significant measure of reproductive isolation (e.g., pre- and postzygotic isolation in *Mastomys* and prezygotic isolation in sympatric *Tatera* and *Gerbillurus* species) and cannot really be regarded as actively speciating. They perhaps represent an older speciation event, somewhat similar to the class 1 series (A–B–C–D) described by King (1993:172) although differing in their sympatric, rather than parapatrically linear, relationship, that is, "A relic, colonising radiation in which all species in a sequence A–D have numerous fixed differences between them." Sympatrically distributed chromosomal complexes or species pairs are not reported frequently worldwide, but a recent case involving 2 forms of *Dipodomys agilis* in

California was reported by Sullivan and Best (1997).

THE ROLE OF CHROMOSOMAL CHANGE IN SPECIATION

Pattern 1 merits further research to investigate conditions under which chromosomal rearrangements may become fixed in peripheral populations; a similar approach has provided valuable insight into the speciation process in *Mus* and *Sorex* in Europe. Patterns 3–5 appear too advanced to be able to extrapolate the role that chromosomal change may have played during the past speciation event. In pattern 2, represented by the actively speciating *O. irroratus* complex, the current evolutionary role of observed chromosomal patterns can best be understood. In this instance, both chromosomal and nonchromosomal characters appear to be associated with the initiation and maintenance of the 5 recognized races. In the case of the tandem fusion marker for the A1 chromosome race, severely reduced hybrid fertility has resulted in an immediate potential species barrier. In other chromosome races, chromosomal differences are unlikely to result in meiotic problems, yet behavioral differences indicative of premating isolation have begun to evolve. In such cases, observed chromosomal differences cannot be implicated in the divergence process, and it can be argued that a measure of prezygotic isolation (e.g., between A1 and A) has developed in the absence of significant measurable genotypic divergence at the gene (allozyme and immunoblot data) or DNA (mtDNA and PCR–RAPD data) level. The acquisition of reproductive isolation and incipient speciation in the *O. irrortus* complex thus appears to be mediated by chromosomal (postzygotic) and nonchromosomal (prezygotic, i.e., behavioral or ecological) processes. The precise role of behavioral and ecological factors in speciation of *Otomys* warrants further research. Behavioral differences between races are rather subtle, and tests have been performed on only relatively few combinations of chromosomal races (with only 1 population representing each race). The strong correlation between chromosome races and climate zones suggests that ecological factors may be playing a vital role in speciation, but the causal basis of this association is unknown.

In terms of the role of chromosomal change in the onset of reproductive isolation, the case of the allopatric species pair, *Tatera afra–T. brantsii* is potentially informative because this appears to be an explicit example of Haldane's (1922) rule, resulting in male (but not female) sterility. Such a process was argued to be involved in the speciation of collared lemmings, whereby only interracial chromosomal differences involving sex chromosomes, and not autosomal differences, resulted in reproductive isolation (Engstrom 1997). However, in the case of the allopatric *Tatera* species pair, individuals never meet in nature, making it impossible to test predictions of postzygotic versus prezygotic isolation in nature (i.e., at hybrid zones). Accumulation of genetic differences during allopatry makes it difficult to exclude the possibility of gene differences resulting in the observed reduced fertility. In the laboratory, prezygotic isolation is undeveloped, while postzygotic isolation, in the form of impaired male fertility, is developed.

TAXONOMIC CONSIDERATIONS

In the case of pattern 6 species, nomenclatural problems arise where sympatry has been demonstrated in the geographic vicinity of type localities. For example, the recognition of *M. natalensis* (type locality = Durban, KwaZulu–Natal) and *M. coucha* (type locality = Kimberley, Western Cape) as valid names for the $2n = 32$ and $2n = 36$ chromosomal species, respectively, was based on the premise of distributional parapatry, whereby the $2n = 36$ form occupied drier western regions and the $2n = 32$ form moister eastern regions. The recent morphometric identification of *M. coucha* in the Durban area (Njobe 1997) casts doubt on

the name *natalensis,* making it imperative to examine cranial type material in museums (if reasonably unbroken skulls are available). A similar problem afflicts the *Thallomys paedulcus–T. nigricauda* and *Aethomys chrysophilus–A. ineptus* species pairs, which have been shown on morphometric grounds to occur sympatrically and not parapatrically.

CONCLUSIONS

Many gaps exist in our knowledge of the evolutionary biology of chromosomally variable rodent species and species complexes in southern Africa. Several chromosomally variable species for which few chromosomal data are available, such as *Dasymys incomtus* and *Rhabdomys pumilio,* require more extensive cytogenetic surveys so that distribution patterns of chromosomally defined taxa can be comprehensively mapped. To establish evolutionary homologies and relationships within chromosomally complex species complexes, such as *Saccostomus campestris* and *Thallomys paedulcus,* studies employing chromosome banding and fluorescent in situ hybridization (FISH) methods are urgently required. Studies of pre- and postzygotic reproductive isolation are required, especially in the *Thallomys* and *Aethomys* complexes, for example, laboratory breeding and behavioral studies, ecological studies of sympatrically occurring sibling species (e.g., *Aethomys, Mastomys,* and *Thallomys*), histological studies, and cytogenetic studies of synaptonemal complexes in experimental or natural hybrids. Molecular methods, such as DNA sequencing, microsatellites, PCR–RAPDs, fragment-length polymorphism of restriction endonucleases, and the modern, shape-based geometric morphometrics approach, have yet to be applied but promise to unravel taxonomic and evolutionary relationships and adaptive processes within actively speciating chromosomal species complexes.

To date, no natural hybrids have been detected despite some collecting at the borders between chromosomal races of *Otomys irroratus.* Future studies will attempt to document such zones, especially where they are predicted (e.g., between races differing in minor, neutral chromosomal arrangements).

The 10 chromosomally polytypic southern rodent species and species complexes reviewed here reveal a diversity of distributional patterns and chromosomal mechanisms, as well as important differences, compared with worldwide patterns, in the frequency of sympatric species pairs, compared with parapatric chains, the scarcity of karyotypic orthoselection, and the absence, so far, of any hybrid zones so characteristic of classical cases of chromosomal variation. The actively speciating *O. irroratus* complex holds promise for further investigation into the role of chromosomal change in speciation, and this complex also requires taxonomic revision to give taxonomic recognition to the reproductively isolated, higher-altitude A1 cytotype.

ACKNOWLEDGMENTS

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