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The fossil record of turtles from the Pleistocene of Crete (Greece)

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ABSTRACT
The Isle of Crete contains an important endemic fossil fauna that has been studied extensively in the past. An endemic fossil tortoise, *Testudo marginata cretensis* Bachmayer, Brinkerink & Symeonidis, 1975, had previously been named from Pleistocene cave deposits in the island, presumably being larger than the mainland species and having some important morphological differences as well. In this paper I revise these type specimens and describe for the first time numerous additional fossil specimens from the Pleistocene sites of Gerani IV, Zourida, Koumpes, Liko, Mavro Mouri IV, and Simonelli Caves (near Herakleion), Rethymnon fissure, and from the open site of Sitia in the eastern part of the Island. These specimens belong mostly to the marginated tortoise, but the presence of a terrapin is confirmed as well. These new fossils help to refute the validity of the Cretan subspecies, and change the range of the marginated tortoise during Pleistocene/Holocene times in the southern Balkans.

KEY WORDS
Pleistocene,
Crete,
Endemism,
Testudo,
Mauremys.

RÉSUMÉ
Les fossiles de tortues du Pléistocène de l'île de Crète (Grèce).
L'île de Crète contient une importante faune fossile endémique qui a été largement étudiée dans le passé. Une tortue fossile endémique, *Testudo marginata cretensis* Bachmayer, Brinkerink & Symeonidis, 1975, nommée à partir des dépôts de grottes du Pléistocène dans l'île, est vraisemblablement plus grande que l'espèce continentale et présente avec celle-ci d'importantes différences morphologiques. Dans cet article, je révise ces spécimens types et décris pour la première fois de nombreux spécimens fossiles supplémentaires des sites du Pléistocène de Gerani IV, Zourida, Koumpes, Liko, Mavro Mouri IV et les grottes de Simonelli près d'Héraklion, Crète, la fissure de Rethymnon, et du site ouvert de Sitia dans la partie orientale de l'île. Ces spécimens appartiennent pour la plupart à la tortue marginée, mais la présence d'un terrapin est également confirmée. Ces nouveaux fossiles permettent de réfuter la validité de la sous-espèce crétoise et les changements dans l'aire de répartition de la tortue marginale à l'époque du Pléistocène/Holocène dans le sud des Balkans.

MOTS CLÉS
Pléistocène,
Crète,
endémisme,
Testudo,
Mauremys.

INTRODUCTION

Crete is the largest island of Greece and is located in a key position in the eastern part of the Mediterranean Sea. The rich and diverse fossil fauna of Crete has attracted the interest of palaeontologists for more than a century, because of its importance in understanding the phenomenon of endemism of insular faunas (Lyras *et al.* 2022; and references therein). Crete has been isolated from the surrounding continental landmasses during the last five million years, and its ancient fauna is considered to be the result of the colonization of animals that could reach Crete either by flying (e.g. birds, bats, and insects) or through the sea; this could happen by swimming, rafting, or floating through a shallow marine corridor that connected Peloponnesus with Crete (Lomolino 2000; van der Geer *et al.* 2017; and references therein). As a result, several mammalian species including elephants, mammoths, hippos, deer, and some rodents could colonize the island and experience the effects of isolation. Consequently, the insular fauna of Crete includes dwarf species of otherwise large animals (e.g. dwarf mammoths) or giant forms of otherwise small rodents, as well as deer with spectacular and diverse adaptations (Lyras *et al.* 2022; and references therein).

As far as turtles are concerned, geoemydid species have the possibility of rapid expansion aided by some tolerance to salty water (Vamberger *et al.* 2014; and references therein), whereas tortoises have the capability of floating and rafting through the sea, especially if their size is considerable (Gerlach *et al.* 2006). It is not strange, therefore, that these are the turtle clades that we encounter in Crete. Shortly after their discovery, the specimens of the Pleistocene tortoises from Crete were deemed to be part of this endemic fauna with the new subspecies *Testudo marginata cretensis* Bachmayer, Brinkerink & Symeonidis, 1975, considered larger than its extant representatives.

Half a century ago, Siegfried E. Kuss explored numerous Pleistocene caves in Crete (Kuss 1970), collecting several fossils of mammals and some turtle fossils from Mavro Mouri IV Cave. These fossils were in Freiburg, Germany, for decades, but are currently stored permanently in the collections of the Natural History Museum of Crete (NHMC). Shortly afterward, other collections were made in the island. Brinkerink (1996) briefly summarized the exploration of joint teams of the National and Kapodistrian University of Athens (NKUA) and the University of Utrecht (UU), collecting specimens in Gerani, Zourida, Koumpes, Liko, Mavro Mouri IV, and Simonelli Caves and the open site Siteia (or Sitia). These specimens have been, since then, in Brinkerink's possession in Utrecht and only briefly presented in a form of a preliminary list (Brinkerink 1996). Most of the specimens were identified as representatives of the marginated tortoise *Testudo marginata* Schoepff, 1793 and its new subspecies from Crete, whereas some occurrences of freshwater turtles were noted in Rethymnon fissure (as cf. *Emys orbicularis*) and Siteia (as *Clemmys* cf. *caspica*) (Brinkerink 1996); he also mentioned a curious and larger femur, a specimen that is further discussed below. Currently, these fossils are stored permanently in the collection of the Athens Museum of Palaeontology and Geology of the NKUA (AMPG). In 1975, an Italian team collected fossils from a newly discovered cave, Bate Cave, including some specimens of the marginated tortoise (Kotsakis 1977), currently stored in the University of Roma Tre, Rome, Italy. All these cave sites are located in the coastal area near Rethymnon, whereas Siteia is located on the eastern part of the island. Besides these Pleistocene records, more fossil turtles are known from earliest late Miocene locality of Plakias, including a trionychid and a geoemydid taxon (Georgalis *et al.* 2016).

The objective of this paper is to describe for the first time the fossil turtles and tortoises from the Pleistocene of Crete in detail, based on the study of the great majority of the recovered material from the island. The most complete specimens from the shell and appendicular skeleton are described and figured in detail. Previously published specimens are revised herein and the validity of *Testudo marginata cretensis* is evaluated.

MATERIAL AND METHODS

The majority of the material has been studied based on personal observations on the specimens in AMPG and NHMC during my doctoral thesis (Vlachos 2015). The only material that has been reviewed based on the published information (Kotsakis 1977) is that from Simonelli Cave. The description and figuration of the studied specimens is given below, divided per taxon and within each taxon per locality.

Abbreviations

Institutions

AMPG	Athens Museum of Palaeontology and Geology of the National and Kapodistrian University of Athens, Athens;
NHMC	Natural History Museum of Crete, Herakleion, Crete;
NKUA	National and Kapodistrian University of Athens, Athens;
UU	University of Utrecht, Utrecht.

SYSTEMATIC PALAEONTOLOGY

Order TESTUDINES Batsch, 1788
Suborder CRYPTODIRA Cope, 1868
Family Testudinidae Batsch, 1788
Genus *Testudo* Linnaeus, 1758

Testudo marginata Schoepff, 1793
(Figs 2-13)

Testudo marginata cretensis Bachmayer, Brinkerink & Symeonidis, 1975: 111.

Temporal distribution in Greece. — Recent-Pleistocene.

Type locality. — Crete.

Geographical distribution in Greece. — Extant *Testudo marginata* is known from almost the entire country, excluding most islands in the Aegean and Ionian Seas and Crete as well (Vlachos

2015; TTWG 2017; Speybroeck *et al.* 2020; and references therein). In Crete, it is known from cave sites in the Rethymnon area, Crete, such as Gerani IV (type locality of *T. m. cretensis*), Zourida, Koumpes, Liko, Mavro Mouri IV, Simonelli, Bate. Outside Crete, this species is known from Xerias in Kavala, Lakonia in Peloponnesus, Kythera Island, Kos Island, and Charkadio Cave in Tilos Island. See Vlachos (2015) and references therein for more information.

MATERIAL EXAMINED. — **Gerani Cave, Crete** (1 specimen) (Figs 2; 3): AMPG 3/1974, shell, holotype of *Testudo marginata cretensis*.
Zourida Cave, Crete (9 specimens) (Figs 4; 5): AMPG no number, almost complete carapace; AMPG 577, posterior carapace; AMPG 578, fragment of the posterior lobe; AMPG 600, left hyoplastron fragment; AMPG 601, plastron fragment; AMPG 602, left humerus; AMPG 603, right femur; AMPG 604, left scapula; AMPG 605, right humerus.
Koumpes Cave, Crete (18 specimens) (Figs 6; 7): AMPG 576, left part of a shell; AMPG 579, costal fragment; AMPG 580, right epiplastron; AMPG 581, peripheral; AMPG 582, plastron fragment; AMPG 583, costal fragment; AMPG 584, hyo/hypo fragment; AMPG 585, hyo/hypo fragment; AMPG 586, plastron fragment; AMPG 587, plastron fragment; 595, costal fragment; 596, left epiplastron fragment; 597, right humerus; 598, femur diaphysis; 599, femur head; 618, left hypoplastron fragment; 619, peripheral; 620, humerus diaphysis.
Liko Cave (70 specimens) (Figs 8-10): AMPG 551, left shell part; AMPG 552, part of the bridge; AMPG 553, costal; AMPG 554, peripheral; AMPG 555, right xiphiplastron; AMPG 556, suprapygal; AMPG 557, peripheral; AMPG 558, peripheral fragment; AMPG 559, costal fragment; AMPG 560, left hypoplastron fragment; AMPG 561, plastron fragment; AMPG 562, costal fragment; AMPG 563, peripheral; AMPG 564, hyo/hypo fragment; AMPG 565, costal fragment; AMPG 566, costal fragment; AMPG 567, left hypoplastron fragment; AMPG 568, peripheral; AMPG 569, left epiplastron; AMPG 570, plastron fragment; AMPG 571, costal fragment; AMPG 572, anterior plastral lobe; AMPG 573, peripheral & costal fragment; AMPG 574, peripheral; AMPG 575, left hyoplastron; AMPG 588, hyoplastron fragment; AMPG 589, entoplastron; AMPG 590, peripheral; AMPG 591, suprapygal; AMPG 592, costal fragment; AMPG 593, tibia; AMPG 594, posterior ungual; AMPG 610, left hypoplastron fragment; AMPG 611, left hyoplastron fragment; AMPG 612, costal fragment; AMPG 613, cervical vertebra; AMPG 614, 1st dorsal vertebra; AMPG 615, left shoulder girdle; AMPG 616, humerus; AMPG 617, pelvis fragment; AMPG 625, scapula; AMPG 626, peripheral; AMPG 627, costal; AMPG 628, costal fragment; AMPG 672, costal fragment; AMPG 673, plastron fragment; AMPG 674, coracoid; AMPG 675, femur fragment; AMPG 676, femur fragment; AMPG 677, tibia distal part; AMPG 732, plastron fragment; AMPG 733, plastron fragment; AMPG 734, plastron fragment; AMPG 780, peripheral 11; AMPG 781, peripheral 8; AMPG 782, peripheral; AMPG 783, shell fragment; AMPG 784, costal fragment; AMPG 785, costal fragment; AMPG 787, humerus; AMPG 797, costal fragment; AMPG 798, costal fragment; AMPG 799, peripheral; AMPG 800, peripheral; AMPG 801, left epiplastron; AMPG 802, carapace fragment; AMPG 803, carapace fragment; AMPG 804, carapace fragment; AMPG 805, carapace fragment; AMPG 806, costal fragment; AMPG 807, peripheral; AMPG 808, ulna; AMPG 809, tibia; AMPG 810, fibula.
Mavro Mouri IV, Crete (122+ specimens) (Figs 11; 12): NHMC FS38/60, anterior lobe; NHMC FS38/61, right hyoplastron; NHMC FS38/62, left hyoplastron; NHMC FS38/63, right hyoplastron; NHMC FS38/64, anterior peripherals; NHMC FS38/65, posterior peripherals; NHMC FS38/66, peripheral; NHMC FS38/67, xiphiplastron fragment; NHMC FS38/68, xiphiplastron fragment; NHMC FS38/69, hyoplastron fragment; NHMC FS38/70, left humerus fragment; NHMC FS38/71, right humerus fragment; NHMC FS38/72, humerus diaphysis; NHMC FS38/73, humerus diaphysis; NHMC FS38/74, humerus diaphysis; NHMC FS38/75, humerus diaphysis; NHMC FS38/76, scapula fragment; NHMC FS38/77, femur diaphysis; NHMC FS38/78, group of 9 fragments; AMPG 678, right hyoplastron; AMPG 679, left hyoplastron; AMPG 680, left hypoplastron; AMPG 681, left hypoplastron; AMPG 682, left hyoplastron; AMPG 683, right hyoplastron; AMPG 684 right hyoplastron; AMPG 685, left hyoplastron; AMPG 686, costal fragment; AMPG 687, peripheral; AMPG 688, peripheral; AMPG 689, costal fragment; AMPG 690, posterior peripheral; AMPG 691, posterior peripheral; AMPG 692, posterior peripheral; AMPG 693, posterior peripheral; AMPG 694, posterior peripheral; AMPG 695, posterior peripheral; AMPG 696, peripheral; AMPG 697, posterior peripheral; AMPG 698, costal fragment; AMPG 699, costal fragment; AMPG 700, costal fragment; AMPG 701, costal fragment; AMPG 702, peripheral fragment; AMPG 703, peripheral; AMPG 704, peripheral fragment; AMPG 705, costal fragment; AMPG 706, costal fragment; AMPG 707, peripheral fragment; AMPG 708, carapace fragment; AMPG 709, neural fragment; AMPG 710, peripheral; AMPG 711, right hyoplastron; AMPG 712, hypoplastron fragment; AMPG 713, left hyoplastron; AMPG 714, peripheral; AMPG 715, costal fragment; AMPG 716, left 7th peripheral; AMPG 717, right epiplastron; AMPG 718, left epiplastron; AMPG 719, left epiplastron; AMPG 720, left hyoplastron; AMPG 721, right 3rd peripheral; AMPG 722, left 3rd peripheral; AMPG 723, left hyoplastron; AMPG 724, peripheral; AMPG 725, peripheral; AMPG 726, costal fragment; AMPG 727, humerus diaphysis; AMPG 728, cervical vertebra; AMPG 729, vertebra fragment; AMPG 730, osteoderm; AMPG 731, ungual; AMPG 742, left xiphiplastron fragment; AMPG 743, left xiphiplastron fragment; AMPG 744, plastron fragment; AMPG 745, hypoplastron fragment; AMPG 746, peripheral fragment; AMPG 747, plastron fragment; AMPG 750, left epiplastron; AMPG 751, left and right epiplastron; AMPG 752, entoplastron fragment; AMPG 755, nuchal; AMPG 756, posterior peripheral; AMPG 757, costal fragment; AMPG 758, hyoplastron fragment; AMPG 759, left hyoplastron; AMPG 760, hypoplastron fragment; AMPG 761, hyoplastron fragment; AMPG 762, plastron fragment; AMPG 763, plastron fragment; AMPG 764, plastron fragment; AMPG 765, plastron fragment; AMPG 766, plastron fragment; AMPG 767, plastron fragment; AMPG 768, plastron fragment; AMPG 769, plastron fragment; AMPG 770, plastron fragment; AMPG 771, plastron fragment; AMPG 772, plastron fragment; AMPG 773, plastron fragment; AMPG 774, plastron fragment; AMPG 775, plastron fragment; AMPG 776, plastron fragment; AMPG 777, plastron fragment; AMPG 794, hyoplastron fragment; AMPG 795, plastron fragment; AMPG 796, plastron fragment; AMPG 811, group appr. 100 frs.; AMPG 812, peripheral fragment, AMPG 813, costal fragment; AMPG 814, 8th costal fragment; AMPG 815, costal fragment; AMPG 816, neural fragment; AMPG 817, costal fragment; AMPG 818, ilium fragment; AMPG 854, anterior lobe; AMPG 855, right xiphiplastron.
Simonelli Cave, Crete (4 specimens) (Fig. 13): AMPG 606, right humerus; AMPG 607, humerus diaphysis; AMPG 607, distal femur; AMPG 608, sacral vertebra.

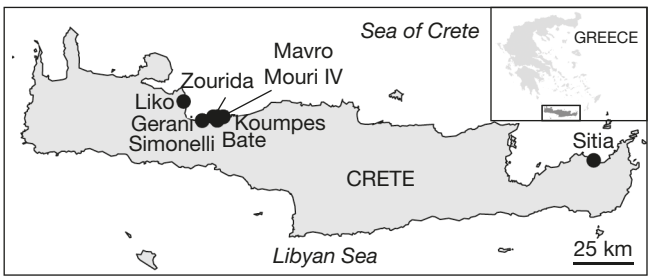

FIG. 1. — Map of Crete, showing the localities mentioned in the text.

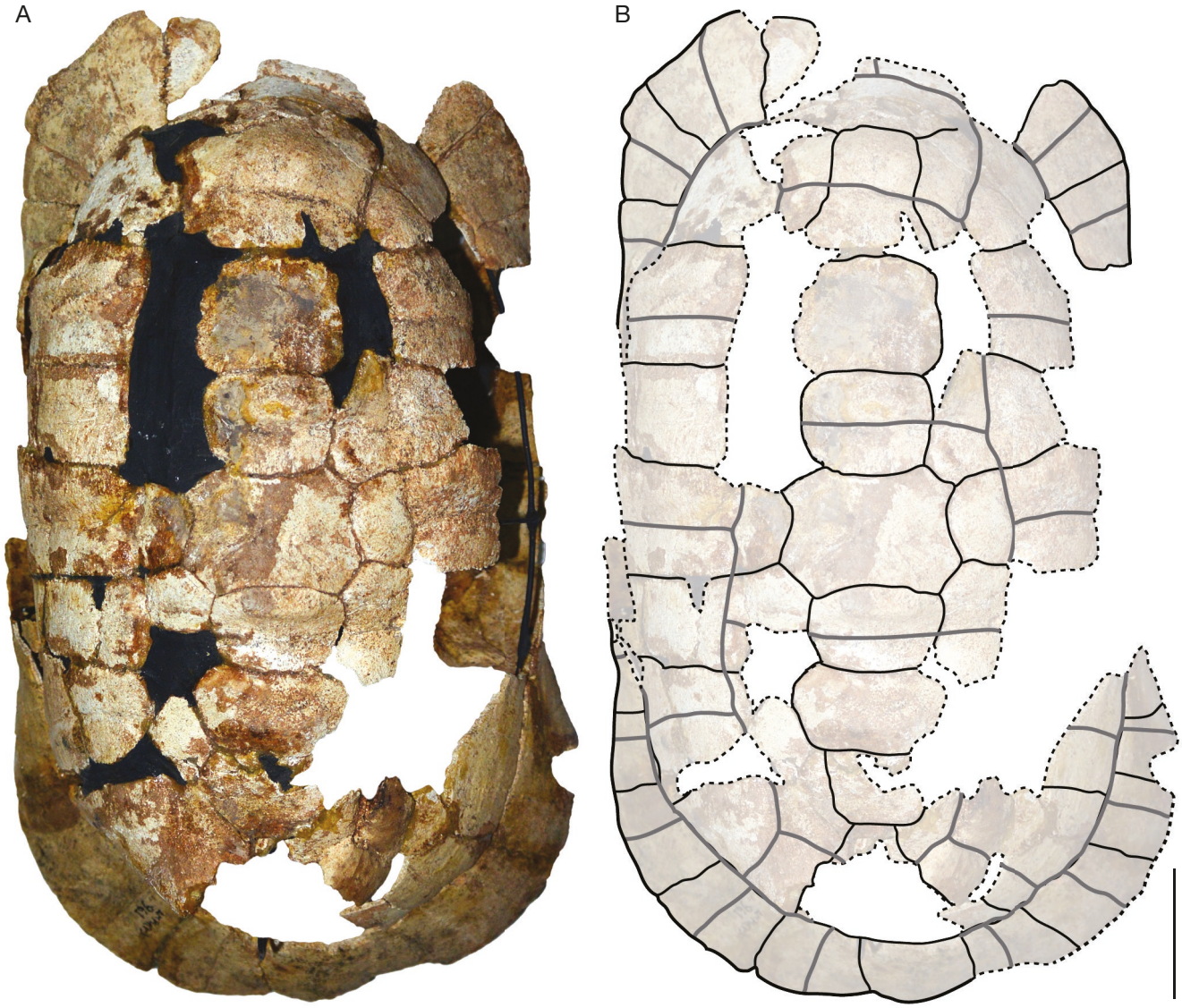

Fig. 2. — The holotype of *Testudo marginata cretensis* Bachmayer, Brinkerink & Symeonidis, 1975 (AMPG 3/1974) from the Pleistocene of Gerani Cave (Crete): **A**, carapace in dorsal; **B**, drawing of the dorsal view. Scale bar: 5 cm.

Gerani IV Cave, Crete

The known material from Gerani IV Cave represents a shell AMPG 3/1974 (Figs 2; 3) that is the holotype of the endemic taxon *Testudo marginata cretensis*. The specimen is almost complete, measuring up to 310 mm. From the carapace (Fig. 2), only some plates are missing from the anterior, from the right bridge and from the medial parts. From the plastron (Fig. 3), only some parts of the medial hyo- and hypoplastra are missing. The specimen is very fragile and is safely supported by a metal scaffold. This setting, however, does not allow clear observation of the visceral sides.

The nuchal is partially preserved and is certainly wider than long. The neural 1 is hexagonal, longer than wide, with short posterior lateral sides. The posterior part of the neural 1 is much wider than the anterior one, almost double in width. Bachmayer *et al.* (1975) described this neural as rectangular, whereas it actually is hexagonal. The shape of the first neural is subject to variation in *T. marginata*. For example, it is hexagonal in the recent *T. marginata* in figure 3 of Bachmayer *et al.* (1975). The neural 2 is octagonal with rounded edges, slightly wider than long. Neural 3 is quadrangular, wider than long. Neural 4 is octagonal, wider than long. Neural 5 is quadrangular, wider than long, whereas the posterior part is narrower than the anterior. Neural 6 is hexagonal, wider than long, wider than neural 5 and with short anterior lateral sides. Neural 7 is also hexagonal, narrower than neural 6. In the neurals that are crossed by the vertebral sulci (neurals 1, 3, 5), small, pointed, dorsal bumps are noted. The suprapygal/pygal area is incomplete, but a small trapezoidal suprapygal 1 is present. The costals are well differentiated to match the alternating pattern of the neurals. The costal 1 is quite large, making contact with the nuchal, the first two neurals, the costal 2 and the peripherals 1-3. Costal 2 is trapezoidal, being shorter medially and longer laterally. Costal 4 shows a similar shape, and they are alternated with the costals 3 and

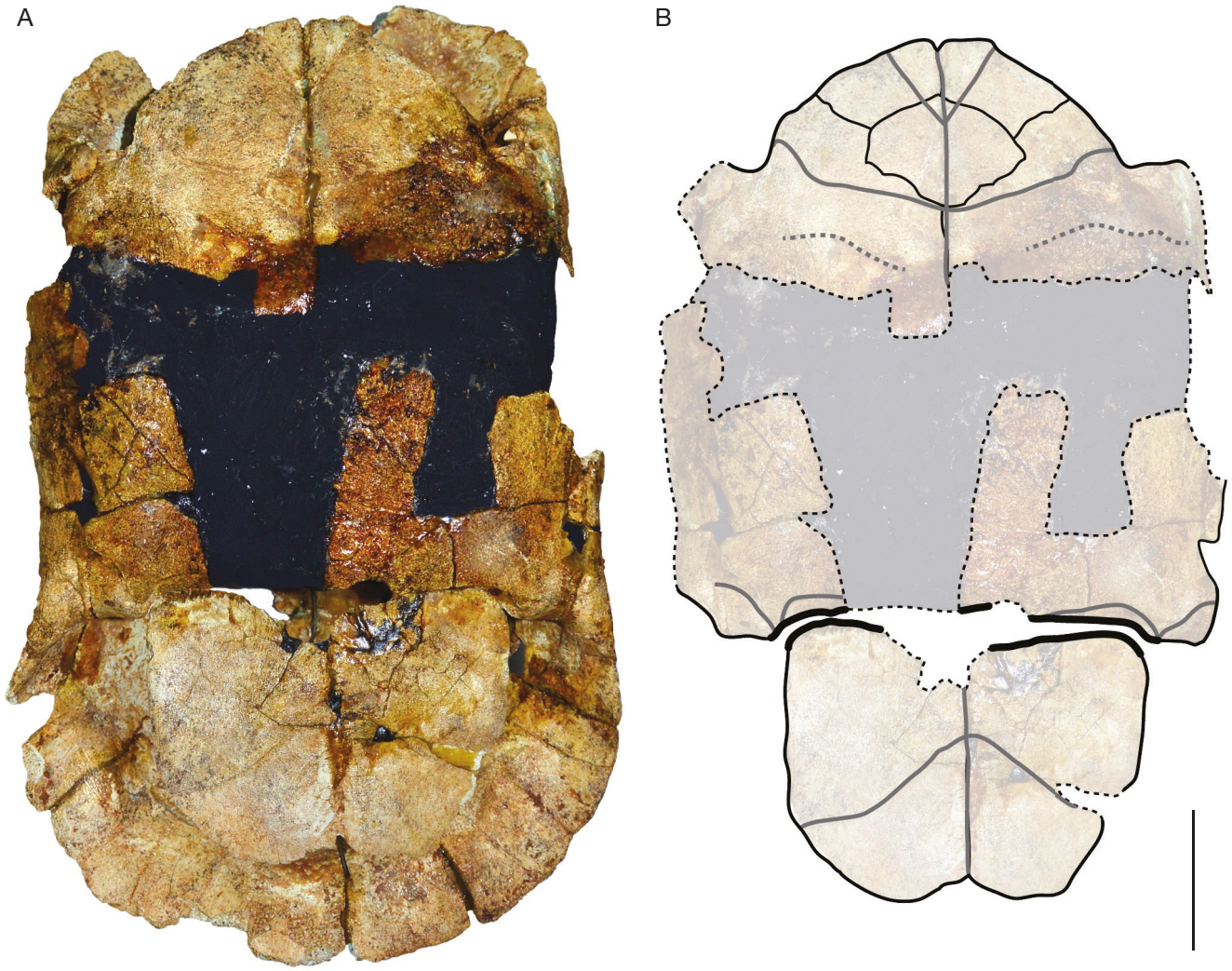

Fig. 3. — The holotype of *Testudo marginata cretensis* Bachmayer, Brinkerink & Symeonidis, 1975 (AMPG 3/1974) from the Pleistocene of Gerani Cave (Crete): **A**, plastron in ventral; **B**, drawing of the ventral view. Scale bar: 5 cm.

5 that are medially longer and laterally shorter. Costals 6 and 7 are different in shape, showing a double medial suture for the hexagonal neurals. The peripherals are quite long. The anterior peripherals, as well as the posterior ones, are flared. Especially, the posterior peripherals are quite elongated and flared posteriorly. The same is true for the pygal that is as long as wide. This orientation of the posterior border creates the characteristic posterior carapace of *T. marginata*. In this specimen, however, the posterior rim is not horizontally flared, but rather posteroventrally oriented. Given that the suprapygal area is incomplete, this configuration could be the result of the preparation of the specimen, and the border could have been even more flared.

The anterior lobe of the plastron is short and wide, whereas the posterior lobe is comparatively longer. The epiplastra are short and narrow. Viscerally, a thick convex epiplastral lip is formed, with a deep gular pocket. The entoplastron is wide and short, roughly hexagonal with a narrowed posterior part. The hyo- and hypoplastra are long and wide. The posterior lobe is formed entirely by the xiphiplastra, and is not sutured with the hypoplastra. Posteriorly, a wide and shallow anal notch is formed. The gulars are narrow and long, covering the medial part of the epiplastra and the anterior part of the entoplastron. The gularo-humeral sulcus is V-shaped, forming an acute angle with the midline. The rest of the entoplastron is covered only by the humerals. The humero-pectoral sulcus is broadly concave in the midline, strongly convex laterally. It is situated medially on the posterior end of the entoplastron. The limits between the pectorals and the abdominals cannot be confidently observed because of the state of preservation, but most probably had the typical morphology of this species. The femorals show a small covering on the lateral posterior parts of the hypoplastra, whereas medially the abdomino-femoral sulcus represents the posterior hypoplastral suture. The anterior part of the posterior lobe is covered by the femorals that are short medially and long laterally. Alternatively, the anals are medially long and laterally short. Therefore, the femoro-anal sulcus is pointed anteriorly, being strongly convex medially and slightly concave laterally on each side. The absence of a

tight suture between the hypoplastra and the posterior lobe, the long xiphiplastra forming the entire posterior lobe and the small covering of the femorals on the hypoplastra are features suggesting a mobile posterior lobe. Therefore, the presence of a hypo-xiphiplastral hinge can be hypothesized for this specimen.

Zourida Cave, Crete

The known material of the marginated tortoise from Zourida Cave representsis represented by an almost complete shell from the AMPG collection (Fig. 4), and additional shell and appendicular elements from the former UU collection (Fig. 5, now in the AMPG). The AMPG specimen (no number, Fig. 4) has been also described by Bachmayer *et al.* (1975) as belonging to *T. marginata cretensis*. A drawing of the dorsal carapace is provided here for the first time (Fig. 4). It is an almost complete carapace, missing only some plates that have been reconstructed with plaster, measuring up to 290 mm. The nuchal is wider than long, showing a small nuchal notch in the area of the cervical scute. The neural 1 is partially preserved, probably being longer than wide, with a wider posterior side than the anterior one. The neural 2 is octagonal, wider than long. Neural 3 is quadrangular, longer than wide. Neural 4 is octagonal, slightly wider than long. Neural 5 is quadrangular, slightly longer than wide. Neural 6 is hexagonal, wider than long, wider than neural 5 and with short anterior lateral sides. Neural 7 is also hexagonal, narrower than neural 6. In the neurals crossed by the vertebral sulci (neurals 1, 3, 5) dorsal bumps are noted. The suprapygal/pygal area is incomplete, but there is a single trapezoidal suprapygal. The pygal is trapezoidal, and its posterior border is slightly wider than the anterior one. The costal 1 is quite large, making contact with the nuchal, the first two neurals, the costal 2 and the peripherals 1-3. Costals 2 and 4 are shorter medially and longer laterally, alternating with the costals 3 and 5 that are longer medially and shorter laterally. This alternating pattern is typical for the testudinids, to match the octagonal/quadrangular neurals. Costals 6 and 7 are different in shape, showing a double medial suture for the hexagonal neurals. The peripherals are quite long. The anterior peripherals, as well as the posterior ones, are flared. Especially the posterior ones are quite elongated and flared posteriorly. The same is true for the pygal, which is as wider than long, with a wider posterior side. The posterior rim of the carapace is horizontally flared, much more so than the Gerani IV specimen. A short and narrow cervical is present anteriorly, showing a shallow nuchal notch. The vertebrals are hexagonal, wider than long. Their sulci cross longitudinally neural 1, neural 3, neural 5 and probably the suprapygal 1. In the limits of the vertebrals, dorsal bumps are formed in the neurals. The pleurals are rectangular, crossing costals 2, 4, 6 and 7. The borders of the pleurals with the marginals show a good correspondencecorrespondence with the sutures between the costals and the peripherals. The marginals are long and narrow. The marginals 12 are fused into a wide, trapezoid supracaudal. The anterior side of the supracaudal is narrower than the posterior.

Additional material from Zourida Cave is known from the UU collection (now in AMPG). AMPG 577 (Fig. 5A-G) comprises the major part of the posterior carapace. Parts of the last costals are found on each side of a single trapezoidal suprapygal. On the visceral side of the last costals we find the end of the sacral vertebrae. The peripherals are long and narrow. The pygal is trapezoidal, being slightly wider posteriorly. The posterior carapacial border is elongated and flared, horizontally oriented and with an even more curved posteriormost lip (Fig. 5A). The last vertebral scute covers the suprapygal and the posterior parts of the last costals. There is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. The same is true for the suprapygal-pygal suture and the vertebra-supracaudal sulcus. The marginals are long and narrow. The marginals 12 are fused into a trapezoid supracaudal, with a wider posterior part. Viscerally, however, the suprapygal is divided.

AMPG 578 (Fig. 5H-J) consists of the posterior parts of both xiphiplastra of a long and wide posterior lobe, showing a deep anal notch posteriorly. Ventrally, the femoro-anal sulcus is convex medially and concave laterally. The anals are longer medially, but laterally short. AMPG 600 (not figured) is a small fragment of the left hyoplastron, preserving the lip of the visceral covering of the humerals. AMPG 601 (not figured) is an unidentified fragment of the plastron, as inferred by the shape and morphology of the visceral side.

This collection from Zourida Cave also preserves some appendicular elements. AMPG 604 (Fig. 5K) comprises most of the left scapula, with a preserved length of 41 mm. The acromion is missing. The scapular prong extends vertically, and is straight. AMPG 602 (Fig. 5L) is the proximal and medial part of the left humerus, with a preserved length of 52 mm. The head is spherical. The two trochanters are slightly diverging to parallel, the major trochanter extending well beyond the humeral head. The diaphysis is strongly curved. AMPG 605 (Fig. 5M) represents the proximal and medial parts of the right humerus, but the minor trochanter is missing, with a preserved length of 48 mm. The specimen is eroded. The head is spherical. The major trochanter extends well beyond the humeral head, and the diaphysis is curved. AMPG 603 (Fig. 5N) represents the proximal and medial parts of the right femur, with a preserved length of 44 mm. The head is elliptical, oriented at an obtuse angle with the midline. The trochanters are fused, and the diaphysis is straight in the preserved part.

Koumpes Cave

The known material of the marginated tortoise from Koumpes comprises mainly a partial shell, accompanied by isolated carapace and plastron fragments and some appendicular elements (Figs 6; 7). AMPG 576 (Fig. 6) represents the left part of the shell of a marginated tortoise. From the carapace, the lateral parts of the anterior and medial costals are preserved. The costals show the typical alternating pattern of the costals of the testudinids, being alternatively long and short, matching the alternating neurals (not preserved). Almost the entire left peripheral rim is preserved, from the partial

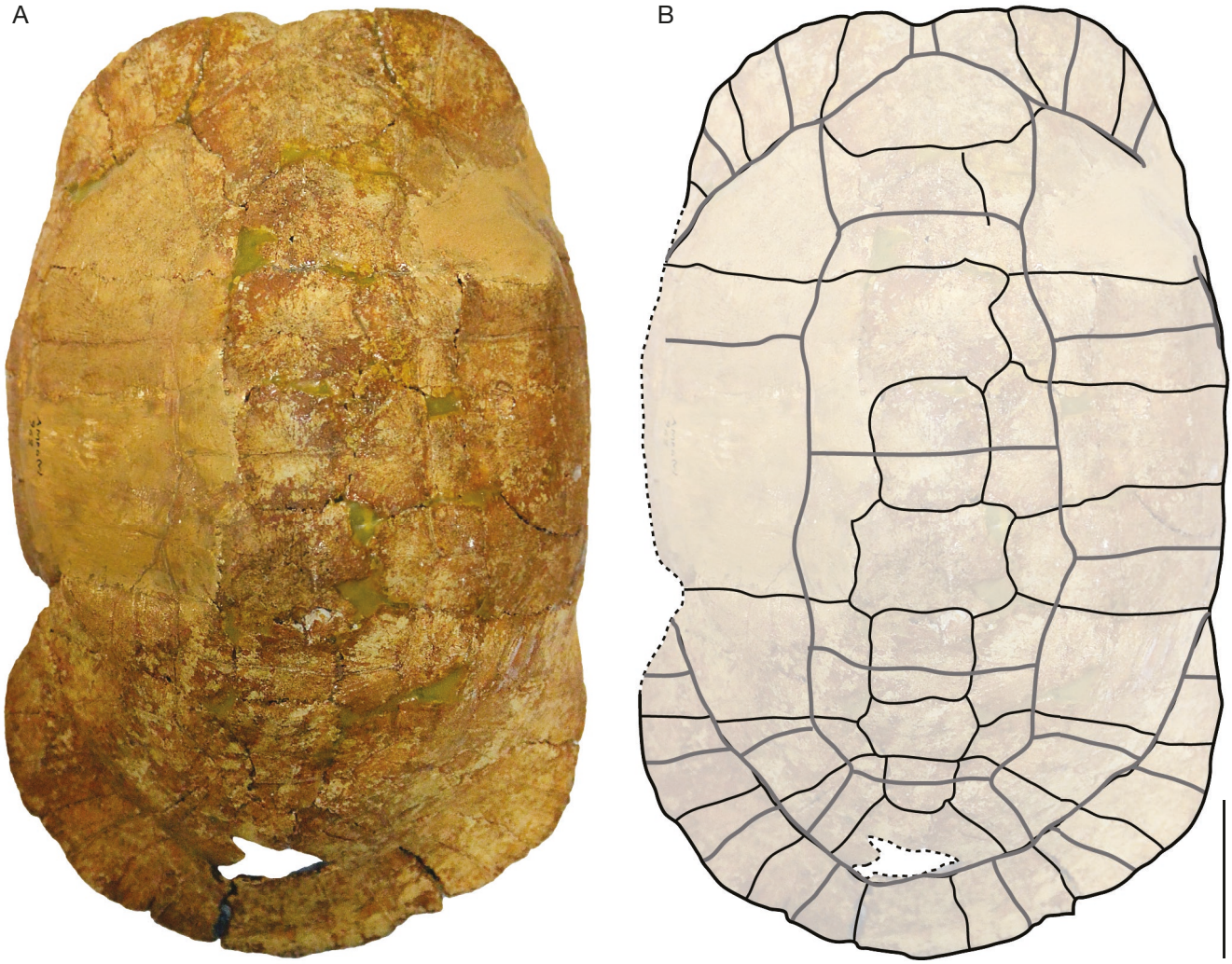

FIG. 4. — The referred specimen (AMPG, no number) to *Testudo marginata cretensis* Bachmayer, Brinkerink & Symeonidis, 1975 from the Pleistocene of Zourida Cave (Crete): **A**, carapace in dorsal; **B**, drawing of the dorsal view. Scale bar: 5 cm.

peripheral 2 until the peripheral 11. The anterior peripherals are long and narrow, the peripherals of the bridge are tall and narrow, and the posterior peripherals are horizontally flared, creating the characteristic posterior carapacial border of the marginated tortoise. There is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. In the anterior part of the bridge, in the axillary notch, a single axillary scute is present, in contact with the marginal 3, and the humeral and pectoral scutes of the plastron.

A good portion of the left part of the plastron is preserved. The anterior lobe appears to be short and wide. The border of the anterior lobe is rounded. The lateral part of the left epiplastron is preserved and it is medially thickened, indicating that viscerally a thick epiplastral lip was present. The left part of the entoplastron is preserved, allowing us to reconstruct a hexagonal, wider than long entoplastron. The hyo- and hypoplastra are long and wide. The hypoplastra terminate at the end of the bridge, indicating that the posterior lobe was formed entirely by the xiphiplastra. As far as the scute sulci are concerned, few sulci are observed. The humero-pectoral sulcus is situated medially in the posterior end of the entoplastron, whereas laterally it crosses the hyoplastron to reach the axillary scute. The edges of the pectorals and the abdominals are not visible as a result of the preservation of the specimen. In the posterior part of the hypoplastra, however, the abdomino-femoral sulcus is observed, close to the end of the bridge and strongly convex. All the above suggest the presence of a hypo-xiphiplastral hinge in this specimen.

The isolated specimens from Koumpes Cave provide some additional information on the anatomy of the Koumpes marginated tortoises; the most important specimens are figured in Figure 7.

AMPG 583 (Fig. 7A) is the medial part of a narrow costal, articulating with a single octagonal neural. AMPG 579 (Fig. 7B) and AMPG 595 (Fig. 7C) represent the distal parts of two costals, laterally short, whereas AMPG 619 (Fig. 7D) is likewise the distal part of a costal but is laterally longer. These costal fragments demonstrate the alternating pattern of costals in the marginated tortoise. AMPG 581 (Fig. 7E) is an almost entire peripheral that is crossed longitudinally by the marginal sulci.

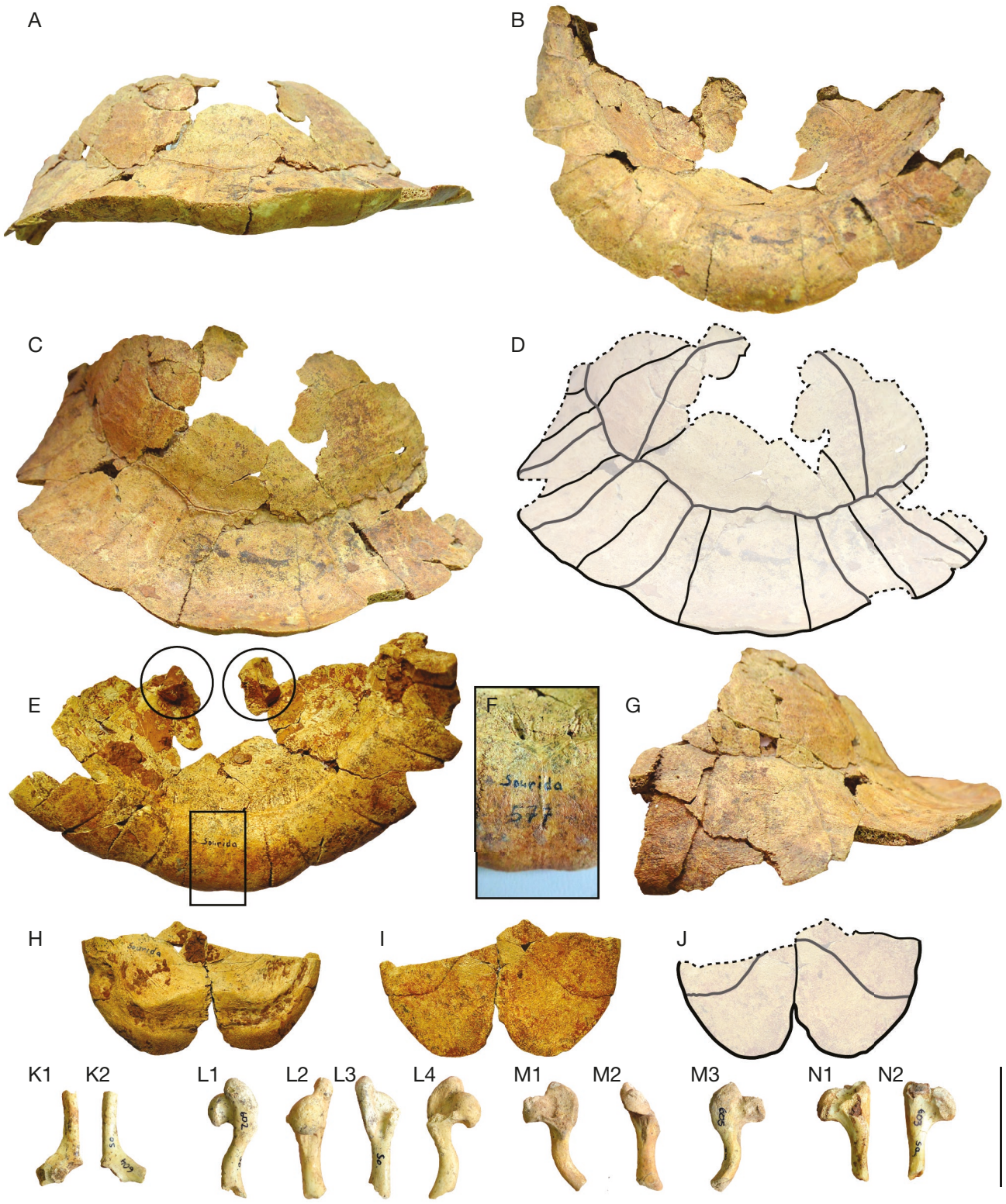

FIG. 5. — Additional material of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Zourida Cave (Crete): **A**-**G**, AMPG 577, posterior carapace views: **A**, posterior; **B**, dorsal; **C**, dorso-posterior; **D**, drawing of the dorso-posterior; **E**, visceral; **F**, detail of pygal in visceral; **G**, left lateral; **H**-**J**, AMPG 578, posterior lobe views: **H**, visceral; **I**, ventral; **J**, drawing of the ventral; **K**, AMPG 604, left scapula views: **K1**, posterior; **K2**, anterior; **L**, AMPG 602, left humerus views: **L1**, posterior; **L2**, dorsal; **L3**, ventral; **L4**, anterior; **M**, AMPG 605, right humerus views: **M1**, anterior; **M2**, dorsal; **M3**, posterior; **N**, AMPG 603, right femur views: **N1**, anterior; **N2**, posterior. Scale bar: 5 cm.

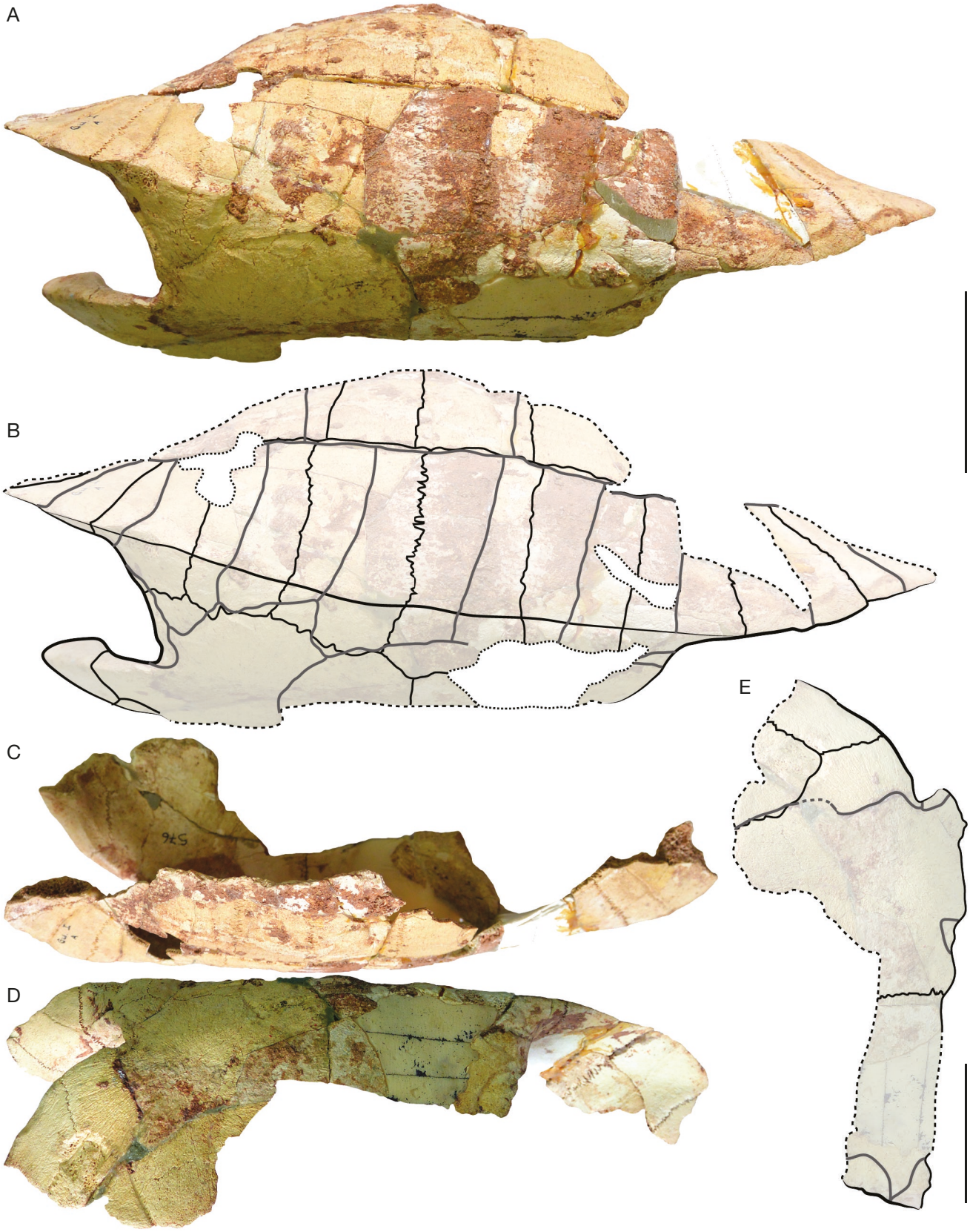

FIG. 6. — Shell material of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Koumpes Cave (Crete), AMPG 576, partial shell views: **A**, left lateral; **B**, drawing of the left lateral; **C**, dorsal; **D**, ventral; **E**, drawing of the ventral views. Scale bars: 5 cm.

A pointed tip is noted in the borders between the marginals in the carapacial rim. Based on the preserved part, the peripheral appears to have been horizontally flared. Moreover, the two sides are not parallel to each other. Compared with the material preserved from this site and other localities from Crete described here, this peripheral most probably corresponds to the right peripheral 11 of the flared carapacial border of *T. marginata*. Compared to the peripherals of AMPG 576 (Fig. 6), this peripheral is larger and thicker, corresponding to a larger individual. AMPG 620 (not figured), corresponds to the most part of a posterior peripheral, that is long and narrow, being crossed by the marginal sulcus. Based on the known material from this site, it resembles in length and morphology the anterior peripherals.

From the plastron several fragments are preserved, including AMPG 580 (Fig. 7F), which represents a part of the right epiplastron. Viscerally, the epiplastral lip thickens gradually towards the middle. The epiplastra are short and wide. The entoplastron is wider than long. The gulars are long and narrow, covering probably the anterior part of the entoplastron. Another partial right epiplastron is preserved (AMPG 596, Fig. 7G), showing the suture between the epiplastron and the entoplastron, as well as the visceral thickening of the epiplastral lip. AMPG 584 (Fig. 7H) is very thin and does not show any evidence of sulci. Two sides, however, show sutural surfaces. Based on the preserved part it could represent the medial part of the hyo/hypoplastra, but further identification is not possible. AMPG 618 (Fig. 7I) is the posterior part of the left hypoplastron. The posterior suture of the hypoplastron is broad and rounded, indicating the presence of a hinge. The ventral surface is eroded and no sulci can be observed. There are additional plastron fragments in the material, including a part of the hyo/hypoplastra (AMPG 585), a fragment that is probably the axillary part of the hyoplastron (AMPG 586, as inferred by the presence of a process that resembles the axillary process), and some unidentifiable fragments (AMPG 582, 587).

A few appendicular elements are also preserved from Koumpes. AMPG 597 (Fig. 7J) represents the proximal and medial part of the left humerus, with a preserved length of 34 mm. The head is mostly spherical, although its outline is irregular with a part that is straight. The two trochanters are slightly diverging to parallel. The tips of the trochanters are broken, but certainly the major trochanter extended well beyond the humeral head. AMPG 621 (not figured) corresponds to a partial diaphysis of a humerus. AMPG 598 (Fig. 7K) is the slightly curved diaphysis of a femur, with a preserved length of 35 mm. AMPG 599 (not figured) is an elliptical femoral head.

Liko Cave, Crete

The fossil tortoise material from Liko Cave is probably the anatomically richest material of the marginated tortoise known from Crete, preserving numerous elements from the carapace (Fig. 8), many well-preserved plastral elements (Fig. 9), as well as several appendicular elements (Fig. 10). Liko might not have complete shells like other Cretan caves, but the material is exceptionally preserved, allowing the documentation of most of the anatomical features of this species. The appendicular elements are also quite diverse, including besides the more frequently recovered humeri and femora also vertebrae, elements of the scapular girdle, an ulna, radii, and even an ungual phalanx.

From the carapace, the most complete specimen is AMPG 551 (Fig. 8A), the left part of a tortoise shell. Of the costals, the medial and lateral parts of the left costal 3 to costal 6 are preserved, along with a tiny part of the costal 7. Most of the bridge is preserved. The costals show the alternating pattern known in *T. marginata*, with medially long and laterally short costals alternated with medially short and laterally long costals. The costal 3 and costal 5 are crossed by the pleural sulci. The peripherals are tall and narrow. The last preserved peripheral (probably the peripheral 8) displays a widening and a degree of flaring, which is characteristic of the posterior carapace border of *T. marginata*. The peripherals of the bridge area are strongly curved ventrally and are tightly sutured with the hyo- and hypoplastra. The marginals cover the peripheral, and their sulci cross them transversely. There is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. The sulci between the marginals and the scutes of the plastron are situated on the peripherals. In the posterior part of the bridge, a single inguinal triangular scute mainly covers the hypoplastron and is slightly expanded on the sutured peripheral. In the posterior part of the hypoplastron, a hinge is formed with the posterior lobe. As a result of erosion, no sulci can be observed on the plastron.

The remaining carapacial elements belong mostly to isolated or partial plates. AMPG 553 (Fig. 7B) is an almost complete costal that is medially long, and laterally short. On the medial part, the borders between the vertebrals and the pleurals are clear. AMPG 562 (Fig. 8C) is the distal part of a partial costal that is crossed by the pleural sulci. Even smaller parts of costals can be identified in the material, such as AMPG 566 (Fig. 8D) and AMPG 559 (Fig. 8.E), that are not crossed by any sulci, and others that preserve the sulci such as AMPG 798 (Fig. 8F), AMPG 565 (Fig. 8G), and AMPG 797 (Fig. 8H), and many smaller ones without much anatomical information (AMPG 571, 592, 612, 627, 628, 672, 673, 784, 785, 806).

Additional specimens that document the morphology and variation of the peripheral rim in the tortoises from Liko Cave are preserved. AMPG 552 (Fig. 8I) represents the anterior part of the left bridge of the shell. Only parts of two peripherals are preserved, being sutured to the lateral part of the left hyoplastron. A crest in the lateral part of the bridge is anterodorsally oriented. There is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. The sulci between the marginals and the scutes of the plastron are situated on the hyoplastron, contrary to the morphology observed in AMPG 551. A small axillary scute is noted anteriorly, situated mostly on the hyoplastron. AMPG 558 (Fig. 8J) is a fragment of a peripheral from the bridge area, showing the change of curvature toward the plastron; it is crossed by the marginal sulci transversely. AMPG 557 (Fig. 8K) is a short, narrow, and flared peripheral, crossed by the marginal sulci transversely; it could be an anterior

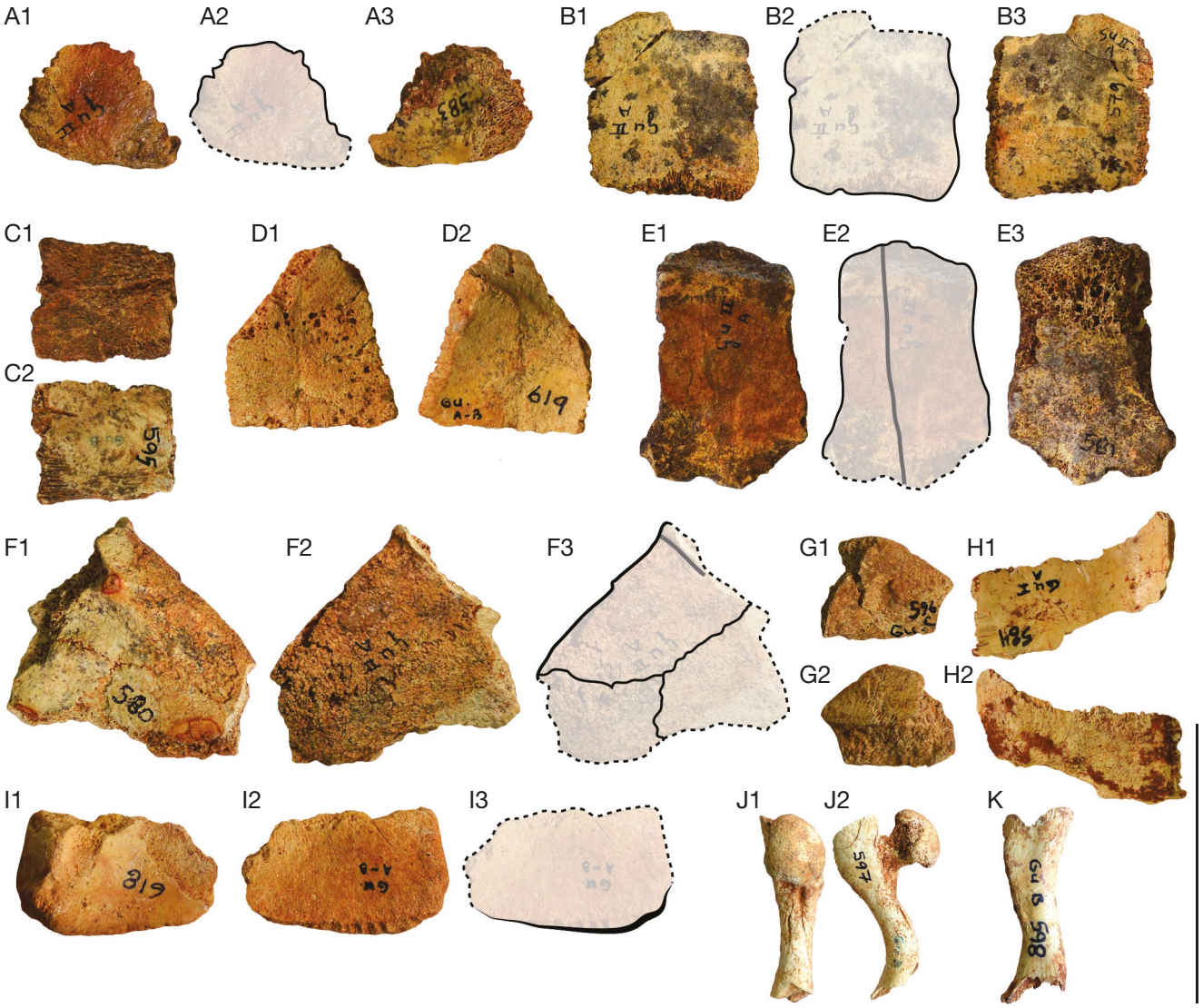

Fig. 7. — Additional material of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Koumpes Cave (Crete): **A**, AMPG 583, costal fragment partial shell views: **A1**, dorsal; **A2**, drawing of the dorsal; **A3**, visceral; **B**, AMPG 579, costal fragment partial shell views: **B1**, dorsal; **B2**, drawing of the dorsal; **B3**, visceral; **C**, AMPG 595, costal fragment partial shell views: **C1**, dorsal; **C2**, visceral; **D**, AMPG 619, costal fragment partial shell views: **D1**, dorsal; **D2**, visceral; **E**, AMPG 581, peripheral partial shell views: **E1**, dorsal; **E2**, drawing of the dorsal; **E3**, visceral; **F**, AMPG 580, right epiplastron partial shell views: **F1**, visceral; **F2**, ventral; **F3**, drawing of the ventral; **G**, AMPG 596, fragment of the right epiplastron partial shell views: **G1**, visceral; **G2**, ventral; **H**, AMPG 584, hyo/hypoplastron partial shell views: **H1**, visceral; **H2**, ventral; **I**, AMPG 618, left hypoplastron partial shell views: **I1**, visceral; **I2**, ventral; **I3**, drawing of the ventral; **J**, AMPG 597, left humerus partial shell views: **J1**, dorsal; **J2**, posterior; **K**, AMPG 598, femur in lateral view. Scale bar: 5 cm.

peripheral, which are usually shorter than the posterior ones in this species. For example, AMPG 563 (Fig. 8L) is a tall and narrow peripheral that is partly covered by calcitic material. It is crossed by the marginal sulci transversely, and appears moderately flared. This peripheral probably comes from the posterolateral rim. AMPG 568 (Fig. 8M) is a short and narrow peripheral, crossed by the marginal sulci transversely and flared. Compared to AMPG 557, its anterior and posterior borders are parallel to each other. It could be one of the free peripherals close to the bridge of a small, probably young individual. AMPG 554 (Fig. 8N) is a tall and narrow peripheral, crossed by the marginal sulci transversely. The costo-peripheral suture corresponds to with the pleuro-marginal sulcus. AMPG 781 (Fig. 8O) is an almost complete, tall and narrow peripheral. It is crossed longitudinally by the marginal sulci. Anteriorly it preserves a broad suture, indicating that is the left peripheral 8, and the last one on the left bridge of the shell. AMPG 780 (Fig. 8P) is a complete peripheral that is crossed longitudinally by the marginal sulci. Based on the preserved part, the peripheral appears to have been horizontally flared. Moreover, the two sides are not parallel to each other. Compared to the material preserved from this site and other localities from Crete, this peripheral most probably represents the right peripheral 11 of the flared carapacial border. AMPG 573 (Fig. 8Q) is a large fragment of the bridge, preserving parts of the peripherals and a fragment of the costal. There is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. Many more isolated peripheral plates are known in the Liko material. AMPG 574 and 800

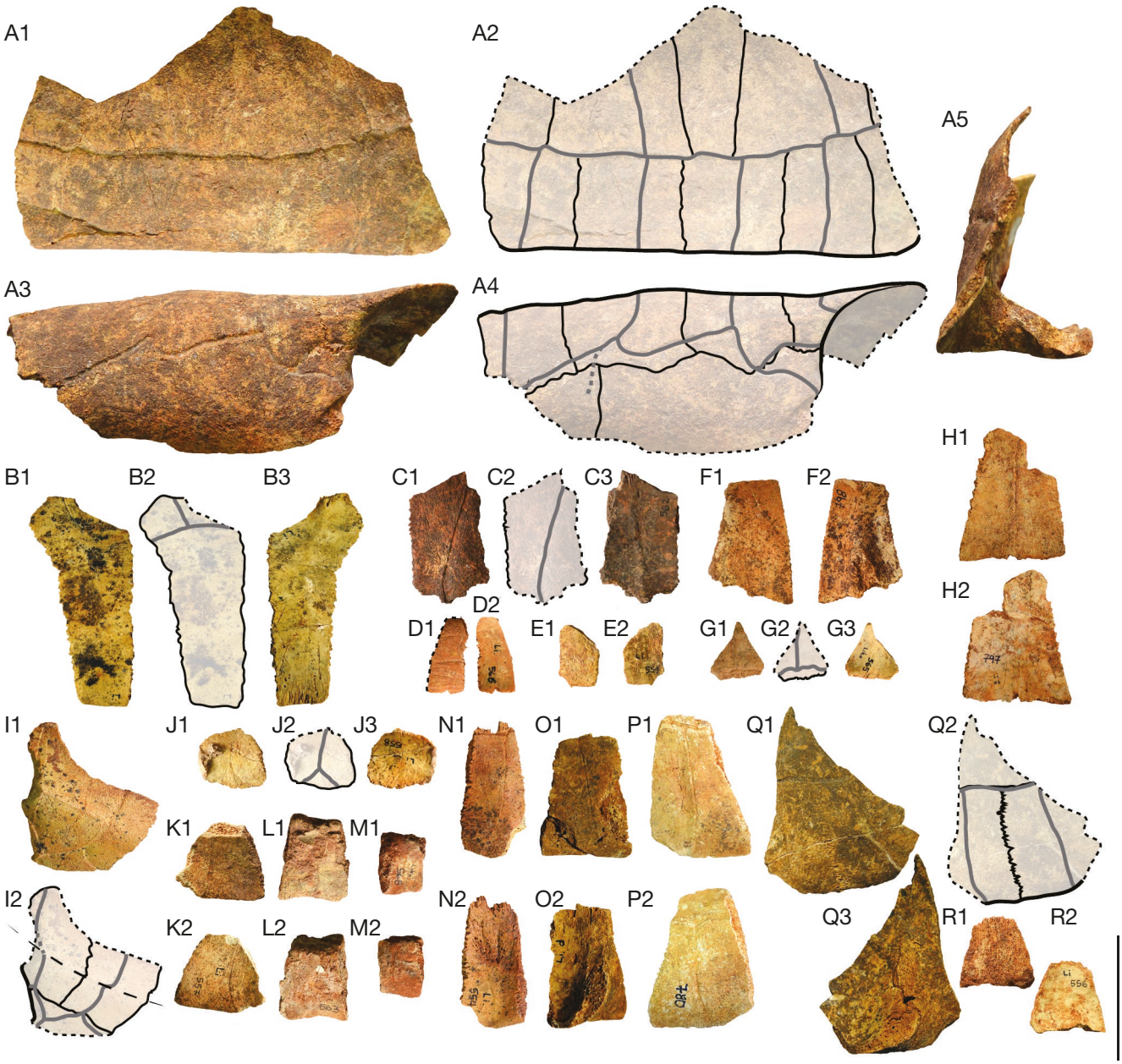

Fig. 8. — Carapace material of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Liko Cave (Crete): **A**, AMPG 551, left part of the shell partial shell views: **A1**, lateral; **A2**, drawing of the lateral; **A3**, ventral; **A4**, drawing of the ventral; **A5**, posterior; **B**, AMPG 553, costal partial shell views: **B1**, dorsal; **B2**, drawing of the dorsal; **B3**, visceral; **C**, AMPG 562, costal fragment partial shell views: **C1**, dorsal; **C2**, drawing of the dorsal; **C3**, visceral; **D**, AMPG 566, costal fragment partial shell: **D1**, dorsal; **D2**, visceral; **E**, AMPG 559, costal fragment partial shell views: **E1**, dorsal; **E2**, visceral; **F**, AMPG 798, costal fragment partial shell views: **F1**, dorsal; **F2**, visceral; **G**, AMPG 565, costal fragment partial shell views: **G1**, dorsal; **G2**, drawing of the dorsal; **G3**, visceral; **H**, AMPG 797, costal fragment partial shell views: **H1**, dorsal; **H2**, visceral; **I**, AMPG 552, anterior part of the left bridge partial shell views: **I1**, dorsal; **I2**, drawing of the dorsal; **J**, AMPG 558, peripheral partial shell views: **J1**, dorsal; **J2**, drawing of the dorsal; **I3**, visceral; **K**, AMPG 557, peripheral: **K1**, dorsal; **K2**, visceral; **L**, AMPG 563, peripheral partial shell views: **L1**, dorsal; **L2**, visceral; **M**, AMPG 568, peripheral partial shell views: **M1**, dorsal; **M2**, visceral; **N**, AMPG 554, peripheral partial shell views: **N1**, dorsal; **N2**, visceral; **O**, AMPG 781, peripheral partial shell views: **O1**, dorsal; **O2**, visceral; **P**, AMPG 780, peripheral partial shell views: **P1**, dorsal; **P2**, visceral; **Q**, AMPG 573, bridge fragment partial shell views: **Q1**, dorsal; **Q2**, drawing of the dorsal; **Q3**, visceral; **R**, AMPG 556, probable suprapygal partial shell views: **R1**, dorsal; **R2**, visceral. Scale bar: 5 cm.

are short and narrow, horizontally flared peripherals, crossed by the marginal sulci transversely; they probably come from the anterior border. On the other hand, AMPG 590, 626, and 782 are much taller and also horizontally flared, coming probably from the posterior border. AMPG 799 is an almost complete peripheral from the bridge area, showing the distal change of curvature for the contact with the plastron.

AMPG 556 (Fig. 8R) is a relatively flat and thin fragment. It is narrower anteriorly and widens posteriorly, trapezoidal in shape. It is not crossed by any sulci and there is no evidence of a rib on the visceral surface. Based on the comparative material presented here, this plate could be a single fused suprapygal, but this identification is uncertain. A similar morphology is noted in AMPG 591 (not figured here).

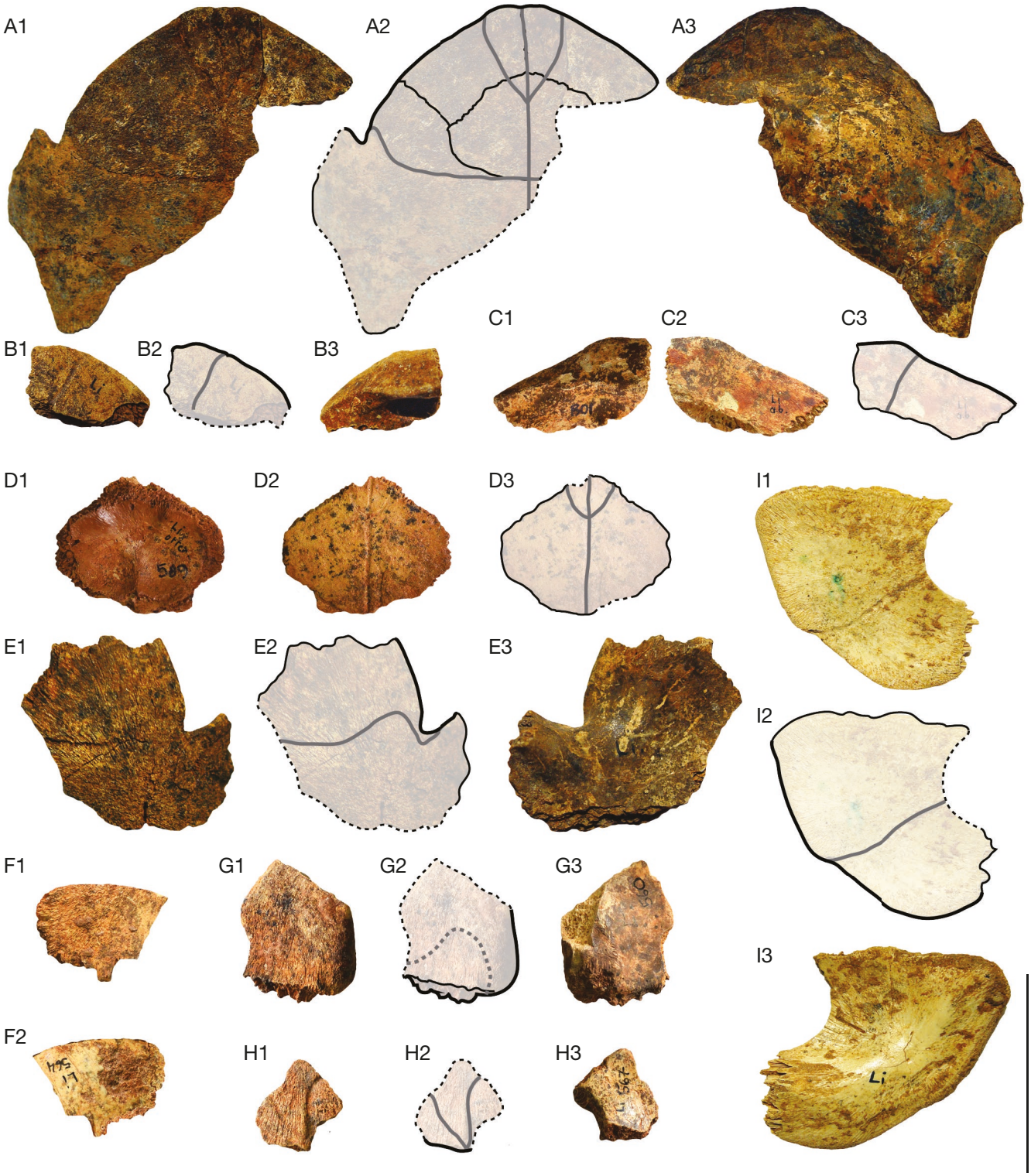

FIG. 9. — Plastron material of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Liko Cave (Crete): **A**, AMPG 572, anterior lobe partial shell views: **A1**, ventral; **A2**, drawing of the ventral; **A3**, visceral; **B**, AMPG 569, left epiplastron partial shell views: **B1**, ventral; **B2**, drawing of the ventral; **B3**, visceral; **C**, AMPG 801, left epiplastron partial shell views: **C1**, visceral; **C2**, ventral; **C3**, drawing of the ventral; **D**, AMPG 589, entoplastron partial shell views: **D1**, visceral; **D2**, ventral; **D3**, drawing of the ventral; **E**, AMPG 588, left hyoplastron partial shell views: **E1**, ventral; **E2**, drawing of the ventral; **E3**, visceral; **F**, AMPG 564, hyo/hypoplastral fragment partial shell views: **F1**, ventral; **F2**, visceral; **G**, AMPG 560, left hypoplastron fragment partial shell views: **G1**, ventral, **G2**, drawing of the ventral; **G3**, visceral; **H**, AMPG 567, left hypoplastron fragment partial shell views: **H1**, ventral, **H2**, drawing of the ventral; **H3**, visceral; **I**, AMPG 555, right xiphiplastron partial shell views: **I1**, ventral, **I2**, drawing of the ventral; **I3**, visceral. Scale bar: 5 cm.

There are several elements from the plastron of the Liko marginated tortoise, most of which are isolated (or fragments of isolated) plates that nevertheless document almost the entire morphology of the plastron. The most complete specimen is AMPG 572 (Fig. 9A), which represents most of the anterior plastral lobe, missing part of the left hyoplastron. The anterior lobe is rounded, short and wide. The epiplastra are short and wide, showing a thickened visceral part forming a convex epiplastral lip with a gular pocket. Ventrally and medially they are covered by long and narrow gulars that overlap the anterior part of the entoplastron. The entoplastron is wide and short, roughly rhomboidal and with a slightly rounded posterior side. The humero-pectoral sulcus is broadly concave and is situated medially on the posterior end of the entoplastron. Additional epiplastral remains include the almost complete AMPG 569 (Fig. 9B) and the complete AMPG 801 (Fig. 9C). Both are identified as left epiplastra, being short and wide, showing a thickened visceral part forming a convex epiplastral lip with a gular pocket. Ventrally and medially they are covered by long and narrow gulars that overlap the anterior part of the entoplastron. AMPG 589 (Fig. 9D) is a complete entoplastron, which is hexagonal, short and wide, and with a slightly curved posterior border. Anteriorly it is overlapped by the gular scutes, whereas the rest is covered by the humerals. AMPG 588 (Fig. 9E) is a flat fragment of an almost complete left hyoplastron. Its visceral surface is smooth, and part of the medial suture is preserved. Ventrally it is crossed by the humero-pectoral sulcus that is straight medially and wavy toward the lateral border. A similar morphology is also observed in the almost complete left hyoplastron AMPG 575 (not figured here), but in this case the humero-pectoral sulcus is situated clearly posterior to the entoplastron. The morphology of these additional specimens matches well the morphology of the partial anterior lobe (AMPG 572).

The posterior lobe of the Liko marginated tortoise is known only from isolated fragments. AMPG 564 (Fig. 9F) is a small fragment of the plastron, as inferred from the relatively flat shape and the smooth visceral surface. It belongs to the medial part (hyo/hypoplastron) but further identification is not possible. AMPG 560 (Fig. 9G) is a small fragment of the posterior area of the left hypoplastron. Although the surface of the specimen is eroded, I the imprint of a strongly convex abdomino-femoral sulcus is preserved. The posterior part of the hypoplastron is thick and the suture is rounded. The morphology of the preserved part is consistent with the presence of a hypo-xiphiplastral hinge in this specimen. AMPG 567 (Fig. 9H) is a small fragment of the posterior area of another left hypoplastron. On the ventral side of the specimen is the lateral part of a convex abdomino-femoral sulcus and a single inguinal scute. The posterior part of the hypoplastron is thick and the suture is rounded. The morphology of the preserved part is consistent with the presence of a hypo-xiphiplastral hinge. AMPG 555 (Fig. 9I) is an almost complete right xiphiplastron, missing only some of the medial suture. The suture with the hypoplastron appears to have been broad and rounded, suggesting the presence of a hypo-xiphiplastral hinge. On the posterior end, a deep and wide anal notch is noted. Ventrally, the femorals are medially short and laterally long. Contrary, the anals are medially long and laterally short. The femoro-anal sulcus is V-shaped anteriorly, and nearly straight on each side. AMPG 610 and 611 comprise fragments of the left hypoplastron. AMPG 610 is eroded and no sulci can be observed, whereas AMPG 611 is crossed probably by the abdomino-femoral sulcus. The posterior part of this hypoplastron is thick and the suture is rounded. The best preserved plastral elements confirm the presence of the hypo-xiphiplastral hinge in the Liko tortoise. Several other plastron fragments are not further identifiable (AMPG 561, 570).

At least 16 appendicular elements are preserved from the Liko marginated tortoise, including some vertebrae, parts of the girdles, long bones, and an ungual.

Two cervical vertebrae are preserved. AMPG 613 (Fig. 10A) is almost complete, missing only some tips of the dorsal processes. The centrum of the vertebra is long and is amphicoelous with doubled anterior and posterior joints indicating that it is probably the seventh cervical vertebra; it articulates quite well with the eighth cervical vertebra (AMPG 614; Fig. 10B). AMPG 614 (Fig. 10B) is an almost complete eighth cervical vertebra. The centrum is short, biconvex and doubled anteriorly. Posteriorly, two long and curved apophyses are present for the articulation with the dorsal vertebra, developed mostly horizontally and only slightly bent posteriorly. This is the typical condition seen in most Testudinidae.

The shoulder and pelvic girdles are represented by few specimens. AMPG 625 (Fig. 10C) represents most of the scapula, missing only the acromion process. The scapular prong is long and straight, forming a right angle with the acromion. AMPG 615 (Fig. 10D) is an almost complete shoulder girdle, missing only some of the coracoid. The specimen is deformed, and therefore it is not possible to observe the original angles between the shoulder girdle elements. AMPG 674 (Fig. 10E) is an almost complete coracoid with a preserved length of 29 mm; some parts of this element are covered by calcitic material. The neck of the coracoid is long and narrow, whereas the end is wider and rounded. AMPG 617 (Fig. 10F) comprises most of the ischium, partly covered by calcitic materal.

Two well preserved humeri are presented in the Liko material. AMPG 787 (Fig. 10G) is a complete left humerus, with a preserved length of 60.6 mm. The head is spherical. The two trochanters are slightly diverging to parallel. The major trochanter extends well beyond the humeral head. The diaphysis is strongly curved. AMPG 616 (Fig. 10H) is a complete right humerus, with a preserved length of 64 mm. The head is spherical. The two trochanters are slightly diverging to parallel. The major trochanter extends well beyond the humeral head. The diaphysis is strongly curved. Because of the small difference in size and the quite different colors of the specimens I speculate that they probably belong to two different individuals. From the rest of the anterior limb a complete right ulna (AMPG 808, Fig. 10I) is preserved. The proximal part is wide, wider than the narrow distal end. The proximal articular surface is broadly wide, whereas the distal is convex. The medial part of the bone is curved. The cross-section of the bone is triangular. Laterally a thin crest is formed.

FIG. 10. — Appendicular elements of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Liko Cave (Crete): **A**, AMPG 613, cervical vertebra partial shell views: **A1**, anterior; **A2**, right lateral; **A3**, ventral; **A4**, left lateral; **A5**, dorsal; **B**, AMPG 614, cervical vertebra 8 partial shell views: **B1**, anterior; **B2**, posterior; **B3**, ventral; **B4**, left lateral; **B5**, dorsal; **C**, AMPG 625, scapula: anterior view; **D**, AMPG 615, shoulder girdle partial shell views: **D1**, ventral view of the acromion; **D2**, anterior; **D3**, posterior; **E**, AMPG 674, coracoid partial shell views: **E1**, dorsal; **E2**, ventral; **F**, AMPG 617, ischium, dorsal view; **G**, AMPG 787, left humerus partial shell views: **G1**, anterior; **G2**, dorsal; **G3**, ventral; **G4**, posterior; **H**, AMPG 616, right humerus partial shell views: **H1**, dorsal; **H2**, ventral; H3, posterior; **I**, AMPG 808, right ulna partial shell views: **I1**, dorsal; **I2**, lateral; **I3**, medial; **I4**, ventral; **J**, AMPG 676, left femur partial shell views: **J1**, posterior; **J2**, dorsal; **J3**, anterior; **K**, AMPG 675, femur partial shell views: **K1**, dorsal; **K2**, ventral; **L**, AMPG 593, right tibia partial shell views: **L1**, dorsal; **L2**, ventral views; **M**, AMPG 809, left tibia partial shell views: **M1**, dorsal; **M2**, medial; **M3**, lateral; **M4**, ventral; **N**, AMPG 594, ungual partial shell views: **N1**, dorsal; **N2**, ventral. Scale bar: 5 cm.

The posterior limb is represented by several specimens. AMPG 676 (Fig. 10J) corresponds to the proximal and medial part of a left femur, with a preserved length of 44 mm. The head is rounded and elliptical. Its longer axis is oriented with an obtuse angle with the midline. The proximal part is wide, and the trochanters are fused. The diaphysis is straight with a preserved length of 44 mm. AMPG 675 (Fig. 10K) represents the medial and distal part of a femur, with a preserved length of 42 mm. The diaphysis is straight and the distal end is wide. AMPG 593 (Fig. 10L) and AMPG 809 (Fig. 10M) are two complete right tibiae that are relatively straight in the proximal and medial parts, but display a significant degree

of curvature in the distal parts. In the distal part of the shaft a rugosity is noted. The proximal part is wide, triangular in cross-section and with a well-developed and broad cnemial crest. The proximal articular surface is broadly concave. The distal articular surface is more complex, being concave medially and convex laterally. AMPG 593 is slightly longer than AMPG 809. AMPG 677 (not figured here) is the distal part of a tibia, largely covered by calcitic material. AMPG 810 (not figured here) is an almost complete fibula, but the bone is too eroded to allow further description. AMPG 594 (Fig. 10N) is a complete ungual that is long, straight, and with a pointed tip. Based on the elongated and pointed morphology, this ungual probably comes from the posterior limb of the marginated tortoise.

Mavro Mouri IV, Crete

Mavro Mouri IV is one of several caves in Mavro Mouri area in Crete, and the only one among them to provide chelonian remains (Kuss 1970). This material is the richest known from Crete in terms of number of identified specimens but less anatomically diverse compared to the material from the Liko Cave. It represents nearly all the shell and many appendicular elements of a marginated tortoise. The Mavro Mouri IV fossils are stored in the collections of NHMC and AMPG, and will be described separately. This is done because they represent different collections: the NHMC material comes from the collections by Kuss, whereas the AMPG material comes from the collections by the joint expeditions of AMPG and UU.

The NHMC collection from Mavro Mouri IV

This collection contains some shell remains (mainly from the plastron) and some appendicular elements. The carapace is poorly known with only some isolated peripheral plates. NHMC FS38/64 (not figured here) is a continuous series of anterior peripherals. Based on the available comparative material they are the right peripherals 2-4. They are crossed by the marginal sulci, whereas there is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. They are moderately flared. NHMC FS38/66 (not figured here) is a fragment of an anterior peripheral. On the preserved part I cannot observe any evidence of sulci. NHMC FS38/65 (Fig. 11A) corresponds to a continuous series of posterior peripherals. The lateral sides of the peripheral 11 are not parallel to each other, indicating that the corresponding pygal must have been trapezoidal with a narrow posterior side. They are crossed by the marginal sulci, whereas there is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. They are long and posteriorly flared. Based on comparative material they are the right peripherals 10-11. Although limited, this material attests to the presence of a marginated tortoise in the NHMC material from Mavro Mouri IV cave.

The best preserved plastral element is NHMC FS38/60 (Fig. 11B), which represents the entire anterior lobe of the plastron. The lobe is short and wide, having a rounded triangular outline. The epiplastra are short and wide, covering the anterior part of the lobe. Viscerally, the epiplastra are thick, forming a convex epiplastral lip and a significant gular pocket, partly covered by sediment and calcitic material. The entoplastron is hexagonal, slightly wider than long. The anterior parts of the hyoplastra are also preserved. The gulars are narrow and long, covering the medial epiplastra and the anterior part of the entoplastron. The gularo-humeral sulcus is V-shaped, forming an acute angle with the midline. The humerals medially are slightly shorter than the gulars, covering the remaining part of the entoplastron, whereas laterally they are longer. The humero-pectoral sulcus is nearly straight to slightly sinuous, being situated medially in the posterior end of the entoplastron. NHMC FS38/61 (Fig. 11C) is an almost entire right hyoplastron. It is crossed anteriorly by the humero-pectoral sulcus. Based on the preserved part the sulcus is situated posterior to the posterior end of the entoplastron. The remaining surface of the hyoplastron is eroded and it is not possible to confidently identify the pectorals. NHMC FS38/62 and NHMC FS38/63 (Fig. 11D) belong to the same individual and represent the anterior and medial part of the left and right hyoplastron. They are crossed anteriorly by the humero-pectoral sulcus. Based on the preserved part the sulcus is situated posterior to the posterior end of the entoplastron. The pectorals are medially short and laterally longer. The pectoro-abdominal sulcus is slightly convex on each side. NHMC FS38/67 (Fig. 11E) represents the posterior part of the left xiphiplastron. Based on the preserved part we can infer the presence of a wide anal notch in the posterior part of the posterior lobe. It crossed by the femoro-anal sulcus that is oriented medio-anteriorly. The visceral covering of the anal scutes forms a short, narrow and convex lip on the xiphiplastron. NHMC FS38/68 (Fig. 11F) represents the posterior part of the left xiphiplastron. Based on the preserved part we can infer the presence of a wide anal notch in the posterior part of the posterior lobe. The preserved part is not crossed by any sulci. The visceral covering of the anal scutes forms a short, narrow and convex lip on the xiphiplastron. Additional fragments are identified in the material, including NHMC FS38/69 that is a small fragment of the plastron, most probably from the hyoplastral area, and NHMC FS38/78, a group of nine small fragments of the shell.

Several appendicular elements are also identified in the NMHC material from Mavro Mouri IV. NHMC FS38/70 (Fig. 11G) represents the proximal and medial part of the left humerus. The head of the humerus is spherical, developed at a right angle with the proximal part of the bone. The two trochanters are unequal in size, and are developed slightly diverging from parallel to each other. The major trochanter extends well beyond the humeral head, whereas the minor one is poorly developed in some cases. The diaphysis is strongly curved, especially in the distal part. NHMC FS38/72 (Fig. 11H) represents the diaphysis of a humerus. The diaphysis is strongly curved, especially in the distal part. NHMC FS38/71 (Fig. 11I): this specimen represents the proximal part of the right humerus. The head of the humerus is spherical, developed at a right angle with the proximal part of the bone. The two trochanters are unequal in size, and

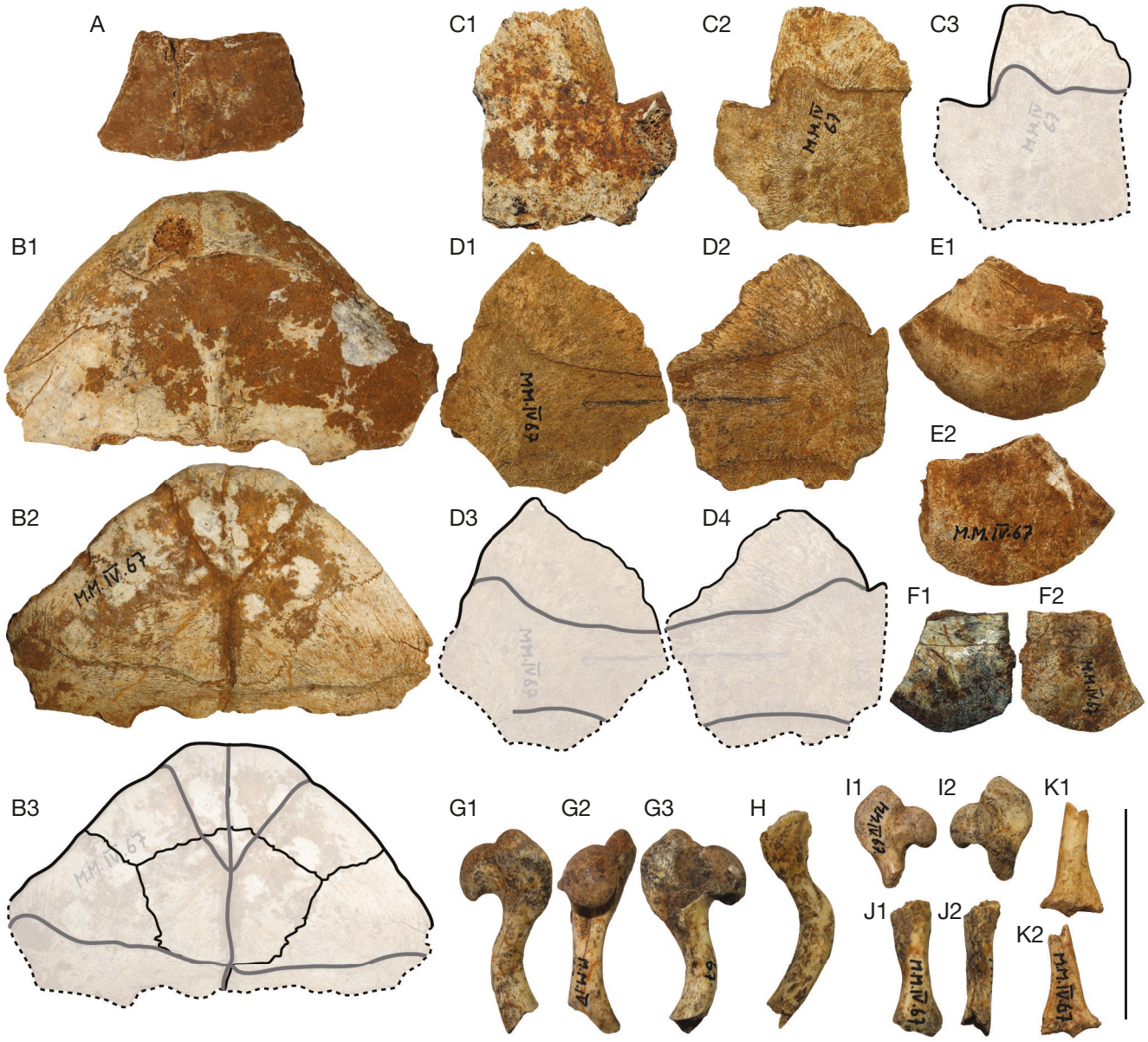

Fig. 11. — Shell and appendicular elements of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Mavro Mouri IV Cave (Crete). NHMC collection: **A**, NHMC FS38/65, peripheral in dorsal view; **B**, NHMC FS38/60, anterior plastral lobe partial shell views: **B1**, visceral; **B2**, ventral; **B3**, drawing of the ventral; **C**, NHMC FS38/61, left hyoplastron partial shell views: **C1**, visceral; **C2**, ventral; **C3**, drawing of the ventral; **D**, NHMC FS38/62-63, left, right hyoplastra partial shell views: **D1**, **D2**, ventral; **D3**, **D4**, drawing of the ventral; **E**, NHMC FS38/67, left xiphiplastron partial shell views: **E1**, visceral; **E2**, ventral; **F**, NHMC FS38/68, left xiphiplastron partial shell views: **F1**, visceral; **F2**, ventral; **G**, NHMC FS38/70, left humerus partial shell views: **G1**, posterior; **G2**, dorsal; **G3**, anterior; **H**, NHMC FS38/72, humerus in lateral view; **I**, NHMC FS38/71, right humerus partial shell views: **I1**, posterior; **I2**, anterior; **J**, NHMC FS38/77, femur partial shell views: **J1**, dorsal; **J2**, lateral; **K**, NHMC FS38/76, ilium partial shell views: **K1**, dorsal; **K2**, ventral. Scale bar: 5 cm.

are developed slightly diverging from parallel to each other. The major trochanter extends well beyond the humeral head, whereas the minor one is poorly developed in some cases. NHMC FS38/73, NHMC FS38/74, and NHMC FS38/75 (none figured herein) correspond to fragments of the diaphysis of three different humeri. The diaphysis is strongly curved, especially in the distal part. NHMC FS38/77 (Fig. 11J) represents the diaphysis of a femur. The diaphysis is straight, thicker proximally, thinner medially. The distal part widens compared to the proximal one. NHMC FS38/76 (Fig. 11K) is a small fragment of an ilium, which is relatively straight in the preserved part.

The AMPG collection from Mavro Mouri IV

This collection contains several carapacial remains and plastral fragments, as well as a couple of appendicular remains. The most important specimens are figured in Figure 12 and are described below.

AMPG 755 (Fig. 12A) represents the anterior left part of the nuchal, which is wide, probably wider than long, and hexagonal. No evidence of a nuchal notch is noted in the preserved part. Anteriorly, a long and wide cervical is present, both dorsally and viscerally; the posterior part of the cervical appears to be a bit wider than the anterior one. The covering of the marginal 1 is extensive on the nuchal,

and the marginal-vertebral sulcus on each side is straight. AMPG 709 (Fig. 12B) and AMPG 816 (Fig. 12C) represents fragments of octagonal neurals that are not crossed by any sulci. Viscerally the attachment of the corresponding dorsal vertebra is observed on both cases.

Numerous partial costals are preserved in the AMPG collection from Mavro Mouri IV. AMPG 686 (Fig. 12D) represents the distal part of a costal plate, crossed by the pleural sulci transversely. Based on the preserved part, there is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. AMPG 715 (Fig. 12E) represents a fragment of a costal of a young individual. Viscerally, the inserted rib can be observed. Ventrally it is not crossed by any sulci. AMPG 813 (Fig. 12F) represents the medial part of a costal that is medially long and is crossed transversely by the pleural sulci. AMPG 815 (Fig. 12G) represents the distal part of a costal that is medially long and is crossed transversely by the pleural sulci. There is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. Several isolated specimens (AMPG 689, 698, 699, 700, 701, 705, 706, 726, 757, 817; not figured here) correspond to fragments of various parts of costal plates, most of which are crossed by the pleural sulci. Some of these costal fragments (e.g. AMPG 689, 726, 757) are quite small and thin and could belong to juvenile individuals. AMPG 814 (not figured here) represents the medial part of the costal 8, as viscerally the attachment processes of the sacral vertebra are noted.

Several peripherals are preserved as well, most of which exhibit the typical flared morphology of the marginated tortoise (AMPG 688, 690-697, 702-704, 708, 710, 714, 716, 721, 722, 724, 725, 746, 812). AMPG 687 (Fig. 12H), for example, forms part of a moderately flared peripheral. It is crossed by the marginal sulci, and there is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. Medially there is a change in the curvature, whereas anteriorly a broad suture with the successive peripheral is noted. Therefore, this peripheral represents the left peripheral 7, right after the end of the bridge. The change in the curvature indicates that the carapacial rim widens at this point, as in the marginated tortoise. AMPG 756 (not figured here) represents a long and almost horizontally flared peripheral of the posterior region of the carapace. It is crossed by the marginal sulci, and there is good correspondence between the costo-peripheral sutures and the pleuro-marginal sulci. Practically, parts of the entire peripheral rim are preserved in this collection, showing that the anterior peripherals were much shorter and less flared compared to the posterior ones.

The plastron is represented by several specimens that preserve several characters of the Mavro Mouri IV marginated tortoise. AMPG 854 (Fig. 12I) represents almost the entire anterior lobe of the plastron. The lobe is short and wide, with a rounded triangular outline. The epiplastra are short and wide, covering the anterior part of the lobe. Viscerally, the epiplastra are thick, forming a convex epiplastral lip and a significant gular pocket. The entoplastron is hexagonal, slightly wider than long. The anterior parts of the hyoplastra are also preserved. The gulars are narrow and long, covering the medial epiplastra and the anterior part of the entoplastron. The gularo-humeral sulcus is V-shaped, with an acute angle with the midline. The humerals medially are slightly shorter than the gulars, covering the remaining part of the entoplastron, whereas laterally they are much longer. The remaining part is eroded and I cannot see the trace of the humero-pectoral sulcus. AMPG 751 (Fig. 12J) represents the left and right epiplastron, forming the anterior part of a wide and rounded lobe. The epiplastra are short and wide. The gulars are long and narrow, covering the medial epiplastra and expanded on the anterior part of the entoplastron. A small irregularity is noted in the right gular scute, being slightly expanded on the left epiplastron. Viscerally, a thick convex epiplastral lip is formed, with a deep gular pocket. Based on the preserved part I can estimate that the entoplastron was short and wide. AMPG 717 (Fig. 12K) represents a complete right epiplastron. The gulars are long and narrow, covering the medial epiplastra and overlapping the anterior part of the entoplastron. A small constriction is noted in the gularo-humeral sulcus. Viscerally, a thick convex epiplastral lip is formed, with a gular pocket. AMPG 718 (Fig. 12L) represents a complete left epiplastron, possibly from the same individual as AMPG 717. The gulars are long and narrow, covering the medial epiplastra and expanded on the anterior part of the entoplastron. A small constriction is noted in the gularo-humeral sulcus. Viscerally, a thick convex epiplastral lip is formed, with a deep gular pocket. AMPG 719 (not figured here) represents an almost complete right epiplastron. The gulars are long and narrow, covering the medial epiplastra and overlapping the anterior part of the entoplastron. Viscerally, a thick convex epiplastral lip is formed, with a gular pocket. AMPG 750 (not figured here) represents a fragment of a left epiplastron. The gulars are long and narrow, covering the medial epiplastra and expanded onto the anterior part of the entoplastron. AMPG 752 (Fig. 12M) represents the posterior part of a short and wide entoplastron, overlapped by the gular scutes.

AMPG 682 (Fig. 12N) represents the anterior part of the left hyoplastron. Anteriorly I can observe the suture with the epiplastron, antero-medially with the entoplastron, and medially with the right hyoplastron. It is crossed anteriorly by the humero-pectoral sulcus, which is medially straight and laterally convex. Based on the preserved part, the sulcus coincides medially with the posterior end of the entoplastron. AMPG 679 (Fig. 12O) represents the anterior part of the left hyoplastron. Anteriorly I notice the suture with the epiplastron and antero-medially with the entoplastron. It is crossed anteriorly by the humero-pectoral sulcus, which is medially straight and laterally convex. Based on the preserved part, the sulcus is situated posterior to the posterior end of the entoplastron. AMPG 720 and 723 (not figured here) are the anterior parts of the left hyoplastron. They are crossed anteriorly by the humero-pectoral sulcus. Based on the size of the preserved part we can estimate that these specimens belonged to small individuals. AMPG 678 (Fig. 12P) represents the anterior and medial part of the right hyoplastron. It is crossed anteriorly by the humero-pectoral sulcus.

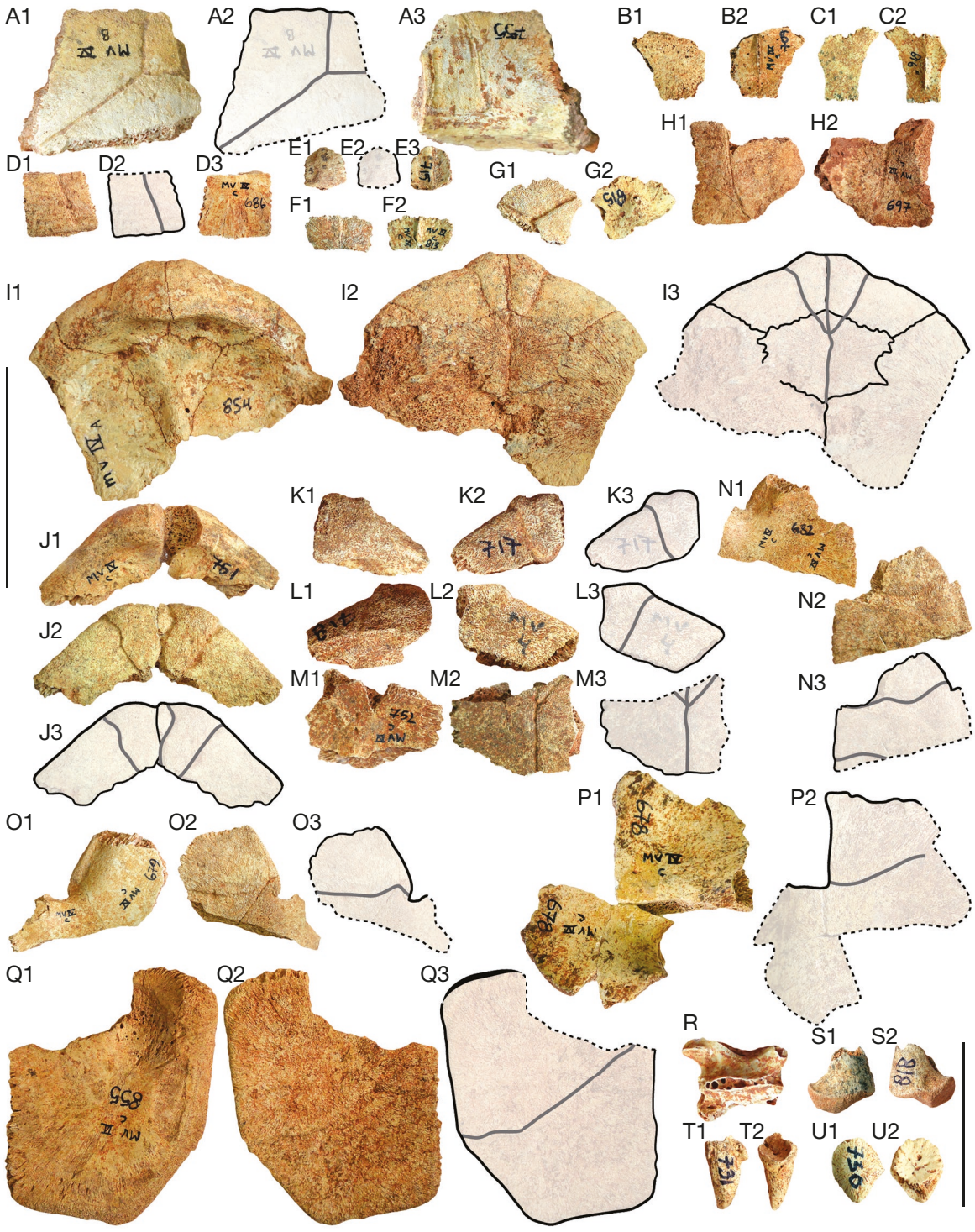

Fig. 12. — Shell and appendicular elements of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Mavro Mouri IV Cave (Crete). AMPG collection: **A**, AMPG 755, nuchal fragment partial shell views: **A1**, dorsal; **A2**, drawing of the dorsal; **A3**, visceral; **B**, AMPG 709, neural fragment partial shell views: **B1**, dorsal; **B2**, visceral; **C**, AMPG 816, neural fragment partial shell views: **C1**, dorsal; **C2**, visceral; **D**, AMPG 686, costal fragment partial shell views: **D1**, dorsal; **D2**, drawing of the dorsal; **D3**, visceral; **E**, AMPG 715, costal fragment partial shell views: **E1**, dorsal; **E2**, drawing of the dorsal; **E3**, visceral; **F**, AMPG 813, costal fragment partial shell views: **F1**, dorsal; **F2**, visceral; **G**, AMPG 815, costal fragment partial shell views: **G1**, dorsal; **G2**, visceral; **H**, AMPG 697, peripheral partial shell views: **H1**, dorsal; **H2**, visceral; **I**, AMPG 854, anterior lobe partial shell views: **I1**, visceral; **I2**, ventral; **I3**, drawing of the ventral; **J**, AMPG 751, left and right epiplastra partial shell views: **J1**, visceral; **J2**, ventral; **J3**, drawing of the ventral; **K**, AMPG 717, right epiplastron partial shell views: **K1**, visceral; **K2**, ventral; **K3**, drawing of the ventral; **L**, AMPG 718, left epiplastron partial shell views: **L1**, visceral; **L2**, ventral; **L3**, drawing of the ventral; **M**, AMPG 752, entoplastron fragment partial shell views: **M1**, visceral; **M2**, ventral; **M3**, drawing of the ventral; **N**, AMPG 682, left hyoplastron partial shell views: **N1**, visceral; **N2**, ventral; **N3**, drawing of the ventral; **O**, AMPG 679, left hyoplastron partial shell views: **O1**, visceral; **O2**, ventral; **O3**, drawing of the ventral; **P**, AMPG 678, right hyoplastron partial shell views: **P1**, visceral; **P2**, drawing of the ventral; **Q**, AMPG 855, right xiphiplastron partial shell views: **Q1**, visceral; **Q2**, ventral; **Q3**, drawing of the ventral; **R**, AMPG 728, cervical vertebra in dorsal view; **S**, AMPG 818, ilium partial shell views: **S1**, dorsal; **S2**, ventral; **T**, AMPG 731, ungual partial shell views: **T1**, dorsal; **T2**, ventral; **U**, AMPG 730, osteoderm partial shell views: **U1**, dorsal; **U2**, ventral. Scale bars: 5 cm.

Based on the preserved part, the sulcus is situated posterior to the posterior end of the entoplastron. The remaining surface of the hyoplastron is eroded and it is not possible to confidently observe the pectorals. Therefore, some morphological variability exists in the position of the humero-pectoral sulcus relative to the posterior end of the entoplastron. Additional hyoplastra are known (AMPG 683-685, 711, 713, 758, 759, 761, 795) and they are consistent with the morphology indicated by the rest of the most complete specimens that are figured here.

The posterior lobe is known from fewer specimens. AMPG 680 (not figured here) represents a fragment of the left hypoplastron, based on the shape and curvature. As it is not crossed by any sulci, further description of the preserved part is not possible. AMPG 760 (not figured here) represents a fragment of the right hypoplastron. Although the ventral surface is eroded, I can see the abdomino-femoral sulcus and the edges of a single inguinal scute. The posterior hypoplastral suture is wide and rounded, showing a hypo-xiphiplastral hinge. Additional hypoplastral specimens are known (AMPG 681, 712), but they are too small and poorly preserved to add more information. AMPG 855 (Fig. 12Q) represents an almost complete right xiphiplastron; some of the medial part is missing. The posterior lobe is formed entirely by the xiphiplastra, and is not sutured to the hypoplastra. Posteriorly, a wide and deep anal notch is formed. The anterior part of the posterior lobe is covered by the femorals, which are short medially and long laterally. Alternatively, the anals are medially long and laterally short. Therefore, the femoro-anal sulcus is slightly concave laterally. The absence of a tight suture between the hypoplastra and the posterior lobe and the long xiphiplastra forming the entire posterior lobe suggests a mobile posterior lobe. Therefore, the presence of a hypo-xiphiplastral hinge can be hypothesized for this specimen. AMPG 742 and 743 (not figured here) represent small fragments of a left xiphiplastron. Several other poorly preserved specimens from the plastron (AMPG 744, 745, 747, 762-711, 795, 796) and the shell (AMPG 811; group of approximately 100 small fragments) have been collected as well, but do not offer more anatomical information.

A few specimens from the appendicular skeleton are also preserved in the AMPG Mavro Mouri IV collection. AMPG 728 (Fig. 12R) is an almost complete procoelous cervical vertebra. The centrum is long, and the apophyses are missing. AMPG 729 (not figured here) represents another small fragment of a cervical vertebra. AMPG 818 (Fig. 12S) represents an ilium fragment, preserving part of the deep articular surface for the femur. AMPG 731 (Fig. 12T): a complete ungual, long and pointed, probably comes from the posterior limb of the tortoise. AMPG 730 (Fig. 12U) represents a complete half-pointed osteoderm. AMPG 727 (not figured here) represents the curved diaphysis of a humerus.

Simonelli Cave, Crete

The first material mentioned from Simonelli Cave is by Kotsakis (1980). This material (stored in Roma Tre University, Rome, Italy) consists of several limb bones, such as a left femur, three diaphysis of humerus, a tibia, and an ulna. As Kotsakis (1980) mentioned, the morphology of these specimens is consistent with *T. marginata*. The previously undescribed elements from the AMPG collection presented here (Fig. 13) are similar in morphology to the material presented by Kotsakis (1980). It must be noted that no shell remains are known up to now from Simonelli Cave.

AMPG 609 (Fig. 13A) represents an almost complete sacral vertebra, with a preserved length of 21.7 mm. It shows significant lateral processes and a long procoelous body. It shows no attachments for the carapace. AMPG 608 (Fig. 13B) represents the distal part of a straight femur with a preserved length of 18 mm. AMPG 607 (Fig. 13C) represents the curved diaphysis of a humerus with a preserved length of 27 mm. Finally, AMPG 606 (Fig. 13D) represents an almost complete right humerus, only the distal part missing, and with a preserved length of 52 mm. The head is spherical. The two trochanters are slightly diverging to parallel. The major trochanter extends well beyond the humeral head. The diaphysis is strongly curved.

Discussion

The marginated tortoise, *Testudo marginata*, is one of the traditionally recognized species of *Testudo*, named by Schoeppf in 1793. Among the various species of *Testudo* it is certainly the largest, as it can exceed 40 cm in carapacial length (Vlachos 2015; and references therein). It is distributed across the mainland of Greece and Peloponnesus, and in a few Aegean islands. It is also found in Albania. This species is easily recognized by the presence of a long carapace with posteriorly flared peripherals and pygal (Vlachos 2015; and references therein). Among the Cretan material presented above, several specimens preserve the posteriorly flared carapace allowing a clear attribution to this taxon. Also, it is relatively easy to attribute all the isolated peripheral plates presented above to this taxon as well, as this character can be undoubtedly identified even in isolated materials. However, the degree of the flaring of the posterior carapacial rim varies in the material. For example, some specimens (e.g. Gerani; Fig. 2) show a posterior rim that is not horizontally flared, whereas others (e.g. Zourida; Fig. 4) show a rim that is horizontal (paratype of *T. m. cretensis*) or even more curved (AMPG 577; Fig. 5A-G). The presence of the posteriorly flared peripheral rim, including the pygal of course, and the presence of a typical hypo-xiphiplastral hinge identifies the Cretan tortoise as *Testudo marginata*.

Previously, the marginated taxon that has been identified in Crete was *Testudo marginata cretensis*, a new subspecies described by Bachmayer *et al.* (1975). In this section some information on the potential validity of this subspecies is provided. It is diagnosed as: "Neurale I hat eine rechteckige und Neurale II eine achteckige Umrissform. Das Pygale ist vorne und hinten gleich breit. Gulare ist viel schmäler. Der Hinterrand des Xiphiplastrons ist bei der Unterart viel breiter als bei der Art *Testudo marginata*" (Neural I has a rectangular shape and Neural II has an octagonal outline. The pygal is equally wide. Gulars are much narrower. The rear edge of the xiphiplastron is much wider in the subspecies than in the species *Testudo marginata*) (Bachmayer *et al.* 1975: 111). Based on my observations of the holotype, the neural 1 is

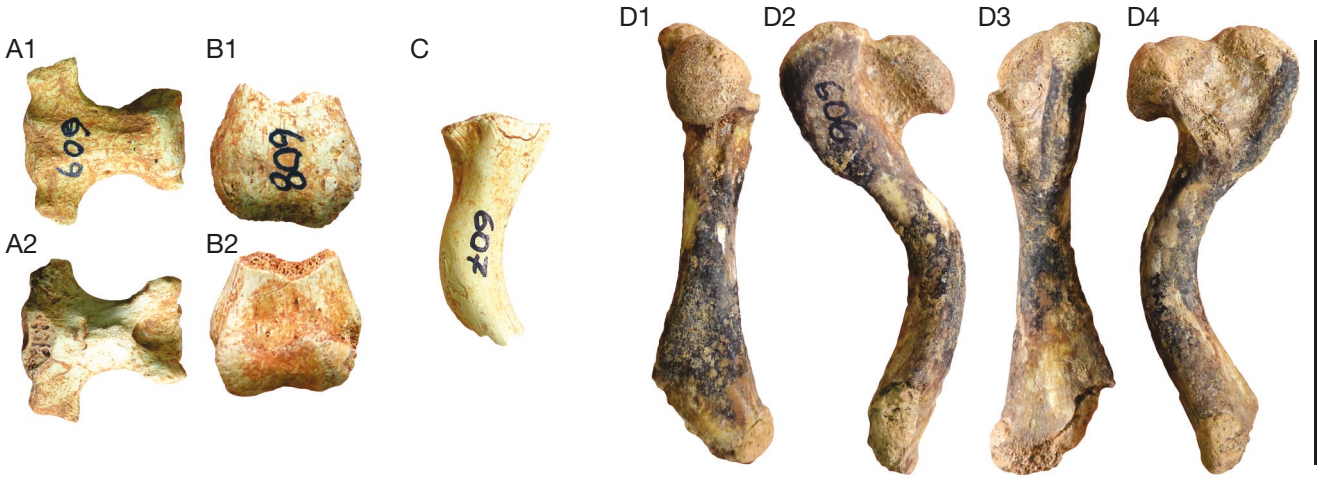

FIG. 13. — Additional appendicular elements of *Testudo marginata* Schoepff, 1793 from the Pleistocene of Simonelli Cave (Crete). AMPG collection: **A**, AMPG 609, sacral vertebra partial shell views: **A1**, dorsal; **A2**, ventral; **B**, AMPG 608, femur partial shell views: **B1**, dorsal; **B2**, ventral; **C**, AMPG 607, diaphysis of a femur in lateral view; **D**, AMPG 606, right humerus partial shell views: **D1**, dorsal; **D2**, posterior; **D3**, ventral; **D4**, anterior. Scale bar: 5 cm.

hexagonal with short postero-lateral sides (Fig. 2B), and not rectangular as described by Bachmayer *et al.* (1975). Note that Bachmayer *et al.* (1975: fig. 3) showed the neural region of a recent *T. marginata* as having an hexagonal neural 1. Several other extant specimens that were examined have rectangular and hexagonal neural 1. In the paratype (from Zourida Cave; Fig. 4) the limits of neural 1 are not clearly visible. Therefore, the first character (neural 1 rectangular) for the differential diagnosis of *T. m. cretensis* is subject to the intraspecific variability of *T. marginata*. The second character (neural 2 octagonal) is the normal condition seen not only in *T. marginata* but in other *Testudo* as well. The third character (pygal of equal anterior and posterior width) is even more variable. Although the holotype (Gerani Cave; Fig. 2) shows this condition, the paratype (Zourida; Fig. 4) shows a pygal that is posteriorly wider (also seen in other specimens from Zourida). In most extant specimens of *T. marginata* the pygal is posteriorly narrower than anteriorly (e.g. Schleich 1982). The fourth character (narrow gulars) is also quite variable, not only in the studied specimens from Crete, but within *T. marginata* in general. Similar is the variability within *T. marginata* in the last character (wider xiphiplastra). It seems that all these differences can be within the range of the intraspecific variation and/or sexual dimorphism of the marginated tortoise. Also, many of the comparative specimens that have been examined (and also the one figured by Bachmayer *et al.* 1975: fig. 3) show many irregularities in the shape of the neurals. For example, in some specimens the last neurals could be missing and the costals contact each other medially.

A recent attempt to define another species within the *T. marginata* complex was made by Bour (1996) with the erection of a "dwarf" species of *T. marginata*, named *Testudo weissingeri*. But study of its mitochondria (Fritz *et al.* 2005) does not support this distinctiveness. Also, Fritz *et al.* (2005: 399) conclude that: "[…] tortoises are capable of modifying their morphology within a few hundred or thousand years, due to genetic bottlenecks or environmental pressure. This argues for caution when erecting further new *Testudo* species or subspecies without accompanying genetic studies".

Based on all the available morphological evidence and the current genetic context it seems that the small differences observed in the Gerani and Zourida specimens are not adequate enough in order to successfully distinguish the Crete tortoises from *T. marginata*.

Whether a new taxon or not, the presence of the marginated tortoise in Crete is an important finding. The stratigraphic range for this taxon is established in Greece for the entire Pleistocene, with fossils that are within the natural distribution of the extant *T. marginata* (Vlachos 2015; TTWG 2017). However, we know of some fossils that expand the range of this taxon in the Pleistocene more to the south and southeast: the few fossils from Kos and the appendicular-dominated collection from Tilos (see Vlachos 2015) are the easternmost occurrences of this taxon, whereas the numerous occurrences in Crete herein (see also Brinkerink 1996 and Vlachos 2015) are the southernmost records for the marginated tortoise. The Cretan tortoise is identified as one of the taxa that have suffered extinction during the end of the Pleistocene by TEWG (2015). Obviously, two important issues play a role in evaluating this possible extinction event. First, the subjective taxonomic opinion on the distinction or not of the Cretan tortoise as a different subspecies (or even species) could affect the interpretation. Perhaps ancient DNA sampling (if available and traceable) in the future could help to solve this issue. Second, the unclear stratigraphic placement and imprecise dating of the specimens does not allow placing them in a refined chronostratigraphic scale in the Pleistocene. That placement would important in order to establish the timing and/or extinction factors of this taxon in Crete and southern Greece. For the moment, the most conservative interpretation is that the Pleistocene geographical range of the marginated tortoise was more extensive compared to the extant one, with several occurrences in southeastern and southern regions of the Aegean Sea.

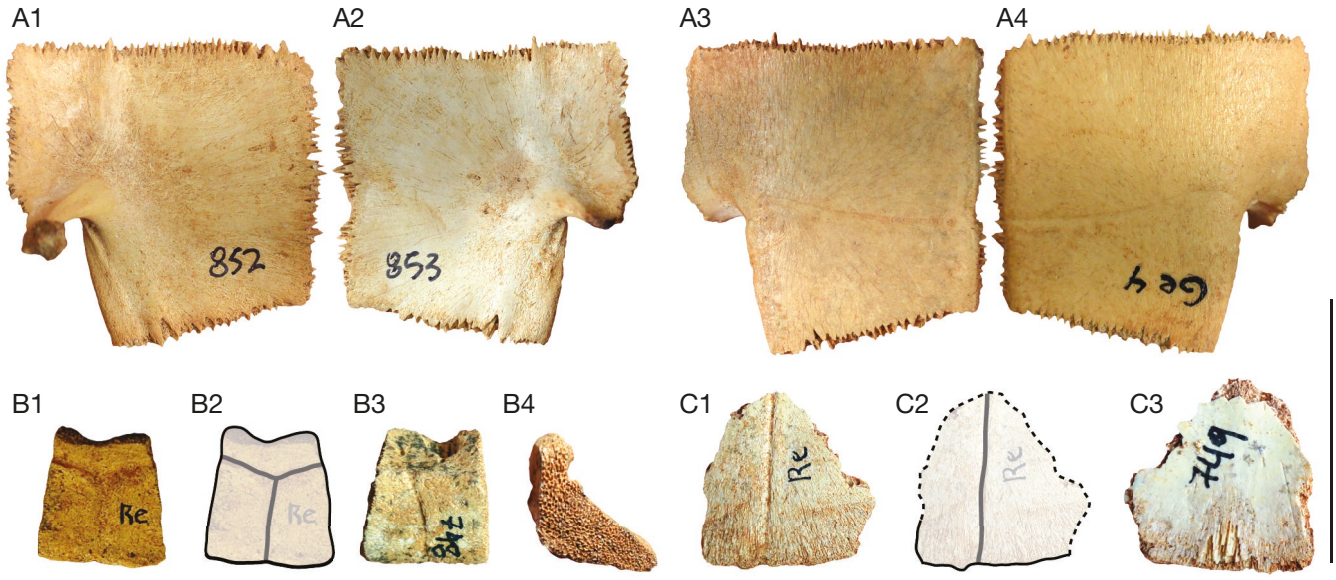

Fig. 14. — *Mauremys* cf. *rivulata* Valenciennes *in* Bory de Saint-Vincent, 1833 from Gerani Cave and Rethymnon fissure (Crete): **A**, Gerani Cave (recent), AMPG 852 and 853, left and right hypoplastra partial shell views: **A1**, **A2**, visceral; **A3**, **A4**, ventral; **B**, **C**, Rethymnon fissure (Pleistocene): **B**, AMPG 748, peripheral views: **B1**, dorsal; **B2**, drawing of dorsal; **B3**, visceral; **B4**, medial; **C**, AMPG 749, costal fragment views: **C1**, dorsal; **C2**, drawing of the dorsal; **C3**, visceral. Scale bar: 5 cm.

A final note needs to be made on the mysterious humerus from Katharo. Brinkerink (1996) brings into attention a distal humerus (AMPG 787; not figured here) from Katharo basin in Crete, suggesting that this is an element of a large *Testudo*. My inspection of the specimen found no similarities with a turtle/tortoise humerus. The diaphysis of the specimen is almost straight, compared to the curved humerus of testudinids. Moreover, there is no ectepicondylar foramen. Finally, a transverse constriction is found that is lacking in chelonian humeri. Therefore, based on the available material we can probably refute the presence of tortoises in Katharo basin.

Family Geoemydidae Theobald, 1868
Genus *Mauremys* Gray, 1869

Mauremys cf. *rivulata* (Vallenciennes *in* Bory de Saint-Vincent, 1833) (Figs 14-19)

Emys rivulata Valenciennes *in* Bory de Saint-Vincent, 1833: planches, pl. 9 (14: 25). — Restricted to "Morée…Modon" [Greece] by Bory de Saint-Vincent (1836: 110), and emended to "Umgebung von Modon, Morea, Griechenland" [Greece] by Mertens & Müller (1928: 22). See TTWG 2017 for more information.

Temporal distribution in Greece. — Extant-Pleistocene.

Type locality. — Not designated.

Geographical distribution in Greece. — Extant *Mauremys rivulata* is known from almost the entire country, excluding some islands in the Aegean and Ionian Seas, including Crete (Vlachos 2015; TTWG 2017; and references therein). In Crete it is probably known from the Cave sites in Rethymnon area, Crete Island such as Koumpes, Liko, Mavro Mouri IV, Rethymnon fissure, and the open site of Siteia. Outside Crete, this species is known from Vraona Cave in Attica (subrecent), Megalopolis in Peloponnesus, and Kos Island. See Vlachos (2015) and references therein for more information.

Material examined. — **Gerani Cave, Crete** (Pleistocene, 2 specimens) (Fig. 14): AMPG 852, left hypoplastron; AMPG 853, right hypoplastron.
Rethymnon fissure, Rethymnon, Crete (Pleistocene, 2 specimens) (Fig. 14): AMPG 748, peripheral; AMPG 749, costal fragment.
Koumpes Cave, Crete (Pleistocene, 4 specimens) (Fig. 15): AMPG 621, fragment of the carapace; AMPG 622, costal; AMPG 623, neural; AMPG 624, peripheral.
Liko Cave, Crete (Pleistocene, 9 specimens) (Fig. 16): AMPG 735, neural; AMPG 736, humerus; AMPG 737, humerus diaphysis; AMPG 738, coracoid; AMPG 739, ungual; AMPG 753, peripheral; AMPG 754, humerus distal part; AMPG 778, right xiphiplastron; AMPG 779, peripheral.
Mavro Mouri IV, Crete (Pleistocene, 6 specimens) (Fig. 17): AMPG 788, entoplastron; AMPG 789, costal; AMPG 790, costal fragment; AMPG 791, peripheral; AMPG 792, peripheral fragment; AMPG 793, peripheral.
Sitia, Crete (Pleistocene, 72+ specimens) (Figs 18; 19): AMPG 629, suprapygal 2; AMPG 630, costal; AMPG 631, costal fragment; AMPG 632, costal fragment; AMPG 633, costal fragment; AMPG 634, costal fragment; AMPG 635, peripheral; AMPG 636, right epiplastron; AMPG 637, entoplastron; AMPG 638, hypoplastron fragment; AMPG 639, hypoplastron fragment; AMPG 640, plastron fragment; AMPG 641, plastron fragment; AMPG 642, humerus diaphysis; AMPG 643, femur diaphysis; AMPG 644, costal fragment; AMPG 645, peripheral fragment; AMPG 646, nuchal fragment; AMPG 647, peripheral; AMPG 648, costal fragment; AMPG 649, xiphiplastron fragment; AMPG 650, humerus; AMPG 651, scapula; AMPG 652, costal fragment; AMPG 653, costal fragment; AMPG 654, peripheral; AMPG 655, peripheral fragment; AMPG 656, plastron fragment; AMPG 657, costal fragment; AMPG 658, costal fragment; AMPG 659, costal fragment; AMPG 660, costal fragment; AMPG 661, costal fragment; AMPG 662, costal fragment; AMPG 663, costal fragment; AMPG 664, costal fragment; AMPG 665, pygal; AMPG 666, peripheral; AMPG 667, peripheral; AMPG 668, left epiplastron; AMPG 669, left xiphiplastron fragment; AMPG 670, plastron fragment; AMPG 671, hypoplastron fragment; AMPG 819, peripheral; AMPG 820, peripheral; AMPG 821, periph-

eral; AMPG 822, peripheral; AMPG 823, peripheral; AMPG 824, peripheral; AMPG 825, peripheral; AMPG 826, peripheral; AMPG 827, left costal; AMPG 828, costal fragment; AMPG 829, costal fragment; AMPG 830, costal fragment; AMPG 831, costal fragment; AMPG 832, costal fragment; AMPG 833, costal fragment; AMPG 834, plastron fragment; AMPG 835, peripheral; AMPG 836, hyoplastron fragment; AMPG 837, costal fragment; AMPG 838, plastron fragment; AMPG 839, plastron fragment; AMPG 840, plastron fragment; AMPG 841, plastron fragment; AMPG 842, left epiplastron; AMPG 843, left xiphiplastron; AMPG 844, peripheral fragment; AMPG 845, neural fragment; AMPG 846, costal fragment; AMPG 847, hyoplastron fragment; AMPG 848, hyoplastron fragment; AMPG 849, costal fragment; AMPG 850, neural; AMPG 851, costal fragment.

Gerani Cave, Crete

Two of the specimens collected in the Gerani Cave do not belong to the marginated tortoise (Fig. 14A). Based on the type of preservation the material is not fossilized and could be recent to sub-recent, as it has been also noted in the first mention of this material by Brinkerink (1996). AMPG 852 and 853 (Fig. 14A) represent a complete left and right hypoplastron respectively, and probably belonged to the same individual. Both the visceral and the ventral surfaces are smooth and the specimen is thin. The femoral covering on the visceral side of the hypoplastra is relatively broad, creating a convex lip. Ventrally, the specimen is crossed by the abdomino-femoral sulcus that is nearly straight to slightly concave medially and broadly convex laterally. The hypoplastra contribute significantly to the formation of the posterior lobe. Clearly, as no evidence of a movable hinge is noted on any of the anterior or posterior sides, these specimens differ from the marginated tortoise or the pond turtle, and are as such attributed to the Balkan terrapin.

Rethymnon fissure

Additional material of this species comes from the Rethymnon fissure. AMPG 748 (Fig. 14B) is a short and wide peripheral, crossed by the pleuro-marginal sulcus medially and the marginal sulci transversely, thus lacking the typical correspondence seen in tortoise peripherals. The peripheral is horizontally flared, resembling those in the posterior carapacial rim of a terrapin. AMPG 749 (Fig. 14C) represents the lateral part of a costal, crossed by the pleural sulci. The smooth surface is consistent with that of a terrapin and not of a tortoise.

Koumpes Cave

Two specimens from Koumpes Cave can be attributed to the Balkan terrapin. AMPG 621 (Fig. 15A) represents a part of the medial carapace of a terrapin. The presence of rib ends and areas of vertebrae attachments on the visceral side allows the identification of two neurals and a fragment of a costal. The anterior neural is partially preserved, whereas both are hexagonal with short anterior lateral sides. The costal articulates with both neurals, through a long suture with the anterior, and a shorter suture with the posterior one. As far as scute sulci are concerned, the border with two vertebrals is noted, crossing the anterior neural and the costal. This morphology differs from the neural pattern of the marginated tortoise that is defined by quadrangular and octagonal neurals in alternation. AMPG 623 (Fig. 15B) is an almost complete neural, hexagonal, with short anterior lateral sides, and is not crossed by any sulci. AMPG 622 (Fig. 15C) represents the medial part of a costal, crossed only by the vertebra-pleural sulcus. It is associated with terrapins because of the color and texture similarity with the other confirmed terrapin specimens. AMPG 624 (not figured here) is a fragment of a peripheral. Although no sulci can be observed, the small size and the degree of flaring is consistent with the morphology of the posterior peripherals of a terrapin.

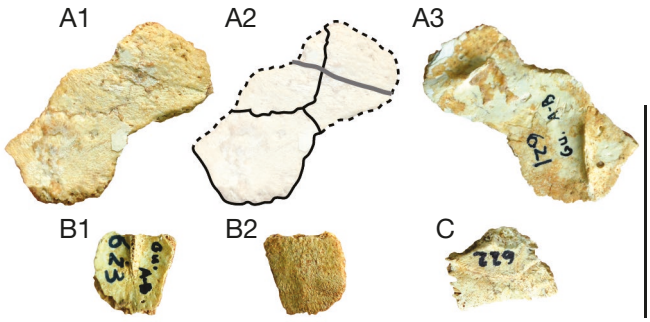

Fig. 15. — *Mauremys* cf. *rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833 from the Pleistocene of Koumpes Cave (Crete): **A**, AMPG 621, neurals and costal fragment views: **A1**, dorsal; **A2**, drawing of the dorsal; **A3**, visceral; **B**, AMPG 623, neural views: **B1**, visceral; **B2**, dorsal; **C**, AMPG 622, costal fragment in dorsal view. Scale bar: 5 cm.

Liko Cave, Crete

Some specimens that can be attributed to the terrapin are also found in the AMPG Liko collection. Besides several anatomical characters, these specimens are distinguished from the tortoise specimens from the same cave because of their color, that is more greenish-to-yellowish. AMPG 735 (Fig. 16A) represents a complete neural, which is hexagonal, with short anterior sides, not crossed by any sulci. AMPG 779 (Fig. 16B) represents a complete peripheral of the bridge area. It is overlapped by the pleural scutes and laterally displays a lateral ridge like a gutter. AMPG 753 (Fig. 16C) is a wide and short peripheral, overlapped by the pleural scutes. AMPG 778 (Fig. 16D) is an almost complete right xiphiplastron. The anterior part is missing. The lateral sides converge posteriorly. Posteriorly, a deep and rounded anal notch is noted. The anals are quite long. The femoro-anal sulcus is straight, being oriented anteriorly.

Some appendicular elements from Liko could also belong to the terrapin, although their identification is less certain. AMPG 738 (Fig. 16E) represents an almost complete coracoid of a juvenile individual. The neck of the coracoid is narrow and long, with a wide distal end. AMPG 736 (Fig. 16F) and AMPG 737 (not figured here) are almost complete and moderately curved humeri of juvenile individuals. AMPG 754 (Fig. 16G) represents the medial and distal part of a humerus, being moderately curved. AMPG 739 (Fig. 16H) represents a long and pointed ungual of a terrapin.

Mavro Mouri IV

A few specimens from Mavro Mouri IV cave could belong to the Balkan terrapin *Mauremys rivulata*, and are clearly

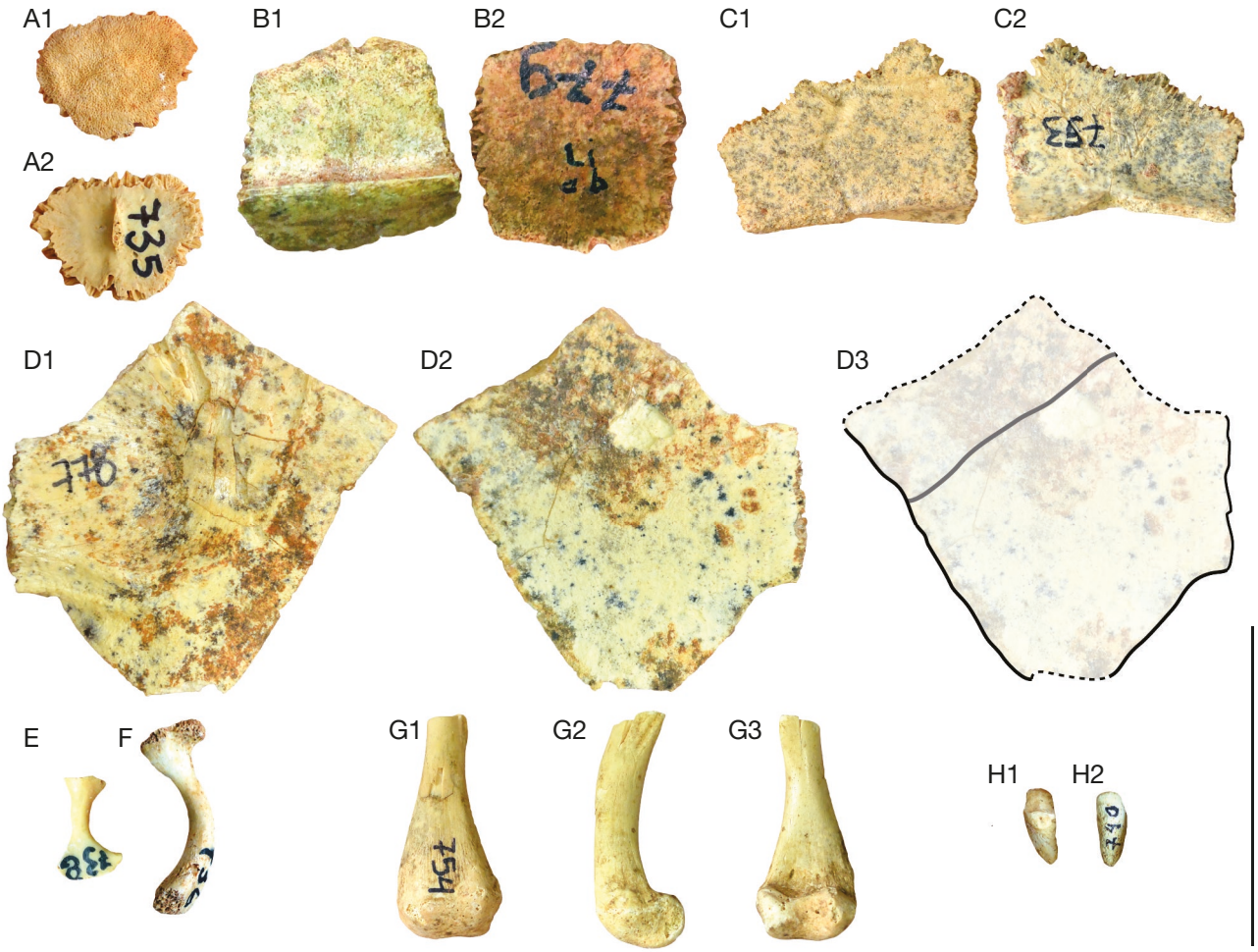

Fig. 16. — *Mauremys* cf. *rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833 from the Pleistocene of Liko Cave (Crete): **A**, AMPG 735, neural views: **A1**, dorsal; **A2**, visceral; **B**, AMPG 779, peripheral views: **B1**, dorsal; **B2**, visceral; **C**, AMPG 753, peripheral views: **C1**, dorsal; **C2**, visceral; **D**, AMPG 778, right xiphiplastron views: **D1**, visceral; **D2**, ventral; **D3**, drawing of the ventral; **E**, AMPG 738, coracoid of a juvenile in dorsal view; **F**, AMPG 736, humerus of a juvenile in lateral view; **G**, AMPG 754, humerus views: **G1** dorsal; **G2**, posterior; **G3**, ventral; **H**, AMPG 739, ungual views: **H1**, ventral; **H2**, dorsal. Scale bar: 5 cm.

distinct from the tortoise specimens collected from the same locality. AMPG 789 (Fig. 17A) represents a complete costal that is hexagonal and very wide. The medial and lateral sides are of equal width. The medial side shows one long suture surface anteriorly and one short posteriorly, representing hexagonal neurals with short anterolateral sides. Dorsally, the limits of the vertebrals and the pleural scutes can be observed. AMPG 790 (not figured here) represents a fragment of a costal that is crossed transversely by the pleural sulci, and is identical to the AMPG 789 specimen. AMPG 791 (Fig. 17B) is an almost complete peripheral that is short and moderately flared, crossed transversely by the marginal sulci. In the medial part the short overlapping of the pleural scutes is noted. Similarly, AMPG 792 and 793 (not figured here) are partial peripherals of similar morphology, being short and moderately flared, crossed transversely by the marginal sulci. AMPG 788 (Fig. 17C) represents a complete entoplastron. It is hexagonal, slightly longer than wide. Anteriorly it is overlapped by the gular scutes. Compared to the entoplastra of the marginated tortoise, this is longer than wide, with a quite short anterior part.

Sitia, Crete

The best material of the Balkan terrapin from Crete comes from Sitia, a site that has not provided so far any specimens of a marginated tortoise. The material comprises isolated plates from the carapace and plastron, as well as some appendicular elements.

AMPG 646 (not figured here) is very small, but most probably represents a fragment of the nuchal. The sulci on the dorsal side could represent the cervical and the marginals, but the specimen is too small to allow a confident assessment. AMPG 850 (Fig. 18A) represents a part of a neural that is rounded and is crossed by the vertebral sulci. Dorsally, the crossing of the vertebral sulci is seen. AMPG 845 (not figured here) is also a small neural fragment. AMPG 629 (Fig. 18B) represents an almost complete suprapygal 2. It is hexagonal with wider anterior part, being wider than long. The plate is also convex in shape. Dorsally is crossed by the vertebro-marginal sulci. Moreover, the presence of two marginals posteriorly (marginals 12) is noted, and the anterior part of the marginal sulcus (the vertebro-marginal sulcus) is preserved in the posterior part of the suprapygal. AMPG 665 (Fig. 18C) represents an

FIG. 17. — *Mauremys* cf. *rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833 from the Pleistocene of Mavro Mouri IV Cave (Crete): **A**, AMPG 789, costal views: **A1**, dorsal; **A2**, drawing of the dorsal; **A3**, visceral; **B**, AMPG 791, peripheral views: **B1**, dorsal; **B2**, visceral; **C**, AMPG 788, entoplastron views: **C1**, visceral; **C2**, ventral; **C3**, drawing of the ventral. Scale bar: 5 cm.

almost complete pygal plate. The pygal is strongly curved transversely. It is covered only by the marginals 12 and their limit crosses the pygal longitudinally.

Numerous costals and costal fragments are preserved in the Sitia material. AMPG 630 (Fig. 18D) represents an almost complete costal plate. The medial part shows two sutured sides, one longer and one short, representing hexagonal neurals. Dorsally I can observe the crossing of the vertebral and pleural sulci. The vertebrals are narrower than the pleurals. AMPG 633 (Fig. 18E) represents the medial part of a costal. Dorsally, a single sulcus is noted, crossing the plate anterio-posteriorly. Therefore, this specimen could be identified as the costal 8, from the left side. It could represent a young individual. AMPG 631 (Fig. 18F) represents the distal part of a costal. The costal is crossed by the pleural sulci. AMPG 662 (Fig. 18G) represents the medial part of a costal plate, whose medial part shows two sutured sides, one longer and one short, corresponding to hexagonal neurals. Dorsally I can observe the crossing of the vertebral sulci. AMPG 652 (Fig. 18H) represents the lateral part of a costal. It is not crossed by any sulci. The presence of a free rib end laterally indicates a young individual. AMPG 664 (Fig. 18I) represents the medial part of a costal plate. The medial part shows one rounded sutured surface, probably corresponding to the last neurals. Dorsally the crossing of the vertebral sulci can be observed. AMPG 831-833 (Fig. 18J) correspond to the middle parts of costals that are crossed by the pleural sulci. AMPG 828 (Fig. 18K) represents the middle part of a costal that is not crossed by any sulci. AMPG 827 (Fig. 18L) is a complete long and narrow costal. Dorsally a wide covering of the vertebrals and no pleural sulci are observed. Viscerally, the presence of the rib end is noticed. Based on the outline of the plate, this is the left costal 1. AMPG 653 (Fig. 18M) represents the medial part of a costal that is dorsally crossed by vertebral and pleural sulci. Viscerally, it shows the attachments of the vertebra. Most probably belongs to the costal 7 or 8. AMPG 849 (Fig. 18N) represents the medial part of a costal plate. The medial part shows two sutured sides, one longer and one short, representing hexagonal neurals. Dorsally the crossing of the vertebral sulci is observed. Based on the size it is presumed to be a young individual. AMPG 657 (Fig. 18O) represents a middle part of a costal, crossed by the pleural sulci. There are several fragmented costals in the Sitia collection with a morphology consistent with the one described above (AMPG 632, 634, 644, 648, 658, 659-661, 663, 829, 830, 837, 846, 851; not figured here).

There are several peripherals preserved in the Sitia material: AMPG 823 (Fig. 18P), AMPG 635 (Fig. 18Q), AMPG 654 (Fig. 18R), AMPG 666 (Fig. 18S), AMPG 820 (Fig. 18T), AMPG 645, 647, 665, 667, 819, 821, 822, 824-826, 835, and 844, representing different parts of the anterior and posterior peripheral rim. The majority of the peripherals are long and narrow, and moderately flared. All are overlapped by the pleurals and crossed by the pleural and marginal sulci.

Several specimens of the anterior and posterior lobe are known as well from Sitia (Fig. 19). AMPG 636 (Fig. 19A) represents an almost complete right epiplastron. The epiplastron is long and narrow. Viscerally, a thin lip is formed that is medially concave. Ventrally, the gulars are narrow and long, covering the medial part of the epiplastra and overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is straight and causes a small constriction in the anterior lobe. AMPG 668 (Fig. 19B) represents a fragment of the left epiplastron. Ventrally no sulci are observed, whereas viscerally the gularo-humeral sulcus is noted. AMPG 842 (Fig. 19C) represents an almost complete left epiplastron.

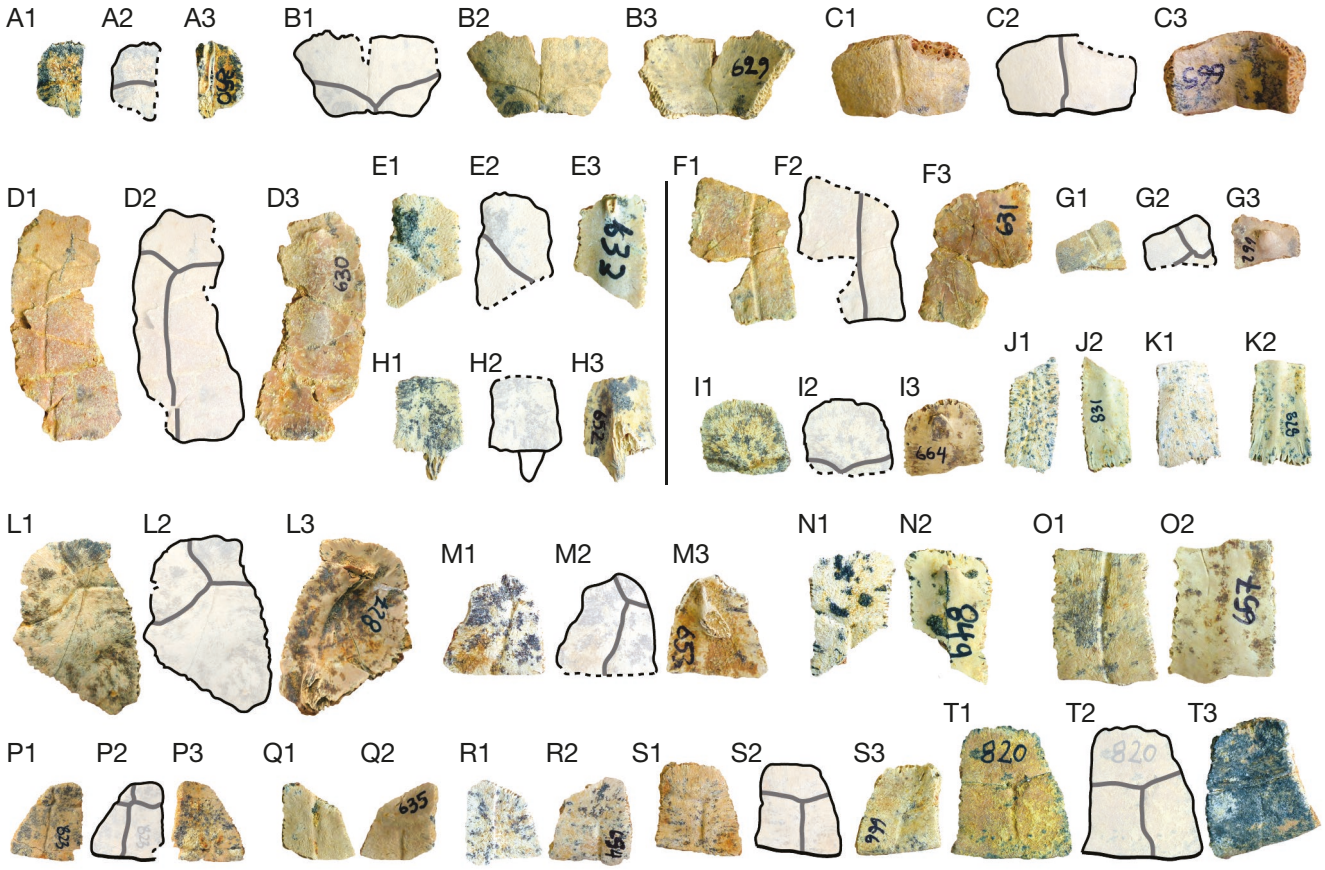

Fig. 18. — Carapace remains of *Mauremys* cf. *rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833 from the Pleistocene of Sitia (Crete): **A**, AMPG 850, neural views: **A1**, dorsal; **A2**, drawing of the dorsal; **A3**, visceral; **B**, AMPG 629, second suprapygal views: **B1**, drawing of the dorsal; **B2**, dorsal; **B3**, visceral; **C**, AMPG 665, pygal views: **C1**, dorsal; **C2**, drawing of the dorsal; **C3**, visceral; **D**, AMPG 630, costal views: **D1**, dorsal; **D2**, drawing of the dorsal; **D3**, visceral; **E**, AMPG 633, costal views: **E1**, dorsal; **E2**, drawing of the dorsal; **E3**, visceral; **F**, AMPG 631, costal views: **F1**, dorsal; **F2**, drawing of the dorsal; **F3**, visceral; **G**, AMPG 662, costal views: **G1**, dorsal; **G2**, drawing of the dorsal; **G3**, visceral; **H**, AMPG 652, costal views: **H1**, dorsal; **H2**, drawing of the dorsal; **H3**, visceral; **I**, AMPG 664, costal views: **I1**, dorsal; **I2**, drawing of the dorsal; **I3**, visceral; **J**, AMPG 831, costal views: **J1**, dorsal; **J2**, drawing of the dorsal; **J3**, visceral; **K**, AMPG 828, costal views: **K1**, dorsal; **K2**, drawing of the dorsal; **K3**, visceral; **L**, AMPG 827, costal views: **L1**, dorsal; **L2**, drawing of the dorsal; **L3**, visceral; **M**, AMPG 653, costal views: **M1**, dorsal; **M2**, drawing of the dorsal; **M3**, visceral; **N**, AMPG 849, costal views: **N1**, dorsal; **N3**, visceral; **O**, AMPG 657, costal views: **O1**, dorsal; **O2**, visceral; **P**, AMPG 823, peripheral views: **P1**, dorsal; **P2**, drawing of the dorsal; **P3**, visceral; **Q**, AMPG 635, peripheral views: **Q1**, dorsal; **Q2**, visceral; **R**, AMPG 654, peripheral views: **R1**, dorsal; **R2**, visceral; **S**, AMPG 666, peripheral views: **S1**, dorsal; **S2**, drawing of the dorsal; **S3**, visceral; **T**, AMPG 820, peripheral views: **T1**, dorsal; **T2**, drawing of the dorsal; **T3**, visceral. Scale bar: 5 cm.

Anteriorly, a shallow notch is noted. The epiplastron is long and narrow. Viscerally, a thin lip is formed that is medially concave. Ventrally, the gulars are narrow and long, covering the medial part of the epiplastra and overlapping the anterior part of the entoplastron. The gularo-humeral sulcus is curved and causes a small constriction in the anterior lobe. AMPG 637 (Fig. 19D) represents an almost complete entoplastron. It is roughly hexagonal and rounded, with a slightly wider posterior part. Anteriorly is overlapped by the gular scutes, whereas posteriorly is overlapped by the pectorals. The humerals are medially short. The humero-pectoral sulcus is nearly straight medially.

AMPG 638 (Fig. 19E) represents the lateral part of the right hypoplastron, and is rather flat and is crossed by the abdomino-femoral sulcus. Additional hypoplastral fragments are preserved (AMPG 639, 656, 671) with a morphology that is consistent with AMPG 638. AMPG 649 (Fig. 19F) and AMPG 669 (Fig. 19G) correspond to the posterior part of the left xiphiplastron. Posteriorly a deep anal notch is noted. The preserved part of the xiphiplastra is not crossed by any sulci indicating that the anals had a long covering on the posterior lobe. AMPG 843 (Fig. 19H) represents an almost complete left xiphiplastron. The lateral sides of the posterior lobe are converging posteriorly. On the posterior part, a deep and rounded anal notch is noted. The xiphiplastral extremities are rather pointed. The femorals cover the anterior part of the xiphiplastron, whereas the anals show a long covering on the posterior part of the lobe. The femoro-anal sulcus is straight, being oriented transversely. Finally, several isolated and unidentifiable plastral fragments are also preserved (AMPG 640, 641, 670, 834, 838-841).

Finally, some appendicular elements of the Sitia terrapin are known. AMPG 651 represents an eroded partial scapula. AMPG 642 represents a diaphysis of a humerus that is moderately curved and belongs to a slender humerus. AMPG 650 represents a diaphysis of a humerus that is moderately curved and rather robust. AMPG 643 represents a diaphysis of a femur that is almost straight throughout its length.

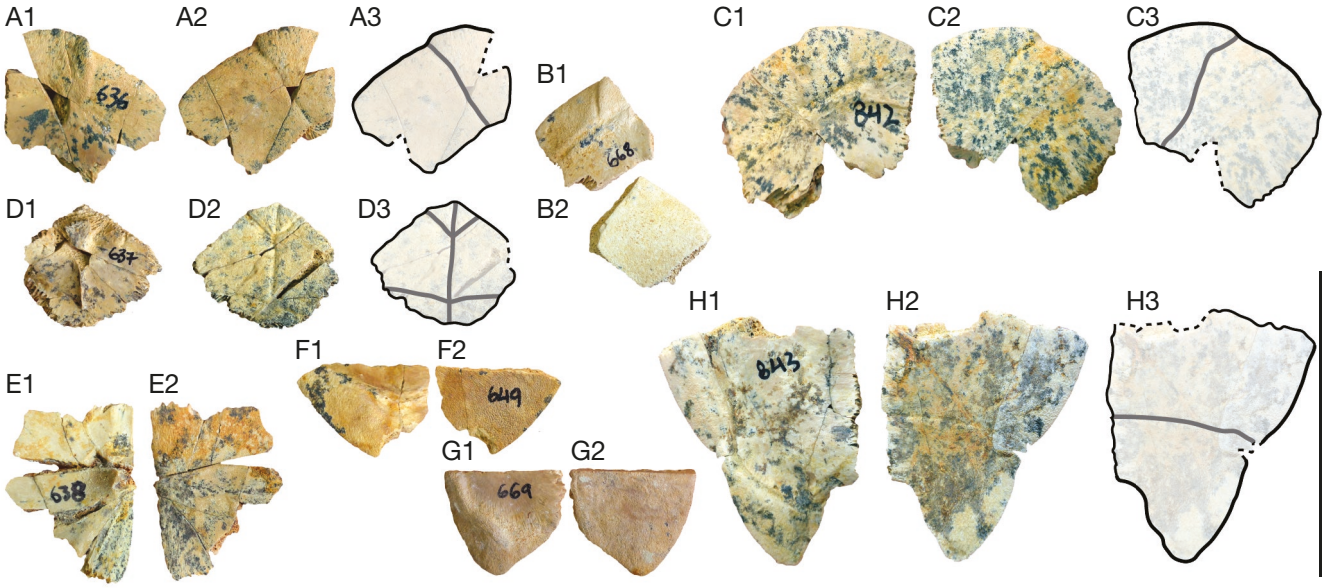

Fig. 19. — Plastron remains of *Mauremys* cf. *rivulata* Vallenciennes *in* Bory de Saint-Vincent, 1833 from the Pleistocene of Sitia (Crete): **A**, AMPG 636, right epiplastron views: **A1**, visceral; **A2**, ventral; **A3**, drawing of the ventral; **B**, AMPG 668, left epiplastron fragment views: **B1**, visceral; **A2**, ventral; **C**, AMPG 842, left epiplastron views: **C1**, visceral; **C2**, ventral; **C3**, drawing of the ventral; **D**, AMPG 637, entoplastron views: **D1**, visceral; **D2**, ventral; **D3**, drawing of the ventral; **E**, AMPG 638, right hyoplastron fragment views: **E1**, visceral; **E2**, ventral; **F**, AMPG 649, left xiphiplastron fragment views: **F1**, visceral; **F2**, ventral; **G**, AMPG 669, left xiphiplastron views: **G1**, visceral; **G2**, ventral; **H**, AMPG 843, left xiphiplastron views: **H1**, visceral; **H2**, ventral; **H3**, drawing of the ventral. Scale bar: 5 cm.

Discussion

The phylogeography of the *Mauremys* complex was recently reviewed by Fritz *et al.* (2008). In the area of the south Balkans, Middle East and Caspian regions, two species occur, *M. caspica* and *M. rivulata*. These two taxa have been often considered synonymous, but considerable mtDNA differentiation confirms their treatment as full species (Fritz *et al.* 2008; and references therein). As shown in Figure 2 of Fritz *et al.* (2008), the differences between the two species are practically in the color of the plastron, whereas their morphological differences in the suture/sulci pattern are very small. In Greece and in the coastal region of Asia Minor only *Mauremys rivulata* occurs.

Although limited, the specimens presented above allow a safe attribution to the geoemydid *Mauremys* based on the peripherals that are overlapped by the pleurals, the entoplastron crossed by the gulars anteriorly and by the humero-pectoral sulcus posteriorly, as well as the deep anal notch (see Vlachos & Delfino 2016; and references therein). The overall similarity (both metrically and morphologically) with extant and extinct members of *M. rivulata*, and the fact that the specimens are of Pleistocene age allow attribution to *M.* cf. *rivulata*. Also, the presence of *M. rivulata* in Crete during the Pleistocene is within the extant geographic range of this taxon. Besides the specimens described above, the presence of *M. rivulata* in the Pleistocene of Crete has been mentioned from Simonelli Cave (note in Kotsakis 1977) and during the Holocene in Vraona Cave (Rauscher 1995). *Mauremys rivulata* is considered to be adapted to a warm Mediterranean climate, contrary to the adaptation of *M. caspica* to a winter-cold continental climate (Fritz & Wischuf 1997). If at some point we will be able to identify such isolated fragments safely and precisely to the species level, it might be possible to use them for some level of palaeoclimatic inference.

CONCLUSIONS

This paper expands significantly the knowledge of the fossil turtles and tortoises from Crete, presenting for the first time numerous new fossil specimens and revising previously published material from Gerani IV, Zourida, Koumpes, Liko, Mavro Mouri IV, and Simonelli Caves near Herakleion, Rethymnon fissure, and from the open site of Sitia in the eastern part of the Island. These specimens are dated to the Pleistocene, but their exact chronostratigraphic position is not clear. The vast majority of the specimens belong to the marginated tortoise *Testudo marginata*, previously considered a new endemic subspecies from Crete called *Testudo marginata cretensis*. The new information presented here documents the morphology of the carapace and plastron in great detail and the appendicular skeleton to some extent, which refutes the validity of this subspecies. Tortoise specimens are numerous and present only in cave sites (not in Sitia). Sitia contains more than 72 specimens of the Balkan terrapin *Mauremys* cf. *rivulata*, which is also identified with a few specimens in Gerani IV, Koumpes, Liko, Mavro Mouri IV, and the Rethymnon fissure. In all these cases of sympatry in the central-west parts of the island, the tortoise was far more abundant compared to the terrapin; more than 224 fossils belong to the tortoise compared to 21 specimens of the terrapin. Whereas the terrapin still survives in Crete at present, the tortoise does not, suggesting a significant range reduction of this species during the Quaternary.

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REFERENCES

BACHMAYER F., BRINKERINK J. P. & SYMEONIDIS N. 1975. — Pleistozäne Schildkröten aus Höhlen der Insel Kreta. *Annales Geologiques des Pays Helleniques* 27: 110-122.

BATSCH A. J. 1788. — *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. Akademische Buchhandlung, Jena, 528 p.

BORY DE SAINT-VINCENT J. 1833. — Vertébrés à sang froid. Reptiles et poissons, *in* GEOFFROY SAINT-HILAIRE E. (ed.), *Expédition Scientifique de Morée*. Vol. 3, Part 1, Atlas, pl. 6. F. Buisson, Paris, 295-337.

BOUR R. 1996. — Une nouvelle espèce de tortue terrestre dans le Péloponnèse (Grèce). *Dumerilia* 2: 23-54.

BRINKERINK H. P. 1996. — Tortoises and turtles from the Pleistocene of Crete, *in* REESE D. (ed.), Pleistocene and Holocene Fauna of Crete and Its First Settlers. *Monographs in World Archaeology* 28: 207-209.

COPE E. D. 1868. — On the Origin of Genera. *Proceedings of the Academy of Natural Sciences of Philadelphia* 20: 242-300. https://www.jstor.org/stable/4059902

FRITZ U. & WISCHUF T. 1997. — Zur Systematik westasiatisch-südosteuropäischer Bachschildkröten (Gattung *Mauremys*)(Reptilia: Testudines: Bataguridae). *Zoologische Abhandlungen-Staatliches Museum fur Tierkunde in Dresden* 49: 223-260.

FRITZ U., ŠIROKÝ P., KAMI H. & WINK M. 2005. — Environmentally caused dwarfism or a valid species — Is *Testudo weissingeri* Bour, 1996 a distinct evolutionary lineage? New evidence from mitochondrial and nuclear genomic markers. *Molecular Phylogenetics and Evolution* 37 (2): 389-401. https://doi.org/10.1016/j.ympev.2005.03.007

FRITZ U., AYAZ D., BUSCHBOM J., KAMI H. G., MAZANAEVA L. F., ALOUFI A. A., AUER M., RIFAI L., ŠILIĆ T. & HUNDSDÖRFER A. K. 2008. — Go east: phylogeographies of *Mauremys caspica* and *M. rivulata*-discordance of morphology, mitochondrial and nuclear genomic markers and rare hybridization. *Journal of Evolutionary Biology* 21 (2): 527-540. https://doi.org/10.1111/j.1420-9101.2007.01485.x

VAN DER GEER A. A. E., LOMOLINO M. V. & LYRAS G. A. 2017. — "Island Life" before man: biogeography of palaeo-insular mammals. *Journal of Biogeography* 44 (5): 995-1006. https://doi.org/10.1111/jbi.12857

GEORGALIS G. L., VILLA A., VLACHOS E. & DELFINO M. 2016. — Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. *Geobios* 49 (6): 433-444. https://doi.org/10.1016/j.geobios.2016.09.004

GERLACH J., MUIR C. & RICHMOND M. D. 2006. — The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History* 40 (41-43): 2403-2408. https://doi.org/10.1080/00222930601058290

GRAY J. E. 1869. — Description of *Mauremys laniaria*, a new freshwater tortoise. *Proceedings of the Zoological Society of London* 37 (1): 499-500. https://doi.org/10.1111/j.1469-7998.1869.tb07358.x

KOTSAKIS T. 1977. — I resti di anfibi e rettili pleistocenici della grotta "Bate" (Rethymnon, Creta). *Rendivoti dell' Accademia Nazionale dei Lincei* 8 (63): 571-582.

KOTSAKIS T. 1980. — Short account on the elephant remains of the Simonelli Cave, *in* MALATESTA A. (ed.), *Dwarf deer and other Late Pleistocene fauna of the Simonelli cave in Crete*. Accademia Nazionale dei Lincei, Roma: 115-119.

KUSS S. E. 1970. — Abfolge nud Alter der Pleistozanen Sangetierfannen der Insel Kreta. *Berichte Naturforschemte Gesellschaft zu Freiburg im Breisgau* 60: 35-81.

LINNAEUS C. 1758. — *Systema Naturae, per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, differentiis, synonymis, locis*. Tomus I. Editio Decima, Reformata. 10th edition, Laurentii Salvii, Holmiae, Stockholm: 824 p.

LOMOLINO M. V. 2000. — Ecology's most general, yet protean pattern: the species-area relationship. *Journal of Biogeography* 27 (1): 17-26. https://doi.org/10.1046/j.1365-2699.2000.00377.x

LYRAS G. A., ATHANASSIOU A. & VAN DER GEER A. E. E. 2022. — The fossil record of insular endemic mammals from Greece, *in* VLACHOS E. (ed), *The Fossil Vertebrates of Greece*. Vol. 2. Springer, Cham: 661-701. https://doi.org/10.1007/978-3-030-68442-6_25

RAUSCHER K. L. 1995. — Die herpetofauna der Vraona-Hoehle (Attika) in Griechenland. *Annales Géologiques des Pays Helléniques* 36: 39-41.

SCHLEICH H. H. 1982. — *Testudo marginata* Schoepff aus plio/pleistozänen Ablagerungen SE-Lakoniens (Peloponnes, Griechenlans). *Palaontologische Zeitschrift* 56: 259-264. https://doi.org/10.1007/BF02988802

SCHOEPFF J. 1793. — *Historia Testudinum Iconibus Illustrata*. Erlangae, Ioannis Iacobi Palm, 136 p. https://www.biodiversitylibrary.org/page/32540981

SPEYBROECK J., BEUKEMA W., DUFRESNES C., FRITZ U., JABLONSKI D., LYMBERAKIS P., MARTÍNEZ-SOLANO I., RAZZETTI E., VAMBERGER M., VENCES M. & VÖRÖS J. 2020. — Species list of the European herpetofauna–2020 update by the Taxonomic Committee of the Societas Europaea Herpetologica. *Amphibia-Reptilia* 41 (2): 1-51. https://doi.org/10.1163/15685381-bja10010

TEWG [TURTLE EXTINCTIONS WORKING GROUP] 2015. — Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians, *in* RHODIN A. G. J., PRITCHARD P. C. H., VAN DIJK P. P., SAUMURE R. A., BUHLMANN K. A., IVERSON J. B. & MITTERMEIER R. A. (eds), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs* 5:1-66.

THEOBALD W. 1868. — Catalogue of Reptiles in the Museum of the Asiatic Society of Bengal. *Journal of the Asiatic Society* Extra Number, 88 p. https://www.biodiversitylibrary.org/page/4381715

TTWG [TURTLE TAXONOMY WORKING GROUP] 2017. — Turtles of the world: annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status, *in* RHODIN A. G. J., IVERSON J. B., VAN DIJK P. P., SAUMURE R. A., BUHLMANN K. A.,

PRITCHARD P. C. H. & MITTERMEIER R. A. (eds), *Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. 8th edition. *Chelonian Research Monographs* 7: 1-292.

VAMBERGER M., STUCKAS H., AYAZ D., LYMBERAKIS P., ŠIROKÝ P. & FRITZ U. 2014. — Massive transoceanic gene flow in a freshwater turtle (Testudines: Geoemydidae: *Mauremys rivulata*). *Zoologica Scripta* 43 (4): 313-322. https://doi.org/10.1111/zsc.12055

VLACHOS E. 2015. — *The fossil chelonians of Greece. Systematics – evolution – stratigraphy – palaeoecology*. Ph.D. dissertation, Aristotle University of Thessaloniki, Thessaloniki, 479 p.

VLACHOS E. & DELFINO M. 2016. — Food for thought: Sub-fossil and fossil chelonian remains from Franchthi Cave and Megalopolis confirm a glacial refuge for Emys orbicularis in Peloponnesus (S. Greece). *Quaternary Science Reviews* 150: 158-171. https://doi.org/10.1016/j.quascirev.2016.08.027

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