General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

The chelonians from the Latest Miocene–Earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia, Greece)

Les chéloniens du Miocène terminal–Pliocène basal de Allatini et Pyléa (Est de Thessalonique, Macédoine, Grèce)

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A R T I C L E   I N F O

A B S T R A C T

During recent years, our knowledge of fossil turtles from northern Greece has improved, as a result of both the discovery and description of new specimens and the revision of previously published material. The sites of Allatini and Pylea are among the classic Latest Miocene–Earliest Pliocene localities of northern Greece and have produced notable chelonian material. The purpose of this paper is to revise the previously published specimens from these sites and describe a new specimen of a turtle from Allatini. Taken together, these specimens constitute a diverse Macedonian chelonian assemblage, comprising a small tortoise, a large tortoise and a turtle. Our results augment previous knowledge of the composition of the Greek paleochelonofaunas in three main respects: first, they show that *Testudo amiatae* was not present in the Greek fossil record; second, they bring to light the earliest mention of a giant tortoise in Greece; finally, they provide the most ancient confirmed record of a fossil geoemydid in Greece.

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R É S U M É

Au cours des années récentes, notre connaissance des tortues fossiles du Nord de la Grèce s'est enrichie, en raison, d'une part, de la découverte et de la description de nouveaux spécimens et, d'autre part, de la révision de matériel déjà publié. Les sites d'Allatini et Pylea figurent parmi les localités Miocène terminal–Pliocène basal du Nord de la Grèce ; elles ont produit une quantité importante de matériel chélonien. Le propos de cet article est de réviser les spécimens de ces sites antérieurement publiés et de décrire un nouveau spécimen provenant d'Allatini. Considérés dans leur ensemble, ces spécimens constituent un assemblage chélonien macédonien varié comportant une petite et une grande

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tortues aquatiques et une tortue terrestre. Nos résultats augmentent les connaissances relatives aux faunes paléochéloniennes de Grèce sur trois principaux points. Premièrement, ils montrent que *Testudo amiatae* n'était pas présente dans le registre fossile de la Grèce ; deuxièmement, ils mettent en lumière la mention la plus précoce d'une tortue aquatique géante en Grèce ; enfin, ils fournissent l'enregistrement confirmé le plus ancien d'une tortue géoémydidée fossile en Grèce.

1. Introduction

The fossil site of Allatini is among the first known sites with chelonian remains in northern Greece. This locality has been referred to by various names, all of which refer to the same area in the east part of the city of Thessaloniki. The name Allatini derives from that of the private company that formerly exploited the clay pits in the area (Fig. 1A). Close to Allatini is the area of Pylea, also called Capundjlar (the Turkish name of Pylea; Fig. 1A). Clay pits existed in Pylea as well, probably yielding many fossil specimens. The two areas are drained by the same river system, and have been erroneously grouped together in many studies under the name of Allatini. The specimens used in this study probably come from both localities, but is currently impossible to determine their precise origin.

There is a long history of fossil discoveries in this area, which has been summarized by Syrides (1990). Specimens have been collected from both the clay deposits of East Thessaloniki and the overlying sand deposits, but some specimens are of uncertain stratigraphic position. The first studies were carried out by Nelli (1914) on the invertebrate fauna found in the clay pits, which was regarded as Pontian in age. A few years later, Del Campana (1917, 1919) described a shell of a tortoise he identified as *Testudo amiatae* Pantanelli, 1893 and a clutch of giant tortoise eggs, both of which are still stored in the collections of the Museum of Natural History in Florence (Italy). According to a note in the catalogue of the Museum, the tortoise was later identified as *Testudo marmorum* Gaudry, 1862b by A. Azzaroli in 1965. Further information on the invertebrate fauna of Allatini is given by several authors (see Syrides, 1990). Marinos (1964) proposed a Late Pliocene age for the Allatini clay deposits based on ostracods, also stating that the overlying sands were of Pleistocene age. Bachmayer and Symeonidis (1970) reported a partial shell of *T. amiatae* from Allatini (stored in the Museum of Geology and Paleontology, National Kapodistrian University of Athens, Greece). Sickenberg (1972) described a mandible of *Nyctereutes donnezani* (Depéret, 1890) from the sands overlying the clay deposits of Allatini, leading him to date these sand deposits to the Pliocene. Steffens et al. (1979) suggested a Pontian age for the clay deposits and a Ruscinian age for the sands. Close to Allatini and Pylea is the fossil locality of Megalo Emvolon, which has yielded several mammalian fossils of Ruscinian age (Koufos et al., 1991).

The chelonian material from this locality is currently poorly known and has never been reviewed with a modern approach. Del Campana (1917) provided only photographs of the shell specimen he described, in which the sutures and most sulci are difficult to perceive clearly. Bachmayer and Symeonidis (1970) provided both drawings and photographs, but continued to refer the specimen to *T. amiatae* without clear justification.

A recent attempt by Georgalis and Kear (2013) to summarize the fossil turtles of Greece complicated our scientific understanding of the Allatini fauna. First of all, the site was erroneously placed by these authors in the Mygdonia basin, rather than within the city limits of Thessaloniki (see our Fig. 1A). Second, there was no mention of the giant tortoise eggs (in Del Campana, 1919). Finally, they confused the Athens specimen (described by Bachmayer and Symeonidis, 1970) with the Florence specimen (studied by Del Campana, 1917). In detail, they write: "[...] the only other extinct small-bodied testudinid species documented from Greece is *T. amiatae* from the Latest Miocene (Messinian-Zanclean) Trilophos Formation of Allatini, near Thessaloniki (Campana, 1917). This taxon was first described from Tuscany [...], with the only known Greek specimen [...] consisting of a poorly-preserved shell (AMPG(y) 1917/1970/2) referred solely on the basis of its immobile xiphiplastra, a distinguishing feature of *Testudo* sensu lato [...]. However, our inspection of AMPG(y) 1917/1970/2 found the posterior plastron to be missing, thus its taxonomic assignment is impossible to substantiate." (Georgalis and Kear, 2013:304). Therefore, it is clear that these authors considered the AMPG specimen (first described by Bachmayer and Symeonidis, 1970) as the original specimen in Del Campana (1917). Indeed the posterior plastron is missing in the Athens specimen, but is preserved completely in the Florence specimen studied by Del Campana (1917).

The above historical summary indicates that the available published information on the chelonians of these localities is either outdated or erroneous. In this contribution we revise the chelonian fauna from Allatini, presenting up-to-date information on the Florence (found in Pylea) and Athens (found in Allatini) specimens. Further information on the chelonian fauna of this locality comes from an unpublished geoemydid specimen that has been found in the collections of the Museum of Geology and Paleontology (Aristotle University of Thessaloniki, Greece). The
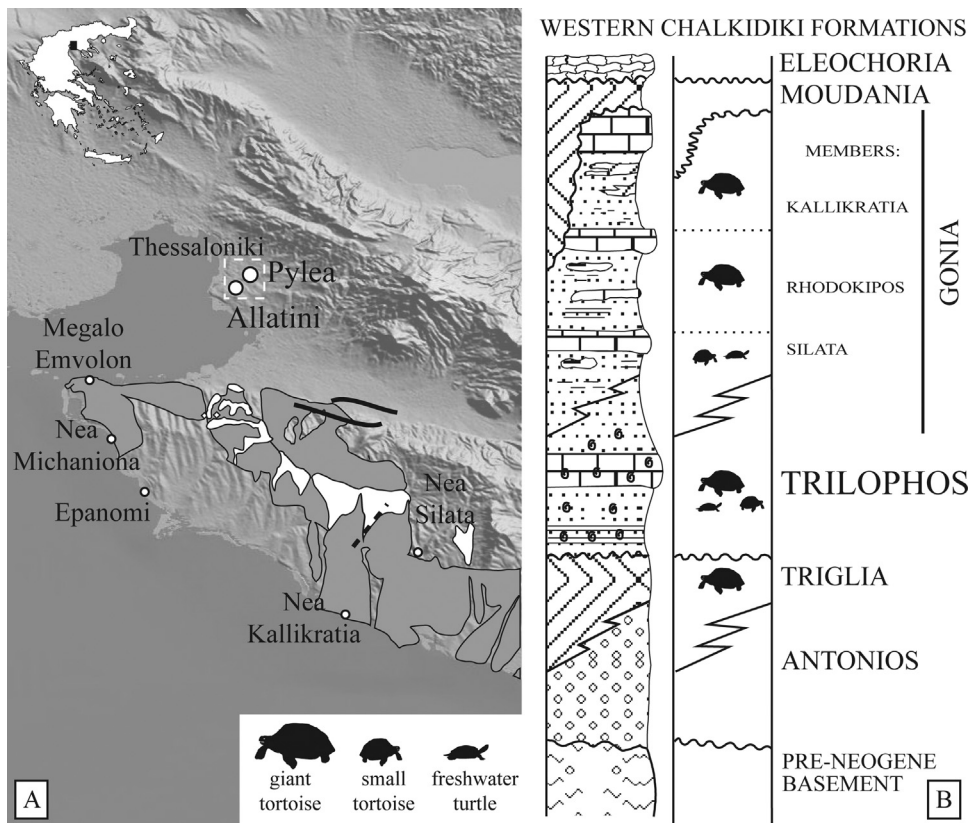
Fig. 1. A. The positions of Pylea and Allatini, in the eastern part of the city of Thessaloniki, in addition to those of other sites mentioned in this paper that have yielded fossils of turtles and tortoises. Dark gray indicates surface exposure of Neogene deposits. White color indicates surface exposure of Trilophos Formation. B. Simplified stratigraphical column (modified by Syrides, 1990; Vasileiadou et al., 2003) showing the Neogene/Quaternary formations of the western Chalkidiki peninsula. Simplified drawings of turtles indicate the presence of giant tortoises, small tortoises, and turtles in these formations.
Fig. 1. A. Localisation de Pylea et d'Allatini dans la partie orientale de la ville de Thessalonique, ainsi que des autres sites mentionnés dans l'article et ayant fourni des fossiles de tortues aquatiques et terrestres. En gris clair, les dépôts néogènes exposés superficiellement ; en blanc, l'exposition super-ficielle de la formation Trilophos. B. Colonne stratigraphique simplifiée (modifiée par Syrides, 1990 ; Vasileiadou et al., 2003) montrant les formations Néogène–Quaternaire de la péninsule de Chalkidiki ouest. Des dessins simplifiés de tortues indiquent la présence de tortues aquatiques géantes et petites ainsi que de tortues terrestres dans ces formations.

information presented here on the composition of the pale-ochelonofauna from Allatini reveals it to be one of the most diverse fossil chelonian assemblages from Greece. Finally, we provide some additional information on the Italian taxon *T. amiatae*.

Anatomical Abbreviations: Bony plates are indicated with small letters, scutes with capitals. ABD, abdominal; AN, anal; CE, cervical; cos, costal; en, entoplastron; ep, epi-plastron; FE, femoral; GU, gular; hyo, hyoplastron; hypo, hypoplastron; HU, humeral; MA, marginal; ne, neural; nuc, nuchal; PEC, pectoral; per, peripheral; PLE, pleural; VE, ver-tebral; xi, xiphiplastron.

Institutional Abbreviations: AMPG, Museum of Palaeon-tology and Geology of the National and Kapodistrian University of Athens, Greece; IGF, Sezione di Geologia e Paleontologia, Museo di Storia Naturale di Firenze, Florence, Italy; LGPUT, Laboratory of Geology and Pale-ontology, University of Thessaloniki, Greece; MNHN, Muséum national d'histoire naturelle, Paris, France; MPUM, Museo di Paleontologia dell'Università di Mod-ena, Italy; NHMW, Naturhistorisches Museum, Vienna, Austria.

2. Geological setting

The sediments of the study area are among the Neogene/ Quaternary outcrops of the western Chalkidiki peninsula, which spans from the city of Thessaloniki in the north part till the Kassandra peninsula in the south. These deposits were divided into six formations by Syrides (1990): the Antonios Formation (Middle–Late Miocene), Triglia For-mation (Vallesian–Early Turolian, Late Miocene), Trilophos Formation (Latest Miocene = Pontian), Gonia Formation (Early–Late Pliocene), Moudania Formation (Pleistocene), and Eleochoria Formation (Late Pleistocene–Holocene) (Fig. 1B). The deposits in Allatini and Pylea have now been fully exploited and/or covered by domestic areas, but the majority of them belong to the Trilophos Formation. These well stratified sediments of Trilophos Formation con-tain fossiliferous sands, clays, sandstones and limestones with abundant brackish mollusks of Paratethyan origin (Vasileiadou et al., 2003). The Trilophos Formation passes via a gradual transition into the overlying fluvial-lacustrine sediments of the Gonia Formation (Fig. 1B), which contains numerous fossils of giant tortoises (Vlachos et al., 2014),

and unconformably overlies the red beds of the Triglia Formation.

The available information regarding the provenance of the specimens considered in this study is as follows. Del Campana (1917, 1919) stated that the IGF specimens were from Pylea. The testudinid specimen from APMG originates from Allatini (Bachmayer and Symeonidis, 1970). The IGF specimens are brownish to reddish (Fig. 2) whereas the AMPG specimen is gray (Fig. 3), supporting the interpretation that the specimens come from different localities. The new LGPUT turtle specimen is also from Allatini according to a handwritten accompanying label stating that this "*freshwater turtle comes from the clay layer b' of the clay pits of Allatini, Thessaloniki, 13 November 1933*". The gray color of the sediment filling the AMPG and LGPUT specimens is consistent with their being from the Allatini locality. Since both localities mainly expose strata of the Trilophos Formation, it is likely that all the fossils considered in this study are from this formation. The lack of information on the discovery and collection of the specimens makes this assumption impossible to test, unless new specimens are found in situ or the sediment filling the shells is analyzed and compared with samples collected from various stratigraphic levels at the localities mentioned above (something which is outside the scope of this paper). Therefore, the specimens are very likely of Latest Miocene age but we cannot presently exclude the possibility that they date to the earliest Pliocene.

3. Material and methods

The material discussed here is stored in the collections of three institutions. The material described by Del Campana (1917, 1919) is stored in the IGF (shell, IGF 11602; eggs, IGF 11603). The material mentioned by Bachmayer and Symeonidis (1970) is stored in the collections of the AMPG (AMPG 1970/2). The new turtle material is stored in the collections of the LGPUT (LGPUT GG 23). The characters used for the phylogenetic analysis of this taxon are listed in the Appendix and the TNT file is provided as supplementary material. As comparative material we used published specimens from Greece stored in the AMPG, LGPUT, MNHN, and NHMW, as well as unpublished LGPUT specimens that are part of the doctoral thesis of one of us (EV). Measurements were taken using BMI calipers (0.01 mm precision).

4. Systematic paleontology

TESTUDINES Batsch, 1788
CRYPTODIRA Cope, 1868
TESTUDINIDAE Gray, 1825
Testudo Linnaeus, 1758
Testudo graeca Linnaeus, 1758
The Florence specimen: IGF 11602, partial shell of a small tortoise (total length: 167 mm), Fig. 2.
Locality: Pylea, East Thessaloniki.
Preservation: The specimen is almost complete. The lithified sediment preserved inside the shell masks the morphology of the visceral surfaces of the bones. Most plates of the carapace are preserved (Fig. 2A), apart from the left anterior carapacial margin and the entire posterior carapacial margin (partial seventh and complete eighth

costals; posterior peripherals; suprapygals). The right bridge is also missing, but the imprints of the bony plates that formed the bridge can be observed on the sediment filling the shell. The scute sulci are clearly visible on the entire surface of the carapace, but the bony sutures are not clearly visible on the anterior part (Fig. 2B). The plastron is almost completely preserved (Fig. 2C), lacking only some small parts of the xiphiplastra and hypoplastra. Parts of the medial and hypo-xiphiplastral sutures are covered by sediment. The shell is slightly deformed and compressed. The most significant deformation affects the plastron, which is deeply concave because its central area is depressed; proof of the existence of this deformation is furnished by a V-shaped space that separates the epiplastra in anterior view (see Fig. 2D).

Description
Carapace–Bony plates
Nuchal. The nuchal outline is only partially visible, but indicates that the nuchal is slightly wider than long and hexagonal in shape. The anterior border of the nuchal is nearly straight, lacking a nuchal notch.

Neurals. Nearly all the neurals are preserved (except the posterior part of the seventh and the eighth). The shape of the first neural cannot be directly observed, but based on the remaining plates we estimate that it is longer than wide, probably quadrangular. The second neural is octagonal, although the location of the anterior border of this plate is uncertain, and its posterior part is slightly wider than its anterior part. The second neural is not crossed by any sulci. The third neural is quadrangular, and wider than long. The fourth neural is octagonal, with anterior and posterior parts of equal width, and is not crossed by any sulci. The fifth neural is quadrangular and wider than long, but is narrower than the third neural. The anterior and posterior ends of the fifth neural are more convex and more concave, respectively, than those of the third neural. The sixth neural is octagonal, and its anterior part is wider than its posterior part. The sixth neural, like the preserved part of the seventh neural, is not crossed by any sulci. The seventh neural is not complete, and its edges are only faintly visible, but this plate can be estimated to be quadrangular and longer than wide.

Costals. Nearly all the costals are present and well preserved, although the posterior parts of the seventh costals are missing. The sutural margins of the first costals cannot be clearly observed, but we can estimate that the first costals are long and wide, making contact with the nuchal, the first and second neurals, the second costals and the first to third peripherals. They are the largest costals of the carapace. The remaining costals show the typical alternating pattern of the testudinids, corresponding to the quadrangular–octagonal pattern of the neurals (described above). The second, fourth, and sixth costals are medially short (in the anteroposterior dimension) and laterally long, and are crossed transversely by the pleural sulci. They alternate with the third, fifth, and seventh costals, which are medially long and laterally short. The medial parts of the third, fifth and seventh costals are crossed by the vertebral sulci.

Peripherals. Few peripherals are preserved. Those of the anterior margin are longer than wide, whereas those of the
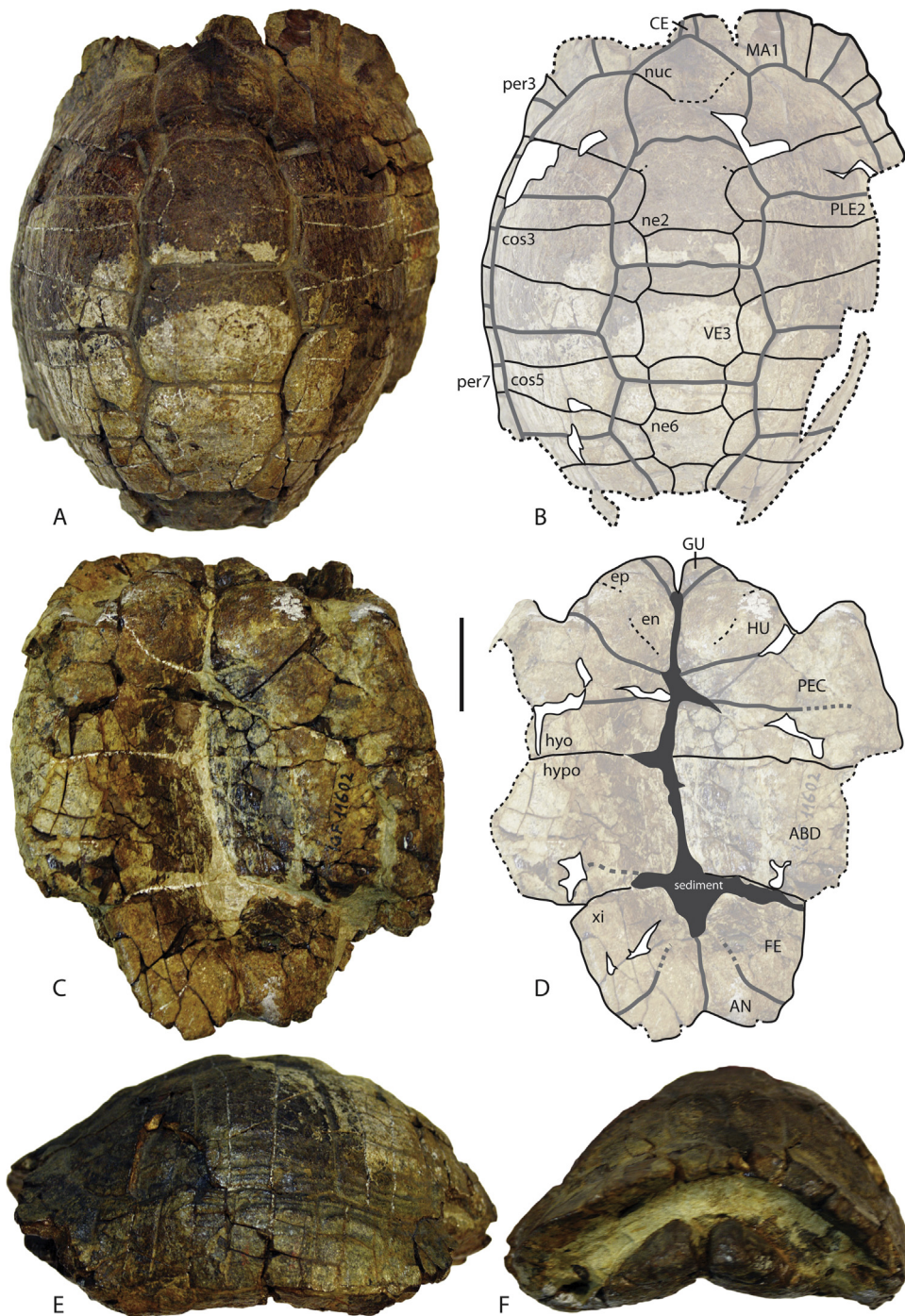
Fig. 2. (Color online.) The Florence specimen (IGF 11602) of *Testudo graeca* from the Latest Miocene–Earliest Pliocene of Pylea, Thessaloniki, Greece. A. Dorsal view of the carapace. B. Simplified drawing of the carapace in dorsal view. C. Ventral view of the plastron. D. Simplified drawing of the plastron in ventral view. E. Left lateral. F. Anterior views of the shell. The scale bar equals 5 cm.

Fig. 2. (Couleur en ligne.) Spécimen Florence (IGF 11602) de *Testudo graeca* du Miocène supérieur–Pliocène inférieur de Pylea, Thessalonique, Grèce. A. Vue dorsale de la carapace. B. Dessin simplifié de la carapace en vue dorsale. C. Vue ventrale du plastron. D. Dessin simplifié du plastron en vue ventrale. Vues latérale gauche (E) et antérieure (F) de la carapace. Barre d'échelle = 5 cm.
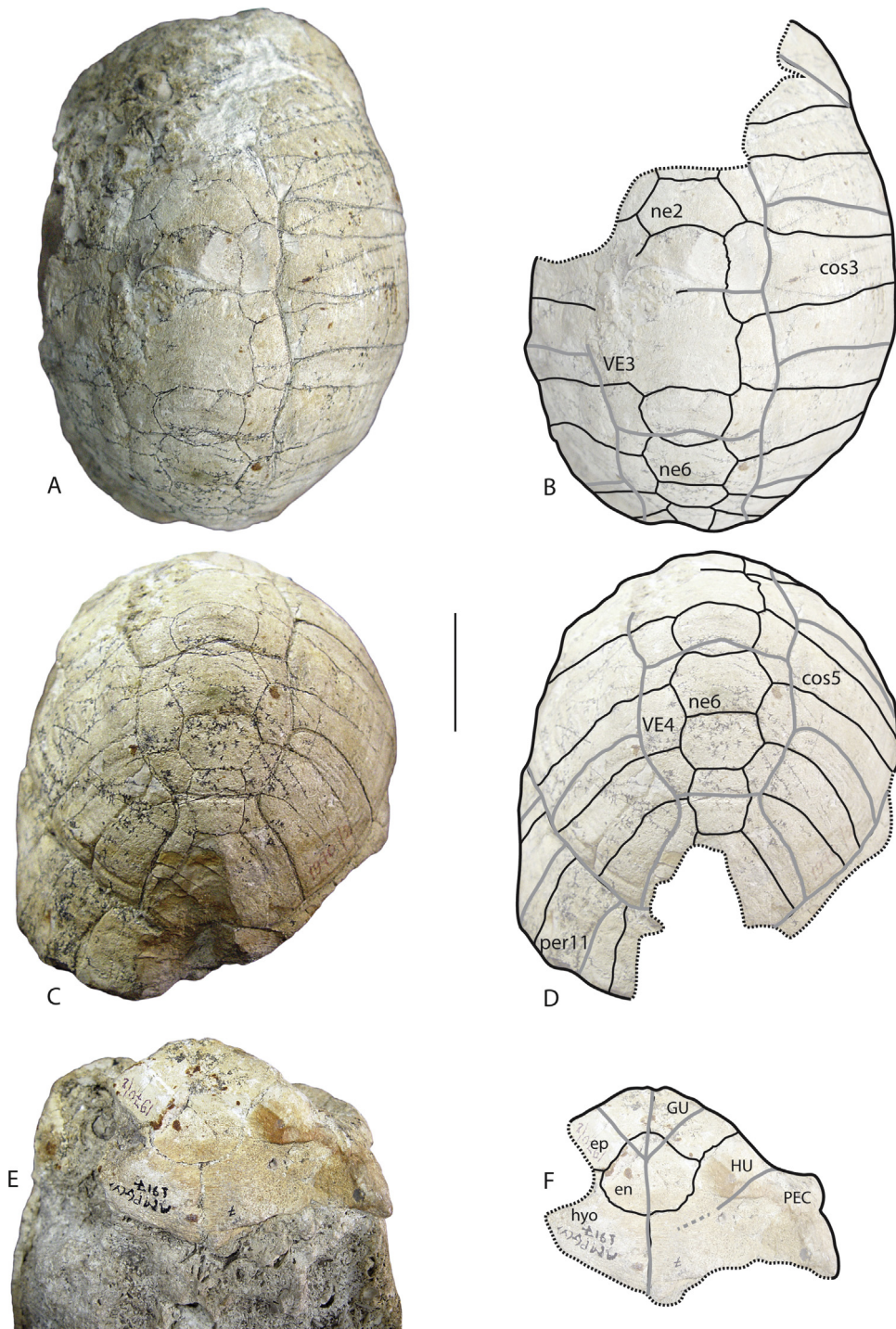
Fig. 3. (Color online.) The Athens specimen (AMPG 1970/2) of *Testudo graeca* from the Latest Miocene–Earliest Pliocene of Allatini, Thessaloniki, Greece. A. Dorsal view of the carapace. B. Simplified drawing of the carapace in dorsal view. C. Posterodorsal view of the shell. D. Simplified drawing of the shell in posterodorsal view. E. Ventral view of the plastron. F. Simplified drawing of the plastron in ventral view. The scale bar equals 5 cm.

Fig. 3. (Couleur en ligne.) Spécimen Athènes (AMPG 19702) de *Testuido graeca* du Miocène supérieur–Pliocène inférieur d'Allatini, Thessalonique, Grèce. A. Vue dorsale de la carapace. B. Dessin simplifié de la carapace en vue dorsale. C. Vue postérodorsale de la carapace. D. Dessin simplifié de la carapace en vue postérodorsale. E. Vue ventrale du plastron. F. Dessin simplifié du plastron en vue ventrale. Barre d'échelle = 5 cm.

bridge area are much taller than long. All peripherals are crossed by the intermarginal sulci. The anterior peripherals are anteriorly curved, being sub-horizontally oriented.

Carapace–Scutes

Cervical. A cervical scute is visible on the anterior part of the carapace. This scute is longer than wide, being approximately one-fourth as long as the nuchal, and broadens slightly in the posterior direction.

Vertebrals. The first four vertebrals are preserved. The vertebral scutes are wide, approximately equaling the pleurals in width, but appear significantly broader than the pleurals in dorsal view. The first vertebral overlaps the nuchal, first peripherals, first neural, and first costals. It is longer than wide and has convex lateral margins. The sulcus between the first and second vertebrals crosses the first neural and is slightly wavy. The second vertebral is slightly longer than wide, and the anterior part of this scute is narrower than the posterior part. The second vertebral covers the posterior part of the first neural, the second neural, the anterior part of the third neural, and the medial parts of the first three costals. The sulcus between the second and third vertebrals becomes anteriorly convex over a short interval crossing the midline. The third vertebral is slightly wider than long, covering the posterior part of the third neural, the fourth neural, and the anterior part of the fifth neural, as well as medial parts of the third to fifth costals. The sulcus between the third and the fourth vertebrals is straight. The fourth vertebral is longer than wide, with a narrow posterior end. It covers the posterior part of the fifth neural, the sixth neural, and the anterior part of the seventh neural, as well as the medial parts of the fifth to seventh costals. The area of the shell overlain by the fifth vertebral is not preserved.

Pleurals. The pleurals cover only the costal plates, as the pleuro-marginal sulci roughly coincide with the costo-peripheral sutures. The first two pairs of pleurals are longer than wide, whereas the last two are wider than long (although this is uncertain in the case of the last pair because of imperfect preservation). The first pleural covers the first costal, and the anterior part of the second costal. The second pleural covers the posterior part of the second costal, the third costal and the anterior part of the fourth costal. The third pleural covers the posterior part of the fourth costal, the fifth costal and the anterior part of the sixth costal. The fourth pleural covers the posterior part of the sixth costal, as well as the seventh costal, although not all of the area covered by the fourth pleural is preserved.

Marginals. The marginal scutes are morphological similar to the peripherals. The anterior marginals are wide and short, whereas those of the bridge area are much taller than long.

Plastron–Bony plates

Epiplastra. The paired epiplastra have convex ventral surfaces and are greatly thickened in the area corresponding to the epiplastral pads. In lateral view, their anterior portion is clearly deflected dorsally. Because the shell is filled with sediment, it is not possible to evaluate the presence and degree of development of the gular pocket, which is usually present when the epiplastral pads are as well developed as is the case in this specimen. The epiplastra are short and wide, and are restricted to the anterior part

of the lobe. The anterior edge of the lobe is approximately rounded. The posterior margins of the epiplastra cannot be confidently observed.

Entoplastron. The margins of the entoplastron are not clear, but this plate is probably broad and rhomboid. The entoplastron probably contributes to the dorsally deflected portion of the anterior lobe.

Hyoplastra/Hypoplastra. The hyoplastra and the hypoplastra are the largest plates of the plastron, and are long and wide. They are medially depressed, but it is not possible to infer if this is an effect of deformation or an indication that this specimen represents a male. The anterior suture between the hyoplastra and the entoplastron is not clearly visible. The hyo-hypoplastral suture is straight. The midline suture separating the left and right hyo- and hypoplastra is covered by sediment. The posterior margin of the hypoplastra is mostly covered by sediment as well, but the visible part indicates that this suture is located close to the end of the bridge. Therefore, the hypoplastra do not contribute to the posterior lobe of the plastron.

Xiphiplastra. The xiphiplastra are slightly longer than broad. Compared to the hypoplastra, they are relatively long, constituting the entire posterior lobe. The lateral edge of each xiphiplastron is rather straight anteriorly, becoming convex only towards the posterior tip. A wide (approximately 120 degrees) but relatively shallow anal notch separates the posterior parts of the two xiphiplastra.

Plastron–Scutes

Gulars. The gulars are wide and short, covering the epiplastra. They converge posteriorly and probably cover the anterior part of the entoplastron.

Humerals. The humerals are wide and anteroposteriorly short, covering the posterior parts of the epiplastra, the entoplastron and the anterior parts of the hyoplastra. The humero-pectoral sulcus has a wide V-shape, and crosses the hyoplastra posterior to the entoplastron.

Pectorals. The pectorals are the anteroposteriorly shortest scutes of the plastron, but they are very wide. They cover only the middle parts of the hyoplastra.

Abdominals. The abdominals are the longest scutes of the plastron, covering the posterior parts of the hyoplastra and nearly all of the hypoplastra. Medially, the posterior ends of the abdominals apparently coincide with those of the hypoplastra. Laterally, they contact the anterior parts of the femorals, which prevent them from covering the posterolateral corners of the hypoplastra.

Femorals. The femorals cover the anterior parts of the xiphiplastra, whereas a small part of each femoral, strongly convex in shape, covers the posterolateral part of the corresponding hypoplastron. As a result of the presence of the hinge, the median part of the abdomino-femoral sulcus coincides with the hypo-xiphiplastral suture. The medial parts of the femorals are anteroposteriorly shorter than the lateral parts.

Anals. The anals cover the posterior parts of the xiphiplastra. Although they are not completely visible, they appear to be medially long and laterally short. The femoro-anal sulcus is slightly anteriorly concave.

The Athens specimen: AMPG 1970/2, partial shell of a small tortoise, Fig. 3.

Locality. Allatini, east Thessaloniki.

Preservation. The shell is partially preserved, and its internal surface is covered by lithified sediment. The right side of the carapace is almost complete, lacking only a part of the first costal. The right side is preserved from the third till the eighth costal (Fig. 3A–D). The pygal–suprapygal area is fragmented and incomplete, with only a part of the suprapygal being visible. Only a part of the anterior lobe of the plastron is preserved (Fig. 3E–F). The sutures and sulci are not entirely visible in some areas, such as in the medial region of the carapace and the hyoplastral region.

Description
Carapace-Bony plates

Neurals. Only the posterior part of the first neural is preserved, but this plate was probably quadrangular and very wide. The second neural is hexagonal, with short posterolateral sides. The third neural is quadrangular, and markedly wider than long. The fourth neural is partially visible in this specimen, and possibly deformed. However, it displays an octagonal shape. The fifth neural is quadrangular and longer than wide, with rounded lateral sides. The sixth neural is hexagonal, and wider than long. The seventh neural is also hexagonal, but is narrower in proportion to its length than the sixth. The eighth neural is also hexagonal, but markedly longer than wide.

Suprapygal. Only a partial suprapygal is preserved. Its state of preservation does not allow its morphology to be clearly assessed, but the suprapygal is probably single and pyramidal in shape, with a narrow anterior end and a wide posterior one.

Costals. The right costals (from the second to the sixth) show the alternating pattern that is typical of testudinids, as plates that are medially short and laterally long alternate with ones that are medially long and laterally short.

Peripherals. The only preserved peripherals are those on the posterior part of the left side. They are short, tall and almost vertically oriented.

Carapace–Scutes

Vertebrals. Four vertebrals are preserved, and only the first one is missing. The vertebrals are wide, being almost equal in width to the pleurals in dorsal view. The second vertebral covers the posterior part of the first neural, and the entirety of the second and third neurals. The third vertebral covers the posterior part of the third neural, the fourth neural, and the anterior part of the fifth neural. The sulcus between the second and third vertebrals is slightly convex anteriorly. The fourth vertebral is longer than wide, covering the posterior part of the fifth neural, all of the sixth and seventh neurals, and the anterior part of the eighth neural. The sulcus between the third and fourth vertebrals is again convex anteriorly.

Pleurals. The pleurals show the typical morphology for *Testudo*. They cover only the costals, are quadrangular, and are slightly wider than long. The pleuro-marginal sulcus coincides with the costo-peripheral suture in the preserved portion of the carapace.

Marginals. The marginal scutes are similar in shape to the peripherals, being short and tall.

Plastron

Description. Due to the poor preservation of the plastron, we will not describe each plate separately.

The epiplastra are narrow and anteroposteriorly short. Although covered with sediment, both epiplastra are thickened anteriorly, suggesting the presence of an epiplastral lip. The entoplastron is wider than long, being rhomboid to subcircular in shape. Among the scutes, only the gulars are clearly distinguishable. They are long and narrow, covering the anterior part of the entoplastron. The humero-pectoral sulcus is preserved only on one side, and is only partially visible, but is located posterior to the entoplastron.

Comments and comparisons

Among other features, the presence of a thickened epiplastral lip and the alternating pattern of the costals provide a basis for referring the Allatini and Pylea specimens to Testudinidae. The presence of a cervical scute, the pattern of the neural plates, the fact that the costo-peripheral sutures coincide with the pleuro-marginal sulci, and the fact that the gulars cover the anterior part of the entoplastron (among other features) indicate that they belong to the genus *Testudo* (e.g., Młynarski, 1976; Lapparent de Broin et al., 2006; and references therein). The updated morphological description presented above implies that the tortoises from Allatini should be attributed to the *Testudo* s.s. lineage, and in particular to *Testudo graeca*. Among other features, the wide vertebrals of the carapace are characteristic of *Testudo* s.s., and differ from the narrower vertebrals of *Testudo hermanni* (Amiranashvili, 2000; Lapparent de Broin et al., 2006). Further evidence comes from the plastron. Several characters suggest the presence of a hypo-xiphiplastral hinge in the Florence specimen (for details on the morphology of the hinge in *Testudo* s.s., see Lapparent de Broin et al., 2006). First, the posterior lobe is formed entirely by the xiphiplastra and is elongated compared to the hypoplastra. In all hingeless taxa, the anterior part of the posterior lobe is contributed by the hypoplastra. Second, the extent to which the femoral scutes cover the posterior parts of the hypoplastra is much reduced medially. Third, the posterior lobe is preserved in a position of slight displacement, indicating a loose connection with the hypoplastra. Finally, the abdomino-femoral sulcus coincides medially with the hypo-xiphiplastral suture, as is typical in taxa with a hinge (Amiranashvili, 2000; Lapparent de Broin et al., 2006; Delfino et al., 2009).

The Florence and Athens specimens display some important morphological differences with regard to the bony elements of the carapace, despite similarities in the positions of the scute sulci of the carapace and the morphology of the plastron that strongly support their referral to the same species. In particular, the neural series is different. In the Florence specimen we observe the typical differentiated condition of *Testudo* with alternating quadrangular and octagonal neurals. The Athens specimen on the other hand, shows a less differentiated (more primitive) neural series. The second neural is hexagonal. Unfortunately, this region cannot be clearly studied in the Florence specimen, but a hexagonal second neural (or even an octagonal one with very short anterolateral sides) is a relatively normal feature that can be found in several extant specimens of *Testudo graeca*. Moreover, the sixth and seventh neurals

of the Athens specimen are also hexagonal, a condition that is rare in the *Testudo* s.s. lineage (Lapparent de Broin et al., 2006: 334). Similarly, the sulci separating the vertebrals differ in position between the Athens and Florence specimens, being located near the posterior margin of the neurals in the Florence specimen.

The most relevant comparison that can be made is to the complete shell from the Pliocene of Megalo Emvolon, which was described as *Testudo* cf. *graeca* by Bachmayer et al. (1979). This specimen (NHMW 1980z0069/0000) is more similar to the Florence specimen than the Athens specimen in having a well differentiated neural region, which differs only in two minor respects. First, the fourth neural of the Megalo Emvolon specimen is significantly wider than the other neurals, a condition not observed in the Florence specimen. Second, the sulci between the vertebrals in the Megalo Emvolon specimen are straight, in contrast with the wavy condition in the Florence specimen. Few differences in plastron morphology exist between the two specimens as well, and these concern mainly the shape of the entoplastron. In the Megalo Emvolon specimen, the entoplastron is much narrower and longer than in either of the specimens from Allatini and Pylea. Other specimens of the *Testudo graeca* lineage are known from the Lowermost Pleistocene of Lesvos (figured in Lapparent de Broin, 2002) and from the Upper Miocene–Pliocene of Thessaloniki (precise locality unknown; mentioned in Arambourg and Piveteau, 1929). The available information on these specimens is limited.

The specimens from the Mio-Pliocene boundary revised here can also be compared with the other Late Miocene form known from Greece, namely *Testudo marmorum* Gaudry (1862b) from the undoubtedly older deposits of Pikermi, Attica (precise locality unknown). Albert Gaudry briefly described and figured this taxon in three publications (Gaudry, 1862a, b, 1862-1867). This taxon is known from two specimens housed at the MNHN and six housed at the AMPG. Both MNHN specimens are labeled "type", but neither was named as a holotype by A. Gaudry. The AMPG specimens were described by Bachmayer and Symeonidis (1970). The known material of *T. marmorum* is in need of revision and is part of the doctoral thesis of one of us (EV). In the present study we focus on the type material from the MNHN in our comparisons. Like the specimens revised above, the small tortoise from Pikermi is also characterized by the presence of a hinge between the hypoplastra and the xiphiplastra. It has always been regarded as a close relative with the extant species *Testudo marginata* (see Lapparent de Broin, 2001 amongst others), but without any detailed justification. Neither of the MNHN specimens retains the posterior pygal region. In AMPG specimens that retain this part of the shell, the pygal lacks the posterior flaring seen in the extant marginated tortoise. As preserved, the plastron of MNHN PIK 3683 shows a posterior widening of the posterior lobe (as in *T. marginata*), but this is probably a result of deformation. In any case, *Testudo marmorum* differs in many respects from the Allatini and Pylea specimens. First, *T. marmorum* has a longer and narrower cervical scute. In the MNHN specimens of *T. marmorum*, the cervical scute is in fact so narrow that Gaudry's original figures of this taxon did not depict a cervical. Second, the pleural scutes overlap the nuchal and anterior peripherals to a significant

degree in *T. marmorum*, whereas in the Pylea specimen the pleuro-marginal sulci coincide with the costo-peripheral sutures. Third, the first vertebral scute is much longer and narrower in *T. marmorum* than in the Pylea specimen. Finally, the entoplastron is always longer and narrower in *T. marmorum* than in the specimens revised here.

Looking beyond Greece, the material described above can be compared with the recently named species *Testudo oughlamensis* from the Upper Pliocene of Ahl al Oughlam, Morocco (Gmira et al., 2013). The Pylea and Allatini specimens are certainly distinct from the Moroccan tortoise in having narrower vertebral scutes, and differences also exist in the neural series. The third and fifth neurals are quadrangular in the specimens studied here, being also much shorter and narrower than in *T. oughlamensis*. While the neural formula of the Pylea specimen is ?4-8-4-8-4-6-?6-?, that of the Moroccan specimen is completely different and irregular, being 4-8-7-5-6-5-6-6. This condition could be the result of anomalous growth of the plates.

So far, the morphology of the specimens redescribed above (AMPG 1970/2, IGF 11602) is consistent with the known morphology of extant and extinct examples of *T. graeca* from Greece. According to de Lapparent de Broin (2001), specimens of *T. marmorum* and *Testudo* sp. from the Late Miocene of "Salonique", Greece (we keep the name "Salonique" as in Arambourg and Piveteau, 1929 due to the uncertainty of the precise locality; see Vlachos et al., 2014) constitute the oldest record of *Testudo* s.s. However, many Mio-Pliocene *Testudo* fossils remain unidentified at the species level, so that the actual oldest record of *T. graeca* remains an open question. In other words, how far back in time can we confidently identify this taxon based on morphological characters that can be found in fossils? The *T. graeca* complex has a convoluted taxonomic history, characterized by numerous nominal species and subspecies (see for example Fritz et al., 2007, and references therein). In many cases, characters relating to scute coloration or keratinous features (thigh-spurs in *T. graeca*) are used to distinguish the subspecies, but such characters are not preserved in fossil specimens.

The two small tortoises from Allatini, namely the Florence and Athens specimens, have been previously attributed to the Late Miocene species *Testudo amiatae* Pantanelli, 1893. This taxon was described on the basis of a relatively well-preserved shell from "Fosso Merlaccione" close to Cinigiano (Tuscany, Italy; Pantanelli, 1893a, b), now housed in the collections of the Museo di Paleontologia dell'Università di Modena with the collection number MPUM 25. Auffenberg (1974) lists *T. amiatae* as a junior synonym of *T. antiqua*. Chesi (2008) redescribed the holotype and remarked that it represents a small *Testudo*-like male, being a domed shell 140 mm long, 110 mm wide and 84 tall. The plastron is moderately concave, with a wide anal notch. MPUM 25 is further characterized by broad vertebrals and a sutural connection between the hypoplastra and xiphiplastra. The absence of a hinge is also supported by the considerable distance between the abdomino-femoral sulci and the hypo-xiphiplastral sutures. After Chesi (2008) tentatively accepted the validity of *T. amiatae*, but questioned its generic identification and suggested that it could belong

to the *Testudo hermanni-Testudo horsfieldi* lineage because of the sutural relationships between the hypoplastra and xiphiplastra. As described above, the Allatini and Pylea material clearly differs from *T. amiatae* and cannot be referred to this species. *T. amiatae* is therefore known only from its type locality (despite being abundant, all other fossil *Testudo* specimens from Tuscany are referred to extant species or remain unidentified at the species level; Chesi, 2008; Rook et al., 2013).

GEOEMYDIDAE Theobald, 1868
Mauremys sp.
The Thessaloniki specimen: LGPUT GG 23, partial compressed shell.
Locality. Allatini, East Thessaloniki.
Preservation. This specimen was collected in November 1933 in the clay pits of Allatini, and delivered to the LGPUT. When the fossil was discovered, only the dorsal side was visible, the ventral side being covered with sediment. On the dorsal side, only a few plates were preserved, in their original position (Fig. 4A). However, compression of the specimen caused the missing bony plates to leave clear imprints on the matrix filling the shell, providing additional information on the structure of the carapace. The visceral surface of the left xiphiplastron was also exposed in dorsal view, indicating that at least some of the plastron was preserved (Fig. 4B). The ventral side of the specimen was recently prepared by one of us (EV), revealing the nearly complete plastron. Due to the severe compression of the specimen, the surface of the shell is badly fractured, but in most cases the sutures and sulci are clearly visible (Fig. 4C). The only missing parts of the plastron are the right epiplastron and a portion of the left (Fig. 4D).

Description
Carapace. The general shape of the carapace, as inferred from the imprints of the plates on the sediment, resembles that seen in a turtle. The carapace is longer than wide, is relatively flattened (even allowing for the compression it has undergone), and has short and almost horizontally oriented peripherals (those not involved in the bridge). The imprints of the neurals indicate a poorly differentiated neural series, with quadrangular and hexagonal neurals. The first neural appears to be quadrangular, and longer than wide. The second is hexagonal with short anterolateral sides, and slightly wider than long. The fourth is quadrangular. The fifth is hexagonal, with short anterolateral sides, and is slightly longer than wide. This neural is crossed by a sulcus. The remaining neurals appear to be hexagonal, with short anterolateral sides, and markedly wider than long. The costals are not differentiated, all being quadrangular with almost parallel sides. Only one costal, possibly the left fourth costal, is crossed by sulci. Two sulci, which could correspond to the boundaries between a vertebral and two adjacent pleurals, are visible on this plate. If the fourth costal plate is in its correct anatomical position, the vertebrals must have been very short and wide.
*Plastron.* Due to the imperfect preservation of the plastron, we will not describe each plate separately. The partial left epiplastron is thin, without any protruding epiplastral lip, and is covered by the gular scute medially. The part of the plastron covered by the gulars is incompletely

preserved, but these scutes appear to be long and narrow. The entoplastron is rhomboid in shape, being equally long and wide, and is covered by the gulars anteriorly. The humero-pectoral sulcus crosses the posterior part of the entoplastron. The hyo- and hypoplastra are long and wide. The hyoplastra are crossed anteriorly by the humero-pectoral sulcus, whereas the hypoplastra are crossed posteriorly by the pectoro-abdominal sulcus. The xiphiplastra are strongly constricted at the level of the lateral termination of the femoro-anal sulcus. The anals are medially long and laterally short. A deep and somewhat rounded anal notch separates the posterior ends of the xiphiplastra.

Comments and comparisons
The neural pattern and the presence of the anal notch allow attribution of the Allatini specimen to Geoemydidae. Given that few morphological details can be discerned on the dorsal surface of the carapace, the best available information comes from the plastron. In many geoemydids the entoplastron is covered anteriorly by the gular scutes and posteriorly crossed by the humero-pectoral sulcus. In the Allatini specimen, however, the humerals are medially very short, increasing the area of the entoplastron that is covered by the gulars and pectorals. This condition is found only in some species of *Mauremys* (e.g., *Mauremys caspica, Mauremys leprosa, Mauremys sarmatica, Mauremys gaudryi*; see character 49, state 4, and fig. 3.21 in Hervet, 2003), whereas the gulars and pectorals cover less of the entoplastron in *Mauremys portisii, Mauremys pygolopha, Mauremys thainensis* and some species of *Palaeochelys*. Another character supporting the taxonomic placement of the Allatini geoemydid in *Mauremys* is the narrow and deep anal notch. The anal notch of the Allatini *Mauremys* is somewhat rounded as in *M. sarmatica* and *M. pygolopha*, but is more similar to the angular notch seen in *M. caspica* and *M. leprosa*. However, the anal notch is wider in these two extant taxa than in the Allatini geoemydid. Claude et al. (2007) listed a number of additional diagnostic characters of the carapace of *Mauremys* that cannot be observed on the Allatini specimen.

Compared to *Mauremys* sp. from San Giovanni di Sinis, Italy (Chesi et al., 2007), the Allatini turtle shows a deeper and narrower anal notch. Compared to the Late Miocene *Mauremys campanii* (new combination in Chesi et al., 2009), the Allatini specimen has a more posteriorly located humero-pectoral sulcus. Among the measurements and ratios used by Chesi et al. (2009), only ratio of the length of the humerals to that of the entoplastron can be confidently assessed in the Allatini specimen (HuL/Ent = 8.38 mm/21.42 mm = 0.391). The calculated value of 0.391 is similar to those previously obtained for *M. campanii* ($0.132 < x < 0.5$), *M. gaudryi* (0.352) and *M. sarmatica* ($0.164 < x < 0.586$), but significantly lower than the value for *M. portisii* (0.613) (from Chesi et al., 2009). Also, the median length of the humerals is much shorter than that of the pectorals. The length ratio between these elements cannot be determined precisely, but appears to fall within the range expected for *Mauremys*. Regarding the Asian *Mauremys*, Takahashi et al. (2013) list a number of differences among hingeless geoemydids
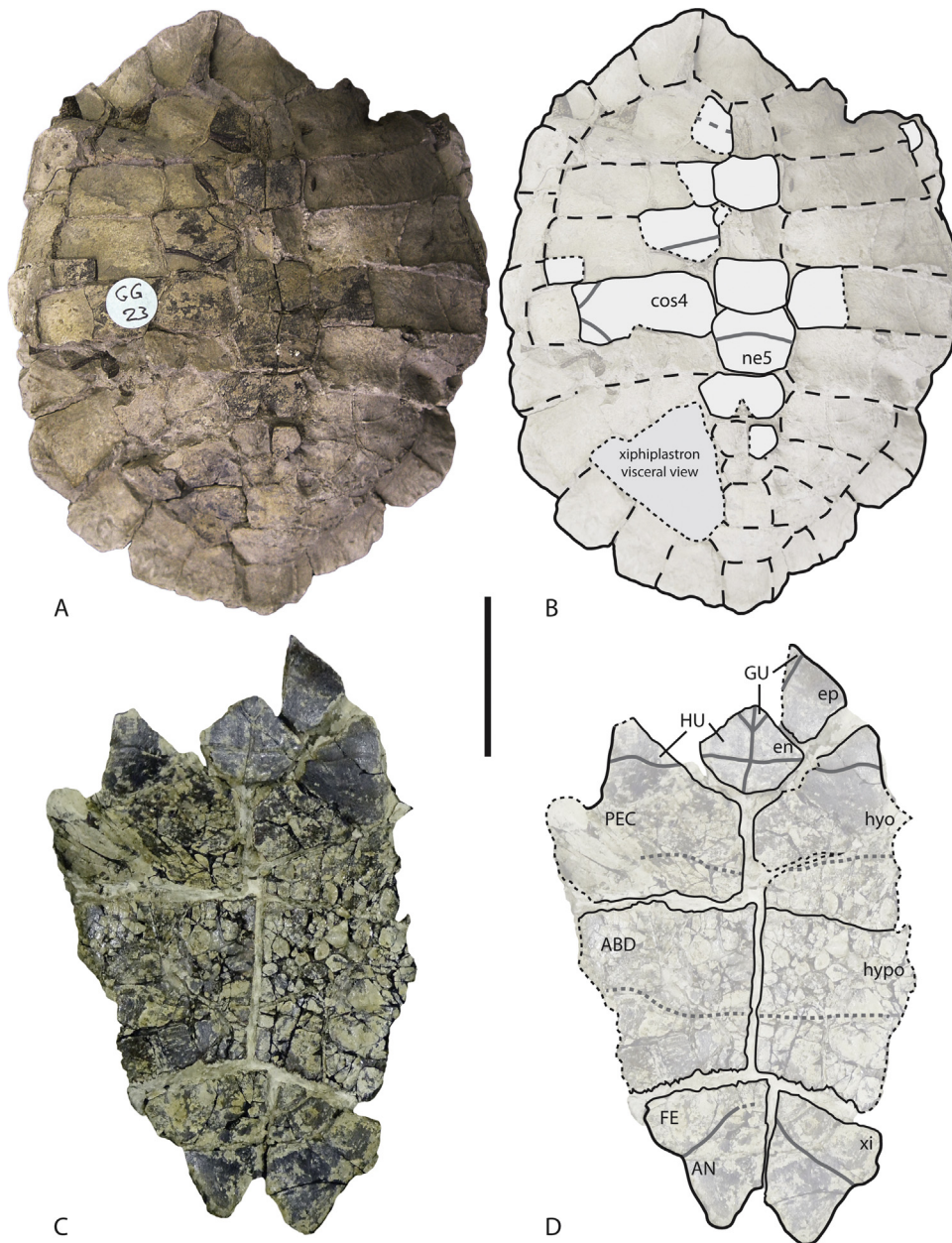
Fig. 4. (Color online.) The Thessaloniki specimen (LGPUT GG 23) of *Mauremys* sp. from the Latest Miocene–Earliest Pliocene of Allatini, Thessaloniki, Greece. A. Dorsal view of the carapace. B. Simplified drawing of the carapace in dorsal view. C. Ventral view of the plastron. D. Simplified drawing of the plastron in ventral view. The scale bar equals 5 cm.

Fig. 4. Spécimen Thessalonique (LGPUT GG 23) de *Mauremys* sp. du Miocène supérieur–Pliocène inférieur d'Allatini, Thessalonique, Grèce. A. Vue dorsale de la carapace. B. Dessin simplifié de la carapace en vue dorsale. C. Vue ventrale du plastron. D. Dessin simplifié du plastron en vue ventrale. Barre d'échelle = 5 cm.

from Asia and Europe with an entoplastron crossed by the humero-pectoral sulcus. The main differences are found on the carapace, which is not preserved in the Allatini specimen. The only character that is preserved in our specimen is the length of the entoplastron relative to the interhyoplastral suture (character 8 in Takahashi et al., 2013). The length of the entoplastron in the Allatini specimen is shorter than the interhyoplastral length, similar to *M. japonica* but contrasting the condition in *M. mutica* and *M. yabei*.

Several of the characters mentioned above, however, are potentially subject to the intraspecific variation that is present in *Mauremys*, a matter that has received some attention in the literature. For example, Gómez de Soler et al. (2012) suggested that the differences between the Pliocene *M. gaudryi* and the extant *M. leprosa* were small enough to be attributed to intraspecific variation. The two taxa are indeed fairly similar in many respects, although *M. gaudryi* may differ from *M. leprosa* in having wider

cervical, a slightly deeper anal notch, and a humero-pectoral sulcus that is more posteriorly placed on the entoplastron. We consider that this example illustrates one of the main problems encountered when comparing fossil and extant taxa, involving the distinction between discrete and continuous characters (see for example the discussion in Escapa and Pol, 2011 and references therein). Most of the differences noted above cannot be adequately coded as discrete characters (e.g., presence/absence) because they are actually shape changes that are more appropriately analyzed with a combination of morphometrics and cladistics (see Escapa and Pol, 2011 and references therein).

Documenting the presence of a turtle referable to *Mauremys* sp. in the Uppermost Miocene–Lowermost Pliocene of Greece is of particular interest, as this constitutes the oldest confirmed record of this genus in Greece. Gad (1990) reported some fragmentary remains of *Mauremys* from the Uppermost Miocene of Maramena (Serres basin), but the material is too poorly preserved to allow a confident assessment of its taxonomic affinities. Further *Mauremys* specimens from near the Miocene/Pliocene boundary are known from the Nea Silata locality (EV unpubl. data; information by G. Syrides and K. Vassileiadou). Identifying the Allatini specimen at the species level is rather difficult, because the carapace provides only limited morphological information.

One taxonomically important point, however, lies in the shape of the vertebral scutes. Although information from the dorsal carapace is limited in the Allatini specimen, the vertebrals were evidently extremely wide (approximately two-thirds of the width of the carapace, or even more) and short. A similar condition has been noted by one of us (EV) in isolated costal plates from the Late Miocene/Pliocene of the Nea Silata locality, close to Thessaloniki. Extant specimens of *Mauremys* (*M. caspica*, *M. leprosa)* always have narrow and longer vertebrals. Among the known fossil forms of *Mauremys*, the only taxon in which the vertebrals approach a comparable width is *M. campanii* (see Chesi et al., 2009), but even in this species the vertebrals are still narrower than in the Allatini specimen. Other fossil *Mauremys* specimens from Italy (e.g., *M. portisii*, *M. etrusca*; see Chesi, 2008) have narrower and longer vertebrals as well. The vertebrals of *Hardella thurjii* are wider than in other extant geoemydids, but still almost twice as long as those of the Allatini geoemydid. As summarized by Danilov (2005: Fig. 80) some geoemydids show wide vertebrals as well. The Pliocene *Clemmydopsis mehelyi* from Hungary (see Danilov, 2005: Fig. 80A, B) lacks the first pleural scutes, showing very wide vertebrals as a result. However, the plastron of *Clemmydopsis* shows a short anal notch compared to the Allatini geoemydid. The Pliocene *Sakya kolakovskii* from Georgia (see Danilov, 2005: Fig. 80C, D) also shows wide vertebrals that reach the lateral parts of the costals, in contact with narrow pleurals. In this case however, the number of vertebrals is higher than normal, showing 10 wide and narrow vertebral scutes. The Miocene *Sarmatemys lungui* from Moldova (see Danilov, 2005: Fig. 80E, F) shows some similarities with the Allatini geoemydid in the shape of the vertebrals and in the shape of the anal notch, but *Sarmatemys* shows an entoplastron that is not overlapped by the gular scutes. The Allatini geoemydid differs from all these taxa in having a sinuous humero-pectoral sulcus (as in *Mauremys*). Obviously, the few preserved carapacial information on the Allatini geoemydid does not allow further comparison with the above-mentioned taxa.

The peculiar morphology of the vertebral scutes seems to distinguish the Allatini geoemydid from known extant and extinct forms, suggesting that the Late Miocene *Mauremys* from the Thessaloniki area could belong to a new species. However, the specimen is too poorly preserved for clear conclusions to be drawn at present, since many diagnostic parts of the carapace are missing. Nevertheless, we will attempt below to assess the phylogenetic position of the Allatini geoemydid within known extant and extinct geoemydids from Europe. Hopefully new specimens will allow a more detailed description, and a more secure taxonomic identification, in the future.

Phylogenetic analysis

Given that the Thessaloniki specimen (LGPUT GG 23) is one of the oldest geoemydids from Greece, and possibly represents a new taxon (see above), we tried to assess its phylogenetic position among the various European *Mauremys* species (and other closely related taxa). We used the data matrix of Hervet (2003), incorporating the modifications suggested by Chesi et al. (2009) for *M. portisii* and *M. campanii* (excluding *Borkenia* aff. *B. oschkinisi*). Since the characters have only been published in French, in the thesis of Hervet (2003), they are listed here in English (see Appendix). We also accepted the proposal by Claude and Tong (2004) that the following species represent junior synonyms of other taxa: *Juvemys*, *Francellia*, *Owenemys* and *Euroemys* (junior synonyms of *Palaeoemys*); *Bergounioux-chelys*, *Cuculemys* and *Provencemys* (junior synonyms of *Palaeochelys*); *Francellia sallouagmirae* and *Juvemys labarrei* (junior synonyms of *Palaeoemys testudiniformis*); and *Palaeoemys occitana* (junior synonym of *Palaeoemys hessiana*). The data matrix contained 30 taxa and 54 characters (see Appendix). We performed a traditional search with TNT v. 1.0 (Goloboff et al., 2008), using a tree-bisection algorithm with 1,000 replicates. All characters were considered unordered and equally weighted. A total of 28 most parsimonious trees, each having a length of 145 steps, were recovered.

The strict consensus of the recovered trees is presented in Fig. 5A. The Allatini specimen is clearly a member of the *Mauremys* clade, and in particular the clade containing *M. leprosa*, *M. caspica*, *M. gaudryi*, *M. campanii* and *M. portisii*, being clearly separated from the older forms like *M. sarmatica* and *M. pygolopha*. Because few characters could be scored for the specimen, its exact phylogenetic position remains unresolved. The Allatini specimen occupies different positions within the *Mauremys* clade: either outside to the clade containing *M. leprosa*, *M. caspica, M. gaudryi*, *M. campanii*, and *M. portisii*, or as the sister taxon of *M. caspica*, or as the sister of one of two Italian taxa, the Early Pliocene *M. portisii* and the Late Miocene *M. campanii*. To further analyze this instability, we employed the iter-PCR script developed by Pol and Escapa (2009). This script not only analyzes the positions of unstable taxa, but also reports the characters that support alternative placements.
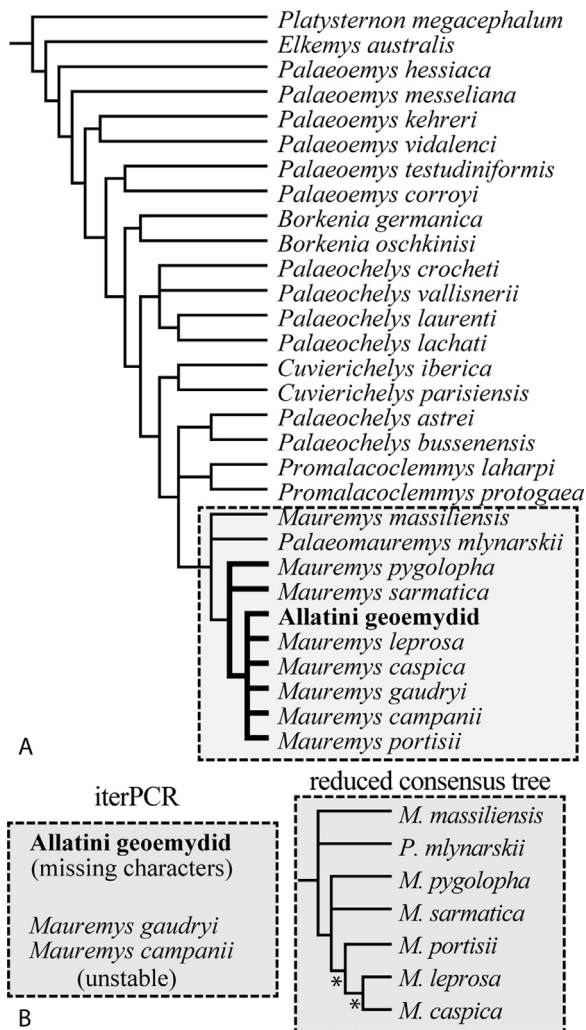
Fig. 5. A. Strict consensus of 28 most parsimonious trees (length = 145), from on an analysis of 54 characters in 30 taxa, based on the analysis proposed by Hervet (2003), following several modifications explained in the text. The Allatini specimen (LGPUT GG 23) is clearly a member of the *Mauremys* clade. B, Reduced consensus tree (from the iterPCR script of Pol and Escapa, 2009), showing the possible positions (with asterisk) of the unstable taxa within *Mauremys*.

Fig. 5. A. Strict consensus des 28 arbres les plus parcimonieux (longueur 145), obtenu à partir d'une analyse de 54 caractères dans 30 taxa, basée sur l'analyse proposée par Hervet (2003) suivant différentes modifications expliquées dans le texte. Le spécimen d'Allatini (LGPUT GG 23) est clairement un membre du clade *Mauremys*. B. Arbre de consensus réduit (d'après le script iterPCR de Pol et Escapa, 2009) montrant les positions possibles (avec astérisque) des taxa instables au sein de *Mauremys*.

Furthermore, it identifies characters that, if coded, could potentially resolve the positions of taxa for which many codings are lacking (Pol and Escapa, 2009). The script also produces a reduced consensus tree without the unstable taxa (Fig. 5B). The iterPCR results showed that the Allatini geoemydid, *M. campanii* and *M. gaudryi* were all unstable, but for different reasons. The Allatini geoemydid was found to be unstable as a result of missing data, mainly pertaining to carapace characters (1, 2, 3, 5, 6, 7, 8, 12, 16, 18, 50). New

material from the same locality or nearby sites will hopefully help to resolve this issue in the future. On the other hand, *M. campanii* and *M. gaudryi* were found to be unstable because of several characters (1, 2, 3, 7, 8, 12, 16, 25, 26, 49, 50) that could be scored but supported alternative positions for these two taxa. Based on all available published information, and on direct observations, we have confirmed that the scorings taken from previous analyses for *M. gaudryi* (Hervet, 2003) and *M. campanii* (Chesi et al., 2009) are correct. Therefore, we interpret this instability as an indication that the characters used in the analysis, although useful for analyzing relationships at the generic level and above, were unable to provide good resolution at the specific level. Hopefully our results will encourage a search for further characters that might be of use in resolving species-level relationships within *Mauremys*.

Based on the above, it is clear that more specimens must be described from nearby localities exposing Early Pliocene–Late Miocene boundary strata in northern Greece in order to shed light on faunal changes across this boundary. Our analysis also highlights the problematic state of the taxonomy of European geoemydids. For example, some taxa are placed within *Mauremys* in our analysis (e.g., *Palaeomauremys mlynarskii*). Also, taking into account the synonymies suggested by Claude and Tong (2004) our analysis reveals that *Palaeochelys* may be polyphyletic, and *Palaeoemys* paraphyletic. However, we acknowledge that our analysis includes only European taxa, and therefore fails to encompass the entire diversity and range of *Mauremys* given that this genus has numerous representatives in Asia as well. Hervet (2004) suggested the presence of a *Palaeochelys* s.l.–*Mauremys* lineage, contradicting both molecular phylogenetic analysis of geoemydids and the Asian fossil record (see Claude et al., 2007 and references therein). For example, molecular evidence suggests that the clade containing *M. caspica* and *M. rivulata* has a sister-group relationship with a clade containing such Asian taxa as *M. annamensis*, *M. mutica* and *M. pritchardi* (Spinks et al., 2004), and the position of *M. leprosa* is not fully resolved. Similar results were also obtained by Barth et al. (2004). Phylogenetic relationships within *Mauremys*, and the Geoemydidae in general, could be better resolved by analyzing further morphological characters to the morphological matrix introduced by Hervet (2003), and by including extant and extinct Asian geoemydids, and combine the results with the information produced by molecular studies. Such an analysis is far beyond the scope of this paper, but is needed in order to fully understand geoemydid phylogenetic relationships.

TESTUDOOLITHIDAE *indet.* (sensu Hirsch, 1996)

IGF 11603. Six structures that could represent eggs are preserved as internal molds of lithified sediment (Fig. 6) that each retains several eggshell fragments adhering to the surface (white areas in Fig. 6). Notably, some of the poorly preserved specimens are broken in ways that reveal fragments of eggshell embedded in the matrix. If the identification of these structures as eggs is correct, they must have had a complex taphonomic history.

Locality. Pylea, east Thessaloniki.
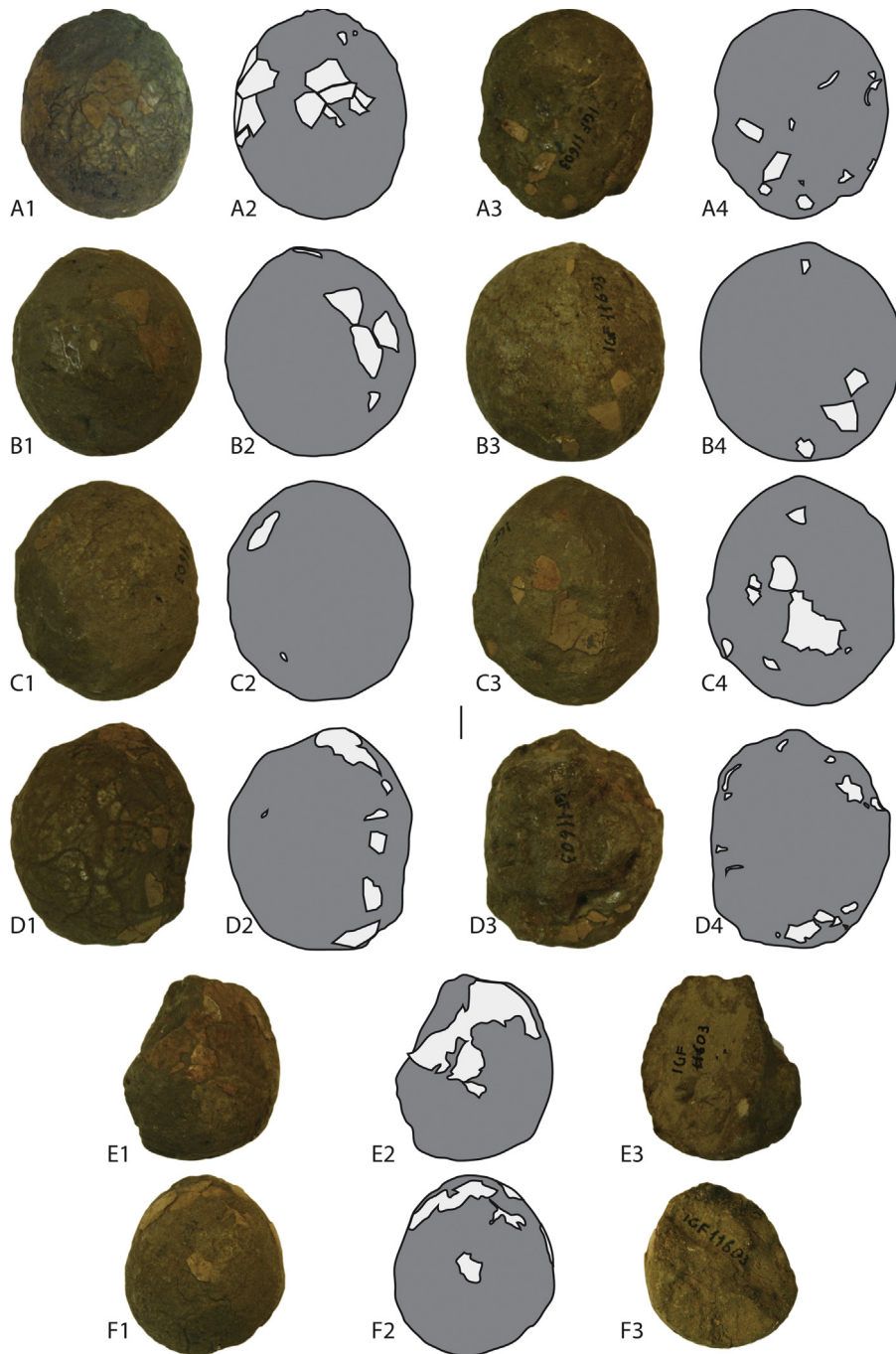
Fig. 6. A–F. (Color online.) Clutch of possible giant tortoise eggs (IGF 11603) from the Uppermost Miocene–Lowermost Pliocene of Pylea, Thessaloniki, Greece. The simplified drawings indicate the patches of preserved eggshell (white) and the lithified sediment (gray). The scale bar equals 1 cm.
Fig. 6. (Couleur en ligne.) Couvée d'œufs d'une éventuelle tortue aquatique géante (IGF 11603) du Miocène supérieur–Pliocène inférieur de Pylea, Thessalonique, Grèce. Les dessins simplifiés indiquent des fragments de coquilles d'œufs préservés (en blanc) dans le sédiment lithifié (en gris). Barre d'échelle = 1 cm.

Description. The putative eggs are elliptical in shape and somewhat flattened. The best-preserved specimens (A–C in Fig. 6) have the following dimensions (in mm): A = 61-52-43; B = 59-53-47, C = 60-49-47. The others are too fragmentary to be worth measuring. The external surface of the eggshell is light brown in color and generally smooth, but in some cases is slightly pitted.

Comments and comparisons

All of the specimens can be referred to the parataxonomic family Testudoolithidae Hirsch, 1996, based on their

ellipsoid shape. The preserved eggs are larger than previously known *Testudo* eggs (e.g., the eggs of *T. marginata* measure 38×32 mm, and those of *T. ibera* measure 35×25 mm; Bonin et al., 2006). In comparison, eggs of extant large testudinids may exceed 50 mm in length (e.g., *Centrochelys sulcata*, *Chelonoidis nigra;* from Bonin et al., 2006). The specimens correspond in their dimensions and external morphology to previously described chelonian eggs from the Pliocene of Apolakkia, Rhodes (Mueller-Töwe et al., 2011) and the Pliocene of Gran Canaria (Hirsch and Lopez-Jurado, 1987). According to Hirsch (1996), turtle eggs are characterized by the presence of an aragonite calcareous shell layer. Therefore, only an X-ray diffraction analysis (following Mueller-Töwe et al., 2011) would confidently identify the IGF specimens. Sampling the IGF specimens for such an analysis was not possible. However, the fact that the Pylea deposits belong to the Gonia Formation, which is rich in large tortoise material (see Vlachos et al., 2014), supports the possibility that these structures represent the eggs of giant tortoises.

The possible presence of giant tortoise eggs is among the interesting features of the Pylea locality. Although these are the first chelonian eggs reported from Greece (in Del Campana, 1919), they were not mentioned by Mueller-Töwe et al. (2011) or Georgalis and Kear (2013). In fact, these specimens may represent the oldest Greek record of a giant tortoise. The presence of giant tortoises was further reported in the Thessaloniki area by Arambourg and Piveteau (1929; from Axios or Megalo Emvolon) and by Bachmayer et al. (1979; from Megalo Emvolon). Recently, the new species "*Cheirogaster*" *bacharidisi* has been reported (Vlachos et al., 2014) from localities at Epanomi, Nea Michaniona and Nea Kallikratia that, like Megalo Emvolon, are within the Gonia Formation. Unfortunately, no fossil giant tortoise shells are known from Allatini, making it impossible to know if the eggs can be attributed to this species. Together with previously reported eggshell fragments from the Pliocene of Apolakkia (Rhodes Island; Mueller-Töwe et al., 2011), these specimens are the only examples of preserved turtle eggshell known from Greece.

5. Conclusions

This paper comprehensively revises the chelonian fauna from the Miocene/Pliocene boundary strata of East Thessaloniki (Macedonia, Greece). All fossil chelonians from this area have been described, in some cases erroneously, as being from the locality Allatini in Museum catalogues and the literature. Here we present evidence that the specimens originate from two localities, Pylea and Allatini, which are very close together but nevertheless distinct. The fossil chelonian assemblage from these sites is among the most diverse in Greece. Two specimens are attributed to the hinged *Testudo graeca*, a taxon with extant representatives in Greece today. Both of these specimens had previously been attributed to the Italian taxon *Testudo amiatae*, but the updated morphological information presented here proves that this taxon was not present in Greece. The two *T. graeca* specimens make it possible to document intraspecific variation in the neural series. We also point out the

presence of a giant tortoise, indicated by the findings of six eggs. Giant tortoises are well known from this area, but these specimens are the only fossil eggshell material from northern Greece. Finally, a new specimen represents the oldest confirmed record of the turtle *Mauremys* from Greece. Although the morphological information provided by the carapace is limited, a phylogenetic analysis confirms the placement of this specimen within the *Mauremys* clade. This clade is present in the extant Greek fauna, but only very limited fossil material of *Mauremys* was previously known from Greece. At the end of Miocene, the area that is now Thessaloniki was characterized by the presence of lake and river systems, which are ideal for the survival and diversification of turtles and tortoises. However, the Miocene-Pliocene transition was marked by significant climatic and faunal changes in the east Mediterranean region. Although the effect of these changes on fossil mammal assemblages is relatively well-known, little attention has been given to their effect on reptiles. Revisions of poorly known published specimens, and descriptions of new ones, contribute significantly to our knowledge of the diversity of the fossil chelonians from this region.

Appendix.

Morphological characters used in the analysis, based on Hervet (2003: 201-237; original characters in French). These are brief and simplified descriptions; please see Hervet (2003) for detailed information and drawings of the alternative character states.

0, Presence of inframarginal scutes: (0) yes; (1) no, presence only of axillary and inguinal scutes.

1, Length of the contact of the axillary process with the first costal (COS1): (0) no contact; (1) long process, touching a third to half of the COS1; (2) narrow process, touching a third of PL1; (3) narrow process, touching less than a third of COS1; (4) narrow process, touching only an extremity of COS1.

2, Contact of the inguinal process with the fifth and/or sixth costal: (0) no contact; (1) long process, touching a third to half of the pleurals; (2) narrow process, touching less than a third of the pleurals.

3, Axillary and inguinal notches: (0) large; (1) reduced.

4, Nuchal notch: (0), wide notch, affecting the first and second peripherals as well; (1) reduced, affecting the first peripheral and sometimes the second; (2) almost absent.

5, Contact of the first vertebral with the nuchal: (0), narrow vertebral, the first pleurals cover the lateral parts of the nuchal; (1) wide vertebral, extending on first peripherals and the pleuro-marginal sulcus crosses the peripheral; (2) wide, could extend behind the suture of the first two peripherals.

6, Width/length ratio of the first vertebral: (0) below 1.2; (1) between 1.2 and 1.7; (2) above 1.7.

7, Contact of the first vertebral with the second marginal: (0), absent; (1) large contact.

8, Shape of the first vertebral: (0) lyre-shaped; (1) straight lateral borders that diverge anteriorly; (2) rounded lateral borders that converge anteriorly.

9, Width of the second and third vertebral in respect to the nuchal: (0) always below 75%; (1) more than 70%.

10, Width of the vertebral in respect to the pleurals: (0) narrow; (1) wide, width of third vertebral/width of second and third pleurals more than 80%; (2) wider, width of third vertebral/width of second and third pleurals more than 100%

11, Width of fourth and fifth vertebral: (0) fifth vertebral wider than the fourth; (1) fifth vertebral narrower than the fourth.

12, Width of the cervical in respect to the nuchal (cervical width/nuchal width): (0) less than 25%; (1) more than 25%.

13, Covering of the cervical viscerally: (0) short; (1) long.

14, Covering to the first and second marginals viscerally on the nuchal and on the border: (0) long on nuchal and reducing towards the border, small or absent on the border; (1) well developed on nuchal and moderate on the border; (2) well developed on the nuchal, more developed on the border.

15, Contact between the costals 1-2 and the peripherals: (0) costals 1-2 suture in the middle of peripheral 3; (1) costals 1-2 suture roughly corresponds to the peripheral 3-4 suture.

16, Correspondence of the costal sutures with the peripheral sutures in the anterior carapace: (0) good correspondence in general; (1) weak correspondence.

17, Position of the pleuro-marginal sulci on the peripherals (excluding peripherals 11 and the pygal): (0) pleuro-marginal sulcus crossing the peripherals, marginals 1-3 always being shorter than peripherals 1-2; (1) coincidence (excluding the pygal and peripheral 11, and moderate coincidence of marginals 1-3 anteriorly).

18, Contact between the marginal 1 and/or marginal 2 and the costal 1: (0) absent or sometimes present (intraspecific variation); (1) always present.

19, Contact between the pleural 3 and the marginal 6: (0) absent; (1) present.

20, Contact between the pleural 4/vertebral 5 sulcus and the marginal 10: (0) absent, sulcus on marginal 11; (1) present, sulcus on marginal 10/11 or on marginal 10.

21, Position of vertebral 5 in respect to the suprapygal 2 and the pygal: (0) marginals 12 sulcus is short and marginals are on the same level as the suprapygal/pygal suture; (1) marginals 12 sulcus is short, but the marginals extend on the suprapygals; (2) vertebral 5 does not extend on the pygal.

22, Shape of the nuchal: (0) short, wider than long, with wide anterior border; (1) long, moderately wide, with wide anterior border; (2) long, moderately wide, but with narrower anterior border than state 1; (3) long, longer than wide, with narrow anterior border.

23, Neural series: (0) completely irregular; (1) neural 1 is quadrangular and neurals 2-8 hexagonals with short anterior lateral borders.

24, Shape of suprapygals 1: (0) trapezoidal, with a wide posterior side; (1) trapezoidal, with narrow posterior side (more rectangular).

25, Shape of suprapygals 2: (0) inversed trapezoidal; (1) trapezoidal to hexagonal; (2) hexagonal, with anterolateral and posterolateral borders of equal width; (3) hexagonal, with longer posterolateral borders.

26, Shape of pygal: (0) long, as long as wide or longer than wide; (1) short, wider than long, rectangular; (2) short, much shorter than state 1.

27, Shape of the anterior lobe of the plastron: (0) quadrangular to slightly trapezoidal; (1) trapezoidal.

28, Size of the plastron in respect with the carapace: (0) shorter, the lobes not reaching the level of the marginals; (1) long, the anterior and/or the posterior lobe reaching the level of the marginals.

29, Type of dorsal epiplastral lip: (0) weakly developed medially and laterally; (1) epiplastral lip developed, but is non-existent in the symphysis; (2) epiplastral lip more developed than in state 1, as well as in the posterior ends of the epiplastra; (3) epiplastral lip even more developed, with the presence of two thickenings one each side, medially of the humero-pectoral sulcus.

30, Length of the gularo-humeral sulcus in respect to the width of the gulars: (0) less than 0.2; (1) between 0.2 and 0.3; (2) more than 0.3.

31, Elongation of the epiplastral lip in the symphysis: (0) absent; (1) present.

32, Position of the posterior point of the gulars in respect with the entoplastron: (0) contacting the entoplastron, often with the presence of a small entoplastral scute; (1) not contacting the entoplastron; (2) covering the anterior area of the entoplastron.

33, Comparison of the width and length of gulars (length/width ratio): (0) less than 45%; (1) more than 45%.

34, Angle of the gularo-humeral sulci: (0) almost 180°; (1) equal or more than 90°; (2) always below 90°.

35, Shape of the gularo-humeral sulcus: (0) straight or sinuous; (1) becomes narrower towards the medial part.

36, Narrowing of the anterior lobe at gularo-humeral sulcus: (0) absent or slightly developed; (1) present.

37, Shape of the anterior lobe: (0) straight to slightly rounded; (1) well rounded.

38, Length of the abdominal and femoral scutes (abdominal/femoral length ratio): (0) more than 175%; (1) less than 175%.

39, Length of the humeral and pectoral scutes (humeral/pectoral length ratio): (0) more than 70%; (1) less than 70%.

40, Length of the gular and humeral scutes (gular/humeral length ratio): (0) less or equal than 100%; (1) more or equal than 100%.

41, Length of the humeral scute relative to the entoplastron (humeral/entoplastron length ratio): (0) more than 70%; (1) less than 70%.

42, Length of the gular scute relative to the length of the anterior lobe, measured till the axillary process (humeral/anterior lobe length ratio): (0) less than 30%; (1) between 30 and 45%; (2) more than 40%.

43, Shape of entoplastron: (0) long and oval; (1) rhomboid; (2) piriform.

44, Orientation of the epi-hyoplastral suture in ventral view: (0) diverges posteriorly; (1) almost perpendicular; (2) converge posteriorly.

45, Length of epiplastra in symphysis: (0) short; (1) long; (2) elongated.

46, Median length of hyoplastra in the posterior border of the entoplastron in respect to the axillary notches: (0) hyoplastra medially long and the posterior border of the entoplastron is situated anterior to the axillary notches; (1) hyoplastra medially short and the posterior border of the entoplastron is situated slightly anterior to the axillary notches; (2) hyoplastra medially much shorter and the posterior border of the entoplastron is situated posterior to the axillary notches;

47, Length of the hyoplastron in the symphysis in respect to the length of the anterior lobe (hyoplastron/anterior lobe length ratio): (0) more than 55%; (1) less than 55%.

48, Shape of the humero-pectoral sulcus: (0) sinuous; (1) rounded; (2) straight or slightly sinuous.

49, Position of the humero-pectoral sulcus medially, in respect with the entoplastron: (0) posterior to the entoplastron; (1) still posterior to the entoplastron, but in a more advanced position compared to the previous state; (2) in contact with the posterior end of the entoplastron; (3) crossing the posterior part of the entoplastron; (4) in an advanced position on the entoplastron.

50, Length of the bridge in respect to the length of the plastron (till the xiphiplastral tips, bridge/plastron length ratio): (0) less than 20%; (1) more than 40%; (2) between 30 and 40%.

51, Thickening of the lip covered by the humeral and femoral scutes in visceral view: (0) slight to moderate; (1) moderate to large.

52, Anal notch: (0) large and wide, sometimes deep; (1) narrow and deep.

53, Size of anal scute in respect to the xiphiplastron: (0) anals cover more than 80% of the xiphiplastra; (1) anals cover less than 80% of the xiphiplastra.

Character/Taxon Matrix, based on Hervet (2003), following modifications of Chesi et al. (2009), including the synonymies proposed by Claude and Tong (2004).

Platysternon_megacephalum	00000?101?11000000100000000000000000000000??2?0000
Elkemys_australis	0??0??000?00???10000100101011???0201011000011100021000
Palaeoemys_hessiaca	1110?0002000000100000?11010001002010000000011100101001
Palaeoemys_messeliana	11101000000000??10000001112000??02010000000011100211?01
Palaeoemys_vidalenci	11102000000?0001?000??11????12001010000000011101011001
Palaeoemys_kehreri	11102000000000010000000112001?12001010000000111?1021001
Palaeoemys_corroyi	111020000000000001?0011?11???11310201000000011101111001
Palaeoemys_testudiniformis	1110200000000??10001121112011?1?201000000011101111?01
Borkenia_oschkinisi	11101000100010010000???21???11310101000000011111221001
Borkenia_germanica	11101000100010010000?1221120113101010000000011112211001
Cuvierichelys_parisiensis	1110?110110?1021000?0221??011311101000000011221031101
Cuvierichelys_iberica	1?10?1?0110???2?0?00122112011311101000?000111221021101
Palaeochelys_vallisnerii	1??0211010001001?0010021120113002010100000111121031001
Palaeochelys_crocheti	1210?0?0000????110010?21???103002010?00000111121031001
Palaeochelys_lachati	1??0211010001?01?11??0211201130020100000111?1021001
Palaeochelys_laurenti	121021101?00??0111110221120113002010100000111121031001
Promalacoclemmys_protogaea	12?0222111201??1001100311201131021111110002112110211101
Promalacoclemmys_laharpi	1??0222111201111000110311201130020111110001111110210?01
Palaeochelys_bussenensis	?????1201000???1?00?0131121??????????????????????????
Palaeochelys_astrei	????212010001??100001131121??????????????????????????
Palaeomauremys_mlynarskii	?21?211011101??10001023112??????????????????????????
Mauremys_massiliensis	1??12110111?1??1100?0231211132021111101112?122103?111
Mauremys_sarmatica	13212110111101110001023112111320212110111222221041111
Mauremys_pygolopha	131121101?1?0111000?1231211132021211101112222221031111
Mauremys_portisii	1??0211101111??11001023113?11?2?21211101112222210031?11
Mauremys_campanii	14?12221111111?110110[0 1 2]3112111?2?212111?11122221042?11
Mauremys_gaudryi	14?122211111111010023113211???21211101112222210?4??11
Mauremys_caspica	14212111111111110010231132113202121110111222221042111
Mauremys_leprosa	14212111111111110010231132113202121110111222221042111
Allatini_geoemydid	1???????????????????????3113211??021211?0111?22?2?04??11

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.crpv.2015.01.005.

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