



A tale of two African mongooses (Carnivora: Herpestidae): differing genetic diversity and geographical structure across a continent

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Received: 6 April 2022 / Accepted: 28 September 2022 / Published online: 13 October 2022
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Abstract

Phylogeographies of African mammals reveal patterns that correlate with Pleistocene environmental fluctuations and geographical barriers, which may affect species differently according to their habitat preferences and dispersal capabilities. The marsh mongoose *Atilax paludinosus*, a widely distributed African carnivoran, is a good model to compare with other African mammals. Here, we aimed to determine if its phylogeographical patterns depend on habitat preferences or other factors, such as dispersal capabilities. One nuclear and two mitochondrial markers were sequenced for marsh mongooses sampled throughout the species range, and sequences were also analysed for another widely distributed African mongoose, the white-tailed mongoose *Ichneumia albicauda*, previously studied, but more completely for this study. In the marsh mongoose we observed a deep divergence between West + Central Africa and East + South Africa, a pattern also observed in both forest and savanna mammals. With good dispersal capabilities and a preference for riparian habitats, the marsh mongoose may have been confined to forest refugia during Quaternary dry periods and may have used rivers as dispersal corridors. In contrast, in the white-tailed mongoose, the haplogroups were strongly divergent which may indicate more limited dispersal capabilities, but also reflect the preference of this species for more open habitats. These results suggest that life history traits, in addition to habitat preferences, had an impact on how these species were affected by past environmental changes, which is reflected in the geographical genetic structure today.

Keywords Herpestidae · Africa · Phylogeography · Dispersal capabilities · Mitochondrial DNA

Introduction

Comparison of phylogeographical patterns in different species is an important approach to understand the factors driving the diversification and distribution of biodiversity, especially when comparing species with similar and contrasting

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habitat preferences or life history traits. The diversity and distribution of African mammal species are suggested to have been impacted by the climatic fluctuations of the Pleistocene (2.58–0.012 Myr; Walker et al. 2018) and by past and present geographical barriers (see e.g., Nicolas et al. 2008; Olayemi et al. 2012; Jacquet et al. 2014; Bohoussou et al. 2015; Hassanin et al. 2015; Mizerovska et al. 2019). Indeed, the retreat of rainforests resulting from drier climates during glacial periods of the Pleistocene, which created forest refugia separated by drier habitats, has been proposed as a driver of forest species diversification (Moritz et al. 2000). Pleistocene climatic changes affected both savanna and forest vegetation; glacial periods led to expansion of savanna into tropical regions that were previously occupied by rainforest, and to its recession in northern regions, where deserts expanded (Donkpegan et al. 2020). During interglacial periods rainforest replaced savanna in the tropical region and savanna expanded. While rainforest survived in fragmented refugia during cold periods, savanna vegetation was not necessarily fragmented during interglacial humid periods (Donkpegan et al. 2020), although some studies on mammals suggest otherwise (see e.g. Lorenzen et al. 2012; Cuyper et al. 2022). At least five major Pleistocene rainfall and drought cycles provoked shifts in vegetation (Szabo et al. 1995), and glacial forest refugia have been identified in the Afrotropics (see e.g. Maley 1996; Anthony et al. 2007; Born et al. 2011; Stribna et al. 2019).

Several phylogeographies of African mammals display patterns that distinguish for instance populations from West and Central Africa (e.g., fruit bats, Hassanin et al. 2015); West + Central African populations from East + South African populations (see review in Bertola et al. 2016; bushbucks, *Tragelaphus* spp., Hassanin et al. 2018); West + Central, East, and South populations (e.g., African buffalos, *Syncerus caffer*, Lorenzen et al. 2012), as well as North from South (e.g. lions, *Panthera leo*, Bertola et al. 2016; giraffes, *Giraffa* spp., Petzold et al. 2020), highlighting the role of variation in the extent of dry deserts, savannas, dense rainforests and hydrographical networks during the Pleistocene. Compared with small carnivores and herbivores, Werdelin (2008) pointed out that large carnivores do not show a strong geographical structuring of their populations due to their high mobility, which prevents population isolation.

The Herpestidae (Carnivora) are small species that mainly feed on small prey and live in various habitats in Africa and Asia (Jennings and Veron 2019). The family comprises 25 African and nine Asian mongoose species (Veron et al. 2022). A few mongooses are widely distributed in Africa, including the marsh mongoose *Atilax paludinosus*, the common slender mongoose *Galerella sanguinea*, the Egyptian mongoose *Herpestes ichneumon*, the white-tailed mongoose *Ichneumia albicauda*, and the banded mongoose *Mungos mungo* (Jennings and Veron 2019). The genetic structure of

a few mongoose species has been studied, among them the white-tailed mongoose (Dehghani et al. 2008) and the Egyptian mongoose (Gaubert et al. 2011); both species occur in a wide diversity of habitats, but avoid rainforests (Do Linh San 2015; Do Linh San et al. 2016). Among the forest species, the geographical genetic structure has been studied in the cusimanses *Crossarchus* spp. (Sonet et al. 2014), but each of the four cusimanse species has a restricted range in the tropical rainforests of Central and West Africa.

The marsh mongoose appears to be an appropriate model to study the geographical pattern of an African species, as this species ranges throughout most of sub-Saharan Africa (Yalden et al. 1996; Gilchrist et al. 2009). It is a quite large (up to 4 kg; head-and-body length up to 50 cm), dark, shaggy mongoose, characterised by unwebbed feet and naked plantar surfaces, and a tail almost as long as head-and-body length (Gilchrist et al. 2009). The species occurs from sea level to 3950 m, from Senegal eastward to Ethiopia and south to southern Africa, where it is present in the eastern parts of the region, as well as along the coast (Gilchrist et al. 2009; Baker et al. 2016). Its populations are estimated to be decreasing, likely in relation to habitat loss and hunting (Do Linh San et al. 2015). The ecology of the marsh mongoose has been studied by Baker (see reviews in Baker 1992 and Baker and Ray 2013), Ray (1997), and more recently by Do Linh San et al. (2020) and Streicher et al. (2020; 2021). These studies showed that the species occurs in various habitats, but is mainly restricted to riparian habitats with suitable vegetation cover in the proximity of water. Although the species can be found in urban mosaics, in such environments it still favours forest and bushland close to natural water sources (Streicher et al. 2021). A camera-trap study in various habitats in Gabon also confirms this preference with much higher capture rates along streams than in forest and no detection in savanna (Nakashima et al. 2022). Thus, the species appears to favour forest habitats, in particular swamp forests in Central Africa, although it also occurs in mixed or degraded habitats in other regions, but with the need for water proximity and dense vegetation. The marsh mongoose consumes mainly aquatic preys, such as amphibians, fishes, crustaceans and other aquatic arthropods, although in some areas, small mammals, terrestrial insects and birds are important food sources (Ray and Sunquist 2001; Baker et al. 2016). The home range of the marsh mongoose covers 0.85–11.8 km², with marked differences between the various studies that may be due to methodology, habitat specificity and prey population density (see Streicher et al. 2020). Marsh mongooses can travel over 4 km in 12 h along streams (Ray 1997).

Using molecular data, the marsh mongoose has been shown to be the closest relative of the long-nosed mongoose *Xenogale naso* by Veron et al. (2004), with both species forming a sister clade to the Asian mongooses (Perez et al.

2006; Patou et al. 2009). Hassanin et al. (2021) estimated that *Atilax paludinosus* and *Xenogale naso* have diverged around 7–6.3 Myr. Ten subspecies have been recognised in the marsh mongoose (see Coetzee 1977; Baker 1992; Gilchrist et al. 2009; Supplementary Figure 1): *A. p. macrodon* Allen, 1924 (Type locality in the Democratic Republic of the Congo, thereafter DRC), *A. p. mitis* (Thomas, 1903) (Ethiopia), *A. p. mordax* (Thomas, 1912) (Tanzania), *A. p. paludinosus* (Cuvier, 1829) (South Africa), *A. p. pluto* (Temminck, 1853) (Ghana), *A. p. robustus* Gray, 1865 (Sudan), *A. p. rubellus* (Thomas and Wroughton, 1908) (Mozambique), *A. p. rubescens* (Hollister, 1912) (Tanzania), *A. p. spadiceus* Cabrera, 1921 (Equatorial Guinea), and *A. p. transvaalensis* Roberts, 1933 (South Africa). The subspecies descriptions have been based on differences in coat colour (varying from brown to blackish), body size, skull robustness, and number of premolars (three or four premolars, the first one being always small and sometimes missing). However, no recent taxonomic revision has been conducted, and the validity of these subspecies has never been tested using genetic data.

The main purpose of this study was to determine the genetic polymorphism, geographical structure and population differentiation of marsh mongoose populations, in order to test if the phylogeographical pattern in this species is similar to that observed in other African mammals showing a wide distribution in sub-Saharan Africa. This may reveal whether this species was affected by habitat changes related to the climatic fluctuations of the Pleistocene and geographical barriers in the same way as other species. The results may also provide a framework for future taxonomic revision of the subspecies. To achieve these goals, one nuclear and two mitochondrial markers were sequenced for marsh mongoose individuals sampled throughout the species range. For comparisons with another mongoose species with a large distribution in Africa, sequences were also obtained for the white-tailed mongoose, and available GenBank sequences were gathered for both species. Genetic structure and population differentiation of these wide-ranging African mongoose species could then be compared to the patterns observed in other mammals. Our expectations were that the marsh mongoose, which needs vegetation cover, may have been affected in the past by environmental changes similarly to other forest species, while open-habitat species may display contrasting patterns.

Material and methods

Sampling, extraction, PCR and sequencing

We analysed samples (muscle and skin tissues, hair samples, and dry tissues from museum specimens) from 16 individuals of *Atilax paludinosus* and 25 individuals of *Ichneumia*

albicauda (Supplementary Table 1). DNA was isolated following a cetyltrimethylammonium bromide (CTAB)-based protocol (Winnepenninckx et al. 1993). For museum samples, dithiothreitol (DTT 1 M, ca 8–15 μ L per extract) was added during lysis to break up disulphide bonds, and the lysis time was increased (up to 72 h).

We sequenced two mitochondrial fragments: the whole Cytochrome b (Cytb) and the hypervariable region 1 of the Control Region (CR), using published primers (Cytb: Veron and Heard 2000; Veron et al. 2004, 2014; CR: Palomares et al. 2002). To provide an evolutionary assessment independent from mitochondrial markers, we also sequenced the nuclear marker Beta-fibrinogen intron 7 (FGB), using the primers from Yu and Zhang (2005).

Polymerase chain reactions (PCRs) were performed as in Veron et al. (2014), with annealing temperatures of 50 °C for Cytb, 61 °C for CR, and 59 °C for FGB. PCR products were sent to Eurofins Genomics (Ebersberg, Germany) for purification and sequencing (on Applied Biosystem® 3730XL DNA Analyzer). Sequences were edited and aligned manually using Bioedit (version 7; Hall 1999).

Phylogenetic and haplotypic network analyses

Phylogenetic analyses for each marker were performed using the Maximum Likelihood (ML) method, as implemented in MEGA X (Kumar et al. 2018). We rooted the phylogenetic trees with four representatives of the families Eupleridae (sister-group to the Herpestidae) and Hyaenidae (sister-group to Herpestidae + Eupleridae). The best-fitting model was estimated using MEGAX, following the Akaike information criterion (AIC). The selected model was implemented in the ML analyses and node robustness was assessed through 1000 bootstrap replicates.

We compared resulting topologies and node support; nodes were considered as supported when bootstrap values were $\geq 70\%$.

We employed DNAsp6 (Rozas et al. 2017) for defining haplotypes, and PopART (<http://popart.otago.ac.nz/>; Leigh and Bryant 2015) to construct haplotype median-joining networks (Bandelt et al. 1999) for each fragment. We computed genetic distances using MEGA X, and genetic diversity and population differentiation using DNAsp6.

Results

Sequencing results

We obtained 35 new Cytb sequences, 19 new CR sequences, and 21 new FGB sequences for the marsh mongoose and the white-tailed mongoose (GenBank # OL362113 to OL362191, Supplementary Table 1).

New Cytb and CR sequences were also obtained for two individuals of the long-nosed mongoose. The GenBank sequences were from Palomares et al. 2002; Yoder et al. 2003; Gaubert et al. 2004; Veron et al. 2004; Koepfli et al. 2006; Markotter et al. 2006; Perez et al. 2006; Morley et al. 2007; Dehghani et al. 2008; Fernandes et al. 2008; Patou et al. 2009; Fernandes 2011; Gaubert et al. 2011; Rapson et al. 2012; Sonet et al. 2014; Veron et al. 2015a; Barros et al. 2016; Hassanin and Veron 2016; Gryseels et al. 2020.

The whole Cytb gene (1140 bp) was used to reconstruct the Herpestidae phylogeny and species phylogeographies. Due to missing data in some sequences (in museum and badly preserved samples) and in some of the GenBank sequences, Cytb haplotypes and analyses of population differentiation were computed using a shorter fragment (601 bp located between the position 159 and 759 on the Cytb gene). The CR fragment obtained was 360 bp long for the marsh mongoose and 364 bp long for the white-tailed mongoose. The FGB fragment was 619 bp long.

The Cytb alignment includes 1140 bp for 129 samples, representing 21 mongoose species (19 African species and two Asian species), as well as two species of Eupleridae and two species of Hyaenidae as outgroups (563 variable sites, including 473 informative sites; ML model: HKY + G + I). The phylogenetic analyses suggested the re-identification of three samples initially identified as the marsh mongoose (see “Discussion” section), including two samples from Tanzania (FMNH 208458 and FMNH 211260), which appeared to be the bushy-tailed mongoose *Bdeogale crassicauda*, and another from Guinea (MNHN PP054), which was found to be a white-tailed mongoose *Ichneumia albicauda*.

The divergence between the Herpestidae species ranges from 4.57% (between the *Bdeogale* species) to 18.42% (between *Suricata* and *Mungos*). Among the 16 African mongoose species represented by more than one individual, the highest intraspecific Cytb distances (> 4%; Table 1) are found in the wide-ranging species, i.e., in the common slender mongoose *Galerella sanguinea*, then in the white-tailed mongoose *Ichneumia albicauda*, the marsh mongoose *Atilax paludinosus* and the banded mongoose *Mungos mungo*.

Genetic structure of the two wide-ranging African mongoose species

Marsh mongoose *Atilax paludinosus*

The dataset includes sequences from 17 individuals from nine countries in Africa (see sample localities on Fig. 1).

The Cytb phylogeography of the marsh mongoose (alignment length: 1140 bp, Model ML HKY + G + I) shows two main well-supported clades (Fig. 2). One clade includes all the four samples from South Africa, one sample from

Table 1 Comparison of Cytb genetic diversity in African mongoose species. Length of fragment used : 1140 bp

Species	N	Mean dist (%)	V	Pi
<i>Atilax paludinosus</i>	16	4.14	130	86
<i>Bdeogale crassicauda</i>	3	2.46	40	0
<i>Crossarchus alexandri</i>	4	1.52	31	7
<i>Crossarchus obscurus</i>	2	1.07	12	0
<i>Crossarchus platycephalus</i>	3	1.11	19	0
<i>Cynictis penicillata</i>	4	0.65	14	3
<i>Galerella nigrata</i>	14	0.56	27	13
<i>Galerella pulverulenta</i>	2	1.27	14	0
<i>Galerella sanguinea</i>	13	5.04	136	108
<i>Helogale parvula</i>	2	3.77	38	0
<i>Herpestes ichneumon</i>	21	0.56	27	8
<i>Ichneumia albicauda</i>	23	4.45	135	121
<i>Liberiictis kuhni</i>	2	0.00	0	0
<i>Mungos mungo</i>	4	4.10	78	7
<i>Suricata suricatta</i>	2	2.47	27	0
<i>Xenogale naso</i>	4	1.16	26	0

Marsh and white-tailed mongooses in bold

N: number of samples; mean dist: overall mean distance; V: number of variable sites; Pi: number of parsimony informative sites

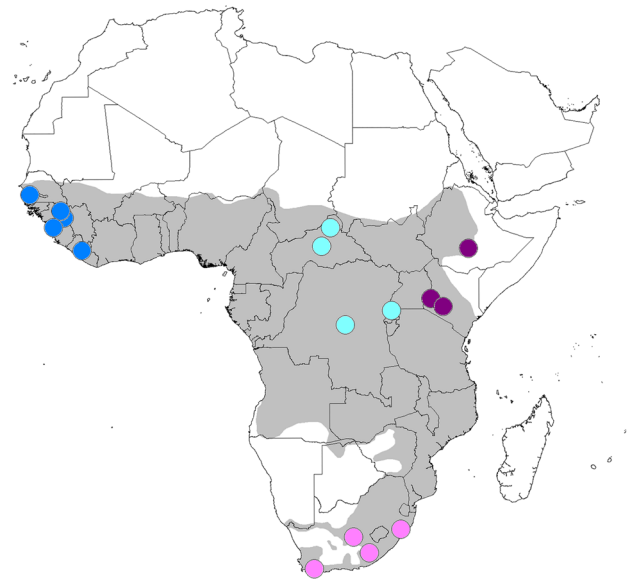


Fig. 1 Localities of the samples of the marsh mongoose *Atilax paludinosus* used in this study. The distribution of the species according to the IUCN Red List map (Do Linh San et al. 2015) is shown in grey shading. Localities are coloured by regions: West (blue), Center (light blue), East (purple) and South (pink)

Ethiopia, and one sample from eastern Kenya. The other clade comprises two well-supported sub-clades; one West African clade (Guinea and Liberia); and one Central African

Fig. 2 ML Cytb tree for the marsh mongoose *Atilax paludinosus* (Alignment length: 1140 bp; model: HKY + G + I), with countries of origin. The boxes indicate the main regions (colour as on Fig. 1). The sample ApF9668 is from the western part of Kenya, while the sample ApTC059 is from the eastern part of Kenya (see the text)

clade (Central African Republic, DRC, Uganda, and also one sample from western Kenya).

Cytb haplotypes were computed using the reduced Cytb alignment of 601 bp (see Table 2). All the samples have a unique haplotype, except four samples: ApDQ512859 and ApTC161, which are both from South Africa and share the same haplotype; ApF9668 (from Kenya) and ApMN597509 (from the DRC), which share the same haplotype. The Cytb haplotype network (Fig. 3) shows one haplogroup (South + East Africa), including samples from South Africa, Ethiopia and eastern Kenya; another group (Central Africa) with samples from Uganda, DRC, Central African Republic and western Kenya; and a third haplogroup (West Africa) with samples from Guinea and Liberia. The two latter haplogroups (Central + West Africa) are separated by at least seven mutations, while the South + East Africa group is much more distant, and separated from the two other haplogroups by at least 28 mutations. Within the South + East Africa group, the Ethiopian sample is the most distant (nine mutations).

The two samples from Kenya are thus found in two different haplogroups; one found in the Central African haplogroup (ApF9668) is from a locality in the West of Kenya, not far from the border with Uganda (Kakamega Forest National Park), while the sample found within the South + East African group (ApTC059) is located further East (Naivasha).

The Cytb sequence obtained for the museum sample from Senegal (ApM1995, specimen MNHN 1995-427) was too short (263 bp) to be included in the haplotype network analyses; however, this sequence belongs to the West African haplogroup, where it is close to a sample from Guinea (ApPP001).

The CR haplotype network (see Table 2) shows a similar pattern (Fig. 3). The South + East African haplogroup is separated by at least 24 mutations from the other haplogroups, and the West + Central African haplogroups are separated by at least 11 mutations from each other.

The FGB haplotype network (see Table 2 for details; Fig. 3) includes only four haplotypes, each separated by one mutation; West Africa is represented by two unshared haplotypes; Central Africa is also represented by two haplotypes, one unshared, and one shared with South and East Africa.

White-tailed mongoose *Ichneumia albicauda*

The dataset includes sequences from 53 individuals from 14 countries (see sample localities on Fig. 4).

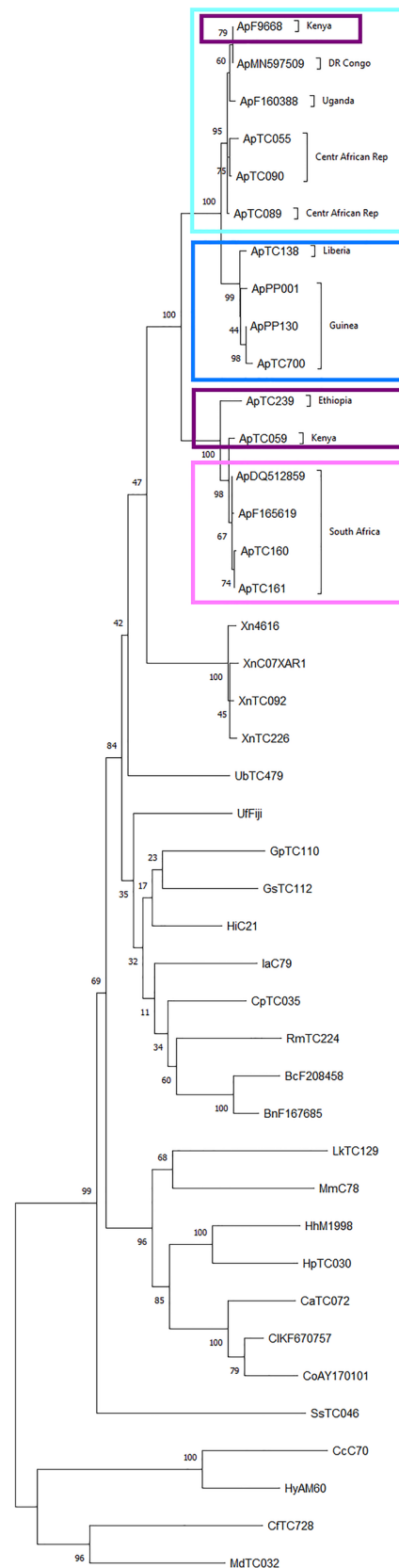


Table 2 Haplotype genetic diversity estimates within African mongoose species for each marker. The length of the fragments used was for Cytb: 601 bp; for CR: 360-364 bp; and for FGB: 619 bp

	Cytb						
	<i>N</i>	<i>n</i>	<i>h</i>	Hd	Pi	<i>S</i>	<i>k</i>
<i>Atilax paludinosus</i>	16	578	14	0.9830	0.0363	60	21.00
<i>Ichneumia albicauda</i>	22	567	16	0.9740	0.0414	63	23.45
	CR						
	<i>N</i>	<i>n</i>	<i>h</i>	Hd	Pi	<i>S</i>	<i>k</i>
<i>Atilax paludinosus</i>	12	350	12	1.0000	0.0513	45	17.9
<i>Ichneumia albicauda</i>	55	303	26	0.9360	0.0466	53	14.1
	FGB						
	<i>N</i>	<i>n</i>	<i>h</i>	Hd	Pi	<i>S</i>	<i>k</i>
<i>Atilax paludinosus</i>	10	578	4	0.6444	0.0024	3	1.36
<i>Ichneumia albicauda</i>	12	578	4	0.6970	0.0015	3	0.88

N: number of samples; *n*: number of sites used (among the total number of sites in the dataset; sites with missing data were excluded); *h*: number of haplotypes; Hd: haplotype diversity, Pi: nucleotide diversity; *S*: number of polymorphic sites; *k*: average number of nucleotide differences

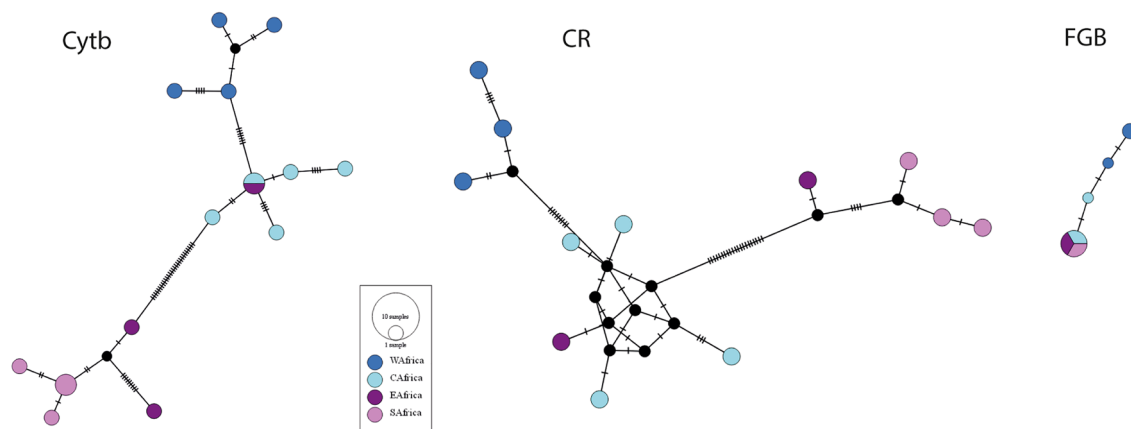


Fig. 3 Median-joining networks of Cytb (left), CR (center) and FGB (right) haplotypes for the marsh mongoose *Atilax paludinosus*. One bar corresponds to one mutation and the size of each circle is pro-

portional to the haplotype frequency. The East African sample whose haplotype is shared with a Central African sample is from Kakamega Forest in the Western part of Kenya (see the text for details)

The Cytb phylogeography of the white-tailed mongoose (alignment length: 1140 bp, Model ML GTR + G + I) shows five well-supported clades; a Central African clade, sister to an Arabian Peninsula clade, both sister to an East African clade; a South African clade; and a West African clade (Fig. 5).

The Cytb haplotype network (see Table 2; Fig. 6) shows five main haplogroups; the West African group is separated by 29 mutations from a South African group, and by 33 from an East African group; the latter is separated by 13 mutations from the Central African group; the Central African group is separated by seven mutations from the Arabian Peninsula group.

The Cytb sequence obtained for the museum sample from Senegal (IaM2003, specimen MNHN 2003-129) was too short to be included in the network analyses (307 bp); however, it is close to two samples from Guinea (IaPP027 and IaPP099) of the West African haplogroup.

The CR haplotype network (see Table 2; Fig. 6) shows a South African haplogroup separated by 17 mutations from a West African haplogroup, itself separated by 18 mutations from the closest East African haplotype. The eight East African haplotypes cluster in three groups; one with Ethiopian and Kenyan individuals and one with Eritrean individuals separated by at least 15 mutations; and one with Ethiopian individuals, separated by one mutation from Central African

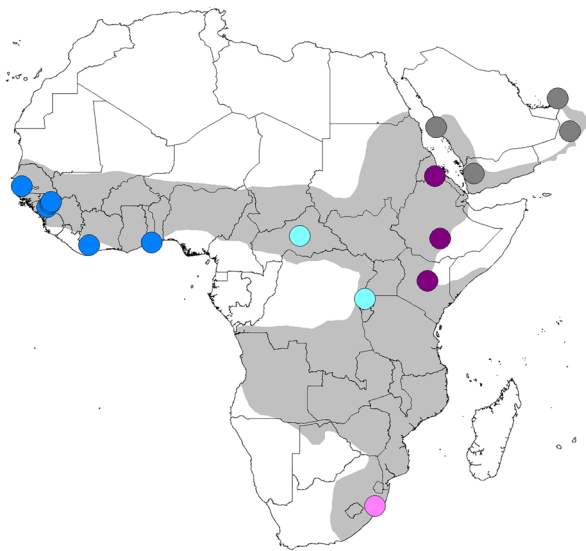


Fig. 4 Localities of the samples of the white-tailed mongoose *Ichneumia albicauda* used in this study. The distribution of the species according to the IUCN Red List map (Do Linh San 2015) is shown in grey shading. Localities are coloured by regions: West (blue), Center (light blue), East (purple), South (pink), and Arabian Peninsula (grey)

haplotypes, and by six mutations from the Eritrean haplotypes and by 13 mutations from the other Ethiopian individuals. The two Central African haplotypes are separated by one, five and 12 mutations from the three closest East African haplotypes. The Arabian Peninsula haplogroup is separated by only two mutations from the closest Central African haplogroup.

The two CR sequences of Dehghani et al. (2008) from Ethiopian samples, which have the same haplotype (IaTC242 and IaTC246) and which are close to the Central African haplotypes (separated by one mutation; see Fig. 5), may be the result of sample contamination, as they were found to be very distant from the other Ethiopian samples from the same locality (IaTC237, IaTC238, IaTC240, IaTC241, IaTC244 and IaTC247). This cannot be checked using *Cytb* analyses from the same samples, as they did not provide readable sequences, due to DNA degradation. Thus, the CR sequences of these two Ethiopian samples were removed from the population divergence analyses (results below).

These two Ethiopian individuals, which are close to Central African haplotypes and distant from the other Ethiopian haplotypes, are absent from the *Cytb* dataset. In addition, two Eritrean individuals are represented by GenBank CR sequences, but are absent in the *Cytb* dataset too. These differences in the CR and *Cytb* datasets should be considered when comparing the *Cytb* and CR networks.

The FGB network (see Table 3; Fig. 6) shows four haplotypes, separated from each other by one mutation. South

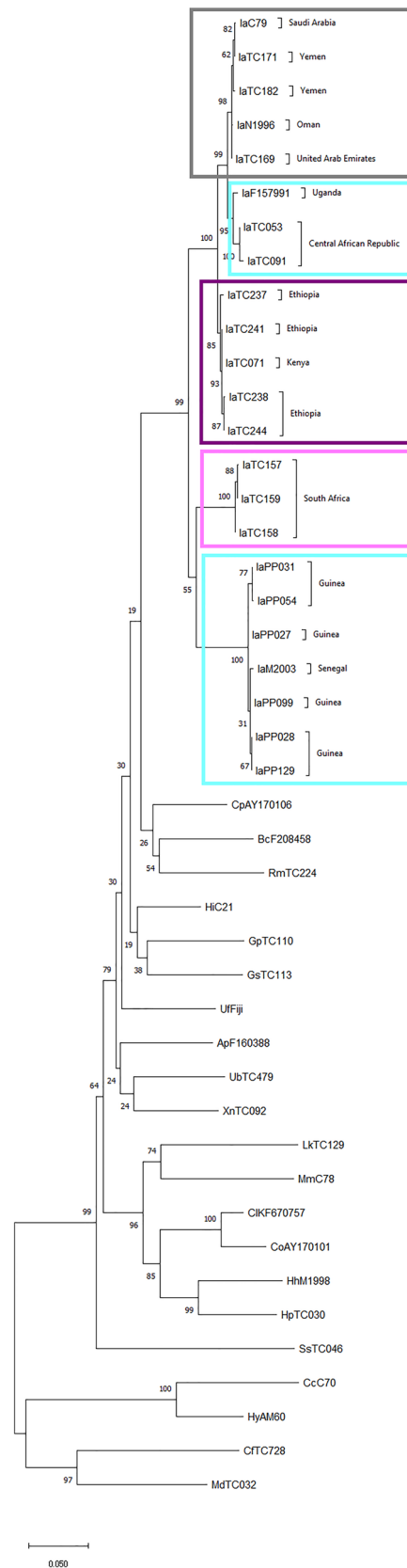


Fig. 5 ML *Cytb* tree for the white-tailed mongoose *Ichneumia albicauda* (Alignment length: 1140 bp; model: GTR+G+I), with countries of origin. The boxes indicate the main regions (colours as in Fig. 4)

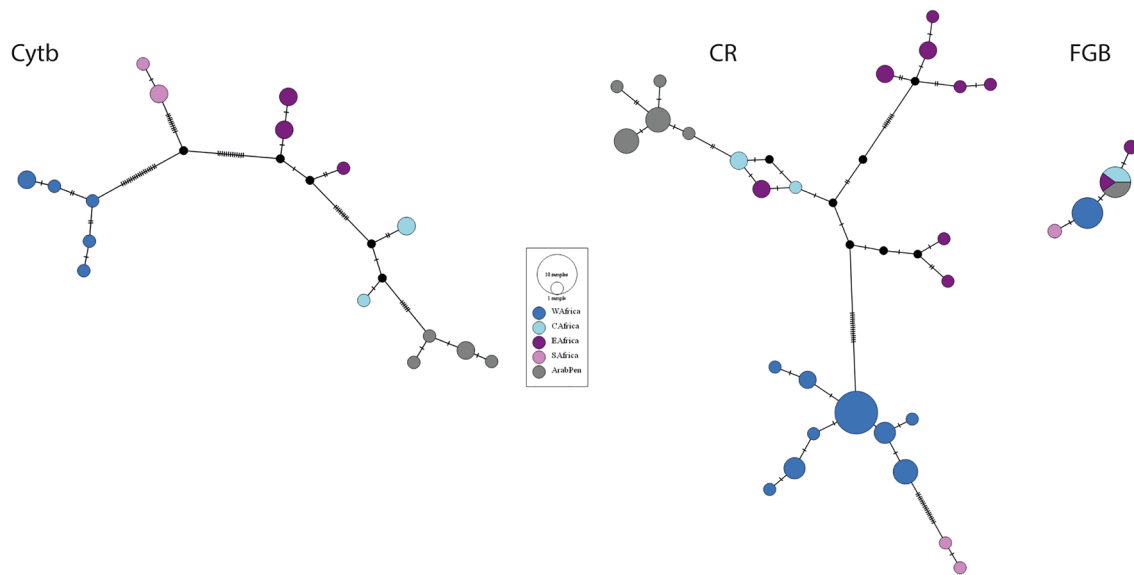


Fig. 6 Median-joining networks of Cytb (left), CR (center) and FGB (right) haplotypes for the white-tailed mongoose *Ichneumia albicauda*. One bar corresponds to one mutation and the size of each circle is proportional to the haplotype frequency

Table 3 Cytb divergence and genetic differentiation between haplogroups (length of fragment used: 601 bp)

	W Africa	C Africa	E Africa	S Africa	
<i>Atilax paludinosus</i>					
W Africa	1.00	0.6403	0.8098	0.9254	
C Africa	2.04%	0.93	0.7899	0.9181	
E Africa	6.83%	6.06%	1.00	0.2581	
S Africa	6.97%	5.99%	1.43%	0.83	
	W Africa	C Africa	E Africa	S Africa	Arabian Pen
<i>Ichneumia albicauda</i>					
W Africa	0.93	0.9319	0.9173	0.9390	0.9447
C Africa	8.17%	0.67	0.8184	0.9485	0.7837
E Africa	6.07%	2.36%	0.80	0.9430	0.8657
S Africa	6.10%	6.13%	4.76%	0.67	0.9659
Arabian Pen	7.85%	1.65%	2.40%	5.73%	0.90

Above the diagonal: pairwise F_{st} ; below the diagonal: percentage of pairwise divergence; on the diagonal in bold: haplotype diversity within haplogroups (Hd)

Africa and West Africa are each represented by one unshared haplotype; East Africa is represented by two haplotypes, one unshared and one shared with Central African and Arabian Peninsula individuals.

Intraspecific genetic diversity and population differentiation in the two wide-ranging African mongooses

The polymorphism in the marsh mongoose is comparable to that observed in the other mongoose species with wide distributions (Tables 1, 2).

Population differentiation was analysed using the 601 bp Cytb fragment (used to compute haplotypes), based on haplogroups observed in the networks (see Table 3).

According to the Cytb data, the marsh mongoose displays a high global fixation index (F_{st}) (0.8168); between pairs of populations (corresponding to the four haplogroups), the lowest pairwise F_{st} is between South and East Africa (0.2581) and the highest between South and West Africa (0.9254). In the white-tailed mongoose the global F_{st} is also high (0.9257), and pairwise F_{st} is high between all pairs of regions (0.7837 to 0.9659).

Population differentiation was also analysed using the CR fragment (360–364 bp, Table 4) for the marsh mongoose and the white-tailed mongoose. In the marsh mongoose the global F_{st} is high (0.8332), and the pairwise F_{st} between Central and West Africa is lower (0.6493) than the other pairwise F_{st} s. However, population differentiation cannot be tested between the different regions and East Africa (only one CR sequence from this region). In the white-tailed mongoose the global F_{st} is also high (0.89963), and the lowest pairwise F_{st} is between Eritrea and Central Africa, and the highest between South Africa and the Arabian Peninsula.

Genetic divergence (Cytb and CR) between haplogroups within the two mongoose species can be found in Tables 3 and 4.

For the marsh mongoose, the genetic divergence between haplogroups (see Tables 3, 4) ranges from 1.43 to 6.97% for Cytb and from 1.84 to 8.98% for CR; the lowest divergence is found between the South and East African haplogroups, and the highest between South Africa and regions other than East Africa.

For the white-tailed mongoose the genetic divergence between haplogroups (Tables 3, 4) ranges from 1.65 to 8.17% for Cytb, and from 1.90 to 11.13% for CR; the lowest divergence is found between Arabian Peninsula and Central Africa, and the highest between West Africa and other regions for Cytb, and between South Africa and the other regions for CR.

Discussion

This study provides new insights into the genetic polymorphism and structure of a widely distributed mongoose, the marsh mongoose *Atilax paludinosus*. Although based on a small sample size, these results can be compared to results from another wide-ranging African mongoose species, the white-tailed mongoose *Ichneumia albicauda*, which was studied previously (Dehghani et al. 2008), but completed and reanalysed for this study. Our results show geographical patterns that can be compared to those obtained for other African mammals, in order to evaluate if these species may have been affected by the same palaeo-environmental events or geographical barriers.

This work highlights the difficulty in obtaining samples of the elusive marsh mongoose, as unfortunately samples of only 17 individuals were available, and it also points out the difficulty of the identification of mongoose species. Indeed, among the sampled specimens originally identified as marsh mongoose, two (FMNH 208458 and FMNH 211260, both from Tanzania) appeared to be the bushy-tailed mongoose *Bdeogale crassicauda*, and another (MNHN PP054 from Guinea) was a white-tailed mongoose *Ichneumia albicauda*. DNA extractions, PCR and sequences of the various fragments were repeated, in order to check the authenticity of the sequences obtained. Also, the molecular identification of the two FMNH specimens was confirmed by re-examination of the specimens by Adam W. Ferguson, curator at the FMNH (pers. comm.), and the molecular identification of MNHN PP054 was confirmed by checking the specimen photograph taken by the collector. These three species can easily be confused by a non-specialist, because of their similar size

Table 4 CR divergence and genetic differentiation between haplogroups (length of fragment used: 360–364 bp)

	W Africa	C Africa	E Africa	S Africa		
<i>Atilax paludinosus</i>						
W Africa	1.00	0.6493	NA	0.8824		
C Africa	4.50%	1.00	NA	0.8747		
E Africa	7.60%	7.81%	NA	NA		
S Africa	8.89%	8.98%	1.84%	1.00		
	W Africa	C Africa	E Africa_Eritrea	E Africa	S Africa	Arabian Pen
<i>Ichneumia albicauda</i>						
W Africa	0.78	0.9241	0.8819	0.9006	0.9310	0.9379
C Africa	6.62%	0.67	0.6061	0.8456	0.9565	0.6763
E Africa_Eritrea	7.20%	3.09%	1.00	0.7894	0.9273	0.7454
E Africa	8.02%	5.61%	6.48%	0.90	0.9314	0.8587
S Africa	7.60%	9.80%	10.05%	10.82%	1.00	0.9631
Arabian Pen	7.85%	1.90%	3.45%	6.01%	11.13%	0.78

Above the diagonal: pairwise F_{st} ; below the diagonal: percentage of pairwise divergence; on the diagonal in bold: haplotype diversity within haplogroups (Hd)

and shape with a dark coat. Although the tail of the white-tailed mongoose is usually white, it is also frequently black (Dehghani et al. 2008), leading to misidentification of this species.

Owing to these difficulties the number of samples for the marsh mongoose remains low, which limits the types of analyses that can be conducted, and thus the interpretation of the results should be taken with caution. However, the observed geographical structure is consistent with results obtained for African forest species (e.g. roussetine fruit bats, Stribna et al. 2019; and other taxa, see Bertola et al. 2016) and also for open habitat mammals (e.g. *Mus minutoides*, Mboumba et al. 2011; Bryja et al. 2015; and see review in Bertola et al. 2016), and is interesting in the context of species comparisons, in order to understand the factors that may affect the distribution of these species.

Genetic polymorphism in African mongooses

The genetic polymorphism within the marsh mongoose is quite similar to that of the other widely distributed mongooses with similar body size, which may not be surprising as these mongooses may have similar dispersal capabilities. Unfortunately, their exact dispersal capabilities are unrecorded, although the marsh mongoose can travel up to 4 km along streams (Ray 1997). Also, Streicher et al. (2020) observed differences in their home-range sizes in South Africa, with a larger home range (95% KDE mean \pm SE) in the marsh mongoose (13.7 ± 5.30 km²) than in the white-tailed mongoose (0.9 ± 0.06 km²). However, home-range sizes may vary depending on sites, habitats and prey population density.

The level of Cytb divergence in the marsh mongoose is quite high, with values reaching *ca.* 7% between West Africa and either South Africa or East Africa (see Table 3). Similarly, Cytb divergences range from 6 to 8% between West Africa and other regions in the white-tailed mongoose. The level of divergence in these widely distributed species (*ca.* 7–9% of Cytb divergence between main haplogroups for the 601 bp fragment) may suggest that the taxonomic status of some of the haplogroups should be reviewed, if criteria for mammal species recognition based on the level of Cytb divergence are followed (>5%, Baker and Bradley 2006; >1.5–2.5%, Tobe et al. 2010). Although this degree of separation has been suggested for some Carnivora, such as the kinkajou *Potos flavus* (Nascimento et al. 2017), quite similar levels of intraspecific divergence (over 6%) were observed within other mongoose species (e.g., an Asian species, the short-tailed mongoose *Urva brachyura*; Veron et al. 2015a) or other carnivorans (e.g., the small-toothed palm civet *Arctogalidia trivirgata*; Veron et al. 2015b). Such genetic divergence could result from strong structuring of the populations, in particular for the maternal lineages,

although the presence of unrecognised species cannot be excluded and would need further testing using nuclear data. The level of haplotype diversity of the nucleotide marker FGB in the marsh mongoose and white-tailed mongoose (0.64 and 0.69 respectively) was higher than that observed, for instance, in closely related Eupleridae species (between 0 and 0.39 in Galidiinae species, and 0 in the fosa *Cryptoprocta ferox*; Veron et al. 2017, 2018). However, more nuclear markers and more samples should be analysed, as well as morphological data, before any conclusions can be made about the taxonomic status of the main haplogroups observed in this study.

The mitochondrial Control Region is known to evolve faster than mitochondrial protein-coding genes in mammals (see e.g. Saccone et al. 1993; Alter and Palumbi 2009), including in the Carnivora (see e.g. Jansen van Vuuren et al. 2012; Veron et al. 2017, 2018). For instance, in the ring-tailed vontsira *Galidia elegans* (Eupleridae, sister family to the Herpestidae), the average number of nucleotide difference and the haplotype and nucleotide diversities were higher for CR than for Cytb (see Veron et al. 2017). In contrast, in the marsh mongoose and white-tailed mongoose we observed a similar level of genetic diversity for Cytb and CR. In the marsh mongoose the average number of nucleotide differences in our data set was *ca.* 18 for CR and 21 for Cytb, and the haplotype and nucleotide diversities had similar values for CR and Cytb. Similar trends were observed for the white-tailed mongoose (see Table 2).

Geographical patterns

Our study suggests a clear genetic structure in the populations of marsh mongooses, and their geographical pattern is similar to that seen in some other African mammals, with a genetic proximity of the South and East African populations, and of the Central and West African populations, respectively. Such a pattern was observed in roussetine fruit bats (Stribna et al. 2019), bushbucks (Moodley and Bruford 2007; Hassanin et al. 2018), the savannah pygmy mice (Mboumba et al. 2011; Bryja et al. 2015) and in several other mammals (see review in Bertola et al. 2016 and Lorenzen et al. 2012).

Reconstructions of forest cover at the Last Glacial Maximum (LGM) suggest that the Cameroon Highlands, the Congo Basin and south-eastern South Africa experienced the densest forest cover (Cowling et al. 2008); similarly, a high concentration of climatically suitable ranges of birds and mammals aggregates in Upper Guinea, the Cameroon Highlands, the Congo Basin, the Ethiopian Highlands, the Angola–Namibia area and south-eastern South Africa (Levinsky et al. 2013), which suggests the existence of refugia during the LGM in these regions. North–South and West–East dispersals of forest species may have been

impeded by heterogeneous patches of forest during glacial periods (Cowling et al. 2008), which may explain the structuring in West + Central and East + South groups. During and after environmental fluctuations, connections and dispersal may have occurred through riverine forests for riverine species with good dispersal capabilities, such as the marsh mongoose. However, humid interglacial periods have shaped the hydrographical network, creating further physical barriers, which may have impeded gene flow, such as between the populations of Central Africa and southern Africa (see Petzold et al. 2020).

In the marsh mongoose, West and Central African populations are distinct, but much closer to each other than they are to South and East populations. A better geographical coverage of samples would be needed to observe the geographical pattern in more detail, and particularly to check the role of geographical barriers. Genetic distances between West and Central African regions are quite low for the marsh mongoose (Cytb: 2.04%). This may be due to the habitat preference of the species, notably the proximity to water courses, as its dispersal may occur mainly along riverine forests. In addition, although the marsh mongoose is not a rainforest specialist, this habitat does not constitute a barrier to its dispersal, contrary to species preferring more open habitats.

In contrast, in the white-tailed mongoose, populations from all the main regions are genetically distinct from each other and, specifically, the West African populations are distant from Central African populations, which is contrary to what is observed in the marsh mongoose. This may suggest that these two species are affected differently by past and present factors. Importantly, the white-tailed mongoose favours more open habitats, while rainforest areas may be a barrier to dispersal. The geographical structure observed in this species has also been observed in savanna mammals (e.g., rodents, Hanova et al. 2021). The stronger population structure and divergence between all regions found in the white-tailed mongoose may also be a consequence of lower dispersal capabilities. Its recorded home ranges are smaller than those of the marsh mongoose (see Streicher et al. 2020; Admasu et al. 2004), but unfortunately its dispersal capabilities and its maximum daily travel distances are not known.

Surprisingly, white-tailed mongoose samples from the Arabian Peninsula are closer to Central Africa samples than to any others. Colonisation of the Middle East by African mammals are documented only for a few species (e.g., Hamadryas baboon *Papio hamadryas*, Kopp et al. 2014). Although it has been suggested that the white-tailed mongoose may have been introduced to the Arabian Peninsula (Taylor 2013), this hypothesis was not considered by Dehghani et al. (2008) and was ruled out by Fernandes (2011). The latter estimated the colonisation of the Arabian Peninsula ca. 31,000 years before present (with confidence

interval ca. 8000 to 87,000), based on a CR dataset calibrated at 15.8 Myr for the *Ichneumia/Cynictis* divergence. However, this divergence has been recently re-estimated, based on a mitochondrial genome dataset and multiple calibration points, at 7.7–7 Myr (Hassanin et al. 2021), so the date estimated by Fernandes (2011) may have to be re-evaluated. The Green Sahara periods (see e.g., Drake et al. 2013) may have enabled dispersal from Africa to the Arabian Peninsula. As all white-tailed mongoose samples from the Arabian Peninsula cluster in one haplogroup, which is closer to Central Africa samples than to East Africa samples, our result may suggest a unique colonization of the Arabian Peninsula from populations now restricted to Central Africa through an expansion during humid periods, rather than from East African populations, despite their geographical proximity to the Arabian Peninsula. Introduction by humans a few thousand years ago is also still possible as it was suspected for other introduced small carnivorans (Malay civet *Viverra zibethica*, Veron et al. 2014; small Indian civet *Viverricula indica*, Gaubert et al. 2017); indeed, only few mutations (Cytb: 7, CR: 2) were observed between the Arabian Peninsula haplotypes and the closest African haplotypes, which remains compatible with either a recent colonisation or an ancient anthropogenic introduction. Anyway, better sampling from this region and adjacent regions using more markers, including nuclear ones, could help test various hypotheses on their origin.

The white-tailed mongoose occurs mainly in open habitats and avoids rainforests (Do Linh San 2015) in contrast to the marsh mongoose, and thus it may have been affected strongly by the forest–savanna contractions and expansions during the Pleistocene, and rainforest may be a barrier to dispersal for this species. During warm interglacial periods, central lowland forests may have expanded and isolated open-habitat species in the West, East and South of Africa (Cowling et al. 2008), which may explain the pattern observed in the white-tailed mongoose.

In contrast, in the marsh mongoose, the East and South populations are very close to each other, as was observed for other mammals (see review in Bertola et al. 2016). However, among the Kenyan samples of marsh mongoose, one (from Naivasha, ApTC059) falls close to the South African haplogroup, while the other one (from Kakamega forest in western Kenya, close to the Uganda border, ApF9668, specimen FMNH 231276/JCK9668) shares its haplotype with a Central African Republic sample, and falls within the Central African haplogroup. Further samples would be needed to determine the precise geographical limit between the East–South African group and the East–Central African group; also, nuclear markers would be needed to test if this pattern may result from hybridisation between lineages. However, the separation of eastern individuals obtained for this species fits with Kingdon's Line (see Grubb et al. 1999;

Joordens et al. 2019), separating the eastern coastal forest from the central African forest, which may correspond to former forest refugia. Kakamega forest has been recognised biogeographically as the easternmost forest with a central African fauna (see e.g., Roth and Cords 2015; Nicolas et al. 2020), and our study confirms that marsh mongooses from this area belong genetically to the Central African region.

Implications for marsh mongoose taxonomy

Within the marsh mongoose the main population divergence is between a South + East group and a West + Central Africa group, with Cytb divergences of ca. 6–7% between these two main groups. Within these two groups the divergence is low and is for instance stronger between some haplotypes within East Africa than between East and South Africa. Divergence is a little higher between Central and West Africa. More sampling would be needed to confirm these patterns and determine the factors that have driven this divergence pattern. However, considering that only two main groups were found, the validity of the ten subspecies of marsh mongoose (Coetzee 1977; Baker 1992; Gilchrist et al. 2009) needs re-evaluation.

Although further genetic and morphological data would be needed in order to revise the taxonomy of the species, the lack of strong divergence between the South and East, provisionally suggest that an eastern-southern subspecies may be recognized, which would be, according to priority, *A. p. paludinosus* (Cuvier, 1829). The geographical limit of the subspecies will need to be confirmed, but according to our results, it would include populations from southern Africa, and within East Africa, those from the eastern part of the range (e.g., Ethiopia, Kenya, Tanzania). However, regarding western Kenya, and probably also western Tanzania, our results suggest that populations there belong to the Central + West group. In other words, the West Kenya population belongs to the central African block of rainforest, while the East and Central Kenya population belongs to the coastal forests, corresponding to a separation by Kingdon's Line (Grubb et al. 1999; see above).

The West–Central Africa populations may be provisionally attributed to the subspecies *A. p. pluto* (Temminck, 1853), but further investigations should be conducted to define its exact geographical limit, and if a split between the populations of West Africa (with *A. p. pluto*) and of Central Africa should be made. In the latter case, in Central Africa the subspecies *A. p. mordax* (Thomas, 1912) was described from Tanzania, but the type locality (at the north end of Lake Malawi) seems to fall on the eastern side of Kingdon's Line, and would therefore not correspond to the Central African population. The subspecies *A. p. spadiceus* (Cabrera, 1921), described from Equatorial Guinea, would then be the earliest name available for Central Africa populations.

Unfortunately, as the current sampling does not allow confirmation of a definitive split within the West + Central group, and as no samples were obtained from the type localities of the relevant taxa, further investigations should be conducted to clarify the taxonomy of the marsh mongoose.

Conclusions

The geographical pattern of genetic variation for the African marsh mongoose, with a split between West + Central Africa and East + South Africa, was previously observed in both savanna and forest mammal species (see e.g., Bertola et al. 2016). In contrast, in the white-tailed mongoose the haplogroups of the different regions are strongly divergent, which may be due to more limited dispersal capabilities, as well as a preference for more open habitats. This may suggest that life history traits in addition to habitat preferences have an impact on how these species were affected by past environmental changes and biogeographical barriers. The marsh mongoose is not a rainforest specialist, but as a riverine species needing vegetation cover, it may have used forest refugia during glacial periods. However, the species probably has good dispersal capabilities and could have used riverine forests as corridors during dry and wet periods. This may explain its large distribution and the observed genetic pattern, as rainforest and rivers do not act as barriers for the dispersal of this species.

Further samples and markers would be needed to improve our understanding of the biogeography and taxonomy of these mongooses and determining the factors that may have affected the distribution patterns of the populations. Unfortunately, these mongoose species remain little known and elusive, and samples are difficult to obtain. Moreover, despite being listed as Least Concern in the IUCN Red List (Do Linh San et al. 2015), populations of the marsh mongoose are said to be declining, mainly due to habitat loss (Do Linh San et al. 2015). Conversion of swamplands for agriculture, and possibly water pollution, are likely to affect strongly this riparian species (Do Linh San et al. 2015; Baker et al. 2016), and so it is urgent to monitor its populations and to propose conservation actions. Our results provide preliminary insights into the delimitation of subspecies and further investigations are needed to define possible conservation units.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s42991-022-00321-8>.

Acknowledgements We are grateful to the following people and institutions for providing samples or for the help during this study: F. Catzeflis (ISEM, Université de Montpellier); M. Colyn (Université Rennes 1, Station Biologique de Paimpont); F. de Haas van Dorsser (United Arab Emirates University); C. Denys and A. Lalis (ISYEB, MNHN); A. Dunham (State University of New York at Stony Brook); J. Eger (Royal Ontario Museum); L. Heaney, B. Patterson and J. Phelps (Field

Museum of Natural History); K. Laursen (University of Edinburgh); S. Lavoué (MNHN); I. Parker; P. Taylor (Durban Museum); and P. Vercammen (Breeding Centre for Endangered Arabian Wildlife). We thank Adam W. Ferguson (Field Museum of Natural History, Chicago) for specimens' identification. Molecular work was undertaken at the 'Service de Systématique Moléculaire' (UMS CNRS 2700, MNHN), and we thank the lab staff for their help, and in particular, C. Bonillo. GV received financial support from MNHN and CNRS.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Géraldine Veron and Caroline Daniel. The first draft of the manuscript was written by Géraldine Veron and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Financial support was received from Muséum National d'Histoire Naturelle and Centre National de la Recherche Scientifique.

Data availability The data generated and analysed during the current study are available in GenBank.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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