


The Pikermian tortoises (Testudines, Testudinidae) from the late Miocene of the South Balkans

Evangelos Vlachos, Georgios L. Georgalis, Socrates Roussiakis, Madelaine Böhme & George Theodorou



To cite this article: Evangelos Vlachos, Georgios L. Georgalis, Socrates Roussiakis, Madelaine Böhme & George Theodorou (2020): The Pikermian tortoises (Testudines, Testudinidae) from the late Miocene of the South Balkans, Journal of Vertebrate Paleontology

To link to this article: <https://doi.org/10.1080/02724634.2019.1711520>

 View supplementary material 

 Published online: 27 Feb 2020.

 Submit your article to this journal 

 View related articles 

 View Crossmark data 

THE PIKERMIAN TORTOISES (TESTUDINES, TESTUDINIDAE) FROM THE LATE MIOCENE OF THE SOUTH BALKANS

EVANGELOS VLACHOS,^{*1,2} GEORGIOS L. GEORGALIS,^{3,4} SOCRATES ROUSIAKIS,⁵ MADELAINE BÖHME,^{6,7} and GEORGE THEODOROU⁵

¹CONICET and Museo Paleontológico Egidio Feruglio, Av. Fontana 140, 9100, Trelew, Chubut, Argentina, evlacho@mef.org.ar;

²School of Geology, Faculty of Sciences, Aristotle University of Thessaloniki, Thessaloniki, Greece;

³Department of Earth Sciences, University of Turin, Via Valperga Caluso 35, 10125 Turin, Italy;

⁴Department of Ecology, Laboratory of Evolutionary Biology, Faculty of Natural Sciences, Comenius University in Bratislava, Mlynská dolina, 84215 Bratislava, Slovakia, dimetrodon82@gmail.com;

⁵Department of Historical Geology and Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Panepistimiopolis 15784, Athens, Greece, srousiak@geol.uoa.gr; theodorougeorge@gmail.com;

⁶Terrestrial Palaeoclimatology, Department of Geosciences, Eberhard Karls University Tübingen, Sigwartstrasse 10, 72076 Tübingen, Germany, m.boehme@ifg.uni-tuebingen.de;

⁷Senckenberg Centre for Human Evolution and Palaeoenvironment, Sigwartstrasse 10, 72076 Tübingen, Germany

ABSTRACT—This article deals with the fossil tortoises of one of the most iconic fossil localities of the Neogene of the Old World, the upper Miocene locality of Pikermi, near Athens, Greece. We describe the type, previously published, and new material of the fossil tortoises from Pikermi, along with new material from the coeval Azmaka 6 locality in Bulgaria. This combined information results in the complete revision of the ‘marble tortoise’ *Testudo marmorum*, which is the first turtle species ever named from Greece. Besides the challenges and difficulties of working with material from the old collections of Pikermi, we present a complete revision of this species and identify its presence outside its type locality in the South Balkan Peninsula. The presence of numerous shells of the ‘marble tortoise’ allows us to discuss the observed variation and attempt to interpret it as the result of intraspecific variation, ontogenetic changes, or sexual dimorphism. For the first time, we observe the absence of the characteristic hypo-xiphiplastral hinge in female individuals of *Testudo marmorum*, which in turn challenges the traditional phylogenetic position of this species. We further describe previously published and new material of the giant tortoise *Titanochelon* from Pikermi. Based on the updated information, we can suggest that the Pikermian giant tortoise probably represents a distinct taxon. Our results signal Pikermi as one of the most important localities to understand the evolution of tortoises in the eastern Mediterranean during the last parts of the Neogene.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

Citation for this article: Vlachos, E., G. L. Georgalis, S. Roussiakis, M. Böhme, and G. Theodorou. 2020. The Pikermian tortoises (Testudines, Testudinidae) from the late Miocene of the South Balkans. *Journal of Vertebrate Paleontology*. DOI: 10.1080/02724634.2020.1711520.

INTRODUCTION

Fossil tortoises from the upper Miocene of Pikermi in Attica, Greece, are the first chelonian fossils ever described from Greece and the South Balkans. Gaudry (1862a, 1862b, 1862–1867) named and described the iconic ‘marble tortoise,’ *Testudo marmorum* Gaudry, 1862a, based on material in the Muséum National d’Histoire Naturelle, Paris, France. Much later, Bachmayer and Symeonidis (1970) added to our knowledge more specimens of this species (stored in the collections of Museum of the National and Kapodistrian University of Athens, Athens, Greece). Furthermore, a giant tortoise was reported from Pikermi (Bachmayer, 1967) as well as from the nearby locality of Liossati (or Kiourka) (Bachmayer and Symeonides, 1977).

The fossil site of Pikermi (Figure 1) represents a benchmark for the European late Miocene, with pivotal contributions to

mammal paleontology and paleobiology (Gaudry, 1862a, 1862b; Abel, 1922). Mammalian fossils from Pikermi have contributed significantly to biogeographic ideas and thoughts about the evolution of savannah biomes in the Old World (Bernor, 1983; Solounias et al., 1999). This site actually represented several superimposed bone accumulations (Theodorou et al., 2010) dated to the latest Tortonian between 7.33 and 7.29 Ma (Böhme et al., 2017). Its sedimentary succession comprises alternations of reddish silts and conglomerates, interpreted as Sahara-derived eolian dust and debris-flow deposits (Böhme et al., 2017). In accordance with initial paleoenvironmental interpretations based on mammalian fossils (Gaudry, 1862a, 1862b; Abel, 1922), these sediments represented an open, woodland to woody grassland environment. Stable isotopes and palynology (phytoliths, pollen, microcharcoal) indicate a seasonal, fire-prone savannah biome, with dominance of C4 grasses (Böhme et al., 2017).

In contrast to the mammals, the tortoises from the region, including those from Pikermi, have received little attention. Increased efforts in recent years are beginning to narrow this gap with new turtle records published for numerous regional localities. These include the limit of Miocene/Pliocene of northern

*Corresponding author.

Color versions of one or more of the figures in the article can be found online at www.tandfonline.com/ujvp.



FIGURE 1. Simplified map of the eastern Mediterranean showing the Miocene localities mentioned in the text. Pikermi, the type locality of *Testudo marmorum*, is indicated by the star. Closed circles mark the localities where the presence *Testudo marmorum* is confirmed, whereas open circles mark localities with coeval small-sized testudinids. The landmass configuration in the late Miocene is shown in gray, superimposed on the present configuration (based on Rögl, 1999).

Greece (Vlachos et al., 2015, 2019); the late Miocene of Samos Island (Szalai, 1931), Platania (Drama Basin, Eastern Macedonia and Thrace; Vlachos and Tsoukala, 2014), Plakias (Crete; Georgalis et al., 2016), and Nikiti (Chalkidiki; Garcia et al., 2016); the middle Miocene of Chios (Paraskevaidis, 1955); and the early Miocene of Kastoria (northwestern Greece; Georgalis et al., 2013), Karydia (Rhodope, Eastern Macedonia and Thrace; Georgalis et al., 2019), and Aliveri (Evia Island; Georgalis et al., 2019). This composite fauna, summarized in Georgalis and Kear (2013) and revised in Vlachos (2015), contains at least three small tortoises (*Testudo marmorum*, *Testudo graeca*, and *Testudo* sp.), two giant tortoises (*Titanochelon schafferi* and *Titanochelon* sp.), two freshwater turtles (*Mauremys* sp. and *Mauremys aristotelica*), an indeterminate pan-trionychid, and the only pleurodire from Greece (*Nostimochelone lampra*) (Georgalis et al., 2013, 2016; Vlachos, 2015; Vlachos et al., 2019). In the broader area of southern Balkans, few occurrences of Miocene fossil turtles are known. *Testudo marmorum* is reported from Azmaka (Upper Thrace Basin; Spassov et al., 2012), whereas some poorly preserved specimens are referred from Küçükçekmece (Lower Thrace Basin; Malik and Nafiz, 1933) and Kalimantsi (Sandanski Basin; Kovachev, 2005).

The primary objective of this study is to revise the chelonian material from the late Miocene (MN 12) locality of Pikermi, Greece, focusing on *Testudo marmorum*. We further discuss the distribution of this taxon outside Pikermi based on new material from the upper Miocene locality of Azmaka, Bulgaria, and a reappraisal of all previously published specimens. The new information on this taxon facilitates a discussion on the origin and evolution of the plastral hinge in *Testudo*. We also describe previously published, as well as new, material of the giant tortoise *Titanochelon* from Pikermi and discuss its importance for the Neogene evolution of giant tortoises.

Institutional Abbreviations—**AMPG**, Museum of the National and Kapodistrian University of Athens, Athens, Greece; **LGPOT**, Laboratory of Geology and Paleontology of the School of Geology, Aristotle University of Thessaloniki, Thessaloniki, Greece; **MNHN**, Muséum National d'Histoire Naturelle, Paris,

France; **NHMUK**, Natural History Museum, London, U.K.; **NMNH**, National Museum of Natural History, Sofia, Bulgaria.

MATERIALS AND METHODS

The studied testudinids from Pikermi contain material from the levels of the old excavations of Gaudry, in 1855 and 1860 (reposited in the MNHN), and Woodward and Skoufos, in 1901 (reposited in the NHMUK), as well as material deposited at the AMPG. In addition to these fossils, a single tortoise shell is from the new Pikermi level, PV1, excavated since 2009 (Theodorou et al., 2010). The Liossati material (Bachmayer and Symeonidis, 1977) is stored in the AMPG. The Azmaka material is deposited in the NMNH.

Supplemental Data—Supplemental information for this article includes detailed descriptions of the various shells of *Testudo marmorum* (as Supplemental Data 1) and the files needed to replicate the phylogenetic analysis. In particular, we include the modified (from Vlachos and Rabi, 2018) morphological (as Supplemental Data 2) and total-evidence (as Supplemental Data 3) matrices, the most parsimonious trees (as Supplemental Data 4), and the modified morphological matrix from Luján et al. (2016) (as Supplemental Data 5). See also Appendix 1 for scorings.

LOCALITY INFORMATION

Pikermi, Greece

Pikermi is a famous late Miocene vertebrate locality in the Attica region of Greece (Figure 1). It is situated in the Mesogea Basin, 19 km east-northeast of the center of Athens, by the Megálo Réma rivulet. Perhaps the most reliable information concerning the testudinid fossils in the classical beds of Pikermi comes from Woodward (1901), who mentions the frequent presence of shells of *Testudo marmorum* (mostly fragmented) between and below the red beds, as well as the presence of a well-preserved specimen found in the marl beds between the

upper and lower beds in one pit—these are, most probably, among the NHMUK specimens included in our analysis. Also, it should be noted that it is most likely that both AMPG and NHMUK specimens come from the excavations carried out in Pikermi by Woodward and Skoufos in 1901, because it is documented in various archives that the fossils unearthed from these excavations were shared between NHMUK and AMPG (S.R., pers. observ.). The sedimentology and stratigraphy (bio-, magneto-, and cyclostratigraphy) of the Pikermi site were recently studied by Böhme et al. (2017). Reddish silts, containing vertebrate accumulations, alternate with gravel horizons. The silts are interpreted as aeolian dust deposits, which alternate with debris flows (Böhme et al., 2017). In total, five classical bone-bearing levels (named PV3; Roussiakis et al., 2014) are documented, deposited within 40 ka between 7.33 and 7.29 Ma during the late Tortonian.

In contrast to Gaudry's excavations (1855 and 1860), the excavation of Woodward and Skoufos in 1901 (Woodward, 1901) took place in the upper part of the classical section, dated to between 7.31 and 7.29 Ma (Böhme et al., 2017). The new Pikermi level, PV1 (Theodorou et al., 2010), is situated 500 m downstream from the classical sites. This locality dates slightly younger at 7.27 Ma (Böhme et al., 2017).

Liossati, Greece

Another late Miocene locality in the Attica region was discovered in 1974 by F. Bachmayer and N. Symeonidis near Lake Marathon, 23 km northeast from the center of Athens (Bachmayer and Symeonidis, 1977). The fossil site, published as Liossati, is 4.5 km south-southeast of the city Afidnes (= Kiourka or Liossati; Figure 1). The sediments from which tortoises were discovered can be attributed to the Pikermi Formation (for a description of lithology and definition, see Böhme et al., 2017: suppl. 4 text), based on reddish fine-clastic sediments in alternation with gravels and the associated horse *Cremohipparion mediterraneum* (in Bachmayer and Symeonidis, 1977). The Pikermi Formation is dated to the latest Tortonian and earliest Messinian, from 7.36 to 7.11 Ma (Böhme et al., 2017).

Azmaka 6, Bulgaria

The locality Azmaka is in the Upper Thrace Basin near Chirpan, Bulgaria (Figure 1). The outcropping fluvial to alluvial Ahmatovo Formation has produced, besides a rich mammalian fauna including the oldest potential hominin *Graecopithecus* von Koenigswald, 1972 (Spassov et al., 2012; Fuss et al., 2017), a complete testudinid shell from its uppermost alluvial horizon (AZM6). This layer is dated by magnetostratigraphy to 7.20 Ma at the earliest Messinian (Böhme et al., 2017).

Chronology of Other Referred Material

The stratigraphically oldest tortoise studied here and referred to *Testudo marmorum* is from Nikiti 2 (Central Macedonia, Greece; Garcia et al., 2016). The reddish-brown, fine-clastic sediments from the uppermost part of the Nikiti Formation (Koufos, 2016) are biochronologically dated to between 8.7 and 8.2 Ma (Koufos et al., 2016).

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788, sensu Joyce, Parham, and Gauthier, 2004

CRYPTODIRA Cope, 1868, sensu Joyce, Parham, and Gauthier, 2004

TESTUDINOIDEA Fitzinger, 1826, sensu Joyce, Parham, and Gauthier, 2004

TESTUDINIDAE Gray, 1825, sensu
Joyce, Parham, and Gauthier, 2004
TESTUDONA sensu Parham in Parham et al., 2006a
TESTUDO Linnaeus, 1758
TESTUDO MARMORUM Gaudry, 1862a
(Figs. 2–9)

Nomenclatural Notes—There are some nomenclatural issues concerning *Testudo marmorum* that deserve some detailed explanation. First, we need to clarify which is the publication in which *Testudo marmorum* was originally named. Second, it is necessary to review Gaudry's (1862a, 1862b, 1862–1867) works to understand what kind of type specimens are housed at MNHN (e.g., syntypes, holotypes).

There is considerable discrepancy in the literature regarding original authorship of the name *Testudo marmorum*. The ultimate reason for those discrepancies is that Albert Gaudry named this new taxon in three separate publications using more or less the same words: “J'ai nommé notre tortue de Grèce *Testudo marmorum*, pour rappeler la nature des roches sur lesquelles elle dut se traîner” (in Gaudry, 1862a:504) or “J'ai nommé la tortue fossile de l'Attique *Testudo marmorum* pour rappeler la nature des roches sur lesquelles elle dut se traîner” (in Gaudry, 1862b:635; Gaudry, 1862–1867:317). First of all, the monograph of Gaudry was issued in parts in between 1862 and 1867, and the relevant part containing the description of *Te. marmorum* was issued in 1865; as such, this date is to be adopted (Articles 21.5 and 21.6 of the International Code of Zoological Nomenclature; International Commission on Zoological Nomenclature [ICZN], 1999), and the description certainly postdates the 1862 works. The other two works of Gaudry (1862a, 1862b) refer to the same event, which is the presentation of fossil bones from Pikermi at the meeting of the Academy of Sciences of Paris on March 3, 1862. But, which paper was published first? Because the Comptes Rendus paper (Gaudry, 1862a) is included in the volume of the first semester of 1862 (January to June), whereas the Bulletin paper (Gaudry, 1862b) is included in a volume that includes information from the entire 1862 year, we conclude that the Comptes Rendus paper (Gaudry, 1862a) was published before the Bulletin paper (Gaudry, 1862b) (day of publication incompletely specified; Article 21.3 of the International Code of Zoological Nomenclature [ICZN, 1999]). Also, Comptes Rendus was published on a weekly basis (hence ‘hebdomadaire’); so most likely, Gaudry (1862a) appeared before Gaudry (1862b) and almost immediately after its public presentation on March 3, 1862. Another, indirect, line of evidence supporting this conclusion is that Gaudry (1862–1867:316) cites, in the synonymy of *Te. marmorum*, the Comptes Rendus paper before the Bulletin one. Therefore, the name *Testudo marmorum* should be attributed to Gaudry (1862a).

The second issue concerns the type specimens of *Te. marmorum*. The first publication (Gaudry, 1862a) provides no information regarding the number or identity of the specimens on which the description is based, nor any figure. Gaudry (1862b:634) describes “one of these specimens” (i.e., implying the existence of more than one), which is illustrated in his plate 16, figures 13 and 14; this is a partial shell, preserving both the carapace and the plastron. Later, Gaudry (1862–1867) mentions the existence of three shells, figuring the carapace of a second specimen (Gaudry, 1862–1867:pl. 60, fig. 1) and the plastron of the previously figured specimen (Gaudry, 1862–1867:pl. 60, fig. 2). Both figured specimens were located in the MNHN collections, both under the MNHN PIK 3683 specimen number and both labeled as ‘type’; the third specimen has not been located. As inferred from the original publication(s), Gaudry had clearly worked with more than one specimen when he named the species, and there is no case of a fixed holotype by expression or by monotypy (International Code of Zoological Nomenclature, Articles 73.1.1–73.1.2; ICZN, 1999). In this case, we follow Recommendation 73F

(International Code of Zoological Nomenclature; ICZN, 1999) and treat them as syntypes. We choose the specimen MNHN PIK 3683a (new number; partial shell consisting of both the carapace and the plastron) figured by Gaudry (1862b:pl. 60, fig. 1) and herein (Fig. 3A–G) as the lectotype by present designation. The other specimen, MNHN PIK 3683b (Fig. 3H–J, new number; Gaudry 1862–1867:pl. 60, fig. 2), becomes the paralectotype; should it be discovered, the third specimen implied by Gaudry (1862–1867) would also be a paralectotype.

Type Material—MNHN PIK 3683a (lectotype by present designation; see previous section), a partial shell (Fig. 3A–G).

Type Locality—Pikermi, Attica, Greece; classical layers, 7.33–7.29 Ma, late Miocene, late Tortonian (MN 12).

Referred Material—Pikermi, Greece (late Miocene), MNHN collection (Fig. 3H–J); MNHN PIK 3683b (paralectotype by present designation); AMPG collection (Figs. 4–7): AMPG PIK 1970/1a, partial shell (Fig. 6B); AMPG PIK 1970/1b, partial shell (Fig. 4A); AMPG PIK 1970/1c, partial plastron (Fig. 4C); AMPG PIK 1970/1d, partial shell (Fig. 5); AMPG PIK 1970/1e, highly fragmented shell (Fig. 4D); AMPG PIK 1970/1f, partial shell (Fig. 6A); AMPG PIK 1970/1g, partial shell (Fig. 4B); NHMUK collection (Figs. 7, 8): NHMUK R 4328, partial shell (Fig. 7A); NHMUK R 4329, partial shell (Fig. 7B); NHMUK R 4332, partial plastron (Fig. 8A); NHMUK R 4333, partial shell (Fig. 8E); NHMUK R 4334, costal plate (Fig. 8D); NHMUK R 4335, partial plastron (Fig. 8B); NHMUK R 4336, partial plastron (Fig. 8C). Azmaka 6, Bulgaria, NMNHS collection (Fig. 9): NMNHS AZM-6-2857, almost complete shell. Nikiti 2, Central Macedonia, Greece (late Miocene, early Turolian, MN 11), LGPUT collection: LGPUT NIK-1946, almost complete shell (referred to *Testudo* cf. *marmorum* by Garcia et al., 2016).

Possible Referred Material—Pikermi (late Miocene, Greece): AMPG PV1/1849, partial shell in a block of bones (Fig. 10).

Distribution—South Balkan Peninsula: upper Miocene of Pikermi (Attica) and Nikiti 2 (Chalkidiki, Central Macedonia), Greece, and Azmaka, Bulgaria. The taxon was also mentioned from the upper Miocene of Halmyropotamos, Euboea Island (Melentis, 1970). However, that material was never figured or described, and we were unable to locate that in the collections of the AMPG, or in the specimens list from Halmyropotamos provided by I. Melentis (S.R., pers. observ.). Therefore, the occurrence of *Te. marmorum* in Halmyropotamos cannot be confirmed, but it would fall within the proposed range of this taxon.

Emended Diagnosis—Testudinidae based on the presence of a well-developed epiplastral lip, well-developed anterior and posterior buttresses, lateral coincidence between the costoperipheral sutures and the pleuromarginal sulci, presence of a supracaudal, and short pectoral scutes. Testudona based on the absence of contact between marginal 6 and pleural 3. *Testudo* based on the presence of a hinge between the hypoplastra and the xiphoplastra, at least in male adults. Differs from other species of *Testudo* by the following combination of characters: cervical scute short and narrow, vertebral 1 lyre-shaped, pleural 1 covers lateral parts of the nuchal, there is no coincidence between the anterior pleuromarginal sulci and costoperipheral sutures and the first two marginals expand on costal 1, suprapygal 1 is boomerang-shaped, embracing the smaller suprapygal 2, and gular scutes are short and cover the anterior part of the entoplastron.

Description

The anatomy of male adult individuals of *Testudo marmorum* is summarized in the reconstruction shown in Figure 2. This reconstruction is based mainly on the lectotype and paralectotype from MNHN, whereas the remaining specimens from AMPG and NHMUK helped reconstruct the missing parts. Below, we provide a detailed description of the morphology of *Testudo*

marmorum, and individual specimens are cited when necessary. Detailed anatomical descriptions of each specimen are given in the supplemental information.

Preservation and Measurements—The lectotype (MNHN PIK 3683a; Fig. 3A–G) is incomplete, missing the entire left portion and posterior rim and measures 181 mm, with an estimated minimum carapace length of 185 mm. The carapace is deformed, resulting in an overlap of the costal plates onto the neural series. This prevents a clear observation and description of the neurals. Most of the plastron is preserved, and only the lateral parts of the hyo- and hypoplastra are missing. The sediment filling the shell is preserved, which prevents direct observation of the visceral surfaces. The paralectotype (MNHN PIK 3683b; Fig. 3H–J) preserves most of the carapace and measures 102 mm in length, with an estimated minimum carapace length of 120 mm. We consider this a juvenile specimen based on its small size. Referred specimens (Figs. 4–10) include partial and almost complete shells (AMPG PIK 1970/1a, with an estimated minimum carapace length of 170 mm; AMPG PIK 1970/1d, with a carapace length of 213 mm; AMPG PIK 1970/1e, with an estimated carapace length of 200 mm; AMPG PIK 1970/1f, with a carapace length of 200 mm; NHMUK R 4328, measuring 166 mm, with an estimated minimum carapace length of 180 mm; NHMUK R 4329, measuring 159 mm, with an estimated minimum carapace length of 190 mm; NHMUK R 4333; NMHMS AZM-6-2857, with a carapace length of 196 mm), complete plastra (AMPG PIK 1970/1g, measuring 208 mm, with an estimated carapace length of 210 mm), and partial plastra (AMPG PIK 1970/1c, measuring 62 mm, with an estimated carapace length of 160 mm; NHMUK R 4332, NHMUK R 4335, and NHMUK R 4336).

Carapace—The nuchal plate is hexagonal, slightly wider than long, with a clear nuchal notch in some specimens (e.g., NHMUK R 4328, NMHMS AZM-6-2857) constricted only in the anterior part of the nuchal and not expanding on the peripherals, and without nuchal notch in others (e.g., MNHN PIK 3683a). The first neural is quadrangular, significantly longer than wide. Neurals 2 and 4 are octagonal, whereas neurals 3 and 5 are quadrangular, wider than long. Neurals 6–7 are hexagonal, with the shorter lateral sides placed anteriorly. Neural 8 is quadrangular, wider than long, and quite reduced in size compared with the other neurals. Two suprapygals are present, suprapygal 1 being boomerang-shaped and embracing suprapygal 2, which is much smaller, semicircular, and wider than long. The pygal is elongated, quadrangular, with wider anterior end; no pygal notch is present, and the pygal is curved inward. All costals are wider than long, but costal 1 is significantly longer than the rest. Costal 1 makes contact with the nuchal, anterior peripherals (probably peripherals 1–3), and neurals 1–2. Costals 2–5 show an alternating pattern: costals medially short and laterally long (costals 2 and 4) alternated with others that are medially long and laterally short (costals 3 and 5). Costals 6–7 are not differentiated, corresponding with the hexagonal neurals. In the anterior part, a short and narrow cervical is present. The first vertebral is narrowed anteriorly, and pleural 1 covers the edges of the nuchal in some specimens (e.g., NHMUK R 4328, NMHMS AZM-6-2857). The marginals are long, and the pleuromarginal sulci coincide with the costoperipheral sutures all along the carapace (except on the nuchal of course). The remaining vertebrae are wider than vertebral 1, but all are narrower than the pleurals. Neurals 1, 3, 5, and 8 are crossed transversely by the vertebral sulci. Pleurals 2, 4, and 6 are crossed by the pleural sulci. Marginals 1 and 2 are fused into a supracaudal. Overall, there is good coincidence between the pleuromarginal sulci and the costoperipheral sutures, except on the anterior part of some specimens (e.g., NHMUK R 4328), where the marginals cover the entire peripherals and slightly expand on costal 1.

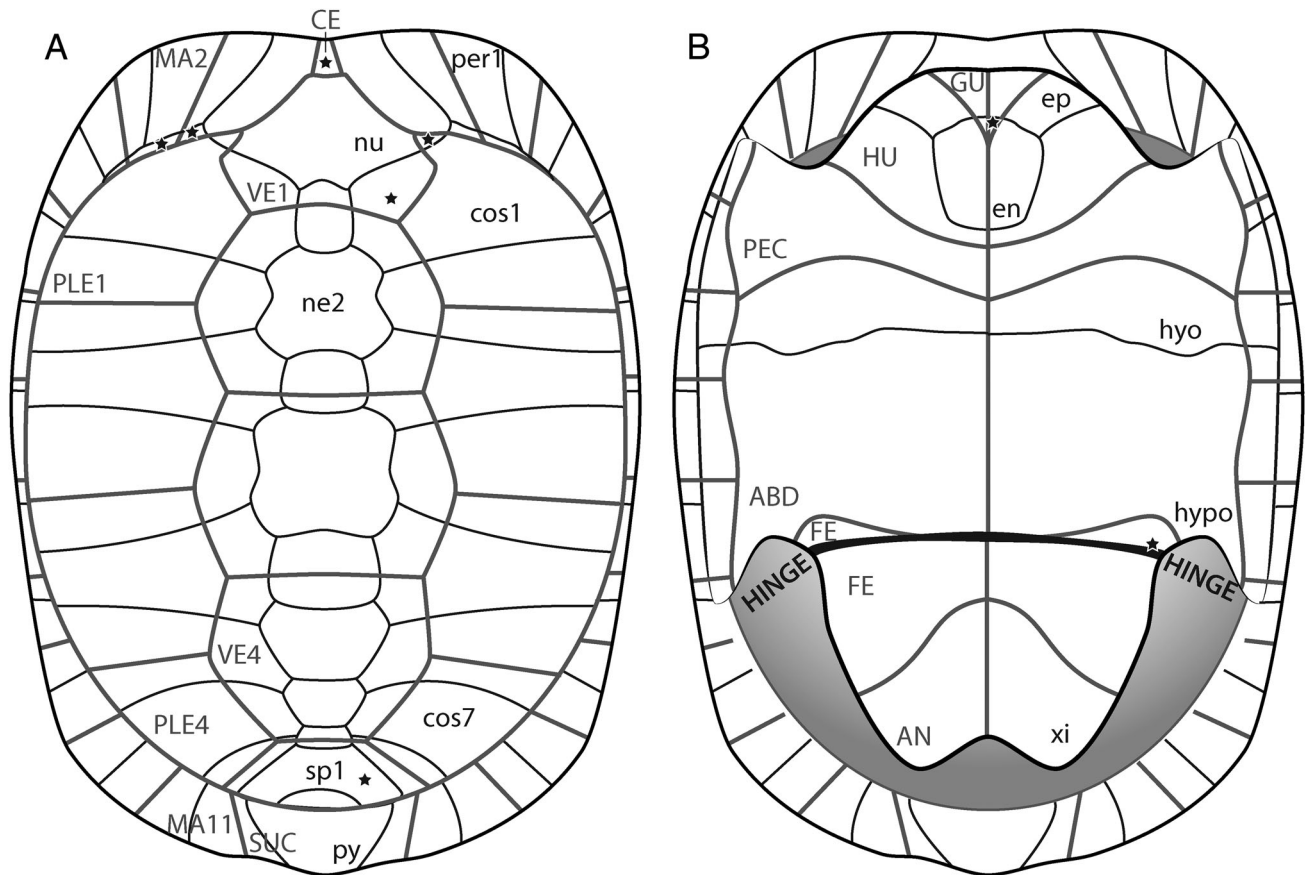


FIGURE 2. *Testudo marmorum* Gaudry, 1862a, reconstruction of the shell morphology of an adult male individual based on the material presented herein. **A**, carapace; **B**, plastron. Thin black lines indicate sutures, thicker black lines represent margins, and thick gray lines represent sulci. Stars indicate areas of the shell important for the diagnosis of this taxon. In the abbreviations, bony plates are indicated with small letters and scutes with capital letters. **Abbreviations:** ABD, abdominal; AN, anal; CE, cervical; cos, costal; en, entoplastron; ep, epiplastron; FE, femoral; GU, gular; HU, humeral; hyo, hypoplastron; hypo, hypoplastron; MA, marginal; ne, neural; nu, nuchal; PEC, pectoral; per, peripheral; PLE, pleural; sp, suprapygal; SUC, supracaudal; VE, vertebral; xi, xipliplastron.

Plastron—The epiplastra are short and wide, being restricted in the anterior part of the lobe. The anterior border of the epiplastra is rounded in some specimens (e.g., NHMUK R 4328) and straight in others (e.g., NMHMS AZM-6-2857). The entoplastron is long, narrow, and hexagonal. Hyo- and hypoplastra are long and wide. The gulars are long and narrow, covering the anterior part of the entoplastron. The gularohumeral sulcus forms an acute angle with the midline. The remaining part of the entoplastron is covered by the humerals. The humeropectoral sulcus is wide, forming a wide angle with the midline, and is located posterior to the entoplastron. The pectorals are short and wide. The pectoroabdominal sulcus is curved, being concave medially and convex laterally. The abdominals are long, covering the posterior parts of the hypoplastra and nearly the entire ventral surface of the hypoplastra. Only the posterior lateral parts of the hypoplastra are covered by the femorals. Most of the specimens had a hypo-xipliplastral hinge (e.g., MNHN PIK 3682a, AMPG PIK 1970/1b, 1d–1f, NHMUK R 4328, NHMUK R 4333, NMHMS AZM-6-2857). In those specimens, there is a medial coincidence of the abdominofemoral sulcus with the hypo-xipliplastral suture, a small covering of the femoral onto the hypoplastra, and absence of a sutured connection between the hypoplastra and the xipliplastra (as indicated by the absence of the xipliplastra), all indicative of the presence of the hinge. In some specimens (e.g., NMHMS AZM-6-2857), the xipliplastra are completely missing, further indicating the presence of a

movable lobe. However, some specimens do not share this morphology. In the plastron of AMPG PIK 1970/1f (Fig. 6A), the posterior parts of the hypoplastra make a slight contribution to the posterior lobe, and the abdominofemoral sulcus is situated anterior to the suture. However, the xipliplastra make a large contribution to the posterior lobe, especially when compared with hingeless taxa. Also, the anterior side of the xipliplastra is straight and almost perpendicular to the axis. This indicates that a hinge may have been present, but incompletely developed; this would be similar to the hinge in some older female individuals of *Chersine hermanni* (Gmelin, 1789). Similarly, the plastron of AMPG PIK 1970/1a (Fig. 6B) has a posterior lobe that is not formed entirely by the xipliplastra. The hypoplastron is crossed by the abdominofemoral sulcus, which is strongly convex. Although the preserved part is small, it seems possible that the sulcus is not situated close to the hypo-xipliplastral suture. See Discussion for further information on the presence of hinge in this species. The femoroanal sulcus is generally omega-shaped, except in some specimens (e.g., AMPG PIK 1970/1d, 1f) where it is straight and forms an acute angle. In all cases, however, the medial length of the anals is longer than the medial length of the femorals.

Based on the presence of a concavity in the hyo-hypoplastral region, we can estimate that MNHN PIK 3683a, AMPG PIK 1970/1d, NHMUK R 4328, and NMHMS AZM-6-2857 were male individuals, whereas AMPG PIK 1970/1f was a female.

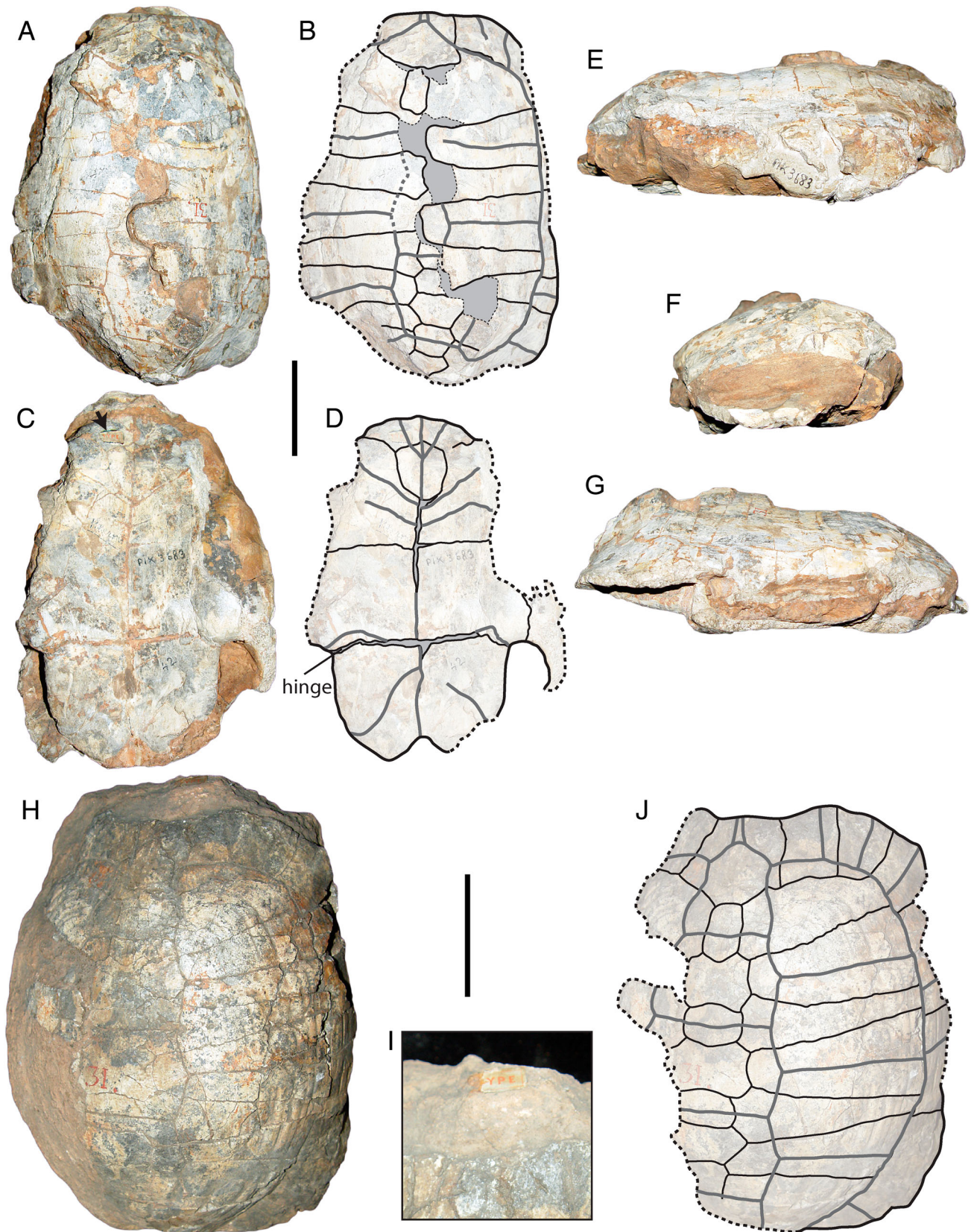


FIGURE 3. *Testudo marmorum* Gaudry, 1862a, type material. A–G, MNHN PIK 3683a, lectotype: A, dorsal view; B, drawing of the dorsal view; C, ventral view; D, drawing of the ventral view; E, left lateral view; F, anterior view; G, right lateral view. H–J, MNHN PIK 3683b, paralectotype: H, dorsal view; I, detail (showing the label 'TYPE'); J, drawing of the dorsal view. Scale bars equal 50 mm.

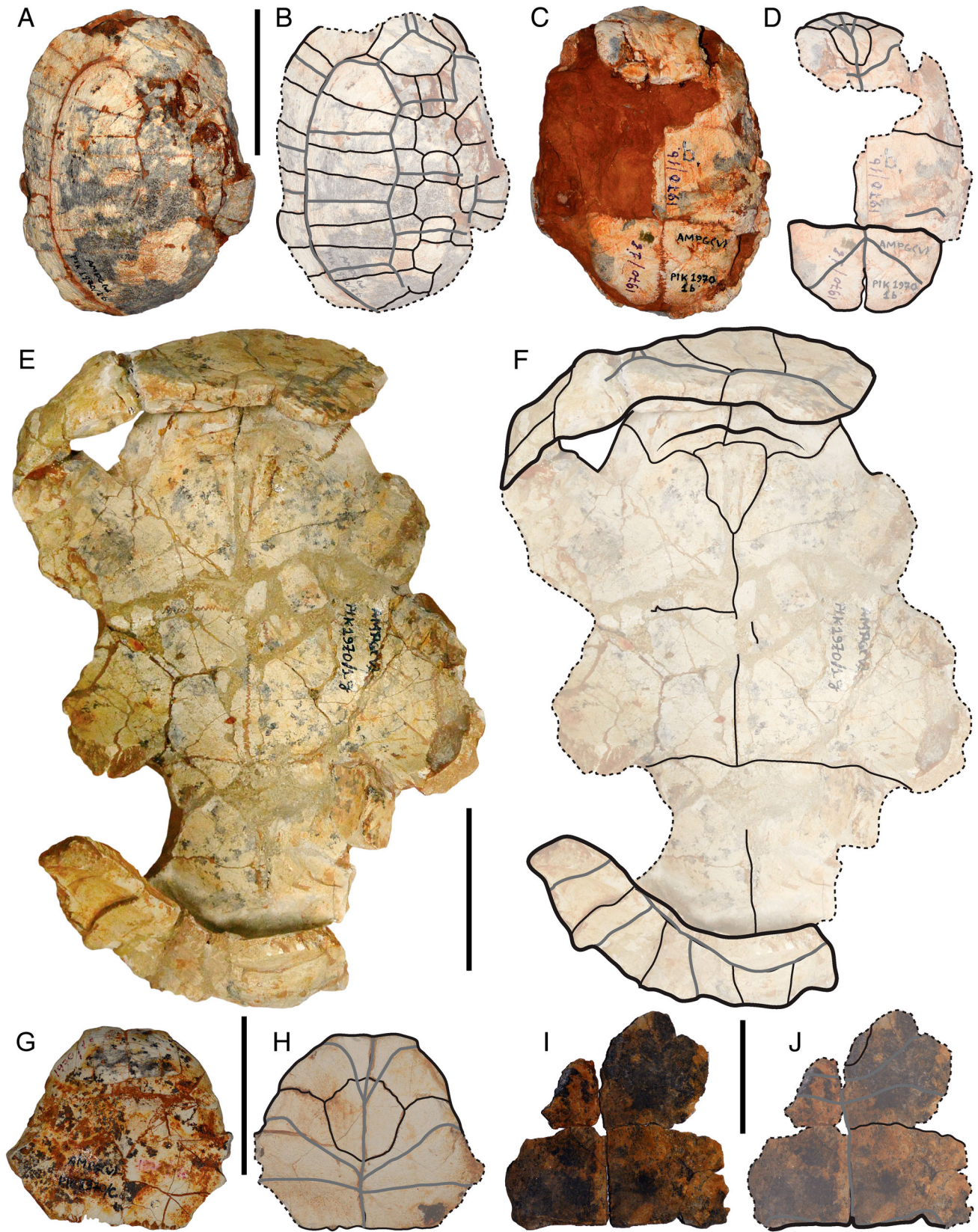


FIGURE 4. *Testudo marmorum* Gaudry, 1862a, referred material. **A–D**, AMPG PIK 1970/1b, partial shell: **A**, dorsal view; **B**, drawing of the dorsal view; **C**, ventral view; **D**, drawing of the ventral view. **E, F**, AMPG PIK 1970/1g, partial shell: **E**, visceral view; **F**, drawing of the visceral view of the plastron. **G, H**, AMPG PIK 1970/1c, anterior plastron: **G**, visceral view; **H**, drawing of the ventral view. **I, J**, AMPG PIK 1970/1e, partial plastron: **I**, ventral view; **J**, drawing of the ventral view. Scale bars equal 50 mm.

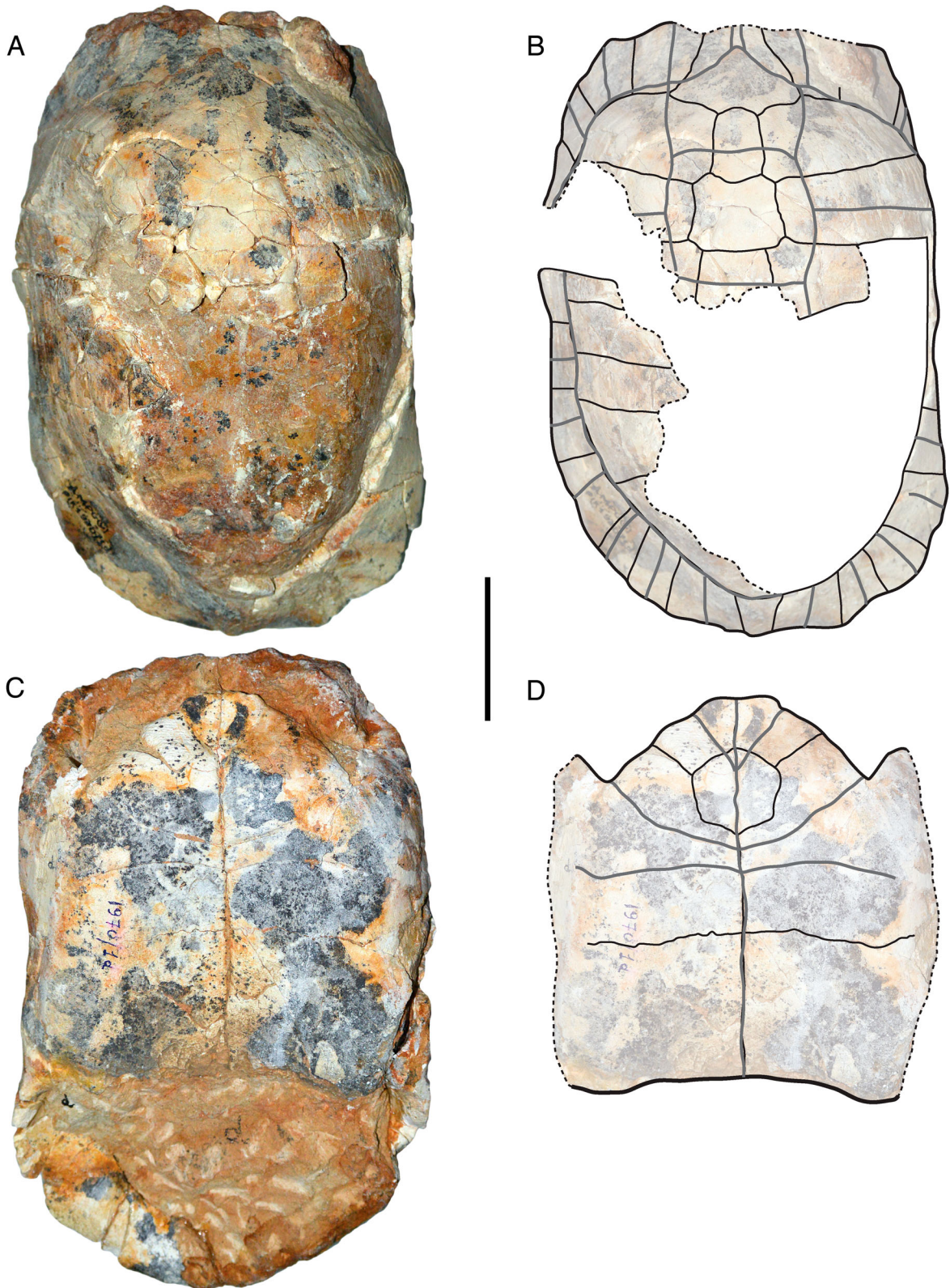


FIGURE 5. *Testudo marmorum* Gaudry, 1862a, AMPG PIK 1970/1d, referred material, partial shell. **A**, dorsal view; **B**, drawing of the dorsal view; **C**, ventral view; **D**, drawing of the ventral view. Scale bar equals 50 mm.

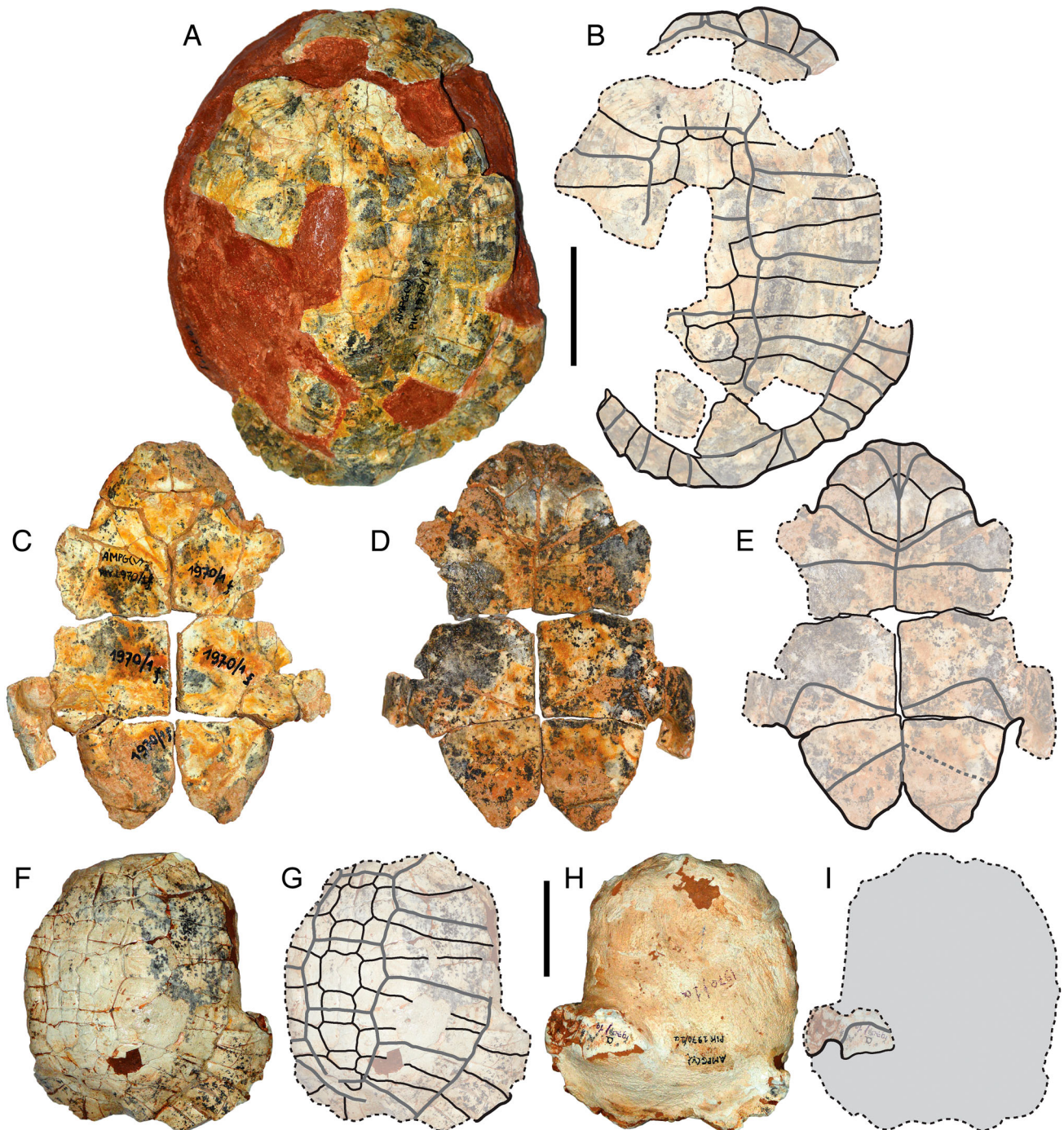


FIGURE 6. *Testudo marmorum* Gaudry, 1862a, referred material from the upper Miocene of Pikermi, Attica. **A–E**, AMPG PIK 1970/1f, a partial shell, with an incompletely developed hinge: **A**, dorsal view; **B**, drawing of the dorsal view; plastron: **C**, dorsal/visceral view; **D**, ventral view; **E**, drawing of the ventral view. **F–I**, AMPG PIK 1970/1a, a partial shell: **F**, dorsal view; **G**, drawing of the dorsal view; **H**, ventral view; **I**, drawing of the ventral view. Scale bars equal 50 mm.

TESTUDO cf. *MARMORUM*
(Fig. 10)

AMPG PIK PV1/1849

This specimen preserves the entire plastron and parts of the anterior carapace. Its recovery position in a big block of bones hinders observation of most of its morphological characters.

The specimen measures 135 mm, allowing the estimation of a minimum carapace length of 150 mm for this individual. Based on the observable characters, there is no evidence of a hypoxiphiplastral hinge, because the xiphiplastra appear to be firmly attached to the hypoplastra. The inability to observe the ventral side does not allow confirming the presence of a hingeless small testudinid in Pikermi or its attribution to *Testudo marmorum* (see above for specimens with a not so evident hinge and below for further discussion). The flat surface of the visceral side of

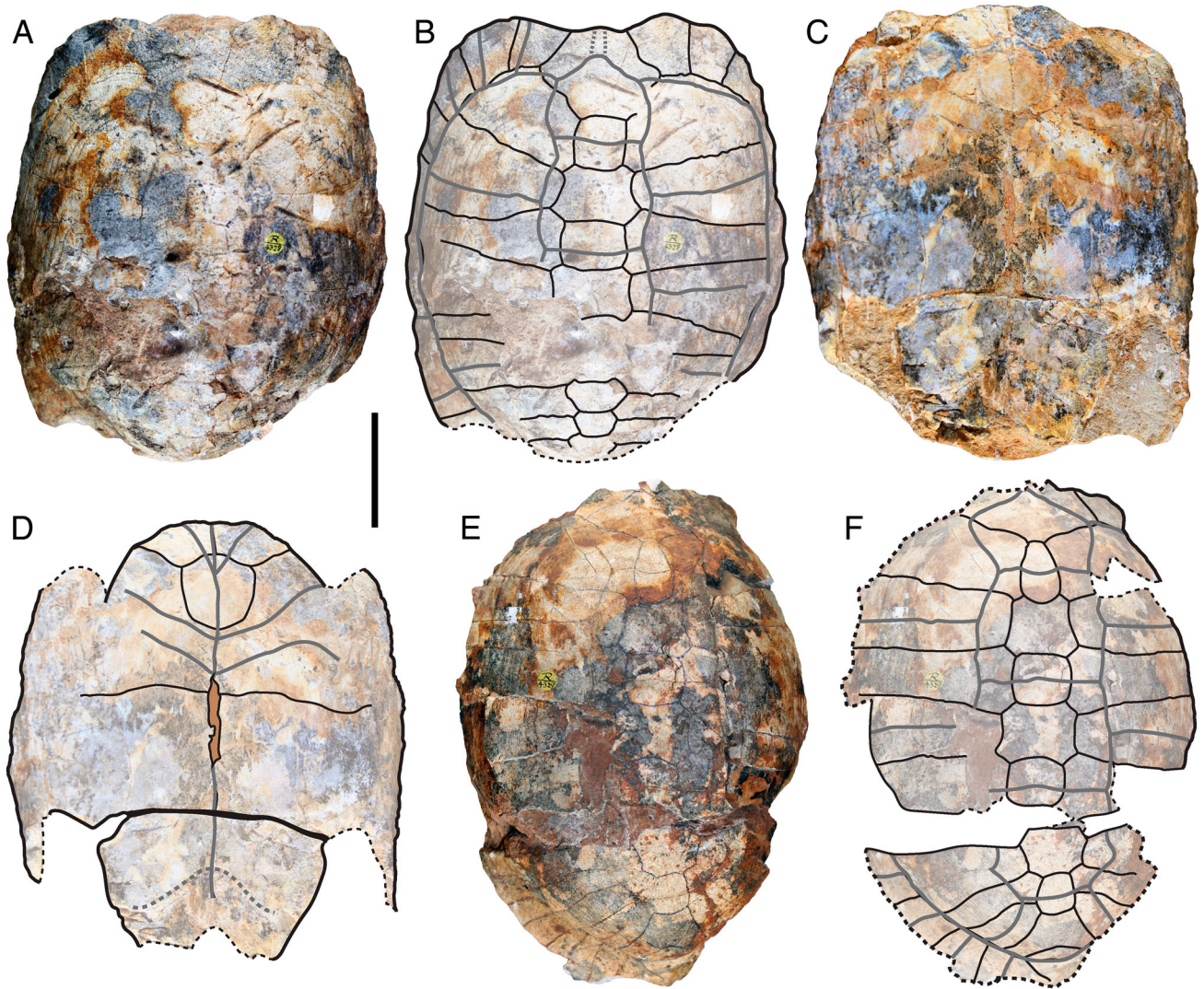


FIGURE 7. *Testudo marmorum* Gaudry, 1862a, referred material from the upper Miocene of Pikermi, Attica. **A–D**, NHMUK R 4328, an almost complete shell: **A**, dorsal view; **B**, drawing of the dorsal view; **C**, ventral view; **D**, drawing of the ventral view. **E, F**, NHMUK R 4329, an almost complete carapace: **E**, dorsal view; **F**, drawing of the dorsal view. Scale bar equals 50 mm.

the plastron tentatively indicates a female individual. In the absence of clear evidence of other species of small-sized testudinids in Pikermi, we tentatively refer this specimen to *Te. marmorum*, pending a further preparation of the specimen.

Remarks

Other Specimens—Recently, Garcia et al. (2016) described a complete shell of a tortoise (LGPOT NIK 1956) from the late Miocene of Nikiti 2, northern Greece. It was attributed to *Testudo* cf. *marmorum* because some of the observed characters were outside the known morphological variation of *Testudo marmorum*. In particular, Garcia et al. (2016) pointed out the well-rounded carapace shape and the presence of a quadrangular, elongated, and well-curved pygal as differences between the Nikiti and *Te. marmorum* specimens. Where no deformation is present, complete shell specimens from Pikermi indicate that this rounded shape (e.g., Figs. 5, 7A) and even a similar size can be reconstructed for the MNHN paralectotype. Also, where preserved, the pygal from Pikermi specimens has the same

morphology as in the Nikiti one, although some, probably intraspecific, differences can be noted in the width of the pygal. These morphologies are evident in the material from the type locality, as well as the specimen from Azmaka, Bulgaria (Fig. 9). Therefore, we refer the Nikiti specimen of Garcia et al. (2016) to *Testudo marmorum*. As mentioned by Garcia et al. (2016), a ventral concavity in the hyo-hyoplastral region suggests that it was a male.

Another locality and fauna that merits discussion from a temporal and geographic point of view is the late Miocene (late Vallesian, MN 10, ~9.5 Ma; Kostopoulos and Sen, 2016) Küçükçekmece site from the Lower Thrace Basin (European Turkey; Malik and Nafiz, 1933; Nicolas, 1978). Malik and Nafiz (1933) identified a *Testudo* cf. *marmorum* and a large-sized tortoise. These occurrences were reidentified by Nicolas (1978; as *Testudo* sp. of small and large sizes, respectively) and Staesche et al. (2007; as *Testudo* cf. *graeca* and *Cheirogaster* cf. *bolivari*, respectively). Although older than our investigated samples, it is possible that this material belongs to *Te. marmorum*, but a revision of these specimens is necessary. Similarly, Staesche et al. (2007) identified several other small testudinid specimens from

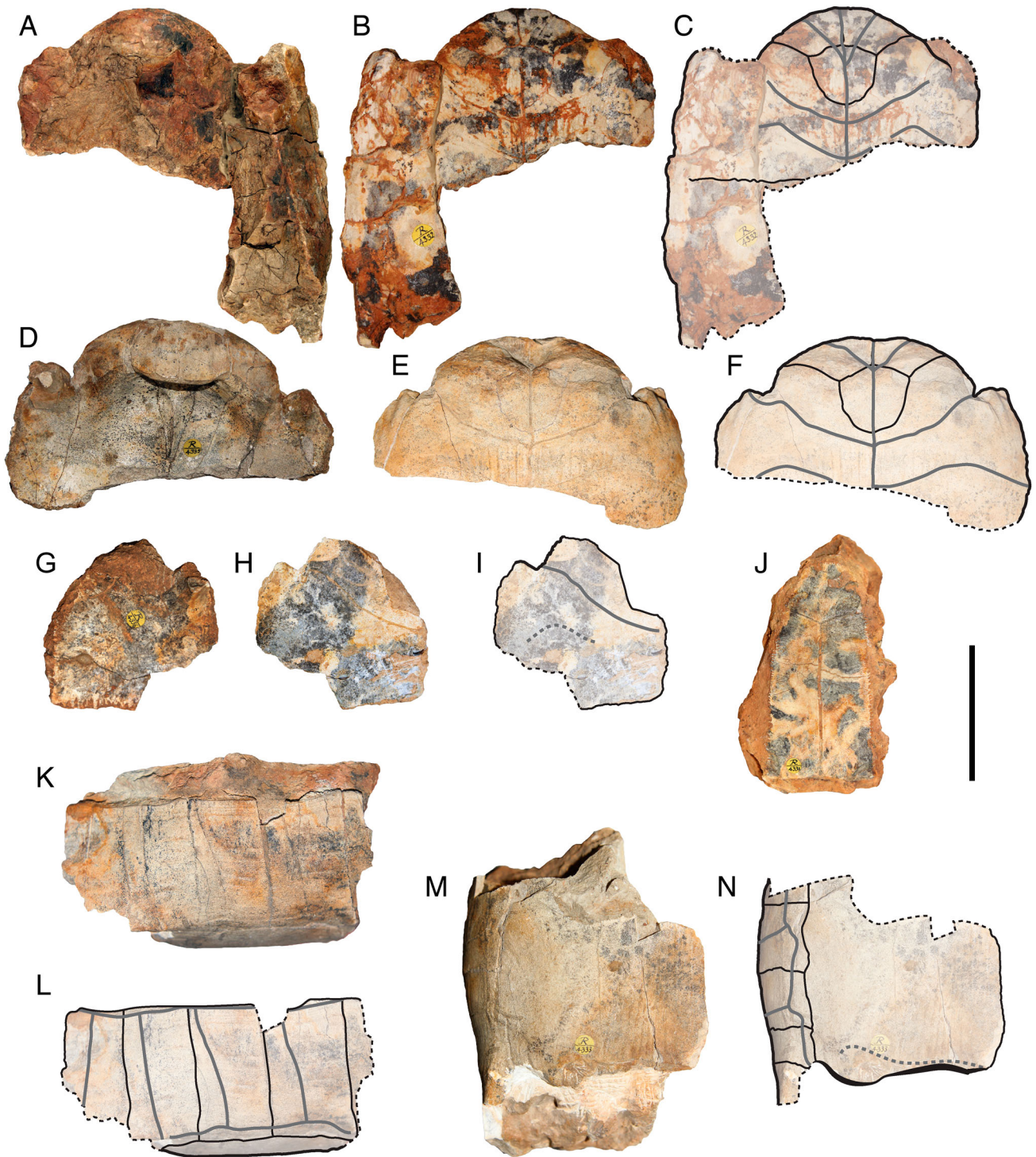


FIGURE 8. *Testudo marmorum* Gaudry, 1862a, referred material from the late Miocene of Pikermi, Attica. **A–C**, NHMUK R 4332, a partial plastron: **A**, visceral view; **B**, ventral view; **C**, drawing of the ventral view. **D–F**, NHMUK R 4335, a partial plastron: **D**, visceral view; **E**, ventral view; **F**, drawing of the ventral view. **G–I**, NHMUK R 4336, a partial hyoplastron: **G**, visceral view; **H**, ventral view; **I**, drawing of the ventral view. **J**, NHMUK R 4334, a costal plate in dorsal view. **K–N**, NHMUK R 4333, a partial shell: **K**, lateral view; **L**, drawing of the lateral view; **M**, ventral view; **N**, drawing of the ventral view. Scale bar equals 50 mm.

mainland Turkey as *Testudo* cf. *graeca* (for further information, see Fig. 1). Regarding their most complete specimen, identified as a juvenile of *Cheirogaster* cf. *bolivari*, Pérez-García and Vlachos (2014) showed that it is not representative of a giant

tortoise taxon but rather a small-sized one (possibly *Agrionemys*). It is nevertheless essential to revise those specimens to delimit the temporal and geographic distribution of *Te. marmorum*. Kovachev (2005) described some tortoise specimens from the upper

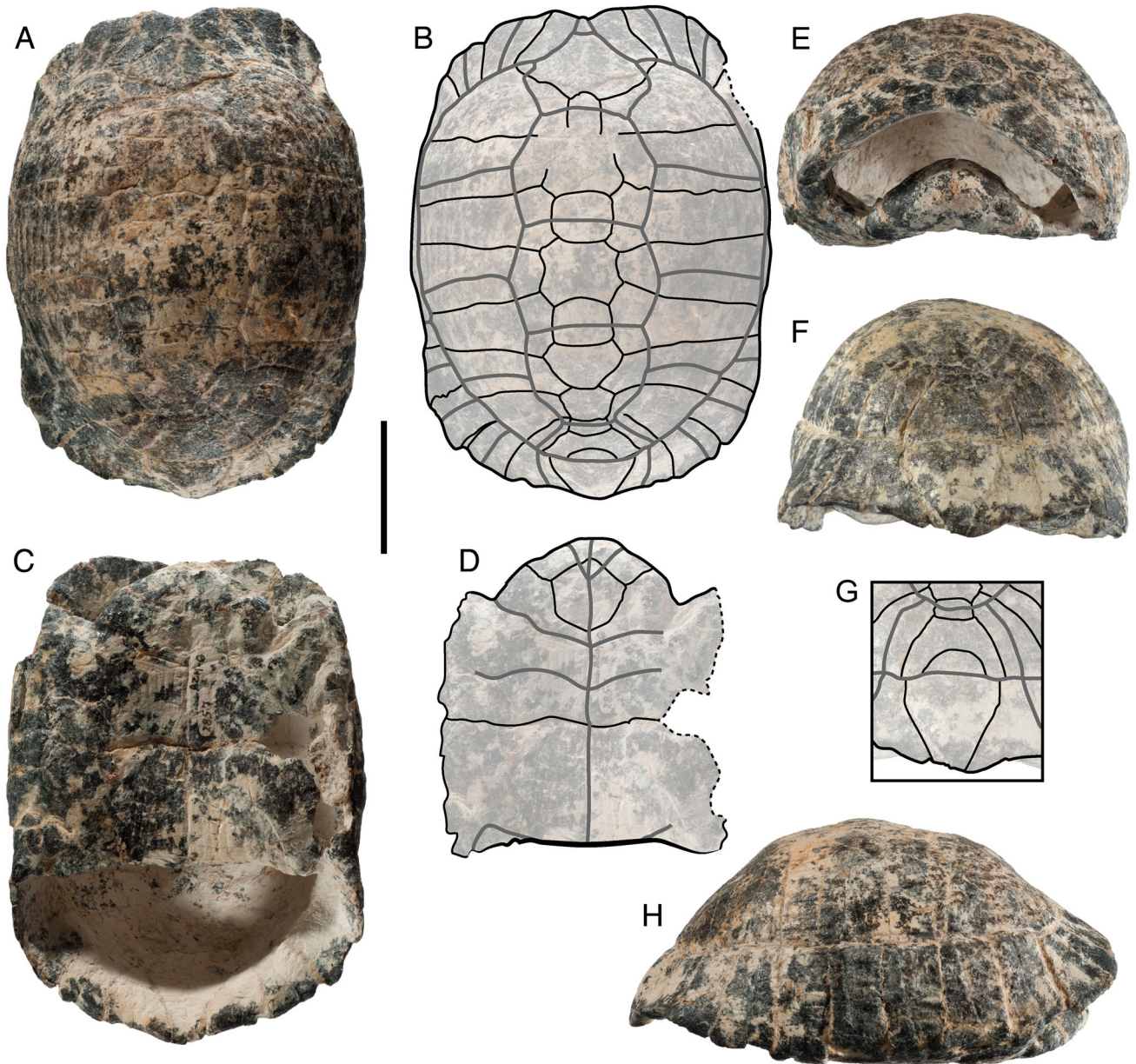


FIGURE 9. *Testudo marmorum* Gaudry, 1862a, AZM-6-2857, a new specimen from the late Miocene of Azmaka, Bulgaria. **A**, dorsal view; **B**, drawing of the dorsal view; **C**, ventral view; **D**, drawing of the ventral view; **E**, anterior view; **F**, posterior view; **G**, drawing of the posterior view; **H**, right lateral view. Scale bar equals 50 mm.

Miocene of Kalimantsi (Bulgaria), attributing them to *Testudo* cf. *antiqua* and *Testudo* sp. These specimens should be revised in the future, because some of them (especially the partial shell figured in Kovachev, 2005:pls. 1.1–1.3) show a general morphology that could be consistent with *Testudo marmorum* (presence of a hypo-xiphiplastral hinge, pleural 1 possibly expanding onto the nuchal).

Ontogenetic Changes in *Testudo marmorum*—The existence of several shells of different sizes and sexes allows us to codify and analyze with an ontogram the morphological variability from various points of view (see Ezcurra and Butler, 2015, and references therein), including intraspecific variation, sexual dimorphism, and ontogeny. In this method, the specimens are first arranged in an ontogenetic order. In the absence of any other

potential source of information, we use the total estimated carapace length as a guide to relative ontogenetic stage. In this sense, AMPG PIK 1970/1b, the smallest specimen, is classified as a possible juvenile, AMPG PIK 1970/1a is classified as possibly close to the subadult/adult limit, whereas the rest (exceeding 180 mm in length) are ordered by increasing size as adults (Fig. 11). The next step is to map the variable characters to this constructed ontogram and observe their distribution. Some of them do not show any clear distribution, for example, the presence/absence of a hinge (only in the confirmed females; see the next section for more information), the presence/absence of nuchal notch, and the presence/absence of coincidence between the costoperipheral sutures and the pleuromarginal sulci. The first character could be associated with sexual dimorphism (because it coincides

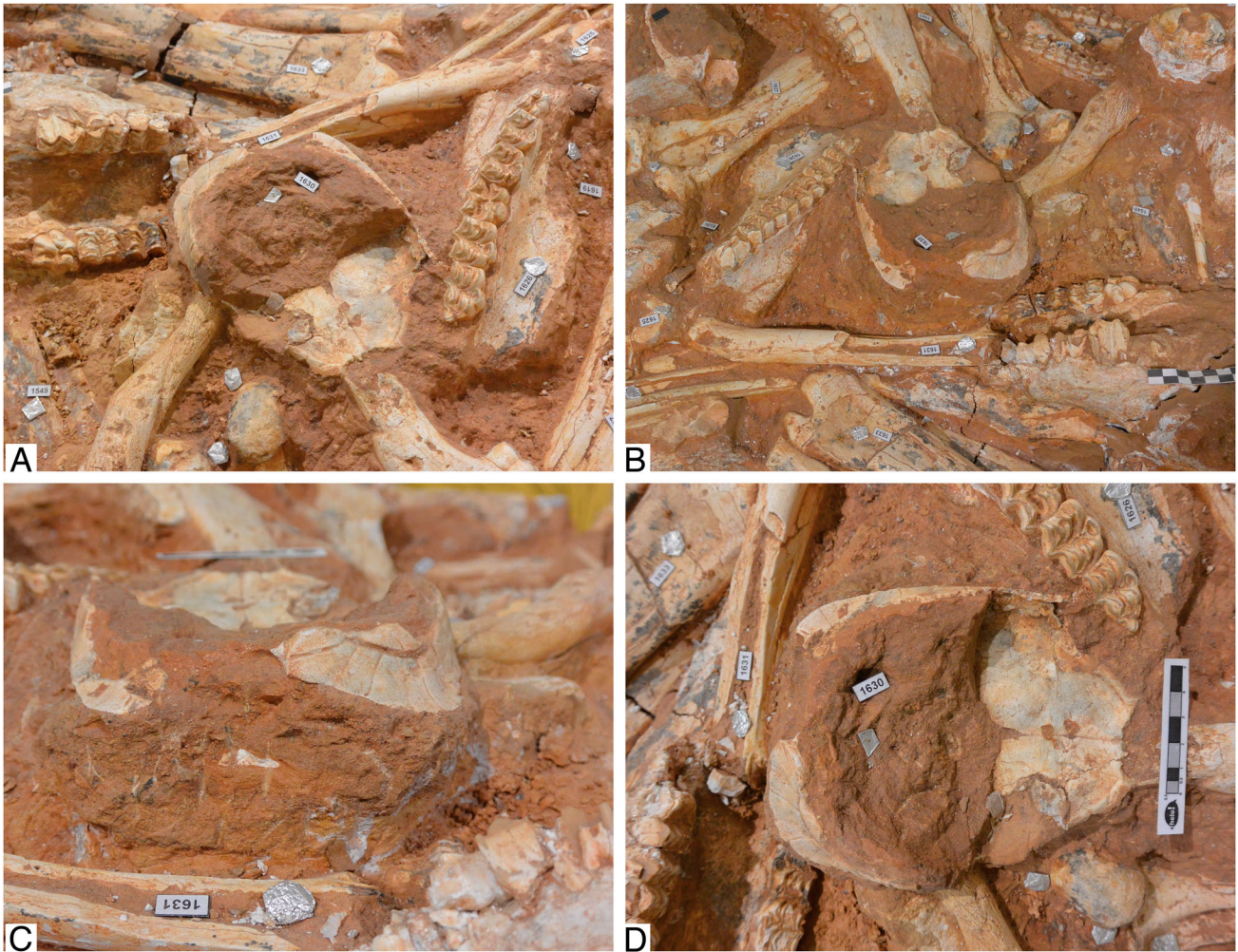


FIGURE 10. *Testudo* cf. *marmorum*, AMPG PIK PV1/1849, partial shell, referred specimen from the late Miocene of Pikermi, Attica, preserved in a big block of fossils collected during recent excavations in the PV1 locality. The shell lies on its plastron in **A**, posterolateral, **B**, anterolateral, **C**, anterior, and **D**, dorsal views. Scale bar equals 50 mm.

with the female specimen), whereas the distribution of the last two characters suggests that this character is due to intraspecific variation (because it does not show any sexual or ontogenetic coincidence). But because we have only one confirmed female individual, we cannot exclude the possibility that the presence of the hinge is also due to intraspecific variation. However, other variable characters show a clearer distribution on the tree, as revealed through mapping of the scored characters on this constructed topology. For example, the smallest specimen does not have an anal notch. The two smaller specimens demonstrate a vertebral 1 with equal anterior and posterior lengths and a pleural 1 that does not cover the lateral parts of the nuchal. Finally, the largest specimens show a femoroanal sulcus that forms an acute angle with the midline. We therefore interpret and suggest that these changes are the result of ontogenetic changes that occur in the shell of *Te. marmorum*.

Testudo Taxonomy Hinges upon the Hinge—The presence of the hypo-xiphialastral hinge is a crucial character for the taxonomy of the *Testudo* complex, allowing the distinction of a derived *Testudo* s.s. group (sensu Lapparent de Broin et al., 2006, and references therein) that contains the extant *Te. graeca* Linnaeus, 1758, *Te. marginata* Schoepff, 1793, *Te. kleinmanni* Lortet, 1883, and possibly several extinct taxa such as *Te.*

marmorum. The taxonomy of hingeless taxa such as ‘*Testudo*’ *hermanni* has been controversial (Lapparent de Broin et al., 2006; Parham et al., 2006a), and currently it is considered to be nested within *Chersine* Merrem, 1820 (Fritz and Bininda-Emonds, 2007). However, Lapparent de Broin et al. (2006:281) mentioned that old females of *Chersine hermanni* (*Eurotestudo hermanni* therein) “[...] feature a hypo-xiphialastral partial hinge (lateral), without the coincidence of the abdomino-femoral sulcus and the hinge (the suture) laterally.” This is further confirmed by examination of extant specimens (E.V., pers. observ. of extant tortoise specimens in LGPUT and MNHN). Just as some stem *Testudo* could develop a hinge (i.e., *Chersine hermanni*), the opposite scenario is observed in some populations of crown *Testudo*. There is a specific population in the Araks River Valley that comprises tortoises with a low-domed shell and hingeless plastron; this is considered to represent the typical *Testudo armeniaca* Chkhikvadze and Bakradze, 1991, morphotype, which is currently mostly considered to be a subspecies of *Testudo graeca* (Parham et al., 2006b; Arakelyan et al., 2018, and references therein). Another testudinid taxon, *Pyxis* Bell, 1827, presents a hypo-xiphialastral hinge in old females, as well as a hinge on the anterior plastral lobe in some cases (see Bour, 1981). Outside Testudinidae, the presence of a hinge is related to sexual dimorphism in *Heosemys*

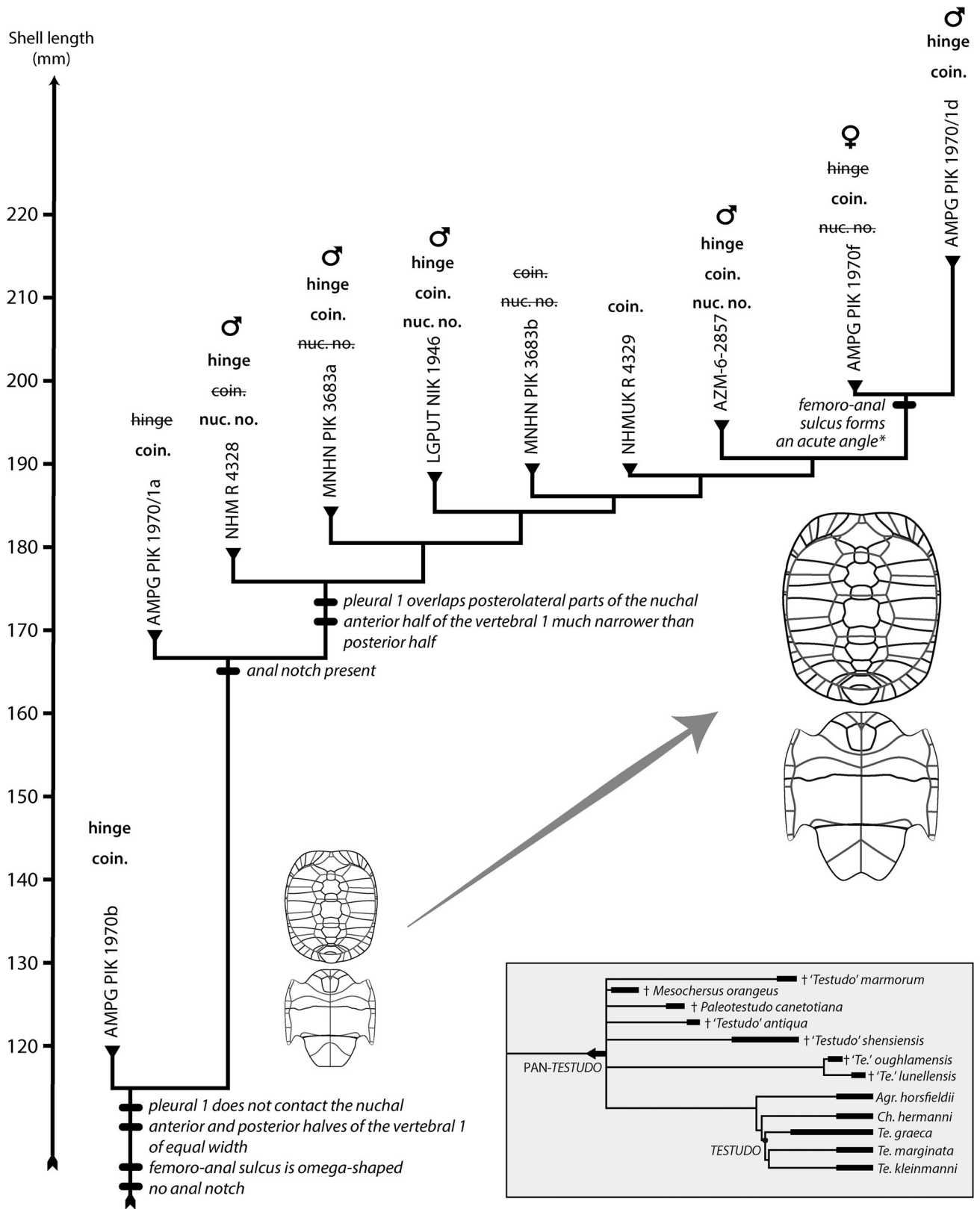


FIGURE 11. Ontogram showing the relative ontogenetic changes in the shell of *Testudo marmorum*. Specimens are ordered according to their estimated length. Selected characters that could be due to ontogenetic changes are mapped on the nodes. Selected characters that could be due to sexual dimorphism or intraspecific variation (presence/absence of the hinge, the coincidence [coin.] between sutures and sulci, and presence/absence of the nuchal notch [nuc. no.]) are shown next to the terminals. Strikethrough text indicates absence. * A character that we clearly interpret as the result of ontogenetic change. **Abbreviations:** Agr, *Agrionemys*; Ch, *Chersine*. See text for more details. Inset shows the Pan-*Testudo* clade, from the strict consensus of 30 most parsimonious trees, based on the cladistic analysis herein.

spinosa (Bell in Gray, 1830), where a hyo-hypoplastral hinge is present in females (Pritchard, 2008). Viewed from a phylogenetic context, it appears that plastral kinesis evolved multiple times in Emydidae, Geoemydidae, and Testudinidae (see Feldman and Parham, 2002, for discussion).

In the material described and presented herein, there are some specimens of *Testudo marmorum* (AMPG PIK 1970/1a, AMPG PIK 1970/1f, AMPG PV1/1849) that do not show a hinge, and those that allow observations of the ventral side (AMPG PIK 1970/1a, AMPG PIK 1970/1f) show a morphology similar to that mentioned above by Lapparent de Broin et al. (2006). Interestingly, two of these specimens (AMPG PIK 1970/1f, AMPG PV1/1849) are probably female individuals (sex cannot be determined in AMPG PIK 1970/1a). On the other hand, all specimens identified as male individuals (MNHN PIK 3683a lectotype, AMPG PIK 1970/1d, NMNHS AZM-6-2857, NHMUK R 4328, LGPUT NIK 1946) show a clear hypo-xiphiplastral hinge. One possibility to explain this difference would be to attribute these specimens to different taxa and propose the presence of two small-sized testudinids in Pikermi. However, the distribution of the presence/absence of hinge in the available specimens is correlated with the sex (males have a hinge; females are hingeless), the remaining shell morphology is consistent with *Te. marmorum*, and there is at least one example in the closely related *Chersine hermanni* that this kind of a morphological difference could exist between the sexes (but inverted in the case of the ‘marble tortoise’). As such, and based on the available evidence, we propose that the absence of hinge in the female individuals is a sexually dimorphic character of *Te. marmorum*. Perhaps the early *Testudo* s.s. ‘experimented’ with the derived presence of hinge in one sex (in this case the males), whereas the females retained the plesiomorphic condition. The presence of kinesis in the plastron of turtles is suggested to serve as a protection mechanism for the limbs (so that they are completely enclosed within the shell) or to facilitate oviposition for species with unusually large eggs (Pritchard, 2008). In *Te. marmorum*, it could serve as extra protection. In any case, further sampling would help to clarify this hypothesis. As it will be addressed in the next section, scoring the presence of the hinge as polymorphic in *Testudo marmorum* challenges its traditional placement within *Testudo*.

Phylogenetic Position—Recently, the phylogenetic position of *Testudo marmorum* was analyzed in several publications (Corsini et al., 2014; Luján et al., 2016; Vlachos and Tsoukala, 2016; Vlachos and Rabi, 2018). All analyses agree that *Te. marmorum* holds a derived position within *Testudo* and that it belongs to the subclade *Chersus* (in Parham et al., 2006a), together with *Testudo marginata* and *Testudo kleinmanni*. Whereas Corsini et al. (2014) recover it as the sister taxon of *Te. marginata* and Luján et al. (2016) recover it as sister to the *Te. marginata* + *Te. brevitesta* clade (both are analyses of morphological characters), Vlachos and Tsoukala (2016; morphological characters with constrained molecular topology) and Vlachos and Rabi (2018; total-evidence analysis) suggest that it is the sister taxon of *Te. kleinmanni*. The former position would make more sense from a paleobiogeographic point of view (because both *Te. marmorum* and *Te. marginata* share a South Balkan distribution), whereas the latter would imply a late Miocene dispersal of *Te. kleinmanni* clade to northern Africa (see Parham et al., 2006a, and Vlachos and Tsoukala, 2016, for further discussion). Another alternative is proposed by Parham et al. (2006a), who explain the distribution of the mentioned species on either side as a result of vicariance after the separation of the two areas in post-Messinian times. Finally, the topology retrieved by Luján et al. (2016) provides a logical, from a chronostratigraphic point of view, position of *Te. brevitesta* as well.

The new information presented herein allows us to explore the phylogenetic position of *Te. marmorum* further. However, the

observed variation (see above) poses some problems on the phylogenetic analysis, mainly because of the variation of the presence/absence of the hinge. All previous analyses treated this species as having a hinge. As seen above, we treat this difference as part of the sexual dimorphism of this species and accordingly update the scorings of *Testudo marmorum* in the matrix of Vlachos and Rabi (2018) and that of Luján et al. (2016); see Appendix 1 and Supplemental Data 2–5 for the updated scorings and further information, respectively. The first analysis of the total-evidence matrix (with the updated *Te. marmorum*) resulted in an unsuccessful Traditional TBR (tree bisection and reconnection) in TNT (Goloboff et al., 2008) because the best score was hit few times only (best score hit 7 of 1,000 replicates). A New Technology search resulted in 30 trees of 18,141 steps, with a best score hit 27 times, first run resulting in 28 trees and expanded to 20 most parsimonious trees (MPTs) after a Traditional TBR with the trees from memory. *Testudo marmorum* is now placed in a more basal position, on the basal unresolved polytomy in the stem of *Testudo* (Fig. 11, inset)—in this case, the presence of the hinge is treated as an autapomorphy. Note that this topology is one step shorter than the solution of Vlachos and Rabi (2018). On the other hand, the updated information on the matrix of Luján et al. (2016) does not alter the position of *Te. marmorum* within *Testudo* (1 tree, 68 steps; implicit enumeration). For the moment, and until we have a more robust explanation (and thus a way to codify it) on the hinge morphology in *Te. marmorum*, we tentatively support the original position within *Testudo*. However, if the presence of a hinge is a matter of sexual dimorphism, it is likely that *Te. marmorum* holds a more basal position, outside *Testudo*; this position would imply some taxonomic changes for the generic combination of the species.

GEOCHELONA sensu Vlachos and Rabi, 2018
(unranked clade)
TITANOCHELON Pérez-García and
Vlachos, 2014
TITANOCHELON sp.

Referred Material—Pikermi, classical layers (late Miocene, late Tortonian, Greece; AMPG collection): AMPG 1871, left ulna; AMPG 2072, right ulna; AMPG 1872, left radius; AMPG 1873, ungual; AMPG PA 2935/91, ungual; AMPG 2073, ungual; AMPG 1874, ulnare?; AMPG 1875, distal carpal; AMPG 1877, phalanx; AMPG 1878, metacarpal; AMPG 1879, metacarpal; AMPG 1880, left epiplastron; AMPG 1881, peripheral; AMPG 1882, shell fragment; AMPG 1883, carapace fragment; AMPG 1884, costal fragment; AMPG 2074, distal carpal; AMPG 2075, right intermedium; AMPG 2078, metacarpal; AMPG 2079, ungual; AMPG 2077, 23+ osteoderms; AMPG PA 1851/91, phalanx; AMPG 1868/91, shell elements of a small individual. Kiourka or Liossati (late Miocene; AMPG collection): AMPG 2070, several fragments of the shell of one individual.

DESCRIPTION

The Pikermi Giant Tortoise

AMPG 1880—Almost complete left epiplastron (Fig. 12A–C), with only a small part of the anteromedial border missing. The epiplastron is long and wide. Viscerally, the epiplastra are thickened, forming a long, slightly convex epiplastral lip, without any gular pocket. Ventrally, the gulars are narrow and long, overlapping the anterior part of the entoplastron. The gularohumeral sulcus is nearly straight and causes a constriction in the epiplastra. Therefore, the anterior part of the epiplastra protrudes anteriorly.

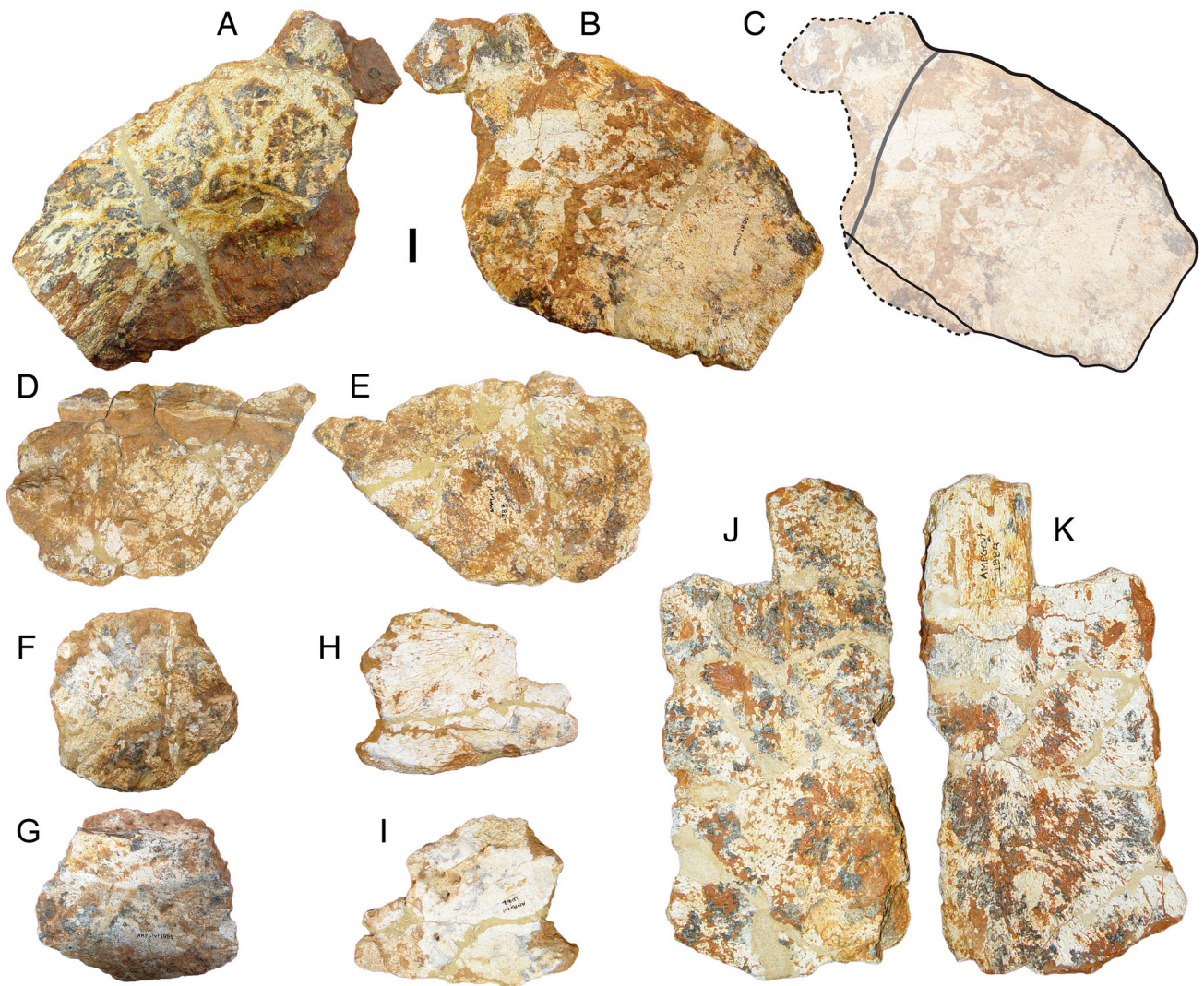


FIGURE 12. *Titanochelone* sp., shell elements from the upper Miocene of Pikermi, Attica. **A–C**, AMPG 1880, left epiplastron in **A**, visceral and **B, C**, ventral views. **D, E**, AMPG 1883, carapace fragment in **D**, dorsal and **E**, visceral views. **F, G**, AMPG 1881, peripheral fragment in **F**, dorsal and **G**, visceral views. **H, I**, AMPG 1882, shell fragment. **J, K**, AMPG 1884, costal fragment in **J**, dorsal and **K**, visceral views. Scale bar equals 50 mm.

AMPG 1883—Fragment of the carapace (Fig. 12D, E), which possibly comes from the bridge area. Further description is not possible.

AMPG 1881—A peripheral (Fig. 12F, G), whose marginal sulci are partially visible as a result of erosion. The peripheral is moderately flared.

AMPG 1882—A fragment of the shell (Fig. 12H, I). Further description is not possible.

AMPG 1884—A medial and a lateral part of a costal (Fig. 12J, K). No sulci are observed dorsally. The inserted rib is noted viscerally.

AMPG 1872—An almost complete left radius (Fig. 13A); only the proximal part is missing. The shaft is circular in diameter and narrow. The distal part of the radius is enlarged, being long and narrow with a convex articular surface. The articulation area with the ulna is tall. When articulated, the radius and ulna show a short, tear-shaped fenestra between them. The distal part of the articulated radius and ulna is not straight but leaves a broad space for the articulation of the first carpal row.

AMPG 1871 and AMPG 2072—A complete left (Fig. 13B) and a complete right (Fig. 13C) ulna, respectively. The ulna is straight, with a small curvature in the distal part. The proximal part is roughly triangular, narrow, and long. The proximal articulation for the humerus is slightly concave. The distal part is narrower and longer than the proximal part, showing a convex articulation surface.

AMPG 1874—A complete ulnare (Fig. 13D). It is cubic in shape and taller than wide. Proximally, the ulnare articulates with the ulna with an elongated concave surface. Medially, it articulates with the intermedium with two small and flat surfaces. Distally, it shows two slightly concave surfaces, which are developed in an obtuse angle.

AMPG 2075—This specimen (Fig. 13E) corresponds to a complete right intermedium. It shows a triangular cross-section. Proximally, it shows a concave articular surface for the ulna. Proximomedially, it shows a slightly concave surface for the radius. Distally, it shows a concave surface for the centralia.

AMPG 1875—A complete distal carpal (Fig. 13F). It shows a small protuberance proximally and a discoid part distally. Compared with the other distal carpal, the distal discoid part is

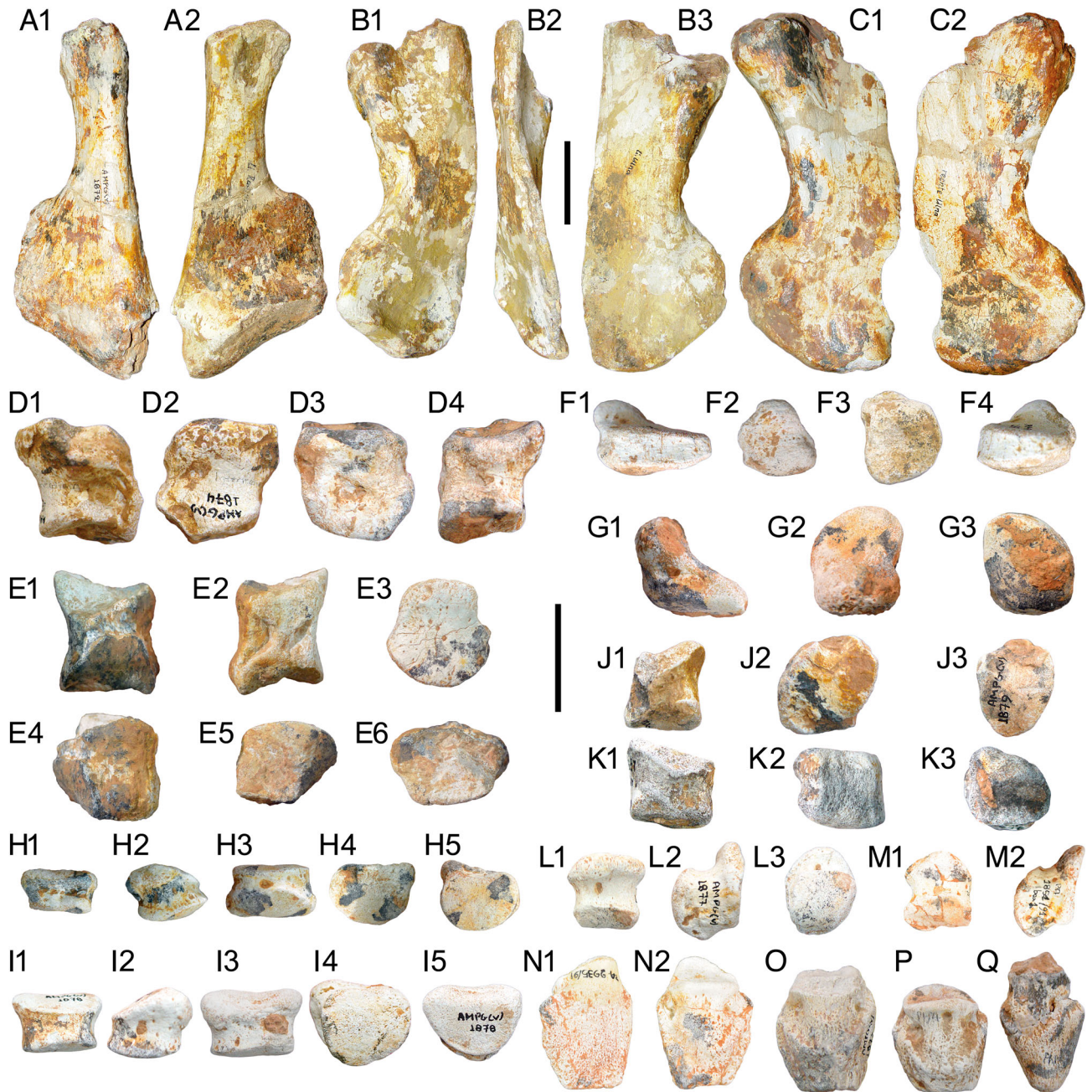


FIGURE 13. *Titanochelon* sp., appendicular elements from the upper Miocene of Pikermi, Attica. **A**, AMPG 1872, left radius in **A1**, ventral and **A2**, dorsal views. **B**, AMPG 1871, left ulna in **B1**, dorsal, **B2**, lateral, and **B3**, ventral views. **C**, AMPG 2072, right ulna in **C1**, ventral and **C2**, dorsal views. **D**, AMPG 1874, ulnare in **D1**, medial, **D2**, dorsal, **D3**, ventral, and **D4**, lateral views. **E**, AMPG 2075, right intermedium in **E1**, medial, **E2**, lateral, **E3**, dorsal, **E4**, ventral, **E5**, proximal, and **E6**, distal views. **F**, AMPG 1875, distal carpal in **F1**, dorsal, **F2**, proximal, **F3**, distal, and **F4**, lateral views. **G**, AMPG 2074, distal carpal in **G1**, lateral, **G2**, proximal, and **G3**, distal views. **H**, AMPG 2076, metacarpal in **H1**, ventral, **H2**, medial, **H3**, dorsal, **H4**, distal, and **H5**, proximal views. **I**, AMPG 1878, metacarpal in **I1**, ventral, **I2**, medial, **I3**, dorsal, **I4**, distal, and **I5**, proximal views. **J**, AMPG 1879, metacarpal in **J1**, medial, **J2**, proximal, and **J3**, distal views. **K**, AMPG 1876, metacarpal in **K1**, medial, **K2**, lateral, and **K3**, distal views. **L**, AMPG 1877, phalanx in **L1**, dorsal, **L2**, lateral, and **L3**, distal views. **M**, AMPG PA 1851/91, phalanx in **M1**, ventral and **M2**, lateral views. **N**, AMPG PA 2935/91, ungual in **N1**, dorsal and **N2**, ventral views. **O**, AMPG 1873, ungual in ventral view. **P**, AMPG 2073, ungual in ventral view. **Q**, AMPG 2079, ungual in ventral view. Scale bars equal 5 cm.

highly asymmetric, with a longer medial part and a much shorter lateral part. Ventrally, there is a convex-to-flat surface for the metacarpals.

AMPG 2074—A complete distal carpal (Fig. 13G). It is tall and narrow. It shows a large protuberance proximally and a discoid part distally. Ventrally, there is a convex-to-flat surface for the metacarpals.

AMPG 2076—A complete metacarpal (Fig. 13H). It shows a convex surface proximally for the distal carpals and a distal convex surface for the first phalanx.

AMPG 1878, AMPG 1879, and AMPG 1876—Three complete metacarpals (Fig. 13I–K). They show a convex surface proximally for the distal carpals and a distal convex surface for the first phalanx.

AMPG 1877 and AMPG PA 1851/91—Two complete phalanges of the anterior limb (Fig. 13L, M), with a concave proximal surface for the metacarpal and a convex distal surface for the unguis.

AMPG PA 2935/91, AMPG 1873, and AMPG 2073—Three almost complete unguis (Fig. 13N–P). They are short and wide with a rounded tip. The proximal surface for the phalanx is concave. These unguis originate from the anterior limb.

AMPG PA 1868/91—This specimen (Fig. 14) consists of various shell elements that belong to the same individual. Based on the size and the thickness of the plates, we can estimate that they belong to a relatively small, young individual. Two fragments from the carapace are of a particular size to allow further detailed description, whereas the remaining elements are small fragments of the same carapace that we cannot find any connections.

The first fragment (Fig. 14A–C) corresponds to a part of the neural series, with some associated costal plates. Viscerally, the attachments for the vertebra are visible in most preserved plates. From the first plate, only the posterior part is preserved. This part shows no vertebra attachments viscera. Therefore, this part could be the posterior part of a nuchal plate. This is in accordance with the configuration of the remaining neural plates. Posterior to the nuchal, parts of the first four neurals are noted. From neural 1, the middle part is preserved. The plate appears to be longer than wide, having a concave anterior border for the nuchal. It is crossed transversely by the vertebral sulcus. Neural 2 preserves the middle and the right part. It is octagonal in shape, having a concave anterior border and a nearly straight posterior border. It is wider than long. Neural 3 preserves also the middle and the right part. It is quadrangular, with rounded edges, wider than long. It is crossed transversely

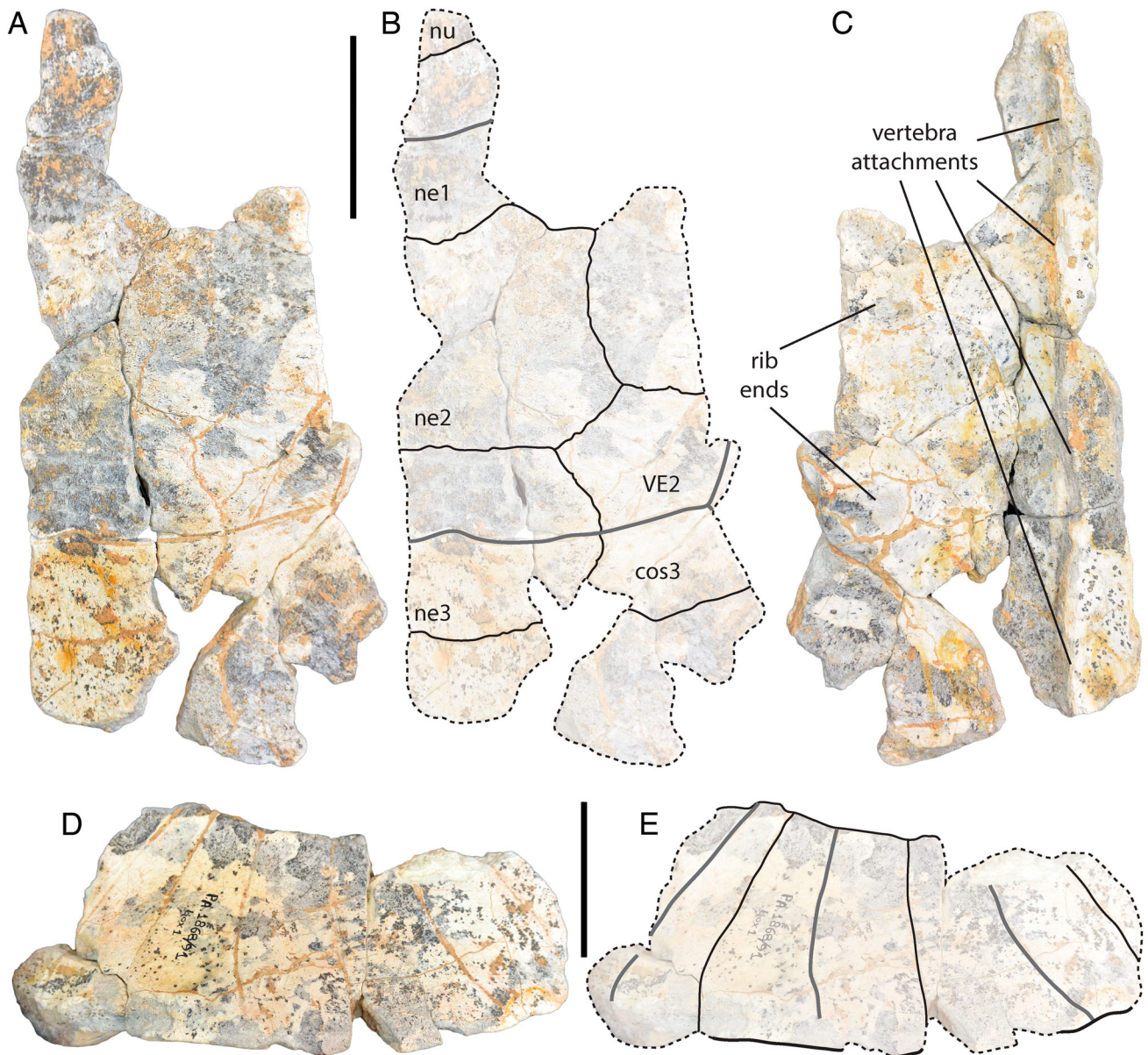


FIGURE 14. AMPG PA 1868/91, shell material of a juvenile individual from the upper Miocene of Pikermi, Attica. **A–C**, fragment of the dorsal carapace in **A**, dorsal view; **B**, interpretation of dorsal view; **C**, visceral view. **D, E**, part of the posterior peripheral rim in **D**, dorsal view; **E**, interpretation of dorsal view. **Abbreviations:** **cos**, costal; **ne**, neural; **nu**, nuchal; **VE**, vertebral. Scale bars equal 50 mm.

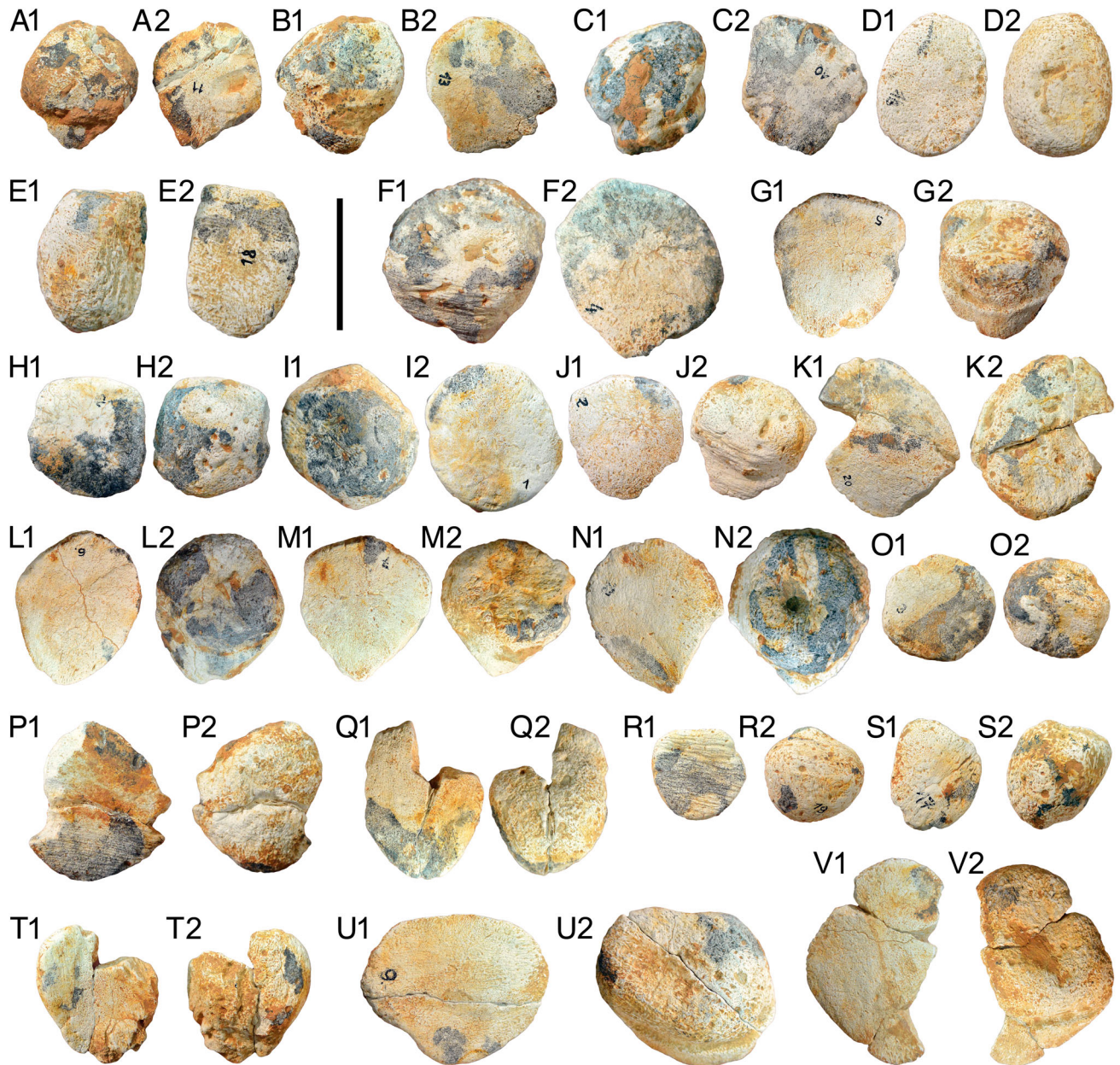


FIGURE 15. *Titanochelone* sp., AMPG 2077, osteoderms from the late Miocene of Pikermi, Attica. **A**, half-pointed osteoderm in **A1**, ventral and **A2**, dorsal views. **B**, half-pointed osteoderm in **B1**, ventral and **B2**, dorsal views. **C**, half-pointed osteoderm in **C1**, ventral and **C2**, dorsal views. **D**, rounded osteoderm in **D1**, ventral and **D2**, dorsal views. **E**, rounded osteoderm in **E1**, ventral and **E2**, dorsal views. **F**, half-pointed osteoderm in **F1**, ventral and **F2**, dorsal views. **G**, half-pointed osteoderm in **G1**, ventral and **G2**, dorsal views. **H**, rounded osteoderm in **H1**, ventral and **H2**, dorsal views. **I**, rounded osteoderm in **I1**, ventral and **I2**, dorsal views. **J**, half-pointed osteoderm in **J1**, ventral and **J2**, dorsal views. **K**, rounded osteoderm in **K1**, ventral and **K2**, dorsal views. **L**, half-pointed osteoderm in **L1**, ventral and **L2**, dorsal views. **M**, half-pointed osteoderm in **M1**, ventral and **M2**, dorsal views. **N**, half-pointed osteoderm in **N1**, ventral and **N2**, dorsal views. **O**, rounded osteoderm in **O1**, ventral and **O2**, dorsal views. **P**, half-pointed osteoderm in **P1**, ventral and **P2**, dorsal views. **Q**, half-pointed osteoderm in **Q1**, ventral and **Q2**, dorsal views. **R**, rounded osteoderm in **R1**, ventral and **R2**, dorsal views. **S**, rounded osteoderm in **S1**, ventral and **S2**, dorsal views. **T**, half-pointed osteoderm in **T1**, ventral and **T2**, dorsal views. **U**, half-pointed osteoderm in **U1**, ventral and **U2**, dorsal views. **V**, half-pointed osteoderm in **V1**, ventral and **V2**, dorsal views. Scale bar equals 50 mm.

by the vertebral sulcus, which is anteriorly convex in the middle. Neural 4 preserves only the anterior part, but most probably is octagonal. The medial parts of costals 2–4 are preserved. As we can infer from the shape of costal 3, the costals showed the alternating pattern of costals medially short with one sutured area alternated with costals medially long with three sutured areas. This alternating pattern corresponds to the quadrangular/octagonal neurals.

The second fragment (Fig. 14D–E) corresponds to a part of the carapacial margin, showing four consecutive peripherals. The margin is thickened, and the peripherals are only slightly flared. They are crossed by the marginal sulci. There is a good coincidence between the costoperipheral sutures and the pleuromarginal sulci.

AMPG 2077—Several osteoderms are known from Pikermi (Fig. 15). They are all large in size and flattened. Two types of

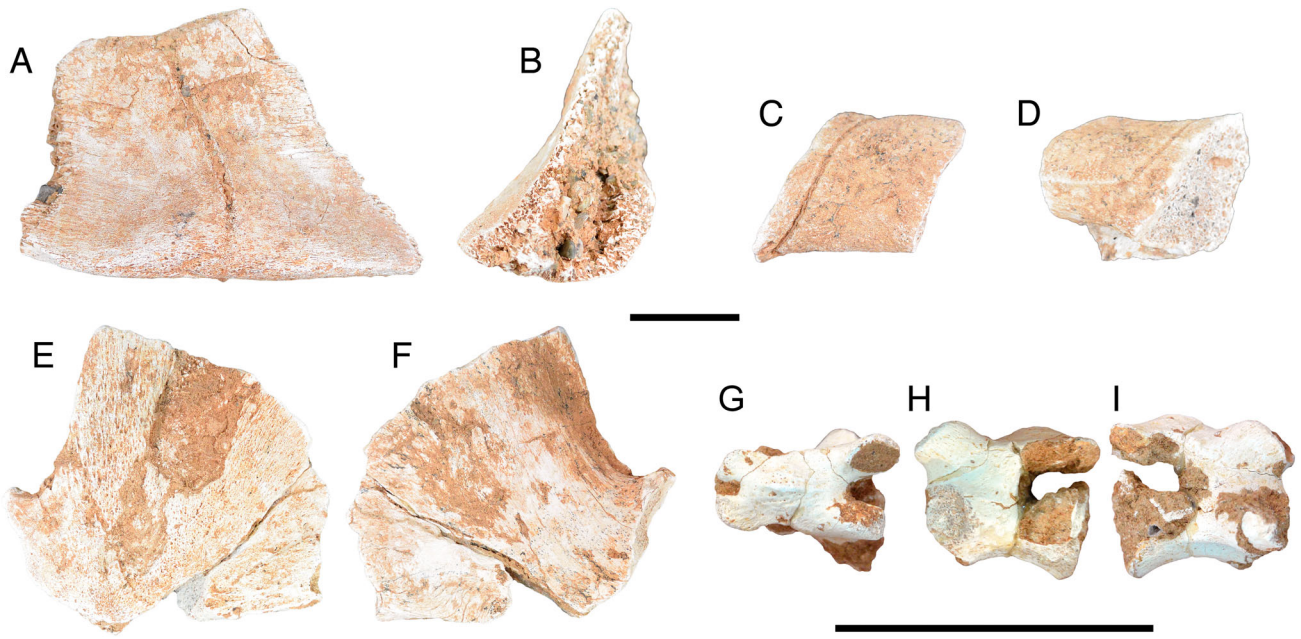


FIGURE 16. AMPG 2070, material from a giant tortoise from the upper Miocene of Kiourka (Liossati), near Pikermi, Attica. **A, B**, peripheral plate in **A**, dorsal and **B**, lateral views. **C, D**, plastron fragment in **C**, ventral and **D**, visceral views. **E, F**, hyoplastron fragment in **E**, ventral and **F**, visceral views. **G–I**, caudal vertebra in **G**, dorsal, **H**, left lateral, and **I**, right lateral views. Scale bars equal 50 mm.

osteoderms are noted: the so-called half-pointed osteoderms (e.g., Fig. 15J, U) and the rounded ones (Fig. 15O, P).

Comments—The specimens from the classical Pikermi layers mentioned above are of similar size, morphology, and type of fossilization. Because overlapping parts of the skeleton are not preserved, it is possible that they belong to the same individual.

The Liossati Giant Tortoise

The material from the late Miocene locality of Liossati (or Kiourka), near Pikermi in Attica, is highly fragmented (AMPG 2070; Fig. 16). Unfortunately, it is not possible to connect the numerous shell fragments in a way that would permit meaningful description. The specimens correspond probably to the same individual of medium size, which could have reached 1 m in length. Several specimens preserve sutures and sulci, but they are too few to allow a clear identification. Some specimens are complete. A complete peripheral is preserved (Fig. 16A), being medially short and laterally long. A part of the epiplastron (Fig. 16B) preserves some of the sulci covering the epiplastral lip. Also, a part of the hyoplastron is identified (Fig. 16C). Some caudal vertebrae are recovered (e.g., Fig. 16D), preserving mainly the centrum and missing the transversal processes.

Remarks

The presence of a giant tortoise in the classical layers of Pikermi was first reported by Woodward (1901:484), who mentioned that “[t]he only striking discovery consists in fragmentary evidence of a gigantic tortoise, at least as large as the largest hitherto found in Europe,” suggesting a rather massive size for the Pikermi large tortoise. Unfortunately, the author provided no figures or description of that material (Woodward, 1901), neither was it possible to locate any giant tortoise specimen in NHMUK. A few decades later, Bachmayer (1967) provided the first actual documentation of a giant tortoise from Pikermi, by describing and figuring some shell fragments, limb bones, and

osteoderms stored in AMPG. The exact excavational provenance of these specimens is not known, but because it is mentioned in the locality information, it is likely that they come from the excavations carried out in Pikermi by Woodward and Skoufos in 1901 (S.R., pers. observ.; see locality information as well). In any case, all these specimens, as well as several others not referred by Bachmayer (1967), are revised and described here in detail, while also indicating certain erroneous identifications originally provided by that author. For example, the specimen AMPG 1880 was reported by Bachmayer (1967) as parts of the costals 7 and 8, whereas we herein demonstrate that this specimen corresponds actually to the left epiplastron (see also Vlachos et al., 2014). At the same time, new important specimens from Pikermi are presented. For example, the specimen AMPG PA 1868/91, which was discovered and preserved in excellent condition by one of us (S.R.), presents the only known example of the neural series of a giant tortoise from Greece. All this new and updated information, aided by the knowledge on comparative material from Greece that is now available, allows us to update the taxonomic status of the large testudinid from Pikermi.

Bachmayer (1967) attributed the specimens to *Testudo* cf. *schafferi* but without providing any morphological evidence, because the material from Pikermi is not overlapping with the type material of the latter species from Samos. Lapparent de Broin (2002) also listed this material as cf. *Cheirogaster* cf. *schafferi* (or as ?*Cheirogaster* cf. *schafferi* in Lapparent de Broin, 2001), a view followed also subsequently by Georgalis and Kear (2013). However, even with the updated information presented here, it is not possible to find comparable or overlapping preserved parts between the Samos and the Pikermi material. The only exceptions are the new carpal elements reported from Samos, i.e., the distal carpal and the phalanx. Similar elements exist in Pikermi. Although similar in size, the Samos elements are always taller and narrower than those from Pikermi. However, such elements are not adequate to form the basis of a taxonomic distinction, but they nevertheless show some differences between the material from Pikermi and Samos, although ontogenetic variation may

well explain such differences. The Samos material, on the other hand, is clearly distinguished by comparable fossils from the Thessaloniki area, i.e., from localities such as Salonique (sensu Arambourg and Piveteau, 1929) or Epanomi, Nea Michaniona and Nea Kallikratia in western Chalkidiki. These differences were first reported by Vlachos et al. (2014) and are further discussed herein. Based on the above points and all the available fossils, we suggest that a close relationship between the Pikermi and Samos large testudinids should not be adopted unless new findings with comparable parts prove this similarity.

Leaving the obvious difference in size aside, the Pikermi form is also different from *Ti. bacharidisi* from Thessaloniki area. The epiplastron from Pikermi shows a shallow epiplastral excavation and a narrowing of the anterior lobe at the gularohumeral sulcus, causing a protrusion of the epiplastral lip. This protrusion is missing in *Ti. bacharidisi*. The preserved sulci show that the anterior part of the entoplastron was overlapped by the gulars. The entoplastron of *Ti. bacharidisi*, however, is covered only by the humerals. The radius from Pikermi is more robust, showing a large and wide distal part. At the same time, the distal articulation with the ulna in the Pikermi form is much taller than in *Ti. bacharidisi*. The Pikermi intermedium (AMPG 2075) is quite large, almost cubic, with an angular articular surface for the medial and lateral centralia, whereas it is triangular with a rounded articular surface for the fused medial and lateral centralia in *Ti. bacharidisi*. The distal carpals of AMPG 2075 are taller and much narrower than in *Ti. bacharidisi*. Based on the few available comparable skeletal elements, we can infer that the morphology of the anterior limb of the Pikermi form *Ti. bacharidisi* was different from that of the Pliocene form. The differences in the morphology of the epiplastron are even greater between the two forms. However, it is necessary to obtain more information on the Pikermi giant tortoise, which would allow confirming these differences, mentioned herein, and exclude the possibility that these changes are due to ontogenetic or other variation.

Summarizing, there is no sufficient overlapping material to relate the Pikermi form with *Ti. schafferi* from Samos, and at the same time the Pikermi specimens are different from the comparable elements in *Ti. bacharidisi*; it is possible that the Pikermi giant tortoise represents another giant tortoise morphotype in the South Balkans. However, due to the limited information on the shell, it is not possible to identify and properly diagnose the Pikermi form at the species level.

CONCLUSIONS

The late Miocene locality of Pikermi (near Athens, Greece) is among the most iconic Neogene sites in Eurasia. Its late Miocene fauna (i.e., Pikermian fauna) represents a landmark for the evolution of the biota in the eastern Mediterranean and is commonly used as a standard reference for the late Miocene. As such, Pikermi fossils are intensely studied by almost everyone with a serious interest in the late Miocene of Europe. However, because most of the material is the result of old collections with uncertain stratigraphic and chronological framework, recent field work in Pikermi was able to provide a more precise chronology. We now know that the classical layers of the Pikermi Formation span the time between the latest Tortonian and earliest Messinian (7.36–7.11 Ma).

In this updated framework, we provide the revision of previously published turtle specimens from Pikermi, as well as the description of new material from Pikermi and the coeval site of Azmaka 6 in Bulgaria. We reaffirm the presence of at least two different testudinid species: the small *Testudo marmorum* and the giant tortoise *Titanochelon* sp., and we provide valuable new information on their morphology, relationships, and distribution.

Testudo marmorum is the first fossil turtle species to be named from Greece. Based on our analysis, we are able to resolve two important nomenclatural issues of this species: first, we provide evidence that the proper authorship of this species name should be attributed to Gaudry (1862a); and second, we designate the most complete specimen from the MNHN syntype series as the lectotype of the ‘marble tortoise.’ All previously published material from MNHN and AMPG is refigured and redescribed, together with new information from unpublished material from NHMUK and AMPG; the new AMPG specimen comes from the new excavations in Pikermi and confirms the presence of this species there.

This species is further identified outside Pikermi. We describe an almost complete shell from the coeval locality Azmaka 6 in Bulgaria and fully refer the complete shell from the older Nikiti locality in northern Greece to *Testudo marmorum*. Considering the possible presence of this species in other nearby late Miocene localities as well, we conclude that the ‘marble tortoise’ is a typical small-testudinid species for the late Miocene from the South Balkans.

Altogether, the morphological information allows the description of the complete shell morphology of this species and, more importantly, to discuss issues related to intraspecific variation, sexual dimorphism, and ontogenetic changes. With the use of an ontogram analysis, we are able to propose that the presence of a completely developed hypo-xiphiplastral hinge and the presence of a nuchal notch are related to sexual dimorphism, that the coincidence between costoperipheral sutures and pleuromarginal sulci in the lateral parts of the carapace is related to intraspecific variation, and that the other variable characters are attributable to ontogenetic changes.

The presence of a hinge in the adult males of *Testudo marmorum* (confirmed females do not have a hinge) is an analogous, but exactly the opposite, case such as the one of the extant *Chersine hermanni*: old female individuals of Hermann’s tortoise can develop a kind of a hypo-xiphiplastral hinge (which is not homologous to that of *Testudo graeca*). This polymorphy challenges the traditional placement of the ‘marble tortoise’ within *Testudo* s.s. It is more parsimonious to consider that this species holds a more basal position in the stem leading to modern *Testudo* than a derived placement within the *Chersus* clade as suggested by all other analyses.

The other testudinid from Pikermi is a member of the widespread *Titanochelon* clade. The previously published material comprises shell fragments, limb bones, carpal bones, and osteoderms, all of which have been redescribed and refigured. We also report a new specimen of a juvenile individual of *Titanochelon*, which presents for the first time in Greece information on the neural series. Based on the updated information, we provide additional evidence that the Pikermian giant tortoise was different from the coeval taxon from the upper Miocene of Samos Island, as well as from the younger Pliocene species from northern Greece. However, the incomplete nature of the material does not allow us to erect a new species formally.

The new information on the fossil tortoises from Pikermi, Azmaka, and other coeval localities is crucial in order to understand the evolution of tortoises in the eastern Mediterranean, for two of the most important and successful testudonian and geocheilonian clades.

ACKNOWLEDGMENTS

We thank A. Ayvazyan for providing the photos of the Azmaka specimen; the following colleagues for providing access to study material under their care: R. Allain and N.-E. Jalil (MNHN), S. Chapman (NHMUK), and N. Spassov (NMHMS); and L. Hristova for preparation of the Azmaka specimen. We thank

N.-E. Jalil (MNHN) for providing new numbers for the syntypes of *Testudo marmorum*. A visit to NHMUK was supported by a SYNTHESYS GB-TAF-6591 grant to G.L.G. Research in Pikerimi by G.T. and S.R. was supported by the Special Account for Research Grants of the National and Kapodistrian University of Athens 70/3/9494, 70/3/10437, 70/4/3570, 70/4/11078, and 70/3/12977. We would like to thank J. Parham, M. Rabi, and editor G. Bever for comments that improved the revised version of the manuscript. The Willi Hennig Society sponsors the use of TNT software.

LITERATURE CITED

- Abel, O. 1922. In der Buschsteppe von Pikerimi in Attika; pp. 75–165 in O. Abel (ed.), *Lebensbilder aus der Tierwelt der Vorzeit*. Gustav Fischer Verlag, Jena.
- Arakelyan, M., O. Türkozan, N. Hezaveh, and J. F. Parham. 2018. Ecomorphology of tortoises (*Testudo graeca* complex) from the Araks river valley. *Russian Journal of Herpetology* 25:245–252.
- Arambourg, C., and J. Piveteau. 1929. Les Vertébrés du Pontien de Salonique. *Annales de Paleontologie* 18:57–139.
- Bachmayer, F. 1967. Eine Riesenschildkröte aus den altploziänen Schichten von Pikerimi (Griechenland). *Praktika Akademiae Athenae* 42:303–317.
- Bachmayer, F., and N. Symeonidis. 1970. Die fossilen Schildkrötenreste des geologisch-paläontologischen Institutes der Universität von Athen. *Annales Géologiques des Pays Helléniques* 22:227–246.
- Bachmayer, F., and N. Symeonidis. 1977. Eine neue ‘Pikerimi’ Fundstelle im Gebiet von Liossati (Kiourka) nördlich von Athen (Griechenland) (Beschreibung einer Riesenschildkröte). *Annales Géologiques des Pays Helléniques* 28:8–16.
- Batsch, A. J. 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien. Akademische Buchhandlung, Jena, 528 pp.
- Bell, T. 1827. On two new genera of land tortoises. *Transactions of the Linnean Society of London* 15:392–401.
- Bernor, R. L. 1983. Geochronology and zoogeographic relationships of Miocene Hominoidea; pp. 21–64 in R. L. Ciochon and R. S. Corruccini (eds.), *New Interpretations of Ape and Human Ancestry*. Plenum Press, New York.
- Böhme, M., N. Spassov, M. Ebner, D. Geraads, L. Hristova, U. Kirscher, S. Kötter, U. Linnemann, J. Prieto, S. Roussiakis, G. Theodorou, G. Uhlig, and M. Winkhofer. 2017. Messinian age and savannah environment of the possible hominin *Graecopithecus* from Europe. *PLoS ONE* 12:e0177347.
- Bour, R. 1981. Etude systématique du genre endémique Malgache *Pyxis* Bell, 1827 (Reptilia, Chelonii). *Bulletin Mensuel de la Société Linnéenne de Lyon* 5:154–176.
- Chkhikvadze, V. M., and M. A. Bakradze. 1991. About systematics of tortoises along Araks River Valley. *The Works of Tbilisi State University* 305:59–63. [Russian]
- Cope, E. D. 1868. On the origin of genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20:242–300.
- Corsini, J. A., M. Böhme, and W. G. Joyce. 2014. Reappraisal of ‘*Testudo antiqua*’ (Testudines, Testudinidae) from the Miocene of Hohenhöwen, Germany. *Journal of Paleontology* 88:948–966.
- Ezcurra, M. D., and R. J. Butler. 2015. Post-hatchling cranial ontogeny in the Early Triassic diapsid reptile *Proterosuchus fergusi*. *Journal of Anatomy* 226:387–402.
- Feldman, C. R., and J. F. Parham. 2002. Molecular phylogenetics of emydine turtles: taxonomic revision and the evolution of shell kinesis. *Molecular Phylogenetics and Evolution* 22:388–398.
- Fritz, U., and O. R. Bininda-Emonds. 2007. When genes meet nomenclature: tortoise phylogeny and the shifting generic concepts of *Testudo* and *Geochelone*. *Zoology* 110:298–307.
- Fitzinger, L. 1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Verlag J. G. Heubner, Vienna, 66 pp.
- Fuss, J., N. Spassov, D. R. Begun, and M. Böhme. 2017. Potential hominin affinities of *Graecopithecus* from the Late Miocene of Europe. *PLoS ONE* 12:e0177127.
- Garcia, G., D. S. Kostopoulos, X. Valentin, and G. D. Koufos. 2016. Testudines. *Geobios* 49:23–27.
- Gaudry, A. 1862a. Résultats des fouilles exécutées en Grèce sous les auspices de l’Académie. *Comptes Rendus de l’Académie des Sciences de Paris* 52:297–300.
- Gaudry, A. 1862b. Note sur les débris d’Oiseaux et de Reptiles trouvés à Pikerimi, Grèce, suivie de quelques remarques de paléontologie générale. *Bulletin de la Société Géologique de France* 19:629–640.
- Gaudry, A. 1862–1867. *Animaux fossiles et geologie de l’Attique*. Savy, Paris, 475 pp.
- Georgalis, G. L., and B. P. Kear. 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. *Geobios* 46:299–311.
- Georgalis, G. L., E. Velitzelos, D. E. Velitzelos, and B. P. Kear. 2013. *Nostimoachelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the Early Miocene of Northern Greece; pp. 277–287 in D. Brinkman, P. Holroyd, and J. Gardner (eds.), *Morphology and Evolution of Turtles*, Proceedings of the Gaffney Turtle Symposium, Drumheller, Canada, 17–18 June, 2009. Springer, Dordrecht, The Netherlands.
- Georgalis, G. L., A. Villa, E. Vlachos, and M. Delfino. 2016. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. *Geobios* 49:433–444.
- Georgalis, G. L., A. Villa, M. Ivanov, S. Roussiakis, P. Skandalos, and M. Delfino. 2019. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia—bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. *Historical Biology* 31:1045–1064.
- Gmelin, J. F. 1789. *Caroli a Linné, Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*, thirteenth edition. G. E. Beer, Leipzig, pp. 1033–1516.
- Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Gray, J. E. 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. *Annals of Philosophy* 10:193–217.
- Gray, J. E. 1830. *Illustrations of Indian Zoology, Chiefly Selected from the Collection of Major-General Hardwicke*. Treuttel, Wurtz, Treuttel, Jun. and Richter, London, 77 pp.
- International Commission on Zoological Nomenclature [ICZN]. 1999. *International Code of Zoological Nomenclature*, fourth edition. International Trust for Zoological Nomenclature, London, 306 pp.
- Joyce, W. G., J. F. Parham, and J. A. Gauthier. 2004. Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology* 78:989–1013.
- Kostopoulos, D. S., and S. Sen. 2016. Suidae, Tragulidae, Giraffidae, and Bovidae. *Geodiversitas* 38:273–298.
- Koufos, G. D. 2016. History, stratigraphy and fossiliferous sites. *Geobios* 49:3–10.
- Koufos, G. D., D. S. Kostopoulos, and T. D. Vlachou. 2016. Revision of the Nikiti 1 (NKT) fauna with description of new material. *Geobios* 49:11–22.
- Kovachev, D. 2005. Turtles from Maeotian near Kalimantsi village, Blagoevgrad region (SW Bulgaria). *Review of the Bulgarian Geological Society* 66:61–70. [Bulgarian]
- Lapparent de Broin, F. de. 2001. The European turtle fauna from the Triassic to the Present. *Dumerilia* 4:155–217.
- Lapparent de Broin, F. de. 2002. A giant tortoise from the Late Pliocene of Lesvos Island (Greece) and its possible relationships. *Annales Géologiques des Pays Helléniques* 34:99–130.
- Lapparent de Broin, F. de, R. Bour, and J. Perälä. 2006. Morphological definition of *Eurotestudo* (Testudinidae, Chelonii): first part. *Annales de Paléontologie* 92:255–304.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. Laurentii Salvii, Stockholm, 824 pp.
- Lortet, L. 1883. Poissons et reptiles du lac de Tibériade et de quelques autres parties de la Syrie. *Archives du Muséum d’Histoire Naturelle de Lyon* 3:99–194.
- Luján, Á. H., M. Delfino, J. M. Robles, and D. M. Alba. 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* 178:312–342.

- Malik, A., and H. Nafiz. 1933. Küçükçekmece fosil fıkralı hayvanlar mecmuası. Darülfünun Jeoloji Enstitüsü 8:64–65.
- Melentis, J. K. 1970. Die Pikermifauna von Halmypopotamos (Euböa, Griechenland)—2. Teil: Osteologie. Annales Géologiques des Pays Helléniques 19:285–411.
- Merrem, B. 1820. Versuch eines Systems der Amphibien. Tentamen Systematis Amphibiorum. J. C. Krieger, Marburg, 191 pp.
- Nicolas, P. 1978. New deposit of vertebrates in Chersonian-West Kutchuk-Tchekmedje (Turkish Thrace). Comptes Rendus Hebdomadaires des Seances de l'Academie des Sciences, Serie D 287:455–458.
- Paraskevaidis, I. 1955. Zwei schildkrötenreste aus dem obermiozän von Chios. Annales Géologiques des Pays Helléniques 6:133–141.
- Parham, J. F., J. R. Macey, T. J. Papenfuss, C. R. Feldman, O. Türközan, R. Polymeni, and J. Boore. 2006a. 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.
- Parham, J. F., O. Türközan, B. L. Stuart, M. Arakelyan, S. Shafei, J. R. Macey, and T. J. Papenfuss. 2006b. Genetic evidence for premature taxonomic inflation in Middle Eastern tortoises. Proceedings of the Californian Academy of Sciences 4:955–964.
- Pérez-García, A., and E. Vlachos. 2014. New generic proposal for the European Neogene large testudinids (Cryptodira) and the first phylogenetic hypothesis for the medium and large representatives of the European Cenozoic record. Zoological Journal of the Linnean Society 172:653–719.
- Pritchard, P. C. H. 2008. Evolution and structure of the turtle shell; pp. 45–84 in J. Wyneken, M. H. Godfrey, and V. Bels (eds.), Biology of Turtles. CRC Press, Boca Raton, Florida.
- Rögl, F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologica Carpathica 50:339–349.
- Roussiakis, S., A. Athanassiou, D. Michailidis, V. Mitsopoulou, C. Solomos, and G. Theodorou. 2014. Remarks on new proboscidean remains from the classical Late Miocene locality of Pikermi and their associated fauna; pp. 171–172 in D. S. Kostopoulos, E. Vlachos, and E. Tsoukala (eds.), Proceedings of the VIth International Conference on Mammoths and Their Relatives, Grevena-Siatista, N. Greece, 5–12 May 2014. Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Greece, 102.
- Schoepff, J. 1793. Historia testudinum iconibus illustrata. Ioannis Iacobi Palm, Erlangen, 136 pp.
- Solounias, N., J. M. Plavcan, J. Quade, and L. Witmer. 1999. The paleoecology of the Pikermian Biome and the savanna myth; pp. 436–453 in J. Agusti, L. Rook, and P. Andrews (eds.), Hominoid Evolution and Climatic Change in Europe. Volume I, The Evolution of Neogene Terrestrial Ecosystems in Europe. Cambridge University Press, Cambridge, U.K.
- Spassov, N., D. Geraads, L. Hristova, G. N. Markov, G. Merceron, T. Tzankov, K. Stoyanov, M. Böhme, and A. Dimitrova. 2012. A hominid tooth from Bulgaria: the last pre-human hominid of continental Europe. Journal of Human Evolution 62:138–145.
- Staesche, K., H. V. Karl, and U. Staesche. 2007. Fossile Schildkröten aus der Türkei; pp. 91–149 in U. Staesche (ed.), Fossile Schildkröten aus drei Kontinenten. Geologisches Jahrbuch 98. German Geological Survey BGR, Hannover.
- Szalai, T. 1931. *Testudo schafferi* nov. sp. eine Riesenschildkröte aus dem Pliozän von Samos. Annalen des Naturhistorischen Museums Wien 46:153–163.
- Theodorou, G., S. Roussiakis, A. Athanassiou, and A. A. Filippidis. 2010. Mammalian remains from a new site near the classical locality of Pikermi (Attica, Greece). Scientific Annals, School of Geology, Aristotle University of Thessaloniki, Greece 99:109–120.
- Vlachos, E. 2015. The fossil chelonians of Greece. Systematics-evolution-stratigraphy-palaeoecology. Ph.D. dissertation, Aristotle University of Thessaloniki, Thessaloniki, Greece, 479 pp.
- Vlachos, E., and M. Rabi. 2018. Total evidence analysis and body size evolution of extant and extinct tortoises (Testudines: Cryptodira: Pan-Testudinidae). Cladistics 34:652–683.
- Vlachos, E., and E. Tsoukala. 2014. *Testudo* cf. *graeca* from the new Late Miocene locality of Platania (Drama basin, N. Greece) and a reappraisal of previously published specimens. Bulletin of the Geological Society of Greece 48:27–40.
- Vlachos, E., and E. Tsoukala. 2016. The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae). Papers in Palaeontology 2:72–86.
- Vlachos, E., J. Sterli, K. Vasileiadou, and J. Corsini. 2014. *Cheirogaster bacharidisi* sp. nov., a new species of a giant tortoise from the Pliocene of Thessaloniki (Macedonia, Greece). Journal of Vertebrate Paleontology 34:560–575.
- Vlachos, E., M. Delfino, and T. Kotsakis. 2015. The chelonians from the latest Miocene-earliest Pliocene locality of Allatini and Pylea (east Thessaloniki, Macedonia, Greece). Comptes Rendus Palevol 14:187–205.
- Vlachos, E., J. Sterli, K. Vasileiadou, and G. Syrides. 2019. A new species of *Mauremys* (Testudines, Geoemydidae) from the late Miocene–Pliocene of Central Macedonia (northern Greece) with exceptionally wide vertebral scutes. Papers in Palaeontology 5:177–195.
- Woodward, A. S. 1901. On the bone beds of Pikermi, Attica and on similar deposits in Northern Euboea. Geological Magazine 8:481–486.

Submitted November 17, 2018; revisions received September 16, 2019; accepted October 12, 2019.
Handling editor: Gabriel Bever.

APPENDIX 1. Updated scorings of *Testudo marmorum* for the matrices of Vlachos and Rabi (2018) and Luján et al. (2016), in TNT format. See Supplemental Data 2–5 for complete matrices. Missing characters are indicated with a question mark (?). Polymorphisms: **A**, 0, 1; **B**, 0, 1, 2; **C**, 0, 2.

Vlachos and Rabi (2018) Matrix

Testudo marmorum
 ?????????? ?????????? ?????????? ??????????
 ?????????? ?????????? ?????????? ?????0001B0
 AAA1132210 10??00A000 0101000000 1100022001
 22210–010C 01111C1000 0????????? ??????????
 ???????????

Luján et al. (2016) Matrix

Testudo marmorum
 11?A00?100 1001200000 01003?1000 1100211