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A revision of African helmeted terrapins (Testudines: Pelomedusidae: *Pelomedusa*), with descriptions of six new species

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Abstract

Using nearly range-wide sampling, we analyze up to 1848 bp of mitochondrial DNA of 183 helmeted terrapins and identify a minimum of 12 deeply divergent species-level clades. Uncorrected *p* distances of these clades equal or clearly exceed those between the currently recognized species of *Pelusios*, the genus most closely related to *Pelomedusa*. We correlate genetic discontinuities of *Pelomedusa* with data on morphology and endoparasites and describe six new *Pelomedusa* species. Moreover, we restrict the name *Pelomedusa subrufa* (Bonnaterre, 1789) to one genetic lineage and resurrect three further species from its synonymy, namely *P. galeata* (Schoepff, 1792), *P. gehafie* (Rüppell, 1835), and *P. olivacea* (Schweigger, 1812). In addition to these ten *Pelomedusa* species, we identify two further clades from Cameroon and Sudan with similar levels of genetic divergence that remain unnamed candidate species. We also note that some problematical terrapins from South Africa and Somalia may represent two additional candidate species. Some of the *Pelomedusa* species are morphologically distinctive, whilst others can only be identified by molecular markers and are therefore morphologically cryptic taxa.

Key words: Africa, Arabian Peninsula, integrative taxonomy, Madagascar, nomenclature, Reptilia, revision, species description

Introduction

Species delimitation has been flagged as a Renaissance issue in zoology (Sites & Marshall 2003), and to this end new DNA-based approaches have been developed (see the reviews in Carstens *et al.* 2013; Miralles & Vences 2013). Basically, two major approaches have gained much attention. One, DNA barcoding (e.g. Hebert *et al.* 2003), relies on genetic distances of typically a single marker gene, whilst the later proposed multilocus coalescent-based methods (e.g. Yang & Rannala 2010) seem at first glance much more sophisticated. It is well known that DNA barcoding suffers from several shortcomings, such as relying on a single (mitochondrial) marker and a rigid threshold for inferring species status. Moreover, hybridization, introgression, paralogues (in particular numts), incomplete sorting and recently split species pose serious challenges (e.g. Meyer & Paulay 2005; Galtier *et al.* 2009). For these reasons, DNA barcoding has been severely criticized as massive oversimplification (e.g. Will &

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Rubinoff 2004; Will *et al.* 2005). However, the multilocus coalescent approach has recently been shown prone to massive oversplitting (Miralles & Vences 2013). A further caveat is that many conflicting phylogenies can be derived from selecting different multilocus sets from whole genomes (*cf.* Dikow & Smith 2013). Together these concerns underline that also the multilocus coalescent approach, whilst methodologically refined, is far from an ideal solution. In view of this background, an 'Integrative Taxonomy' approach has been suggested (Dayrat 2005; Will *et al.* 2005; Padial *et al.* 2010; Schlick-Steiner *et al.* 2010), integrating as many lines of evidence as possible (e.g. different genetic methods, morphology, behaviour, natural history, etc.).

Irrespective of the chosen method, there is another issue in 'real scientific life'. There is a plethora of taxa for which only limited or compromised sampling is available, not allowing a range-wide assessment. This is especially true for widely distributed taxa with ranges dissected by many political borders. In such cases, range-wide sampling is extremely difficult or impossible. Here we present an exemplar study for such a widely distributed taxon, the helmeted terrapin *Pelomedusa subrufa* (Bonnaterre, 1789), and use, as far as possible, an integrative approach to revise its taxonomy.

The helmeted terrapin is currently thought to represent a pan-African species (Wong *et al.* 2010; Barlow *et al.* 2013), distributed throughout most of sub-Saharan Africa, Madagascar and the southwestern Arabian Peninsula (Boycott & Bourquin 2008; Branch 2008). Recent studies have questioned the earlier belief (Gasperetti *et al.* 1993) that *P. subrufa* is a monotypic species, and have identified ten deeply divergent genetic lineages of helmeted terrapins (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010; Fritz *et al.* 2011, 2014). For only four of these lineages, however, are names available (Fritz *et al.* 2014). In the present paper, we examine whether these genetic lineages represent distinct species. To enable this we expand the geographical sampling of the earlier studies considerably, using additional fresh material and historical museum specimens to generate mitochondrial DNA sequences. Our sampling now covers nearly the complete distribution range of *P. subrufa*. We use this data set for inferring phylogenetic relationships of the distinct lineages, and compare the divergence values of two mitochondrial genes to variation among the species of the most closely related genus *Pelusios*. In addition, we use the obtained genetic information for assigning museum specimens to genetic lineages and compare these morphologically. As far as possible, we also integrate data on endoparasites in our considerations, and use this comprehensive data set for a taxonomic revision of the *Pelomedusa* complex.

Materials and Methods

Pelomedusa holdings in the following natural history museums were studied, corresponding to approximately 350 specimens: Muséum d'Histoire naturelle Genève, Museum für Naturkunde (Berlin), Museum für Tierkunde (Senckenberg Dresden), Naturhistorisches Museum Wien, The Natural History Museum (London), Port Elizabeth Museum, Senckenberg-Museum (Frankfurt am Main), Staatliches Museum für Naturkunde Stuttgart, Zoologisches Forschungsmuseum Alexander Koenig (Bonn), and Zoologische Staatssammlung München. In addition, selected terrapins from the collections of the Muséum National d'Histoire naturelle (Paris) and the National Museum Prague were studied. Straight-line standard measurements of the shell (Fritz 1995) were taken and external morphology, colouration and pattern were recorded. Of many museum specimens from localities for which no genetic data were available, tissue samples were extracted for genetic investigation. In addition, fresh samples from different localities in Angola, Namibia and South Africa were studied (Table S1).

Following Fritz *et al.* (2014), parts of three phylogenetically informative mitochondrial genes were sequenced, the 12S rRNA gene (12S), the cytochrome *b* gene (cyt *b*), and the ND4 gene plus adjacent DNA coding for tRNAs. Laboratory procedures for samples from historical museum specimens ($n = 29$) and for fresh samples ($n = 77$) are described in detail in Fritz *et al.* (2014). For generating sequences of museum specimens, all necessary precautions were taken as described in Fritz *et al.* (2014), including DNA extraction in a clean room being physically isolated from the normal DNA processing facilities. The obtained DNA sequences were concatenated for phylogenetic analyses and merged with the partially overlapping data sets of Vargas-Ramírez *et al.* (2010), Wong *et al.* (2010) and Fritz *et al.* (2011, 2014), resulting in an alignment of 183 *Pelomedusa* sequences of 1848 bp length. *Pelusios sinuatus* was added as outgroup (Table S1; see there for GenBank accession numbers). The 12S sequences of fresh samples were up to 356 bp long; 12S sequences from museum specimens, up to 253 bp. The cyt *b* sequences of fresh samples were of 674 bp length, and those from museum specimens, 319 bp. The mtDNA fragment containing

the partial ND4 gene plus adjacent DNA coding for tRNAs was 810–813 bp long in fresh samples, and up to 437 bp long (ND4 only) for historical material.

The alignment was examined using the following partition schemes: (i) unpartitioned, (ii) partitioned by gene, i.e., each gene corresponds to a distinct partition, but all DNA coding for tRNAs was treated as only one additional partition, and (iii) maximum partitioning, i.e., using each codon of the protein-coding genes, the 12S gene and the lumped DNA coding for tRNAs as a distinct partition. To find the best scheme and optimal substitution models for phylogenetic analyses, the software PARTITIONFINDER (Lanfear *et al.* 2012) was applied, resulting in the selection of the maximum partitioning scheme. Based on this, phylogenetic relationships were then inferred using Bayesian Inference (BI) and Maximum Likelihood (ML). BI calculations were performed with MRBAYES 3.2.1 (Ronquist *et al.* 2012) using the best-fit models for nucleotide substitution for each partition (Table S2), two parallel runs (each with four chains) and default parameters. The chains ran for 10 million generations with every 100th generation sampled. The calculation parameters were analysed using the software TRACER 1.6 (http://tree.bio.ed.ac.uk/software/tracer/) and a burn-in of 2.5 million generations to assure that both runs converged. Subsequently, only the plateau of the most likely trees was sampled using the same burn-in, and a 50% majority rule consensus tree was generated. The posterior probability of any individual clade in this consensus tree corresponds to the percentage of all trees containing that clade, and is a measure of clade frequency and credibility. ML analyses were conducted using RAxML 7.2.8 (Stamatakis 2006) and the default GTR+G model. Five independent ML searches were run using different starting conditions and the fast bootstrap algorithm to explore the robustness of the branching patterns by comparing the best trees. Subsequently, 1000 non-parametric thorough bootstrap replicates were calculated and the values plotted against the best tree.

Several recent papers have used uncorrected *p* distances of the cyt *b* gene as a tool for species delimitation in chelonians (e.g. Vargas-Ramírez *et al.* 2010, 2012, 2013; Praschag *et al.* 2011; Fritz *et al.* 2012a, b; Kindler *et al.* 2012). In the present study, divergences among *Pelomedusa* lineages are compared to those of the 17 species of African hinged terrapins (*Pelusios*), which represent the genus most closely related to *Pelomedusa*. For this purpose, previously published sequence data of *Pelusios* (Fritz *et al.* 2011, 2012c, 2013; Stuckas *et al.* 2013) are used. Uncorrected *p* distances were calculated using the software MEGA 6.06 (Tamura *et al.* 2013). Since for many historical museum specimens only 12S sequences could be generated, uncorrected *p* distances were also obtained for this gene.

Results

Mitochondrial phylogeny and geographical distribution of genetic lineages

The results of our phylogenetic analyses (Fig. 1) closely resemble the tree presented in Fritz *et al.* (2014), which was calculated using the merged data sets of Vargas-Ramírez *et al.* (2010), Wong *et al.* (2010), and Fritz *et al.* (2011), plus new sequences, mainly from historical type specimens. Based on this data set of 76 helmeted terrapins, Fritz *et al.* (2014) found 10 deeply divergent clades. Our present analyses expanded this data set with sequences from 107 additional terrapins and revealed two further clades. Furthermore, we made some new country or province records for previously known genetic lineages (all new records are marked below with asterisks; for detailed localities, see Table S1).

The topologies of the trees resulting from our ML and Bayesian analyses are virtually identical (Fig. 1). A well-supported major clade contains all lineages from the northern part of the distribution range of *Pelomedusa*. Another major clade (which under Bayesian analyses is moderately supported, and under Maximum Likelihood only weakly supported) embraces two clades from the southern part of the distribution range.

The northern clade (Fig. 1) consists of 10 deeply divergent clades from Cameroon (lineage I of Vargas-Ramírez *et al.* 2010), Sudan* (newly identified lineage XI), the Central African Republic and South Sudan* (lineage IV of Vargas-Ramírez *et al.* 2010), Eritrea and perhaps Sudan* (lineage X of Fritz *et al.* 2014), Kenya and Tanzania* (lineage V of Vargas-Ramírez *et al.* 2010), Tanzania* (newly identified lineage XII), Ghana and the Ivory Coast (lineage II of Vargas-Ramírez *et al.* 2010), Benin, Burkina Faso, Niger, Nigeria and Senegal (lineage III of Vargas-Ramírez *et al.* 2010), Saudi Arabia and Yemen (lineage VII of Vargas-Ramírez *et al.* 2010), and Somalia (lineage VI of Vargas-Ramírez *et al.* 2010; Fig. 2). The Somali clade is comprised of two deeply divergent subclades, which correspond to samples from sites only 40 km distant (Table S1).

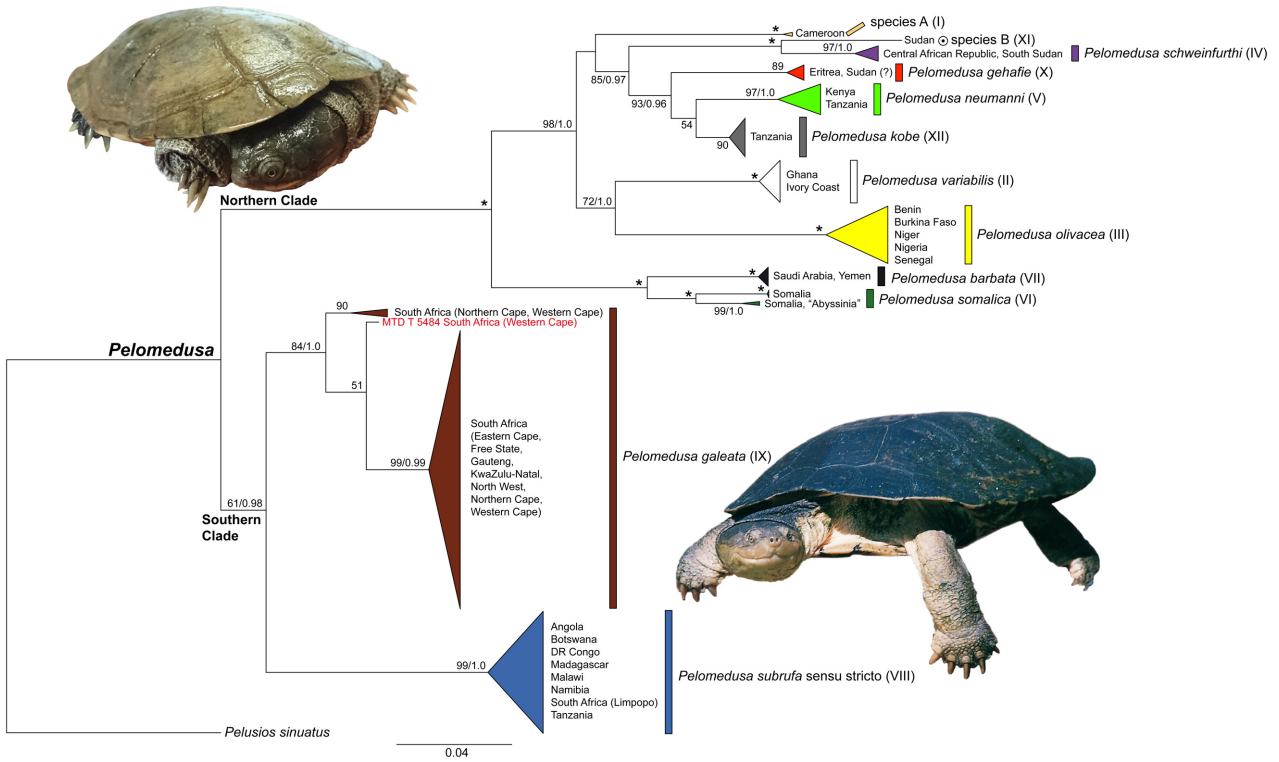

FIGURE 1. Maximum Likelihood tree for helmeted terrapins (*Pelomedusa* spp.) using 1848 bp of mitochondrial DNA (12S, cyt *b*, ND4+tRNAs), rooted with *Pelusios sinuatus*. Terminal clades collapsed to cartoons. The topology of the Bayesian 50% majority rule consensus tree was identical. Numbers along branches indicate bootstrap support and clade support under BI (posterior probabilities) greater than 50 or 0.95, respectively. Asterisks represent maximum support under both methods. Colours and symbol correspond to the map (Fig. 2). On the right, proposed species names indicated; in brackets, mtDNA lineages. For clade membership of individual samples, see Table S1. The questionable sample MTD T 5484 from Swellendam District (Western Cape), South Africa, is highlighted in red (see text). The shown terrapins are *Pelomedusa neumanni* (top; Kakamega, Kenya) and *P. galeata* (bottom; Port Elizabeth, South Africa—photos: H. Prokop and W.R. Branch).

Lineages VII and VI together are, with high support, sister to a clade containing the other northern lineages. Within the latter clade, lineages II and III are sister taxa, and this clade II + III is sister to a weakly supported clade containing the remaining northern lineages. Among those, the sister group relationship of lineages XI and IV is maximally supported, and this clade XI + IV is sister to a well-supported clade containing lineages X, V and XII. However, the phylogenetic relationships within the latter clade are only weakly resolved, as is the placement of lineage I. In particular, support values are low under BI, which could be related to the fact that most concerned clades contain many short mtDNA sequences of historical museum specimens. Obviously, MrBAYES cannot cope with this situation.

The southern clade (Fig. 1) is comprised of a clade corresponding to lineage IX of Vargas-Ramírez *et al.* (2010) from South Africa (Eastern Cape, Free State*, Gauteng, KwaZulu-Natal, North West*, Northern Cape, Western Cape) and another clade corresponding to lineage VIII of Vargas-Ramírez *et al.* (2010). The latter clade contains sequences from southern Angola*, Botswana, the southeastern Democratic Republic of the Congo, Madagascar, Malawi, Namibia, the South African Limpopo province*, and Tanzania* (Fig. 2). Clade IX has pronounced structure, with three distinct subclades. One of these subclades is comprised of most sequences from South Africa, whilst the two others contain only one or three sequences from South Africa, respectively. The sequences of the different subclades are not geographically separated (Table S1).

A remarkable finding is that three distinct lineages (V, VIII, XII) occur in sympatry or at least close proximity in the regions of the Kilimanjaro and Arusha, Tanzania (Fig. 2). Human translocation is unlikely as the studied museum specimens are 50 to more than 100 years old. Thus, this is strong evidence for the specific distinctness of the involved genetic lineages.

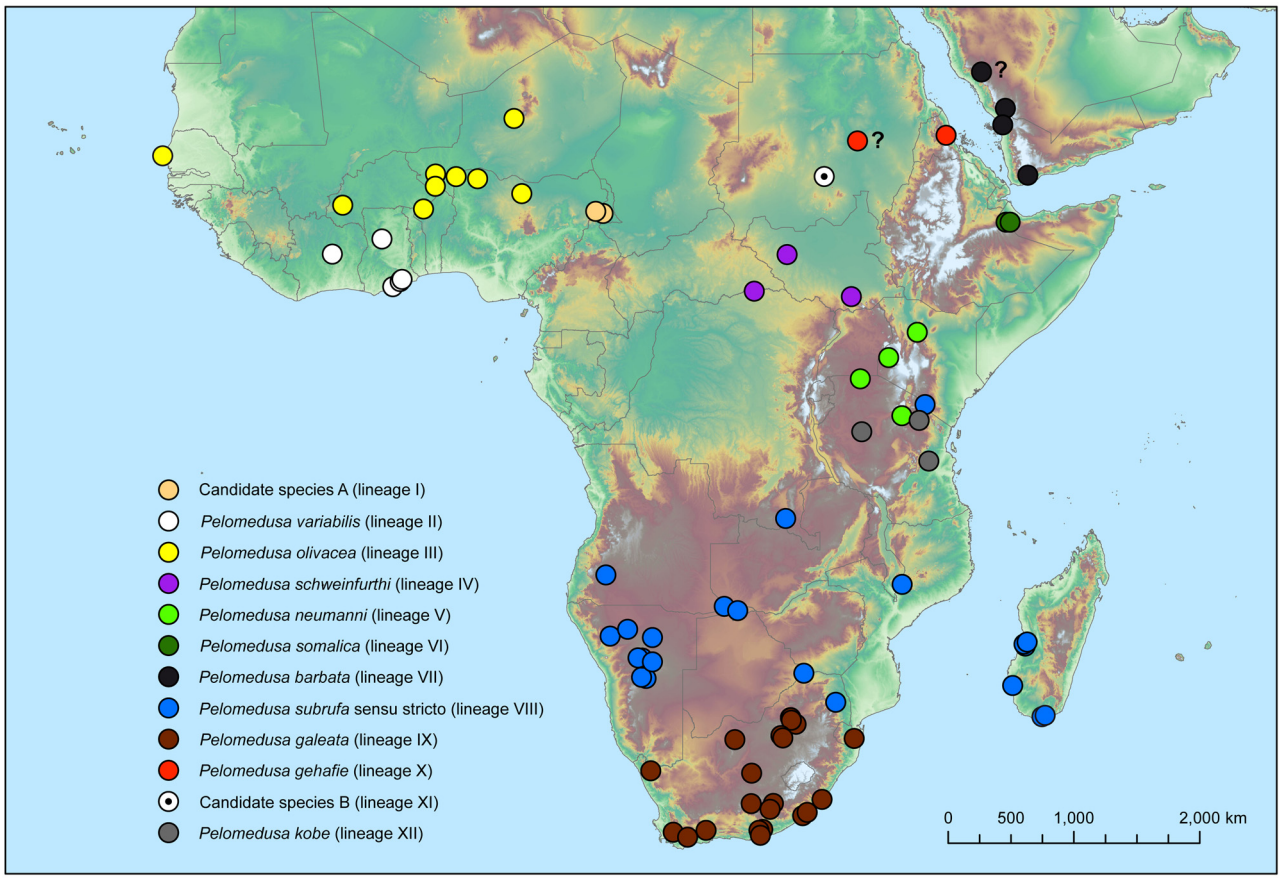

FIGURE 2. Genetically verified records of *Pelomedusa* species. Question marks denote doubtful or uncertain localities.

Uncorrected *p* distances

For the 12S gene, uncorrected *p* distances among the 12 lineages of *Pelomedusa* range on average between 2.60% and 12.15% (Table 1). The lowest values occur between lineages V and XII (2.63%) and lineages X and XII (2.60%); the next-lowest values are already clearly higher with 3.48% (lineages II and III), 3.59% (lineages VI and VII), and 3.79% (lineages V and X). The highest value (12.5%) occurs between lineages IV and VIII. With respect to the within-lineage divergence, the highest average value is found in lineage V (1.34%). The two subclades within lineage VI differ by 1.83%, with within-group divergences of 0%. The average divergence between the two subclades of lineage IX for which 12S sequences are available amounts to 1.79% (within-group divergences of 0% and 0.26%). When these figures are compared to *Pelusios* (Table 2), it is obvious that the values of *Pelomedusa* equal or clearly exceed those between the currently recognized species of *Pelusios*. Between-species divergences in *Pelusios* range on average from 0.32% to 7.92%, and the highest average within-species divergence (*Pelusios carinatus*: 0.73%) is more than twice the value observed between *Pelusios castaneus* and *P. chapini* (0.32%), underlining previous doubts on the validity of the latter species (Fritz *et al.* 2011).

With the more variable cyt *b* gene, the general pattern remains the same. Uncorrected *p* distances among the 12 lineages of *Pelomedusa* range on average between 5.64% and 18.60% (Table 3), with the lowest value found between lineages IV and XI. Similar values of 5.97%, 5.99% and 5.93% do also occur between some other lineages (IV and XII, V and XII, X and XII). The highest value of 18.60% occurs between lineages V and VIII, and most lineages differ by average values greater than 10%. The greatest average distance within a single lineage is found in lineage VI from Somalia (3.72%). When the two subclades within this lineage are compared, they differ on average even by 5.98%, with within-clade divergences of 0% and 1.26%. The average divergences of the three deeply divergent subclades within lineage IX are 1.06%, 7.50% and 8.14%, with within-clade divergences of 0.49% to 1.85%. Average uncorrected *p* distances among *Pelusios* species range from 1.38% to 15.40% (Table 4). The three lowest values (*Pelusios bechuanicus vs. P. upembae*: 1.38%; *P. carinatus vs. P. rhodesianus* from Burundi: 2.02%; *P. castaneus vs. P. chapini*: 1.84%) resemble the largest within-species divergence (*P. castaneus*: 1.95%), challenging

the species status of the concerned taxa. Unlike *Pelusios*, the within-lineage divergences of *Pelomedusa* for the 12S and cyt *b* genes are always clearly lower than the values among the distinct lineages (Tables 1–4).

TABLE 1. Average uncorrected *p* distances (percentages) for a 360-bp-long alignment of the 12S gene of *Pelomedusa* species using the pairwise deletion option of MEGA 6.06. Between-group divergences below diagonal; within-group divergences on the diagonal in boldface. Roman numerals denote the mitochondrial lineage followed by the suggested species name; *n* = number of sequences.

	n	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
I species A	1	**n/a**											
II *variabilis*	11	5.89	**0**										
III *olivacea*	16	8.07	3.48	**0.19**									
IV *schweinfurthi*	5	9.11	7.55	8.24	**0.17**								
V *neumanni*	9	7.52	5.38	6.33	6.95	**1.34**							
VI *somalica*	5	9.50	5.89	6.92	8.22	7.68	**1.10**						
VII *barbata*	6	8.93	6.09	6.88	9.74	7.17	3.59	**0.31**					
VIII *subrufa*	26	11.14	8.52	9.85	12.15	7.71	10.37	9.62	**0.67**				
IX *galeata*	74	8.94	6.43	8.22	8.59	6.99	7.58	7.68	5.82	**0.38**			
X *gehafie*	5	7.53	6.81	7.73	7.26	3.79	7.44	8.12	7.15	6.78	**0.49**		
XI species B	1	11.16	8.89	9.45	6.39	8.50	10.60	10.07	11.72	10.22	8.98	**n/a**	
XII *kobe*	11	6.75	5.81	6.96	6.96	2.63	7.78	7.24	6.85	5.75	2.60	7.57	**0**

Discussion and taxonomic conclusions

In the past, the taxonomy of *Pelomedusa* was entirely morphology-based. Much emphasis was given to the shape of the pectoral scutes of the plastron, in particular whether the pectorals are in midseam contact or not. Many previous authors assigned northern populations, having often widely separated pectorals not in contact in the plastral midline, to the subspecies *Pelomedusa subrufa olivacea* (Schweigger, 1812). The nominotypical southern subspecies, *Pelomedusa subrufa subrufa* (Bonnaterre, 1789), was thought to have the pectorals in contact. Later, Gasperetti *et al.* (1993) questioned the reliability of these characters, and since then *P. subrufa* was treated by most authors as a monotypic species. However, the situation became much more complicated when it turned out that *P. subrufa* consists of deeply divergent genetic lineages, and that some of these genetic lineages completely match with the mentioned character states, but others not (see the recent review in Fritz *et al.* 2014 and below).

According to the present investigation, *P. subrufa* embraces at least 12 deeply divergent mitochondrial lineages that show a consistent geographical distribution, corresponding to a group of ten northern and two southern lineages. In Tanzania, the ranges of the northern and southern group overlap. The 12 lineages differ on average by uncorrected *p* distances of the 12S gene ranging from 2.60% to 12.15% (Table 1) and by uncorrected *p* distances of the cyt *b* gene ranging from 5.64% to 18.60% (Table 3).

Many recent papers have used uncorrected *p* distances of mtDNA, in particular the cyt *b* gene, as a tool for systematics and species delimitation of chelonians (e.g. Vargas-Ramírez *et al.* 2010, 2012, 2013; Praschag *et al.* 2011; Stuckas & Fritz 2011; Fritz *et al.* 2012a, b; Kindler *et al.* 2012; Iverson *et al.* 2013; Todd *et al.* 2014). Important insights of these studies were that there is a wide range of divergence values among congeneric species, and that there is no general threshold of sequence divergence that 'axiomatically' indicates distinct species (see also Shen *et al.* 2013). However, whilst there are several species known that differ not or only by minor sequence divergences in mtDNA (*Cuora*: Spinks *et al.* 2012; *Cyclemys*: Fritz *et al.* 2008; *Emys*: Fritz *et al.* 2005, 2006; *Graptemys*: Lamb *et al.* 1994; *Pseudemys*: Spinks *et al.* 2013; *Rhinoclemmys*: Vargas-Ramírez *et al.* 2013; *Trachemys*: Fritz *et al.* 2012b), there is not a single case known in which chelonians harbouring deeply divergent mitochondrial lineages are taxonomically undifferentiated. In other words, a shallow or absent mitochondrial differentiation does not necessarily contradict taxonomic differentiation or species distinctness, but deep divergence is a reliable indicator for taxonomic differentiation.

TABLE 2. Average uncorrected *p* distances (percentages) for a 388-bp-long alignment of the 12S gene of *Pelusios* species using the merged data sets of Fritz *et al.* (2011, 2012c, 2013) and Stuckas *et al.* (2013) and the pairwise deletion option of MEGA 6.06. Between-group divergences below diagonal; within-group divergences on the diagonal in boldface; *n* = number of sequences.

	n	*ada*	*bec*	*bro*	*car*	*c'us*	*c'es*	*cha*	*cup*	*gab*	*mar*	*nan*	*nig*	*rho* A	*rho* B	*sin* SA	*sin* B	*sub*	*sub* DRC	*upe*	*wil*
adansonii	1	**n/a**																			
bechuanicus	2	4.71	**0**																		
broadleyi	6	2.08	5.50	**0**																	
carinatus	5	5.00	6.13	5.00	**0.73**																
castaneus	11	1.87	4.66	3.39	4.07	**0.21**															
castanoides	31	5.42	5.97	5.94	4.63	3.73	**0.11**														
chapini	3	1.56	4.71	3.13	3.75	0.32	3.85	**0**													
cupulatta	4	5.76	5.26	5.50	4.71	4.54	4.13	4.71	**0**												
gabonensis	2	4.41	5.76	5.08	4.81	3.98	5.41	3.74	4.29	**0.27**											
marani	4	6.21	4.61	7.03	7.14	6.34	7.38	6.08	6.25	5.97	**0**										
nanus	1	5.76	6.58	5.24	4.29	5.58	5.72	5.24	3.95	4.29	6.39	**n/a**									
niger	2	4.70	4.99	4.96	5.17	4.32	4.50	4.44	2.36	3.73	5.27	4.45	**0**								
rhodesianus Angola	1	5.21	6.54	5.73	1.25	3.94	4.63	3.65	4.71	4.94	7.03	4.97	5.22	**n/a**							
rhodesianus Burundi	1	5.22	6.56	5.22	0.73	3.95	4.39	3.66	4.72	4.95	7.32	4.45	5.24	0.52	**n/a**						
sinuatus South Africa	1	5.47	4.71	5.73	7.24	5.10	4.74	5.21	4.97	5.34	6.07	5.76	3.92	7.55	7.57	**0**					
sinuatus Botswana	2	5.21	4.45	5.47	7.03	4.76	5.25	4.95	5.50	4.54	6.07	6.28	4.44	7.29	7.31	1.56	**n/a**				
subniger	45	6.01	3.65	6.80	6.90	5.82	6.45	6.01	6.85	6.82	6.90	7.62	6.81	6.80	7.35	6.25	5.73	**0.07**			
subniger DR Congo	2	6.30	3.94	7.09	7.19	6.12	6.74	6.30	7.39	7.66	7.20	7.92	7.11	7.09	7.63	6.02	6.02	1.81	**0**		
upembae	3	5.15	1.13	5.93	6.74	5.12	6.41	5.15	5.70	6.21	5.61	7.02	5.42	7.16	7.17	5.15	4.89	4.26	4.55	**0.18**	
williamsi	2	5.73	5.76	6.25	5.21	4.06	1.10	4.17	3.93	5.20	6.61	5.50	3.66	5.21	5.22	3.91	4.69	6.01	6.30	6.20	**0**

Among the congeneric species reviewed by Vargas-Ramírez *et al.* (2010) and Fritz *et al.* (2012a), the divergences of the mtDNA lineages of *Pelomedusa* belong to the highest ones observed, and this is also true when the recently reported values for kinosternid turtles (Iverson *et al.* 2013) are considered. When the divergences among the lineages of *Pelomedusa* are compared with *Pelusios* species, which represent the genus most closely related to *Pelomedusa*, it is obvious that the *Pelomedusa* lineages are highly differentiated and their divergences often exceed those among distinct *Pelusios* species (Tables 1–4). Consequently, we argue that each of the lineages of *Pelomedusa* should be recognized as a distinct species, and this taxonomic assessment is in line with the observation that three lineages (V, VIII, XII) occur in sympatry or at least close proximity in the Kilimanjaro and Arusha regions of Tanzania.

In the following, we distinguish 10 species of *Pelomedusa* which were hitherto lumped together as *P. subrufa*. In doing so, we describe six species as new to science, restrict *P. subrufa* (Bonnaterre, 1789) to genetic lineage VIII and resurrect three further species from its synonymy. We refrain from describing two additional species from Cameroon and Sudan formally because each is represented by only one genetically verified museum specimen. We treat these taxa as unconfirmed candidate species (Padial *et al.* 2010), pending further study. Moreover, two of the species recognized below (*P. galeata*, *P. somalica*) contain clearly divergent genetic lineages, which could correspond to two additional candidate species. Since some *Pelomedusa* species are morphologically difficult to tell apart (so-called 'cryptic species'), we complement our morphological diagnoses by sequence data of the 12S rRNA gene, facilitating genetic determination.

Below, the species are arranged alphabetically, with the two candidate species following the formally recognized species. Museum specimens are ethanol-preserved, if not otherwise noted.

TABLE 3. Average uncorrected *p* distances (percentages) for a 674-bp-long alignment of the cyt *b* gene of *Pelomedusa* species using the pairwise deletion option of MEGA 6.06. Between-group divergences below diagonal; within-group divergences on the diagonal in boldface. Roman numerals denote the mitochondrial lineage followed by the suggested species name; *n* = number of sequences.

	n	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
I species A	2	**0.35**											
II *variabilis*	9	9.95	**0.49**										
III *olivacea*	12	9.25	12.21	**1.29**									
IV *schweinfurthi*	1	8.93	11.86	11.12	**n/a**								
V *neumanni*	7	7.71	13.36	11.84	10.42	**0**							
VI *somalica*	5	12.83	14.46	14.97	13.78	13.63	**3.72**						
VII *barbata*	5	12.98	13.30	13.70	13.31	14.44	8.33	**0.36**					
VIII *subrufa*	27	17.50	17.80	15.73	17.63	18.60	16.07	15.36	**1.38**				
IX *galeata*	64	16.57	16.98	15.24	16.48	17.45	16.40	16.47	10.24	**1.15**			
X *gehafie*	3	10.34	8.47	10.61	8.70	9.35	15.01	14.30	16.51	13.70	**0.44**		
XI species B	1	11.81	14.45	12.95	5.64	12.23	15.37	12.85	16.53	15.39	10.96	**n/a**	
XII *kobe*	4	6.35	9.42	8.78	5.97	5.99	11.66	11.76	16.91	12.87	5.93	8.07	**0**

Pelomedusa barbata sp. nov.

Diagnosis: Medium-sized, light-coloured helmeted terrapins with a known maximum straight carapacial length of 21.6 cm (Gasperetti *et al.* 1993). Pectorals with narrow to broad midseam contact. Two small temporal scales (rarely only one large scale) on each side of head. Two or three large to very large barbels under chin. In adults, carapace light coloured, plastron entirely yellow. *Pelomedusa barbata* differs from all other *Pelomedusa* species by a gap instead of adenine (A), cytosine (C) or thymine (T) at position 122 and by the presence of guanine (G) instead of adenine (A) at position 330 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information).

TABLE 4. Average uncorrected *p* distances (percentages) for a 795-bp-long alignment of the cyt *b* gene of *Pelusios* species using the merged data sets of Fritz *et al.* (2011, 2012c, 2013) and Stuckas *et al.* (2013) and the pairwise deletion option of MEGA 6.06. Between-group divergences below diagonal; within-group divergences on the diagonal in boldface; *n* = number of sequences.

	n	*ada*	*bec*	*bro*	*car*	*c'us*	*c'es*	*cha*	*cup*	*gab*	*mar*	*nan*	*nig*	*rho* A	*rho* B	*sin*	*sub*	*sub* DRC	*upe*	*wil*
adansonii	1	**n/a**																		
bechuanicus	2	11.59	**0**																	
broadleyi	7	3.05	13.15	**0**																
carinatus	3	10.16	12.98	11.20	**0.63**															
castaneus	10	6.27	13.88	7.74	11.87	**1.95**														
castanoides	29	9.57	11.50	9.88	10.87	11.50	**0.57**													
chapini	1	5.49	13.58	7.53	11.01	1.84	10.88	**n/a**												
cupulatta	4	10.98	10.79	11.24	11.12	12.56	10.76	12.01	**0.19**											
gabonensis	3	12.80	11.95	12.15	10.84	12.26	11.47	11.70	11.10	**0.17**										
marani	5	12.80	11.21	12.68	12.92	14.09	12.50	13.24	11.82	11.84	**0.05**									
nanus	1	11.59	12.20	12.55	12.86	13.06	11.06	12.58	10.66	11.95	13.19	**n/a**								
niger	2	11.76	13.38	13.90	11.86	15.20	11.85	15.64	9.10	12.73	14.14	12.97	**0**							
rhodesianus Angola	1	7.93	12.66	10.77	4.32	11.57	11.35	10.98	11.27	11.89	12.66	12.40	13.46	**n/a**						
rhodesianus Burundi	1	9.76	13.10	10.13	2.02	11.72	10.51	11.08	10.99	10.83	12.69	12.72	11.93	3.88	**n/a**					
sinuatus South Africa	2	14.02	11.42	13.05	12.46	14.44	13.60	13.97	11.26	11.88	11.02	12.56	14.34	11.82	11.67	**0.13**				
subniger	39	14.63	5.31	12.26	12.72	13.76	11.89	13.74	10.92	11.90	11.23	11.78	11.63	12.26	12.39	10.05	**0.03**			
subniger DR Congo	2	13.41	5.83	11.93	12.90	12.90	11.96	12.94	10.87	11.07	10.87	11.85	11.70	12.37	12.50	10.84	3.13	**0**		
upembae	3	10.98	1.38	13.15	13.11	14.61	11.50	14.21	10.91	12.33	11.82	12.20	13.56	12.92	13.22	11.80	5.40	6.02	**0**	
williamsi	2	9.15	10.91	10.87	10.18	11.70	03.89	10.41	11.01	10.61	11.33	10.41	13.69	11.11	10.71	13.31	12.35	10.89	11.31	**0**

Holotype: Museum für Tierkunde, Senckenberg Dresden (MTD D 24637, male, Zinjibar, Abyan, Yemen, N13°7.75 E45°22.81; leg. W. Wranik, 3 June 1985; Fig. 3 top).

Description of the holotype: Straight carapacial length 12.3 cm, plastral length 10.4 cm. Pectoral scutes triangular and in narrow contact at the midline. Temporal scale divided on left side, undivided on right side of head. Two large barbels below chin. Carapace horn-coloured, plastron yellow with sparse grey mottling. Dorsal side of soft parts grey to horn-coloured, ventral side cream-coloured with a yellow tinge. Tail long.

Paratypes: Muséum d'Histoire Naturelle Genève (MNHG 2310.062, adult male, Al Sukhna, Yemen; MNHG 2455.073–075, adult male and two juveniles, Wadi Warazan, Lahij, Yemen); Museum für Tierkunde, Senckenberg Dresden (MTD D 24638, adult female, Lahij, Yemen); The Natural History Museum, London (BMNH 1985.1475, mummified adult, Al Kadan, Tihama, Al Hudaydah, Yemen; BMNH 1985.1478–1479, adult male and female, Amanat Al Asimah, Sana'a Area, Yemen); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK 87122, juvenile, Asir Region, Saudi Arabia).

Derivatio nominis: The scientific name (Latin: bearded) refers to the large barbels beneath the chin of the new species.

Distribution: Southwestern Arabian Peninsula (Saudi Arabia, Yemen; Gasperetti *et al.* 1993; Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010).

Remarks: *Pelomedusa barbata* corresponds to mtDNA lineage VII of Vargas-Ramírez *et al.* (2010). According to our analyses of mtDNA, *P. barbata* belongs to the northern species group of *Pelomedusa* and is most closely related to *P. somalica* (Fig. 1).

Gasperetti *et al.* (1993) mention that they have studied helmeted terrapins from southwestern Arabia that "more or less encompass all of the plastral variations" described for *Pelomedusa* and "all of the colour descriptions, from the lightest tan colour to almost black". However, their figures show only terrapins with pectoral scutes in contact, matching our observations. We never encountered dark coloured Arabian terrapins.

Pelomedusa barbata is the only chelonian species endemic to the Arabian Peninsula. Due to the paucity of local freshwater habitats, *P. barbata* should be regarded as an endangered species.

Pelomedusa galeata (Schoepff, 1792)

1792 *Testudo galeata* Schoepff—Restricted type locality (Hewitt 1935): environs of Cape Town, South Africa; lectotype (Fritz *et al.* 2014): Biological Museum of Lund University, ZMUL 6481 (Fig. 3 bottom in Fritz *et al.* 2014)

1835 *Pentonyx capensis* Duméril & Bibron—Restricted type locality (by lectotype designation, Fritz *et al.* 2014): Cape of Good Hope, South Africa; lectotype (Fritz *et al.* 2014): Muséum National d'Histoire naturelle, Paris, MNHN 9506 (Fig. 4 in Fritz *et al.* 2014)

1863 *Pelomedusa nigra* Gray—Type locality: Natal, South Africa; lectotype (Fritz *et al.* 2014): The Natural History Museum, London, BMNH 1849.1.30.27 (Fig. 6 top in Fritz *et al.* 2014)

1935 *Pelomedusa galeata devilliersi* Hewitt—Type locality: Besondermeid, Steinkopf, Northern Cape, South Africa; holotype: Port Elizabeth Museum, PEM R14962 (Fig. 7 bottom in Fritz *et al.* 2014)

1935 *Pelomedusa galeata orangensis* Hewitt—Type locality: Kimberley neighbourhood (?), Northern Cape, South Africa; holotype: McGregor Museum, Kimberley, lost (Fig. 4 of Plate XXXII in Hewitt 1935)

Diagnosis: Large-sized, often dark-coloured helmeted terrapins with an exceptional maximum straight carapacial length of 32.5 cm (Hewitt 1935, discussed in Branch *et al.* 1990). However, the normal shell length of adult terrapins is around 26 cm. Pectoral scutes always with broad or very broad contact at plastral midseam. In approximately 50% of all terrapins two small temporal scales present on each side of head, the others having one large undivided temporal scale. Two small barbels below chin. Soft parts dorsally darker than ventrally. Carapace and plastron of adults often mainly or entirely dark. However, in the western and northwestern parts of the range adults may be light-coloured with mainly or entirely yellow plastra. *Pelomedusa galeata* differs from all other *Pelomedusa* species except *P. subrufa* sensu stricto by the presence of cytosine (C) instead of adenine (A) or guanine (G) at position 148, by the presence of guanine (G) instead of adenine (A) at position 159, by the presence of cytosine (C) instead of thymine (T) at position 167, and by the presence of guanine (G) instead of adenine (A) or thymine (T) at position 343 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information). In addition, *P. galeata* differs from all other *Pelomedusa* species except *P. subrufa* sensu stricto (and

FIGURE 3. Dorsal and ventral aspects of the holotype of *Pelomedusa barbata* **sp. nov.** (MTD D 24637, male, Zinjibar, Abyan, Yemen; top) and of the holotype of *Pelomedusa kobe* **sp. nov.** (ZSM 334/1978:1, juvenile, Naberera, Manyara, Tanzania; bottom). Scale bars, 3 cm. Photos: E. Morawa.

possibly *P. gehafie*, *P. kobe* and candidate species B, in which the respective character states are unknown) by the presence of thymine (T) instead of cytosine (C) at position 26 and by the presence of cytosine (C) instead of thymine (T) at position 38. *Pelomedusa galeata* differs from *P. subrufa* sensu stricto by the presence of cytosine (C) instead of thymine (T) at positions 60 and 191, by the presence of thymine (T) instead of cytosine (C) at positions 117 and 298, by the presence of adenine (A) instead of thymine (T) at position 169, by the presence of guanine (G) instead of adenine (A) at positions 180 and 233, by the presence of adenine (A) instead of guanine (G) at positions 223, 226 and 296, by the presence of cytosine (C) instead of adenine (A) at position 280, and by the presence of guanine (G) instead of thymine (T) or cytosine (C) at position 289.

Distribution: South Africa (Eastern Cape, Free State, Gauteng, KwaZulu-Natal, North West, Northern Cape, Western Cape; Vargas-Ramírez *et al.* 2010; Fritz *et al.* 2014; this study).

Remarks: *Pelomedusa galeata* corresponds to mtDNA lineage IX of Vargas-Ramírez *et al.* (2010). It is one of the two southern species of *Pelomedusa* which constitute together a weakly supported clade based on phylogenetic analyses of mtDNA (Fig. 1).

According to phylogenetic analyses, *P. galeata* is composed of three distinct clades, one being represented by many samples from most of South Africa and two represented by only one and three samples, respectively (Fig. 1). However, the clade represented by only one sample (MTD T 5484, Swellendam District, Western Cape) is questionable. For MTD T 5484 are cyt *b* and ND4 sequences available, published in Vargas-Ramírez *et al.* (2010). The cyt *b* sequence is identical with or closely resembles those of the widely distributed South African clade. The ND4 sequence is highly distinct and identical to the ND4 sequence of another sample from the same province (MTD T 5897, Chelance, Western Cape), which is placed together with two other samples in the second small clade. Thus, it is evident that the distinct phylogenetic position of MTD T 5484 is an artefact caused by erroneously concatenated cyt *b* and ND4 sequences of two different terrapins.

Yet, if MTD T 5484 is disregarded, there still remain two deeply divergent clades within *P. galeata* which are unambiguous. Their average uncorrected *p* distances for the 12S gene (1.79%) and the cyt *b* gene (7.50%) are pronounced and suggest taxonomic distinctness (*cf.* Tables 1 and 3). The remaining small clade is represented only by two samples from the Northern and Western Cape provinces and by the lectotype of *Pentonyx capensis* Duméril & Bibron, 1835, lacking an exact geographical provenance. The sequences from the Northern and Western Cape correspond to topotypic material of *Testudo galeata* Schoepff, 1792 and to the holotype of *Pelomedusa galeata devilliersi* Hewitt, 1935 (Fritz *et al.* 2014). The widely distributed second clade contains, besides fresh material, also sequences of the types of *Pelomedusa nigra* Gray, 1863 (Fritz *et al.* 2014) and of a terrapin from the Western Cape (MTD T 10511, Groenfontein near Calitzdorp; Table S1). MTD T 10511 can also be considered topotypic for *Testudo galeata* Schoepff, 1792. Because topotypes of *Testudo galeata* Schoepff, 1792 are represented in both clades, the situation is nomenclaturally intricate. Moreover, the rarity of material of the small clade does not allow a morphological assessment of the situation. Therefore, we feel it is prudent to recognize for the moment only one species from South Africa, pending further study.

Unlike *P. subrufa* and some northern *Pelomedusa* species (see below), *P. galeata* is not parasitized by monogenean flatworms of the genus *Polystomoides* (Polystomatidae). These flatworms are generally found in the urinary bladder, cloaca, eye cavity, nose, mouth and pharynx of terrapins (Morrison & Du Preez 2011). They are known to be site-specific, and more than one species can be found in a single host species (Du Preez & Lim 2000). However, more than 200 *Pelomedusa galeata* from localities throughout its known geographical range were screened for the presence of polystomatids but none were found (Du Preez, unpubl.), indicating that this species is not susceptible to these parasites.

Pelomedusa gehafie (Rüppell, 1835)

1835 *Pentonyx gehafie* Rüppell—Type locality: eastern slope of coastal mountains, Eritrea; lectotype (Mertens 1937): Senckenberg-Museum, Frankfurt am Main, SMF 7947 (Fig. 5 top in Fritz *et al.* 2014)

1910 *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier—Restricted type locality (by lectotype designation, Fritz *et al.* 2014): eastern slope of coastal mountains, Eritrea; lectotype (Fritz *et al.* 2014): Muséum National d'Histoire naturelle, Paris, MNHN 7870

Diagnosis: Medium-sized, light-coloured helmeted terrapins with a known maximum straight carapacial length of 17.8 cm. Pectoral scutes triangular and in adults widely separated from plastral midseam (in hatchlings the tips of the triangular pectorals may meet at the plastral midseam). One large undivided temporal scale on each side of head. Two small barbels under chin. Carapace unpatterned light coloured. Plastron in adults completely yellow. *Pelomedusa gehafie* differs from all other *Pelomedusa* species except *P. schweinfurthi* and *P. somalica* by the presence of guanine (G) instead of adenine (A) at position 256 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information). *Pelomedusa gehafie* differs from *P. schweinfurthi* and *P. somalica* by the presence of thymine (T) instead of cytosine (C) at positions 125, 267, 287 and 345, by the presence of adenine (A) instead of guanine (G) at position 180, by the presence of guanine (G) instead of adenine (A) at position 223, by the presence of cytosine (C) instead of thymine (T) at position 236, and by the presence of adenine (A) instead of cytosine (C) or thymine (T) at position 268. Furthermore, *P. gehafie* differs from *P. schweinfurthi* by the presence of cytosine (C) or guanine (G) instead of adenine (A) at position 147, by the presence of adenine (A) instead of guanine (G) at positions 148 and 297, by the presence of cytosine (C) instead of adenine (A) at positions 166, 191 and 303, by the presence of thymine (T) instead of cytosine (C) at positions 266 and 326, by the presence of cytosine (C) instead of thymine (T) at position 279, by the presence of cytosine (C) instead of a gap at position 298, and by the presence of guanine (G) instead of adenine (A) at position 305. In addition to the above mentioned characters, *P. gehafie* differs from *P. somalica* by the presence of adenine (A) instead of thymine (T) at position 94, by the presence of cytosine (C) instead of thymine (T) at positions 95, 122 and 131, by the presence of adenine (A) instead of cytosine (C) at position 123, by the presence of thymine (T) instead of cytosine (C) at position 124, and by the presence of adenine (A) instead of guanine (G) at position 332.

Distribution: Genetically verified specimens of *P. gehafie* are only known from the type locality in Eritrea and from a second questionable site (Gebel Arary, Naturhistorisches Museum Wien, NMW 24448). The latter locality could to be identified with Jabal Karari, Omdurman near Khartoum, Sudan, because the specimen originates from Joseph Russegger (18 November 1802–20 June 1863), who is known to have collected near Khartoum. We tentatively identify therefore Gebel Arary with Jabal Karari and show this site in our map (Fig. 2) with a question mark. In the Museum für Naturkunde, Berlin, there is a further genetically verified and morphologically typical specimen originating in "Abyssinia" (ZMB 15693, coll. W. Jesse).

Remarks: This is a morphologically distinctive species (*cf.* the figures in Fritz *et al.* 2014 and this study). *Pelomedusa gehafie* corresponds to mtDNA lineage X of Fritz *et al.* (2014). It belongs to the northern species group of *Pelomedusa*, which is well supported in phylogenetic analyses of mtDNA. These reveal that the East African species *P. neumanni* and *P. kobe* are closely related to *P. gehafie* (Fig. 1). These two species are morphologically easy to tell apart from *P. gehafie*. Adults of *P. gehafie* consistently have triangular pectoral scutes not reaching the plastral midseam, whereas the pectorals in the two other species are always in contact in the midline.

***Pelomedusa kobe* sp. nov.**

Diagnosis: Medium-sized to, perhaps, large-sized helmeted terrapins with a known maximum straight carapacial length of 15.9 cm. Pectoral scutes rectangular with wide midseam contact or triangular with narrow midseam contact. Normally one large undivided temporal head scale present. Two, rarely three, small barbels under chin. Larger specimens with chestnut carapace and yellow plastron with darker elements along the distal seams; soft parts ventrally lighter than dorsally. *Pelomedusa kobe* differs from all other *Pelomedusa* species except *P. gehafie*, *P. subrufa* sensu stricto and candidate species B by the presence of guanine (G) instead of adenine (A) at position 223 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information). *Pelomedusa kobe* differs from these three species by the presence of cytosine (C) instead of thymine (T) at position 188 and from the individual species as shown in Table 5.

Holotype: Zoologische Staatssammlung München (ZSM 334/1978:1, juvenile, Naberera, Manyara, Tanzania, S4°11.66 E36°55.74; leg. J. Popp, 16 July 1960; Fig. 3 bottom).

Description of the holotype: Straight carapacial length 7.5 cm, plastral length 6.5 cm. Pectoral scutes with wide midseam contact. One large undivided temporal scale on each side of head. Two small barbels under chin. Carapace chestnut; plastron yellow with some darker elements concentrated along the seams; gulars, intergular and anals mostly dark. Soft parts dorsally greenish brown, ventrally ochre.

TABLE 5. Diagnostic sites of *Pelomedusa kobe*, *P. gehafie*, *P. subrufa* sensu stricto and *Pelomedusa* candidate species B in the 360-bp-long reference alignment of 12S sequences (Supporting Information).

Position	*P. kobe*	*P. gehafie*	*P. subrufa*	Candidate species B
95	C	C	T	C
103	C	C	C	T
109	T	T	T	C
117	T	T	C	T
122	C	C	C	A
125	T	T	T	C
126	gap	gap	gap	T
147	C	C/G	C	A
148	A	A	C	G
152	T	T	T	C
154	A	A	A	G
159	A	A	G	A
166	C	C	C	A
167	T	T	C	T
168	gap	gap	gap	T
169	A	A	T	A
180	A	A	A	G
188	C	T	T	T
191	A	C	T	A
226	A	A	G	A
233	G	G	A	A
256	A	G	A	A
266	T	T	T	C
268	C	A	C/A	T
274	C	C	C	T
280	C	C	A	C
287	T	T	T	C
296	A	A	G	A
298	T	C	C	gap
302	T	T	T	A
303	C	C	C	A
326	T	T	T	C
337	T	T	C	T
343	A	A	G	A
345	C	T	C/T	C

Paratypes: Museum für Naturkunde, Berlin (ZMB 11741, female, Pumbo creek, Monda/Unguru, Morogoro, Tanzania; ZMB 11742, juvenile, Tabora, Tanzania); Zoologische Staatssammlung München (ZSM 285/1937:1–3, male and two juveniles, Tanganyika; ZSM 334/1978:2, hatchling, same data as holotype; ZSM 96/1960:1–5, two hatchlings and three juveniles, same data as holotype).

Derivatio nominis: The species name *kobe* is the Swahili word for terrapin. It is used as a noun in apposition (ICZN 1999: Art. 31.1).

Distribution: Only known from Tanzania, where it occurs in the Arusha region in close proximity to, or in sympatry with, *P. neumanni* and *P. subrufa*.

Remarks: The genetic lineage corresponding to *P. kobe* was previously unknown. *Pelomedusa kobe* belongs to the northern species group of *Pelomedusa* and is related to *P. gehafie* and *P. neumanni* (Fig. 1).

Pelomedusa kobe most likely reaches a much larger size than *c.* 16 cm because the largest type specimens still have wide fresh growth rings. One of the paratypes (ZMB 11742) has the temporal scales on each side of the head divided into two smaller scales, whilst all other types have large undivided temporal scales. Hatchlings of *P. kobe* have conspicuous light horn-coloured shell margins. The paratype ZSM 96/1960:1 has three barbels under the chin.

***Pelomedusa neumanni* sp. nov.**

Diagnosis: Medium-sized helmeted terrapins with a known maximum straight carapacial length of 19.4 cm. Pectoral scutes rectangular with wide midseam contact. One large undivided temporal head scale. Two small barbels under chin. Colouration variable; specimens with light horn-coloured carapace and completely yellow plastron and individuals with brownish plastron known to occur; soft parts ventrally lighter than dorsally. *Pelomedusa neumanni* differs from all other *Pelomedusa* species except possibly *P. gehafie*, *P. kobe* and candidate species B (in which the respective character states are unknown) by the presence of thymine (T) instead of cytosine (C) at position 57, by the presence of thymine (T) instead of cytosine (C) or guanine (G) at position 349, and by the presence of adenine (A) instead of cytosine (C) or guanine (G) at position 353 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information). *Pelomedusa neumanni* differs from *P. gehafie*, *P. kobe* and candidate species B by the presence of thymine (T) instead of cytosine (C) at position 116, by the presence of adenine (A) or thymine (T) instead of cytosine (C) or guanine (G) at position 147, and by the presence of adenine (A) instead of guanine (G) at position 223. In addition, *P. neumanni* differs from *P. gehafie* by the presence of adenine (A) instead of guanine (G) at position 256, by the presence of cytosine (C) instead of adenine (A) at position 268, and by the presence of cytosine (C) instead of thymine (T) at position 345. *Pelomedusa neumanni* differs from *P. kobe* by the presence of cytosine (C) instead of thymine (T) at position 298. *Pelomedusa neumanni* differs from candidate species B by the presence of cytosine (C) instead of thymine (T) at positions 103, 268 and 274, by the presence of thymine (T) instead of cytosine (C) at positions 109, 125, 152, 287 and 326, by the presence of cytosine (C) instead of adenine (A) at positions 122, 166 and 303, by a gap instead of thymine (T) at positions 126 and 168, by the presence of adenine (A) instead of guanine (G) at positions 148, 154, 180 and 223, and by the presence of thymine (T) instead of adenine (A) at position 302.

Holotype: National Museum Prague (NMP6V 74974, adult male, Kakamega, Kenya, N0°17.04 E34°44.52; leg. P. Široký, 11 September 2003; Fig. 4 top).

Description of the holotype: Dry shell plus head in ethanol. Straight carapacial length 16.6 cm, plastral length 14.9 cm. Carapace wide, dark brown, in dorsal view with pronounced waist. Epidermal scutes of vertebral 2–4 missing, anterior carapacial margin slightly mutilated. Plastron dark coloured; pectoral scutes with midseam contact. Head dorsally dark coloured; throat yellowish, two small barbels under chin.

Paratypes: Museum für Naturkunde, Berlin (ZMB 28356, hatchling, Mangara River, Manyara, Tanzania); Naturhistorisches Museum Wien (NMW 24452, male, Lake Victoria); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK 81951, hatchling, Kakamega Forest, Kenya).

Derivatio nominis: We dedicate this new species to Oscar Neumann (3 September 1867–17 May 1946) who undertook in the late 19th and early 20th centuries influential expeditions to East Africa, Somalia, Ethiopia, and Sudan. Neumann worked voluntarily for over 40 years in the Museum für Naturkunde, Berlin, but was forced by the Nazi government to leave Germany in 1941.

Distribution: Kenya (Vargas-Ramírez *et al.* 2010) and Tanzania (this study). The genetically verified paratype ZMB 28356, collected by Oscar Neumann in the late 19th century in present-day Tanzania, provides evidence for the occurrence of *P. neumanni* in close proximity to genetically verified records of *P. kobe* and *P. subrufa*.

FIGURE 4. Dorsal and ventral aspects of the holotype of *Pelomedusa neumanni* **sp. nov.** (NMP6V 74974, adult male, Kakamega, Kenya; top) and of *Pelomedusa schweinfurthi* **sp. nov.** (SMF 56161, female, Liria, Central Equatoria, South Sudan; bottom). Scale bars, 3 cm. Photos: P. Široký and E. Morawa.

Remarks: *Pelomedusa neumanni* corresponds to mtDNA lineage V of Vargas-Ramírez *et al.* (2010). According to our phylogenetic analyses of mtDNA sequences, *P. neumanni* belongs to the northern species group of *Pelomedusa*. *Pelomedusa neumanni* is phylogenetically most closely related to *P. gehafie* and *P. kobe*. However, the sister group relationships within the clade comprising these three species are not well resolved (Fig. 1).

The ranges of *P. neumanni*, *P. kobe* and *P. subrufa* abut or overlap in the East African savannah. To avoid taxonomic misidentifications, we included only genetically verified museum specimens in our type series. However, it should be noted that all 18 specimens from Kenya we studied have pectoral scutes in wide midline contact.

For the monogenean flatworm *Polystomoides chabaudi* possibly parasitizing *Pelomedusa neumanni*, see below under *P. subrufa* sensu stricto.

Pelomedusa olivacea (Schweigger, 1812)

1812 *Emys olivacea* Schweigger—Restricted type locality: Senegal; holotype: Muséum National d'Histoire naturelle, Paris, MNHN 7971

1884 *Pelomedusa gasconi* Rochebrune—Restriced type locality (by neotype designation, Fritz *et al.* 2014): Dagana, Senegal; neotype (Fritz *et al.* 2014): Zoologisches Forschungsmuseum Alexander Koenig, Bonn, ZFMK 17076 (Fig. 6 bottom in Fritz *et al.* 2014)

Diagnosis: Small to medium-sized helmeted terrapins with a known maximum straight carapacial length of 16.8 cm. Pectoral scutes triangular and either just meeting at their tips along the plastral midseam or more or less widely separated. One large undivided temporal scale on each side of head. Two small barbels under chin. Carapace and plastron light coloured. Soft parts dorsally darker than ventrally. *Pelomedusa olivacea* differs from all other *Pelomedusa* species by the presence of guanine (G) instead of adenine (A) or cytosine (C) at position 123 and by the presence of adenine (A) instead of guanine (G) at position 271 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information).

Distribution: Genetically verified records for *P. olivacea* are known from Benin, Burkina Faso, Niger, Nigeria, and Senegal (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010; Fritz *et al.* 2014).

Remarks: *Pelomedusa olivacea* corresponds to mtDNA lineage III of Vargas-Ramírez *et al.* (2010). Phylogenetically, *P. olivacea* belongs to the northern clade of *Pelomedusa* and is most closely related to *P. variabilis* from Ghana and the Ivory Coast (Fig. 1). In both species, the pectoral scutes may be triangular with or without midseam contact. Among 21 museum specimens of *P. olivacea*, 18 have completely divided pectoral scutes and three have triangular pectoral scutes just meeting at the plastral midline. This matches the description for Senegalese *P. olivacea* given in Rochebrune (1884).

The monogenean flatworm *Polystomoides nabedei* Kulo, 1980 was described from helmeted terrapins from Siborototi, Togo (most likely *Pelomedusa olivacea* or *P. variabilis*). This parasite was described as a distinct species based on morphological differences from *Polystomoides chabaudi*, which is known from *Pelomedusa subrufa* and probably *P. neumanni* (see respective species accounts).

Pelomedusa schweinfurthi sp. nov.

Diagnosis: Small to medium-sized, dark-coloured helmeted terrapins with a known maximum straight carapacial length of 15.7 cm. Pectoral scutes rectangular with wide midseam contact or triangular with narrow midseam contact. Temporal head scales large, mostly undivided. Two small barbels under chin. In adults, carapace and plastron rather dark; soft parts ventrally lighter than dorsally. *Pelomedusa schweinfurthi* differs from all other *Pelomedusa* species by the presence of thymine (T) instead of cytosine (C) at position 279, by the presence of guanine (G) instead of adenine (A) or a gap at position 297, and by the presence of adenine (A) instead of guanine (G) at position 305 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information).

Holotype: Senckenberg-Museum, Frankfurt am Main (SMF 56161, female, Liria, Central Equatoria, South Sudan, N4°38.66 E32°4.83; leg. C. Scherpner, 3 March 1955; Fig. 4 bottom).

Description of the holotype: Straight carapacial length 12.3 cm, plastral length 10.5 cm. Pectoral scutes rectangular with wide midseam contact. Temporal scale divided on left side, undivided on right side of head. Two small barbels under chin. Carapace and plastron dark brown. Dorsal side of soft parts and entire forelegs dark grey, ventral side of hind legs light grey. Tail short.

Paratypes: Senckenberg-Museum, Frankfurt am Main (SMF 56160, 65162, males, same data as holotype); Museum für Naturkunde, Berlin (ZMB 15697, juvenile, Djur River W Wau, Western Bahr el Ghazal, South Sudan).

Derivatio nominis: We dedicate this species to Georg August Schweinfurth (29 December 1836–19 September 1925) who was the last of the great explorers of Africa. Schweinfurth collected the oldest of the paratypes (ZMB 15697) during his famous third Africa expedition (1868–1871) "inside the heart of Africa" (Schweinfurth 1874) in present-day South Sudan.

Distribution: Central African Republic (Vargas-Ramírez *et al.* 2010) and South Sudan (this study).

Remarks: *Pelomedusa schweinfurthi* corresponds to mtDNA lineage IV of Vargas-Ramírez *et al.* (2010), which was previously only recorded from the Central African Republic. Our new 12S sequences of the type specimens provide evidence for the occurrence in South Sudan. The temporal scale is divided on the left side of the head in the holotype, but undivided on the right side, as it is in all paratypes. The largest specimen (SMF 56162) has a straight carapacial length of 15.7 cm. Unlike many other *Pelomedusa* species, *P. schweinfurthi* is overall quite dark coloured, with a predominantly brown plastron.

Pelomedusa schweinfurthi belongs to the northern species group and is with high support sister to candidate species B from Sudan (Fig. 1).

Pelomedusa somalica sp. nov.

Diagnosis: Small to medium-sized, light-coloured helmeted terrapins with a known maximum straight carapacial length of 15.7 cm. Pectoral scutes triangular to rectangular with wide or, rarely, narrow midseam contact. One large undivided temporal scale on each side of head. Two small barbels under chin. In adults, plastron completely yellow; soft parts ventrally lighter than dorsally. *Pelomedusa somalica* differs from all other *Pelomedusa* species by the presence of thymine (T) instead of adenine (A), cytosine (C) or a gap at position 122 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information).

Holotype: The Natural History Museum, London (BMNH 1970.1481, field number 502, adult, Borama district, Awdal, Somaliland/Somalia, N9°55 E43°10, 4500 ft; coll. R.H.R. Taylor, 17 December 1932; Fig. 5 top).

Description of the holotype: Shell. Straight carapacial length 15.7 cm, plastral length 13.7 cm. Pectoral scutes rectangular with very wide midseam contact. Carapace light chestnut; plastron entirely yellow.

Paratypes: The Natural History Museum, London (BMNH 1931.7.20.412–414, juvenile and two shells of adults with heads in alcohol, Buran, Sanaag, Somaliland/Somalia; BMNH 1931.8.1.177, juvenile, Ceerigaabo, Sanaag, Somaliland/Somalia); Naturhistorisches Museum Wien (NMW 24449, juvenile, Abyssinia).

Derivatio nominis: The species name *somalica* refers to the geographical origin of the new species.

Distribution: Somaliland, Somalia (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010; Fritz *et al.* 2014). A genetically verified paratype of *P. somalica* (NMW 24449) was collected in Abyssinia by Baron Carlo von Erlanger (5 September 1872–4 September 1904) in 1901. Abyssinia comprised present-day Eritrea and northern Ethiopia, suggesting that *P. somalica* also occurs in one or both of these countries.

Remarks: *Pelomedusa somalica* corresponds to mtDNA lineage VI of Vargas-Ramírez *et al.* (2010). Our phylogenetic analyses of mtDNA sequences indicate that *P. somalica* is part of the northern species group of *Pelomedusa* and that *P. barbata* from the Arabian Peninsula is its sister species. However, the relatively deep divergences among Somali terrapins from two sites being only 40 km distant (Vargas-Ramírez *et al.* 2010; Table S1) raise the possibility that *P. somalica* consists of more than only one species. This situation warrants further research. That more than one species could be involved is also suggested by two morphologically divergent specimens from Somaliland in the Museum für Naturkunde, Berlin (ZMB 27266, 49719). These relatively small adult males of 13.0 cm and 10.9 cm straight carapacial length differ from the type series from Awdal and Sanaag regions (Somaliland) significantly in their distinctly darker colouration. Without genetic verification, we are reluctant to identify them with *P. somalica* and exclude them explicitly from the type series.

FIGURE 5. Dorsal and ventral aspects of the holotype of *Pelomedusa somalica* **sp. nov.** (BMNH 1970.1481, adult, Borama district, Awdal, Somaliland/Somalia; top) and of *Pelomedusa variabilis* **sp. nov.** (SMF 58075, subadult male, Gold Coast, Ghana; bottom). Scale bars, 3 cm. Photos: A. Petzold and E. Morawa.

Pelomedusa subrufa (Bonnaterre, 1789) sensu stricto

1789 *Testudo subrufa* Bonnaterre—Restricted type locality (Bour 1982): Taolañaro, Madagascar; holotype: Muséum National d'Histoire naturelle, Paris, MNHN 7970 (Fig. 2 in Fritz *et al.* 2014)
1798 *Testudo badia* Donndorff (nomen novum)
1798 *Testudo rubicunda* Suckow (nomen novum)
1935 *Pelomedusa galeata damarensis* Hewitt—Type locality: Quickborn near Okahandja, Namibia; lectotype (Fritz *et al.* 2014): Port Elizabeth Museum, PEM R14953 (Fig. 7 top in Fritz *et al.* 2014)
1937 *Pelomedusa subrufa wettsteini* Mertens—Type locality: Majunga (Mahajanga), western Madagascar; holotype: Senckenberg-Museum, Frankfurt am Main, SMF 7958 (Fig. 8 in Fritz *et al.* 2014)

Diagnosis: Small to medium-sized helmeted terrapins with a known maximum straight carapacial length of 19.7 cm. Yet, the shell length of most adults is below 14 cm. Pectoral scutes in most specimens with broad contact at plastral midseam; however, terrapins with narrow contact or, exceptionally, with triangular pectorals without midseam contact occur. One large undivided temporal scale on each side of head. Two small barbels under chin. Carapace uniform light to dark brown. Plastron in larger individuals mostly light coloured, in younger specimens often with dark markings. *Pelomedusa subrufa* sensu stricto differs from all other *Pelomedusa* species by the presence of cytosine (C) instead of thymine (T) at position 117, by the presence of thymine (T) instead of adenine (A) at position 169, by the presence of thymine (T) instead of adenine (A) or cytosine (C) at position 191, by the presence of guanine (G) instead of adenine (A) at positions 226 and 296, by the presence of adenine (A) instead of cytosine (C) at position 280, and by the presence of cytosine (C) or thymine (T) instead of adenine (A) or guanine (G) at position 289 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information). In addition, *P. subrufa* sensu stricto differs from all other *Pelomedusa* species except *P. galeata* by the presence of cytosine (C) instead of adenine (A) or guanine (G) at position 148, by the presence of guanine (G) instead of adenine (A) at position 159, by the presence of cytosine (C) instead of thymine (T) at position 167, and by the presence of guanine (G) instead of adenine (A) or thymine (T) at position 343. Moreover, *P. subrufa* sensu stricto differs from all other *Pelomedusa* species except *P. galeata* and possibly *P. gehafie*, *P. kobe* and candidate species B (in which the respective character states are unknown) by the presence of thymine (T) instead of cytosine (C) at position 26 and by the presence of cytosine (C) instead of thymine (T) at position 38.

Distribution: Southern Angola (this study), Botswana, southeastern Democratic Republic of the Congo, Malawi (Vargas-Ramírez *et al.* 2010), Namibia (Wong *et al.* 2010; this study), South Africa (Limpopo; this study), and Kilimanjaro region of Tanzania (this study). Introduced to Madagascar (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010).

Remarks: *Pelomedusa subrufa* sensu stricto corresponds to mtDNA lineage VIII of Vargas-Ramírez *et al.* (2010). Besides *P. galeata*, it is one of the two southern species of *Pelomedusa*.

In the course of the present study, we recorded *P. subrufa* sensu stricto for the first time for South Africa, based on one sample from the western border region of the Kruger Park (Hoedspruit, Limpopo, South Africa). To the west and south, the next genetically verified records are approximately 300 km distant and are *P. galeata*. It seems possible that the ranges of the two species abut or overlap in northeastern South Africa.

In the Zoologische Staatssammlung München there are genetically verified specimens of *P. subrufa* sensu stricto collected on 3 May 1937 by Wolfgang Uthmöller (25 October 1904–25 August 1951) at the northern slope of the Kilimanjaro, Tanzania (ZSM 320/1937:1–4), and additional genetically verified specimens with the date 5 May 1937 originating from the same collector, but bearing only "Tanganyika" as locality data (ZSM 285/1937:1–3). The latter specimens represent another species (*P. kobe*, see above), suggesting that both taxa occur in close geographical proximity or even sympatry in Tanzania. This is also supported by further genetically verified specimens of *P. kobe* from the Arusha region, Tanzania, from where also the new species *P. neumanni* is recorded (see above).

The identity of mtDNA sequences of *P. subrufa* sensu stricto from Tanzania and Madagascar points to Tanzania as geographical source region for the introduced Malagasy helmeted terrapins.

Among 94 museum specimens of *P. subrufa*, two terrapins have triangular pectorals without midseam contact, and 19 terrapins have pectoral scutes with narrow plastral midseam contact, whilst the remaining specimens have pectoral scutes with broad contact at the midseam.

Pelomedusa subrufa can cope with extremely arid conditions. For Namibia, there are records from the mouths of temporary streams (so-called riviers) in the Namib Desert (Branch 2008; Boycott & Bourquin 2008; vouchers in the Museum für Naturkunde, Berlin). It is well known that Namibian terrapins burrow underground during arid periods, and if there is no rain, they may evidently survive up to six years burrowed (A. Schleicher, pers. observ., Omaheke, Namibia).

The monogenean flatworm *Polystomoides chabaudi* Euzet & Combes, 1965 was described from *Pelomedusa subrufa* sensu stricto (collected at Betioky, Madagascar). The same polystomatid species was also reported from helmeted terrapins from the Kampala area, Uganda (Tinsley 1973), that is, probably from *P. neumanni*.

Pelomedusa variabilis sp. nov.

Diagnosis: Medium- to large-sized helmeted terrapins with a known maximum straight carapacial length of 24.8 cm. Pectoral scutes mostly triangular without midseam contact, but terrapins with pectorals having narrow or wide midseam contact occur. One large undivided temporal head scale. Two small barbels under chin. Colouration extremely variable; very dark individuals are known, as well as specimens with light horn-coloured carapace and completely yellow plastron. Soft parts ventrally lighter than dorsally. *Pelomedusa variabilis* differs from all other *Pelomedusa* species by the presence of adenine (A) instead of cytosine (C) or thymine (T) at position 189 and by the presence of adenine (A) instead of guanine (G) at position 322 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information).

Holotype: Senckenberg-Museum, Frankfurt am Main (SMF 58075, subadult male, Gold Coast, Ghana; leg. H. Lang, 18 February 1957; Fig. 5 bottom).

Description of the holotype: Straight carapacial length 10.3 cm, plastral length 8.7 cm. Pectoral scutes triangular, widely separated, without midseam contact. Temporal scales undivided; injury on the right side of head. Two small barbels under chin. Carapace covered by algae; plastron dark brown, seams distinctly lighter. Soft parts dorsally dark grey; throat cream-coloured, ventral side of legs greyish brown. Tail long.

Paratypes: Museum für Tierkunde, Senckenberg Dresden (MTD T 33818–33819, male and female, Ghana; MTD T 35041, juvenile, Ghana); The Natural History Museum, London (BMNH 1863.3.27.1, male, Ghana; BMHN 1927.8.27.240–242, juveniles, Ghana); Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK 47521–47523, juveniles, Achimota, Greater Accra Region, Ghana).

Derivatio nominis: The species name *variabilis* is an adjective in female gender, referring to the variable morphology of the new species.

Distribution: Genetically verified records for *P. variabilis* are only known for Ghana and the Ivory Coast (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010; Fritz *et al.* 2014).

Remarks: *Pelomedusa variabilis* corresponds to mtDNA lineage II of Vargas-Ramírez *et al.* (2010). It belongs to the northern clade of *Pelomedusa* and is according to our mtDNA analyses sister to *P. olivacea* (Fig. 1).

Male helmeted terrapins from the Ivory Coast were reported to have red-spotted nearly white heads (Bull & Legler 1980). However, specimens with such colouration were never seen during fieldwork by M.-O. Rödel (pers. comm.). Among the 11 specimens of the type series, there are nine terrapins with triangular pectoral scutes without midseam contact; in another specimen (MTD D 33819) the tip of the left pectoral just reaches the midseam, whereas the right pectoral does not, and in the paratype BMNH 1863.3.27.1 the pectoral scutes are rectangular with wide midseam contact.

For the monogenean flatworm *Polystomoides nabedei* possibly parasitizing *Pelomedusa variabilis*, see under *P. olivacea*.

Pelomedusa candidate species A

This candidate species from Cameroon corresponds to mtDNA lineage I of Vargas-Ramírez *et al.* (2010). It is genetically clearly distinct and differs in 12S and cyt *b* sequences by uncorrected *p* distances resembling the divergences among other *Pelomedusa* species (Tables 1 and 3). Since there is just one genetically verified voucher specimen available (Zoologisches Forschungsmuseum Alexander Koenig, Bonn, ZFMK 15171, Mokolo, Margui-

Wandala, Extreme North Province, Cameroon, coll. Wolfgang Böhme, 14–17 February 1974), we refrain from describing this species formally. ZFMK 15171 is a dark-coloured subadult terrapin of 9.3 cm straight carapacial length, resembling in gross morphology *P. schweinfurthi* or dark-coloured *P. variabilis*. However, unlike *P. schweinfurthi*, the pectoral scutes of ZFMK 15171 are triangular and do not reach the plastral midseam. Another terrapin from the same source region was only sampled, but not collected (Museum of Zoology, Senckenberg Dresden, Tissue Collection, MTD T 5183, Maroua, Extreme North Province, Cameroon) and is genetically very similar. Our phylogenetic analyses of mtDNA sequences place candidate species A in the well-supported northern clade of *Pelomedusa* (Fig. 1). Therein, it is best understood as having a basal position.

Pelomedusa candidate species A differs from all other *Pelomedusa* species by the presence of guanine (G) instead of cytosine (C) at position 212, by the presence of thymine (T) instead of cytosine (C) at position 222, by the presence of cytosine (C) instead of thymine (T) or adenine (A) at position 302, by the presence of cytosine (C) instead of adenine (A) or guanine (G) at position 325, by the presence of thymine (T) instead of adenine (A) or guanine (G) at position 343, and by the presence of adenine (A) instead of cytosine (C) or thymine (T) at position 345 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information). In addition, *Pelomedusa* candidate species A differs from all species except possibly *P. gehafie* and *P. kobe* by the presence of thymine (T) instead of cytosine (C) at position 50 and by the presence of thymine (T) instead of adenine (A) or cytosine (C) at position 65 (character states in *P. gehafie* and *P. kobe* unknown).

Pelomedusa candidate species B

The second candidate species is also represented by only one genetically verified voucher specimen. This terrapin from the Naturhistorisches Museum Wien (NMW 24451) was collected by Franz Werner in March 1914 at Al-Ubayyid (El Obeid), North Kurdufan, Sudan. It is a light-coloured subadult with an entirely yellow plastron and a straight carapacial length of 14.2 cm. Its pectoral scutes are triangular, but reach the plastral midline. As with candidate species A, the genetic distances of this Sudanese terrapin resemble the divergences among other distinct *Pelomedusa* species. The genetic lineage of candidate species B was hitherto unknown. According to our analyses of mtDNA sequences, candidate species B belongs into the northern clade of *Pelomedusa* and is, with maximum support, sister to *P. schweinfurthi*.

Pelomedusa candidate species B differs from all other *Pelomedusa* species by the presence of cytosine (C) instead of thymine (T) at positions 109 and 152, by the presence of adenine (A) instead of cytosine (C) or thymine (T) at positions 122 and 302, by the presence of thymine (T) instead of a gap at positions 126 and 168, and by the presence of guanine (G) instead of adenine (A) at position 154 of the 360-bp-long reference alignment of the 12S rRNA gene (Supporting Information).

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Supporting Information

REFERENCE ALIGNMENT. 12S rRNA sequences (FASTA format) for *Pelomedusa* species.

TABLE S1. Used samples, GenBank sequences and their accession numbers.

TABLE S2. Evolutionary models selected by the Bayesian Information Criterion in PARTITIONFINDER (Lanfear *et al.* 2012).

The Supporting Information is available from the Dryad Repository using the link http://dx.doi.org/10.5061/dryad.288ft

References

Barlow, A., Baker, K., Hendry, C.R., Peppin, L., Phelps, T., Tolley, K.A., Wüster, C.E. & Wüster, W. (2013) Phylogeography of the widespread African puff adder (*Bitis arietans*) reveals multiple Pleistocene refugia in southern Africa. *Molecular Ecology*, 22, 1134–1157.
http://dx.doi.org/10.1111/mec.12157

Bonnaterre, P.J. (1789) *Tableau encyclopédique et méthodique des trois règnes de la nature. Erpétologie.* Panckoucke, Hôtel de Thou, Paris, xxviii + 70 + (1) pp., 35 plates.
http://dx.doi.org/10.5962/bhl.title.59326

Boycott, R.C. & Bourquin, O. (2008) *Pelomedusa subrufa* (Lacépède 1788), helmeted turtle, helmeted terrapin. *In*: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A. & Iverson, J.B. (Eds.), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs, No. 5.* Chelonian Research Foundation, Lunenburg, MA, pp. 007.1–007.6.
http://dx.doi.org/10.3854/crm.5.007.subrufa.v1.2008

Branch, B. (2008) *Tortoises, Terrapins & Turtles of Africa*. Struik Publishers, Cape Town, 128 pp.

Branch, W.R., Baard, E.H.W. & De Villiers, A. (1990) Some exceptionally large Southern African chelonians. *Journal of the Herpetological Association of Africa*, 37, 53–54.
http://dx.doi.org/10.1080/04416651.1990.9650264

Bull, J.J. & Legler, J.M. (1980) Karyotypes of side-necked turtles (Testudines: Pleurodira). *Canadian Journal of Zoology*, 58, 828–841.
http://dx.doi.org/10.1139/z80-115

Carstens, B.C., Pelletier, T.A., Reid, N.M. & Satler, J.D. (2013) How to fail at species delimitation. *Molecular Ecology*, 22, 4369–4383.
http://dx.doi.org/10.1111/mec.12413

Dayrat, B. (2005) Towards integrative taxonomy. *Biological Journal of the Linnean Society*, 85, 407–415.
http://dx.doi.org/10.1111/j.1095-8312.2005.00503.x

Dikow, R.B. & Smith, W.L. (2013) Complete genome sequences provide a case study for the evaluation of gene-tree thinking. *Cladistics*, 29, 672–682.
http://dx.doi.org/10.1111/cla.12020

Donndorff, J.A. (1798) *Zoologische Beyträge zur XIII. Ausgabe des Linnéischen Natursystems. Dritter Band. Amphibien und Fische.* Weidmannsche Buchhandlung, Leipzig, VI + 980 pp., Errata.

Duméril, A.M.C. & Bibron, G. (1835) *Erpétologie générale ou histoire naturelle complète des reptiles. Tome second.* Librairie encyclopédique de Roret, Paris, 680 pp.
http://dx.doi.org/10.5962/bhl.title.46831

Du Preez, L.H. & Lim, L.H.S. (2000) *Neopolystoma liewi* sp. n. (Monogenea: Polystomatidae) from the eye of the Malayan box turtle (*Cuora amboinensis*). *Folia Parasitologica*, 47, 11–16.
http://dx.doi.org/10.14411/fp.2000.003

Euzet, L. & Combes, C. (1965) Parasites des chéloniens malgaches. *Polystomoides chabaudi* n. sp. (Monogenea) chez la tortue d'eau douce *Pelomedusa subrufa* Lacépède 1788. *Annales de Parasitologie Humaine et Comparée*, 40, 455–450.

Fritz, U. (1995) Zur innerartlichen Variabilität von *Emys orbicularis* (Linnaeus, 1758). 5a. Taxonomie in Mittel-Westeuropa, auf Korsika, Sardinien, der Apenninen-Halbinsel und Sizilien und Unterartengruppen von *E. orbicularis*. *Zoologische Abhandlungen*, 48, 185–242.

Fritz, U., Alcalde, L., Vargas-Ramírez, M., Goode, E.V., Fabius-Turoblin, D.U. & Praschag, P. (2012a) Northern genetic richness and southern purity, but just one species in the *Chelonoidis chilensis* complex. *Zoologica Scripta*, 41, 220–232.
http://dx.doi.org/10.1111/j.1463-6409.2012.00533.x

Fritz, U., Branch, W.R., Gehring, P.-S., Harvey, J., Kindler, C., Meyer, L., Du Preez, L., Široký, P., Vieites, D.R. & Vences, M. (2013) Weak divergence among African, Malagasy and Seychellois hinged terrapins (*Pelusios castanoides*, *P. subniger*) and evidence for human-mediated oversea dispersal. *Organisms Diversity & Evolution*, 13, 215–224.
http://dx.doi.org/10.1007/s13127-012-0113-3

Fritz, U., Branch, W.R., Hofmeyr, M.D., Maran, J., Prokop, H., Schleicher, A., Široký, P., Stuckas, H., Vargas-Ramírez, M., Vences, M. & Hundsdörfer, A.K. (2011) Molecular phylogeny of African hinged and helmeted terrapins (Testudines:

Pelomedusidae: *Pelusios* and *Pelomedusa*). *Zoologica Scripta*, 40, 115–125.
http://dx.doi.org/10.1111/j.1463-6409.2010.00464.x
Fritz, U., d'Angelo, S., Pennisi, M.G. & Lo Valvo, M. (2006) Variation of Sicilian pond turtles, *Emys trinacris* – What makes a species cryptic? *Amphibia-Reptilia*, 27, 513–529.
http://dx.doi.org/10.1163/156853806778877095
Fritz, U., Fattizzo, T., Guicking, D., Tripepi, S., Pennisi, M.G., Lenk, P., Joger, U. & Wink, M. (2005) A new cryptic species of pond turtle from southern Italy, the hottest spot in the range of the genus *Emys*. *Zoologica Scripta*, 34, 351–371.
http://dx.doi.org/10.1111/j.1463-6409.2005.00188.x
Fritz, U., Guicking, D., Auer, M., Sommer, R.S., Wink, M. & Hundsdörfer, A.K. (2008) Diversity of the Southeast Asian leaf turtle genus *Cyclemys*: how many leaves on its tree of life? *Zoologica Scripta*, 37, 367–390.
http://dx.doi.org/10.1111/j.1463-6409.2008.00332.x
Fritz, U., Petzold, A., Kehlmaier, C., Kindler, C., Campbell, P., Hofmeyr, M.D. & Branch, W.R. (2014) Disentangling the *Pelomedusa* complex using type specimens and historical DNA. *Zootaxa*, 3795 (5), 501–522
http://dx.doi.org/10.11646/zootaxa.3795.5.1
Fritz, U., Stuckas, H., Vargas-Ramírez, M., Hundsdörfer, A.K., Maran, J. & Päckert, M. (2012b) Molecular phylogeny of Central and South American slider turtles: implications for biogeography and systematics (Testudines: Emydidae: *Trachemys*). *Journal of Zoological Systematics and Evolutionary Research*, 50, 125–136.
http://dx.doi.org/10.1111/j.1439-0469.2011.00647.x
Fritz, U., Vargas-Ramírez, M. & Široký, P. (2012c) Phylogenetic position of *Pelusios williamsi* and a critique of current GenBank procedures (Reptilia: Testudines: Pelomedusidae). *Amphibia-Reptilia*, 33, 150–154.
http://dx.doi.org/10.1163/156853812x627204
Galtier, N., Nabholz, B., Glémin, S. & Hurst, G.D.D. (2009) Mitochondrial DNA as a marker of molecular diversity: a reappraisal. *Molecular Ecology*, 18, 4541–4550.
http://dx.doi.org/10.1111/j.1365-294x.2009.04380.x
Gasperetti, J., Stimson, A.F., Miller, J.D., Ross, J.P. & Gasperetti, P.R. (1993) Turtles of Arabia. *Fauna of Saudi Arabia*, 13, 170–367.
Gray, J.E. (1863) Notice of a new species of *Pelomedusa* from Natal. *Annals and Magazine of Natural History,* 3 (12), 99–100.
Hebert, P.D.N., Cywinska, A., Ball, S.L. & DeWaard, J.R. (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society London, B (Biological Sciences)*, 270, 313–321.
http://dx.doi.org/10.1098/rspb.2002.2218
Hewitt, J. (1935) Some new forms of batrachians and reptiles from South Africa. *Records of the Albany Museum*, 4, 283–357, plates XXVII–XXXVI.
ICZN [International Commission on Zoological Nomenclature] (1999) *International Code of Zoological Nomenclature. Fourth Edition.* International Trust for Zoological Nomenclature, London, XXIX + 306 pp.
Iverson, J.B., Le, M. & Ingram, C. (2013) Molecular phylogenetics of the mud and musk turtle family Kinosternidae. *Molecular Phylogenetics and Evolution*, 69, 929–939.
http://dx.doi.org/10.1016/j.ympev.2013.06.011
Kindler, C., Branch, W.R., Hofmeyr, M.D., Maran, J., Široký, P., Vences, M., Harvey, J., Hauswaldt, J.S., Schleicher, A., Stuckas, H. & Fritz, U. (2012) Molecular phylogeny of African hinge-back tortoises (*Kinixys*): implications for phylogeography and taxonomy (Testudines: Testudinidae). *Journal of Zoological Systematics and Evolutionary Research*, 50, 192–201.
http://dx.doi.org/10.1111/j.1439-0469.2012.00660.x
Kulo, S.-D. (1980) Parasites de chéloniens en Afrique intertropicale. *Polystomoides nabedei* n. sp. (Monogenea, Polystomatidae), parasite de la vessie urinaire de la tortue d'eau douce *Pelomedusa subrufa* Lacépède, 1788 (Chélonien, Pelomedusidae). *Annales de Parasitologie Humaine et Comparée*, 55, 367–377.
Lamb, T., Lydeard, C., Walker, R.B. & Gibbons, J.W. (1994) Molecular systematics of map turtles (*Graptemys*): a comparison of mitochondrial restriction site versus sequence data. *Systematic Biology*, 43, 543–559.
Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PARTITIONFINDER: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29, 1695–1701.
http://dx.doi.org/10.1093/molbev/mss020
Mertens, R. (1937) Bemerkungen über die Rassen von *Pelomedusa subrufa* (La Cépède). *Zoologischer Anzeiger*, 117, 139–142.
Meyer, C.P. & Paulay, G. (2005) DNA barcodes: error rates based on comprehensive sampling. *PLoS Biology*, 3, e422.
http://dx.doi.org/10.1371/journal.pbio.0030422
Miralles, A. & Vences, M. (2013) New metrics for comparison of taxonomies reveal striking discrepancies among species delimitation methods in *Madascincus* lizards. *PLoS ONE*, 8, e68242.
http://dx.doi.org/10.1371/journal.pone.0068242
Morrison, C. & Du Preez, L.H. (2011) *Turtle Polystomes of the World. Neopolystoma, Polystomoidella and Polystomoides*. VDM Verlag Dr. Müller, Saarbrücken, 236 pp.
Padial, J.M., Miralles, A., De la Riva, I. & Vences, M. (2010) The integrative future of taxonomy. *Frontiers in Zoology*, 7, 16.
http://dx.doi.org/10.1186/1742-9994-7-16

Praschag, P., Stuckas, H., Päckert, M., Maran, J. & Fritz, U. (2011) Mitochondrial DNA sequences suggest a revised taxonomy of Asian flapshell turtles (*Lissemys* Smith, 1931) and the validity of previously unrecognized taxa (Testudines: Trionychidae). *Vertebrate Zoology*, 61, 147–160.

Rochebrune, A.-T. de (1884) *Faune de la Sénégambie. Reptiles.* Octave Doin, Paris, 41 + (1) pp., 8 plates.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) Mrbayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61, 539–542.
http://dx.doi.org/10.1093/sysbio/sys029

Rüppell, E. (1835) *Neue Wirbelthiere zu der Fauna von Abyssinien gehörig. Amphibien*. Siegmund Schmerber, Frankfurt am Main, 18 pp., 6 plates.
http://dx.doi.org/10.5962/bhl.title.53778

Schlick-Steiner, B., Steiner, F.M., Seifert, B., Stauffer, C., Christian, E. & Crozier, R.H. (2010) Integrative taxonomy: a multisource approach to exploring biodiversity. *Annual Review of Entomology*, 55, 421–438.
http://dx.doi.org/10.1146/annurev-ento-112408-085432

Schoepff, I.D. (1792) *Historia Testudinum iconibus illustrata*. Ioannes Iacobus Palm, Erlangen, XII + 136 pp., 31 plates.
http://dx.doi.org/10.5962/bhl.title.5109

Schweigger, [A.F.] (1812) Prodromus monographiae Cheloniorum. *In:* Bessel, F.W., Hagen, K.G., Remer, W.H.G., Schweigger, A.F. & Wrede, E.F. (Eds.), *Königsberger Archiv für Naturwissenschaft und Mathematik. Erster Band.* Friedrich Nicolovius, Königsberg, pp. 271–368 + 406–462.

Schweinfurth, G. (1874) *Im Herzen von Afrika. Reisen und Entdeckungen im centralen Aequatorial-Afrika während der Jahre 1868 bis 1871*. Volume 1 and 2. F.A. Brockhaus, Leipzig, XIII + 599 pp. (Vol. 1), XII + 561 pp., 2 maps (Vol. 2).

Shen, Y.-Y., Chen, X. & Murphy, R.W. (2013) Assessing DNA barcoding as a tool for species identification and data quality control. *PLoS ONE*, 8, e57125.
http://dx.doi.org/10.1371/journal.pone.0057125

Sites, J.W. & Marshall, J.C. (2003) Delimiting species: a Renaissance issue in systematic biology. *Trends in Ecology and Evolution*, 18, 462–470.
http://dx.doi.org/10.1016/s0169-5347(03)00184-8

Spinks, P.Q., Thomson, R.C., Pauly, G.B., Newman, C.E., Mount, G. & Shaffer, H.B. (2013) Misleading phylogenetic inferences based on single-exemplar sampling in the turtle genus *Pseudemys*. *Molecular Phylogenetics and Evolution*, 68, 269–281.
http://dx.doi.org/10.1016/j.ympev.2013.03.031

Spinks, P.Q., Thomson, R.C., Zhang, Y., Che, J., Wu, Y. & Shaffer, H.B. (2012) Species boundaries and phylogenetic relationships in the critically endangered Asian box turtle genus *Cuora*. *Molecular Phylogenetics and Evolution*, 63, 656–667.
http://dx.doi.org/10.1016/j.ympev.2012.02.014

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
http://dx.doi.org/10.1093/bioinformatics/btl446

Stuckas, H. & Fritz, U. (2011) Identity of *Pelodiscus sinensis* revealed by DNA sequences of an approximately 180-year-old type specimen and a taxonomic reappraisal of *Pelodiscus* species (Testudines: Trionychidae). *Journal of Zoological Systematics and Evolutionary Research*, 49, 335–339.
http://dx.doi.org/10.1111/j.1439-0469.2011.00632.x

Stuckas, H., Gemel, R. & Fritz, U. (2013) One extinct turtle species less: *Pelusios seychellensis* is not extinct, it never existed. *PLoS ONE*, 8, e57116.
http://dx.doi.org/10.1371/journal.pone.0057116

Suckow, G.A. (1798) *Anfangsgründe der theoretischen und angewandten Naturgeschichte der Thiere. Dritter Theil. Von den Amphibien.* Weidmannische Buchhandlung, Leipzig, 298 pp.
http://dx.doi.org/10.5962/bhl.title.62582

Tamura, K., Stecher, G., Peterson, D., Filipski, A. & Kumar, S. (2013) MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. *Molecular Biology and Evolution*, 30, 2725–2729.
http://dx.doi.org/10.1093/molbev/mst197

Tinsley, R.C. (1973) Observations on Polystomatidae (Monogenoidea) from East Africa with a description of *Polystoma makereri* n. sp. *Zeitschrift für Parasitenkunde*, 42, 251–263.
http://dx.doi.org/10.1007/bf00328887

Todd, E.V., Blair, D. & Jerry, D.R. (2014) Influence of drainage divides versus arid corridors on genetic structure and demography of a widespread freshwater turtle, *Emydura macquarii krefftii*, from Australia. *Ecology and Evolution*, 4, 606–622.
http://dx.doi.org/10.1002/ece3.968

Vaillant, L. & Grandidier, G. (1910) Volume XVII. Histoire naturelle des reptiles. Première partie: Crocodiles et tortues. *In:* Grandidier, A. & Grandidier, G. (Eds.), *Histoire physique, naturelle et politique de Madagascar*. Imprimerie Nationale, Paris, pp. 1–86, plates 1–27.

Vargas-Ramírez, M., Carr, J.L. & Fritz, U. (2013) Complex phylogeography in *Rhinoclemmys melanosterna*: conflicting mitochondrial and nuclear evidence suggests past hybridization (Testudines: Geoemydidae). *Zootaxa*, 3670 (2), 238–254. http://dx.doi.org/10.11646/zootaxa.3670.2.8

Vargas-Ramírez, M., Michels, J., Castaño-Mora, O.V., Cárdenas-Arevalo, G., Gallego-García, N. & Fritz, U. (2012) Weak genetic divergence between the two South American toad-headed turtles *Mesoclemmys dahli* and *M. zuliae* (Testudines: Pleurodira: Chelidae). *Amphibia-Reptilia*, 33, 373–385. http://dx.doi.org/10.1163/15685381-00002840

Vargas-Ramírez, M., Vences, M., Branch, W.R., Daniels, S.R., Glaw, F., Hofmeyr, M.D., Kuchling, G., Maran, J., Papenfuss, T.J., Široký, P., Vieites, D.R. & Fritz, U. (2010) Deep genealogical lineages in the widely distributed African helmeted terrapin: evidence from mitochondrial and nuclear DNA (Testudines: Pelomedusidae: *Pelomedusa subrufa*). *Molecular Phylogenetics and Evolution*, 56, 428–440. http://dx.doi.org/10.1016/j.ympev.2010.03.019

Will, K.W., Mishler, B.D. & Wheeler, Q.D. (2005) The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology*, 54, 844–851. http://dx.doi.org/10.1080/10635150500354878

Will, K.W. & Rubinoff, D. (2004) Myth of the molecule: DNA barcodes for species cannot replace morphology for identification and classification. *Cladistics*, 20, 47–55. http://dx.doi.org/10.1111/j.1096-0031.2003.00008.x

Wong, R.A., Fong, J.J. & Papenfuss, T.J. (2010) Phylogeography of the African helmeted terrapin, *Pelomedusa subrufa*: genetic structure, dispersal, and human introduction. *Proceedings of the California Academy of Sciences*, 61, 575–585.

Yang, Z. & Rannala, B. (2010) Bayesian species delimitation using multilocus sequence data. *Proceedings of the National Academy of Sciences of the USA*, 107, 9264–9269. http://dx.doi.org/10.1073/pnas.0913022107