From: Hannah.O'Regan@nottingham.ac.uk
Subject: Decision on Manuscript ID PALA-05-15-3692-OA.R1Papers in Palaeontology
Date: August 26, 2015 at 10:25 AM
To: evlacho@mef.org.ar, evlacho@gmail.com, lilits@geo.auth.gr

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26-Aug-2015

Dear Dr Vlachos,

It is a pleasure to accept your paper entitled "The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of Testudo Linnaeus, 1758 (Testudines: Testudinidae)" in its current form for publication in Papers in Palaeontology. The comments of the referees who reviewed the manuscript are included at the foot of this letter.

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Yours sincerely,
Dr. Hannah O'Regan
Editor
The Palaeontological Association
Hannah.O'Regan@nottingham.ac.uk

Referee(s)' Comments to Author:

Referee: 1

Comments to the Author
Thank you for making the requested technical changes, the overall resolution of the figures now looks fine. The background image in Fig. 1A looks to be very pixellated - is this deliberate? It may be useful to have it slightly higher resolution (300 dpi) if you want the features to be a little clearer, even though you seem to intend it to be muted in the background. If you can improve this, could you contact me directly to arrange a file transfer please?

Sally Thomas
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The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of Testudo Linnaeus, 1758 (Testudines: Testudinidae)

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Key words:	Chelonians, Testudines, Testudo marginata, Neogene, Chersus, Testudona

The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae)

by EVANGELOS VLACHOS[*1,2] *and* EVANGELIA TSOUKALA[2]

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Abstract: The Late Pliocene (Early Villafranchian, MN 16a) locality of Milia (Grevena, Greece), has yielded numerous remains of mammals such as zygodons, mastodons, rhinocerotids, hipparions, bovids, cervids, suids, carnivorans~~es~~, and tapirs. This locality is of special interest because of the findings of the two pairs of tusks of the zygodon *Mammut borsoni*, the longest tusks in the world, and the discovery of animals such as tapirs and agriotheriums for the first time in the Greek fossil record. Among the various fossils found in the sand deposits of Milia, several specimens of chelonians have also been discovered. Although few, they show a remarkable diversity, with findings of a small testudinid, a geoemydid, and a giant tortoise. The presence of a giant tortoise and a geoemydid with large dimensions further document the trend on gigantism on the diverse fauna of Milia. In terms of taxonomic abundance, ~~This~~ this is so far the richest locality in Greece ~~in terms of taxonomic abundance~~ of extinct turtles. The small testudinid is of particular importance because it preserves a posteriorly flared carapace, as in the extant *Testudo marginata*, but the posterior carapace is much taller and anteroposteriorly shorter. These characters allow us to propose a new species, *Testudo brevitesta* sp. nov., and to discuss the presence of the marginated tortoise and closely related forms in Greece. The new taxon is analyzed in a phylogenetic context within other extant and extinct testudinids, providing new information on the clade *Testudona*. ~~The presence of a giant tortoise and a geoemydid with large dimensions further document the trend on gigantism on the fauna of Milia.~~

Key words: Chelonians, Testudines, *Testudo marginata*, Neogene, *Chersus*, *Testudona*.

THE fossil turtles and tortoises from Greece form a quite diverse fauna in the area of the South Balkans, spanning mainly from the Late Miocene and onwards. This fauna has been poorly understood and as such the chelonian fossils from Greece have received our focus during the last years. With several papers (Tsoukala *et al*. 2011; Vlachos *et al.* 2014; Vlachos and Tsoukala 2014; Vlachos *et al.* ~~in press~~2015) and a doctoral thesis (Vlachos 2015) we have ~~tried to ~~presented new material from Greece and ~~to ~~revised previously published specimens. ~~Our aim is to gain a better understanding~~This study describes more of the Greek fossil chelonian fauna, which represents arguably one of the best fossil records of the Mediterranean Neogene.

In most cases, fossil chelonians were discovered in field works focused in the recovery of fossil mammal remains, and as a result the recovered material was rather limited and fragmented. However, during the last decade, focused fieldwork from the School of Geology, Aristotle University of Thessaloniki (Greece) has ~~provided a wealth of new information on~~unearthed many new chelonian specimens (Vlachos 2015). The Late Pliocene site of Milia (Grevena, NW Greece) was on the main focus of this study for several reasons. First~~ of all~~, dated ~~in ~~to the end of Pliocene based on large mammal biostratigraphy (Early

Villafranchian, MN16a) (Guérin and Tsoukala 2013), Milia is the most representative site of this period in Greece, showing a unique diversity of mammals ~~in Greece~~. This assemblage has only recently ~~started to be~~been studied in detail (see locality information) and ~~needs~~ is the subject of further investigation as it provides valuable information on the final stages of the Pliocene. It is the first time that the biozone MN16a is well-documented in Greece. Finally, the chelonian specimens ~~that have been~~ described herein illustrate one of the most diverse fossil chelonian faunas in South Balkans~~, known up to now~~.

In this paper, we describe and figure in detail the chelonian material from Milia~~,~~. ~~that~~ It represents at least three species: a small and a large testudinid, as well as a geoemydid. Such a diverse assemblage is only known in Greece from ~~the joint area of~~ two localities, Allatini and Pylea (Latest Miocene-Earliest Pliocene; Vlachos *et al.* ~~in press~~2015). Moreover, the small testudinid is designated here as a new species of *Testudo*, showing clear ~~affinities~~ similarities with the marginated tortoise, *Testudo marginata*. This species is currently surviving in continental Greece, ~~and~~ southwestern Albania and Cyprus, being further introduced by humans in Sardinia (Italy) (van Dijk *et al.* 2012). Our recent studies on the Greek fossil record (Vlachos 2015) were able to identify a rather rich fossil record of *Te. marginata* in the Pleistocene of Greece, but no fossils of the marginated tortoise are identified in pre-Pleistocene times.

The taxonomy and palaeobiogeographical history of the tortoise species that surround the Mediterranean Sea is quite complex and in many ways poorly understood up to now, but~~.~~ Parham *et al.* (2006) and Fritz and Bininda-Emmonds (2007) provide ~~the necessary~~a reasonable taxonomic framework from a phylogenetic point of view; thus~~.~~ ~~The~~ the work of Parham *et al.* (2006) is largely used here as a ~~starting~~ reference point ~~and is evaluated with the addition of several fossil taxa~~for our phylogenetic analysis. In this broader ~~scheme~~analysis, species from the circum-Mediterranean area (*Te. graeca, Te. marginata,* *‘Te.’ hermanni, Te. kleinmanni, Agrionemys horsfieldii*) are associated with the African *Malacochersus* and the Asian *Indotestudo*, forming a clade named *Testudona* (sensu Parham *et al.*, 2006). Several molecular analyses (e.g. Parham *et al.* 2006; Fritz and Bininda-Emmonds 2007 amongst others) usually group the marginated tortoise with the Egyptian tortoise *Te. kleinmanni*, this clade (*Chersus* sensu Parham *et al.* 2006) being sister to *Te. graeca*. Parham *et al.* (2006) have argued that the *Chersus* clade originates at least in the beginning of the Pliocene (~5.33 Mya), but no fossils are known yet prior to the Pleistocene. The new species of *Testudo* presented here ~~closes~~ fills a part of this gap, as it demonstrates a posteriorly flared carapace that ~~allows association~~indicates affinity with *Te. marginata*, a position that is supported in our phylogenetic analysis (given the incomplete nature of the studied specimens). Another fossil taxon that ~~is associated with~~appears to be within the clade *Chersus* is the Late Miocene *Testudo marmorum* from Pikermi, Greece. The revision of this taxon is going to be presented elsewhere, but its position in our cladistic~~s~~ analysis is preliminary discussed here (based on the type specimens of MNHN and not the AMPG material) ~~for relevance with~~because is related to the new *Testudo* species. Finally, the members of the clade *Chersus* along with *Testudo graeca* from the clade *Testudo* (sensu Parham et al 2006); this definition for *Testudo* is used herein, which practically groups together the small testudinids with the hypo-xiphiplastral hinge (among other characters as well).

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The fossil specimens from Greece help elucidating the early history of *Chersus* in contrast with *Testudo* clade (sensu Parham *et al.* 2006), which shows both an extensive extant distribution (see Fritz *et al.* 2009 and references therein) and an overwhelming fossil record in the circum-Mediterranean area. New ~~material~~specimens, like those described here, aid in the better understanding of ~~this fossil record~~the relationships of the members of the clade *Chersus*.

Institutional abbreviations. AMPG, Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, Greece; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; LGPUT, Laboratory of Geology and Paleontology of University of Thessaloniki, Greece; MNHN, Muséum National d'Histoire Naturelle, Paris, France.

Anatomical abbreviations. Bony plates are indicated with small letters, horny scutes with capitals. ABD, abdominal; cos, costal; en, entoplastron; ep, epiplastron; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral; MA, marginal; neu, neural; PEC, pectoral; per, peripheral; PLE, pleural; py, pygal; sp, supragygal; VE, vertebral.

Other abbreviations. MN, European Mammal Neogene biozones.

LOCALITY INFORMATION

The locality of Milia is well-known for the gigantic mastodon fossils that have been described by Tsoukala (2000) and Tsoukala and Mol (in press), the rhinoceros, tapir and suid fossils (Guérin and Tsoukala 2013) and other mammalian taxa that ~~are~~ have been preliminarily described: ~~carnivores~~ carnivorans in van Logchem *et al.* (2010) and Tsoukala *et al.* (2014); hipparions in Lazaridis and Tsoukala (2014); bovids and cervids in Crégut-Bonnoure and Tsoukala (2014). The testudine remains have been preliminary mentioned in Vlachos (2014). The fossils ~~are~~ were recovered mainly in loose sediments of the fluvial and lacustrine deposits of loose conglomerates, clays and sands of various grain sizes in alternations, of undivided Plio-Pleistocene age, that cover most of the Grevena basin (Brunn 1956; Savoyat and Monopolis 1972). ~~However, t~~The study of proboscideans in the area

(Tsoukala and Lister 1998, Tsoukala 2000, Tsoukala and Mol in press), provided a more detailed view of these deposits and allowed the distinction of the Pliocene deposits (presence of zygodons and mastodons) from the Pleistocene ones (presence of the straight-tusked elephant).

The fossils are found in several localities around the village of Milia (localities Milia 1-Milia 10; Fig. 1A). The turtle remains in particular were recovered from the localities Milia 4 (Fig. 1B), Milia 5 (sandpit) and Milia 10. All these sites are marked by the presence of the Borson's zygodont, *Mammut borsoni* and the rhinoceros species *Dicerorhinus jeanvireti*. Based on the mammalian fossils, the fauna is of Late Pliocene age (Early Villafranchian, MN16a, Guérin and Tsoukala 2013). Since the turtle material ~~is~~ was recovered in association with those fossils, a similar age is proposed for the turtle and tortoise remains. Most of the isolated fragments from the Milia-5 locality ~~are~~ were found as the result of sieving procedure. The partial carapace from Milia-4 locality ~~has been~~was found in an upturned position showing the visceral side of the carapace (Fig. 1C-D), indicating possible post-mortem ~~modification~~ transport of the specimen.

MATERIAL AND METHODS

The fossil material is part of the collections of LGPUT, under the code MIL (for Milia). Shell nomenclature follows Zangerl (1969). Taxonomy follows Joyce *et al.* (2004), Parham *et al.* (2006) and van Dijk *et al.* (2012). Detailed descriptions of all the specimens are given in the supporting information (Vlachos and Tsoukala 2015). For the phylogenetic analysis of the new species of *Testudo* from the Late Pliocene of Milia, we have used a character/taxon matrix that ~~is introduced~~was developed in the doctoral thesis of one of us (Vlachos~~,~~ 2015). In the supporting information there is additional information for the selected characters from pre-existing matrices, the scorings and the ingroup taxa. This matrix for the analysis of testudinids is part of an ongoing ~~research~~ project with M. Rabi (University of Tübingen; IKYDA project). The version of the matrix used in this paper includes a compilation of characters introduced in previously published papers. In particular, we used characters from ~~Pérez-García and Vlachos (2014),~~ Crumly (1982; 1984), Amiranashvili (2000), Meylan and Sterrer (2000), Gerlach~~,~~ (2001), Claude and Tong (2004), Joyce and Bell (2004), ~~and~~ Lapparent de Broin *et al.* (2006), Pérez-García and Vlachos (2014), consisting of 81 characters from skull, shell and appendicular elements and 37 taxa (21 extant and 16 extinct; see suppl. material for further information). Please note that list of the above mentioned works is not exhaustive, as several summarize the anatomy and character definitions from numerous previous papers (e.g. references in: Crumly 1982; 1984, Meylan and Sterrer 2000; Claude and Tong 2004; Joyce & Bell 2004). The matrix was created in Mesquite software (Maddison and Maddison 2008, version 3.02). The cladistic analysis was performed with the software TNT (Goloboff *et al.* 2008~~a; b~~). Jackknife and Bootstrap indices were calculated in TNT. The analysis of a matrix of 37 taxa and 81 characters (see supporting information) has been performed under a traditional search with TNT v. 1.0 (Goloboff *et al.* 2008~~a~~), using a tree-bisection algorithm with 1,000 replicates. All characters were considered unordered and equally weighted. Two searches for MPTs were made, one unconstrained and one with molecular constrains. The constrained analysis ~~followed~~ was based on the results of Fritz and Bininda-Emmonds (2007) that include a similar taxon sampling as our data. In this paper we will focus only on the relationships within *Testudona* clade (sensu Parham *et al.* 2006).

SYSTEMATIC PALAEONTOLOGY

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Testudines Batsch, 1788 (sensu Joyce *et al.* 2004)

Cryptodira Cope, 1868

Testudinidae Batsch, 1788

Testudo Linnaeus, 1758 (sensu Parham *et al.* 2006)

Testudo brevitesta sp. nov.

LSID. urn:lsid:zoobank.org:act:XXXXXXXXX

Figures 2–5

Derivation of name. For the species name, *brevi*- from Latin, meaning short and *–testa* from Latin for shell. The specific name corresponds to the short, flared posterior carapace of the holotype, as opposed to the elongated one of the *Testudo marginata*.

Type locality. Milia, Grevena, W. Macedonia, N. Greece.

Age. Late Pliocene; MN 16a.

Holotype. LGPUT MIL 495, posterior part of carapace.

Referred Material. (LGPUT collection): MIL 255, plastron fragment; MIL 256a, neural; MIL 256c, pygal region fragment; MIL 982d, left hyoplastron fragment; MIL 1168, left epiplastron & entoplastron fragment; MIL 1396, left hyoplastron; MIL 1592, peripheral fragment; MIL 1633, shell fragment; MIL 1638, carapace fragment; MIL 1753, left part of a plastron (in four fragments a, b, c, d); MIL 1937, costal; MIL 1938, left hypoplastron fragment.

Diagnosis. A member of Testudinidae based on the presence of the alternating pattern of neurals and costals, i.e. the octagonal-quadrangular neurals make contact with costals that are medially short and laterally long, alternated with costals that are medially long and laterally short (seen in the holotype), ~~and~~ on the presence of a thick dorsal epiplastral lip (seen in the referred material) and fused 12th marginal scutes. Differs from extant *Testudo graeca,* ‘*Testudo*’ *hermanni,* and extint *Testudo* spp., ~~and~~and resembles ~~is associated with~~ *Testudo marginata* on the basis of the posteriorly flared pygal region and on the pygal shape, which shows lateral borders that slightly diverge posteriorly (in some *Te. marginata*). Differs from *Te. marginata* in the short posterior carapacial lobe, ~~not being elongated~~in lack of overall elongation, in the narrower vertebrals, and in its shorter posterior peripherals~~, and in the pygal, which shows lateral sides that diverge posteriorly~~. Differs from *Kinixys*, that also shows a posteriorly flared margin, on the absence of a carapacial hinge.

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Description

This taxon is known from the combined anatomical information from several specimens (see supporting information for detailed descriptions) that allow knowing of the morphology of the posterior carapace and anterior-mid part of the plastron.

Carapace. The description of the carapace is mainly based on the specimen MIL 495 (Fig. 2). When the description is based on other specimens as well, additional specimen numbers are provided. The shell is rounded in dorsal outline and tall (Fig. 2). Neurals 1-3 were not recovered. The fourth neural ~~4~~ is octagonal, as long as wide. The fifth neural ~~5~~ (MIL 256a) is quadrangular, wider than long (Fig. 2 and 4A-C). The sixth neural ~~6~~ is roughly octagonal, slightly wider than long. The seventh neural ~~7~~ is hexagonal, with short anterior lateral sides.

~~Most probably t~~The eighth neural ~~8~~ is present, being quadrangular with rounded edges. ~~It seems that o~~Only one suprapygal is present, that being trapezoid with narrow anterior and wider posterior part. The costal plates (MIL 1937) preserve the typical alternating pattern of the testudinids, showing costals that are medially short and laterally long to be alternated with costal that are medially long and laterally short (Fig. 2 and ~~4B~~4D-F). From the peripheral series, those from the right bridge and the entire posterior rim are preserved. The peripherals of the bridge are tall and ~~short~~narrow. The pygal is trapezoid in shape, with slightly narrow anterior and wider posterior side, thus showing lateral sides that appear to slightly diverge posteriorly (Fig. 2D-E). The peripherals of the posterior rim are moderately long and posteriorly flared, including also those of the pygal region (Fig. 2F-G). The isolated pygal (MIL 256b; Fig. 4G-I) is also posteriorly flared, excluding the possibility of any taphonomical alteration of the holotype specimen. Although posteriorly flared, the posterior carapace is not elongated as in *Te. marginata,* but rather of the same relative size (to the complete length) as in *Te. graeca.* ~~The pygal is trapezoid in shape, with narrow anterior and wider posterior side, thus showing lateral sides that diverge posteriorly.~~ The imprints of the scute sulci are clearly visible as they are deeply pronounced on the plates. The vertebrals are slightly longer than wide, but still narrower than the pleurals. The vertebral sulci cross transversely the neural 3, neural 5, and the last neural plate. In the crossing of the sulci on the neurals, significant dorsal bumps are noted. The pleurals are rectangular, wide and short, crossing the costals 2, 4, and 6 transversely. The marginals are long and narrow, crossing the peripherals. The twelfth marginals ~~12~~ are fused into a single supracaudal. ~~In the preserved part~~Were preserved, there is good coincidence between the costo-peripheral suture and the pleuro-marginal sulci (Fig. 2~~) and 4C)~~.

Plastron. The description of the carapace is mainly based on the specimen MIL 1753 (Fig. 3). When the description is based on other specimens as well, additional specimen numbers are provided. The anterior lobe of the plastron is short and wide, with a rounded rim (Fig. 3). The epiplastra (MIL 1168) are short and wide, forming a thick convex epiplastral lip viscerally (Fig. 3 and ~~4D~~4J-L). A deep gular pocket is ~~noted~~present. The entoplastron is longer than wide, roughly hexagonal. The hyo- and hypoplastra are long and wide, showing a moderate concavity ventrally~~. This~~, which suggests that the specimen (MIL 1753) is ~~probably~~ a male individual. The preserved part of the left bridge shows that the peripherals were tall and ~~short~~narrow, being moderately flared posteriorly. The gulars are long and narrow, covering the epiplastra and overlapping the anterior part of the entoplastron. The humerals are long, compared to the short pectorals. The humero-pectoral sulcus is laterally convex and medially slightly concave. It is situated on the hyoplastra, posterior to the end of the entoplastron. The pectoro-abdominal sulcus is curved, being concave medially and convex laterally (Fig. 3 and ~~4E~~4M-O). The abdominals cover the posterior half of the hyoplastra and all the preserved part of the hypoplastra, suggesting a rather long covering of the abdominals. This morphology, together with the thickened plate on the preserved part of the bridge resembles the morphology of the plastra with a movable posterior lobe (Fig. 3D). For measurements see Table 1.

Comments. Regarding the tortoise specimens, the posterior carapace MIL 495 has been found in the site Milia-4, the left plastron MIL 1753 in the site Milia-10, whereas the remaining isolated fragments in the site Milia-5. Although few of the specimens present overlapping fragments, all the material can be attributed to the same species.

Based on its morphology, ~~This~~ this tortoise material ~~is associated~~shows similarities with the marginated tortoise *Te. marginata*. ~~This species is found in Greece, in parts of~~

~~Albania and it has been introduced by humans in Sardinia and Cyprus (van Dijk *et al.* 2012).~~ ~~It~~The marginated tortoise is characterized by the presence of an elongated posterior carapacial lobe, with a peripheral margin that is almost horizontally flared. This distinctive morphology makes the living marginated tortoises and the specimens of its extinct representatives easily recognizable. The other small, extant testudinid species in Greece, *Te*. *graeca* and ‘*Te*’. *hermanni*, show a peripheral margin (pygal and last peripherals) that is curved inwards (Fig. 5). Thus, they are easily distinguished from *Te*. *marginata*. The Greek fossil record is quite rich in specimens of *Te*. *marginata*, all from the Pleistocene. In the mainland Greece ~~few sites~~some fossil chelonians are known, such as those discovered at Xerias (Kavala; Tsoukala et al.~~,~~ 2011) ~~with a shell showing many similarities with *T. marginata*,~~ and Laconia ~~with fragments of the carapacial margin~~ (Schleich~~,~~ 1982). These exhibit a shell showing many similarities with *Te. marginata*, specifically in the shape of the carapacial margin. On the other hand, numerous specimens of *Te*. *marginata* ~~are~~ have been found ~~on cave on~~in island caves~~s~~, such as Charkadio Cave, Tilos Island and various caves in Crete (Vlachos 2015 and references therein). The Milia marginated tortoise clearly differs from all these specimens in the less flared carapacial margin, ~~and~~ in the short posterior carapacial lobe. The shape of the pygal bone is also present on some specimens of the marginated tortoise (in Vlachos 2015) but not in other testudinids with posteriorly flared carapacial margins (e.g. *Kinixys*).~~.~~

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A taxon that has been traditionally ~~associated~~ considered as closely related to~~with~~ the *marginata* group ~~it the~~is *Testudo marmorum* from the Late Miocene of Pikermi (see Vlachos and Tsoukala~~,~~ 2014 and Vlachos *et al.* ~~in press~~2015 for some comments). The Milia testudinid is different from the marble tortoise in the narrower vertebrals, in the posteriorly flared carapacial margin, the presence of dorsal bumps in the neurals and in the shorter and wider entoplastron. Another taxon that is of interest is the recently erected *Testudo* *weissengeri* Bour, 1996. This new extant species, which also preserves a flared carapacial margin, has been distinguished from *Te. marginata* based on the smaller shell size and differences in colorations, presenting a distinct population on the south Peloponnesus. However, genetic evidence from mitochondrial and nuclear genomic markers showed that *Te. weissengeri* is not a distinct evolutionary lineage (Fritz *et al.* 2005). Based on the above, the *Testudo* sp. from Milia is the only *Testudo* taxon that shows a flared carapacial margin similar to ~~the~~ that of *Te. marginata*.

Recently, Gmira *et al.* (2013) described the small testudinid *Testudo oughlamensis* from the Late Pliocene of Ahl al Oughlam (Morocco), that interestingly shows a similar (although probably richer than Milia) turtle fauna containing at least one small testudinid (there are others preliminary identified as *Testudo* spp.), at least one large (?*Centrochelys marocana*) and a freshwater *Mauremys* cf. *leprosa*. The Moroccan small testudinids are clearly different from the Milia taxon on the shape of the posterior carapacial rim that is curved inwards in the Moroccan taxa. Further differences can be found on the shape of the anterior lobe of the plastron, being rounded in Milia taxon but straight or medially notched in the *Te. oughlamensis*. The epiplastral lip is also much longer antero-posteriorly in the Moroccan taxon.

Titanochelon Pérez-García and Vlachos, 2014

Titanochelon sp.

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Figure 6

Material. MIL 1511, coracoid proximal fragment right; MIL 1834, osteoderm fragment.

Description

The material of the giant tortoise is rather limited. MIL 1511 corresponds to the proximal part of the right coracoid. It is large and wide, triagonal in cross-section, and it shows a shallowly concave articular surface for the humeral head, whereas the symphyseal area with the scapula is broken. The coracoid shows a narrow and long neck, leading to the medial part of the bone, which is flattened and with elliptical cross-section. MIL 1834 corresponds to a fragment of a porous, flat and rounded element. Based on ~~the available material and~~ the structure of the broken inner surface, this specimen can be attributed to a rounded osteoderm of a giant tortoise.

Comments. The material of the giant tortoise from the Late Pliocene site of Milia is too scarce to allow a confident identification. It ~~indicates~~is, however, the ~~presence~~ first report of a large testudinid~~s~~ in Western Macedonia~~ for the first time~~;~~, but~~ more material is certainly needed to better characterize this tortoise. The size and morphology of the preserved coracoid is similar to that of the Pliocene species *Ti. bacharidisi*, present in northern Greece (Vlachos *et al.* 2014).

Geoemydidae Theobald, 1868

Mauremys Gray, 1869

Mauremys sp.

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Figure 7

Material. MIL 818, hypoplastron right fragment; MIL 981, epiplastron left; MIL 982, hyoplastron left; MIL 1847, epiplastron left; MIL 1939, neural; MIL 1940, hyoplastron fragment.

Description

From the carapace only a neural is known. MIL 1939 corresponds to an almost complete neural that is hexagonal in shape, with short anterior lateral processes. The anterior part of the neural is wider than the posterior one. It is not crossed by any sulci. Besides this ~~specimen~~neural, ~~mostly~~ parts of the plastron ~~is~~ are ~~known form this turtle~~present. MIL 981 corresponds to a complete left long and narrow epiplastron. Viscerally, a long lip is formed, being concave medially. The gular scutes are wide and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is slightly curved. The length of the medial suture of the epiplastra is 21 mm, the maximum width is 44 mm. MIL 1847 (Fig. ~~7B~~7D-F) shows a similar morphology. The gular scutes are narrow and long, overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is slightly convex, and causes a slight constriction in the anterior part of the lobe. Therefore, the anterior part of the lobe is protruding. This specimen shows a remarkable size. The length of the medial suture of the epiplastra is 34 mm, the maximum width is 54 mm. This suggests that the width of the anterior lobe could reach 11 cm, making this terrapin among the largest known. The hyoplastron is poorly ~~known~~represented by only~~, from~~ a fragment of the right hyoplastron (MIL 1927, Fig. ~~7F~~7P-R) being crossed by the humero-pectoral sulcus. The right hypoplastron (MIL 818, Fig. ~~7E~~7M-O) shows a posterior side that corresponds to the slightly convex suture with the xiphiplastron. Viscerally, there is a wide covering of the femoral scutes. Ventrally, no sulci are noted indicating that the preserved surface was covered only by the femorals.

Comments. The geoemydid material from Milia is relatively scarse and the most diagnostic preserved element is the epiplastron. The presence of a shallow notch, the constriction in the gularo-humeral sulcus, and the presence of a pointed tip on the visceral surface of the epiplastron, ~~associated~~ considered the Milia material ~~with~~ to be closely related to the geoemydid *Mauremys* as opposed to emydids. Based on observations ~~In~~ in various emydids, the anterior lobe is wheel-rounded and there is less coverage of the gulars viscerally. Identification to the specific level is not possible based on the preserved material. One of the most important observations in the Milia *Mauremys* remains is the size of the specimens. Especially ~~specimen~~ MIL 1847 is, to the ~~extent~~ best of our knowledge, among the biggest epiplastra attributed to *Mauremys*. From the literature, Melentis (1966) provides some medial epiplastral lengths of a recent *M. (Clemmys) caspica* (18~~,~~.3mm), *Clemmys steinheimensis* (17~~,~~.5 - 14 - 16~~,~~.5mm). Both specimens from Milia are larger. MIL 981 has a medial length of 22mm, while MIL 1847 reaches a length of 34~~,~~.9mm. In general, ~~Gigantic~~ gigantic proportions are evident among the ~~animals~~ vertebrates from Milia, as emphasized by the presence of one of the largest mastodons that ever lived (Tsoukala 2000; Tsoukala and Mol, in press).

PHYLOGENETIC ANALYSIS

The uncostrained analysis resulted in 72 MPT, with best score (TBR) 300 (hit 121 times out of 1000). The strict consensus tree is given as a supplementary figure (Vlachos and Tsoukala 2015; file 5). Two main polytomies are identified in the consensus tree of the unconstrained analysis, one on the basal taxa and the other on the *Testudona* clade. The Palaeogene taxa *Cheirogaster maurini, 'Hadrianus' castrensis, 'Achilemys' cassouleti* are recovered in a polytomy with *Kinixys erosa*. Within *Testudona*, only the *Indotestudo* clade is recovered, with the remaining taxa recovered in many alternative positions. *Titanochelon* is again recovered as monophyletic, in a larger dataset this time (compared with Pérez-García and Vlachos, 2014). The monophyly of *Chelonoidis*, as a sister of the African *Centrochelys*, and the monophyly of *Gopherus* and the *Testudona* clade are recovered based only on

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morphological characters. These are promising results regarding the use of this character/taxon matrix~~, which was further analyzed with molecular constrains~~.

In order to provide a “molecular scaffold” for the analysis (sensu Crawford *et al.* 2015 and references therein) we constrained the extant taxa based on the results of the MP tree of Fritz and Bininda-Emmonds (2007). The results are significantly ~~better~~different, resulting in only 4 MPT, with best score (TBR) 318 (hit 112 times out of 1000). The strict consensus tree is given in Figure 8A. In the present paper we will focus on the placement of the new taxon from Milia ~~taxon~~ and ~~the~~ its relationships within *Testudona* (see box in Fig. 8A for clade names sensu Parham *et al.* 2006).

In all trees of the constrained analysis, the *Pan-Testudona* clade is united by 3 synapomorphies (rectangular neural 1; no gular protrusion; femoro-anal sulcus with acute angle), whereas the *Testudona* clade (including ‘*Paleotestudo ~~canetoniana~~canetotiana’*) is united by a single synapomorphy (humerals smaller than the gulars). The *Testudona* clade without ‘*Pa. ~~canetoniana~~canetotiana’* is further united by one more synapomorphy (humero-pectoral sulcus coinciding medially with the posterior part of the entoplastron). Within *Testudona*, the *Indotestudo* clade is united by 4 synapomorphies in all trees (obtuse gulars; perpendicular humero-pectoral sulcus; straight or slightly rounded ~~femore~~femoro-anal sulcus; no posterior maxillary process). The *Testudo* clade is also supported by 4 synapomorphies in all trees (humerals longer than gulars; hypo-xiphiplastral plastral hinge; S-shaped femoro-anal sulcus; latissimus dorsi scar present). As a result of the molecular constrains, the clade including *‘Testudo’ hermanni* and *Agrionemys horsfieldii* is recovered, united by 2 synapomorphies (octagonal nuchal; short maxilla/premaxilla height). This clade is united with *Testudo* with 3 synapomorphies (reduction of neurals; fusion of suprapygals; one phalanx in the first and fifth digit). Besides ‘*Pa. ~~canetoniana~~canetotiana’* that is recovered within and outside *Testudona*, three other forms are placed in the stem of *Testudona*. The

Middle Miocene Namibian *Namibchersus namaquensis* is the most basal taxon in *Pan-Testudona*, excluded from the rest by the pleural 1 not touching or overlapping the nuchal. The position of the Late Oligocene '*Ergilemys' bruneti* from France would place the origin of the *Pan-Testudona* in the Oligocene. *'Testudo' antiqua* is recovered also in the stem of *Testudona*, united by 3 synapomorphies (narrow vertebrals; position of the posterior sulcus of the vertebral 5; humero-pectoral sulcus not perpendicular to the axial plane).

Testudo graeca is always recovered as the most basal taxon within *Testudo*. The new taxon presented here, *Testudo brevitesta* sp. nov. from the Late Pliocene of Milia is recovered within the *Testudo* clade in the constrained analysis (Fig. 8A). In 2 trees (Fig. 8B-C) is united with *Te. marginata* by 1 synapomorphy (posteriorly flared carapace), whereas in the remaining 2 trees (Fig. ~~8C~~8D-E) is basal to the clade containing *Te. marmorum* and *Te. kleinmanni*, with the humero-pectoral sulcus posterior to the entoplastron uniting the three taxa. We interpret these alternative positions as the result of two reasons: first, many characters of the anterior carapace and posterior plastron are not scored in *Te. brevitesta.* Second, the presence of a posteriorly flared carapace in other ingroup taxa (e.g. *Kinixys*) makes this character homoplastic and could support different topologies. Interestingly, the Late Miocene *Te. marmorum* from Pikermi (scored on the MNHN specimens; revision of this taxon currently in prep.) is nested within *Testudo* in all trees (Fig. 8). This position would push the origin of *Testudo* prior to the Late Miocene, which is in accordance with the results of Parham *et al.* (2006). The Pikermian tortoise is always recovered together with *Te. kleinmanni* (Fig. 8~~C,D~~B-E). In 2 trees, two synapomorphies group them together (pleural 1 overlapping the lateral parts of the nuchal; no protrusions in the peripherals) (Fig. 8B-C), whereas in the other 2 trees no synapomorphies unite this clade (Fig. 8D-E).

The result of the sister-group relationship of the Egyptian tortoise *Te. kleinmanni* with *Te. marmorum* is also confirmed in the unconstrained analysis, having only some trees where

Te. brevitesta is placed inside this clade. In all unconstrained trees we also failed to recover a direct sister-group relationship between the Egyptian tortoise and *Te. marginata*. In the constrained MPT's no synapomorphy is recovered for the node that groups *Te. kleinmanni* and *Te. marginata*. Note that our sampling did not include unfortunately any skull specimens of both taxa. These results could build upon the view of Delfino *et al.* (2009:850) that shell osteology does not reflect the recovered molecular sister-group relationship between the marginated and the Egyptian tortoise. Although certainly the presence of a hypo-xiphiplastral hinge places them within *Testudo*, Delfino *et al.* (2009:858) failed to find any significant synapomorphy between the two taxa. It is clear the two taxa have distinct shell morphology: the Egyptian tortoise shows some plesiomorphic features within the clade *Testudo* (e.g. the covering of first pleural on the lateral parts of the nuchal), whereas the marginated tortoise shows apomorphic ones (the posterior shell border morphology and overall elongation). Our results also show, both in the unconstrained analysis and even in the constrained analysis that forces the relationship of these two extant species, that certainly some extinct taxa could be placed in between (e.g. *Te. marmorum* and perhaps *Te. brevitesta*). If we tentatively accept their closer sister-relationship compared to *Te. graeca* based on molecular evidence (strong support in both Parham *et al.* 2006 and Fritz and Bininda-Emmonds 2007), maybe our analysis points out a possible solution to this problem (besides the lack of cranial information). It could be possible that these two extant species with distinct shell morphology are the present-day remnants of a larger clade (*Chersus*) with their last common ancestor traced back at least in the Late Miocene; thus the significant difference on their shell morphology might not be strange after all.

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The most recent phylogeny of the Mediterranean tortoises, with focus on naming possible clades, is that of Parham *et al.* 2006, and is therefore important to compare our results with the taxonomy proposed in that paper. By comparing the unconstrained analysis with the results of Parham *et al.* (2006), we are able to identify (although in a large polytomy), the *Testudona* clade based on morphological characters. In the constrained analysis, our ~~use~~ application of the results of Fritz and Bininda-Emmonds (2007) as a “molecular-scaffold” does not force the sister-group relationship of *‘Testudo’ hermanii* + *Agrionemys horsfieldii* with *Indotestudo* (as in Parham *et al.* 2006). This relationship was ~~neither~~ also not supported in the unconstrained analysis ~~as well~~ (see supporting information). The two fossil taxa (*Te. brevitesta* sp. nov. and *Te. marmorum*) are placed within *Testudo,* and particularly within *Chersus* clade (sensu Parham *et al.* 2006), strengthening the distinction of *Chersus* from *Testudo*. Our results would favor the dispersal hypothesis of Parham *et al.* (2006), i.e. dispersal from the NE part to the SE Mediterranean giving rise to the *Te. kleinmanni* lineage, but further taxon sampling is needed for a confident assessment. A recent morphological analysis within *Testudona* is presented by Corsini *et al.* (2014), including revised information on *‘Testudo’ antiqua* and on the matrix of Lapparent de Broin *et al.* (2006). Although, we used the updated information on *‘Testudo’ antiqua* from Corsini *et al*. (2014), our results, both the unconstrained and constrained analysis, greatly differ from the phylogeny of Corsini *et al.* (2014). Briefly, the main differences are summarized in the position of the fossil taxa *‘Er.’ bruneti, ‘Te.’ antiqua,* and *‘Pa.* ~~*canetoniana*~~*canetotiana’* that are mostly recovered here in the stem of *Testudona.* The relationships within *Testudo* clade are, however, in good accordance with Corsini *et al.* (2014), with some differences on the position of *Te. marmorum* (sister to *Te. marginata* in Corsini *et al.* 2014). Those differences are certainly caused by the updated information on some taxa from Greece (e.g. *Te. marginata* and *Te. marmorum*), the smaller taxon sampling of fossil testudonans in our case and in the smaller taxon sampling within testudinids in the case of Corsini *et al.* (2014). These points, however, clearly illustrate that the phylogenetic relationships of fossil testudinids are still immature but hopefully this work will spur research for more robust results in the future.

CONCLUSIONS

In this paper a new member of *Testudo* is described, from the Late Pliocene deposits of Milia, Grevena (NW Greece). This new tortoise, *Testudo brevitesta* sp. nov., differs from most *Testudo* on the posteriorly flared carapace, which allows association with the marginated tortoise, *Testudo marginata*. It differs, however, from the extant and extinct marginated tortoise, and consequently from other related small testudinids, on the less extended posterior carapace and the distinct morphology of the pygal plate. A new phylogenetic analysis based on morphological characters of the new taxon, supports its placement within *Testudo* and our unconstrained results are in good accordance with recent molecular analyses. The constrained analysis on the other hand, provides a more confident placement of fossil taxa within well-supported crown clades. The clade of interest in this paper, *Chersus* (sensu Parham *et al.* 2006) that includes the extant *Te. marginata* and *Te. kleinmanni*, is found to contain *Te. brevitesta* (possibly as a sister taxon of *Te. marginata*) and most probably the Late Miocene *Te. marmorum*. These results strengthen the temporal and geographical distribution of the clade *Chersus* and help elucidate~~ing~~ ~~each~~ the early history of this clade in the Pliocene. Our preliminary results question the placement of some fossil testudinids (e.g. ‘*Testudo*’ *antiqua*~~’~~ and ‘*Paleotestudo* ~~*canetoniana*~~*canetotiana*’) within *Testudona* and this result should be explored in a much broader context (in prep.). Inclusion of more fossil testudonans in this emerging picture would help to clarify the position of ‘*Testudo*’ *hermanni* (see Fritz and Bininda-Emmonds 2007). Also attention should be raised in the expansion of the complex of *Testudo graeca* complex (sensu Fritz *et al.* 2009) with more fossil species, as *Te. graeca* is recovered as the most basal taxon within *Testudo*.

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Strengthening *Te. graeca* clade with some fossil representatives might provide a better understanding of the anatomy of the members of the clade *Chersus* as well, an open question also discussed in this paper. All these further steps would shed light to the palaeobiogeographical history of these testudinids on the area surrounding the Mediterranean, already shown as quite complex based on the extant species.

Besides this new testudinid, the Milia deposits contain an unidentified large testudinid that is the first one from NW Greece and a species of *Mauremys*. All together, our findings bring into attention the most diverse chelonian fauna in Greece, and further increase the taxonomic diversity of chelonians in the Pliocene. The Milia chelonian fauna joins a roughly coeval and similar faunal composition that was reported recently from the southern Mediterranean in Ahl al Oughlam (Morocco; Gmira *et al.* 2013). Although the taxa from Milia are different, and the Moroccan locality is probably richer in taxa, this work increases our knowledge of the turtles from known Late Pliocene localities (e.g. Ahl al Oughlam, Ichkeul, Perpignan, Wadi Natrun, Hamada Damous; from Gmira *et al.* 2013). The large documented proportions of the new *Testudo*, the *Mauremys*, and of course the large testudinid, further depict the favorable conditions in Milia, as emphasized by the gigantism of the mastodons that lived in the area during the Late Pliocene. This warm and humid environment would evolve into less favorable conditions ~~become extinct~~ with the onset of the Pleistocene climate changes.

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SUPPORTING INFORMATION

DATA ARCHIVING STATEMENT

Data for this study are available in the [Dryad Digital Repository]: http://dx.doi.org/10.5061/dryad.6970v

Supplementary File 1. Document containing detailed descriptions of the specimens and information on the characters of the phylogenetic analysis.

Supplementary File 2. The character/taxon matrix in TNT format.

Supplementary File 3. The consensus tree of the constrained analysis with the list of common synapomorphies.

Supplementary File 4. The 4 most parsimonious trees of the constrained analysis with the list of common synapomorphies.

Supplementary File 5. Strict consensus tree of the unconstrained (A) and the constrained (B) analysis. Extinct taxa are marked with an asterisk. See text for further details.

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EXPLANATIONS OF FIGURES AND TABLES

FIG. 1. The Late Pliocene site of Milia, near Grevena (NW Greece). A, map of the area, showing the fossil localities around the village of Milia. The sites containing fossil chelonians are shown with solid circles. B, site Milia-4, which provided the partial carapace MIL 495. C, the partial carapace MIL 495 on recovery position in visceral and D, on anterior views.~~ Red circle marks the position of the carapace finding, shown in C and D.~~

FIG. 2. *Testudo brevitesta* sp. nov. from the Late Pliocene of Milia (Grevena). MIL 495, partial carapace in: ~~(A)~~A, dorsal~~, ~~; ~~(~~B,~~)~~ drawing of the dorsal~~, ~~; ~~(~~C,~~)~~ visceral~~, ~~; D, dorso-posterior; E, drawing of the dorso-osterior; ~~(D~~F,~~)~~ right lateral; and ~~(E~~G,~~)~~ left lateral views. Scale bar equals 5 cm. Abbreviations: cos, costal; MA, marginal; neu, neural; per, peripheral; PLE, pleural; py, pygal; sp, supragygal; VE, vertebral.

FIG. 3. *Testudo brevitesta* sp. nov. from the Late Pliocene of Milia (Grevena). MIL 1753, partial plastron in: ~~(~~A,~~)~~ visceral;~~,~~ ~~(~~B,~~)~~ ventral;~~,~~ ~~(~~C,~~)~~ drawing of the ventral;~~,~~ ~~(~~D,~~)~~ posterior; and ~~(~~E,~~)~~ detail of the left lateral views. Scale bar equals 5 cm. Abbreviations: ABD, abdominal; en, entoplastron; ep, epiplastron; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral; PEC, pectoral.

FIG. 4. *Testudo brevitesta* sp. nov. from the Late Pliocene of Milia (Grevena). Additional shell material: A-C, MIL 256a, 4th neural in: ~~(~~A,~~1)~~ dorsal;~~,~~ ~~(A2)~~B, drawing of the dorsal; and ~~(A3)~~C, visceral views. ~~B~~D-F, MIL 1937, costal in: ~~(B1)~~D, dorsal~~, ~~; ~~(B2)~~E, drawing of the dorsal; and ~~(B3)~~F, visceral views. ~~C~~G-I, MIL 256b, pygal in: ~~(C1)~~G, dorsal;~~,~~ ~~(C2)~~H, drawing

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of the dorsal; and ~~(C3)~~I, visceral views. ~~D~~J-L, MIL 1168, left epiplastron in: ~~(D1)~~J, ventral;~~,~~ ~~(D2)~~K, drawing of the ventral; and ~~(D3)~~L, visceral views. ~~E~~M-O, MIL 1938, left hypoplastron fragment in: ~~(E1)~~M, ventral~~,~~; ~~(E2)~~N, drawing of the ventral; and ~~(E3)~~O, visceral views. ~~F~~P-R, left hyoplastron fragment in: ~~(F1)~~P, ventral~~,~~; ~~(F2)~~Q, drawing of the ventral; and ~~(F3)~~R, visceral views. ~~G~~S-U, MIL 982d, left hyoplastron fragment in: ~~(G1)~~S, ventral~~,~~; ~~(G2)~~T, drawing of the ventral, and ~~(G3)~~U, visceral views. ~~H~~V-Y, MIL 255, shell fragment in: ~~(H1)~~V, ventral~~,~~; ~~(H2)~~X, drawing of the ventral; and ~~(H3)~~Y, visceral views. Scale bar equals 5 cm.

FIG. 5. Comparison of the morphology of the posterior carapace of: ~~(~~A,~~)~~ extant *Testudo graeca*~~,~~; ~~(~~B,~~)~~ extant *Testudo marginata*; and ~~(~~C,~~)~~ ~~*the Milia testudinid*~~*Testudo brevitesta* sp.nov. from Milia. Cross-sections of the medial plane of the pygal are shown.

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FIG. 6. *Titanochelon* sp. from the Late Pliocene of Milia (Grevena). Right coracoid in: ~~(~~A,~~)~~ dorsal~~,~~; ~~(~~B,~~)~~ anterior;~~,~~ ~~(~~C,~~)~~ ventral~~,~~; ~~(~~D,~~)~~ posterior views; and ~~(~~E~~)~~ detail of the articulation. Scale bar equals 5 cm.

FIG. 7. *Mauremys* sp. from the Late Pliocene of Milia (Grevena). A-C, MIL 1939, neural in: ~~(A1)~~A, dorsal~~,~~; ~~(A2)~~B, drawing of the dorsal; and ~~(A3)~~C, visceral views. ~~B~~D-F, MIL 1847, left epiplastron in: ~~(B1)~~D, visceral;~~,~~ ~~(B2)~~E, ventral; and ~~(B3)~~F, drawing of the ventral views. ~~C~~G-I, MIL 1928, left epiplastron in: ~~(C1)~~G, visceral~~,~~; ~~(C2)~~H, ventral; and ~~(C3)~~I, drawing of the ventral views. ~~D~~J-L, MIL 981, left epiplastron in: ~~(D1)~~J, visceral~~,~~; ~~(D2)~~K, ventral; and ~~(D3)~~L, drawing of the ventral views. ~~E~~M-O, MIL 818, right hypoplastron in: ~~(E1)~~M, visceral~~,~~; ~~(E2)~~N, ventral; and ~~(E3)~~O, drawing of the ventral views. ~~F~~P-R, right hyoplastron in: ~~(F1)~~P, visceral~~,~~; ~~(F2)~~Q, ventral; and ~~(F3)~~R, drawing of the ventral views. ~~G~~S-U, MIL 1940, left

hyoplastron in: ~~(G1)~~S, visceral~~, ;~~ ~~(G2)~~T, ventral; and ~~(G3)~~U, drawing of the ventral views. Scale bar equals 5 cm. Abbreviations: ep, epiplastron; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral.

FIG. 8. Phylogenetic analyses of ~~*the new taxon from*~~*Testudo brevitesta* from Milia. A, constrained analysis, consensus tree of 4 MPTs. The clade *Pan-Testudona* is shown fit in the stratigraphy. Names of clades (sensu Parham *et al.* 2006) are shown in the box. B~~1-2~~-C, two of the MPTs of the constrained analysis recovering the Milia tortoise as a sister group of *Testudo marginata*. ~~C1-2~~D-E, two of the MPTs of the constrained analysis recovering the Milia tortoise as basal to *Testudo kleinmanni* + *Testudo marmorum*. Asterisk indicates the wild-card taxa.

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Table 1. Measurements of the left anterior plastron MIL 1753 of *Testudo brevitesta* sp. nov. from Milia. Abbreviation: pr, preserved.

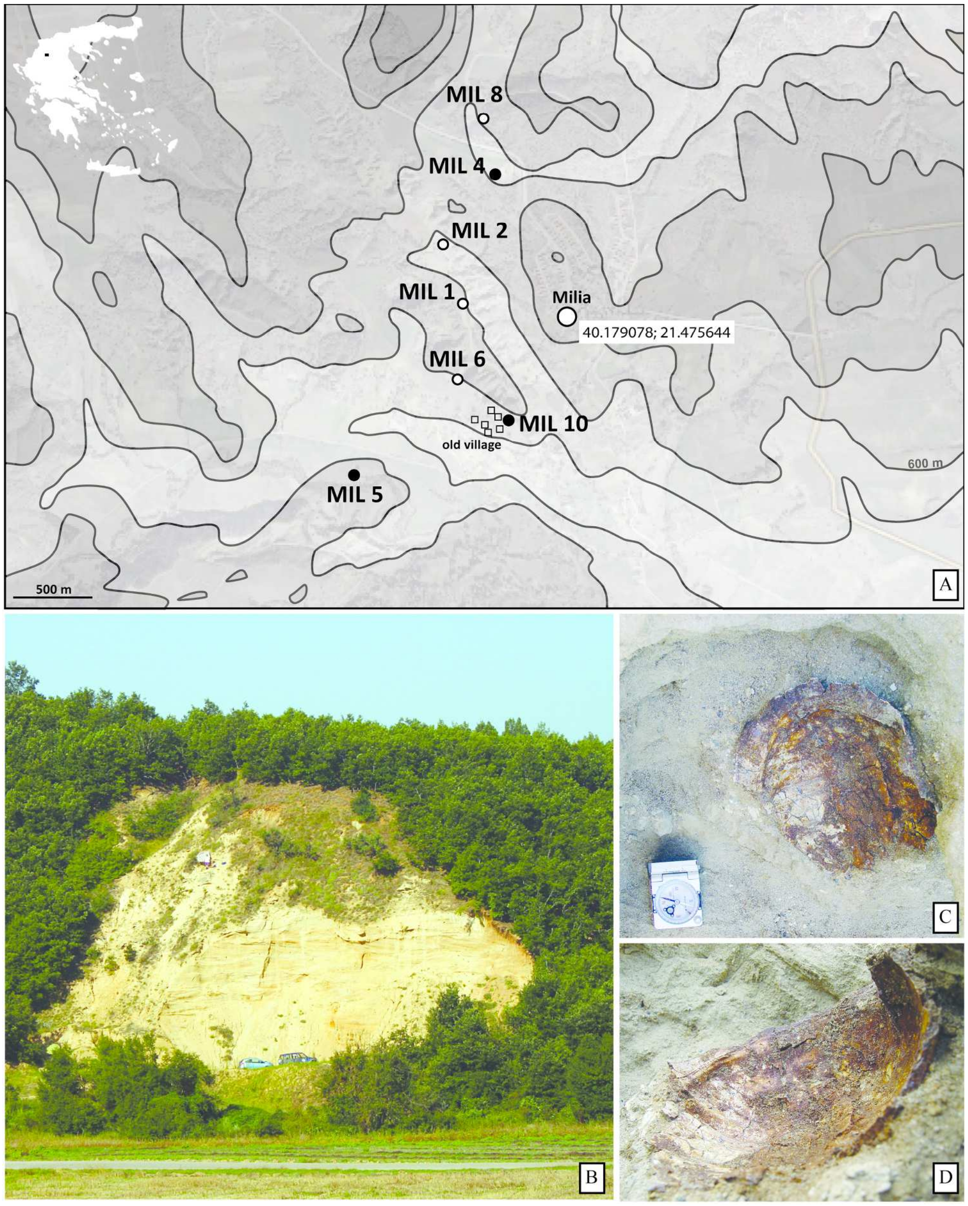
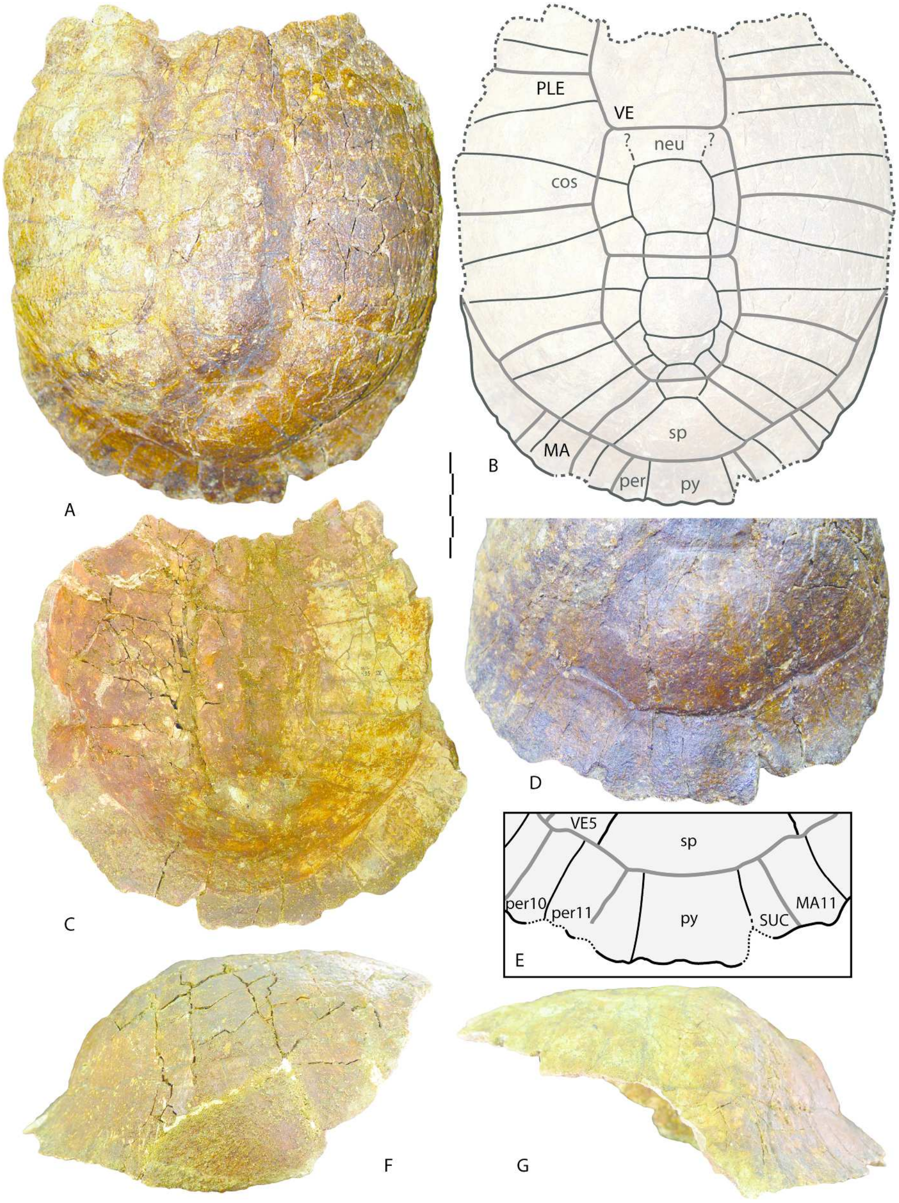


FIG. 1. The Late Pliocene site of Milia, near Grevena (NW Greece). A, map of the area, showing the fossil localities around the village of Milia. The sites containing fossil chelonians are shown with solid circles. B, site Milia-4, which provided the partial carapace MIL 495. C, the partial carapace MIL 495 on recovery position in visceral and D, on anterior views.
207x258mm (300 x 300 DPI)



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221x295mm (300 x 300 DPI)

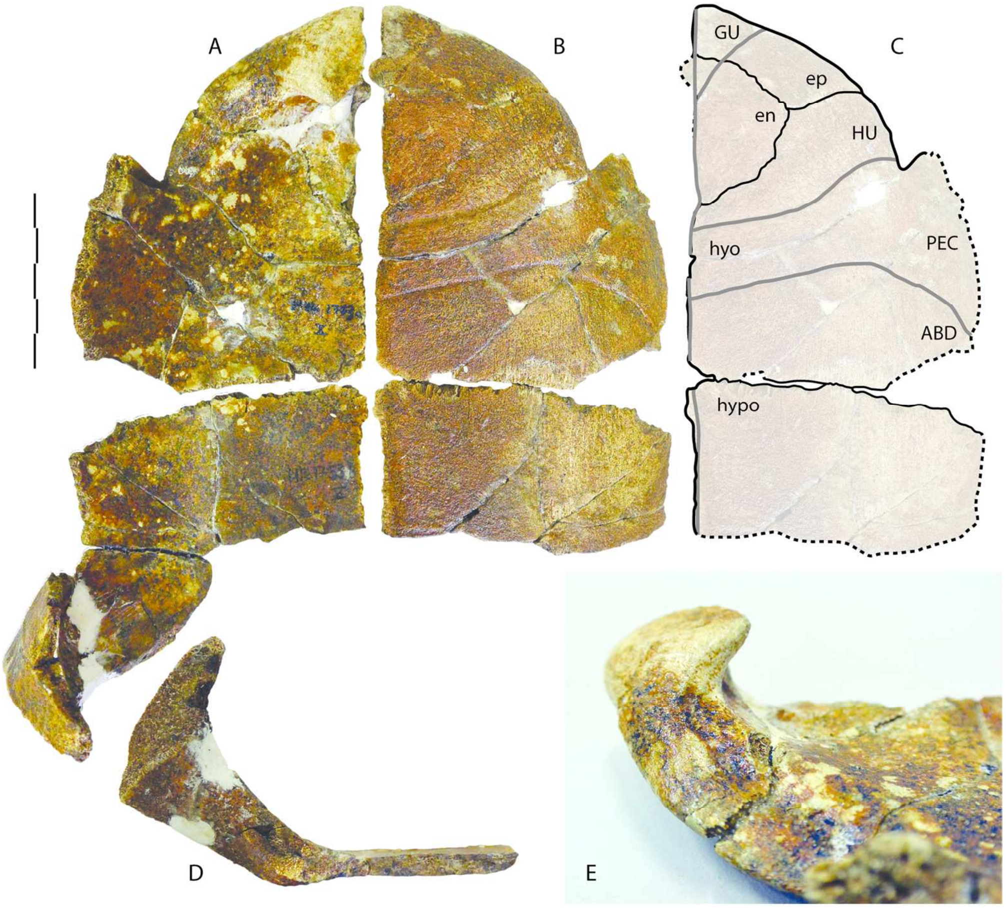
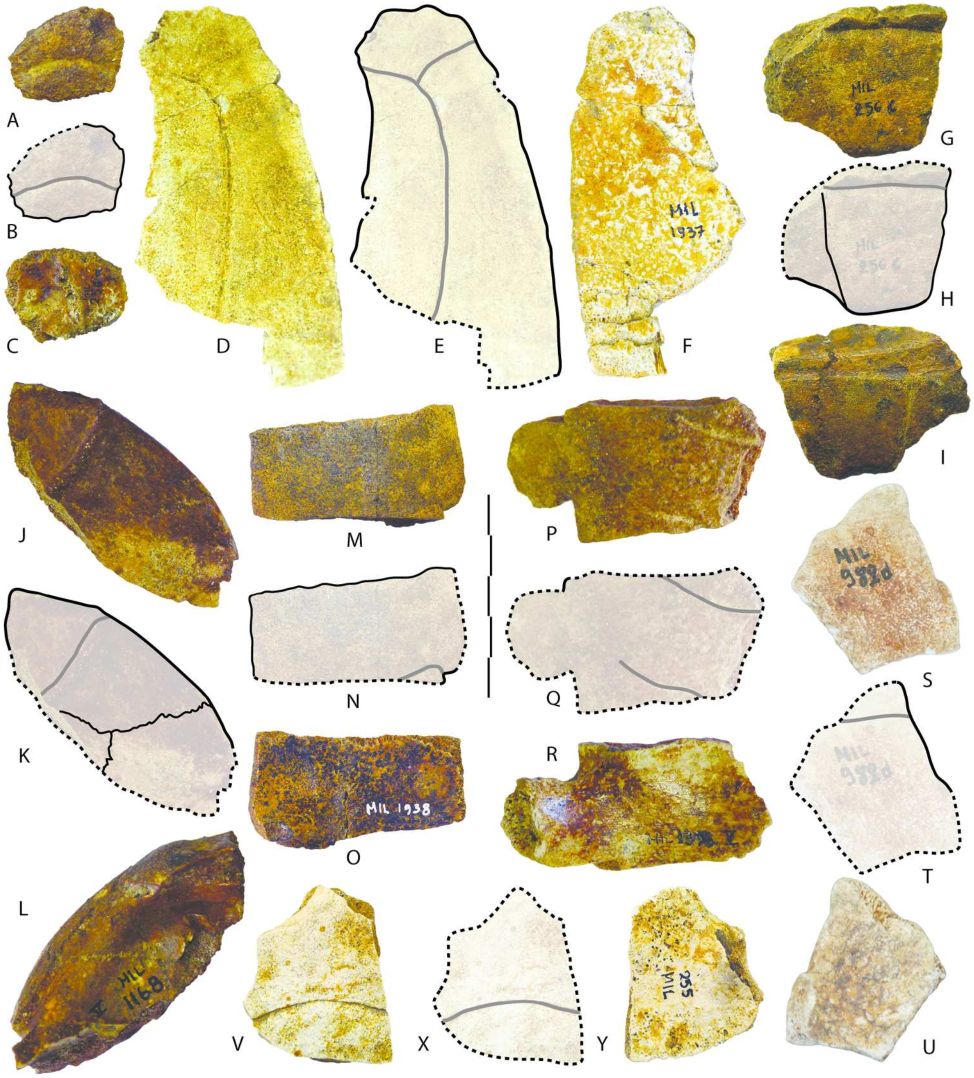


FIG. 3. Testudo brevitesta sp. nov. from the Late Pliocene of Milia (Grevena). MIL 1753, partial plastron in: A, visceral; B, ventral; C, drawing of the ventral; D, posterior; and E, detail of the left lateral views. Scale bar equals 5 cm. Abbreviations: ABD, abdominal; en, entoplastron; ep, epiplastron; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral; PEC, pectoral.
150x135mm (300 x 300 DPI)



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185x207mm (300 x 300 DPI)

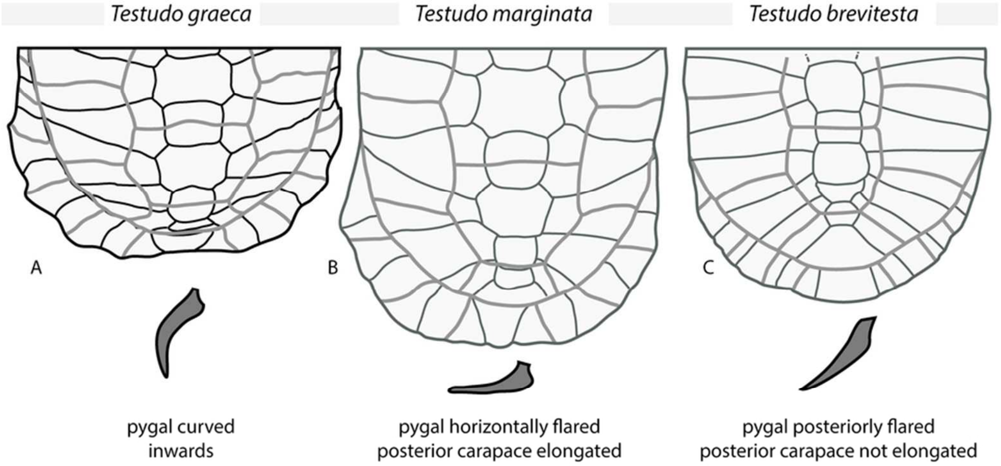
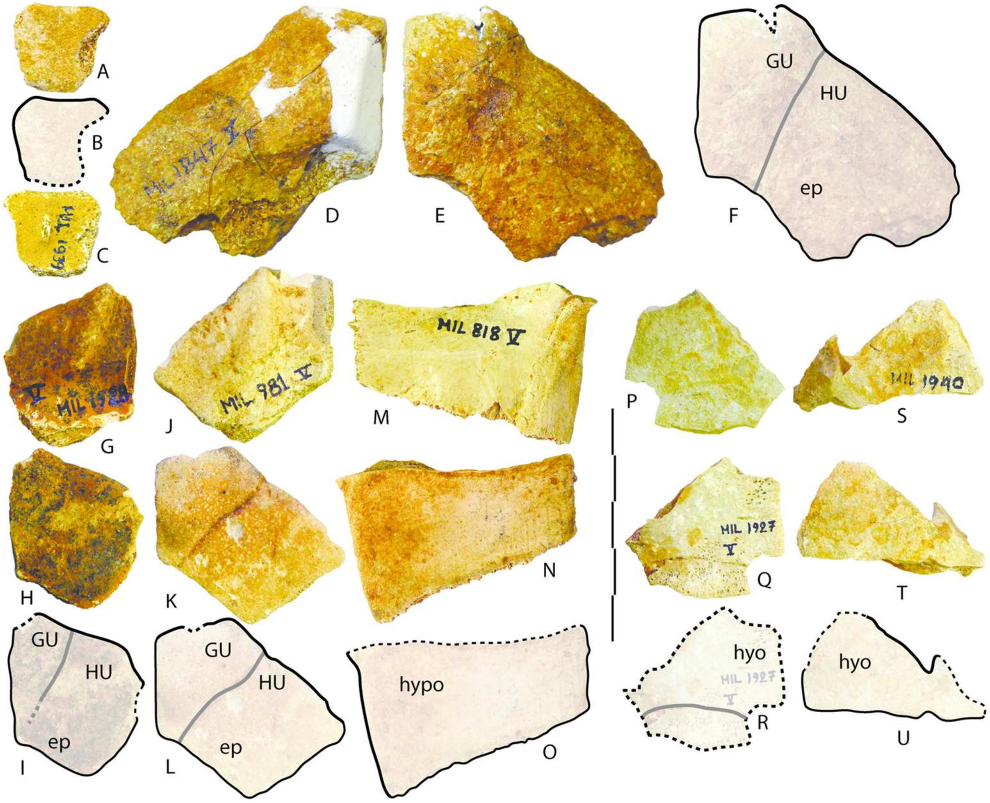


FIG. 5. Comparison of the morphology of the posterior carapace of: A, extant Testudo graeca; B, extant Testudo marginata; and C, Testudo brevitesta sp.nov. from Milia. Cross-sections of the medial plane of the pygal are shown.
81x39mm (300 x 300 DPI)

FIG. 6. Titanochelon sp. from the Late Pliocene of Milia (Grevena). Right coracoid in: A, dorsal; B, anterior; C, ventral; D, posterior views; and E detail of the articulation. Scale bar equals 5 cm.
63x24mm (300 x 300 DPI)



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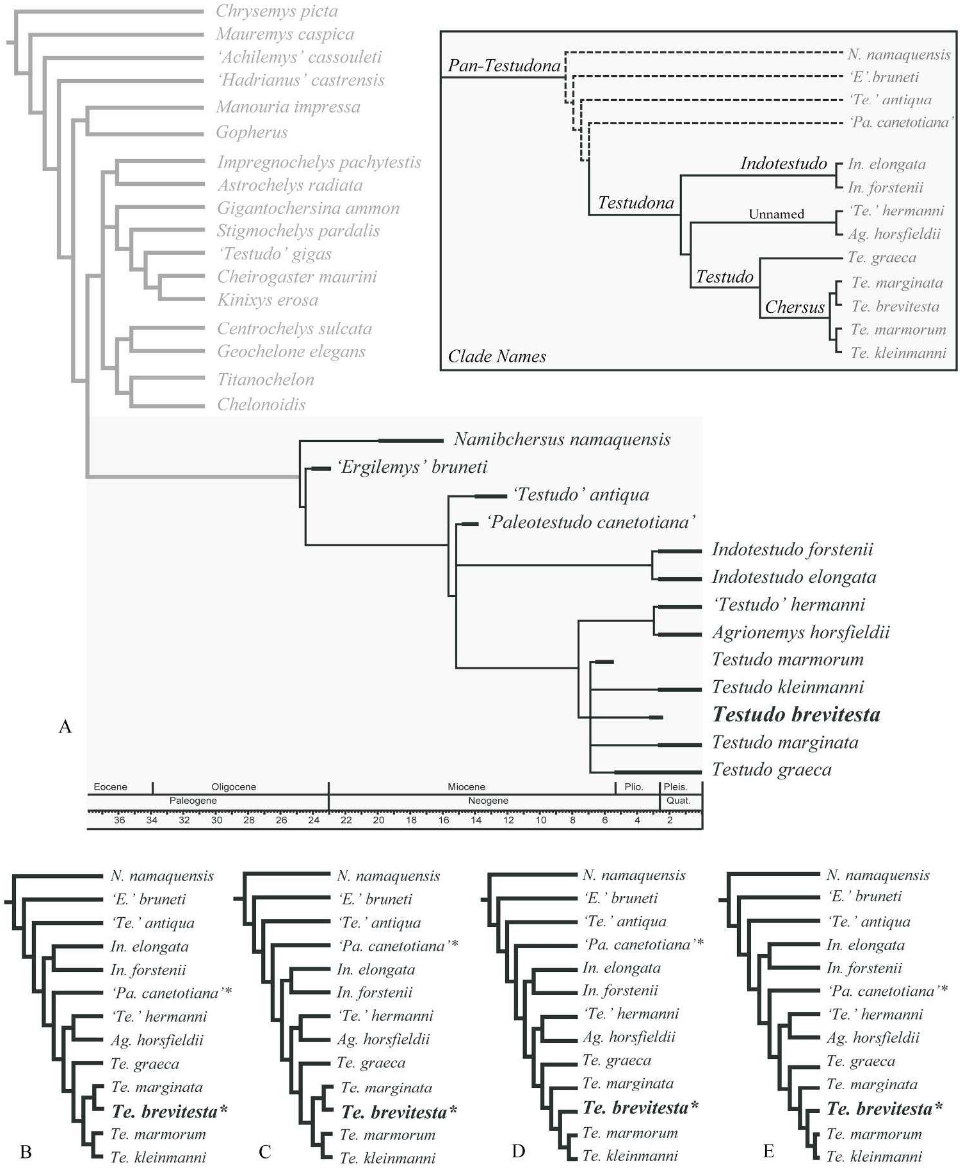
134x108mm (300 x 300 DPI)



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206x256mm (300 x 300 DPI)

	Antero-posterior Length at symphysis (mm)	Maximum Width (mm)	Thickness (mm)
Epiplastron	18.5	45.8	26.5
Epiplastral lip	Length: 32.8. Width: 22.3. Height:29.6		
Entoplastron	41.4	26	12.3-9.4
Hyoplastron	47.3	82.6	6.6-5.4
Hypoplastron	42.8	41.7 (pr)	6.5-6.1
Gular	25.9	22.1	-
Humeral	37.6	56.74	-
Pectoral	20.9	82.2	-
Abdominal	65.6	81.4	-