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## Disentangling the *Pelomedusa* complex using type specimens and historical DNA (Testudines: Pelomedusidae)

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### Abstract

Recent research has shown that the helmeted terrapin (*Pelomedusa subrufa*), a species that occurs throughout sub-Saharan Africa, in Madagascar and the southwestern Arabian Peninsula, consists of several deeply divergent genetic lineages. Here we examine all nominal taxa currently synonymized with *Pelomedusa subrufa* (Bonnaterre, 1789) and provide mitochondrial DNA sequences of type specimens or topotypic material for most taxa. Lectotypes are designated for *Testudo galeata* Schoepff, 1792, *Pentonyx capensis* Duméril & Bibron, 1835, *Pelomedusa nigra* Gray, 1863, *Pelomedusa galeata* var. *disjuncta* Vaillant & Grandidier, 1910, and *Pelomedusa galeata damarensis* Hewitt, 1935. For *Pelomedusa gasconi* Rochebrune, 1884, a taxon without preserved type material, a neotype is designated. Type material of *Pentonyx americana* Cornalia, 1849, a nominal species without credible type locality, is lost and its identity remains questionable. Also the holotype of *Pelomedusa galeata orangensis* Hewitt, 1935 is lost, but its allocation to the only genetic lineage occurring in South Africa is unambiguous. Phylogenetic analyses of type sequences or topotypic material reveal that the remaining nominal taxa represent three of the nine previously identified lineages of *Pelomedusa*. Among these three lineages is the South African one. Type specimens of *Pentonyx gehafie* Rüppell, 1835 correspond to an additional distinct lineage. The present study provides a sound basis for a subsequent integrative taxonomic revision of the *Pelomedusa* complex.

**Key words:** Africa, Arabian Peninsula, Madagascar, nomenclature, type specimen

### Introduction

Helmeted terrapins (*Pelomedusa subrufa*) are widely distributed over sub-Saharan Africa, Madagascar and the southwestern Arabian Peninsula (Iverson 1992; Ernst *et al.* 2000; Boycott & Bourquin 2008) and thought to represent an example of a pan-African reptile species (Wong *et al.* 2010; Barlow *et al.* 2013). With maximum shell lengths of 20–32.5 cm (Ernst *et al.* 2000), helmeted terrapins are a small to medium-sized species and adapted to a peculiar life style. These terrapins use small, often temporary water bodies. If these dry out, the terrapins burrow underground and remain there until more favourable conditions return. Moreover, the terrapins are able to move great distances overland, allowing them to occur in quite arid regions. Helmeted terrapins thus occupy a unique ecological niche among African freshwater turtles (Boycott & Bourquin 2008; Branch 2008).

Currently, *P. subrufa* is treated as monotypic (Gasperetti *et al.* 1993; Fritz & Havaš 2007; Boycott & Bourquin 2008; van Dijk *et al.* 2012), even though many previous authors recognized two or three distinct subspecies before Gasperetti *et al.* (1993) questioned the reliability of their diagnostic morphological characters. However, using mitochondrial and nuclear DNA sequences, two recent papers (Vargas-Ramírez *et al.* 2010; Wong *et al.* 2010) revealed deep genealogical lineages in *P. subrufa*, suggesting that *Pelomedusa* represents rather a species complex

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

**TABLE S2.** Primer sequences for mtDNA fragments for fresh samples. Nucleotides in brackets represent variable positions.

**TABLE S3.** Primer sequences and lengths of amplified PCR products of mtDNA fragments of the 12S, cyt b and ND4 genes for historical samples.

**TABLE S4.** PCR conditions for historical and fresh samples.

**TABLE S5.** Degree of overlap for individual mtDNA fragments yielding 251–252 bp of the 12S rRNA gene.

**TABLE S6.** Degree of overlap for individual mtDNA fragments yielding 319 bp of the cyt b gene.

**TABLE S7.** Degree of overlap for individual mtDNA fragments yielding 437 bp of the ND4 gene.

**TABLE S8.** Partitioning scheme and models selected by the Akaike Information Criterion in MrMODELTEST 2.3 (Nylander 2004).

The Supporting Information is available from the Dryad Repository using the link <http://dx.doi.org/10.5061/dryad.rd37p>

## 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>
- Bauer, A.M. & Günther, R. (2013) Origin and identity of the von Borcke collection of amphibians and reptiles in the Museum für Naturkunde in Berlin: a cache of Seba specimens? *Zoosystematics and Evolution*, 89, 167–185.  
<http://dx.doi.org/10.1002/zoots.201300005>
- Bauer, A.M. & Wahlgren, R. (2013) On the Linck collection and specimens of snakes figured by Johann Jakob Scheuchzer (1735) – the oldest fluid-preserved herpetological collection in the world? *Bonn zoological Bulletin*, 62, 220–252.
- 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>
- Boulenger, G.A. (1880) Sur l'existence d'une seule espèce du genre *Pelomedusa* Wagler. *Bulletin de la Société zoologique de France*, 5, 146–151.
- Boulenger, G.A. (1889) *Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum (Natural History). New Edition*. British Museum (Natural History), London, x + 311 pp., 6 plates.  
<http://dx.doi.org/10.5962/bhl.title.13541>
- Bour, R. (1982) *Pelomedusa subrufa* (Lacepède, 1788), *Pelusios subniger* (Lacepède, 1788) (Reptilia, Chelonii) et le séjour de Philibert Commerson à Madagascar. *Bulletin du Muséum National d'Histoire naturelle*, 4<sup>e</sup> Série, Section A, 4, 531–539.
- Bour, R. (1985) Les tortues terrestres et d'eau douce de Madagascar et des îles voisines. *Madagascar Recherches Scientifique*, 18, 54–80.
- Bour, R. (1986) Note sur *Pelusios adansonii* (Schweigger, 1812) et sur une nouvelle espèce affine du Kenya (Chelonii, Pelomedusidae). *Studia Geologica Salmanticensia, Volumen Especial*, 2 (Studia Palaeocheloniologica, II), 23–54.

- 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.
- Cornalia, E. (1849) *Vertebratorum synopsis in museo mediolanense extantium quae per novam orbem cajetanus osculati collegit annis 1846–47–48. Speciebus novis vel minus cognitis adjectis nec non descriptionibus atque iconibus illustratis*. Corbetta, Milan, pp. 301–315, 5 plates.
- 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.
- Ernst, C.H., Altenburg, R.G.M. & Barbour, R.W. (2000) *Turtles of the World. World Biodiversity Database, Version 1.2*. Biodiversity Center of ETI, Amsterdam, CD-ROM.
- Ernst, C.H. & Barbour, R.W. (1989) *Turtles of the World*. Smithsonian Institution Press, Washington, D.C., xii + 313 pp., 16 plates.
- 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., 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. & Havaš, P. (2007) Checklist of chelonians of the world. *Vertebrate Zoology*, 57, 149–368.
- 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. (1831) *Synopsis Reptilium; or Short Descriptions of the Species of Reptiles. Part I.—Cataphracta. Tortoises, Crocodiles, and Enaliosaurians*. Treuttel, Wurtz, and Co., London, viii + 85 pp.
- Gray, J.E. (1856 [“1855”]) *Catalogue of Shield Reptiles in the Collection of the British Museum. Part I. Testudinata (Tortoises)*. British Museum, London, (1) + 79 + (2) pp., 42 plates.  
<http://dx.doi.org/10.5962/bhl.title.5491>
- Gray, J.E. (1863) Notice of a new species of *Pelomedusa* from Natal. *Annals and Magazine of Natural History, Series 3*, 12, 99–100.
- Hall, T.A. (1999) BIOEDIT: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
- Herrmann, H.-W. & Branch, W.R. (2013) Fifty years of herpetological research in the Namib Desert and Namibia with an updated and annotated species checklist. *Journal of Arid Environments*, 93, 94–115.  
<http://dx.doi.org/10.1016/j.jaridenv.2012.05.003>
- 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.
- ICZN [International Commission on Zoological Nomenclature] (2005) Opinion 2104. *Bulletin of Zoological Nomenclature*, 62, 55.
- Iverson, J.B. (1992) *A Revised Checklist with Distribution Maps of the Turtles of the World*. Privately Printed, Richmond, IN, xiii + 363 pp.
- Lacepède, [B.G.] de (1788) *Histoire naturelle des quadrupèdes ovipares et des serpens. Tome premier*. Hôtel de Thou, Paris, (17) + (1, errata) + 651 pp., 1 folded table, 41 plates.  
<http://dx.doi.org/10.5962/bhl.title.5036>
- Linnaeus, C. (1758) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Regnum animale. Editio decima, reformata*. Laurentius Salvius, Stockholm, (3) + 823 + (1) pp.  
<http://dx.doi.org/10.5962/bhl.title.542>
- Loveridge, A. (1941) Revision of the African terrapin [sic] of the family Pelomedusidae. *Bulletin of the Museum of Comparative Zoology*, 88, 467–524.
- Mertens, R. (1937) Bemerkungen über die Rassen von *Pelomedusa subrufa* (La Cépède). *Zoologischer Anzeiger*, 117, 139–142.
- Nylander, J.A.A. (2004) Mrmodeltest, v2. Evolutionary Biology Centre, Uppsala University, Uppsala. Available from: <http://www.abc.se/~nylander/> (accessed 29 January 2011)
- Parker, H.W. (1936) Reptiles and amphibians collected by the Lake Rudolf Rift Valley Expedition, 1934. *Annals and Magazine of Natural History*, 18, 594–609.  
<http://dx.doi.org/10.1080/00222933608655232>

- Praschag, P., Sommer, R.S., McCarthy, C., Gemel, R. & Fritz, U. (2008) Naming one of the world's rarest chelonians, the southern Batagur. *Zootaxa*, 1758, 61–68.
- Rhodin, A.G.J. & Carr, J.L. (2009) A quarter millennium of uses and misuses of the turtle name *Testudo scabra*: identification of the type specimens of *T. scabra* Linnaeus 1758 (= *Rhinoclemmys punctularia*) and *T. scripta* Thunberg in Schoepff 1792 (= *Trachemys scripta scripta*). *Zootaxa*, 2226, 1–18.
- 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>
- 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.
- 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>
- Strauch, A. (1865) Die Vertheilung der Schildkröten über den Erdball. Ein zoogeographischer Versuch. *Mémoires de l'Académie impériale des Sciences de St.-Pétersbourg, VII Série*, VIII (13), 1–207.
- Stuart, B.L. & Fritz, U. (2008) Historical DNA from type museum specimens clarifies diversity of Asian leaf turtles (*Cyclemys*). *Biological Journal of the Linnean Society*, 94, 131–141.  
<http://dx.doi.org/10.1111/j.1095-8312.2008.00966.x>
- 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>
- 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.
- van Dijk, P.P., Iverson, J.B., Shaffer, H.B., Bour, R. & Rhodin, A.G.J. (2012) Turtles of the world, 2012 update: annotated checklist of taxonomy, synonymy, distribution, and conservation status. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., Iverson, J.B. & Mittermeier, R.A. (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. 000.243–000.328.  
<http://dx.doi.org/10.3854/crm.5.007.checklist.v5.2012>
- 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>
- Wermuth, H. & Mertens, R. (1961) *Schildkröten, Krokodile, Brückenechsen*. VEB Gustav Fischer, Jena, XXVI + (1) + 422 pp.
- Wermuth, H. & Mertens, R. (1977) Testudines, Crocodylia, Rhynchocephalia. *Das Tierreich*, 100, I–XXVII + 1–174.
- 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.
- Wren-Sargent, M. (1999) Fieldguides, past and present. Part 2: South African publications. *Bird Numbers*, 8, 26–31.