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Phylogeography and genetic diversity of the Serrated Hinge-back Tortoise *Kinixys erosa* (Schweigger): implications for taxonomy and conservation

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Abstract

The Serrated Hinge-back Tortoise *Kinixys erosa* inhabits moist forests across Central and West Africa and is known to show phylogeographic structure. Based on extended geographic sampling, we re-examined its phylogeography using three mitochondrial genes and up to 17 nuclear loci. The observed mtDNA variation was considerable and corresponds to two major and well-supported clades from the western and the eastern part of the distribution range. Within the western clade, samples from Ghana represent a well-supported subclade. Nuclear loci support the genetic distinctness of these groups showing the Ghanian population as the most divergent. This suggests that *K. erosa* comprises hitherto unrecognized distinct taxa. Since no sufficient morphological data are available, and it is unclear to which clade the name *K. erosa* (Schweigger) refers, we abstain from taxonomic conclusions, but identify the genetic clusters as distinct Management Units for conservation.

Key words: Africa, biogeography, genetics, nuclear DNA, phylogeography, taxonomy

Introduction

With a straight carapace length of up to 400 mm, the Serrated Hinge-back Tortoise *Kinixys erosa* (Schweigger) is the largest representative of the genus *Kinixys* Bell (Chirio & LeBreton 2007; Luiselli & Diagne 2014). The species of this genus are characterized by their eponymous dorsal "shell hinge" allowing the partial or complete closure of the posterior carapace, a unique trait among chelonians (Cordero *et al*. 2023). The distribution range of *K. erosa* extends from Gambia eastwards to the Democratic Republic of the Congo (DRC) and Uganda, and south to northern Angola (Branch 2008; Spawls *et al.* 2018; TTWG 2025). *Kinixys erosa* and the closely related Home's Hinge-back Tortoise *Kinixys homeana* Bell inhabit moist forest habitats such as lowland evergreen, marsh, and gallery forests in Central and West Africa (Lawson 1993, 2006).

Previous studies examining mitochondrial or nuclear DNA sequences of *Kinixys* did not focus on the phylogeography of *K. erosa* (Le *et al.* 2006; Fritz & Bininda-Emonds 2007; Kindler *et al.* 2012; Thomson *et al.* 2021; Kehlmaier *et al*. 2023), even though Kindler *et al.* (2012) found for the species some phylogeographic structuring. However, since that study aimed at the overall relationships within the genus, it was limited in *K. erosa*

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to a few samples from only six localities. In the present investigation, we re-examine the phylogeography and genetic diversity of *K. erosa* based on increased sampling, mainly from Central Africa, using three mitochondrial genes and up to 17 nuclear loci.

Materials and methods

We produced new sequence data for 49 individuals of *K. erosa,* covering most of the species' range (Fig. 1; Table S1), as well as 24 additional samples corresponding to three individuals each of all eight currently recognized *Kinixys* taxa. The final dataset also included sequences of 20 *K. erosa* from Kinder *et al.* (2012); our new material originated mainly from Central Africa. For all individuals three mitochondrial (12S, ND4, cyt *b*) and three nuclear DNA fragments (CMOS, ODC, R35) were sequenced using the laboratory procedures outlined in Kindler *et al.* (2012). For a subset of 19 *K. erosa* from Ghana, Cameroon, Congo, and the DRC, 14 additional nuclear loci that have been used successfully to unravel relationships in other chelonian species (Vargas-Ramírez *et al.* 2010; Thomson *et al.* 2021) were sequenced (AIING, BDNF, HMGB2, HNF1α, NB22519, P26S4, PAX1P1, RAG1, RAG2, TB01, TB29, TB53, TB73, TB82).

For sequencing, additional internal primers were used for cyt *b*, ODC, and R35, while PCR primers were used for all other loci. For a complete list of primers and annealing temperatures, see Table S2. European Nucleotide Archive (ENA) accession numbers and sampling sites are summarized in Table S1.

Mitochondrial and nuclear marker systems are frequently conflicting (see the general review in Wüster 2025 and the review for turtles in Fritz *et al*. 2024). Therefore, analyses were performed separately. Phylogenetic analyses were conducted for an alignment containing the concatenated mtDNA fragments of 77 *Kinixys* samples and the three outgroups (12S: 371 bp, cyt *b*: 1035 bp + 23 bp adjacent DNA coding for tRNA-Thr, ND4: 656 bp + 182 bp adjacent DNA coding for tRNAs) using Bayesian Inference (BI) and Maximum Likelihood (ML) approaches. As outgroups, sequences of *Manouria emys* (Schlegel & Müller), *Stigmochelys pardalis* (Bell), and *Testudo graeca* Linnaeus were downloaded from GenBank. A Bayesian tree was constructed with MrBayes 3.2.1 (Ronquist *et al.* 2012) and the implemented Markov chain Monte Carlo (MCMC) algorithm using the optimal partition scheme and nucleotide substitution model (Table S3). Two independent runs (each with 4 chains) were conducted with 10 million generations each and sampled every 500th generation until the average standard deviation of split frequencies dropped below 0.01. Results of the MCMC runs were summarized after discarding the initial 25% of each run as burn-in. Tracer 1.7.1 (Rambaut *et al.* 2018) was used to check parameter convergence of both runs using the Effective Sample Sizes (ESS) of parameters prior to generating consensus trees. Using the same partitioning scheme, an ML tree was built using RAxML 7.2.8 (Stamatakis 2014) and the default GTR+G substitution model across all partitions, following the recommendation of Stamatakis (2016) to avoid the GTR+I+G model. Five independent rapid bootstrap searches were performed, starting from distinct randomized maximum parsimony trees. Subsequently, thorough bootstrap replicates were run until convergence was achieved with a cut-off of 1% (reached after 8000 replicates). The resulting bootstrap support values were mapped onto the best-scoring ML tree. In addition, uncorrected *p* distances of the cyt *b* gene were obtained using MEGA 10.1.8 (Kumar *et al.* 2018) and the pairwise deletion option. This mitochondrial gene has been frequently used to quantify divergence and delimit chelonian species (e.g., Fritz *et al*. 2012; Kindler *et al*. 2012; Petzold *et al*. 2014).

Nuclear loci were phased using DnaSP 6.12.03 (Rozas *et al.* 2017) with 100 iterations, a thinning interval of 1, and a burn-in of 100 iterations. Based on the obtained alleles, parsimony networks were drawn for the individual nuclear loci using TCS 1.2.1 (Clement *et al.* 2000) and the visualization tool TCSbu (Múrias dos Santos *et al.* 2016). Gaps were treated as fifth character state and the connection limit was set to 100 steps. To ensure the reliability of network calculations, which can be compromised by missing data (Joly *et al.* 2007), only individuals with complete sequence data were included in the analyses. Using SplitsTree 4.18.3 (Bryant & Huson 2023), NeighborNets were constructed for a concatenated nuclear alignment with 140 phased sequences of *K. erosa* and all other *Kinixys* species (CMOS: 561 bp, ODC: 921 bp, R35: 1092 bp). In doing so, default parameters were applied, except for enabling the "ignore ambiguous states" option. Using the same settings, a second NeighborNet was drawn for a dataset containing 10 nuclear loci from 15 *K. erosa* samples (HMGB2: 574 bp, ODC: 866, P26S4: 761 bp, PAX1P1: 944 bp, R35: 1087 bp, RAG2: 673 bp, TB29: 558 bp, TB53: 675 bp, TB73: 657 bp, TB82: 677 bp). These loci correspond to the nine most variable ones and one moderately variable locus (TB29).

In addition, Principal Component Analyses (PCAs) were run for *K. erosa* using the Adegenet package (Jombart 2008) for R 3.6.3 based on a haplotype matrix, where rows represented alleles and columns, nuclear loci. The PCAs were based on all 17 phased nuclear loci (AIING: 759 bp, BDNF: 699 bp, CMOS: 560 bp, HMGB2: 574 bp, HNF1α: 843 bp, NB22519: 754 bp, ODC: 866, P26S4: 761 bp, PAX1P1: 944 bp, RAG1: 647 bp, RAG2: 673 bp, R35: 1087 bp, TB01: 679 bp, TB29: 558 bp, TB53: 675 bp, TB73: 657 bp, TB82: 677 bp).

Results

For the concatenated mtDNA dataset, the topologies of the ML and Bayesian trees were similar, with high support for most nodes. Minor differences concerned only the branching patterns of weakly supported nodes (Fig. 2). The *Kinixys* species were assigned to two major clades. One contained the savannah species *K. natalensis* Hewitt, *K. belliana* (Gray), *K. nogueyi* (Lataste), and *K. spekii* Gray, while the other comprised the rainforest species *K. homeana* and *K. erosa* along with the savannah species *K. lobatsiana* (Power) and *K. zombensis* Hewitt. The latter clade was composed of two subclades, one containing *K. homeana* and *K. erosa* and the other, *K. lobatsiana* and *K. zombensis*.

Our analyses revealed two deeply divergent, well-supported terminal clades for *K. erosa* (Fig. 2). One of these clades contained sequences from the western part of the distribution range (Ghana, Cameroon, Congo), with samples from Ghana being the most distinct, and the other clade contained sequences from the east (provinces of Tshopo, Mongala, and northern Tshuapa in north-central and northeastern DRC; Fig. 1). The western and eastern clades of *K. erosa* differ by an uncorrected *p* distance of 3.4% in the cyt *b* gene; within the western clade, samples from Ghana differ from the remaining western samples by 1.3% (Table 1).

The parsimony networks for three phased nuclear genes revealed multiple shared haplotypes (Fig. S1; Table S4). The CMOS network consisted of 15 haplotypes, of which 13 were species-specific, while two were shared between congeners. Notably, *K. natalensis* and *K. nogueyi* exclusively possessed private haplotypes (Table S4), while one haplotype was shared between four taxa (*K. lobatsiana, K. zombensis*, *K. spekii*, *K. belliana*). Western *K. erosa* had two unique haplotypes corresponding to material from Cameroon and the Congo. Eastern *K. erosa* possessed only one private haplotype, while a second was shared with western *K. erosa*, *K. erosa* from Ghana, and *K. homeana*.

The ODC network showed a much larger number of haplotypes (40), and only three of them were shared between distinct taxa. Tortoises from Ghana had two private haplotypes while western *K. erosa* had 12 and eastern *K. erosa* 18. Western *K. erosa* shared one haplotype with *K. homeana* and eastern *K. erosa*.

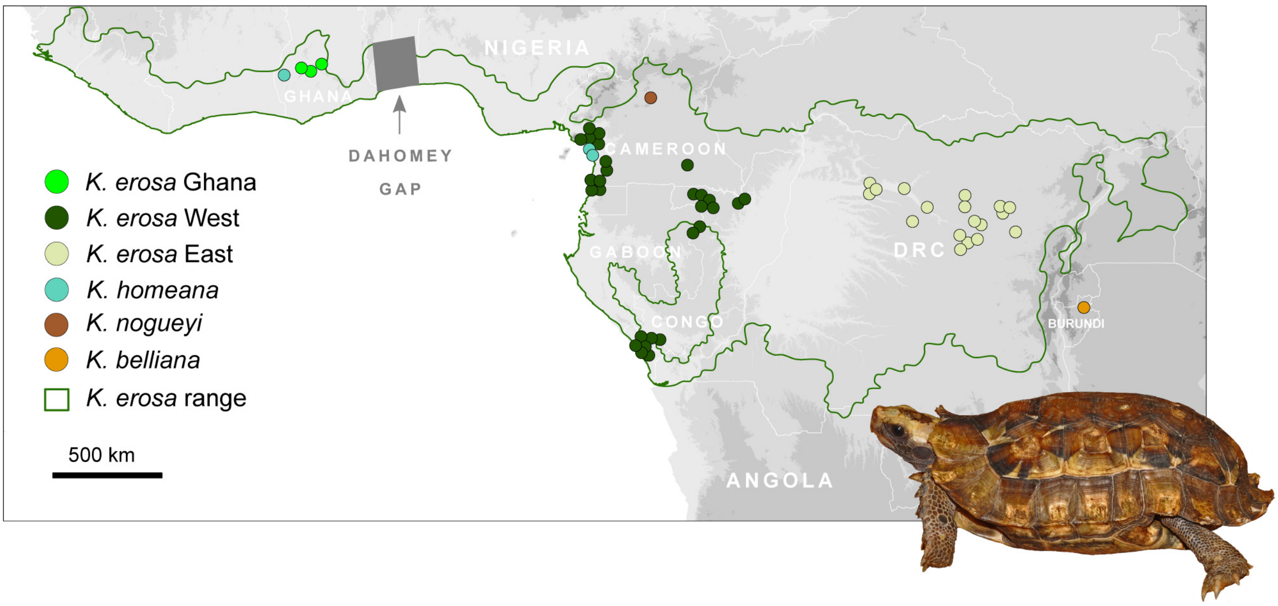

FIGURE 1. Distribution range of the Serrated Hinge-back Tortoise *Kinixys erosa* according to TTWG (2025) with localities of samples used in this study. An arrow indicates the location of the Dahomey Gap. Colors correspond to genetic clades. Inset: juvenile *K. erosa* from Bafwazenge, DRC. Photo: V. Gvoždík.

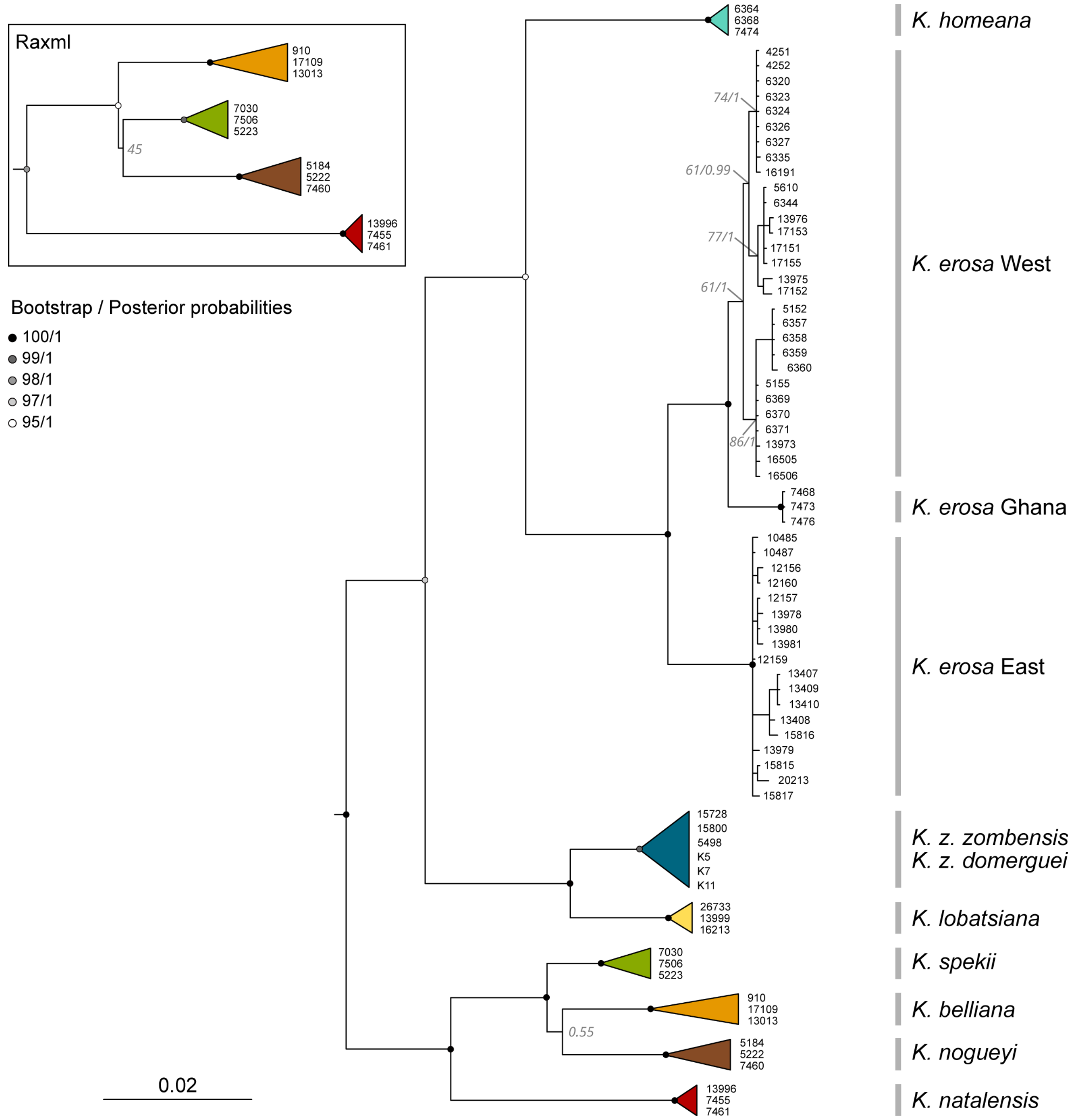

FIGURE 2. Bayesian consensus tree based on sequences for 74 hinge-back tortoises (*Kinixys* spp.) using mtDNA sequences (12S rRNA, ND4 + tRNAs, cyt *b* + tRNA-Thr; total length 2266 bp). Terminal clades of all taxa except *K. erosa* collapsed; outgroups (*Testudo graeca, Manouria impressa, Stigmochelys pardalis*) removed for clarity. The inset shows the different topology of the maximum likelihood tree (RAxML). Terminal numbers are sample codes, see Table S1.

Kinixys zombensis shared one haplotype with *K. nogueyi*. *Kinixys belliana*, *K. natalensis*, and *K. spekii* had only species-specific haplotypes. *Kinixys natalensis* was most differentiated, with two unique haplotypes differing by a minimum of 47 mutation steps from haplotypes of other species.

The parsimony network for R35 contained 40 haplotypes, most of which (36) were species-specific. *Kinixys erosa* from Ghana, *K. lobatsiana, K. natalensis*, *K. nogueyi*, and *K. zombensis* exclusively had private haplotypes. Two haplotypes were shared between western and eastern *K. erosa*, and one haplotype was shared between western and eastern *K. erosa* and *K. homeana*. Another haplotype was shared between *K. belliana* and *K. spekii*.

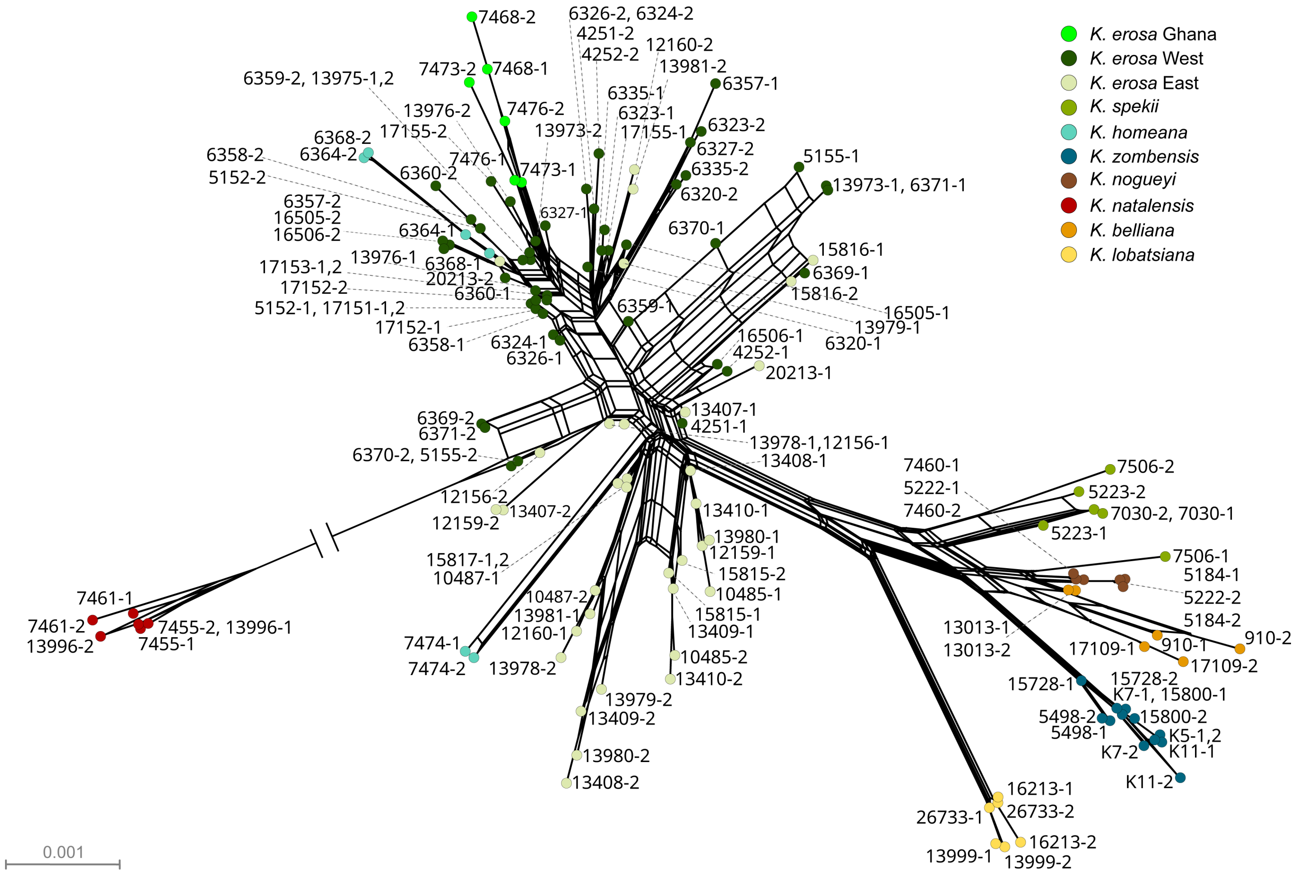

FIGURE 3. NeighborNet for *Kinixys* species, based on alleles of three nuclear loci (ODC, R35, CMOS; total length 2559 bp) of 70 individuals. Numbers are sample codes followed by 1 or 2 to designate alleles. Narrow long branches indicate strong phylogenetic divergence; reticulated edges indicate conflicting phylogenetic signal. Branch of *K. natalensis* shortened by ~80%.

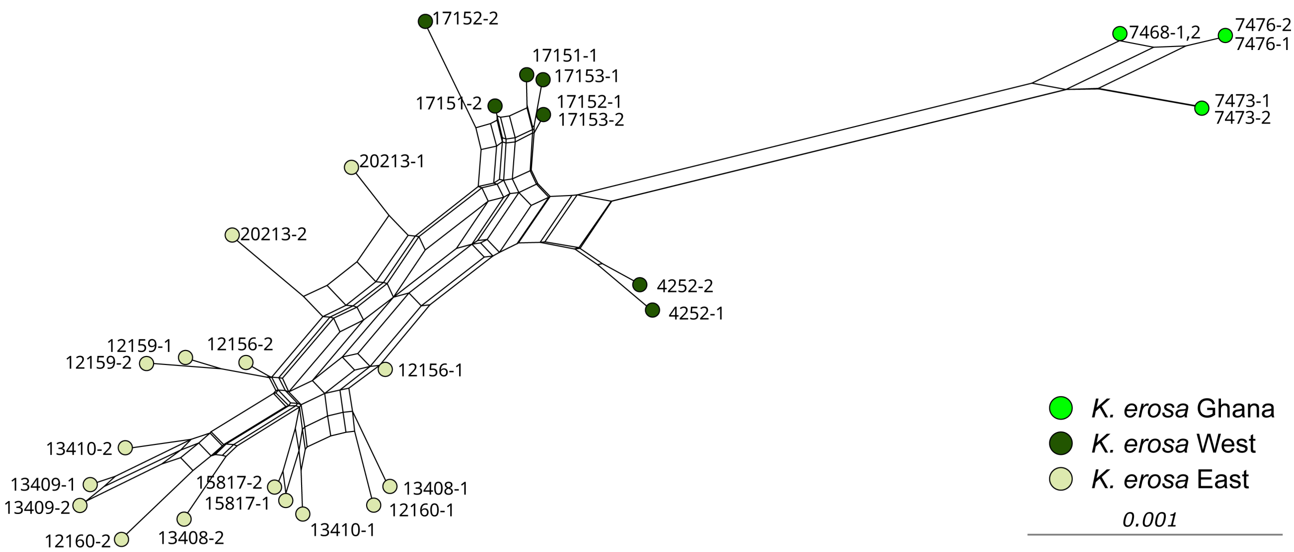

FIGURE 4. NeighborNet for 15 *Kinixys erosa*, based on 10 phased nuclear loci (HMGB2, ODC, P26S4, PAX1P1, R35, RAG2, TB29, TB53, TB73, TB82; total length 7472 bp). For further explanation, see Figure 3.

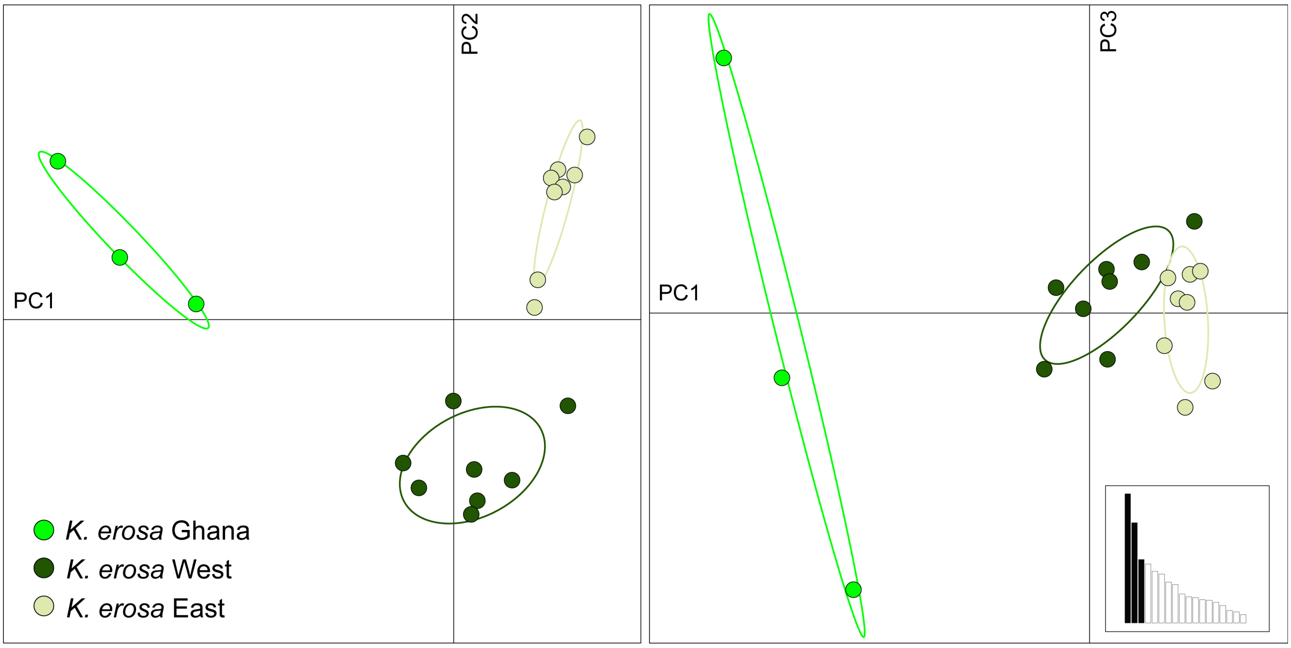

FIGURE 5. PCA plot using alleles of 17 nuclear loci for 19 *Kinixys erosa* individuals. The first, second, and third principal components explain 17.7%, 13.8%, and 8.7% of variation, respectively. Oval outlines represent 95% confidence intervals; colors correspond to Figures 1 and 2.

TABLE 1. Average uncorrected *p* distances for the mitochondrial cyt *b* gene (percentages) of *Kinixys* taxa. Below the diagonal, divergences between clades are given; on the diagonal, divergences within clades in bold. Note that within-clade divergence in *K. z. zombensis* was nearly as high (1.3%) as the divergence between *K. z. zombensis* and *K. z. domerguei* (Vuillemin), despite the dataset included only samples from South Africa and Tanzania. Given that the range of *K. z. zombensis* extends from South Africa in the south to Kenya in the north, this likely does not capture the full genetic diversity within this taxon.

	***K. erosa* Ghana**	***K. erosa* West**	***K. erosa* East**	***K. belliana***	***K. homeana***	***K. lobatsiana***	***K. natalensis***	***K. nogueyi***	***K. spekii***	***K. z. zombensis***	***K. z. domerguei***
K. erosa Ghana (*n*=3)	**0.0**										
K. erosa West (*n*=22)	1.3	**0.3**									
K. erosa East (*n*=18)	3.9	3.4	**0.3**								
K. belliana (*n*=3)	11.0	11.4	11.2	**2.8**							
K. homeana (*n*=3)	7.2	6.9	7.6	10.2	**0.4**						
K. lobatsiana (*n*=3)	8.9	8.8	9.0	10.4	8.4	**0.3**					
K. natalensis (*n*=3)	11.7	11.6	11.9	8.4	10.4	10.4	**0.4**				
K. nogueyi (*n*=3)	11.5	11.3	10.9	5.0	9.6	10.1	8.4	**1.0**			
K. spekii (*n*=3)	11.0	10.7	10.5	4.3	8.9	9.7	7.3	3.8	**0.9**		
K. z. zombensis (*n*=2)	9.4	9.0	9.1	10.0	8.3	3.8	10.4	9.6	9.0	**1.3**	
K. z. domerguei (*n*=3)	9.1	8.7	9.2	9.6	8.5	3.7	9.9	9.4	8.9	1.4	**0.0**

Across all three loci only *K. natalensis* consistently exhibited exclusively species-specific haplotypes, whereas all other taxa shared some haplotypes with congeners. *Kinixys nogueyi* had only private haplotypes in two loci (CMOS and R35). *Kinixys erosa* from Ghana had exclusively private haplotypes in ODC and R35. Haplotype networks for all 17 nuclear loci sequenced for *K. erosa* are presented as Figure S2; HBMG2, P26S4, ODC, PAX1P1, R35, RAG2, TB82, TB53, and TB73 were revealed as the nine most variable loci. Shared and private alleles were found for samples corresponding to all three mitochondrial clades.

The first NeighborNet using a concatenated dataset of phased sequences for three nuclear loci representing all *Kinixys* species revealed most recognized species to form distinct clusters (Fig. 3). *Kinixys natalensis* was the most distinct species, and *K. lobatsiana* and *K. zombensis* also formed highly distinct clusters. In contrast, alleles of the remaining species were less differentiated. Neither *K. erosa* and *K. homeana* nor the alleles corresponding to the mitochondrial clades of *K. erosa* were clearly distinct.

A second NeighborNet only for *K. erosa* and based on 10 nuclear loci confirmed reticulation but showed more resolution. The western and eastern clades were weakly differentiated, whereas the alleles corresponding to the mitochondrial Ghana clade were more distinct (Fig. 4).

A PCA for *K. erosa* based on the phased haplotypes (alleles) of all 17 nuclear loci supported both the genetic distinctness of the Ghana samples and, to a lesser extent, of the western and eastern clades (Fig. 5).

Discussion

Our phylogeny based on the concatenated mtDNA sequences confirmed the placement of *K. lobatsiana* and *K. zombensis* into the forest clade as previously reported by Kindler *et al.* (2012). In addition, our results revealed two well-supported clades within *K. erosa* that correspond to samples from the eastern and western parts of the range. Within the western clade, the samples from Ghana represent a well-supported subclade. Since the only previous molecular genetic study for *Kinixys* (Kindler *et al.* 2012) was restricted to material from the western clade and Ghana, the eastern clade of *K. erosa* was hitherto unknown.

The divergences among the mitochondrial clades of *K. erosa* are pronounced. This is also mirrored by the average uncorrected *p* distances of the cyt *b* gene (Table 1), a mitochondrial gene which was frequently used in the past as a taxonomic yardstick for freshwater turtles and tortoises (e.g., Fritz *et al*. 2012; Kindler *et al*. 2012; Petzold *et al*. 2014). The maximum divergence among clades of *K. erosa* (3.9%) resembles the lowest values between distinct *Kinixys* species (3.7–3.8% *K. lobatsiana* versus the two *K. zombensis* subspecies and *K. nogueyi* versus *K. spekii*), suggestive of taxonomic differentiation. A similar divergence has also been reported for two other tortoise species (*Indotestudo elongata* versus *I. travancorica*: 3.7%, Iverson *et al*. 2001), while the divergence values of other congeneric tortoise species generally resemble those among *Kinixys* (for a review, see Fritz *et al*. 2012).

Parsimony networks using phased sequences of three nuclear loci (Fig. S1) yielded multiple shared alleles between distinct taxa but could not resolve the mitochondrial clades of *K. erosa*. Nuclear loci evolve slower and thus show less variation than mitochondrial markers, often leading to a poor taxonomic resolution when too few markers are considered (e.g., Wiens *et al.* 2010; Shen *et al.* 2014). Moreover, it is well known that mtDNA phylogenies do not necessarily reflect the species tree (e.g., Fritz *et al*. 2024; Wüster 2025). However, a NeighborNet analysis using 10 variable nuclear loci (Fig. 4) and a PCA based on 17 nuclear loci (Fig. 5) supported the distinctness of tortoises representing the three mitochondrial clades, with the Ghanaian *K. erosa* being the most distinct.

The tripartite differentiation within *K. erosa* matches a general biogeographic pattern. Across West and Central Africa, a mosaic of landscape features and ecological gradients has historically impeded dispersal and gene flow, thereby facilitating allopatric speciation (Couvreur *et al.* 2021). Reconstructions of Pliocene and Pleistocene climate oscillations suggest repeated contractions and expansions of the African rain forest (Maley 1996; Anhuf 2000; Anhuf *et al.* 2006; Hardy *et al*. 2013), fostering vicariance and dispersal events in forest biota. It seems likely that these pulses contributed also to the genetic divergence within *K. erosa*.

Many wide-ranging taxa inhabiting the West and Central African rainforests consist of genetically distinct populations or cryptic species, often with distributions shaped by past forest fragmentation and isolation in historical refugia (e.g., Leaché *et al.* 2019; Ernst *et al*. 2025). One of the most prominent present-day barriers for forest-dwelling species is the Dahomey Gap that intermittently developed during arid Pleistocene periods. It is a 200 km wide dry savannah corridor dividing the Guinea-Congolian rainforest into the Upper Guinean Forest and the

Lower Guinean Forest (Booth 1958; Salzmann & Hoelzmann 2005). Examples for divergence on either side of the Dahomey Gap include forest-dwelling species such as the Gaboon viper *Bitis gabonica* (Duméril, Bibron & Duméril) and tree frogs of the genus *Leptopelis* Günther (Segniagbeto *et al.* 2011; Jaynes *et al.* 2022). Notably, diversification of anurans and squamates distributed across the Dahomey Gap occurred asynchronously and was not exclusively driven by shared ecological or life-history traits but reflects a complex history of speciation events extending beyond the Holocene (Leaché *et al.* 2020).

In Kinixys erosa divergence is likely driven by isolation in geographically distinct forest refugia to the east and west of the Dahomey Gap. Further east, the Congo Basin presumably separates the western from the eastern clade. However, further research is needed as our limited sampling does not allow for a precise delineation of range boundaries and potential secondary contact zones.

Recognizing cryptic or previously not recognized taxa is essential for conservation management, as only a correct taxonomy prevents the loss of biodiversity concealed behind a single species name. This is especially critical for rare, endangered, or heavily exploited taxa, where unrecognized lineages may face different levels of threat and require tailored conservation and management (Bickford *et al.* 2007). In *K. erosa*, pressure from habitat degradation and exploitation for subsistence constantly increases (Lawson 2000; Luiselli 2003; Luiselli & Diagne 2014), so that a taxonomic revision is of utmost importance for conservation.

However, despite compelling genetic evidence, we are reluctant to draw taxonomic conclusions for two main reasons. The first is the absence of sufficient morphological data. The second issue refers to the identity of the name *Kinixys erosa*. Schweigger's (1812) original description of *Testudo erosa* was based on three syntypes, which are all lost. Bour (2006) selected the specimen figured in Shaw (1802) as lectotype, an individual of unknown provenance, thought by Shaw to come from North America. Thus, it is completely unclear to which of the clades of *K. erosa* the species name refers.

Nonetheless, our results support the delineation of three Management Units to guide conservation efforts. In the light of this finding, the conservation status of *K. erosa* warrants re-evaluation. While *K. homeana* has been assessed by the IUCN Red List of Threatened Species in 2021, resulting in an upgrade of its threat category from 'Vulnerable' to 'Critically Endangered' (Luiselli *et al.* 2021), *K. erosa* was not assessed since 1996 and remains classified as 'Data Deficient'. Our findings also offer a robust genetic tool for determining the geographic origin of confiscated *K. erosa*, which may help prevent the release of genetically mismatched individuals.

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Supplementary Information. Tables S1–S4 and Figures S1 and S2 are available from figshare using the link https://doi.org/10.6084/m9.figshare.30165172

Table S1. Studied samples and sequences downloaded from GenBank. Numbers of *Kinixys erosa* samples included in the subset are shown in bold. Samples are housed in the tissue collection of the Museum of Zoology, Senckenberg Dresden.

Table S2. Primers used for amplifying and sequencing DNA fragments for *Kinixys*.

Table S3. Partitions and evolutionary models for the mitochondrial alignment inferred by PartitionFinder 2 (Lanfear *et al.* 2017) using the Bayesian Information Criterion.

Table S4. Number of alleles (n_A) and number of private alleles (n_{AP}) for parsimony networks of phased nuclear sequences for the dataset containing all hinge-back tortoises.

Figure S1. Parsimony networks for three phased nuclear loci of *Kinixys*. Symbol size corresponds to allele frequency; lines connecting alleles represent a single mutation step if not indicated otherwise by numbers. Colors of circles correspond to lineages of Figure 1. Small white circles are missing alleles.

Figure S2. Parsimony networks for alleles of 17 nuclear loci of *Kinixys erosa*. Symbol size corresponds to allele frequency; lines connecting alleles represent a single mutation step. Colors correspond to Figures 1 and 2; small white circles are missing alleles. The most variable loci are HBMG2, P26S4, ODC, PAX1P1, R35, RAG2, TB82, TB53, and TB73.