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Two new African hinged terrapins (Testudines: Pelomedusidae: *Pelusios*)

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Abstract

The African hinged terrapin genus *Pelusios* currently contains 17 recognized species. We describe an additional new species with two subspecies from the Democratic Republic of the Congo and Tanzania. According to phylogenetic analyses of mitochondrial DNA, the new species is closely related to *P. subniger*, whereas three nuclear loci (C-mos, RAG2, R35) suggest a closer relationship to *P. bechuanicus* and *P. upembae*. Morphologically, the new species resembles in plastral shape *P. subniger*, but differs in plastral coloration in having a diffuse dark plastral pattern instead of the blotched pattern of *P. subniger*. The two subspecies of the new species are characterized by distinct mitochondrial clades and private alleles in the nuclear RAG2 and R35 loci. According to an examination of museum specimens and photographic records, the new species occurs largely west of the Rift Valley, while *P. subniger* is distributed east of the Rift Valley. Museum specimens and iNaturalist records suggest that the two species could occur sympatrically in central Tanzania. Furthermore, we found no evidence for any genetic distinctness of *P. subniger* from the Seychelles, supporting that the subspecies from there is invalid.

Key words: Democratic Republic of the Congo, *Pelusios hyneki hyneki* **sp. et subp. nov.,** *Pelusios hyneki tanganyika* **subsp. nov.**, *Pelusios subniger*, Tanzania

Introduction

Pelomedusidae is an African-endemic freshwater turtle family comprising two genera, *Pelomedusa* Wagler, 1830, with currently 10 recognized species, and *Pelusios* Wagler, 1830, with currently 17 recognized species (TTWG 2025). While *Pelomedusa* is less strictly confined to aquatic habitats and at least some species can cope with extended drought periods, *Pelusios* are truly aquatic turtles, with species occurring in lentic or lotic waters. The plastral forelobe of *Pelusios* species is hinged and movable, allowing a more or less complete closure of the front shell, a morphological trait to which their common name "hinged terrapins" refers (Branch 2008; Boycott 2014). For East Africa (i.e., Kenya, Tanzania, Uganda plus the Horn of Africa) six *Pelusios* species are known, some of which extent further westwards and southwards. Among the East African species are two having narrow distributions (*Pelusios broadleyi* Bour, 1986, *P. williamsi* Laurent, 1965). Three other species, *P. castanoides* Hewitt, 1931, *P. sinuatus* (Smith, 1838), and *P. subniger* (Bonnaterre, 1789), occupy large ranges that typically reach southward to Mozambique and South Africa and inland to adjacent countries. *Pelusios rhodesianus* Hewitt, 1927 is an additional species occurring in East Africa (Tanzania and Uganda), but having its main distribution range farther west (TTWG 2025).

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One of these taxa, the black hinged terrapin *P. subniger*, is a small to medium-sized species (20 cm maximum straight carapace length; Branch 2008; TTWG 2025) known from Botswana, Burundi, the Democratic Republic of the Congo (DRC), Madagascar, Malawi, Mozambique, the Seychelles, South Africa, Tanzania, Zambia, and Zimbabwe (TTWG 2025). Black hinged terrapins from Madagascar and the Seychelles are not differentiated from South African and Mozambican populations with respect to mitochondrial DNA (mtDNA), and it has been suggested that these island populations represent old, perhaps prehistoric, introductions (Fritz *et al.* 2013). Nevertheless, for the Seychelles, the IUCN still continues to recognize an endemic subspecies, *P. s. parietalis* Bour, 1983 (TTWG 2025). On the other hand, Fritz *et al.* (2013) found two samples of *P. subniger* from the DRC deeply divergent with respect to mtDNA, suggestive of taxonomic differentiation.

In the present study, we expand the sampling of Fritz *et al.* (2013) for *P. subniger* sensu lato and other *Pelusios* species. For *P. subniger* sensu lato, we add substantial new material from the DRC, Mozambique, South Africa, and Tanzania, including historical DNA sequences from museum specimens. In addition to the previously studied three mtDNA fragments, we use information from three nuclear loci and combine the genetic results with phenotypic information from coloration and pattern.

Materials and Methods

Sampling and wet lab approaches

We extended the sampling of Fritz *et al.* (2013) using the same three mtDNA fragments and three additional nuclear loci. We generated sequences from new samples, supplemented the nuclear sequences for the material used in Fritz *et al.* (2013), and included previously published sequences from some investigations focusing on other *Pelusios* species (Fritz *et al.* 2011, 2012; Stuckas *et al.* 2013; Kindler *et al.* 2016; Vamberger *et al.* 2019) and added new sequences for non-focal *Pelusios* species. Most of our new material consists of blood samples taken in 2012 and 2013 from live turtles kept by the late Hynek Prokop (1972–2023) and samples donated from colleagues. A few of the samples are muscle tissue taken from inside the thighs of historical museum specimens (Museum für Naturkunde Berlin: ZMB 155, ZMB 22828; Zoologische Staatssammlung München: ZSM 106/1960). We studied DNA sequences of 397 *Pelusios*, corresponding to all currently recognized species: *P. adansonii*—8, *P. bechuanicus*—10, *P. broadleyi*—8, *P. carinatus*—20, *P. castaneus*—24, *P. castanoides*—47, *P. chapini*—19, *P. cupulatta*—8, *P. gabonensis*—35, *P. marani*—7, *P. nanus*—27, *P. niger*—8, *P. rhodesianus*—22, *P. sinuatus*—60, *P. subniger* sensu lato—79, *P. upembae*—12, and *P. williamsi*—3. Detailed sample information is provided in Table S1, including provenance and GenBank/ENA numbers for DNA sequences.

Using Sanger sequencing, we targeted the mitochondrial 12S (398 bp), cyt *b* (993 bp), and ND4 (971 bp) genes and the nuclear C-mos (514 bp), RAG2 (926 bp), and R35 (1102 bp) loci. For fresh samples, we applied the wet lab approaches and primers described in Fritz *et al.* (2011, 2012). The mtDNA sequence corresponding to the second half of the ND4 gene (771 bp) also contained additional 200 bp of DNA coding for tRNAs (Table S2). For the historical material, short diagnostic DNA fragments were targeted. Sequencing of the nuclear loci was unsuccessful and only mtDNA fragments were obtained. The processing of the historical material followed the general approach outlined in Stuckas *et al.* (2013) considering all necessary precautions (DNA extraction and PCR setup in a clean room physically isolated from modern DNA processing facilities, etc.) and using the primers and PCR conditions of Table 1.

TABLE 1. PCR details for historical specimens: fragment lengths, primer sequences, number of PCR cycles, and annealing temperatures.

Locus	Length of PCR product excl. primers	5'-For-3'	5'-Rev-3'	PCR cycles	Annealing temperature
12S	77 bp	GATAAACCTTACCACCCTTTGCC	GGCTACACCTGGACCTGAC	40	53°C
ND4	82 bp	CCCTTATCAATCACAGGAGC	GCGTGTTAATAGTAGGGTTCG	40	53°C
cyt *b*	59 bp	GAGGCCAAATATCCTTCTGAG	AGAATCCTCCTCAGATTCATTG	40	53°C

Alignment, phylogenetic and network analyses

Nuclear and mitochondrial DNA sequences of the 397 hinged terrapins were aligned using the MUSCLE algorithm (Edgar 2004) implemented in Geneious 11.0.3. (Kearse *et al*. 2012). A few samples for which only the 12S gene was available were excluded from tree calculations. For the remaining 392 samples, mtDNA was analyzed with maximum likelihood (ML) and Bayesian inference (BI) of phylogeny using concatenated sequences of 2311 bp length; *Pelomedusa olivacea* served as outgroup for tree-rooting (for GenBank/ENA accession numbers, see Table S1).

The best fitting substitution models for the individual genes and the unpartitioned dataset were inferred with ModelTest-NG 0.1.7 (Flouri *et al.* 2015; Darriba *et al*. 2020). An ML phylogeny with non-parametric bootstrapping was then computed using RAxML-NG 1.2.2 (Kozlov *et al.* 2019) with 10 randomized parsimony starting trees and 1000 bootstrap replicates. For the unpartitioned analysis of the entire dataset, the model was fixed to GTR+G4+I. In another RAxML-NG run the dataset was partitioned and the substitution model was set for each individual locus (Table S2).

Bayesian inference of phylogeny was also computed for the concatenated unpartitioned sequences and the dataset partitioned into individual loci using MrBayes 3.2.7 (Ronquist *et al.* 2012). Four runs with 4 chains (one hot) ran for 10 million generations. Using the same evolutionary models as for RAxML, every 1000th generation was saved and the first 20% of generations was rejected as burn-in. Tracer 1.7.2. (Rambaut *et al*. 2018) was used to examine convergence of runs.

Using Hapsolutely (Vences *et al*. 2024) and trimmed alignments without missing sites, nuclear DNA sequences were phased and parsimony networks were drawn for the alleles of each locus applying the TCS algorithm. Concatenated nuclear sequences with up to 0.2% missing data were used for constructing a NeighborNet as implemented in SplitsTree4 (Huson & Bryant 2006).

Morphology

Museum specimens from the following collections were studied: Museum für Naturkunde Berlin (ZMB), Museum of Zoology, Senckenberg Dresden (MTD), National Museum Prague (NMP), and Zoologische Staatssammlung München (ZSM). Basic straight-line measurements of carapace, plastron, and plastral seams, as described and figured in Fritz (1995) and Iverson & Lewis (2018), were taken to the nearest 0.1 cm using a caliper. Specimens were photographed and notes on coloration and pattern were recorded. In addition, photos archived in the Museum of Zoology, Senckenberg Dresden, georeferenced photos present on iNaturalist (http://www.inaturalist.org) by 31 May 2025, and live specimens from the former collection of H. Prokop were examined for coloration and pattern traits.

Results

Mitochondrial phylogeny

Both tree-building methods delivered for the partitioned and the unpartitioned dataset consistent branching patterns that generally corresponded to previous results (Fritz *et al.* 2011, 2012, 2013; Stuckas *et al.* 2013; Kindler *et al.* 2016; Vamberger *et al.* 2019), including the weak resolution for some deeper nodes, the paraphyly of *Pelusios castaneus* with respect to *P. chapini*, and the paraphyly of *P. rhodesianus* with respect to *P. carinatus* (see discussion in Kindler *et al.* 2016). We show here an ML tree based on the unpartitioned dataset (Fig. 1), with collapsed clades, including posterior probabilities from the BI analysis of the unpartitioned dataset. All full trees are presented in the Supplementary Information (Figs S1–S4).

As reported in Fritz *et al.* (2013), samples identified as *Pelusios subniger* sensu lato from the DRC (clade B in Fig. 1) were under ML the deeply divergent sistergroup of *P. subniger* from Madagascar, Mozambique, the Seychelles, and South Africa (clade A, *P. subniger* sensu stricto in Fig. 1). However, the sistergroup relationship of these two well-supported clades was only weakly supported, and they were placed in another maximally supported more inclusive clade. It contained a third novel clade (clade C in Fig. 1). It was also well-supported and comprised two historical samples identified as *P. subniger* from Tanzania and three pet trade turtles of unknown provenance. Under BI, the branching pattern was swapped, and clade A was sister to another clade containing clades B and C, albeit with a support value close to random (0.502). Thus, the relationships of the three clades A–C are best

understood as an unresolved polytomy. The more inclusive clade containing clades A–C was sister to a weakly supported clade consisting of *P. bechuanicus* and *P. upembae*. The divergences among clades A–C resembled those between *P. bechuanicus* and *P. upembae*.

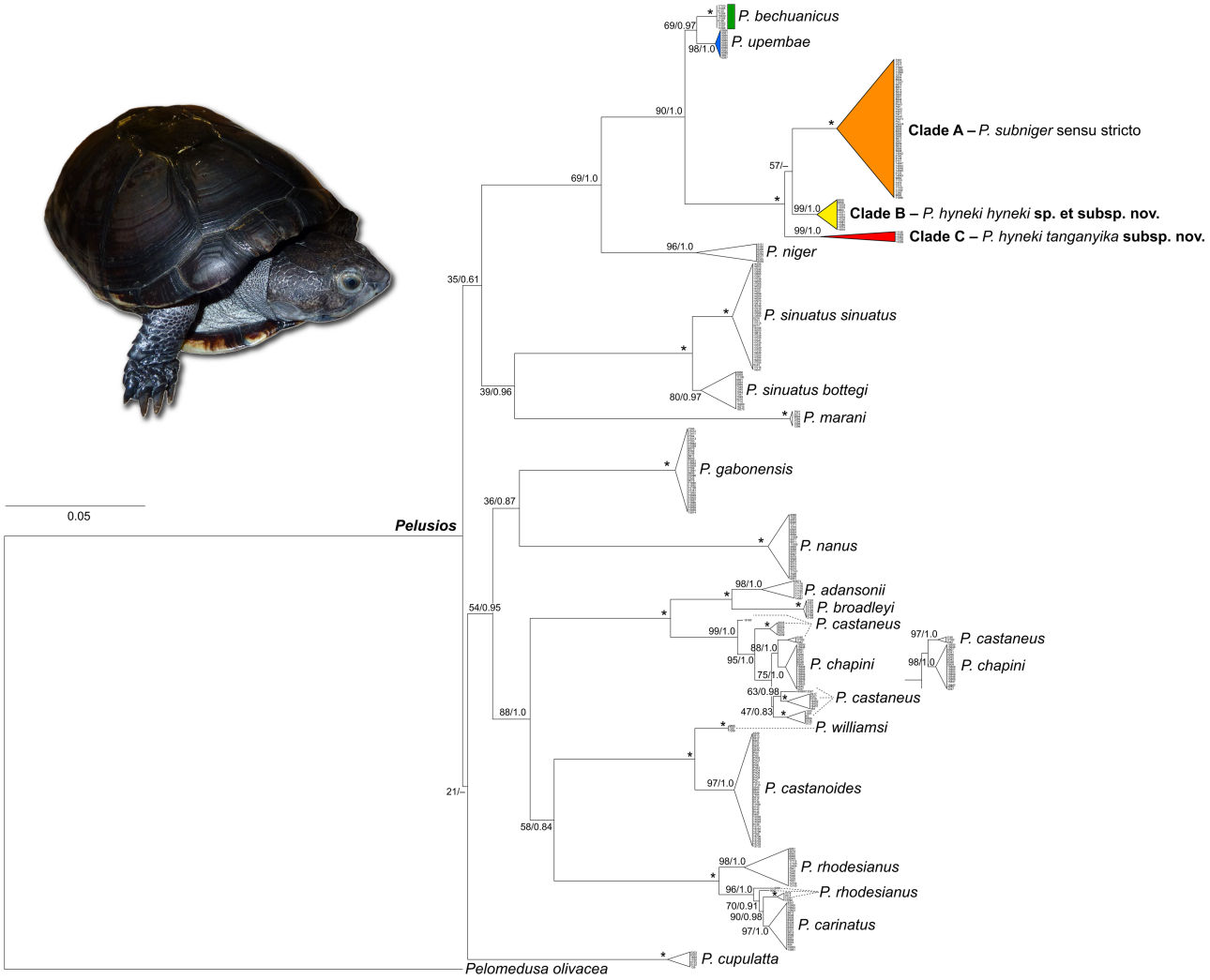

FIGURE 1. Mitochondrial phylogeny of 392 hinged terrapins (*Pelusios* spp.), rooted with *Pelomedusa olivacea*. Shown is an ML tree based on the unpartitioned concatenated dataset (2311 bp). Numbers at nodes are bootstrap values and posterior probabilities from a BI tree with similar topology (unpartitioned concatenated dataset). Asterisks are maximum support under both approaches. Clades collapsed to cartoons. For all four full trees, see Figures S1–S4 (partitioned and unpartitioned datasets, showing intraclade branching patterns). Genetic divergences within *P. adansonii*, *P. niger*, *P. hyneki tanganyika* **subsp. nov.**, and *P. subniger* sensu stricto are probably overestimated due to a few short DNA sequences from degraded or historical samples (see long branches of respective samples in Figs S1–S4). Part of the *P. castaneus*/*P. chapini* clade shown twice to indicate additional support values. Colors for clades correspond to Figures 2–4; *P. bechuanicus* showed no variation, which is why a bar is used to display the green color. Inset picture: *Pelusios subniger* sensu stricto, photo: Hynek Prokop.

Nuclear networks

The network analyses for the individual nuclear loci for the samples from the more inclusive mitochondrial clade corresponding to *P. subniger* sensu lato (Fig. 2) revealed that the samples from the DRC (clade B) and the pet trade turtles placed into the same mitochondrial clade as the museum specimens from Tanzania (clade C) were distinct from samples from Madagascar, Mozambique, the Seychelles, and South Africa (clade A). Only for the R35 locus haplotype sharing was observed in that a single allele from a sample from the DRC (clade B) represented the same haplotype as found in samples from Mozambique, the Seychelles, and South Africa (clade A). On the other hand, haplotype sharing between the turtles from the DRC (clade B) and the pet trade turtles (clade C) occurred for

all three loci, even though the latter possessed also private alleles for RAG2 and R35. Within clade A, samples from Madagascar and the Seychelles were not clearly differentiated from samples from Mozambique and South Africa, even though turtles from Madagascar, but not from the Seychelles, had private haplotypes.

The networks that also included the two *Pelusios* species most closely related to *P. subniger* sensu lato according to the mtDNA phylogeny (Fig. 3), *P. bechuanicus* and *P. upembae*, confirmed the distinctiveness of the three clades within *P. subniger* sensu lato. For all three loci, *P. subniger* sensu stricto (clade A) was completely distinct (C-mos, RAG2) or nearly completely distinct (R35) from the samples corresponding to the two other mitochondrial clades within *P. subniger* sensu lato (clades B and C). Interspecific haplotype sharing was rare and involved *P. bechuanicus* and *P. upembae* and clades B and C, but not clade A of *P. subniger* sensu lato.

SplitsTree analysis

The NeighborNet based on the three concatenated nuclear loci (Fig. 4) found clade A of *P. subniger* sensu stricto clearly distinct from clades B and C, *P. bechuanicus*, and *P. upembae*. Haplotype sharing was restricted to *P. bechuanicus* and *P. upembae*. Clades B and C of *P. subniger* sensu lato clustered closer to *P. bechuanicus* and *P. upembae* than to clade A of *P. subniger* sensu lato.

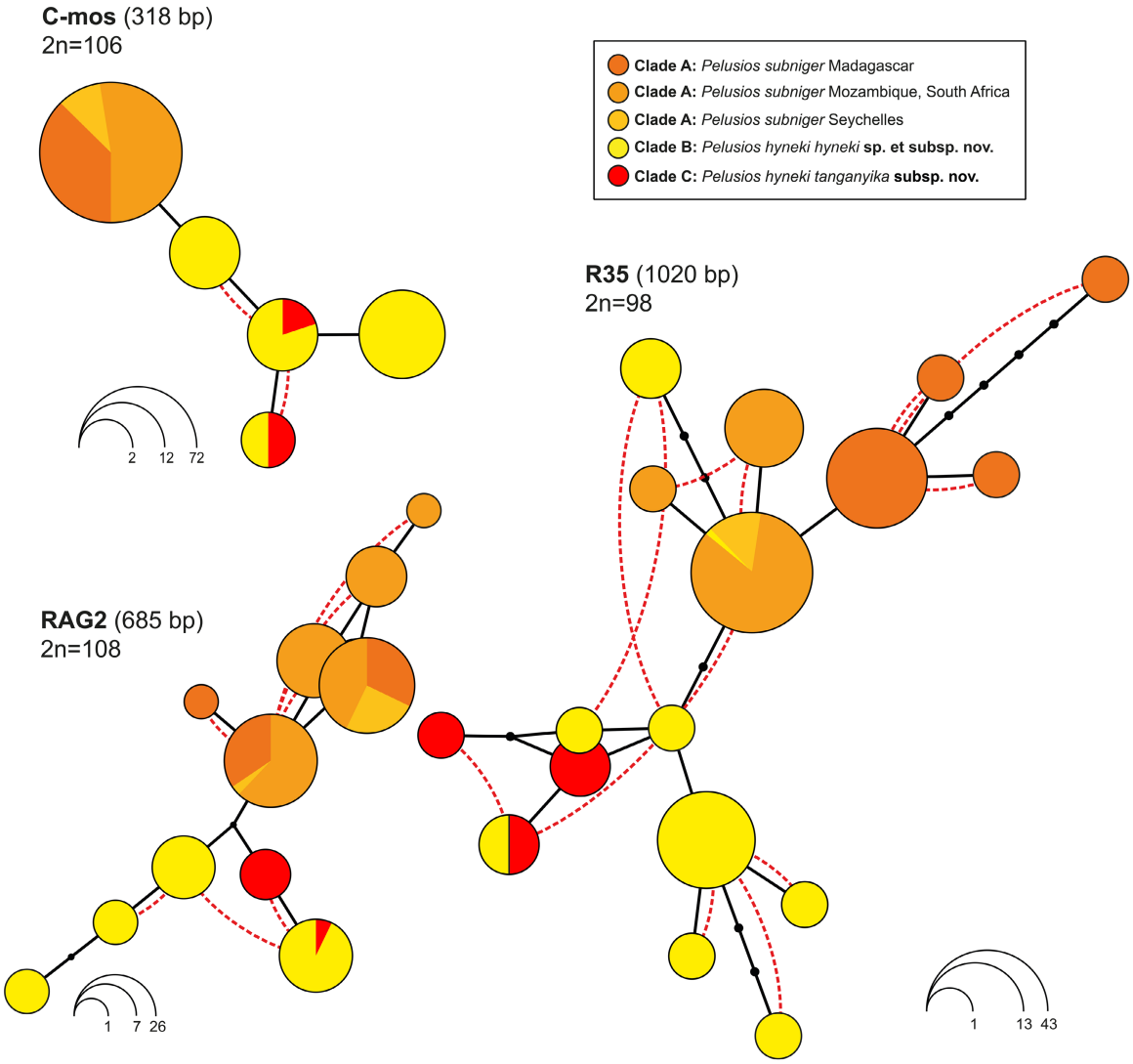

FIGURE 2. Parsimony network for alleles of three nuclear loci of *Pelusios subniger* sensu lato (clades A, B, C). Colored circles represent haplotypes, size corresponds to haplotype frequency. Missing haplotypes are represented by small black circles; lines connecting two haplotypes are one mutation step. Broken red lines connect distinct alleles from the same individual. Sample sizes (2n) refer to alleles. Note that there are no private alleles for the samples from the Seychelles, even though Seychellois black hinged terrapins are currently assigned to a distinct subspecies (*P. s. parietalis*) by the IUCN.

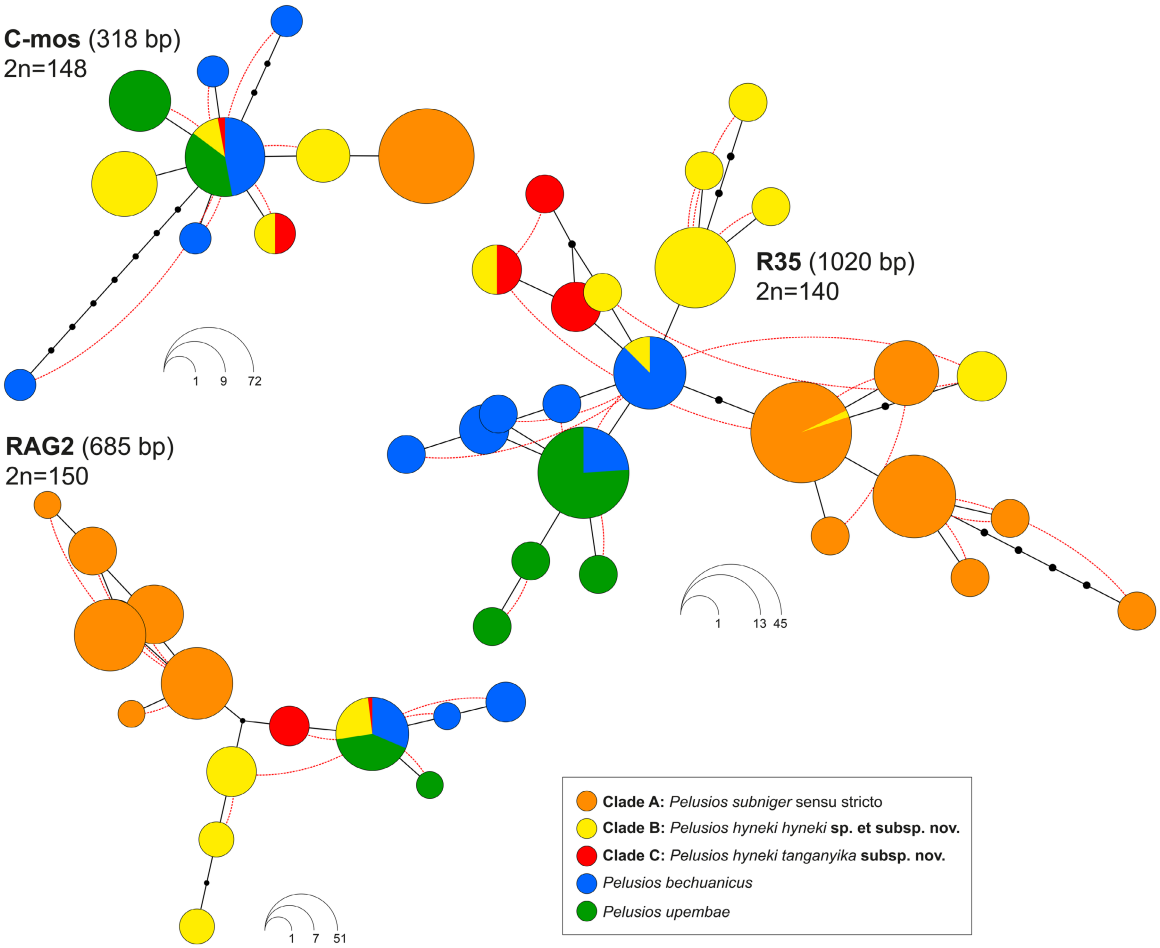

FIGURE 3. Parsimony network for alleles of three nuclear loci of *Pelusios subniger* sensu lato (clades A, B, C), *P. bechuanicus*, and *P. upembae*. Colored circles represent haplotypes, size corresponds to haplotype frequency. Missing haplotypes are represented by small black circles; lines connecting two haplotypes are one mutation step. Broken red lines connect distinct alleles from the same individual. Sample sizes (2n) refer to alleles. Note shared haplotypes of *P. bechuanicus*, *P. upembae*, and clades B and C of *P. subniger* sensu lato.

Plastral coloration

The available museum specimens and photos of *P. subniger* sensu lato (Table S3) reveal that two basic types of plastral coloration exist. One type corresponds to quite distinctive dark blotches along the plastral seams (Fig. 5), with a yellow plastral ground color. For facilitating communication, we refer to this as "blotched pattern" below. The second type is a more diffuse brownish pattern that can cover much of the plastron (Figs 6, 7), without distinct blotches. We refer to this in the following as "diffuse pattern". Also, individuals with a mainly or completely yellow plastron may occur (termed "uniform" in Table S3), in which the gular and anal regions can be dark colored. However, such turtles are rare. Among 80 *P. subniger* sensu lato, including 23 turtles without exact geographic provenance, only five individuals had mainly or entirely yellow plastra, suggesting that this is a rare condition. Two of these turtles were from Tanzania and one each from Madagascar, the Seychelles, and Zimbabwe (Table S3).

Adult and subadult turtles from the distribution range of clade A possess the blotched plastral pattern (Fig. 5). We have seen such specimens or photos from Madagascar (n=21, including the holotype of *Testudo subnigra* Bonnaterre, 1789), Mozambique (n=22 plus 4 juveniles with distinct blotches, see below), the Seychelles (n=3), and South Africa (n=1). Furthermore, four iNaturalist records from Tanzania (Iringa and Manyara Regions) have blotched plastra (Table S3).

Except for one turtle (ZMB 22828, Tanzania) with a yellow plastron, all genetically studied turtles of clades B and C represent the diffuse type of plastral pattern. This is also the case for additional specimens from the same source regions that were not examined genetically. However, there are also photographic records from countries

where no samples were sequenced. Besides seven specimens or photos from the southeastern DRC and one museum specimen from Tanzania (ZSM 106/1960), two turtles from northern Botswana, three turtles from central Zambia, and one from northeastern Zimbabwe show this diffuse plastral pattern (iNaturalist photos, see Table S3).

Figure 8 and Table S3 summarize the geographic distribution of the blotched and diffuse plastral pattern. Accordingly, turtles with blotched and diffuse plastral pattern are largely allopatrically distributed and co-occur in central Tanzania. All turtles with a blotched plastral pattern occur east of the Rift Valley, and turtles with a diffuse plastral pattern are largely distributed west of the Rift Valley, except for Tanzania.

Smaller juveniles generally possess a central dark plastral figure that extends to the plastral rim along the seams; presumably this pattern is present in hatchlings. Some juveniles from Madagascar and Mozambique show already the characteristic blotches along the seams; in four of these individuals, the dark central figure is also still visible but fading. A historical museum specimen from Mossuril, Mozambique, a large juvenile of 12 cm straight shell length sequenced for the present study (ZMB 155), has a clear blotched plastral pattern.

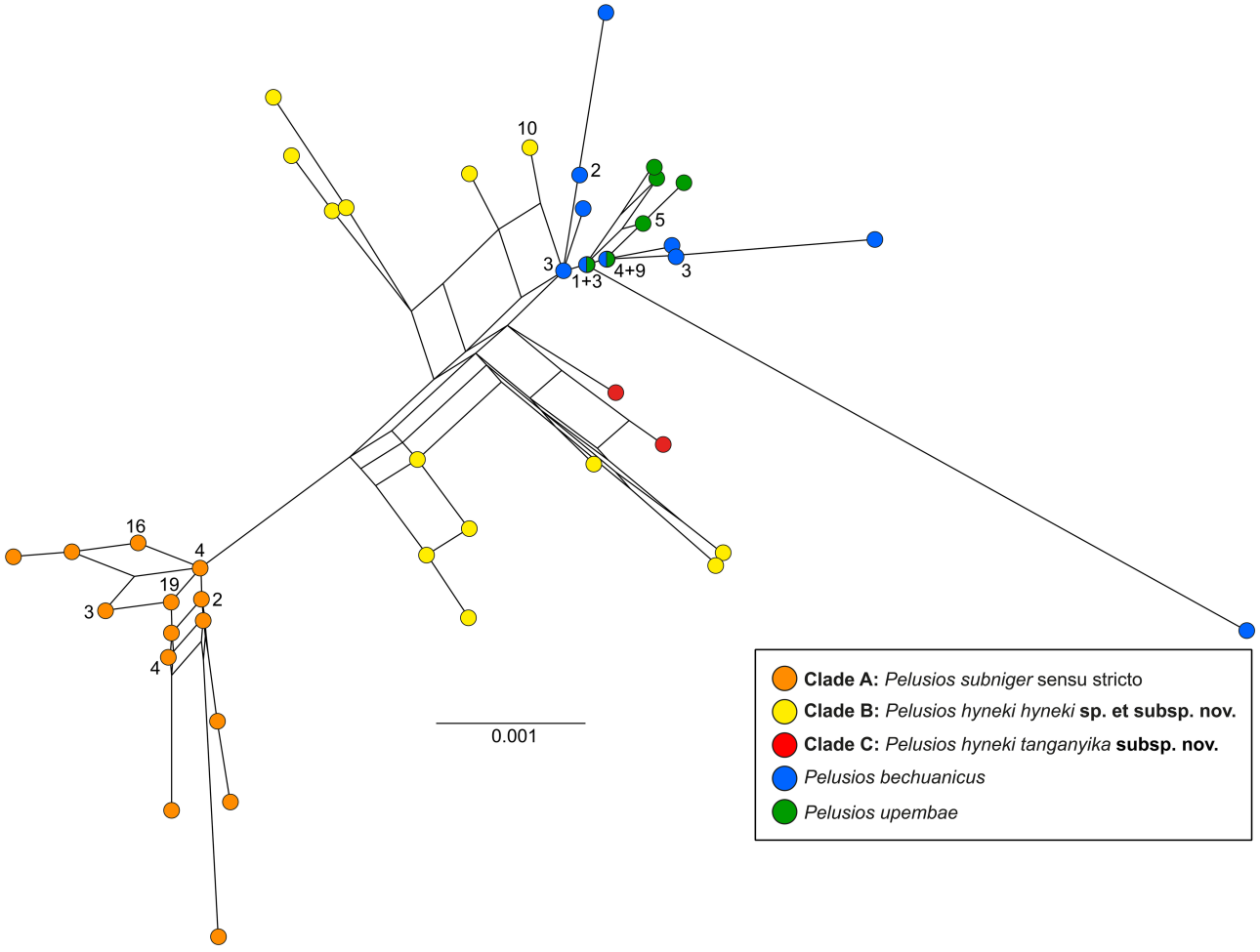

FIGURE 4. NeighborNet using concatenated sequences of three nuclear loci (2136 bp) for *Pelusios subniger* sensu lato (clades A, B, C), *P. bechuanicus*, and *P. upembae* based on 2n=118 alleles. Numbers indicate that the frequency of the respective allele > 1. Note that clades B and C share no haplotypes with clade A, *P. bechuanicus*, or *P. upembae*.

Taxonomy

Using historical evidence, Bour (1979, 1982) identified the type locality of *Testudo nigra* Lacepède, 1788 = *Testudo nigra* Bonnaterre, 1789 with Tamatave (Toamasina), Madagascar (see TTWG 2025 and ICZN 1987 for the usage of Bonnaterre 1789 as describer name). Black hinged terrapins on Madagascar represent clade A and are not genetically distinct from conspecifics from Mozambique and South Africa using mtDNA, suggesting that they were introduced from coastal mainland Africa; the same is true for *P. subniger* sensu stricto from the Seychelles (Fritz *et*

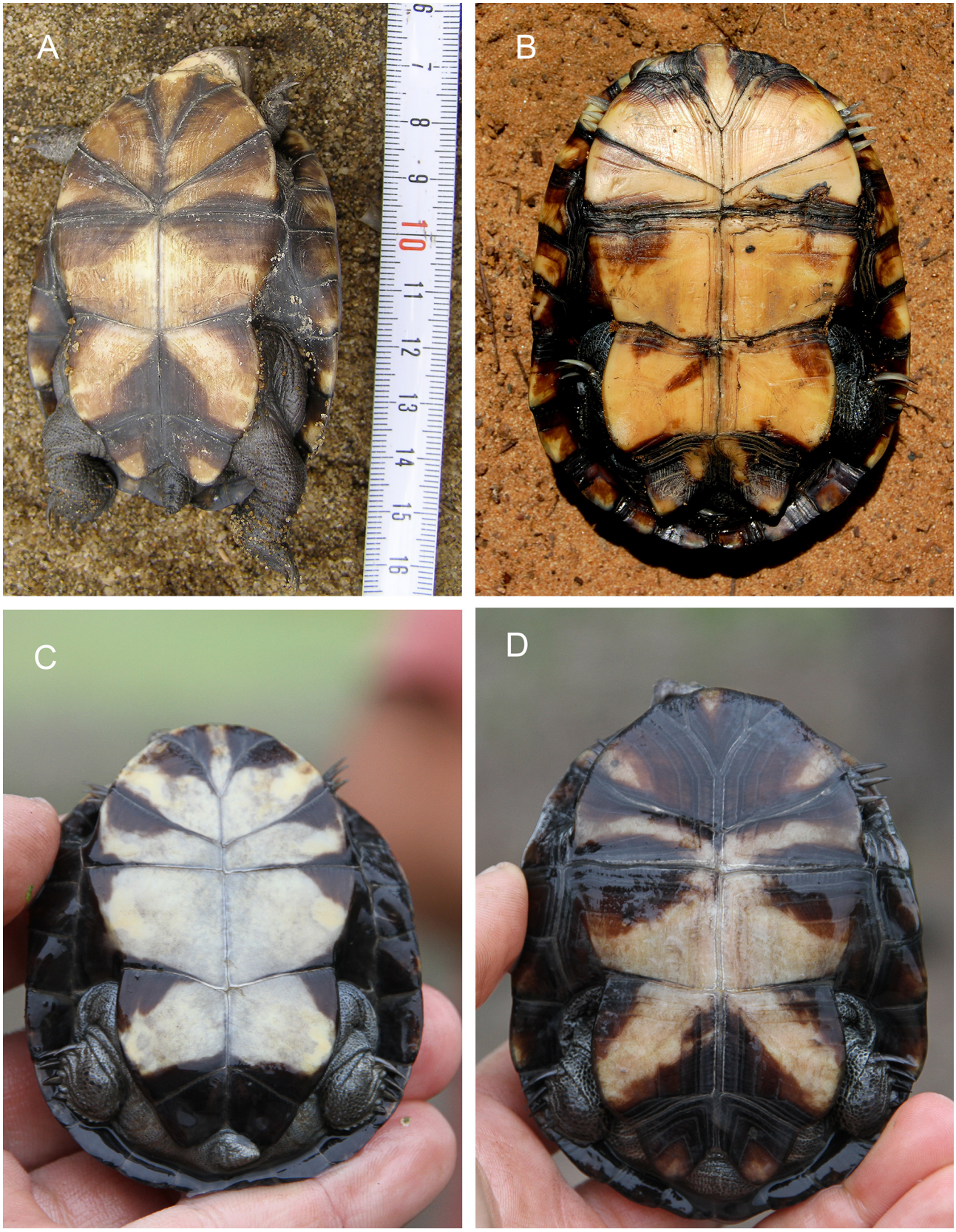

FIGURE 5. *Pelusios subniger* sensu stricto, live individuals, variation of blotched plastral pattern. (A) Adult female from Maroantsetra, Madagascar. Photo: S. Gehring. (B) Adult female from Tembe Elephant Park, South Africa, with weakly blotched pattern. Photo: J. Harvey. (C) Subadult from Chate, Mozambique and (D) subadult male from Macáua, Mozambique, with regular and quite dark pattern. Photos: R. Blažek. B–D not to scale.

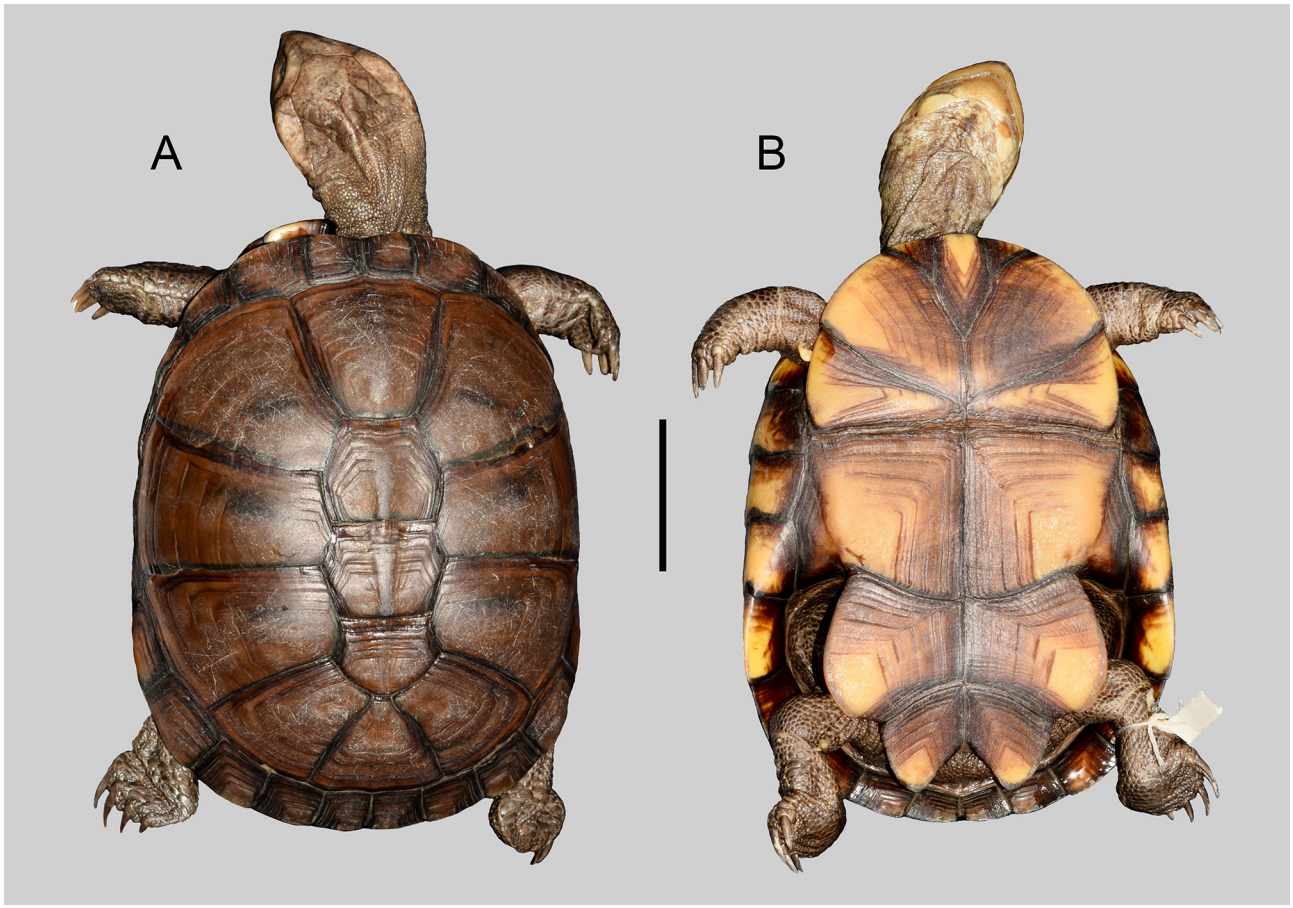

FIGURE 6. *Pelusios hyneki hyneki* **sp. et subsp. nov.** Holotype (NMP-P6V 74976/2), adult female in alcohol, vicinity of Luena (approx. -9.4409, 25.7894), Democratic Republic of the Congo. Note plastral pattern in comparison to Figure 5. Scale bar = 3 cm. Photo: J. Moravec.

al. 2013). According to the present study, *P. subniger* sensu stricto from Madagascar and the Seychelles are also not differentiated with respect to the three studied nuclear genomic markers from populations from Mozambique and South Africa (Fig. 2), reinforcing the previous conclusion (Fritz *et al.* 2013) that the subspecies *Pelusios subniger parietalis* Bour, 1983 is a junior synonym of *Pelusios subniger* (Bonnaterre, 1789). On the other hand, black hinged terrapins from the DRC and Tanzania (clades B and C of *P. subniger* sensu lato, respectively) are distinct in mitochondrial and nuclear DNA as well as in plastral coloration. Therefore, we describe these populations as a distinct species. Acknowledging the mitochondrial and geographical distinctness of clades B and C (Figs 1 and 9), we erect for each a distinct subspecies. This conclusion is also supported by the presence of private haplotypes of both taxa with respect to the nuclear RAG2 and R35 loci (Figs 2 and 3). On the other hand, as a working hypothesis, we regard the representatives of clades B and C as conspecific because of their similar morphology and haplotype sharing in all studied nuclear loci (see also Discussion). In contrast, haplotype sharing between the new species as a whole and *P. subniger* sensu stricto was very limited with respect to the R35 locus, and no haplotype sharing between the two species occurred with respect to the C-mos and RAG2 loci.

Pelusios hyneki hyneki **Široký & Fritz sp. et subsp. nov.**
Hynek's hinged terrapin

Pelusios subniger (partim), Fritz *et al*. (2013), TTWG (2017, 2021, 2025)

Holotype. National Museum Prague (NMP-P6V 74976/2), adult female in alcohol, vicinity of Luena (approx. -9.4409, 25.7894), Democratic Republic of the Congo, leg. Hynek Prokop, 2014 (Fig. 6).

Paratypes. National Museum Prague (NMP-P6V 74975, NMP-P6V 74976/1), adult female and subadult of unknown sex; Museum of Zoology, Senckenberg Dresden (MTD 49501, MTD 49502), subadult of unknown sex and adult male, all same data as the holotype.

Diagnosis. A species closely related to *Pelusios bechuanicus*, *P. upembae*, and *P. subniger* sensu stricto. *Pelusios hyneki* **sp. nov.** resembles *P. subniger* sensu stricto and differs from *P. bechuanicus* and *P. upembae* in the presence of a characteristic constriction of the plastral hindlobe near the bridge region along the abdominal-femoral seam, resulting in an outwards curved contour of the femoral scutes and a pronounced incision between the femoral and anal scutes. Furthermore, *P. hyneki* **sp. nov.** differs from *P. bechuanicus* and *P. upembae* in the distinctly lighter plastral coloration with more or less extensive brownish suffusions that may cover much of the horn-colored or yellow plastron (completely or nearly completely black plastron in *P. bechuanicus* and *P. upembae*). *Pelusios hyneki* **sp. nov.** differs from *P. bechuanicus* also in the absence of a conspicuous symmetrical coarse and contrasting yellow head pattern. *Pelusios hyneki* **sp. nov.** differs from *P. subniger* sensu stricto in its diffuse brownish plastral pattern instead of a contrasting blotched pattern. The nominotypical subspecies *Pelusios h. hyneki* **sp. et subsp. nov.** differs from *P. h. tanganyika* **subsp. nov.** genetically both with respect to mitochondrial and nuclear DNA markers and in its allopatric distribution. A selection of diagnostic sites for the mitochondrial cyt *b* and ND4 genes is listed in Table 2.

TABLE 2. Diagnostic sites for *Pelusios subniger* sensu stricto and the two subspecies of *P. hyneki* **sp. nov.** using the mitochondrial cyt *b* and ND4 genes; positions refer to the reference alignments in the Supplementary Information (Files S1–S2).

Position/Taxon	**cyt *b***	**34**	**55**	**131**	**169**	**234**	**280**	**283**	**319**	**340**	**349**	**418**	**466**
P. subniger sensu stricto		A	A	G	T	T	C	A	A	A	C	G	C
P. h. hyneki **sp. et subsp. nov.**		A	C	A	C	T	C	A	T	A	C	G	T
P. h. tanganyika **subsp. nov.**		T	T	A	C	C	T	C	T	G	A	A	C
Position/Taxon	**ND4**	**21**	**34**	**120**	**144**	**145**	**156**	**177**	**207**	**210**	**234**	**237**	**243**
P. subniger sensu stricto		C	C	T	A	T	C	C	G	C	C	C	T
P. h. hyneki **sp. et subsp. nov.**		C	T	C	A	C	T	T	A	C	T	T	T
P. h. tanganyika **subsp. nov.**		T	T	C	G	C	C	C	A	T	T	T	C
Position/Taxon	**ND4**	**249**	**297**	**363**	**435**	**438**	**439**	**445**	**471**	**579**	**615**	**625**	**654**
P. subniger sensu stricto		C	A	C	C	C	A	T	C	A	T	C	T
P. h. hyneki **sp. et subsp. nov.**		T	G	C	C	C	G	T	T	A	C	T	C
P. h. tanganyika **subsp. nov.**		T	G	A	T	T	G	C	C	C	T	T	T

Description of holotype. Adult female in alcohol, with oval carapacial outline. Plastral hindlobe indented at bridge (along abdominal-femoral seam), outer contour of femorals curved, resulting in an emarginated edge at the femoral-anal seam. Anal scutes deeply notched; notch with straight edges. All following values are maximum measurements in straight line: carapacial length 116 mm, carapacial width 89 mm, plastral length 115 mm, and shell height 45 mm. Length of the elongated diamond-shaped intergular scute 24 mm, separates the small triangular gular scutes completely. Midseam lengths of the remaining plastral scutes as follows: humerals—13 mm, pectorals—3 mm, abdominals—34 mm, femorals—27 mm, and anals—15 mm. Color of carapace chestnut brown; basic color of plastron horn yellow with extensive pale brownish tinge mainly along the plastral seams.

Coloration in life and variation. According to life photographs of the types and additional turtles with the same locality data (Table S3), no significant differences can be discerned in comparison to the alcohol-preserved specimens. The skin of the head is uniform greyish, without fine darker mottling as frequently seen in *P. subniger* sensu stricto. The extent of the diffuse brownish plastral coloration varies. NMP-P6V 74976/1 has a mostly yellowish plastron with some diffuse dark pigment along the seams. In NMP-P6V 74975, approximately one third of the plastron is covered by brownish suffusions, whereas MTD 49501 and the photograph of a not preserved life turtle have the most extensive dark plastral coloration, with more and larger darker suffusions than the holotype. Straight carapacial lengths of the type specimens and live individuals in the former collection of H. Prokop ranged between 82 and 134 mm (n=11); the two smallest individuals were immature. Adult males had straight carapacial lengths

between 106 and 119 mm (*n*=3), adult females, 108 and 134 mm (*n*=6). This suggests that *P. h. hyneki* **sp. et subsp. nov.** is smaller than *P. subniger* sensu stricto, for which a maximum straight carapacial length of 200 mm has been reported (Branch 2008).

Distribution. Genetically confirmed records of *P. h. hyneki* **sp. et subsp. nov.** are presently only known from the type locality in the southeastern DRC. However, there are three iNaturalist records of similar turtles from central Zambia (Kasanka National Park and Mpongwe) that likely represent *P. h. hyneki* **sp. et subsp. nov.** as well, even though their collection sites are approximately 600 km away. This is also likely for the two photographic records of "*P. subniger*" with a diffuse plastral pattern in northern Botswana (Khwai [Kwaai] River and Ngamiland) and another photographic record from northeastern Zimbabwe (Fig. 8; Table S3).

Etymology. We dedicate the nominotypical subspecies to the late Hynek Prokop (1972–2023) who devoted much of his live to keeping and breeding *Pelusios* species. Only his unique live collection of long-term captives, sampled in 2012 and 2013, made the present study possible.

Pelusios hyneki tanganyika Široký & Fritz subsp. nov.

Tanganyika hinged terrapin

Sternotherus nigricans (non *Testudo nigricans* Donndorf, 1798), Sternfeld & Nieden (1911 as "*Sternothaerus nigricans* Smith")

Holotype. Zoologische Staatssammlung München (ZSM 106/1960), subadult female in alcohol, Lake Manyara, Mbugwe (-3.5972, 35.8664), Tanzania, leg. Johann Popp, 22 April 1960 (Fig. 7).

Paratype. Museum für Naturkunde Berlin (ZMB 22828), subadult of unknown sex in alcohol, "Unika, Bezirk Langenburg, D.O. Afrika" (= Unyika, Mbeya District, Tanzania, approx. -8.8900, 33.4651), Hauptmann a. D. Paul Fromm, April 1909.

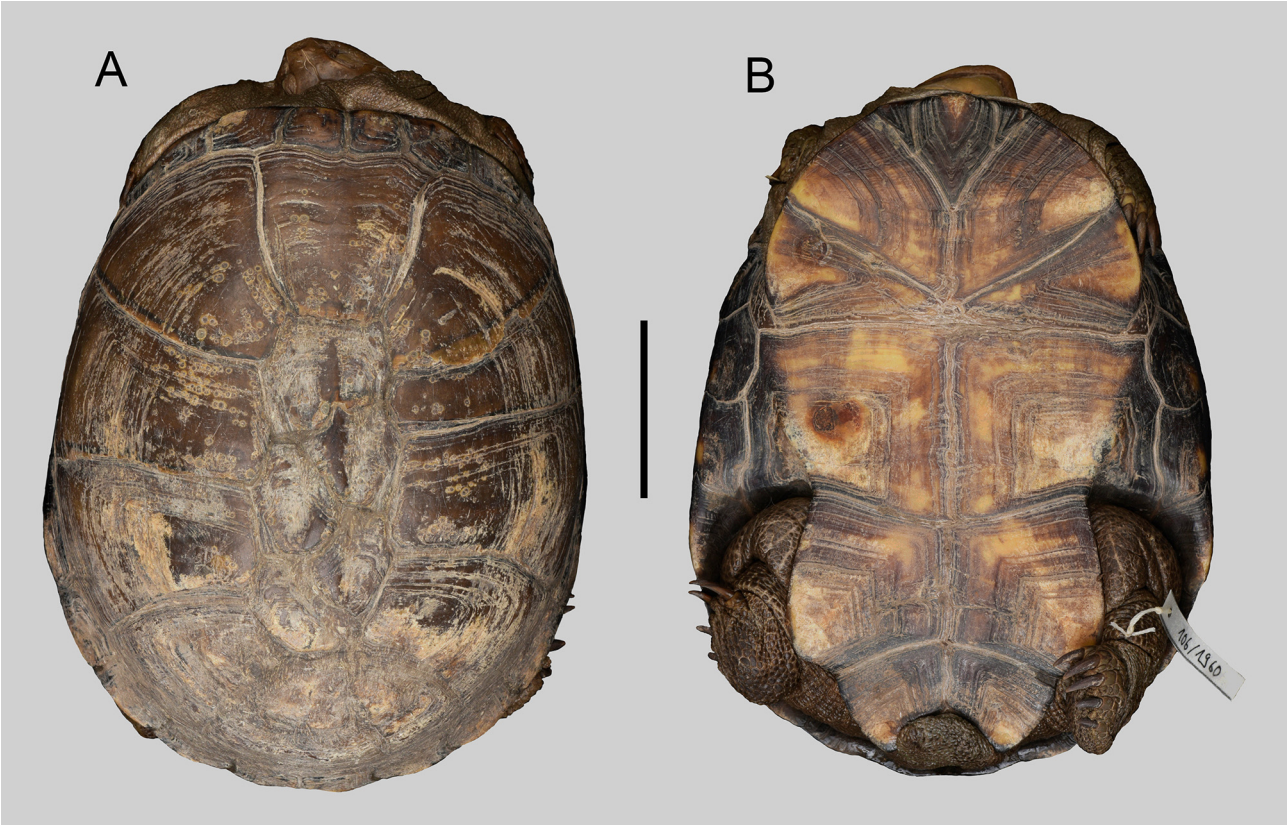

FIGURE 7. *Pelusios hyneki tanganyika* **subsp. nov.** Holotype (ZSM 106/1960), subadult female in alcohol, Lake Manyara, Mbugwe (-3.5972, 35.8664), Tanzania. Note plastral pattern in comparison to Figure 5. Scale bar = 3 cm. Photo: M. Franzen.

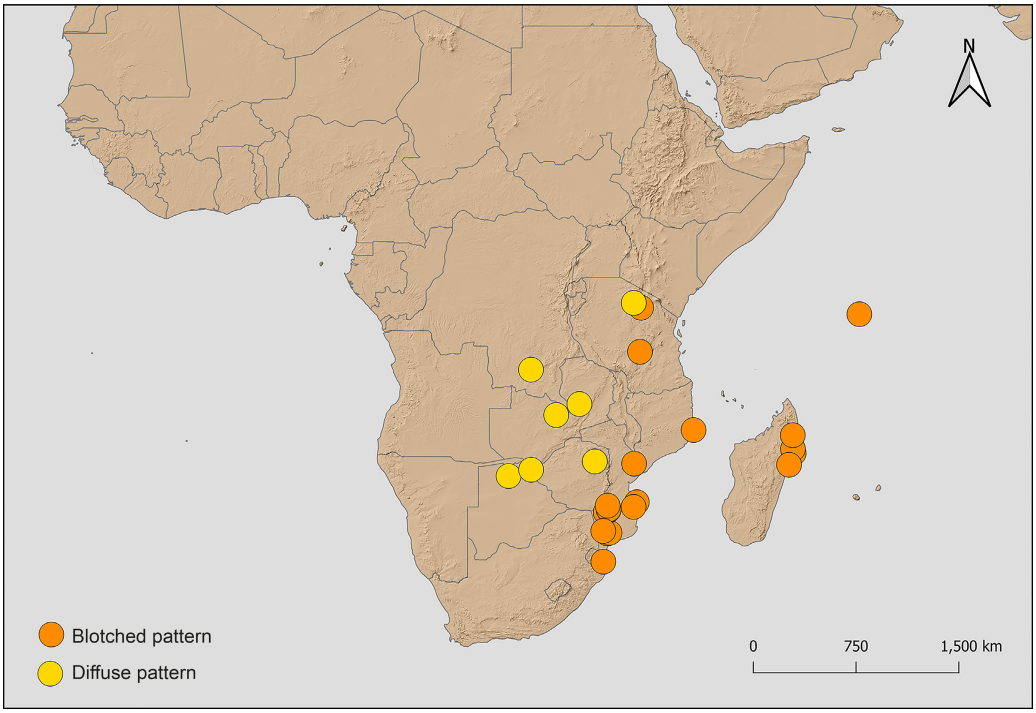

FIGURE 8. Geographic distribution of black hinged terrapins (*Pelusios subniger* sensu lato) with different plastral patterns. Note the occurrence of both patterns in close proximity in northern Tanzania.

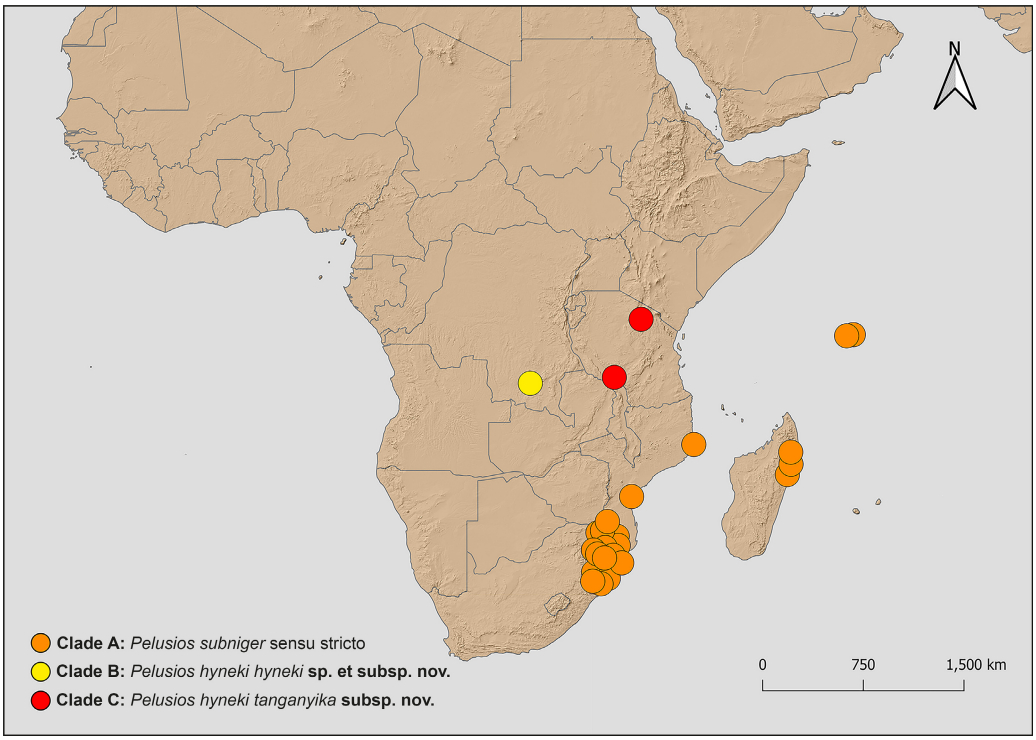

FIGURE 9. Geographic distribution of the three mitochondrial clades of black hinged terrapins (*Pelusios subniger* sensu lato).

Diagnosis. *Pelusios hyneki tanganyika* **subsp. nov.** differs from the nominotypical subspecies in mitochondrial DNA markers, private alleles in the RAG2 and R35 loci, and its allopatric distribution. A selection of diagnostic sites for the mitochondrial cyt *b* and ND4 genes is listed in Table 2.

Description of holotype. Young female in alcohol, with oval carapacial outline. Right side of carapace with abnormal scutation with "dovetailed" vertebral scutes and five irregular costal scutes. Plastral hindlobe indented at bridge (along abdominal-femoral seam), outer contour of femorals curved, resulting in an emarginated edge at the femoral-anal seam. Anal scutes deeply notched; notch with slightly curved edges. Head retracted. All following values are maximum measurements in straight line: carapacial length 150 mm, carapacial width 117 mm, plastral length 140 mm, and shell height 67 mm. Intergular broad, with slightly diverging edges, length 29 mm, separates the small triangular gular scutes completely. Midseam lengths of the remaining plastral scutes as follows: humerals—20 mm, pectorals—5 mm, abdominals—43 mm, femorals—26 mm, and anals—17 mm. Color of carapace olive brownish; basic color of plastron horn yellow with darker brownish suffusions across all shields. Gular, intergular, and anal scutes mainly brownish.

Variation. In contrast to the holotype, the paratype of *P. h. tanganyika* **subsp. nov.** has an almost plain yellow plastron. Its straight carapacial length is 87 mm. Unfortunately, no notes or measurements were taken from the three live individuals in the former collection of H. Prokop (Pardubice).

Distribution. Only known from two sites in central mainland Tanzania.

Remarks. Geographically, the minimum distance between the genetically verified records of *P. h. tanganyika* **subsp. nov.** and the type locality of *P. h. hyneki* **sp. et subsp. nov.** is approximately 800 km. If the black hinged terrapins from Tanzania with blotched plastral pattern represent *P. subniger* sensu stricto (Fig. 8; four iNaturalist records from Iringa and Manyara Regions, see Table S3), *P. h. tanganyika* **subsp. nov.** occurs there sympatrically with *P. subniger* sensu stricto. Together with the photographic records of black hinged terrapins with a diffuse plastral pattern from Botswana, Zambia, and Zimbabwe (Table S3), this suggests that *P. subniger* sensu stricto is rather a coastal and *P. hyneki* **sp. nov.** an inland species (cf. Fig. 8).

Etymology. The subspecies epithet is a noun in apposition and refers to the continental part of Tanzania (Tanganyika) from which the taxon is described.

Discussion

The description of *Pelusios hyneki hyneki* **sp. et subsp. nov.** does not come as a surprise. Fritz *et al.* (2013) already highlighted the mitochondrial distinctness of two turtles from the southeastern DRC, from what is now the type locality and from where all of our samples of the new taxon originate. These turtles were originally identified as "*P. subniger*" and kept by the late Hynek Prokop, who obtained these turtles from the international pet trade. We are confident that the geographic origin is correct according to the information received from H. Prokop. Moreover, morphologically the type series aligns geographically with the examined iNaturalist photos from neighboring countries, providing further support for the reliability of the geographic information (Fig. 8).

The present study showed that *P. h. hyneki* **sp. et subsp. nov.** differs not only in its mtDNA, but also in the studied three nuclear loci and plastral coloration from *P. subniger* sensu stricto. Its nuclear alleles resemble *P. bechuanicus* and *P. upembae* more than *P. subniger* sensu stricto (Figs 3 and 4), with which *P. h. hyneki* **sp. et subsp. nov.** is placed in the same clade based on mtDNA sequences (Fig. 1). Such counterintuitive discordances of mitochondrial and nuclear evidence are not entirely unexpected, since there are many cases of mitochondrial introgression and mitochondrial capture known for different turtle clades (see Kehlmaier *et al.* 2019, 2024, 2025; Fritz *et al.* 2024; Hurtado-Gómez *et al.* 2024 and studies cited therein). Contrary to the nuclear DNA evidence, but in agreement with the mtDNA phylogeny, the similarity of the shape of the plastral hindlobe of *P. subniger* sensu stricto and *P. h. hyneki* **sp. et subsp. nov.** supports that these two taxa are closely related.

The similarity of *P. h. hyneki* **sp. et subsp. nov.**, *P. bechuanicus*, and *P. upembae* in the studied nuclear loci could result either from (1) ancestral polymorphism, (2) introgression/gene flow, or (3) a close phylogenetic relationship of these three species. In the latter case, the mtDNA similarity of the new taxon to *P. subniger* sensu stricto would result from ancient mitochondrial capture. We cannot exclude any of these three possibilities. However, if *P. h. hyneki* **sp. et subsp. nov.** and *P. subniger* sensu stricto should be closely related, as suggested by plastral shape and mtDNA, the similarity of the nuclear loci of *P. h. hyneki* **sp. et subsp. nov.**, *P. bechuanicus*, and *P. upembae* is likely to result from secondary genetic exchange among these species. The collection site of the genetically studied *P. h. hyneki* **sp. et subsp. nov.** in the DRC is close to the distribution range of *P. upembae*, and this could support this option. Studying additional nuclear loci, preferred genome-wide markers (e.g., SNPs or AFLP profiles), could

help to resolve this conundrum. Morphologically, *P. bechuanicus* and *P. upembae* are highly distinct (see Broadley 1981).

The discovery of two black hinged terrapins in central mainland Tanzania representing another deeply divergent mitochondrial clade was unexpected. The mtDNA sequences of these two historical museum specimens align with those of three pet trade turtles and cluster, with maximum support, in an unresolved clade with *P. subniger* sensu stricto and *P. h. hyneki* **sp. et subsp. nov.** One of the Tanzanian specimens has a diffuse plastron coloration resembling the new taxon from the DRC, and the three pet trade turtles match in the studied nuclear markers *P. h. hyneki* **sp. et subsp. nov.** (Figs 2–4). They possess, besides shared haplotypes, also private alleles in the RAG2 and R35 loci. This supports that a third distinct taxon is involved. Unfortunately, the morphology of the pet trade turtles was not recorded. The shape of the plastral hindlobe of the two museum specimens matches *P. subniger* sensu stricto and *P. h. hyneki* **sp. et subsp. nov.**

In the face of the similarity of the third taxon and *P. h. hyneki* **sp. et subsp. nov.** in nuclear markers and plastral morphology, we prefer not to describe another new species. We hypothesize instead that the two taxa are conspecific and identify the third taxon as a subspecies of *P. hyneki, P. h. tanganyika* **subsp. nov.**, which seemingly co-occurs with *P. subniger* sensu stricto in central Tanzania. This taxonomy acknowledges on the one hand the similarity of the two subspecies in the studied nuclear genes as well as in plastral shape and coloration. On the other hand, it accounts for the private alleles and the distinct mitochondrial clade of *P. h. tanganyika* **subsp. nov.** This classification is embedded in a framework recognizing subspecies as allopatric or parapatric taxa that differ in mitochondrial and nuclear genomic markers, but that are still putatively or evidently capable of full genetic amalgamation (Kindler & Fritz 2018), as indicated in this case by their shared alleles (Figs 2 and 3).

The non-monophyly of the mitochondrial clades of the two subspecies does not contradict conspecificity when the many cases of conflicts between mitochondrial and nuclear genomic genealogies in turtles are considered (see above). However, the paucity of specimens with morphological data causes the dilemma that *P. h. tanganyika* **subsp. nov.** currently cannot be diagnosed morphologically from the nominotypical subspecies. We expect that the subspecies description will stimulate further research, allowing for a future morphological characterization.

If we identify all black hinged terrapins with a diffuse plastral pattern as *P. hyneki* **sp. nov.** and all turtles with a blotched plastral coloration as *P. subniger* sensu stricto, a clear geographic pattern emerges: *Pelusios hyneki* **sp. nov.** is then distributed inland, west of the Rift Valley, while *P. subniger* sensu stricto is only known from east of the Rift Valley, from Tanzania south to northeastern South Africa (Fig. 8). Furthermore, *P. subniger* sensu stricto occurs then together with *P. h. tanganyika* **subsp. nov.** in central Tanzania. Remarkably, different species of *Pelomedusa*, the second pelomedusid genus, also co-occur in this region (Petzold *et al*. 2014), although there is no obvious association of the individual distribution ranges of any *Pelomedusa* species with the Rift Valley.

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Supplementary Information (available from figshare using the link: https://doi.org/10.6084/m9.figshare.30019324)

Figure S1. Mitochondrial phylogeny of 392 hinged terrapins (*Pelusios* spp.), rooted with *Pelomedusa olivacea*. Full ML tree for Figure 1 based on the unpartitioned concatenated dataset (2311 bp).

Figure S2. Mitochondrial phylogeny of 392 hinged terrapins (*Pelusios* spp.), rooted with *Pelomedusa olivacea*. Full BI tree for Figure 1 based on the unpartitioned concatenated dataset (2311 bp).

Figure S3. Mitochondrial phylogeny of 392 hinged terrapins (*Pelusios* spp.), rooted with *Pelomedusa olivacea*. Full ML tree based on the partitioned concatenated dataset (2311 bp).

Figure S4. Mitochondrial phylogeny of 392 hinged terrapins (*Pelusios* spp.), rooted with *Pelomedusa olivacea*. Full BI tree based on the partitioned concatenated dataset (2311 bp).

Table S1. Studied samples with GenBank/ENA accession numbers. For heterozygous loci, accession numbers for both alleles are given.

Table S2. Partitioning and best fitting substitution models for mtDNA.

Table S3. Photographic and other records for the plastral pattern of black hinged terrapins.

File S1. Reference alignment for Table 2 (cyt *b*).

File S2. Reference alignment for Table 2 (ND4).