

Recent radiation in West African *Taterillus* (Rodentia, Gerbillinae): the concerted role of chromosome and climatic changes

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West African gerbils of the genus *Taterillus* constitute a complex of seven sibling species distributed from sudano-guinean to saharo-sahelian regions. They display radically rearranged karyotypes despite low genic divergence and a very recent differentiation, that is, within the last 0.4 Myr for the six most derived species. We here provide a comparison of the seven specific karyotypes and perform a cladistic analysis using chromosomal rearrangements character states. When *a posteriori* polarized mutations were mapped onto the phylogenetic tree, 38 rearrangements were identified as fixed during the evolution of these rodents. This makes *Taterillus* one of the most striking examples of accelerated chromosomal evolution within placental mammals. Taking into account the types of chromosomal changes involved, divergence times between lineages, genetic distances, as well as reassessed geographic distributions, we suggest that (1) speciation in West African

Taterillus was driven by chromosomal changes, and (2) the paleoclimatic oscillations of the Sahara desert have played a major role in their evolution. In particular, elevated plasticity of the *Taterillus* genome, as suggested by the patterns observed for some repetitive elements, would have led to a higher probability of mutation. We hypothesize that the process underpinning cladogenesis most probably involved highly underdominant genomic rearrangements that were fixed following pronounced populational bottlenecks resulting from drastic climatic and subsequent environmental changes. Major African rivers formed significant barriers to dispersal, limiting expansion during the more moist and so favorable periods. This scenario would explain the current parapatric species distributions and their relationship to the West African hydrographic features.

Heredity (2005) **95**, 358–368. doi:10.1038/sj.hdy.6800730; published online 17 August 2005

Keywords: chromosome evolution; chromosomal speciation; evolutionary rates; Sahara desert; Sahelian regions; African rivers

Introduction

There has been extensive debate on the role of chromosomal changes in evolution (reviews in Sites and Moritz, 1987; King, 1993; Rieseberg, 2001). In particular, opposite views have persisted about the ability of chromosomal changes to initiate reproductive isolation and thus drive speciation. Arguments against chromosomal speciation are two fold. The first one relies on some examples of important polymorphism in natural populations (Nachman and Myers, 1989), which implies that chromosomal changes are probably not strongly underdominant, and consequently cannot insure reproductive isolation by themselves (Patton and Sherwood, 1983). Although acceptable in some cases, this argument is not generally applicable since many species display very stable karyotypes, high polymorphism being more the exception than the rule. On the contrary,

numerous studies have clearly demonstrated that few or even a single chromosomal rearrangements can have dramatic effects on meiosis in heterozygous carriers (King, 1993).

A second argument against chromosomal speciation is that chromosomal structural rearrangements were too deleterious and required too drastic- and hence rare-population conditions to be fixed (see Patton and Sherwood, 1983; Chesser and Baker, 1986). This argument loses credence however since most species have species-specific karyotypes, meaning that the differences, that is, the karyotypic changes, have necessarily been fixed either during or subsequently to the speciation event.

As with other speciation processes, the difficulty with identifying promoting chromosomal change as a driver of speciation is one usually investigates groups that already display morphologic, eco-ethologic and/or genetic divergences (see Zhang *et al.*, 2004 and references therein, for the example of the highly debated case of human and chimpanzee). It is thus often difficult to assess the exact sequence of events leading to reproductive isolation and to identify the first step of differentiation process. However, several studies have recently suggested that karyotype repatterning plays a significant role in speciation in some organisms. For instance, in

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Received 7 February 2005; accepted 18 July 2005; published online 17 August 2005

Drosophila, inversions have clearly been shown to reduce gene flow between inverted segments, thus allowing differentiation of coadapted genes complexes ('suppressed recombination model' *sensu* Noor *et al*, 2001; Ayala and Coluzzi, 2005; reviewed in Rieseberg, 2001; Hoffman *et al*, 2004; Ayala and Coluzzi, 2005). Similarly, translocations have been proved to lead to a strong decrease in reproductive fitness in engineered yeast hybrids with a controlled genomic background (Delneri *et al*, 2003; 'hybrid dysfunction model' *sensu* Ayala and Coluzzi, 2005).

However, the identification of additional examples, particularly in natural settings is required to further evaluate the importance of chromosomal speciation as an evolutionary process. Unfortunately, experiments involving controlled manipulations in the laboratory, such as the one performed by Delneri *et al* (2003), are hardly realistic when dealing with natural populations. Nevertheless, sibling species complexes offer an opportunity to control some of the myriad of variables associated with natural populations allowing testable hypotheses based on reasonable assumptions. Indeed, sibling species are reproductively isolated but morphologically similar. Therefore, this phenotypic similarity may reflect a recent differentiation, so that not enough time has elapsed for any significant genetical and eco-ethological divergence. Although some examples of sibling but genetically well-differentiated species have been provided (eg, *Arvicanthis* spp, Ducroz *et al*, 1998), many cryptic taxa have been karyotypically differentiated and have proved to be recently diverged (Elder, 1980; Taylor, 2000; Volobouev *et al*, 2002). As such, once these prerequisites are confirmed, sibling species complex constitute valuable biological models for investigating the effect of chromosomal changes in evolution.

Such a complex of sibling species of recent origin is represented by the African genus *Taterillus* (Rodentia, Gerbillinae), and more specially by the West African species. The latter are a monophyletic relative to the Eastern African species, a conclusion which is supported by (1) two synapomorphic autosome-gonosome translocations, one of which results in a sex trivalent XY1Y2 in males (reviewed in Dobigny, 2002), and (2) mitochondrial DNA sequence data (Dobigny, 2002). These murid rodents have previously been shown to exhibit morphological conservatism in both size and shape due to adaptative constraints and/or very recent differentiation (Dobigny *et al*, 2002b). Previous cytotoxic surveys have allowed the identification of several sibling taxa within the West African lineage: *T. gracilis* and *T. pygargus* ($2n=36/37$ and $2n=22/23$, respectively; Matthey and Jotterand, 1972), *T. arenarius* ($2n=30/31$; Robbins, 1974), *T. petteri* ($2n=18/19$, Sicard *et al*, 1988), *Taterillus* sp2 ($2n=24/25$; Dobigny *et al*, 2002c), *T. tranieri* ($2n=14/15$; Dobigny *et al*, 2003a) and *Taterillus* sp1 ($2n=22/23$; Granjon and Dobigny, 2003). Pairwise comparisons between species have shown that these karyotypic differences were sufficient to insure post-zygotic reproductive isolation (Dobigny *et al*, 2002a, 2003a). Molecular analyses using mitochondrial gene sequences showed that the West African *Taterillus* display very low interspecific genetic distances. In particular, they never exceed 15% between *T. gracilis* and the six most derived West African species, whereas variations within the latter range between 7 and 1.9%

(Kimura two parameter model, applied to partial cytochrome *b* sequences of 796 bp; Dobigny, 2002). Therefore, the genetic diversity of these six species lies within the intraspecific range usually observed in rodents (Bradley and Baker, 2001). This low mitochondrial nucleotide divergence was confirmed by nuclear analyses involving nine enzymatic systems for which no variation was observed between *T. pygargus* and *T. petteri* (Benazzou, 1984). Taken together, the species-specific karyotypes, the very low genetic distance and the high morphological similarity make the West African *Taterillus* complex a useful model taxon for testing hypotheses of a causal role for chromosomal rearrangements in speciation.

Finally, admittedly on a limited amount of data, Petter (1974) observed that most of the West African species show geographic patterns shaped by the Senegal and Niger rivers. On this basis, he proposed that these rivers may have been responsible for population isolations and subsequent allopatric speciation, and that these events took place during wet episodes during which rivers would have fragmented populations thus allowing allopatric speciation. Alternatively, Sicard *et al* (1988) favored the hypothesis of differentiation within small isolated demes during dry periods, and proposed that the parapatric distributions currently observed are the result of rivers acting as barriers to subsequent dispersal during wet episodes. To further investigate these two hypotheses, and to provide insights on the tempo and mode of evolution in *Taterillus*, we conducted wide-scale and nonambiguous cytotoxic surveys all over West Africa. We then use chromosomal rearrangements identified by comparative banding patterns in a cladistic analysis of the West African species. By taking the type of karyotypic changes that occurred into account, the extant species distributions, the timeframe provided by our previous molecular analyses, as well as eco-ethological and paleobiogeographical data, we propose an integrated hypothesis for the radiation of this group. This scenario implicates both a predisposition to genome repatterning and drastic populational fluctuations, due to paleoclimatic changes, as drivers of speciation in *Taterillus*.

Materials and methods

In total, 136 specimens were sampled from 41 localities in Mauritania, Senegal, Mali, Burkina-Faso, Niger, and Chad during several rodent surveys (Benazzou, 1984; Volobouev and Granjon, 1996; Dobigny *et al*, 2002a, b, 2003a; Granjon and Dobigny, 2003; Granjon *et al*, 2004; Granjon, unpublished) and used for this study (see Table 1). Fibroblast cell cultures were set up from biopsies for 32 individuals, and metaphases were obtained following standard procedures. Metaphases for the 104 remaining specimens were obtained using direct karyotyping of bone-marrow cells (Lee and Elder, 1980). The diploid and fundamental numbers, as well as the morphology of all chromosomes were assessed for each individual. GTG banding (Seabright, 1971) and CBG banding (Sumner, 1972) were performed on 30 and 27 of the test animal, respectively.

GTG-banding patterns were compared between several representatives of all identified cytotypes (corresponding to eight species; see below), and chromosomal

Table 1 Specific status, geographic origin, sample size (*N*) and karyotypic descriptors (*2n* and *NFa* refer to diploid and fundamental autosomal numbers, respectively) of the biological samples studied here

Species	Country	Locality	N	2n	NFa	
<i>T. arenarius</i>	Mauritania	Chott Boul	1	31	36	
<i>T. congicus</i>	Chad	Zakouma NP	34	54	64	
<i>T. gracilis</i>	Burkina-Faso	Oursi	2	37	44	
	Chad	Bol	2	38/39	44	
	Mali	Emnal'Here	3	36/37	44	
		Kangaba	3	36/37	44	
		Koursalé	1	37	44	
		Balamansala	2	36/37	44	
		Boulou	1	37	44	
		Dialo	10	36/37	44	
		Kalifabougou	2	37	43, 44	
		Makana	1	37	44	
		Nioro du Sahel	2	37	44	
		Samanko	1	36	44	
		Sibi Sibi	2	36/37	44	
		Samaya	1	36	44 or 45	
		Saremama	4	36/37	44	
		Sélingué	1	36	44	
		Niger	Babaganta	3	38/39	42, 44
			Dosso	1	38	44
			Gaya	1	39	42
	Kollo		8	37–39	42, 44	
	Tamou		2	36	42	
	Tondibia	3	38	42		
	Niamey	1	39	44		
Nigeria	Ibadan	2	39	?		
Senegal	Bandia	1	37	44		
<i>T. petteri</i>	Burkina-Faso	Oursi	1	19	24	
	Mali	Endé	9	18/19	28–30	
		Ogoyerou	1	18	30	
		Makana	1	19	32	
<i>T. pygargus</i>	Niger	Oleleoua	1	22	38	
		Tamaya	4	22	38, 39	
		Tanout	1	22/23	40	
		Tara	1	22	40	
	Senegal	Bandia	2	23	40	
		M'Bour	3	22/23	40	
<i>T. tranieri</i>	Mali	Dilly	2	14/15	24	
	Mauritania	Chalkha	2	14/15	22	
<i>Taterillus</i> sp2	Niger	Bosso	3	24	44	
		Chetimari	2	24/25	44	
		Kojimairi	1	24	44	
<i>Taterillus</i> sp1	Chad	Karal	6	22/23	40	

homologies were assessed (Table 2). A phylogenetic analysis was performed according to cladistics concepts and methods as reviewed in Dobigny et al (2004a): 46 nonpolarized structural chromosome rearrangements, excluding heterochromatin changes, were used as binary characters, and their presence/absence was coded as character states (Table 3). The East African species *T. congicus*, which displays XX/XY sex chromosomes, was used as an outgroup. The most parsimonious topologies were retrieved using an exhaustive search in PAUP 4.0b8 (Swofford, 1998). Robustness was evaluated using both decay index and bootstrap support (using 1000 replicates).

Species-specific distribution maps were redefined on the basis of data from literature (see above), this study, and the collections of the Muséum National d'Histoire Naturelle (France) and the Institut de Recherche pour le Développement (France). Only nonambiguous, that is, chromosomally validated sites were considered.

Results

All the karyotypes obtained could be assigned to one of the suite of previously described cytotypes (see above); GTG- and CBG-banding patterns were obtained from representatives of each. Importantly, G-banded karyotypes are presented for the first time for *T. petteri* (Figure 1) *T. gracilis* (Figure 2) and *T. congicus* (Figure 3). Polymorphism was detected in several species, confirming and extending earlier observations: Robertsonian changes in *T. gracilis* ($2n = 36/37$ to $2n = 38/39$; Matthey and Jotterand, 1972; Dobigny et al, 2002a), pericentric inversions in *T. pygargus* (Dobigny et al, 2002b) and *T. petteri* (Tranier, 1974) and heterochromatin amplification in *Taterillus* sp1 (Dobigny et al, 2002b). Note that two cytotypes were considered for the cladistic analysis involving *T. gracilis* ($2n = 36/37$ and $2n = 38/29$) in order to polarize this particular mutational event, although they are clearly conspecific (Dobigny et al, 2002b). Diploid ($2n$), autosomal fundamental (*NFa*) numbers, and the observed variation within each species are summarized in Table 1. C-banding patterns (see Figures 1, 2 and 3 for examples in *T. petteri*, *T. gracilis* and *T. congicus*; see Volobouev and Granjon, 1996; Dobigny et al, 2002a, 2003a, for the others) are markedly different between West and East African species. *T. congicus* possesses well-delineated C-positive heterochromatic blocks on all 18 acrocentric and subtelocentric pairs of its karyotype, whereas the C-positive regions in the other species were generally small and indistinct. Only *T. gracilis* has 10 acrocentric pairs possessing slightly C-positive pericentromeric regions.

G-banding patterns comparison allowed us to assess all the chromosomal homologies between the eight species (Table 2; examples of pairwise comparisons are provided in Dobigny et al, 2002a, 2003a) and to identify the structural differences among karyotypes. A cladistic analysis using these chromosomal rearrangements as characters led to two equally parsimonious ($L = 48$ steps) trees (Figure 4) in which *T. gracilis* was the first taxon to diverge, followed by *Taterillus* sp2 and *Taterillus* sp1, and then *T. arenarius*, *T. pygargus*, *T. petteri* and *T. tranieri*. The only difference between the two topologies lies in the relative position of *Taterillus* sp1 and *Taterillus* sp2, whose relationships are not resolved in one of the topologies whereas *Taterillus* sp2 is more basal in the other one (Figure 4). No differences could be found between the Acctran and Deltran options (data not shown). The chromosomal changes were polarized *a posteriori* using the outgroup comparison criterion and then reported along the cladogram branches (Figure 4). This showed that *Taterillus* karyotype evolution involved at least 11 tandem fusions, six pericentric inversions, 18 or 19 Robertsonian fusions (tree 2 and 1, respectively) and three or four centric fissions (tree 1 and 2, respectively) within the ingroup. Furthermore, two mutations ($n^{\circ}35$ and 21, Table 3) were found homoplastic, which can be explained as two convergent events, or one convergence

Table 2 Chromosomal homologies between the eight species considered in this study

<i>T. congicus</i> 2n = 54	<i>T. gracilis</i> 2n = 36/37	<i>T. arenarius</i> 2n = 30/31	<i>Taterillus sp2</i> 2n = 24/25	<i>Taterillus sp1</i> 2n = 22/23	<i>T. pygargus</i> 2n = 22/23	<i>T. petteri</i> 2n = 18/19	<i>T. tranieri</i> 2n = 14/15
1	Xp, Y2	Xp, Y2	Xp, Y2	Xp, Y2	Xp, Y2	Xp, Y2	Xp, Y2
2	7 dist	6 dist	3q dist	2q dist	2p dist	3p dist	3p dist
3 prox	4 prox	14 prox	10p	3q prox	4p prox	2p med	4 p prox
3 dist	4 dist	14 dist	10q	3p	4p dist	2p dist	4p dist
4	5	4	11	10	8	6	5
5p	9 prox	10 prox	6q prox	3q med dist	9q prox	1p med	1p med
5q	1q prox	5 prox	6p	3q med prox	9p	1p prox	1p prox
6p	6 prox	1q med prox	1q med prox	1q med prox	1q med prox	1q med med	1q med med
6q	17	1q prox	1q prox	1q prox	1q prox	1q med prox	1q med prox
7	8	2p	2p	2p	3q	7 dist	2q med
8	6 dist	1q dist	1q dist	1q dist	1q dist	1q dist	1q dist
9	9 dist	10 dist	6q dist	3q dist	9q dist	1p dist	1p dist
10	10	11	5q	5q	3p (inv)	7 prox	2q dist
11	6 med	1q med dist	1q med dist	1q med dist	1q med dist	1q med dist	1q med dist
12	11	12	4q	4p	5q	8 dist	2p med
13	12	13	4p	5p	5p	8 prox (inv)	2p dist
14	13	2q	7q	7q	6q	4q	6 prox
15	14	8 dist	3p	6q	4q dist	2q prox	4q dist
16 prox	1q med prox	7 prox	2q prox	4q prox	2q prox	3q prox	3q prox
16 dist	1q dist	7 dist	2q dist	4q dist	2q dist	3q dist	3q dist
17	1p	1p	1p	1p	1p	1q prox	1q prox
18	15	5 dist	8q	6p	10q	2q dist	6 dist
19	1q med dist	7 med	2q med	4q med	2q med	3q med	3q med
20	2q	3q	9q	9q	7q	5q	2p prox
21	2p	2p	7p	7p	6p	4p	6 med prox
22	3q	8 prox	8p	8q	4q prox	2p prox (inv)	4q prox
23	16	5 med	5p	8p	10p (inv)	2q med	6 med dist
24	7 prox	6 prox	3q prox	2q prox	2p prox	3p prox	3p prox
25	3p	3p	9p	9p	7p	5p	2q prox
26	Xq dist, Y1q dist	Xq dist, Y1q dist	Xq dist, Y1 dist	Xq dist, Y1 dist	Xq dist, Y1 dist	Xq dist, Y1 dist	Xq dist, Y1 dist
X	Xq prox	Xq prox	Xq prox	Xq prox	Xq prox	Xq prox	Xq prox
Y	Y1q prox+Y1p	Y1q prox+Y1p	Y1q prox+Y1p	Y1q prox+Y1p	Y1q prox+Y1p	Y1q prox+Y1p	Y1q prox+Y1p

Symbols used in this table follow usual cytogenetical standards: 'p' and 'q' mean short and long arm, respectively; 'prox', 'med' and 'dist' stand for proximal, median or proximal segment (relative to the centromere); 'inv' indicates inverted fragment. The numbering nomenclature of chromosomes refer to those used in Figures 1, 2 and 3 for *T. petteri*, *T. gracilis* and *T. congicus*, respectively, and to previous investigations (Dobigny *et al*, 2002a, 2003a) for *T. pygargus*, *T. tranieri*, *Taterillus sp1* and *Taterillus sp2*.

and one reversal, depending on the tree considered (Figure 4). The consistency, retention and rescaled consistency indexes are CI = 0.958, RI = 0.929 and RC = 0.89, respectively. The skewness value is $g_1 = -1.025$. Bootstrap support and decay index values range from 71 to 100% and from 1 to 4, respectively (Figure 4).

Discussion

Phylogenetic relationships between West African *Taterillus*

The consensus topology obtained for the eight cytotypes was well resolved with only one trifurcation. It is well supported by the CI, RI, RC and g_1 statistics and by bootstrap and decay index values. In addition, the majority of the chromosome changes inferred correspond to Robertsonian changes, something which is commonly observed in mammals including gerbilline rodents (Qumsiyeh *et al*, 1987). More importantly, the cladistic method used here implies that character changes are not polarized *a priori*, thus allowing both fusions and fissions to be inferred (reviewed in Dobigny *et al*, 2004a). Yet, 19 (tree 1) or 18 (tree 2) of the rearrangements observed in this study were polarized *a posteriori* using the outgroup comparison criterion as fusions, with only three (tree 1)

or four (tree 2) fissions inferred. In particular, none of the 11 tandem translocations coded here were found to be fission by the analysis. The occurrence of tandem fissions, even if theoretically possible, remains highly unprobable due to the requirement of both a neocentromere and neotelomeres for the fission products to be cytologically viable. As far as we know, this type of mutation has been very rarely documented in mammals (see Table 1 in Modi, 1987 for a possible example in arvicolid rodents). The fact that all of the 11 tandem mutations of our analysis were classified as fusions is, in that sense, reassuring. Finally, the only resolved and supported node previously obtained using molecular phylogenetics, that is, *T. gracilis* as the most basal West African species (Dobigny, 2002), was also retrieved and strongly supported using our chromosomal dataset.

Cladistic analysis of karyotypic rearrangements has been proved to be a highly valuable mean for resolving phylogenetic relationships within several African murid sibling species complexes (Volobouev *et al*, 2002). The well-supported *Taterillus* phylogeny retrieved here, in the absence of sufficient morphological and genetic differences (at least according to current knowledge), provides another example of how the use of chromosomal characters can sometimes provide good insights into phylogenetics.

Table 3 Matrix of chromosomal characters. 'tan', 'rob' and 'inv' refer to tandem translocations (either fusion or fission), centric translocations (either fusion or fission) and pericentric inversions, respectively

n	Characters	Tco	Tgr 38/39	Tgr 36/37	Tar	Tsp2	Tsp1	Tpy	Tpe	Ttr
1	tan(16pr+16dist)	1	0	0	0	0	0	0	0	0
2	tan(16pr+19)	0	1	1	1	1	1	1	1	1
3	tan(16dist+16pr/19)	0	1	1	1	1	1	1	1	1
4	rob(14+21)	0	0	0	1	1	1	1	1	1
5	tan(18+23)	0	0	0	1	0	0	1	1	1
6	rob(22+23)	0	0	0	0	0	1	0	0	0
7	rob(18+22)	0	0	0	0	1	0	0	0	0
8	tan(15+22)	0	0	0	1	0	0	1	1	1
9	tan(24+2)	0	1	1	1	1	1	1	1	1
10	rob(16dist/19/16pr+24/2)	0	0	0	0	0	0	1	1	1
11	rob(6p+6q)	1	0	0	1	1	1	1	1	1
12	rob(8+11)	0	1	1	1	1	1	1	1	1
13	tan(6p+8/11)	0	1	1	1	1	1	1	1	1
14	tan(17+6q/6p/11/8)	0	0	0	1	1	1	1	1	1
15	tan(5q+16pr/19/16dist)	0	1	1	0	0	0	0	0	0
16	rob(17+5q/16pr/19/16dist)	0	0	1	0	0	0	0	0	0
17	tan(9/5p/5q+17/6q/6p/11/8)	0	0	0	0	0	0	0	1	1
18	rob(25+22)	0	1	1	0	0	0	0	0	0
19	rob(21+20)	0	1	1	0	0	0	0	0	0
20	rob(7+16pr/19/16dist)	0	0	0	0	1	0	0	0	0
21	rob(13+12)	0	0	0	0	1	0	1	1	1
22	rob(7+10)	0	0	0	0	0	0	1	1	1
23	rob(25+20)	0	0	0	1	1	1	1	1	1
24	tan(12/13+25/20)	0	0	0	0	0	0	0	0	1
25	tan(25/20+7/10)	0	0	0	0	0	0	0	0	1
26	rob(13+10)	0	0	0	0	0	1	0	0	0
27	rob(23+10)	0	0	0	0	1	0	0	0	0
28	rob(15+24/2)	0	0	0	0	1	0	0	0	0
29	rob(3+22/15)	0	0	0	0	0	0	1	1	1
30	rob(18+15)	0	0	0	0	0	1	0	0	0
31	tan(5q+23/18)	0	0	0	1	0	0	0	0	0
32	rob(7+24/2)	0	0	0	0	0	1	0	0	0
33	tan(3+5q/5p/9)	0	0	0	0	0	1	0	0	0
34	rob(12+16pr/19/16dist)	0	0	0	0	0	1	0	0	0
35	rob(5p+5q)	1	0	0	0	1	1	1	1	1
36	tan(5p+9)	0	1	1	1	1	1	1	1	1
37	tan(18/23+3/22/15)	0	0	0	0	0	0	0	1	0
38	tan(18/23+14/21)	0	0	0	0	0	0	0	0	1
39	tan(1+Xp)	0	1	1	1	1	1	1	1	1
40	tan(Xq/Y+26)	0	1	1	1	1	1	1	1	1
41	inv(14)	0	0	0	0	0	0	0	0	1
42	inv(12/13)	0	0	0	0	0	0	0	1	0
43	inv(22)	0	0	0	0	0	0	0	1	0
44	inv(22)	0	0	0	0	0	0	0	1	0
45	inv(7/10) n°1	0	0	0	0	0	0	0	1	0
46	inv(7/10) n°2	0	0	0	0	0	0	0	0	1

'Tco', 'Tgr', 'Tar', 'Tsp2', 'Tsp1', 'Tpy', 'Tpe' and 'Ttr' represent *T. congicus*, the two *T. gracilis* cytotypes ($2n = 36/37$ and $2n = 38/39$), *T. arenarius*, *Taterillus* sp2, *Taterillus* sp1, *T. pygargus*, *T. petteri* and *T. tranieri*, respectively.

Accelerated rate of chromosomal evolution

Using the *a posteriori* polarized karyotypical rearrangements mapped along the branches of the phylogram (Figure 4), it is possible to evaluate the number of each type of chromosomal changes characterizing specific karyotypes. It should be emphasized that this includes the convergent changes, which remain cryptic when only two karyotypes are compared independently of a phylogenetic framework. This number ranges from 6 between *T. pygargus* ($2n = 22/23$) and *T. tranieri* ($2n = 14/15$) or *T. petteri* ($2n = 18/19$), to 21 between *T. gracilis* ($2n = 36/37$) and *T. petteri* or *T. tranieri* (see Figure 4). In total, at least 38 mutations have been fixed during the course of the West African *Taterillus* investigated here (Figure 4). Divergence times between *Taterillus*-specific lineages were estimated on molecular grounds, suggesting that East and West African species split ~ 3.5 Myr

ago, *T. gracilis* and the other West African species ~ 2 Myr, whereas the six most derived West African species have radiated during the last 0.4 Myr (Dobigny, 2002; see also Chevret and Dobigny, 2005). This is one of the most recent speciation events documented in mammals. As such, it is of interest to compare the tempo of chromosomal change among these species to those observed in eutherian lineages usually considered as the most chromosomally active ones.

Dog-like carnivores provide several examples of quite extensive karyotypical evolution and are thought to display the highest genomic rate of evolution documented so far in placental (see Table 1 in Murphy *et al*, 2003). For instance, the red and arctic foxes diverged only 2 Myr ago (Bininda-Emonds *et al*, 1999) but their karyotypes already differ by more than 30 karyotypical rearrangements (Nash *et al*, 2001). Extant gibbons constitute

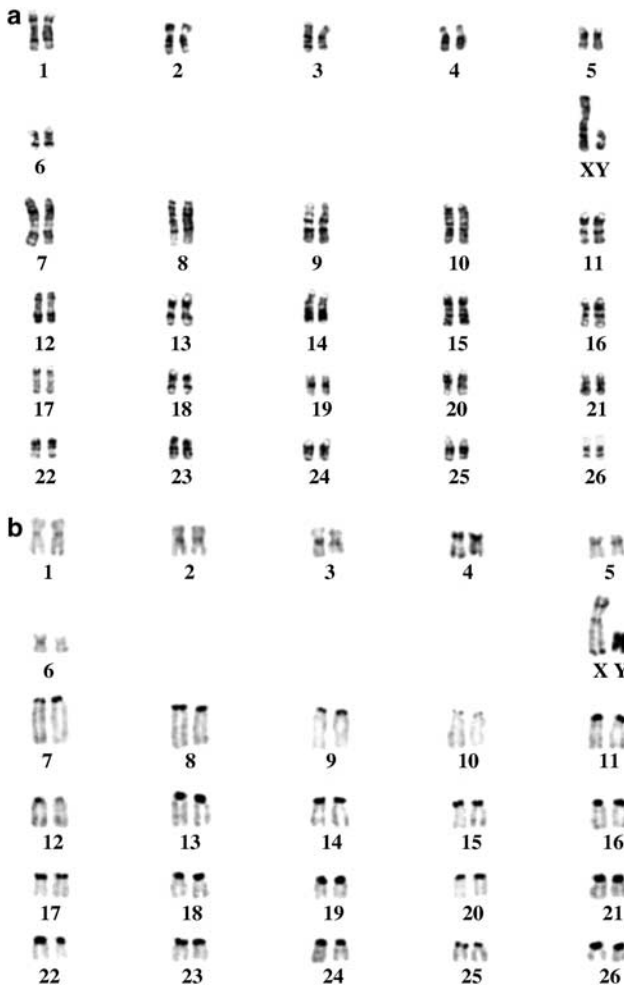


Figure 1 (a) G-banded and (b) C-banded karyotype of *T. congicus*.

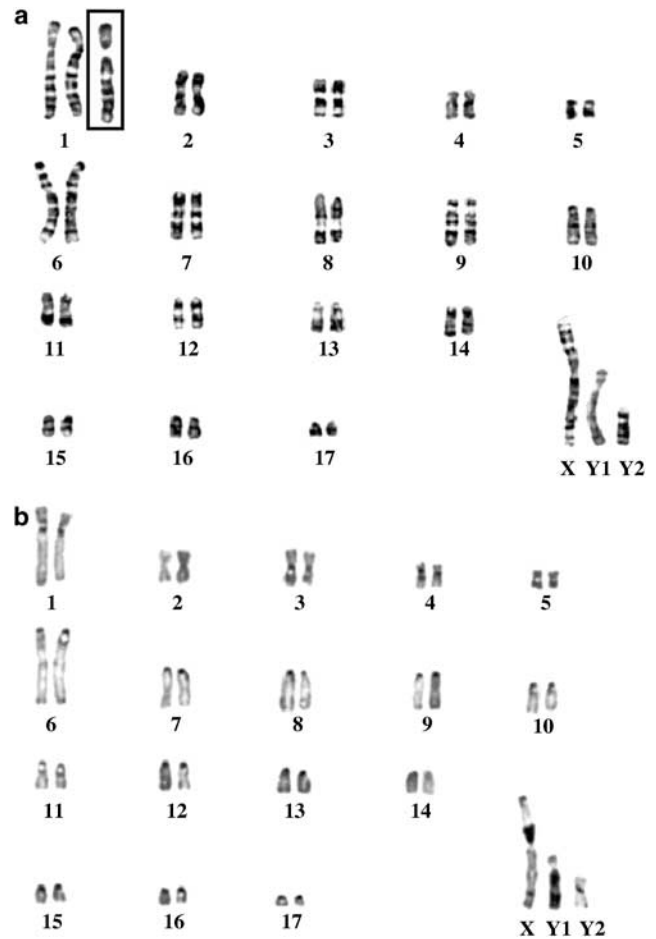


Figure 2 (a) G-banded and (b) C-banded karyotype of *T. gracilis*. The nonfused chromosomes homologous to pair 1 and involved in the Robertsonian polymorphism (see text for details) are presented in the box.

another well-documented case of genome repatterning since *Hylobates hoolock* and *H. leucogenys* differ by 62 (Müller *et al*, 2003) to 83 (Nie *et al*, 2001) rearrangements. Dates of divergence between gibbons lineages are still controversial but they probably diverged from each other soon after the hylobatids/great apes split, that is, approximately 5 Myr ago (Roos and Geissmann, 2001). Explosive chromosomal evolution is also found in equids, where the *E. caballus* karyotype differs from those of *E. burchelli* and *E. zebra hartmannae* by 23 and 32 rearrangements, respectively (Yang *et al*, 2003), whereas the four extant equid lineages are thought to have differentiated only recently (~2.4 myr bp; Oakenfull and Clegg, 1998). Yet, the most striking example is provided by muntjak deer, with more than 30 karyotypic changes which have been fixed between the Indian and the Chinese muntjaks (see Figure 4 in Yang *et al*, 1997) since their last common ancestor between 0.9 and 3.7 Myr ago (Wang and Lan, 2000).

Although we are aware that other factors (such as generation time) should be taken into account for comparing evolutionary rates, we can approximate the tempo of chromosomal evolution by a simple ratio between the number of changes and times of divergence. Considering only the highest values available for the previous examples, the average rate of chromosomal

change per myr reaches 13.3, 15, 16.6 and 33.3 in these equids, carnivores, primates and cervids, respectively. It was suggested that genomic rearrangements between mouse and rat proceed 10 times faster than between human and cat (Stanyon *et al*, 1999) suggesting high rates of chromosomal changes in some rodents. Indeed, several investigations in other rodent groups showed that they sometimes undergo extensive genome repatterning leading and/or accompanying rapid and successive speciation events (Bell *et al*, 2001; Volobouev *et al*, 2002). Although at the intraspecific level, the Robertsonian populations of house mice provide several striking examples of extremely rapid karyotypic evolution in rodents (eg, Britton-Davidian *et al*, 2000; reviewed in Pialek *et al*, 2005). Our analysis of West African *Taterillus* largely support this view as the most recently diverged karyospecies (*T. tranieri* or *T. pygargus* and *Taterillus* sp1 or *Taterillus* sp2; Figure 4) differ by 18 changes, leading to an average rate of 45 changes per myr.

The speciation process in *Taterillus*

The high interspecific chromosomal divergence is in sharp contrast with the low levels of morphological and molecular differences and are hardly compatible with the

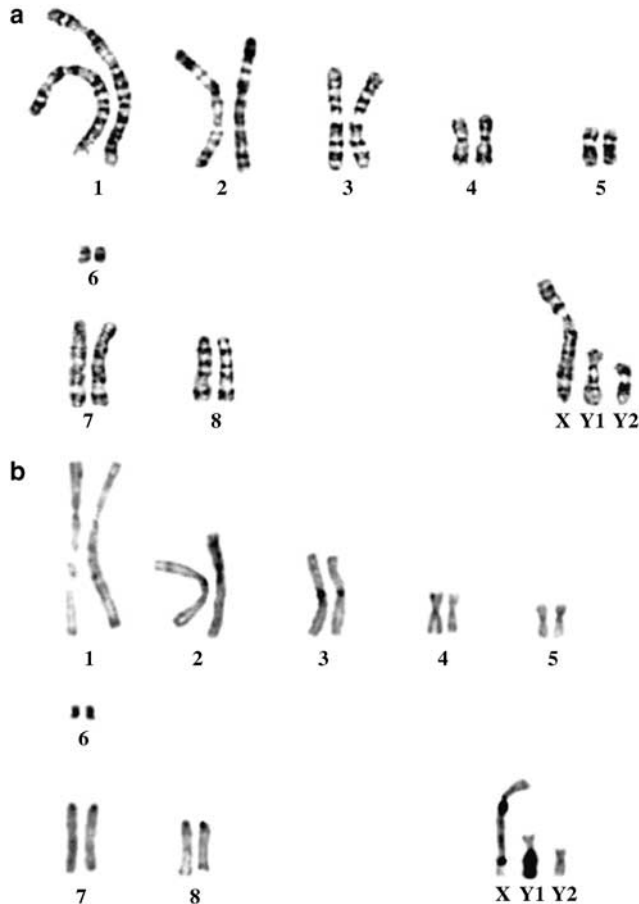


Figure 3 (a) G-banded and (b) C-banded karyotype of *T. petteri*.

speciation models supporting a leading role of genetic divergence (Orr, 2001). Mutations on major genes, which could not have been detected by the molecular analyses (mainly on neutral markers) performed to date in *Taterillus*, may be responsible for these extremely rapid series of speciation events, or at least some of them. However, this type of process has never been demonstrated in mammals and appears quite unlikely to have occurred six times during the last 0.4 Myr (but see Forejt, 1996). As a consequence, although finer-scale genetic investigations would be needed to confirm such a conclusion, it seems probable that genic differences are not a valuable explanation for all speciation events in *Taterillus*.

Ecological and sexual selection speciation models have recently received renewed interest (Panhuis *et al*, 2001; Greenberg *et al*, 2003). These authors propose a role for disruptive selection, which could lead to eco-ethological differentiation and prezygotic isolation. Some evidence regarding these processes is available from eco-ethological and physiological studies were conducted in West African *Taterillus* species (Poulet, 1981; Hubert, 1982; Sicard, 1992). Unfortunately, all of them concentrate on one or two species, and only allow one to compare *T. gracilis* (the most basal and anciently diverged West African species) with *T. pygargus* or *T. petteri* (which both belong to the most recently derived clade). Experiments in captivity showed that F1 hybrids between *T. gracilis* and *T. pygargus* could be produced, but that these

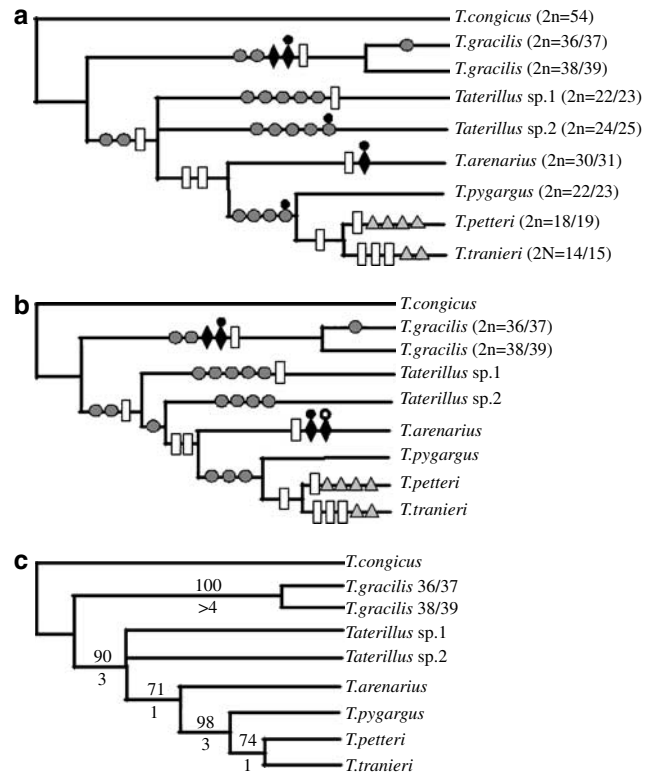


Figure 4 (a, b) The two most parsimonious trees ($L = 48$) retrieved from our cladistic analysis of chromosomal characters in West African *Taterillus*, and (c) their consensus tree. The polarization of each character changes were assessed *a posteriori* using outgroup comparison. Gray circles, black losanges, white blocks and gray triangles represent Robertsonian fusions, centric fissions, tandem fusions and pericentric inversions, respectively. Close and open circles above these symbols correspond to convergent and reversal events, respectively. Bootstrap and decay index values are indicated above and below the branches of the consensus tree, respectively.

hybrids are sterile (Baron *et al*, 1974; Petter, unpublished). Although reproductive features are sometimes different between captivity and nature (eg, Forejt, 1996), this suggests a possible absence of prezygotic isolation and confirms the existence of a post-zygotic barrier. Furthermore, and probably more important, no sister species (as inferred from the topology provided on Figure 4) are known to live in sympatry (Figure 5). On the contrary, species distributions are clearly allopatric. Taken together, these data suggest that ecological and sexual speciation models may not be suitable for *Taterillus* biology and evolution.

We recently presented pairwise comparisons between *Taterillus* sp1, *Taterillus* sp2, *T. petteri* and *T. tranieri* by reconstructing the very complex theoretical meiotic configurations in potential hybrids (see Dobigny *et al*, 2002a, 2003a). The latter strongly suggested postzygotic isolation due to important karyotypic differences. Here, we can extend these results to all West African species. Indeed, mapping of chromosomal changes on the tree demonstrate that all pairwise differences between species include at least one tandem fusion (and up to 8) and/or Robertsonian fusions with monobrachial homologies (Figure 4) which are both known to be highly deleterious (Baker and Bickham, 1986; Elder and Hsu, 1988; King, 1993).

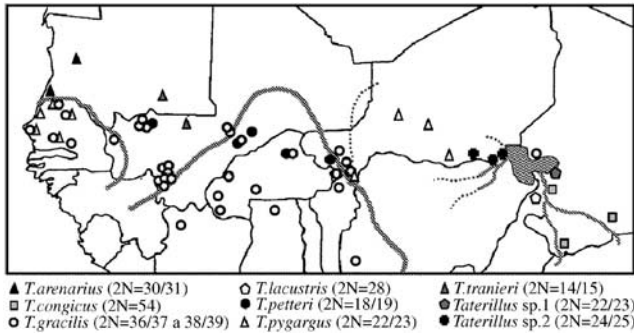


Figure 5 Specific geographic distributions based only on non-ambiguous cytotaxonomic identification. Data were obtained from this study as well as unpublished results from the Muséum National d'Histoire Naturelle and the Institut de Recherche pour le Développement, France. Main permanent and seasonal river courses which may have played a role in shaping *Taterillus*-specific distributions are indicated as solid and dash lines, respectively. Waves symbolize current surface of Lake Chad.

Monobrachial homologies can be fixed very quickly, as observed in domestic mice on Madeira Island where 20 different fusions have been fixed within the last 500 years (Britton-Davidian *et al*, 2000). Tandem translocations have also been fixed in several mammalian lineages (eg, Rodentia: Elder, 1980; Fagundes *et al*, 1997; Artiodactyla: Yang *et al*, 1997; Carnivora: Nash *et al*, 2001; reviewed in King, 1993) although no case of polymorphism has been documented, with the possible exception of the bat *Uroderma bilobatum*. The latter species has been claimed to display cases of double heterozygotes for tandem translocations (see Table 1 in Owen and Baker, 2001). However, no banding data were provided by the authors that would have allowed for a nonambiguous identification of the rearrangements involved. Although prezygotic factors cannot be excluded, crossing experiments between *Otomys* cytotypes (Rodentia, Muridae) differing by a single tandem translocation were only 4% successful (Taylor, 2000). Together these data strongly suggest that (1) tandem translocations are highly deleterious for an heterozygous carrier, and that (2) when they occur and reach the homozygous state, they probably insure an almost instantly and complete reproductive isolation. If this is indeed the case, their presence in the homozygous state within a population would lead either to nearly instantaneous extinction or to the independent evolution (ie speciation) of the nascent cytotype. In *Taterillus*, tandem translocations were particularly numerous, mainly in the most recently speciated groups (Figure 4). The occurrence of this particular class of rearrangements was confirmed by an *in situ* hybridization survey showing the presence of Interstitial Telomeric Signals, which were correlated with the breakpoints of the tandem translocations inferred by the comparison of the GTG-banding patterns (Dobigny *et al*, 2003b). In conclusion, the successive fixation of monobrachial homology and tandem translocations during *Taterillus* genome repatterning must have been rapid events, maybe following an 'all-or-none' rule, and which may not have required other changes than chromosomal ones. This makes it reasonable to assume that the West African *Taterillus* have differentiated following karyotype repatterning, thus illustrating a new case of chromosomal speciation.

The probable role of paleoclimatic changes in West Africa Considering the type of chromosome changes that led to *Taterillus* differentiation, it is also highly probable that the karyotypic changes characterizing the extant species were fixed in very small, isolated populations as predicted by the population cytogenetic models of Lande (1979, 1985) and Chesser and Baker (1986).

Thanks to a growing amount of nonambiguous cytotaxonomic data (see references above, this study, and unpublished data from the Muséum National d'Histoire Naturelle and Institut de Recherche pour le Développement), it is now possible to precisely delimit the West African *Taterillus* species distributions (Figure 5). It is apparent that several of the species' ranges are parapatric and often demarcated by main river courses. In addition, the most derived species display rather narrow geographic ranges compared to the widely distributed *T. gracilis*, which occupies the Sahel and Sudan savannah from Senegal to Chad and Nigeria (Figure 5). Moreover, the six derived species are restricted to the northernmost arid Sahel regions up to the border of the Sahara desert (Figure 5). Interestingly, the latter areas were also the most influenced by the paleoclimatic variations of the Sahara (reviewed in Rognon, 1993). Indeed, during the last 4 Myr, the desert has undergone important changes, rendering its boundaries highly variable. On the one hand, many regions which are now dry where once much more humid, sometimes harboring steppe, savannah or even forest conditions. On the other hand, the desert has displayed periods of expansion, when the extant Sahelian region was a wide desert band of sand dunes (Rognon, 1993). The frequency of the Saharan cycles of desert spread and retraction are estimated to have occurred at cycles of approximately 100 000–20 000 years during the last 3 Myr (Rognon, 1993). *Taterillus* species are not adapted to strictly desert environments and prefer subdesert to more moist conditions (Nowak, 1999). Assuming that their ecological preferences have not significantly changed during the last 4 Myr, it is very likely that these rapid and important paleoclimatic shifts have affected their geographic distribution and evolution.

Petter's (1974) hypothesis of speciation during wet periods following population fragmentation by great rivers does not fit the population cytogenetics patterns observed here, and thus appears highly improbable. Indeed, during such periods, environmental conditions must have been suitable for the expansion of *Taterillus*, allowing wide geographic distributions and consequently preventing cytogenetic drift. On the contrary, their phylogenetic relationships, their redefined geographic ranges and the chromosomal changes that characterize their evolution largely support Sicard *et al*'s (1988) hypothesis. This proposes that during particularly dry periods, *Taterillus* individuals may have been trapped in refuge habitats that still displayed subarid conditions. These small and isolated demes would have provided the necessary population bottlenecks for underdominant karyotypic rearrangements to be stochastically fixed (Lande, 1979, 1985), thus leading to allopatric speciation. It is interesting to note that such refuges have already been identified, including the neighborhood of Lake Chad (cf. Granjon and Dobigny, 2003, and references therein), the coastal and the inner deltas of the Senegal and Niger rivers (see Rognon, 1993).

This hypothesis is further supported by the more southern and wide distribution of the basal species, *T. gracilis*, suggesting this species has never benefited from conditions favoring the fixation of highly deleterious changes. If our conclusions are correct, the current pattern of parapatric-specific distributions result from expansion from discrete refugial areas during more favorable periods. These dispersal phases have subsequently been constrained by the main river courses as *Taterillus* cannot swim (Petter, personal communication).

Conclusion: population and genomic features required for allopatric chromosomal speciation

Since some organisms have fixed no or only a few karyotypical changes during very long periods of time (eg, Marsupialia: Rens *et al*, 2001; Perissodactyla, Rhinocerotidae: Trifonov *et al*, 2003), rapid genome repatterning, like that described here, must imply special conditions. In particular, it requires a high rate of both occurrence and fixation of chromosomal mutations.

As far as the *Taterillus* species are concerned, both the populations' demography and the genomes' lability may be appropriate. As suggested hereabove, the Sahara Desert's variation in both space (leading to the formation of different potential refuge habitats throughout the extant Sahel and Sahara regions) and time (the successive cycles of spreading/contraction of the desert) may have provided the population bottlenecks required for the recurrent fixation of chromosomal rearrangements. Furthermore, the *Taterillus* genome has been shown to display several atypical characteristics, which may reflect a high genomic plasticity. For instance, it displays 28S and 5S rDNA gene clusters that are variable between and within species both in number and location (Dobigny *et al*, 2003b), probably reflecting extensive fine-scale genomic reorganization. In addition, the explosive karyotype repatterning has been accompanied by amplification of LINE-1 retrotransposons (Dobigny *et al*, 2004b). Finally, *T. congicus* possesses C-positive pericentromeric blocks which are not observed in the West African species (Figure 6). Such highly repeated sequences may have favored the occurrence of chromosome mutations such as Robertsonian fusions in the ancestral genome, and have been subsequently lost, as in case of the European house mouse (Garagna *et al*, 2001). All

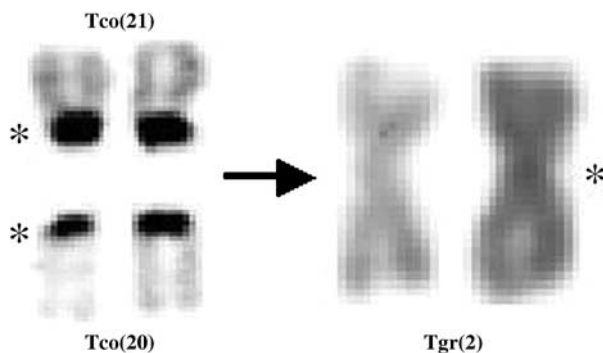


Figure 6 Example of the loss of C-positive pericentromeric heterochromatin after centric fusion of *T. congicus* pairs 20 and 21 homologous to *T. gracilis* pair 2. Asterisks indicate positions of centromeres.

these properties suggest that the *Taterillus* genome is (or has recently been) is particularly plastic and may consequently have a high probability of chromosomal mutation.

This model of simultaneous and favorable conditions at both the populational and genomic levels would explain the very rapid fixation of strongly underdominant mutations. It has been proposed to explain extensive karyotypic evolution in muntjak deer (Wang and Lan, 2000). In the case of *Taterillus*, all genetic, cytogenetic and biogeographic data support such a view. It would be worth testing this hypothesis using population genetics surveys of microsatellite data, in order to detect and date populational bottlenecks in relation to paleoclimatic changes and the temporal phylogenetic framework now available.

Acknowledgements

We are grateful to J Britton-Davidian, TJ Robinson and F Veyrunes for helpful comments and suggestions on the manuscript. S Ag Atteynine, M Angaya, K Bâ, C Denys, A Doukary, J-C Gautun, C Houssin, E Lecompte, A Nomao, A Oumarou, B Sicard, I Sidibé and B Sidiki are gratefully acknowledged for their help in the field. The data from Ibadan, Nigeria, were kindly provided by M Tranier.

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