

Where do you come from, stranger? A scientific-historical digression with discussion on nomenclature and taxonomy of *Testudo graeca* Linnaeus, 1758

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Abstract

It is shown that the location data for the terra typica restricta of *Testudo graeca* and for the terra typica designata for *Testudo graeca* are based on an incorrectly assigned location. In fact, the original place corresponds to Santa Cruz, known today as Agadir (Morocco) and not the old Spanish fortress of Santa Cruz near Oran in Algeria. Accordingly, populations of *Testudo graeca* from the Agadir environment have to be named *Testudo graeca graeca* instead of *Testudo graeca soussensis*. For the populations of *Testudo graeca* from the vicinity of Algiers, “*mauritanica*” is the next available name for this subspecies of *graeca*. Therefore, *Testudo graeca mauritanica* has to be used instead of *Testudo graeca graeca*. For *Testudo graeca mauritanica*, a lectotypus is designated.

Key Words

Algeria, distribution, Morocco, North Africa, Reptilia, Testudines, Testudinidae, Spur thighed tortoise, terra typica designata, terra typica restricta

Introduction

The tenth edition of the first volume of “Systema naturae” – Syst. Nat. (ed.10) – by Carolus Linnaeus 1758 forms the basis of the rules of zoological nomenclature (ICZN 1999, Art. 3.1.). On pages 197–199 eleven turtle and tortoise species are described herein, all of them united within the genus *Testudo*. *Testudo graeca* is listed on page 198 as the sixth species. The description is a brief excerpt from the characterisation of the naturalist George Edwards and refers to the colour image 204 and text on page 204 in the work of Edwards.

The original determination of the origin

The description of the tortoise, to which Linnaeus refers, is in the fourth volume of the “Natural history of birds ...” (Edwards 1751). Together with the colour image, it undoubtedly represents the tortoise species named by Linnaeus as *Testudo graeca* (Fig. 1). Concerning the origin, Edwards notes: “This Tortoise was sent to me from Santa-Cruz in West Barbary, by my late Friend Mr. Thomas Rawlings, Merchant, who died



Figure 1. Plate 204 out of Edwards, G. (1751): “A natural history of birds. The most of which have not hitherto been either figured or described, and the rest, by reason of obscure, or too brief descriptions without figures, or of figures very ill designed, are hitherto but little known: Part IV” etc. Above there is “The African Land-Tortoise”, = *Testudo graeca* Linné.

there [Anno 1748] after some Years Settlement in that Country”.

In the earlier published part 2 of his “Natural history of birds ...” (1747) Edwards had already given some

more precise information on the origin of the objects, which he had received from Thomas Rawlings from Santa Cruz. Describing the “Red legg’d Partridge, from Barbary”, Edwards notes (page 70): “A Pair of these Birds

were sent to me alive by my good Friend, Mr. Thomas Rawlings, Merchant, residing at Santa Cruz, in that Part of Barbary which lies without the Straits of Gibraltar, on the Atlantic Ocean.”

Historical aspects of Agadir

The city was founded by the Portuguese Joao Lopes de Sequeira in 1505 originally a commercial settlement – and was named Santa Cruz do Cabo de Gué. Later, the names “Santa Cruz de Narba” and “Santa Cruz de Aguer” were used. In 1541, the settlement was conquered by the Berbers and expanded to a major trading post. From 1756 its importance as a trading place in favor of Mogador (Essaouira) declined further.

(<https://historiasdeportugalemarrocos.com/2015/02/18/santa-cruz-do-cabo-guer/>; retrieved in August, 2019)

Lempriere (1814), a contemporary source to Edwards, describes in his travel memoirs of 1789 the decay of Santa Cruz: “Santa Cruz is a sea-port, situated on the declivity of a high and steep mountain, forming the western termination of that chain of mountains, which nearly divides the Emperor’s dominions in two parts, so well-known by the name of the Atlas. It formerly belonged to the Portuguese, and till the accession of Sidi Mahomet was the principal place whence Europeans were allowed to trade. It is at present a deserted town, with only a few houses, which are almost hourly mouldering to decay.”

The true type locality

The term “Santa Cruz” in the mentioned sources of Edwards (1747, 1751) together with the historical report of Lempriere (1789) refers therefore without any doubt to today’s Agadir in Morocco.

On the designation of type locality, chronology of misinterpretation

The misinterpretation of the Terra typica of *Testudo graeca* progressively took place, starting from the type locality “Africa” by Linnaeus (1758): 198. Martinus Houttuyn (1764): 56 gives the origin of *Testudo graeca* “Santa Cruz in Barbarie” using the notes of Edwards (1751) without associating this area name with Algeria, as the Turtle Taxonomy Working Group (2017): 152 does. (Additionally, Martinus Houttuyn is named herein under the wrong name “Leven”, see comment under Houttuyn).

Strauch (1862): 67 describes *Testudo graeca* under “*Testudo pusilla* Shaw (nec Linné.)”. However, with a reference in the footnote, he refers to the text and plate 204 of Edwards and thus clearly to *T. graeca* Linnae-

us. Shaw (1802): 53 also based *Testudo pusilla* on Edwards’ specimen, therefore consequently synonymous with *Testudo graeca* Linnaeus 1758, whereas Strauch’s *Testudo graeca* (1862): 73 is a composite, based on *Testudo graeca* Gmelin in Linnaeus (13th ed. Syst. Nat., pars III, p.1043) and defined with features what is today’s *Testudo hermanni*.

Apparently under the influence of having several specimens from the vicinity of Algier in his collection – including several specimens collected by himself in 1861 – Strauch now declares Santa Cruz with the addition of “alte spanische Festung bei Oran in der Algérie” [(old Spanish fortress at Oran in the Algérie)] as Terra typica restricta. Ever since this misinterpretation, the error has been adopted by all other authors.

In any case, Mertens and Müller 1928 do not initially refer to Algeria (page 22: “Santa Cruz in der Westberberei, Nordafrika”) [Santa Cruz in West Barbary, North Africa], but subsequently in 1940 they also formally included the terra typica restricta for *Testudo graeca* to „Santa Cruz, Oran, Nordafrika“ [Santa Cruz, Oran, North Africa] (Mertens and Müller 1940: 20).

Wermuth (1956): 401 assigns in the discussion on the taxonomic position of *Testudo pusilla* Linnaeus, 1758 – the type locality “Santa Cruz in the western Barbary” again to the locality “Santa Cruz, Oran” and, moreover, he declares it to Terra typica designata for the nominate form *Testudo graeca graeca*.

These assignments were retained in all subsequent lists (Loveridge and Williams 1957; Wermuth and Mertens 1961: 209; Wermuth and Mertens 1977: 85; Fritz and Havas 2007: 296). Accordingly, this type locality was also transferred by Mertens and Wermuth (1960): 65 for *Testudo graeca* in the list of amphibians and reptiles in Europe. Most recently, it is quoted by Bour and Ohler (2008) (“presently Djebel Murdjadjo or “pic de l’Aidour” 35°42’N, 0°45’W, Oran, Algeria”) and in the Turtle Taxonomy Working Group [Rhodin AGJ, Iverson JB, Bour R., Fritz U., Georges A., Shaffer HB & van Dijk, P.P.] 2017: 152.

Systematic position and nomenclature of the *Testudo graeca* populations in Algeria and Morocco

The species complex of *Testudo graeca* has been subject to intensive taxonomic investigations in recent years. As a consequence of this, numerous names were established but several ones have been synonymized in subsequent studies. According to the results of mitochondrial and nuclear range wide data, Fritz et al. (2007) present a concept considering all investigated *Testudo graeca* populations as conspecific and propose to reduce the number of subspecies in accordance with the genetic lineages. Concerning the North African populations of



Figure 2. MNHN 0.1937., designated Neotypus of *Testudo graeca mauritanica*, dorsal. (Photograph: A. Ohler).



Figure 3. MNHN 0.1937., designated Neotypus of *Testudo graeca mauritanica*, lateral. (Photograph: A. Ohler).



Figure 4. MNHN 0.1937., designated Neotypus of *Testudo graeca mauritanica*, ventral. (Photograph: A. Ohler).

Testudo graeca, Fritz et al. (2009) investigate the mitochondrial phylogeography in the Western Mediterranean as well as Graciá et al. (2017) in a wider context. In their taxonomic conclusions they assign the four mitochondrial genetic lineages to the six subspecies so far described in this area.

Accordingly, the specimen referred to by Linnaeus in the description of *Testudo graeca* comes from the area assigned to the subspecies *Testudo graeca soussensis* Pieh, 2001 “2000” (= mitochondrial lineage D sensu Fritz et al. 2006). Consequently, due to priority, this subspecies has to be named *Testudo graeca graeca* Linnaeus, 1758. *Testudo graeca soussensis* Pieh, 2001 “2000” therefore is a junior subjective synonym of *Testudo graeca graeca* Linnaeus, 1758. The detailed description of Pieh 2001 “2000” with extensive morphological data can therefore be considered as a redescription of *Testudo graeca graeca*.

The types of *Testudo graeca*

As a matter of fact, Edwards reports a male and female of this species in his holding “I had a male and female of this species; they lived two years with me; in the garden of the College of Physicians, London”. Consequently, the specimen pictured on the iconography has to be designated as lectotype of *Testudo graeca* (ICZN Art. 74) and therefore cannot be the holotype. It is undoubtedly the

male of the two specimens. Consequently, this male is the name bearing lectotype of *Testudo graeca*. Whenever the female of Edwards’ collection emerges it had the rank of a Paralectotype. Bour (1987) wanted to recognise the male depicted in the iconography 204 of Edwards (1751) as the holotype of *Testudo graeca* and at the same time the lectotype of *Testudo mauritanica*. Both findings are not correct; in the case of *Testudo graeca* it must be considered as a lectotype as explained above – and in the case of *T. mauritanica* because these populations have another genetic identity and are treated in the past as their own taxon rather than populations belonging to the nominate subspecies of *Testudo graeca*. To be sure that the two named specimens mentioned by Edwards are not present in a collection, we contacted Patrick Campbell (BMNH) with the result that no specimen in the holdings of the British Museum of Natural History comes into question. It would also have been conceivable that the two Edwardian tortoises would remain or be passed on to Sloane, because Edwards was in contact with Sloane. Afterwards, the collection of Sloane was transferred to the British Museum. Clutton-Brock (1994): 85 states that in Sloane’s Volume 25e the collection of “Quadrupeds” is listed. It comprises 1,903 objects, including 67 tortoises [incl. Sea turtles]. In the comments of Clutton-Brock (pp. 85–90) the turtles are not discussed. In any case, the tortoises of Edwards are not in the collection of the British Museum of Natural History today.

Which name applies to populations of the previous *Testudo graeca graeca*?

Fritz et al. (2009) found a distinct mitochondrial lineage for the Spur thighed tortoises from Algeria and North Eastern Morocco (mitochondrial lineage B 1 sensu Fritz et al. 2006).

The oldest available name is *Testudo pusilla* Linné, 1758. As already Strauch (1862: 67) pointed out, *pusilla* Linnaeus 1766 in part (but not an available name because prior to 1768 ICZN Art.3.2.) together with *pusilla* Shaw 1802 were based on Edwards' specimen(s) of *graeca*. Later, Wermuth (1956: 401) discussed the meaning of *Testudo pusilla* and showed that its origin was declared first to come from India (Linnaeus 1758: 199) and afterwards to come from the Cape of Good Hope but in fact coincides with *Testudo tessellata minor africa* (Edwards), coming from Santa Cruz from Barbary, the same location as given for *T. graeca*. Consequently it was declared as a synonym of *T. graeca* by Strauch and Wermuth.

The next available name is *Testudo mauritanica* Dumeril & Bibron, 1835: 44. Accordingly, the populations of northeastern Morocco and Algeria have to be assigned to *Testudo graeca mauritanica* Dumeril & Bibron instead of *Testudo graeca graeca* Linnaeus, 1758.

Designation of the neotype of *Testudo graeca mauritanica* Dumeril & Bibron, 1835

Because the specimen depicted on plate 204 in Edwards (1751) cannot be the syntypus of *T. g. mauritanica*, a name bearing specimen has to be designated for *T. g. mauritanica* to avoid further confusion. In the description of Duméril and Bibron (1835) a number of different names in several publications are referred to as synonyms of this taxon. One of these synonyms is *Testudo zohalffa* Forsk. (published in Forskål, P. 1775: VIII). Additionally, Duméril and Bibron refer as well to several other tortoises, which were at that time probably popular exotic animals in French and Paris households. It can be assumed that they have had a larger number of animals they examined for their description, but the measurements of only one specimen are given herein (often it was the biggest animal in a series, A. Ohler pers. comm.). In the holdings of the Muséum national d'histoire naturelle we found no specimen fitting the measurements given by Duméril and Bibron (1835: 48), but a specimen with locality specification "Alger" and the note on an old label: "*Testudo zohalffa* Forsk." The measurements of this specimen do not match the data given by Duméril and Bibron (1835: 48). In the last analysis, the circumstances do not give us enough security to value it as a part of the syntypus series, in particular the certainty that the tortoises were acquired from

the Museum Paris during the time of Dumeril and Bibron. Furthermore, we could not trace any further specimens as a part of a possible syntypus series. Therefore, we decide to designate the tortoise MNHN 0.1937 as neotypus of *Testudo graeca mauritanica* (figs 3–5) according Art. 75 ICZN (1999). Measurements: Carapace length (straight length): 87.7 mm, Carapace width (straight) 68.1 mm.

Discussion

From the very beginning, it was the intention of the authors to maintain the subspecies name for *graeca* in place of *mauritanica* to avoid any potential for subsequent confusion. For this purpose, a specimen of *mauritanica* – ideally a type specimen of *mauritanica* – should be selected for it to be designated as Neotypus. Subsequently, an application to the Commission under Art. 75.6. should have been made. A considerable amount of facts would have been necessary to demonstrate that the change of the subspecies name from one population to the other would have a significant impact on the worldwide biological community. Since the chance of such a solution had to be considered low, a corresponding request was not made. After checking other solutions for this problem, we found out that no other option is possible than given in our results.

As a result of the taxonomic changes taken herein, the distribution of the Maghrebian tortoises is as follows:

Testudo g. marokkensis (not affected): north western Morocco: eastwards to the Middle Atlas and south to the northern parts of the Mesata (the large plain in northern Morocco).

Testudo graeca graeca: Morocco: north of the High Atlas mountain chain from the junction with the Middle Atlas in the east westwards to the Atlantic ocean with a few distribution spots in the foreland (Jbilet hills). South of this mountain chain eastwards through the Souss valley and the Ouarzazate basin to Boulmalne du Dades, with questionable records from Erfoud and Alnif, the latter south of the Anti Atlas mountain chain. Along the Atlantic Ocean the distribution of *Testudo g. graeca* runs south to the latitude of the south western end of the Anti-Atlas. Also here are some questionable records close to the border with the Western Sahara (Schweiger 2013).

Testudo graeca mauritanica: from north east Morocco east of the Moulouya river eastwards through northern Algeria to the Tunisian border. A very unlikely finding at Figuig in easternmost south Morocco (Strohl 1923).

Testudo graeca nabeulensis (not affected): north east Tunisia.

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References

- Bour R (1987) L'identité des tortues terrestres européennes: spécimens-types et localités-types. *Revue Française d'Aquariologie* 13(4): 111–122.
- Bour R, Ohler A (2008) *Chersine* Merrem, 1820 and *Chersina* Gray, 1831: a nomenclatural survey. *Zootaxa* 1752: 66–68. <https://doi.org/10.11646/zootaxa.1752.1.4>
- Clutton-Brock J (1994) Vertebrate collections. In: MacGregor A (Ed.) Sir Hans Sloane, Collector, Scientist, Antiquary, Founding Father of the British Museum. British Museum, London, 77–92.
- Duméril AMC, Bibron G (1835) *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles* (Vol. 2). Paris, Librairie Encyclopédique de Roret, (2), (1), 680 pp. [2 folding tables, 12 pls.] <https://doi.org/10.5962/bhl.title.46831>
- Edwards G (1747) A natural history of birds: most of which have not been figured or described, and others very little known, from obscure or too brief descriptions without figures, or from figures very ill designed: Containing the figures of Sixty-One Birds and two quadrupeds, engraved on Fifty-Three Copper Plates, after curious Original Drawings from Life, and exactly Color'd. With full and accurate descriptions. To which is added, An Appendix, by Way of Illustration: part II / by George Edwards – London: Printed for the author, at the College of Physicians in Warwick-Lane, 1743. https://www.europeana.eu/portal/de/record/9200110/BibliographicResource_1000126635400.html
- Edwards G (1751) A natural history of birds. The most of which have not hitherto been either figured or described, and the rest, by reason of obscure, or too brief descriptions without figures, or of figures very ill designed, are hitherto but little known: Part IV: A natural history of uncommon birds: and of some other rare and undescribed animals, quadrupeds, fishes, reptiles, insects, &c., exhibited in two hundred and ten copper-plates, from designs copied immediately from nature, and curiously coloured after life, with a full and accurate description of each figure, to which is added. A brief and general idea of drawing and painting in water-colours; with instructions for etching on copper with aqua fortis; likewise some thoughts on the passage of birds; and additions to many subjects described in this work. Printed for the author, at the College of Physicians in Warwick-Lane, 1743–1751, London. <https://doi.org/10.5962/bhl.title.115782>
- Forsskål P [Forsskål P] (1775) *Descriptiones Animalium: Avium, Amphibiorum, Piscium, Insectorum, Vermium; quae in Itinere Orientali Observavit. Post mortem auctoris edidit Carsten Niebuhr. Hauniae [Copenhagen]: Mölleri*, 164 pp. <https://doi.org/10.5962/bhl.title.2154>
- Fritz U, Havaš P (2007) Checklist of chelonians of the world. *Vertebrate Zoology* 57: 149–368. http://www.senckenberg.de/files/content/forschung/publikationen/vertebratezoology/vz57-2/57-2_fritz_149-368.pdf
- Fritz U, Hundsdoerfer AK, Široký P, Auer M, Kami HG, Lehmann J (2007) Phenotypic plasticity leads to incongruence between morphology-based taxonomy and genetic differentiation in western Palearctic tortoises (*Testudo graeca* complex: Testudines, Testudinidae). *Amphibia-Reptilia* 28: 97–121. <https://doi.org/10.1163/156853807779799135>
- Fritz U, Harris DJ, Fahd S, Rouag R, Graciá E, Giménez A, Široký LP, Kalboussi M, Jdeidi TB, Hundsdoerfer AK (2009) Mitochondrial phylogeography of *Testudo graeca* in the Western Mediterranean: old complex divergence in North Africa and recent arrival in Europe. *Amphibia-Reptilia* 30: 63–80. <https://doi.org/10.1163/156853809787392702>
- Graciá E, Vargas-Ramírez M, Delfino M, Anadón JD, Giménez A, Fahd S, Corti C, Jdeidi TB, Fritz U (2017) Expansion after expansion: dissecting the phylogeography of the widely distributed spur-thighed tortoise, *Testudo graeca* (Testudines: Testudinidae). *Biological Journal of the Linnean Society* 121(3): 641–654. <https://doi.org/10.1093/biolinnean/blx007>
- Houttuyn M (1764) *Natuurlyke historie of uitvoerige beschryving der dieren, planten en mineraalen, volgens het samenstel van den Heer Linnæus. Met naauwkeurige Afbeeldingen. Eerste deels, zesde stuk. Dieren van beiderley leven.* – pp. [1–6], 1–558, [index 1–4], [1–2], Pl. L-LVI [= 50–56]. Amsterdam. (F. Houttuyn). [According to the comment of the SUB library, the true author was Martinus Houttuyn, who was not quoted in the work itself. Title page gave no author and stated “By F. Houttuyn” (“By” = bij, Dutch for “at” or “with”, indicating that Frans Houttuyn was the editor or publisher, not the author). If English, “By” would have indicated authorship, but the work was in Dutch and not in English]
- ICZN (1999) *International Code of Zoological Nomenclature*. Fourth edition. London. (International Trust for Zoological Nomenclature), 306 pp.
- King FW, Burke RL (1989) *Crocodylian, Tuatara, and Turtle Species of the World. A taxonomic and geographic reference Association of Systematics Collections.*
- Lempriere W (1789) *A Tour from Gibraltar to Tangier, Salée, Mogadore, Santa Cruz, and Tarudant; and thence over Mount Atlas to Morocco. Including a particular account of the royal harem, &c. By William Lempriere, surgeon.* In: Pinkerton J (1814) *A general collection of the best and most interesting Voyages and Travels in all parts of the world* (15th edn.). <https://quod.lib.umich.edu/cgi/t/text/text-idx?c=evans;idno=N20724.0001.001>
- Linnaeus C (1758) *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Stockholm (Lars Salvi) (Ed. 10). <https://doi.org/10.5962/bhl.title.542>
- Loveridge A, Williams EE (1957) Revision of the African tortoises and turtles of the suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology at Harvard College* 115: 163–557. [18 pls.] <https://www.biodiversitylibrary.org/page/4779608>
- Mertens R, Müller L (1928) *Liste der Amphibien und Reptilien Europas. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main* 41: 1–62.
- Mertens R, Müller L (1940) *Die Amphibien und Reptilien Europas (Zweite Liste, nach dem Stand vom 1. Januar 1940). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main* 451: 1–56.
- Mertens R, Wermuth H (1960) *Die Amphibien und Reptilien Europas. Frankfurt a. M. : Waldemar-Kramer*, 264 S.
- Pieh A (2001 “2000”) *Testudo graeca soussensis*, eine neue Unterart der Maurischen Landschildkröte aus dem Soustal (Südwest-Marokko). *Salamandra* 36(4): 209–222. <http://www.salamandra-journal.com/index.php/home/contents/2000-vol-36/528-pieh-a/file>
- Schweiger M (2013) *The Tortoises of Morocco. Radiata (English edition)* 22(3): 19–28.
- Shaw G (1802) *General Zoology, or Systematic Natural History* (Vol. 3), Parts 1 + 2 (Amphibia). G. Kearsley, T. Davison, London, 615 pp. <https://www.biodiversitylibrary.org/item/175491>
- Strauch A (1862) *Chelonologische Studien, mit besonderer Beziehung auf die Schildkrötensammlung der Kaiserlichen Akademie der Wis-*

- senschaften zu St. Petersburg. Memoires des l'Académie Impériale des Sciences de St.-Petersbourg, Serie 7, 5(7): 1–196. [1 pl.] https://archive.org/details/bub_gb_PJhFAAAAcAAJ
- Strohl J (1923) Promenade d'un naturaliste á Figuig.-NuméroBulletin de la Société de géographie d'Alger et de l'Afrique du Nord 28: 342–356. <https://gallica.bnf.fr/ark:/12148/bpt6k106556c>
- Turtle Taxonomy Working Group, Rhodin AGJ, Iverson JB, Bour R, Fritz U, Georges A, Shaffer HB, van Dijk PP (2017) Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). In: Rhodin AGJ, Iverson JB, van Dijk PP, Saumure RA, Buhlmann KA, Pritchard PCH, Mittermeier RA (Hrsg) Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 7: 1–292. <https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017>
- Wermuth H (1956) Versuch der Deutung einiger bisher übersehener Schildkröten-Namen. Zoologische Beiträge/Neue Folge, Berlin, (Festgabe für Konrad Herter zum 65. Geburtstage dargebracht von Berliner Freunden und Schülern, herausgegeben von Werner Ulrich) 2(3): 399–423.
- Wermuth H, Mertens R (1961) Schildkröten, Krokodile, Brückenechsen. Jena, Fischer, 422 pp.
- Wermuth H, Mertens R (1977) Testudines, Crocodylia, Rhynchocephalia. Das Tierreich 100: 1–174.