



HAL
open science

The earliest known crown-Testudo tortoise from the late Miocene (Vallesian, 9 Ma) of Greece

Géraldine Garcia, Aurélie Pinton, Xavier Valentin, Dimitris S. Kostopoulos, Gildas Merceron, Louis de Bonis, George Koufos

► **To cite this version:**

Géraldine Garcia, Aurélie Pinton, Xavier Valentin, Dimitris S. Kostopoulos, Gildas Merceron, et al.. The earliest known crown-Testudo tortoise from the late Miocene (Vallesian, 9 Ma) of Greece. PLoS ONE, 2020, 15 (4), pp.e0224783. 10.1371/journal.pone.0224783 . hal-02538523

HAL Id: hal-02538523

<https://hal.science/hal-02538523v1>

Submitted on 20 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

RESEARCH ARTICLE

The earliest known crown-*Testudo* tortoise from the late Miocene (Vallesian, 9 Ma) of Greece

Géraldine Garcia^{1*}, Aurélie Pinton¹, Xavier Valentin¹, Dimitris S. Kostopoulos², Gildas Merceron¹, Louis de Bonis¹, George D. Koufos²

1 PALEVOPRIM, UMR CNRS 7262, Université de Poitiers, Poitiers, France, **2** Department of Geology, Aristotle University of Thessaloniki, Thessaloniki, Greece

* geraldine.garcia@univ-poitiers.fr



Abstract

We here report on fossil remains of the earliest known crown-*Testudo*, an extant clade of Mediterranean testudinid tortoises from the late Miocene (Vallesian, MN 10) from the hominoid locality Ravin de la Pluie (RPI) in Greece. The material studied is a small, nearly complete carapace with a clearly distinct hypo-xiphiplastral hinge. This supports the *sensu stricto* generic assignment. This new terrestrial testudinid specimen is characterized by a possible tectiform, narrow, elongated shell with a pentagonal pygal and a long, posteriorly elevated, lenticular and rounded dorsal epiplastral lip. These unique features differ from those of other known Mediterranean hinged forms and allow the erection of the new species *Testudo hellenica* sp. nov. This taxon is phylogenetically close to two Greek species, the extant *T. marginata* and the fossil *T. marmorum* (Turolian, around 7.3 Ma). This record provides evidence for the first appearance of the genus *Testudo sensu stricto* at a minimum age of 9 Ma.

OPEN ACCESS

Citation: Garcia G, Pinton A, Valentin X, Kostopoulos DS, Merceron G, de Bonis L, et al. (2020) The earliest known crown-*Testudo* tortoise from the late Miocene (Vallesian, 9 Ma) of Greece. PLoS ONE 15(4): e0224783. <https://doi.org/10.1371/journal.pone.0224783>

Editor: Márton Rabi, Eberhard Karls Universität Tübingen, GERMANY

Received: February 22, 2018

Accepted: October 21, 2019

Published: April 8, 2020

Copyright: © 2020 Garcia et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: Field excavations in Greece and this work were supported in part by funding from the RHO/NSF (Revealing Hominid Origins Initiative/National Science Foundation, PIs: L. de Bonis & G. D. Koufos) and also by the budget of our research team (UMR CNRS 7262). The funder had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Introduction

Testudo sensu stricto (s. s. i.e., *Testudo* with a hinge) is defined and restricted to the small tortoise species having a kinetic hinge in its plastron between the hypo- and xiphiplastral (Fig 1) [1, 2]. Based on molecular data [3–7], the *Testudo* s. s. group is monophyletic and restricted to the three extant tortoise species distributed geographically between the Mediterranean region, Caucasus and Iran: *Testudo graeca* [8] (Fig 1), *Testudo marginata* [9] and *Testudo kleinmanni* [10]. This Mediterranean group is supported by a total evidence analysis (morphological and molecular data) as the crown clade arising from the last common ancestor of *T. graeca*, *T. marginata* and *T. kleinmanni*, estimated between 8 to 7 Ma following Vlachos & Rabi [11]. The oldest attested fossil with a hypo-xiphiplastral hinge is *Testudo marmorum* [12, 13] from the classic Pikermi beds, a Turolian locality situated in the North Aegean region near Athens in southern Greece (MN 12) dated from 7.35 to 7.28 Ma by Böhme et al. [14].

A new species of tortoise is described here, that corresponds the earliest *Testudo* s. s. known in the fossil record. It is composed of an almost complete carapace and represents the only

Competing interests: The authors have declared that no competing interests exist.

small tortoise coming from the deposits of the Axios Valley in northern Greece. Historically, the mammal fossiliferous sites of the Axios Valley (Macedonia, Greece) have been known since the beginning of the 20th Century when the paleontologist Camille Arambourg, an officer in the French Army during the First World War at that time, discovered several localities with his soldiers “the Zouaves” and collected some vertebrates still housed today in the Muséum National d’Histoire Naturelle de Paris, France [15]. Decades later, new fieldwork campaigns were reinitiated and have been conducted since the seventies [16]. Numerous outcrops have been revealed in a small perimeter along the Axios Valley from the Vallesian Nea Messimbria Formation to the Turolian Vathylakkos and Dytiko Formations [17]. Among them, Pentelophos (PNT), Xirochori (XIR), and Ravin de la Pluie (RPI) are the three main localities of Vallesian age with the richest faunal assemblages of large mammals (MN 10 9.7 to 8.7 Ma, [18]) (Fig 2). The latter site corresponds to the type locality of the hominid *Ouranopithecus macedoniensis* (see example [19–23]).

While both mammalian diversity and abundance are exceptional in the Vallesian sites, with at least 24 mammal species in RPI [24], reptile remains (lizards and snakes) are scarce. Few terrestrial testudinid specimens were discovered during the numerous field missions of these last decades. Although they are known since the nineteenth century and abundant in Miocene Greek sediments, data on the Testudinidae were limited in the literature, often based on poorly preserved or not formally identified specimens [25] until recently with new published data [26, 27]. There are a few known examples of tortoise remains from the middle Miocene of Chios Island (Keramaria Formation, [28]) but they have not been illustrated or affiliated to the

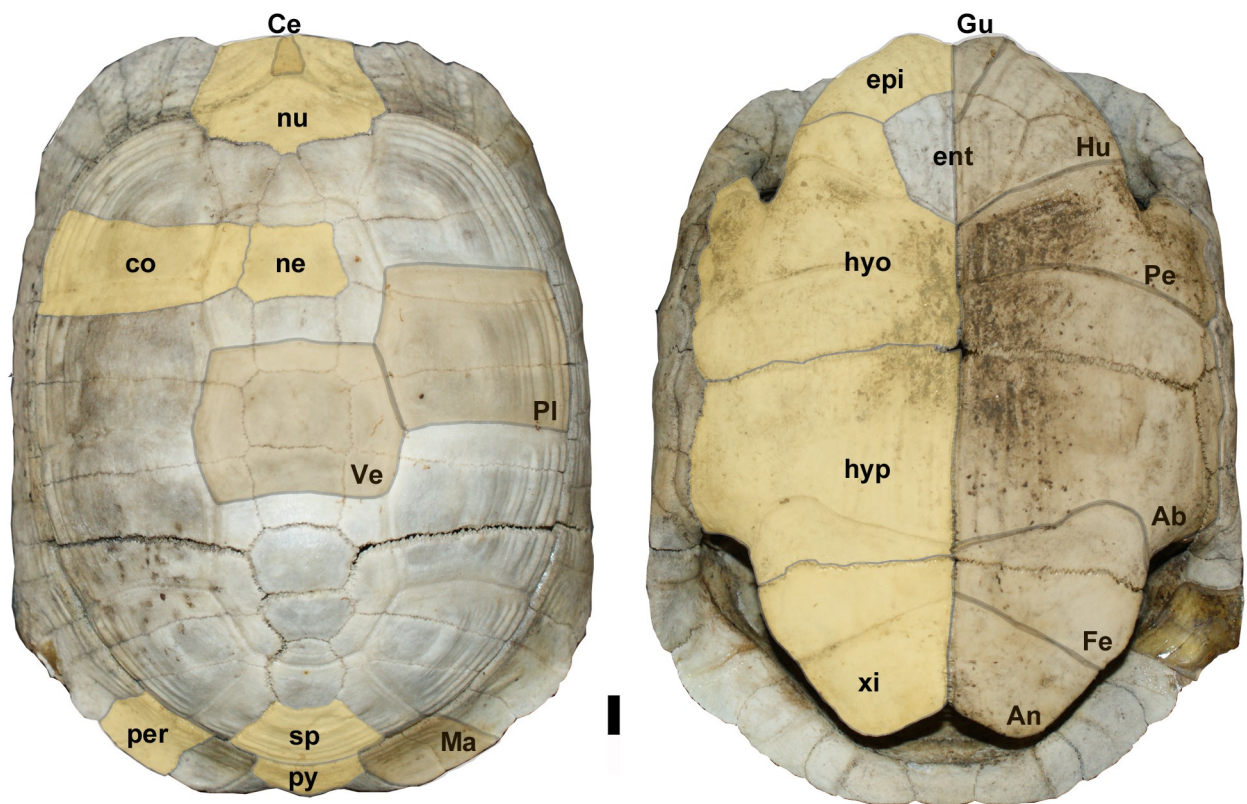


Fig 1. Extant *Testudo graeca* (UP-2015-05) from Greece. nu: nuchal; ne: neural; co: costal; sp: suprapygial; py: pygal; per: peripherals; epi: epiplastron; ent: entoplastron; hypo: hyoplastron; hyp: hypoplastron; xi: xiphiplastron. Scutes: Ce: cervical; Pl: pleural; Ma: marginal; Ve: vertebral; Gu: gular; Hu: humeral; Pe: pectoral; Ab: abdominal; Fe: femoral; An: anal.

<https://doi.org/10.1371/journal.pone.0224783.g001>



Fig 2. The late Miocene site of Ravin de la Pluie, RPI (Thessaloniki Macedonia, northern Greece). View of the dig (A) and its location of the stratigraphy modified after [19] (B) and in the Axios Valley (C), near the two other richest Vallesian vertebrate localities. XIR: Xirochori and PNT: Pentalophos. Source of the satellite image: NASA Earth Observatory.

<https://doi.org/10.1371/journal.pone.0224783.g002>

modern *Testudo* [29]. All other Neogene testudinid fossils from Greece are more recent, from the Turolian (MN 11, around 8 Ma) to the Villafranchian (MN 16, 3 Ma) [30, 31].

Material and methods

The carapace (RPI-216) was collected in the 1980s in the Ravin de la Pluie (RPI), located in the Nea Messimvria Formation (Fig 2). This corresponds to a succession of sands, gravels, conglomerates and reddish clays, reflecting fluvial paleoenvironments [17]. The carapace with plastron is well preserved with relatively low deformations (Figs 3 and 4). In order to observe the detail of the anatomical elements, the specimen was completely prepared. It was found in association with numerous vertebrate fossil remains, including diversified large mammal taxa dominated by herbivorous taxa such as bovids (*Samotragus praecursor*, *Prostrepsiceros vallesiensis*, *Mesembriacerus melentisi* and *Palaeoryx* sp.), giraffids (*Palaeogiraffa macedoniae*, *Palaeotragus* cf. *coelophrys* and *P.* cf. *rouenii* and *Bohlinia* cf. *attica*), equids (*Hipparion primi-genium*, *H. macedonicum* and *H.* aff. *depereti*) and rhinocerotids (Rhinocerotidae indet.).

In order to strengthen the systematic attribution of the fossil and discuss its affinities, a phylogenetic analysis was performed based on a published morphological matrix (Table 1), which includes 20 taxa and 37 characters [32] that helped to resolve the relationships between the various *Testudo* s. l. based on morphological characters. The definition and the coding of some characters were modified (S1 Table). The phylogenetic analyses were performed with PAUP

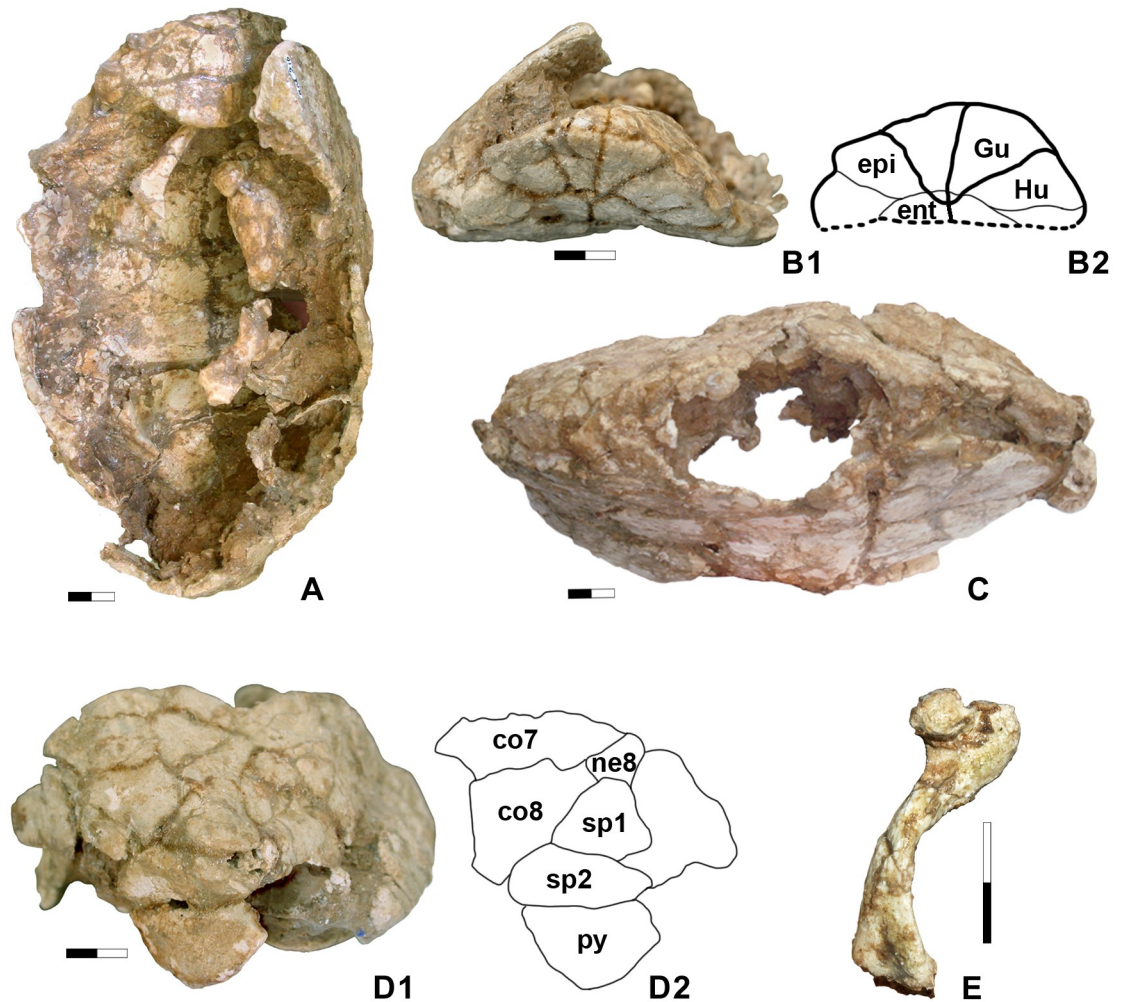


Fig 3. *Testudo hellenica* sp. nov. from Ravin de la Pluie (Greece, late Miocene). Holotype, LGPUT RPI 16. A. Carapace in dorso-lateral view. Note the very obtuse scapula and the deep nuchal notch. B1. Anterior plastral lobe. B2. Interpretative drawing. C. Right lateral view of the carapace. D1. Posterior shell border with suprapygal-pygial configuration. D2. Interpretative drawing. E. Left humerus in lateral view. Scale: 2 cm.

<https://doi.org/10.1371/journal.pone.0224783.g003>

(Phylogenetic Analysis Using Parsimony) version 4.0b10 [33] using the branch and bound algorithm. Following Lujan et al. [34] all characters are treated as unordered and unweighted, branches were set to collapse if minimum length equals zero. However, to ensure the robustness of our topology we performed a run in which multistate characters were ordered. Tree topologies resulting from ordered *versus* unordered analysis (data not shown) are identical. Clade robusticity was assessed by means of bootstrap analysis (10000 replicates) and Bremer support indices, which have been calculated by hand running consecutive analysis and holding trees with one step more each time.

The specimen is stored in the collections of the Geology and Palaeontology laboratory of the Aristotle University of Thessaloniki (LGPUT), accession number RPI-216.

Nomenclatural acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are

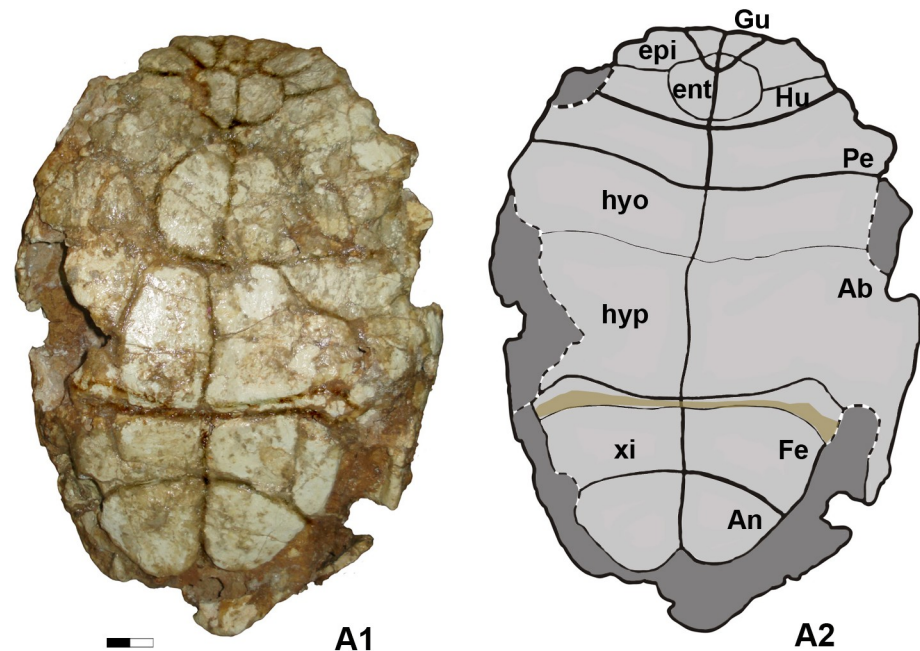


Fig 4. A1. Plastron in ventral view. A2. Interpretative drawing.

<https://doi.org/10.1371/journal.pone.0224783.g004>

available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBankLSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "<http://zoobank.org/>". The LSID for this publication is: urn:lsid:zoobank.org:pub:B6A6B0A2-57F9-4EB6-9C09-CB50DAB1BDB3. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS.

Systematic paleontology

Cryptodira Cope, 1868

Testudinidae Batsch, 1788

Testudo Linnaeus, 1758

Testudo hellenica sp. nov. (Figs 3 and 4)

Testudo hellenica Garcia et al. sp. nov. urn:lsid:zoobank.org:act:3036B41A-88AE-4BE5-ADEE-C7F4C11AC0A1

The name of this new species was already mentioned at the congress communication [34], but it must be considered as a *nomen nudum* because the species was not described according to the rules of the ICZN code.

Holotype. LGPUT RPI-216, a nearly complete carapace with plastron.

Etymology. Named after the Greek word “ελληνικη” (hellenic, adj. of Hellas = Greece) meaning “from Greece”

Type locality. Ravin de la Pluie, lower Axios Valley, Macedonia, Greece; late Miocene (Vallesian Mammal Age, Zone MN 10, correlated with chron C4AR.1N, 9.069–9.149 Ma based on the combination of the evolutionary grade of the mammalian fauna and paleomagnetostratigraphy [35].

Table 1. Data matrix of the cladistic analysis, modified after Lujan et al [32]. Missing data are represented by a question mark. “A” equals (0,1).

| Taxon character | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | |
|-------------------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|
| <i>Malacochersus tornieri</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| <i>Indotestudo elongata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | |
| <i>Testudo Testudo hellenica</i> | 1 | 1 | ? | 1 | ? | 0 | ? | 0 | ? | ? | 1 | 0 | 0 | 1 | 2 | 0 | 0 | ? | 0 | ? | 0 | 0 | ? | 2 | 3 | 0 | ? | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | ? | |
| <i>T. (Testudo) graeca</i> | 1 | 1 | 0 | 1 | A | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | |
| <i>T. (Testudo) marginata</i> | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 2 | A | 1 | |
| <i>T. (Testudo) marmorum</i> | 1 | 1 | ? | 1 | 0 | 0 | ? | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | |
| <i>T. (Testudo) kleinmanni</i> | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | A | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | |
| <i>T. (Testudo) kemitrensis</i> | 1 | 1 | ? | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 1 | ? | 1 | 1 | 0 | 0 | 2 | 1 | 0 | |
| <i>T. (Testudo) oughlamensis</i> | 1 | 1 | ? | 1 | 0 | 0 | ? | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 0 | 0 | 1 | A | 0 | 0 | 2 | 1 | 0 | |
| <i>T. (Testudo) brevitesta</i> | 1 | ? | ? | ? | ? | 0 | ? | 1 | ? | 0 | ? | ? | ? | 1 | 3 | 0 | ? | ? | 1 | ? | ? | ? | 0 | 0 | 3 | 0 | 1 | 1 | ? | ? | 1 | 1 | 0 | 0 | ? | ? | ? | |
| <i>T. (Agrionemys) horsfieldii</i> | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 0 | |
| <i>T. (Agrionemys) bessarabica</i> | 1 | ? | ? | 0 | 0 | ? | ? | 0 | 0 | ? | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | ? | 0 | ? | 0 | 1 | ? | 1 | 0 | 0 | 0 | |
| <i>T. (Chersine) canetoniana</i> | 1 | 1 | 1 | 0 | 0 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>T. (Chersine) hermanni</i> | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | A | 1 | 2 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | |
| <i>T. (Chersine) steinheimensis</i> | 1 | 1 | ? | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | A | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | A | A | 0 | 0 | 0 | 0 | |
| <i>T. (Chersine) catalaunica</i> | 1 | 1 | 1 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | A | 1 | A | A | 0 | 0 | 0 | 0 | |
| <i>T. (Chersine) antiqua</i> | 1 | 1 | ? | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | A | 0 | 2 | 0 | 1 | 0 | 1 | A | 1 | A | 0 | 0 | 0 | 0 | 0 | |
| <i>T. (Chersine) burgenlandica</i> | 1 | 1 | 1 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>T. (Chersine) pyrenaica</i> | 1 | 1 | 1 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | ? | 2 | 0 | 1 | A | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>T. (Chersine) lunellensis</i> | 1 | 1 | 1 | 0 | 1 | 0 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | A | 1 | 1 | 0 | 0 | 1 | 3 | A | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | | |

<https://doi.org/10.1371/journal.pone.0224783.t001>

Diagnosis. Species of *Testudo* s. s. by the hypo-xiphiplastral hinge, characterized by the autapomorphic features of an elongated and quite posteriorly pointed shell shape, with a pentagonal pygal protruding downwards relative to the posterior peripheral border and having a short suture with a peripheral 11, and a lenticular, posteriorly long dorsal epiplastral lip, rounded from side to side and anteriorly to posteriorly convex. Autapomorphies: posterior lobe comprised only by the xiphiplastra with very rounded lateral borders lacking femoro-anal inflexion and with anals slightly medially longer than femorals but without an angular junction of the right and left femoro-anal sulci.

Description. The specimen corresponds to a small, nearly complete carapace, (dimensions: 133 x 228 mm: width/length = 58.33%) with an elongated shape, though it narrows, becoming at least anteriorly angular, nearly tectiform (Fig 3A and 3B1). It lacks the left and dorsal part of the shell. The right peripherals and marginals are hard to distinguish, due to the state of preservation of the dorsal shell. The anterior peripheral shell border is elongated on each side of the middle, particularly protruding at the junction of peripherals 1 and 2, which are visible on the right side. This suggests a somewhat pronounced nuchal notch, with its right part preserved. At the posterior of the shell (Fig 3D1), which is elongated and posteriorly pointed, the suprapygals (sp) compose two transversally separated trapezoids in front of the pygal. They are distinct in their proportions with sp2 more elongated transversely than sp1. The pygal is pentagonal, strongly protruding downwards in relation to the adjacent peripheral border: peripherals 11 are not preserved between the pygal and peripherals 10. However, we can observe in posterior view that the lateral suture between the pygal and the peripheral 11 is short (Fig 3C and 3D1), thus suggesting that the peripheral 11 was reduced. The pygal has no medial sulcus, indicating the presence of a supracaudal formed by the fusion of both marginals 12. The domed pygal plate, curving inwards, indicates a male individual [36]. The posterior peripherals, shifted slightly externally in relation to the pleurals, are barely visible from a dorsal view, dorsally convex, and are neither elevated nor elongated.

Some bones are preserved inside the carapace, such as the left humerus (Fig 3E) and a scapula. The scapula is wide, presenting an obtuse angle as in all the terrestrial testudinids (Fig 3A). The humerus (Fig 3E) is robust and shows the great trochanter moderately close to the minor one, as in *Testudo* species, delimiting a triangular intertrochanteric fossa. The plastral buttresses, erected in columns inside the shell, are somewhat distinguishable and conform to terrestrial testudinids (Fig 3A).

Ventrally, the plastron (Fig 4A1) shows a longitudinal medial concavity, indicating a male specimen. The rounded anterior lobe (58.8 mm long) is semicircular with a slightly straight anterior gular border that is upwardly tilted, and the posterior lobe is slightly longer (61.6 mm) with well-rounded lateral borders and a short anal posterior notch with straight borders. The bridge between these two lobes is relatively long (102.7 mm). The dorsal epiplastral lip is very pronounced, transversally lenticular and medially long, anteroposteriorly convex, rounded from side to side with a flat intermediate part (Fig 3A). It projects dorsally beyond the anterior part of a small entoplastron marked by a slight and small depression: the gular pocket. Due to the strong epiplastral lip, the epiplastra are anteriorly raised in a ledge above the dorsal surface of the anterior lobe (Fig 3B1). Ventrally, the gulars are triangular and their ventral surfaces appear as flat as that of the humerals. The humero-pectoral sulcus (HP) runs lateroposteriorly behind the entoplastron (Fig 4A1), with no contact, in a wide curve. The axillary and inguinal scutes are both large, possibly trapezoidal in shape and the posterior lobe does not completely fill the caudal shell opening. While anterior to the hypo-xiphiplastral suture, the abdomino-femoral sulcus is very close to it, widely and particularly medially, the suture being transformed into a hinge (Fig 4A1) and the posterior lobe is formed exclusively by the xiphiplastra.

Discussion

Testudo hellenica sp. nov. is a new small tortoise from the Vallesian (late Miocene) of Greece. It represents the earliest well-dated record of the genus *Testudo sensu lato* (s. l.) with robust phylogenetic relationships. The shell of this species has the typical features of the genus, such as the plate and scute proportions and configurations (costal/peripheral sutures coinciding with pleural/marginal sulci, contact between marginal/pleural sulci, suprapygial/pygal configuration with trapezoid sp1 and sp2), the trigonous gulars and the dorsal epiplastral lip which is curved onto the entoplastron. The phylogenetic relationships within this genus have been subject of continuous discussions [2, 4, 30, 37, 38, 39 and 40]. According to the latest multi-locus molecular phylogeny [7], this clade includes the extant *T. (Agrionemys) horsfieldi*, *T. (Chersine) hermanni*, the extant hinged species including *T. graeca* and *T. marginata* and *T. kleinmanni* distributed in the Mediterranean basin and Central Asia.

By its autapomorphic features, *T. hellenica* differs from other species of the *Testudo* s. s. group such as *T. graeca*, *T. marginata*, *T. brevitesta* (Villafranchian, Greece; [30]), *T. kleinmanni*, *T. kenitrensis* (Pliocene, Morocco; [41]) and *T. oughlamensis* (upper Pliocene, Morocco; [42]) and in particular from *T. marmorum* (Turolian, Greece) (Figs 5 and 6, [15]). These characters include an angular dorsal shell, not as wide and rounded as that of other species of *Testudo* s. s. and shorter than that of *T. marginata* or *T. marmorum*; the anteroposteriorly elongated and tilted peripherals on the anterior shell border with a possibly pronounced notch at the nuchal border; a long, lenticular, posteriorly elevated and rounded dorsal epiplastral lip that overhangs the dorsal anterior lobe surface; and a protruding pentagonal pygal. *Testudo hellenica* also differs by the configuration of its posterior plastral lobe with curved rather than rectilinear xiphiplastral borders, lacking parallel borders along the femoral part, as is the case in *T. marmorum*, and with curved borders at the femoro-anal sulcus (usually straight and oblique in *Testudo* spp.). The rounded shape of the xiphiplastra is the same as in the short and small Moroccan *T. kenitrensis* and *T. oughlamensis* but *T. hellenica* does not have their angular, less obtuse femoro-anal sulcus. Some characters, such as the shape and the size of the nuchal, the number of neurals and the width of the vertebrae cannot be assessed, due to the state of preservation of the shell. The separation of the xiphiplastra from the hypoplastra indicates the presence of the hinge, allowing movements of the posterior lobe of the plastron. This character, present in both males and females in contrast to *Testudo (Chersine) hermanni*, is a synapomorphy of the *Testudo* s. s. group ([2], this study). *Testudo hellenica* shares with *T. marginata* and *T. marmorum* the elongated shell (ratio of median height and full length in Fig 3A and Fig 3C). The shell dimensions measured for these species are similar to those of all other analysed specimens (Table 2), except for the holotype *T. marmorum* (MNHN F 1862-67(42) PIK 3683, Fig 5A1–5A3). This latter is narrower and has a concave plastron, and is different to the other specimen of *T. marmorum* (MNHN F 1862-67(43), Fig 5B1 and 5B2). They correspond respectively to a male and a female, thus conforming with the sexual dimorphism of *T. marginata*.

In the cladogram (Fig 7), *T. hellenica* is included within the hinged *Testudo* (*T. s. s.*), and this is supported by the angle of the pectoro-abdominal sulcus (11: 1). Moreover, *T. hellenica* appears as the sister taxon of the clade formed by the extant *T. marginata* and the fossil *T. marmorum* and *T. brevitesta* (Fig 7). This group is defined by two characters: a markedly elongated shell contour (15: 2), and a femoro-anal sulcus laterally forming an S-shaped curve, which is very obliquely oriented compared to the axial plane (35: 2). We also note the shared position of the anteriorly reduced part of the femorals with a forwardly protruding V-shape, while the hypo-xiphiplastral hinge slightly juts out beyond the bottom of the inguinal notches. Finally, *T. hellenica* displays the transversally widest hinge and abdomino-femoral sulcus,

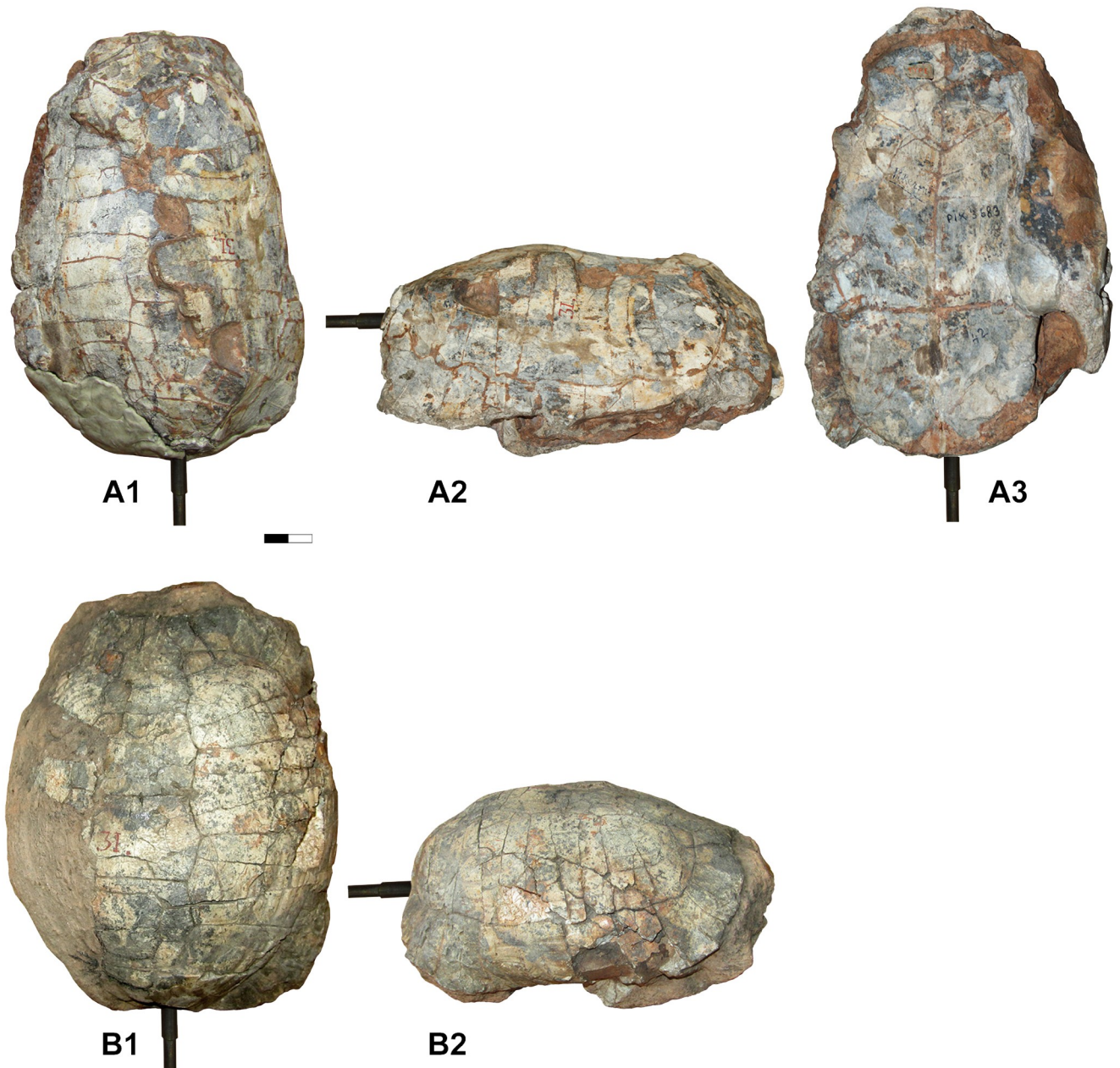


Fig 5. *Testudo marmorum* from Pikermi (Greece, late Miocene) described by Gaudry in 1862, 1862–1867. Holotype MNHN F 1862-67(42) PIK 3683, Carapace in dorsal (A1), lateral (A2) and ventral views. Specimen MNHN F 1862-67(43), Carapace in dorsal (B1) and lateral (B2) views. No plastron is preserved in this specimen.

<https://doi.org/10.1371/journal.pone.0224783.g005>

except on the lateral parts, a condition particularly close to that of *T. marginata*. The position of *T. hellenica* based on this phylogeny analysis is consistent with the late Miocene origin for crown *Testudo*, already suggested by a total evidence analysis of Pan-Testudinidae [11].

Conclusions

Before this study, the earliest occurrence of a hinged testudinid was *T. marmorum*, from the Turolian of Pikermi in Greece (MN 12, around 7.3 Ma [14]). Consequently, *T. hellenica*

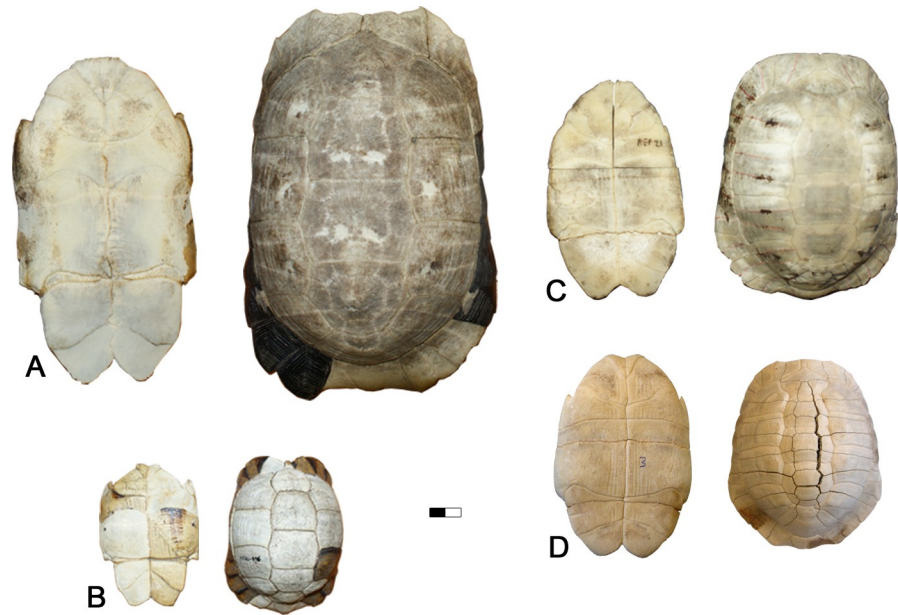


Fig 6. Modern *Testudo*. Carapace in ventral and dorsal views. A. *T. marginata*, 1877–675 MNHN. B. *T. kleinmanni*, 1876–416 MNHN. C. *T. graeca*, REP 21. D. *T. hermanni*, REP 7.

<https://doi.org/10.1371/journal.pone.0224783.g006>

Table 2. Measurements of specimens analyzed and included in the comparative study. Fossil taxa are displayed on a grey background.

| Specimen and catalog number | Localization | Dorsal shell | | | | Plastron | | | | |
|---|------------------------|--------------|-------|------------------------|-------------|--------------|---------------|--------|----------------|------------|
| | | length | width | n3/n4-sp1/sp2 distance | V3 size l/L | Total length | anterior lobe | bridge | posterior lobe | anal notch |
| <i>Testudo marmorum</i> F 1862-67(42) (Type) MNHN | Greece (Upper Miocene) | 18.4 | 11.5 | 8.2 | 4/2.9 | 17.3 | 4 | 7.7 | 5.8 | 1 |
| <i>Testudo marmorum</i> F 1862-67(43) MNHN | Greece (Upper Miocene) | 15.8 | 13 | 8.5 | 4/3.0 | — | — | — | — | — |
| <i>Testudo hellenica</i> RPI-216 Univ. Thessaloniki | Greece (Upper Miocene) | 22.8 | 13.3 | — | — | 21.4 | 5.7 | 9.8 | 5.9 | 1.2 |
| <i>Testudo graeca antakyensis</i> REP 50 MNHN | Syria | 14.9 | 11.6 | 7.5 | 4.5/3 | 14.1 | 3.7 | 7.4 | 3 | less 1 |
| <i>Testudo graeca ibera</i> REP 66 MNHN | Syria | 18.6 | 15 | 8.6 | 6/3.8 | incomplete | 4.3 | 7.5 | — | — |
| <i>Testudo graeca ibera</i> REP 73 MNHN | indeterminate | 21 | 18.8 | 8.8 | 6.5/4 | 17.5 | 4 | 8.5 | 5 | 0.8 |
| <i>Testudo graeca graeca</i> REP 21 MNHN | north of Africa | 15.2 | 11.7 | 6.7 | 4.5/2.9 | 12.9 | 3.2 | 6.4 | 3.3 | 0.9 |
| <i>Testudo hermanni</i> REP 7 MNHN | France | 13.4 | 10.9 | 6.5 | 3.3/2.5 | 12.7 | 2.8 | 6.5 | 3.4 | — |
| <i>Testudo kleinmanni</i> 1876–416 MNHN | Egypte | 11.1 | 7.4 | 4.8 | 2.9/2.2 | 9 | 1.7 | 4.6 | 2.5 | 0.5 |
| <i>Testudo marginata</i> 1877–675 MNHN | indeterminate | 21.8 | 12.5 | 10.2 | 5.7/3.8 | 17.5 | 3.7 | 9.8 | 4.7 | 1.4 |
| <i>Testudo marginata</i> 1887–831 MNHN | indeterminate | 22.6 | 13.4 | 9.4 | 5.3/3.7 | 18 | 3.9 | 9.6 | 4.8 | 1.2 |
| <i>Testudo marginata</i> 1878–199 MNHN | indeterminate | 26.9 | 15.5 | 12.2 | 6.8/4.5 | 22.3 | 5.1 | 10.7 | 5.9 | 2.2 |

<https://doi.org/10.1371/journal.pone.0224783.t002>

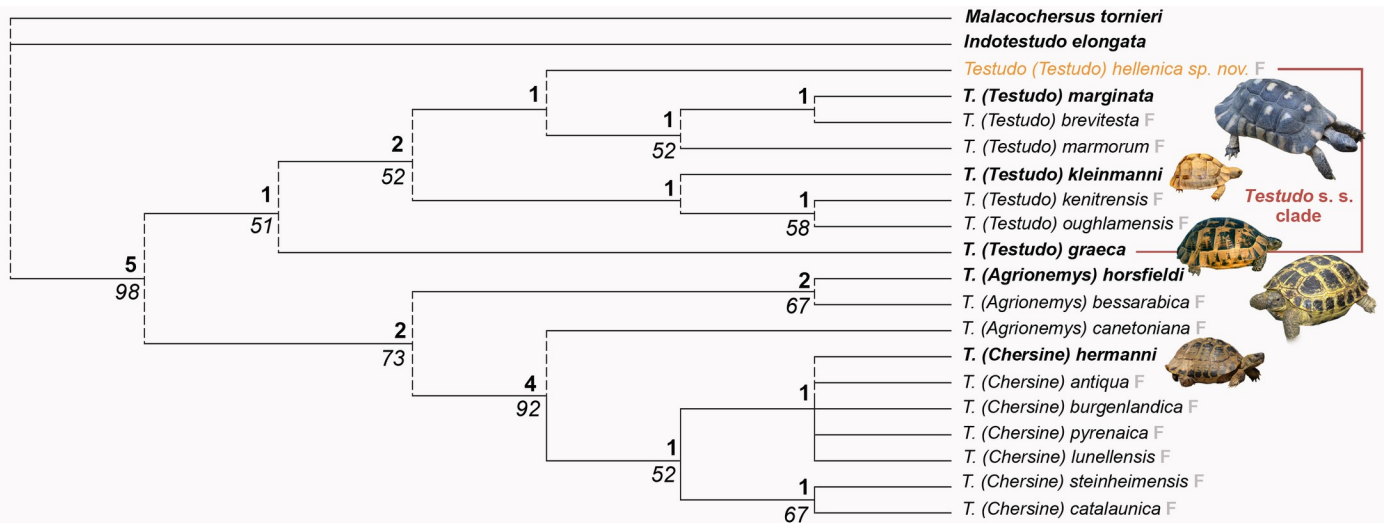


Fig 7. Results of the cladistic analysis corresponding to a strict consensus of 3 equally parsimonious trees of 72 steps (consistency index = 0.61 and retention index = 0.76). The topology of the strict consensus tree obtained is close to the single most parsimonious tree described by Lujan et al. [32] and to the molecular phylogeny tree obtained for the extant taxa [37]. Bremer indices are noted above clades and numbers represents bootstraps values. Extant species are in bold and the fossil species are indicated by an F.

<https://doi.org/10.1371/journal.pone.0224783.g007>

corresponds to the earliest known representative of the *Testudo s. s.* (= hinged *Testudo*) lineage. Its occurrence 9 million years ago in Greece is not unexpected when considering the consistent climatic conditions that prevailed in this region during the late Miocene. The pollen assemblages [43] together with the enamel oxygen stable isotopic analysis [44–48] indicate climatic conditions that were not significantly different from those that are observed today in the southern Balkans, especially in the Axios River Valley. These conditions are characterized by a high seasonal amplitude in terms of temperatures and rainfalls. Both of these parameters play a primary role in shaping the distribution of *T. graeca* [49, 50], particularly at the subspecies level for which some taxa such as *T. g. marokensis* and *T. g. cyrenaica* [51] are considered to be dependent on humid environments.

Due to the absence of either well documented or preserved Mediterranean tortoise fossils from the Miocene, the record from RPI in Greece is also significant in providing an additional data for phylogenetic and molecular studies, in particular for understanding the radiation of the evolutionary history of the *Testudo* lineage, a topic which is still debated [40, 52]. Based on the molecular data [7, 39, 40], the estimated divergence of a crown-*Testudo* with a kinetic plastral hinge originated between the late Oligocene and the late Miocene. A more recent total evidence phylogenetic analysis provided an age estimation of around 8 Ma [11] whereas the Vallesian age of *Testudo hellenica* sp. nov. pushes this divergence back to least 9 Ma and provides important evolutionary information of the carapace of *Testudo s. s.* complex. Finally, our phylogenetic analysis suggests that *T. marmorum* is closer to *T. marginata* (peripheral plates 8–11 posteriorly directed and widened, nuchal plate as long as it is wide) than to *T. kleinmanni*, which is more consistent with the fossil record as it notably reduces the ghost lineage for *T. marginata*.

Supporting information

S1 Table. Character description of the states employed in the cladistic analysis [30, 32, 38, 53–56].

(DOCX)

Acknowledgments

We thank all students and colleagues who have contributed to the field excavations for the last decades. We are grateful to J. Nour-Eddine, R. Allain and S. Bailon (MNHN Paris) for access to comparative reptile material. We are especially indebted to F. de Lapparent, O. Otero and S. Ducrocq for scientific discussions and also to S. Riffaut (Univ. Poitiers) for technical support. We would like to thank the managing editor Iratxe Puebla, and the reviewers, Márton Rabi, Pedro Romano and Evangelos Vlachos, for their helpful comments on earlier versions of this article.

Author Contributions

Conceptualization: Géraldine Garcia.

Data curation: Géraldine Garcia.

Formal analysis: Géraldine Garcia.

Funding acquisition: Géraldine Garcia, Louis de Bonis, George D. Koufos.

Investigation: Géraldine Garcia, Xavier Valentin, Dimitris S. Kostopoulos, Gildas Merceron.

Methodology: Géraldine Garcia, Aurélie Pinton.

Project administration: Louis de Bonis, George D. Koufos.

Resources: Géraldine Garcia, Xavier Valentin, Dimitris S. Kostopoulos, Gildas Merceron.

Software: Aurélie Pinton.

Supervision: Louis de Bonis, George D. Koufos.

Validation: Géraldine Garcia, Aurélie Pinton, Xavier Valentin, Dimitris S. Kostopoulos, Gildas Merceron, Louis de Bonis, George D. Koufos.

Visualization: Géraldine Garcia.

Writing – original draft: Géraldine Garcia.

Writing – review & editing: Géraldine Garcia.

References

1. Lapparent de Broin F de (2001) The European turtle fauna from the Triassic to the Present. *Dumerilia* 4: 155–216.
2. Lapparent de Broin F de, Bour R, Perälä JF (2006a) Morphological definition of *Eurotestudo* (Testudinae, Chelonii): First part. *Annales de Paléontologie* 92 (3): 255–304.
3. Kuyil AC van der, Ballasina DLP, Dekker JT, Maas J, Willemsen RE, Goudsmit J (2002) Phylogenetic relationships among the species of the genus *Testudo* (Testudines: Testudinidae) inferred from mitochondrial 12S rRNA gene sequences. *Molecular Phylogenetics and Evolution* 22: 174–183. <https://doi.org/10.1006/mpev.2001.1052> PMID: 11820839
4. Parham JF, Türkozan O, Stuart BL, Arakelyan M, Shafei S, Macey JR, et al (2006a) Genetic evidence for premature taxonomic inflation in Middle Eastern tortoises. *Proceedings of California Academy of Sciences* 57: 955–964.
5. Fritz U, Harris JD, Fahd S, Rouag R, Gracia Martinez E, Gimenez Casalduero A, et al (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.
6. Guillon JM, Guéry L, Hulin V, Girondot M (2012) A large phylogeny of turtles (Testudines) using molecular data. *Contributions to Zoology* 81 (3): 147–158.
7. Pereira AG, Sterli J, Moreira FRR, Schrago CG (2017) Multilocus phylogeny and statistical biogeography clarify the evolutionary history of major lineages of turtles. *Molecular Phylogenetics and Evolution* 113: 59–66. <https://doi.org/10.1016/j.ympev.2017.05.008> PMID: 28501611

8. Linnaeus C (1758) *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Laurenti Salvii, Holmiae 1: 1–823.
9. Schoepff JD (1792) *Historia Testudinum iconibus Illustrata*. Palmii, Erlangen.
10. Lortet L (1883) *Etudes zoologiques sur la faune de Lac de Tiberiade*. Archives du Muséum d'histoire naturelle de Lyon, 3: 99–189.
11. Vlachos E, Rabi M (2018) Total evidence analysis and body size evolution of extant and extinct tortoises (Testudines: Cryptodira: Pan-Testudinidae). *Cladistics* 34:652–683.
12. Gaudry A (1862) Note sur les débris d'Oiseaux et de Reptiles trouvés à Pikermi, Grèce, suivie de quelques remarques de paléontologie générale. *Bulletin de la Société Géologique de France* 19: 629–640.
13. Gaudry A (1862–1867) *Animaux fossiles et géologie de l'Attique*. Savy, Paris.
14. Böhme M, Spassov N, ebner M, Geraads D, Hristova L, Kirscher U, et al (2017) Messinian age and savannah environment of the possible hominin "*Graecopithecus*" from Europe. *Plos one*: <https://doi.org/10.1371/journal.pone.0177347>.
15. Arambourg C and Piveteau J (1929) Les vertébrés du Pontien de Salonique. *Annales de Paléontologie* XVIII: 8–18.
16. Bonis L de, Bouvrain G, Keraudren B, Melentis J (1973) Premiers résultats des fouilles récentes en Grèce septentrionale (Macédoine). *Comptes Rendus de l'Académie des Sciences de Paris* 277: 1431–1434.
17. Bonis L de, Bouvrain G., Koufos GD (1988) Late Miocene mammal localities of the lower Axios valley (Macedonia, Greece) and their stratigraphic significance. *Modern Geology* 13: 141–147.
18. Steininger FF (1999) Chronostratigraphy, Geochronology and Biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene 'Mammal Zones' (MN-Zones). In Rössner GE and Heissig K. (eds), *Land mammal of Europe*. Verlag Dr F. Pfeil, München, pp. 9–24.
19. Bonis L de, Bouvrain G, Geraads D, Melentis J (1974) Première découverte d'un primate hominoïde dans le Miocène supérieur de Macédoine (Grèce). *Comptes Rendus de l'Académie des Sciences de Paris* 278: 3063–3066.
20. Bonis L de, Bouvrain G, Geraads D, Koufos GD (1990) New hominid skull material from the late Miocene of Macedonia in Northern Greece. *Nature* 345: 712–714. <https://doi.org/10.1038/345712a0> PMID: 2193230
21. Koufos GD, Bonis L de (2004) The deciduous lower dentition of *Ouranopithecus macedoniensis* (Primates, Hominoidea) from the late Miocene deposits of Macedonia, Greece. *Journal of human evolution* 46 (6): 699–718. <https://doi.org/10.1016/j.jhevol.2004.03.007> PMID: 15183671
22. Koufos GD, Bonis L de (2006) New material of *Ouranopithecus macedoniensis* from late Miocene of Macedonia (Greece) and study of its dental attrition. *Géobios* 39 (2): 223–243.
23. Koufos GD, Bonis L de, Kugiumtzis D (2016) New Material of the Hominoid *Ouranopithecus macedoniensis* from the Late Miocene of the Axios Valley (Macedonia, Greece) with Some Remarks on Its Sexual Dimorphism. *Folia Primatologica*, 87(2): 94–122.
24. Bonis L de, Koufos GD (1999) The Miocene large mammal succession in Greece. In: Agustí J, Rook L, Andrews P (eds) *Hominoid Evolution and climatic change in Europe, vol. I, The evolution of the Neogene terrestrial ecosystems in Europe*. Cambridge Univ. Press, London, pp. 205–237.
25. Georgalis GL, Kear BP (2013). The fossil turtles of Greece: an overview of taxonomy and distribution. *Géobios* 46: 299–311.
26. Vlachos E, Tsoukala E, Corsini J (2014) *Cheirogaster bacharidisi*, sp. nov., a new species of a giant tortoise from the Pliocene of Thessaloniki (Macedonia, Greece). *Journal of Vertebrate Paleontology* 34(3): 560–575.
27. Vlachos E, Kotsakis T, Delfino M (2015) The chelonians from the Latest Miocene-Earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia, Greece). *Comptes Rendus Palevol* 14: 187–205.
28. Paraskevaidis I (1955) Zwei schildkrotenreste aus dem obermiozan von Chios. *Annales Géologiques des pays Helléniques* 6: 133–141.
29. Chesi F, Delfino M, Rook L (2009) Late Miocene *Mauremys* (Testudines, Geoemydidae) from Tuscany (Italy): Evidence of terrapin persistence after a mammal turnover. *Journal of Paleontology* 83: 379–388.
30. Vlachos E, Tsoukala E (2016) The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo Linnaeus*, 1758 (Testudines: Testudinidae). *Papers in Palaeontology* 2 1: 71–86.

31. Garcia G, Kostopoulos DS, Koufos GD, Valentin X (2016) Testudines. In Koufos G.D. and Kostopoulos D.S. (eds) Palaeontology of the Upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). *Géobios* 49 (1–2): 23–27.
32. Lujan AH, Delfino M, Robles JM, Alba DM (2016). The Miocene tortoise *Testudo catalaunica* Bataller, 1926 and a revised phylogeny of extinct species of genus *Testudo* (Testudines: Testudinidae). *Zoological Journal of the Linnean Society* <https://doi.org/10.1111/zoj.12414>
33. Swofford DL (2002) PAUP: phylogenetic analysis using parsimony (and other methods) 4.0. Sunderland: Sinauer Associates.
34. Garcia G., Lapparent de Broin de F, Pinton A, Valentin X, Kostopoulos DS, Merceron G, et al (2017) The earliest modern Testudinidae: *Testudo hellenica* a new *Testudo* sensu stricto from the Late Miocene (Vallesian) of Greece. 15th RCMNS Congress Exploring a “physical laboratory”: the Mediterranean Basin.
35. Koufos GD (2013) Neogene mammal biostratigraphy and chronology of Greece. In Wang X., Flynn L.J. and Fortelius M. (eds), Fossil mammals of Asia, Neogene biostratigraphy and chronology. Columbia University Press, New York, pp. 595–621.
36. Bour R (1983) Les tortues terrestres du Paléarctique. In Beaufort F. de (ed.), *Espèces menacées et exploitées dans le monde. Guide pratique pour leur connaissance et leur identification*. Secrétariat de la Faune et de la Flore, Paris, pp. 1–11.
37. Fritz U, Bininda-Emonds ORP (2007) When genes meet nomenclature. Tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*. *Zoology* 110: 298–307.
38. Corsini JA, Böhme M, Joyce WG (2014) Reappraisal of *Testudo antiqua* (Testudines, Testudinidae) from the Miocene of Hohenhüwen, Germany. *Journal of Paleontology* 88(5): 948–966.
39. Lourenço JM, Claude J, Galtier N, Chiari Y (2012) Dating cryptodiran nodes: origin and diversification of the turtle family Testudinoidea. *Systematic Biology* 62: 496–507.
40. Parham JF, Macey JR, Papenfuss TJ, Feldman CR, Türkozan O, Polymeni R, Boore J (2006b) The phylogeny of Mediterranean tortoises and their close relatives based on complete mitochondrial genome sequences from Museum specimens. *Molecular Phylogenetics and Evolution* 38: 50–64. <https://doi.org/10.1016/j.ympev.2005.07.015> PMID: 16150614
41. Gmira S (1993) Une nouvelle espèce de tortue Testudinine (*Testudo kenitrensis* n. sp.) de l’inter Amirien-Tensiftien de Kénitra (Maroc). *Comptes Rendus de l’Académie des Sciences de Paris* 316: 701–707.
42. Gmira S, Lapparent de Broin F de, Geraads D, Lefèvre D, Mohib A, Raynal JP (2013) Les Tortues du Pliocène d’Ahl al Oughlam (Casablanca, Maroc) et de Localités Mio-Pliocènes avoisinantes. *Géodiversitas* 35: 691–733.
43. Jiménez-Moreno G, Popescu SM, Ivanov D, Suc JP (2007) Neogene flora, vegetation and climate dynamics in southeastern Europe and the northeastern Mediterranean. In: Williams M., Haywood AM, Gregory FJ, Schmidt DN (eds) Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies. The Micropalaeontological Society, London, pp 503–516.
44. Merceron G, Kostopoulos DS, Bonis L de, Fourel F, Koufos GD, Lécuyer C, et al (2013) Stable isotope ecology of Miocene bovids from northern Greece and the ape/monkey turnover in the Balkans. *Journal of Human Evolution* 65: 185–198. <https://doi.org/10.1016/j.jhevol.2013.05.003> PMID: 23866679
45. Rey K, Amiot R, Lécuyer C, Koufos GD, Martineau F, Fourel F, et al (2013) Late Miocene climatic and environmental variations in northern Greece inferred from stable isotope compositions ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of equid teeth apatite. *Palaeogeography Palaeoclimatology Palaeoecology* 388: 48–57.
46. Merceron G, Zazzo A, Spassov N, Geraads D, Kovachev D (2006) Bovid paleoecology and paleoenvironments from the late Miocene of Bulgaria: evidence from dental microwear and stable isotopes. *Palaeogeography Palaeoclimatology Palaeoecology* 241: 637–654.
47. Merceron G, Zazzo A, Spassov N, Geraads D, Kovachev D (2006) Bovid paleoecology and paleoenvironments from the late Miocene of Bulgaria: evidence from dental microwear and stable isotopes. *Palaeogeography Palaeoclimatology Palaeoecology* 241: 637–654.
48. Quade J, Solounias N, Cerling TE (1994) Stable isotopic evidence from paleosol carbonates and fossil teeth in Greece for forest or woodlands over the past 11 Ma. *Palaeogeography Palaeoclimatology Palaeoecology* 108: 41–53.
49. Denk T, Zohner CM, Grimm GW, Renner SS (2018) Plant fossils reveal major biomes occupied by the late Miocene Old-World Pliocene fauna. *Nature ecology & evolution* 1.
50. Lambert MRK (1983) Some factors influencing the Moroccan distribution of the western Mediterranean spur-thighed tortoise, *Testudo graeca graeca* and those precluding its survival in NW Europe. *Zoological Journal of Linnean Society* 79: 149–178.

51. Anadón JD, Giménez A, Graciá E, Pérez I, Ferrández M, Fahd S, et al (2012) Distribution of *Testudo graeca* in the western Mediterranean according to climatic factors. *Amphibia-Reptilia* 33, 2: 285–296.
52. Le M, Raxworthy CJ, McCord WP, Mertz L (2006) A molecular phylogeny of tortoises (Testudines: Testudinidae) based on mitochondrial and nuclear genes. *Molecular Phylogenetics and Evolution* 40: 517–531. <https://doi.org/10.1016/j.ympev.2006.03.003> PMID: 16678445
53. Lapparent de Broin F de, Bour R, Perälä JF (2006b) Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): Second part *Annales de Paléontologie* 92 (4): 325–357.
54. Riabinin AN (1918) Tortoises from the Meotian deposits of Bessarabia. *Papers of Geological and Mineralogical Museum Emperor Peter the Great of the Russian Academy of Sciences* 1: 1–16. (in Russian).
55. Loveridge A, Williams EE (1957) Revision of the African tortoises and turtles of the suborder Cryptodira. *Bulletin of the Museum of Comparative Zoology* 115: 163–557.
56. Amiranashvili NG (2000) Differences in shell morphology of *Testudo graeca* and *Testudo hermanni*, based on material from Bulgaria. *Amphibia-Reptilia* 21: 67–81.